

CHEMICAL CUES FROM ANTS INFLUENCE PREDATORY BEHAVIOR IN *HABROCESTUM PULEX*, AN ANT-EATING JUMPING SPIDER (ARANEAE, SALTICIDAE)

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ABSTRACT. The ability of *Habrocestum pulex*, a myrmecophagic jumping spider, to detect olfactory and contact chemical cues from ants was investigated experimentally. When given a choice between walking over clean soil or soil that had housed ants, *H. pulex* spent significantly more time on ant-treated soil. However, *H. pulex* did not appear to discriminate between clean blotting paper and blotting paper over which ants had walked. In tests using a Y-shaped olfactometer, when given a choice between an experimental arm containing air from a cage containing ants, or 6-methyl-5-hepten-2-one, and a control arm containing clean air, *H. pulex* moved into the experimental arm significantly more frequently than the control arm. When on soil that had previously housed ants, agitated walking, undirected leaping, posturing with body raised, and perching on top of corks were each significantly more prevalent than when *H. pulex* was on clean soil. Chemical cues left by ants on soil also affected *H. pulex*'s attention to visual cues from ants: when on treated soil, *H. pulex* initiated and completed stalking sequences more often, and after shorter latency, than when on control soil.

Keywords: Prey detection, myrmecophagy, kairomone, Salticidae, *Habrocestum pulex*

Unique, complex eyes and acute vision in jumping spiders (Salticidae) have led to the evolution of intricate, vision-guided courtship and predatory tactics (Crane 1949; Drees 1952; Land 1969a, 1969b; Forster 1982; Blest et al. 1990; Jackson & Pollard 1996, 1997). However, salticids are not restricted to reliance on optical cues, as tactile, auditory and substrate-vibration cues also influence salticid courtship, either concurrent with or as alternatives to, visual communication (Richman & Jackson 1992; Jackson & Pollard 1997). Pheromone-based intraspecific communication is also widespread in the Salticidae (Crane 1949; Jackson 1987; Pollard et al. 1987; Willey & Jackson 1993; Clark & Jackson 1994a, 1994b, 1995a, 1995b), but little is known about whether salticids are influenced by kairomones (chemicals that provoke a response beneficial to the receiver but not the sender of the signal, where the sender and receiver belong to different species; Brown et al. 1971).

Ants are one of the most abundant prey-size arthropods in the habitats of most spiders (Hölldobler & Wilson 1990), but their defenses (strong mandibles, formic acid and poison-

injecting stings: Wray 1670; Edmunds 1974; Hölldobler & Wilson 1990; Blum 1992) appear to present spiders with formidable challenges. Yet a minority of spiders has overcome the ant's defenses, thereby gaining access to this exceptionally numerous prey (Mackay 1982; Oliviera & Sazima 1985; Nyfeler et al. 1988; Elgar 1993; Cushing 1997).

Within the Salticidae, 21 ant-eating (myrmecophagic) salticids have been studied in detail: *Aelurillus aeruginosus* (Simon 1871), *A. cognatus* (O.P.-Cambridge 1872), *A. kochi* Roewer 1951, six undescribed species of *Chalcotropis* Simon 1902, *Chrysilla lauta* Thorell 1887, *Corythalia canosa* (Walckenaer 1837), *Habrocestum pulex* (Hentz 1846), *Siler semiglaucous* Simon 1901, *Siler* sp. Simon 1889, three undescribed species of *Natta* Karsch 1879, two undescribed species of *Xenocytaea* Berry, Beatty, Prózyński 1998 (formerly called "Euophrys") and *Zenodorus orbiculatus* (Keyserling 1881) (Edwards et al. 1974; Cutler 1980; Jackson & van Olphen 1991, 1992; Li et al. 1996, 1999; Jackson et al. 1998). Although these species feed on a wide variety of insects, they have all been

shown in standardized tests to prefer ants over other prey and to have ant-specific prey-capture behavior (Li & Jackson 1996). Except for *Corythalia canosa* and *Zenodorus orbiculatus*, each of these species has been shown to prefer ants as prey and to use ant-specific prey-capture behavior even when tested with motionless lures (dead insects mounted in life-like posture on corks), implying that optical cues pertaining to shape and form enable them to distinguish ants from other insects (Li & Jackson 1996; Li et al. 1996; Jackson et al. 1998). However, the ability to rely solely on vision for detecting ants does not preclude the possibility that chemical cues also influence the predatory behavior of myrmecophagous salticids.

In the present paper, we investigate how *Habrocestum pulex*, a previously studied myrmecophagous salticid from North America, responds to chemical cues from ants. *Habrocestum pulex* lives in leaf litter, a microhabitat in which numerous visual obstructions might often hinder early visual detection of prey. Ability to detect chemical cues from ants might play an important role in preparing *H. pulex* to respond appropriately to its unusually dangerous prey.

In earlier studies (Cutler 1980; Li et al. 1996), *H. pulex* was tested with prey in a simple laboratory environment. In the present study, we first observe *H. pulex*'s predatory behavior in an environment with leaf litter present, thereby simulating nature more closely than previously. We next consider three hypotheses concerning how *H. pulex* might react to contact chemical cues when in an environment recently occupied by ants. *Habrocestum pulex* might do any combination of the following: remain in the environment, adopt behavior and posture appropriate for capturing ants, or exhibit heightened attention to optical cues from ants. We consider the role of both olfactory and contact chemical cues from ants in moderating the prey-capture behavior of *H. pulex*.

METHODS

General.—Except for minor modifications, maintenance procedures, cage design and data analysis were as in earlier studies (Jackson & Hallas 1986). All experiments were carried out in New Zealand using laboratory cultures of *H. pulex*, originally collected in Kansas,

USA. Each individual salticid was used in a maximum of two tests for any one experiment, and there was no evidence that the identity of individual salticids influenced test outcome. Data from males and females, not being statistically different, were pooled. Body lengths of adults were 3–5 mm. Statistical methods were from Sokal & Rohlf (1995).

In observations and experiments with live ants, we used *Monomorium antarcticum* Smith 1858, a myrmicine ant native to New Zealand (Ettershank 1966; Bolton 1987). The most common prey of *H. pulex* in nature appear to be *Lasius* spp. Fabricius 1804 (Formicinae) (Cutler unpubl. data), which were not available in New Zealand. To test for responses which might be specific to *Lasius* spp., we conducted olfactometer tests using commercially available 6-methyl-5-hepten-2-one (Sigma Chemical Co.), an alarm pheromone of *Lasius* spp. and other ants (Duffield et al. 1977; Blum 1981; Türker 1997a, 1997b). *Monomorium antarcticum* and other myrmicine ants appear not to make this pheromone (Hölldobler & Wilson 1990).

Predation on ants in a complex environment.—The environment was a plastic box (length 170 mm, width 110 mm, depth 60 mm) filled to a depth of 15 mm with soil. Leaf litter was scattered about on top of the soil, covering about 30% of the box surface. Four small corks on which *H. pulex* could stand were spaced within the box, providing perches above the level of leaf litter. Observations were staged by putting *H. pulex* in this environment in the presence of 10–20 prey, where (depending on the test) prey were either ants or vestigial-winged fruit flies (*Drosophila melanogaster* Meigen 1804). The goal was to get qualitative information on how *H. pulex* captured prey in approximately natural environments.

Choice tests using blotting paper.—We adopted, after minor modification, procedures devised earlier for testing the ability of salticids to discriminate between the draglines of different conspecific individuals (Clark & Jackson 1994a, 1995a, 1995b). In each test, *H. pulex* was offered a choice between treated (had been in contact with ants) and untreated (clean) blotting paper. Treated blotting paper was prepared by leaving four ants in a plastic petri dish (diameter 90 mm) for two hours, with one circular piece of blotting paper taped

to the top and another to the bottom. During the two-hour period, ants actively walked about in the petri dish, repeatedly moving over both pieces of blotting paper.

Immediately afterward, each piece of blotting paper was cut in half and the test chamber was prepared. The test chamber was another petri dish (diameter 90 mm) with one half piece of treated blotting paper taped to the top of the dish and another half-piece of treated blotting paper taped to the bottom of the dish directly below the top piece. The other half of the test chamber had control blotting paper taped to the top and bottom. A 15-mm triangle, cut out of the blotting paper and surrounded by a horseshoe-shaped metal divider, served as a "neutral area" into which the test spider was introduced before testing. Having the metal divider in place meant that the salicid could not, all at once, view the entire space within the petri dish (see Clark & Jackson 1994a). A test was defined as having started when the spider moved out of the neutral area and onto the blotting paper. This always happened within 1 min. The test ended 10 min later. For each test, a difference score was obtained (time spent on treated paper minus time spent on control paper). Maximum and minimum possible scores were +600 sec (spent entire time on ant-treated blotting paper) and -600 sec (spent entire time on control blotting paper), respectively.

Choice tests using soil.—Commercial potting mix was placed in a square (160 mm × 160 mm, height 80 mm) plastic storage container filled to a depth of 20 mm and microwaved (900 W) for 10 min, then held in the container (kept closed) for a waiting period of 20–30 days. Treated soil was prepared by keeping about 100 ants in the closed container during the waiting period. Potential contaminants from feeding material were avoided by not feeding the ants during this time. The ants survived the fasting period. Control soil was kept ant free.

The test chamber was a plastic box (length 170 mm, width 110 mm, height 60 mm) filled to a depth of 15 mm with control soil. Two watch glasses (inner diameter 50 mm, inner height 7 mm; outer diameter 65 mm, outer height 15 mm) were placed 10 mm apart (measured from nearest edges) in the center of the box. The watch glasses were filled with soil, then embedded in the surrounding soil

(soil level with rim of watch glass). To facilitate seeing whether test spiders were in the watch glass, the rim of each glass was kept clear of soil. Treated soil was placed in the experimental watch glass (ants removed immediately beforehand) and control soil was placed in the control watch glass. Whether treated soil was on the left or right was decided at random for each test. To start a test, a spider was placed on the soil between the two watch glasses. For the next 60 min, we recorded how much time the test spider spent in each watch glass. Time spent outside the watch glasses was ignored.

Effect of chemical cues in soil on behavior and posture.—Control and treated soils were prepared as in the experiment on choice of soil. Each test spider was tested on one day with treated soil and on the previous or next day (order decided at random) with control soil. During 15-min tests, the test spider's behavior was recorded in detail, but we present data here only where there was statistical evidence of behavior being influenced by soil treatment.

The test chamber was a cylindrical plastic dish (diameter 90 mm, height 40 mm) with soil covering the bottom to a depth of 10 mm. Four corks (diameter 9 mm at the narrow end) were embedded with the upper 5 mm of cork (narrow end) extending above the soil. Corks were evenly spaced in a square centered in the middle of the dish (center of each cork 20 mm from the center of the nearest neighboring cork). Evenly spread around the dish between the corks were four convex 10 × 10 mm pieces of leaf litter (Oak, *Quercus* spp. Linnaeus 1753), each positioned so that the test spider could walk under it.

Effect of chemical cues in soil on attention to optical cues.—We investigated whether *H. pulex*'s attention to optical cues from ants is affected by the presence of chemical cues from ants. Preparation of soil and the test chamber was as described for the experiment on how chemical cues affect behavior and posture, except that no leaf litter was present and there was a glass vial (65 mm long, inner diameter 10 mm) containing two ants on the soil centered between the corks. Latencies to initiate and complete stalking sequences directed at the ants were recorded. Stalking was initiated when the test spider turned toward an ant and began to move steadily toward it, and

completed when the test spider touched the vial. Test spiders were allowed 15 min to begin stalking and subsequently allowed 15 min to complete the stalking sequence.

Olfactometer tests.—A Y-shaped olfactometer (Fig. 1) with airflow adjusted to 1000 ml/min (Matheson FM-1000 flowmeter) was used to assess *H. pulex*'s response to airborne odors from ants. At this airflow setting, there was no evidence that *H. pulex*'s locomotion was impaired. Air flowed from a tap through two separate flowmeters into a stimulus chamber (which contained an odor source) and a control chamber (which was empty). During experimentation, whether the experimental chamber was on the left or right side of the olfactometer was decided at random. Air moved from the stimulus chamber to the stimulus arm and from the control chamber to the control arm. Collectively, the stimulus and control arms are referred to as the "choice arms." Air flowed from each "choice arm" into a single test arm. At one end of the test arm, there was a holding chamber into which a spider was placed prior to testing. A metal barrier, positioned in a slit between the holding chamber and the test arm, blocked the spider's entry into the test arm. Thirty min before each test, an odor source (depending on the experiment, either four ants or 10 μ l of 6-methyl-5-hepten-2-one) was placed in the experimental chamber. This 30-min period allowed the air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer.

During testing, spiders tended to walk about actively in the olfactometer, sometimes entering the experimental or control arm, or both, several times but staying only briefly. For each spider, we recorded both the first and final choice. The first arm the spider entered was its first choice regardless of how long it stayed. By definition, a spider made its final choice when it entered an arm and remained there for a minimum of 30 sec. A maximum of 60 min was allowed for the spider to make a final choice after leaving the holding chamber. Between tests, the olfactometer was dismantled and cleaned first with 80% ethanol and then with water. This was a precaution against the possibility that spiders might be affected by draglines or chemical traces from previously tested spiders.

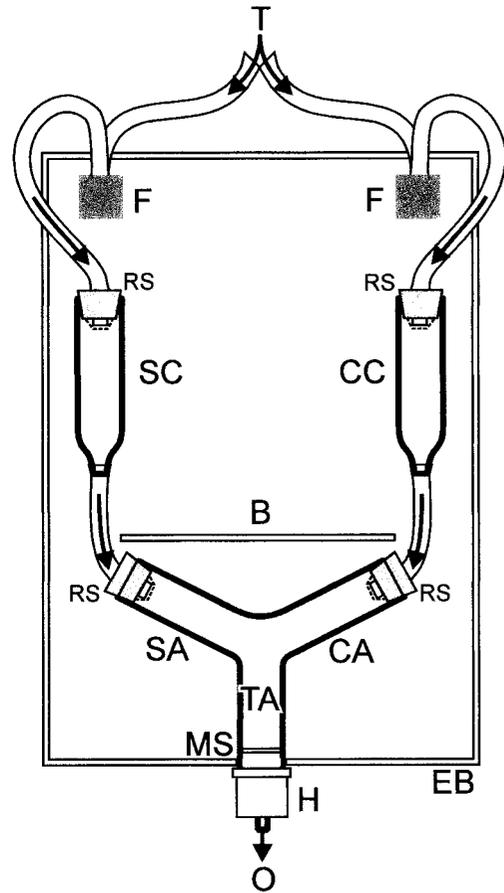


Figure 1.—Olfactometer. Arrows indicate direction of airflow. SC = stimulus chamber (contains odor source); CC = control chamber (empty); H = holding chamber (location of test spider at start of test); TA = test arm; CA = control arm; SA = stimulus arm; MS = metal screen fitted in slit (blocks spider's entry into test arm before test begins); T = tap from which air enters olfactometer; B = opaque barrier (prevents test spider from seeing ants); RS = rubber stopper; O = air leaves olfactometer; EB = edge of box enclosing olfactometer. Diagram not to scale. See text for details.

RESULTS

Predation on ants in a complex environment.—*Habrocestum pulex* tended to leap on fruit flies from any orientation, but attacked ants by repeatedly approaching head on, making stabs with its fangs, then backing away (Fig. 2). Once the ant was more or less quiescent, *H. pulex* approached slowly, grasped the ant and began feeding. During and immediately prior to attacking an ant, the spi-

der's palps were retracted to the sides of the chelicerae, but palps tended not to be retracted during attacks on flies.

Locomotion, when it occurred during tests with flies, tended to be by slow, continuous stepping, and the normal posture was adopted with the body *ca.* 1 mm above the substrate and legs only moderately extended. With ants, prey-capture sequences were normally preceded by distinctive preliminary behavior which included agitated walking, undirected leaping and posturing with the body raised. These sequences were often preceded by periods during which *H. pulex* simply watched (maintained orientation towards) an ant. Agitated walking was a distinctive style of motion in which *H. pulex* repeatedly spurted forward for *ca.* 0.5 sec at 30–50 mm/sec, paused and then spurted forward again. *Habrocestum pulex* made undirected leaps by suddenly propelling itself more or less straight upward with no target being evident. When in the body-elevated posture, *H. pulex* stood with its legs more extended than normal, so that its body was 2–3 mm off the substrate.

When predation was delayed or failed to occur in tests with flies, *H. pulex* spent much of the time sheltering under leaf litter, but *H. pulex* rarely sheltered under leaves in tests with ants. A common preliminary to predation on both ants and flies was for *H. pulex* to stand on corks and watch prey active on the soil below (Fig. 3). Attacks were often made by rushing down from a cork, after which *H. pulex* usually returned to the top of the same cork to feed.

Choice tests using blotting paper.—Scores were spread more-or-less evenly over the range of possible values, providing no evidence that *H. pulex* discriminated between treated and control blotting paper (Fig. 5).

Choice tests using soil.—*Habrocestum pulex* spent more time on treated, rather than control, soil (Fig. 6). In 20 tests, one spider spent more time on control soil, one spent equal time on treated and control soil, and the remaining 18 spent more time on treated soil (McNemar test comparing the number that spent more time on treated versus control soil; $P < 0.001$, $n = 19$).

Effect of chemical cues in soil on behavior and posture.—Agitated walking, undirected leaping, the body-raised posture and perching on corks were more prevalent when

H. pulex was in experimental chambers rather than control chambers (Table 1).

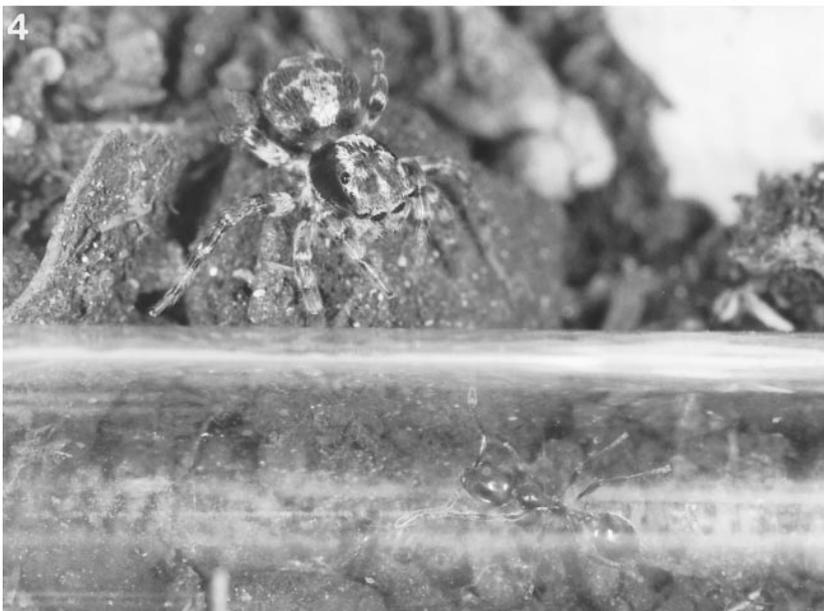
Effect of chemical cues in soil on attention to optical cues.—When on treated soil, *H. pulex* initiated and completed (Fig. 4) stalking sequences against ants more often than when on control soil (Table 1). The latency to initiate and to complete stalking was shorter on treated than control soil (Fig. 7).

Olfactometer tests.—When tested with ants in the stimulus chamber, the first choice was the stimulus arm in 11 tests and the control arm in four tests (binomial, NS). The final choice was the stimulus arm in 13 tests and control arm in two tests (binomial, NS). In all tests in which the stimulus arm contained 6-methyl-5-hepten-2-one, the first and final choices were identical: the stimulus arm in 10 tests and the control arm in one test (binomial, NS). There was no statistical evidence of a relationship between latency to choose and whether the choice was the control or the stimulus arm or, if it was the stimulus arm, whether the stimulus was pheromone or an ant (Mann-Whitney rank-sum tests, NS; Fig. 8).

DISCUSSION

Habrocestum pulex apparently detects and responds adaptively to chemical cues from ants. Our findings support the following hypotheses: (1) *H. pulex* chooses to remain on soil containing chemical cues from ants (choice of soil); (2) ant-derived chemical cues in soil stimulate *H. pulex* to adopt posture and behavior appropriate for capturing ants, even in the absence of optical cues from ants (effect of chemical cues on behavior and posture); (3) ant-derived chemical cues in soil heighten *H. pulex*'s attention to optical cues from ants (effect of chemical cues in soil on attention to optical cues); and (4) *H. pulex* is attracted by olfactory cues from ants (olfactometer tests). Failure to show a preference for treated over control blotting paper in a petri dish suggests that blotting-paper choice tests are excessively artificial.

Rather than demonstrating responses to the particular ant species on which *H. pulex* preys most often in nature, our results suggest that *H. pulex* has evolved the ability to detect and respond adaptively to chemicals secreted by a broader range of ants. In all experiments, we used *Monomorium antarcticum*, a New Zealand myrmicine ant which would not be en-



Figures 2–4.—2. *Habrocestum pulex* (on right) slowly approaches ant (*Monomorium antarcticum*) (on left). Ant now quiescent, having been repeatedly stabbed by *H. pulex*; 3. *Habrocestum pulex* on top of cork watching ant (not in photograph) moving about on soil; 4. *Habrocestum pulex* completes stalking sequence in tests of effect of chemical cues in soil on attention to optical cues (see text). Ant in glass vial (lower right). *H. pulex* (above, left) faces ant and touches glass.

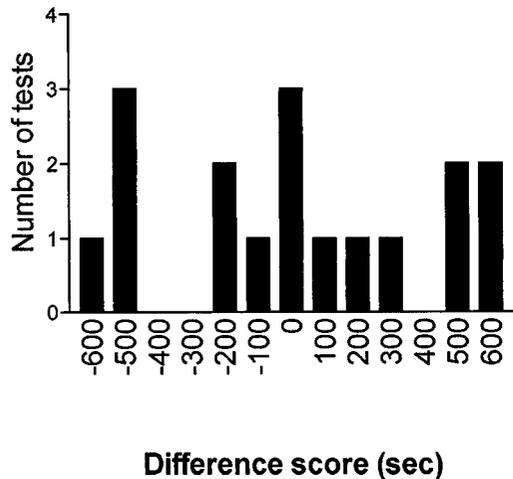


Figure 5.—Distribution of difference scores (time spent on treated blotting paper minus time spent on control blotting paper) from experiment on choice of blotting paper. See text (data more-or-less evenly spread). No statistical evidence of preference (Wilcoxon test for paired comparisons, NS).

countered by *H. pulex* in nature. *Habrocestum pulex* preys especially often in nature on *Lasius* spp., which are formicines. In our experiments, *H. pulex* also was influenced by 6-methyl-5-hepten-2-one, a ketone characteristic of the mandibular gland secretions of many formicine ants and the anal gland secretions of dolichoderine ants (Duffield et al. 1977). In ants, use of chemically-similar pheromones by different species is common (Gabba & Pavan 1970).

The ketone 6-methyl-5-hepten-2-one ap-

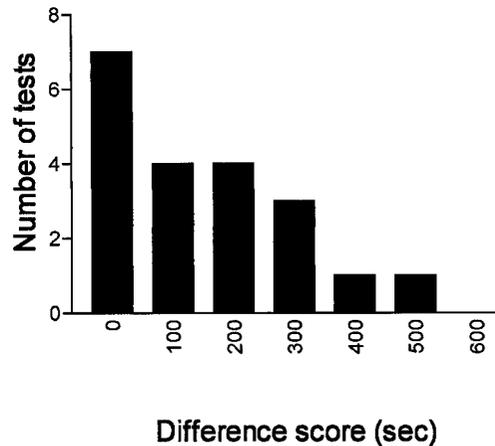


Figure 6.—Distribution of difference scores (time spent in experimental watch glass minus time spent in control watch glass) from experiment on choice of soil, showing preference for treated soil (Wilcoxon test for paired comparisons, $P < 0.001$). Note: There was only one negative score.

pears to be a kairomone not only for *H. pulex* but also for *Habronestes bradleyi* Walckenaer, a myrmecophagic zodariid spider. When tested in a Y-shaped olfactometer, with a choice between chemical cues from disturbed dolichoderine ants (*Iridomyrmex purpureus* Smith 1858) and clean air, *Habronestes bradleyi* most often moved toward the cues from injured or disturbed ants (Allan et al. 1996). Gas chromatography revealed that 6-methyl-5-hepten-2-one is released in high concentrations by injured or disturbed *Iridomyrmex purpureus*. When retested in the Y-shaped ol-

Table 1.—Results from experiments on effects of chemical cues in soil on *Habrocestum pulex*. A. Behavior and posture. B. Attention to optical cues. Each spider tested one day on treated soil (had been in contact with ants) and on alternate day on control soil (had not been in contact with ants). Compared to when on control soil, *H. pulex* on treated soil: A. performed more agitated walking, undirected leaping, holding body raised and perching on wall. B. More often initiated and completed stalking. See text for details. Data analysis: McNemar test for significance of changes (for these tests, only the first two columns of data are used).

Experiment	Response	On treated soil only	On control soil only	On both types of soil	On neither type of soil	McNemar test
A	Agitated walking	8	1	9	2	$P < 0.05$
	Undirected leaping	12	1	2	4	$P < 0.01$
	Holding body raised	12	0	4	4	$P < 0.01$
	Perching on cork	11	1	5	3	$P < 0.01$
B	Initiate stalking	11	1	7	1	$P < 0.01$
	Complete stalking	12	2	4	2	$P < 0.01$

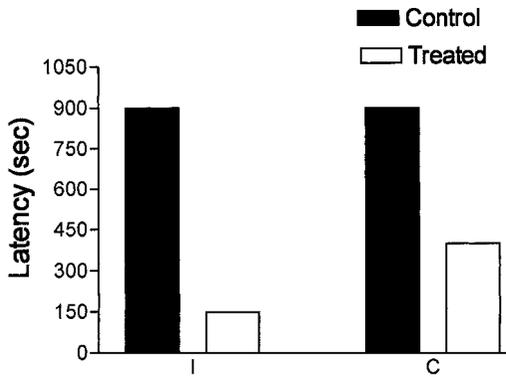


Figure 7.—Latencies (median in sec) to initiate (I) and complete (C) stalking sequence (see text for definitions) in experiment testing for effect of chemical cues in soil on attention to optical cues. Latencies when on treated soil (been in contact with ants) shorter than latencies when on control (clean) soil (Wilcoxon tests for paired comparisons, $P < 0.005$ for both initiating and completing stalking).

factometer, test spiders moved into olfactometer arms which contained 6-methyl-5-hepten-2-one more often than into the clean arms (Allan et al. 1996), implying that this ketone is at least one of the chemicals used by *Habronestes bradleyi* to locate *I. purpureus*.

Detecting 6-methyl-5-hepten-2-one is unlikely to be how *H. pulex* detects *Monomorium antarcticum*. Whether *M. antarcticum* uses alarm pheromones is unknown. Other myrmicine ants are known to do so, but they use another closely related ketone, 4-methyl-3-heptanone (Gabba & Pavan 1970; Hölldobler & Wilson 1990), instead of 6-methyl-5-hepten-2-one. It may be that, for myrmecophagic spiders and for ants, sensory systems are not narrowly tuned to particular ketones, but instead respond to a range of structurally related chemicals (see Türker 1997a, b). Perhaps, *H. pulex* has evolved chemoreceptors sensitive to a series of structurally related chemicals, rather than those secreted by any particular set of ant species. Broad-sensitivity sensors would assist *H. pulex* in predatory sequences against a wide range of ant species, including even New Zealand ants it would never encounter in nature.

Kairomone detection appears to function not only to bring *H. pulex* into proximity with its prey, but also to elicit changes in behavior, body posture and locomotion that prepare *H. pulex* for predation on ants before an ant is

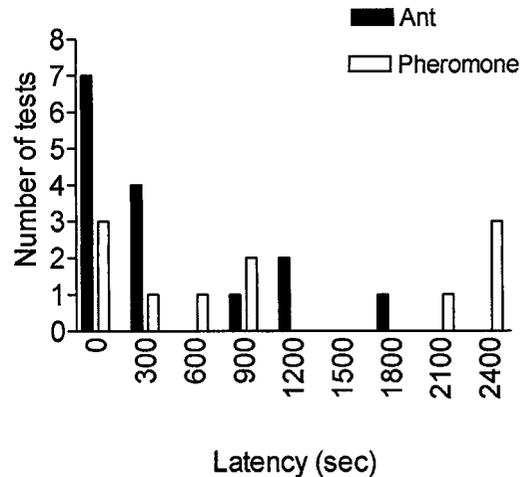


Figure 8.—Latency for test spiders to enter the experimental arm in olfactometer tests. Choice was between experimental arm (contained either live ants ("ant"; $n = 15$) or 6-methyl-5-hepten-2-one ("pheromone"; $n = 11$) or control arm. Instances of choosing control arm are not shown.

seen. In particular, cues from ants caused *H. pulex* to move to higher ground (i.e., perch on corks), where its ability to detect optical cues from ants might be enhanced; and *H. pulex* often launched attacks on ants from elevated positions.

Habrocestum pulex illustrates that the evolution of complex eyes and exceptionally intricate vision-based predatory behavior in salticids is not incompatible with the evolution of kairomone-detection abilities and intricate chemical-mediated predatory behavior in myrmecophagic salticids. In salticids, a vision-based perceptual and behavior system appears to have only minimal, if any, cost to proficiency at using a chemical-based perceptual and behavior system (Jackson & Pollard 1996, 1997). In *H. pulex*, the ways in which chemoreception influences predatory behavior are as intricate as those known for any non-salticid spider. Independently of optical cues, *H. pulex* not only appears to use kairomones for locating and preparing to prey on ants. Kairomones also appear to influence attention to optical cues. When ant-derived cues were present, *H. pulex* located ants faster than when they were absent. This suggests that the chemical and vision-based perceptual systems of salticids may have reached a remarkable level of integration.

ACKNOWLEDGMENTS

We thank Simon Pollard, David Blest, Duane Harland and Philip Taylor for comments on the manuscript. This research was partly funded by a grant from the New Zealand Marsden Fund (UOC512). Voucher specimens of the ants and spiders used are deposited at the Florida State Collection of Arthropods (P.O. Box 147100, Gainesville, Florida, USA) and the Canterbury Museum (Christchurch, New Zealand).

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Manuscript received 12 May 1999, revised 15 December 1999.