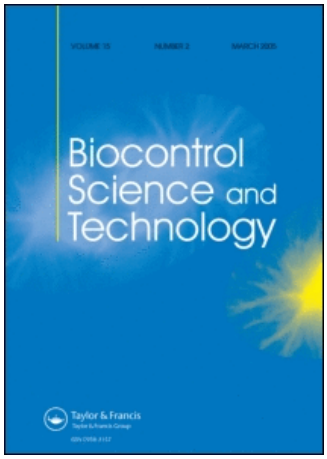

Biocontrol Science and Technology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713409232

Olfactory Responses by the Scale Insect Predator Chilocorus nigritus (F.) (Coleoptera: Coccinellidae)

D. J. Ponsonby; M. J. W. Copland

Online Publication Date: 01 April 1995
To cite this Article: Ponsonby, D. J. and Copland, M. J. W. (1995) 'Olfactory Responses by the Scale Insect Predator Chilocorus nigritus (F.) (Coleoptera: Coccinellidae)', Biocontrol Science and Technology, 5:1, 83 - 94
To link to this article: DOI: 10.1080/09583159550040033
URL: http://dx.doi.org/10.1080/09583159550040033

Biocontrol Science and Technology (1995) 5, 83–93

Olfactory Responses by the Scale Insect Predator *Chilocorus nigritus* (F.) (Coleoptera: Coccinellidae)

D. J. PONSONBY[1] AND M. J. W. COPLAND[2]

[1]*The Science Department, Canterbury, Christ Church College, North Holmes Road, Canterbury, Kent CT1 1QU, UK;* [2]*Department of Biological Sciences, Wye College, University of London, Wye, Ashford, Kent, TN25 5AH, UK*

(*Received for publication 25 March 1994; revised manuscript accepted 3 November 1994*)

Orientation to host plant and host insect volatiles in the coccidophagous coccinellid, Chilocorus nigritus *(F.) was examined using a four-arm olfactometer. Experienced adult females were attracted towards the combination of* Solanum tuberosum *L. and* Abgrallaspis cyanophylli *(Sign.) odours, walked further and spent longer in their presence, and showed an increased turning rate and net speed than in their absence. Host plant volatiles increased speed but decreased turning rates compared with odourless controls, but elicited no strongly directional response. It is postulated that this beetle and other coccinellids have a hierarchical prey-location mechanism which involves host habitat location based on olfactory responses.*

Keywords: Chilocorus nigritus, Abgrallaspis cyanophylli, *prey location, attractants, self-steered, counter-turning, anemotaxis*

INTRODUCTION

Host finding by predaceous coccinellids has been attributed to random chance (with host location occurring only on physical contact) by nearly all authors working in this field prior to 1980 (e.g. Fleschner, 1950; Dixon, 1959; Wratten, 1973). In all cases, larvae or adults were positively phototactic and negatively geotactic, using the prominent features of the plant, such as leaf veins and margins, to guide searching behaviour. Since the prey species show similar photo- and geotaxes and feed largely from the veins, such behaviour tends to concentrate predators at sites of high prey density. All the above studies demonstrated that, after each prey encounter, searching behaviour was modified by decreased orthokinesis (forward speed) and increased klinokinesis (frequency and intensity of turning). Marks (1977) found evidence that larvae of *Coccinella septempunctata* L. chemically marked leaves that had been previously searched, effectively preventing fruitless re-visits in the short term. Colburn and Asquith (1970) suggested that adults of the acarophagous *Stethorus punctum* (LeConte) were attracted to mites and mite-infested leaves by odour, although their apparatus allowed both sight and direct contact during the course of the experiment and the structure of the odour fields was not examined. Allen *et al.* (1970) reported that the pine budworm predator, *Anatis ocellata* (L.), was able to perceive prey from a distance of 1.3–1.9 cm prior to contact, probably by visual cues. Obata (1986) found that adult *Harmonia axyridis* were arrested by sight and odour when beetles were allowed to

0958–3157/95/010083–11

search gauze and plastic bags containing aphid-infested leaves and uninfested leaves. Van den Meiracker *et al.* (1990) found that some adult mealybug predators (*Diomus* and *Exochomus* spp.) were arrested by both wax exuviae and honeydew from cassava and citrus mealybugs, and Heidari and Copland (1993) reported similar behaviour in both adult and larval *Cryptolaemus montrouzieri* (Mulsant) in response to the honeydew of *Pseudococcus affinis* (Maskell). Previously, these authors (Heidari & Copland, 1992) reported that adult *C. montrouzieri* detected prey by both sight and odour, though larvae located prey only after physical contact.

Thus, the assumption that the searching behaviour of coccinellids is purely random has been challenged by several authors. However, with the possible exception of Colburn and Asquith (1970) and Obata (1986), all studies have involved encounters between predator and prey of no more than a few millimetres, even though, in adults, orientation to the host involves both flight and walking. Prey detection over distances greater than a few centimetres has received no attention, despite advances in our understanding of insect olfaction (e.g. Payne *et al.*, 1986). Such a strategy, therefore, remains circumstantial. For example, Taylor (1935), writing on adults of the diaspid feeding *Cryptognatha nodiceps* (Marshall) states, "Their ability to detect small batches of scale, even in densely wooded country at times when the scale is scarce, is most remarkable. In fact, wherever a few scales occur, the beetles are almost invariably present also, even though no appreciable quantity of scale can be found for a mile in any direction". Thompson (1951) reported strong host specificity among diaspid-feeding coccinellids on Bermuda stating (in the absence of experimental evidence but on the strength of field observations), "Predators, like parasites, have a full set of sense organs and there is no doubt that they can perceive their host at a distance, or at least perceive objects at a distance". Apart from Thompson's observations, there are now many known instances of parasitoid attraction to host odours (Jones, 1986). There have been several cases where coleopteran predators are highly specific and attracted to kairomones released by prey concealed underground or within plants, for example, the ant-feeding staphylinids, *Atemeles pubicollis* Bris. and *Amphotis marginata* F., and the bark beetle predators, *Enocleris lecontei* (Wolcott), *Temnochila chlorodia* (Mannerheim), *Thasimanimus dubius* (F.), *T. undulatus* (Wolcott) (Borden, 1977) and *Thanisimus formicarius* L. (Mustaparta, 1986). Indeed, the latter is so specific that electrophysiological recordings from the olfactory cells showed the same degree of specialization in response to the complex of pheromones from the bark beetle prey as the bark beetles showed themselves (Mustaparta, 1986).

If migrating adult coccinellids were able to detect host-bearing plants (or plants capable of bearing hosts) using either sight and/or kairomone attractants, it would place beetles landing on such plants in close proximity to the prey. It would also increase their chance of contact by their switching to close foraging behaviour, which has been shown to be under the control of other factors, such as geo- and phototaxis, arrestant stimuli and sight. Such a behavioural sequence has been proposed as the main mechanism for host detection amongst parasitoids (Vinson, 1976, Jones, 1986) while similar mechanisms occur in phytophagous insects, such as aphids (e.g. Pickett *et al.*, 1992) and bark beetles (Kennedy, 1986). Borden (1977) was unable to find any evidence that coccinellids used kairomones to detect their prey, but behavioural sequences are now known to be so important in host detection that "It is time to look again at cases where—homing-in on a distant odour—appears to be lacking" (Kennedy, 1986).

The current study was begun after *Chilocorus nigritus* adults which had escaped from rearing cages were found to detect quickly their diaspid host (*Abgrallaspis cyanophylli* (Signoret), infesting potato tubers) when the latter were left exposed in the rearing room. The aim was, therefore, to examine the possibility that an economically important predator was able to detect host odours over distances of more than a few centimetres.

MATERIALS AND METHODS

Olfactometer Set-up

A four-arm olfactometer (225 × 225 mm), as described by Vet *et al.* (1983), was used to assess

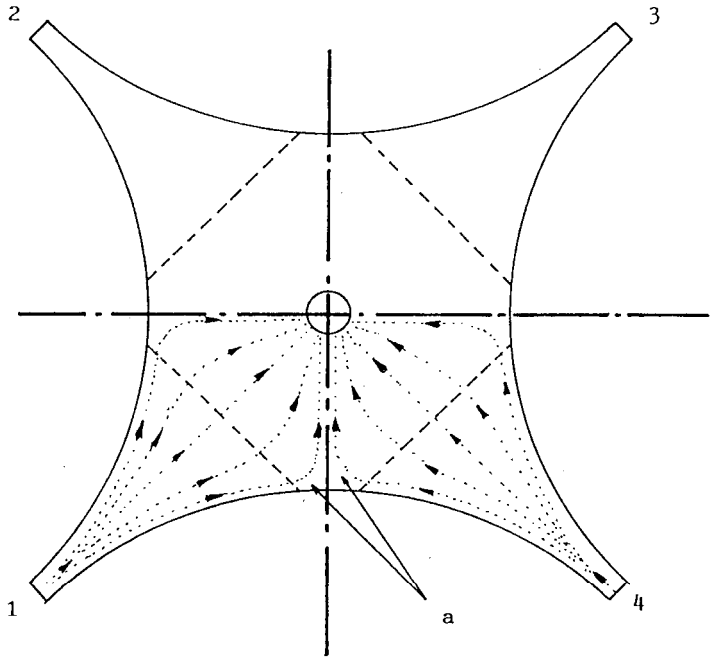

FIGURE 1. Diagramatic representation of odour fields, showing the direction of air movement in two fields (dotted lines) and the position of arbitrary first-choice lines (dashed lines). Odour field 1 represents the direction of the odour source, 2 and 4 the adjacent fields and 3 the opposite fields (each carrying filtered, humidified air). Lines through the centre are odour field boundaries and a is an inert area.

the ability of *C. nigritus* adults to orientate towards host or host plants using olfactory means. The olfactometer was modified in the following way:

- air was drawn through PVC tubing from outside the laboratory and passed through an activated carbon filter before entering the vials containing humidity and odour sources;
- the exposure chamber was edged with 'O' ring rubber held in place by Superglue, and the lid was secured by 12×6 mm bolts with wing-nuts in order to prevent leakage;
- each arm of the olfactometer was connected to a set of three 400-ml glass vials, the first acting as a trap for any beetles reaching that part of the apparatus, the second containing the odour source and the third carrying distilled water through which incoming air was passed in order to create uniform humidity;
- a small chamber was constructed in order to introduce beetles into the arena with minimal stress;
- a 22.5-l reservoir with an adjustable bleed valve (constructed from a Rotaflow fine metering valve) was connected between the vacuum pump and the olfactometer in order to smooth out the airflow;
- the arena was placed inside a black box with a Perspex ceiling through which diffused light was supplied from 2×8 W fluorescent tubes. Activity was viewed using a video camera with an 11–90 mm zoom lens.

The apparatus was tested for leaks using a manometer and found to be completely airtight. Odour fields were visualized by drawing 'smoke' through the arena created by placing NH_4OH in the vials used for containing the odour source and HCl in the trap vials. Results were similar to those of Vet *et al.* (1983), with the sharpest edges to odour fields occuring at 0.3 l min^{-1}. However,

TABLE 1. Directional response of *C. nigritus* to clean air, odour of host plant (*S. tuberosum*) and a mixture of host scale (*A. cyanophylli*) and host plant: first choice of odour field

Treatment	*n*	No. of first choices/odour field		χ^2
		1 (odour source)	2 + 3 + 4 (clean air)	
(1) Control (odourless)	37	9	9 + 8 + 11	0.514 (NS[a]) (1:1:1:1)
(2) Host plant only	71	16	55	0.230 (NS) (1:3)
(3) Host plant plus host scale	94	33	61	5.121 ($P < 0.02$) (1:3)

[a]NS = not significant.

a small inert or possibly turbulent area was found at point a in Figure 1. All trials were run at 26°C with an airflow rate of 0.3 l min^{-1}, the air being exhausted outside the laboratory.

In order to reduce the variability between insects, experienced adult female beetles which were 2–18 days after eclosion and reared at 26°C under a constant light regime were used for all trials. To account for the influence of circadian rhythms (if any), experiments were carried out at the same time each day (10.30–15.30 GMT). No beetle was tested more than once. Each was starved for 18–24 h before being placed individually into the introduction cage. Each beetle was then allowed to enter the arena in its own time, after which its movements were recorded for 10 min. Beetles which did not enter the arena within 4 min were rare, but in such an event, they were replaced by more active individuals. A maximum of 15 beetles were run through the apparatus before the arena was washed thoroughly with Decon 90 (Decon Laboratories Ltd, East Sussex, UK) and rinsed first with distilled water followed by 70% ethanol. At this stage, the odour source was rotated through 90° and the arena through 240° to eradicate any effects of directional bias. Between odour trials, the complete apparatus was soaked overnight in Decon 90 before being rinsed with distilled water and 70% ethanol.

Trials

Odourless trials (treatment 1) were carried out first in order to provide a control and eliminate the possibility of directional bias. These were followed by two trials, each with an odour source in just one arm of the olfactometer. The first odour source was a potato tuber not previously exposed to scale (treatment 2) and the second was a potato tuber upon which all stages of the female host scale, *A. cyanophylli*, were present (i.e. crawlers, second and third instars and ovipositing stages) and early stages of males (crawlers and second instars) (treatment 3).

Directional preferences for all three treatments were assessed when a beetle crossed an arbitrary line drawn on the monitor screen (Figure 1). Six variables—distance walked, amount of time spent in each odour field, time spent walking in each field, degrees turned mm^{-1} (calculated as an average over a 5 mm sampling distance), angular velocity (degrees s^{-1}) and net speed (distance walked/time spent walking)—were analyzed using a computer/video measuring package (Micromeasure V3, Varley *et al.*, 1994).

Statistical Analyses

Directional preferences were tested using the χ^2 goodness-of-fit test (Table 1). Treatment-by-treatment total means (Table 2) and field-by-field means (Table 3) were first tested for an approximation to a normal distribution before carrying out one- or two-way analyses of variance respectively. Skewed or distribution-free data in the field-by-field analysis were tested using Friedman's two-way test by ranks, adjusted for ties. Missing values in this data set were calculated (where appropriate) using the SAS General Linear Model procedure. Because of technical problems with the video camera, recordings of some replicates were 20–30 s short of

TABLE 2. Responses of *C. nigritus* to odours of host plant (*S. tuberosum*) and mixture of host scale (*A. cyanophylli*) and host plant during 600 s of exposure: overall comparison of treatment total means (± SE) using one-way analysis of variance

Treatment	*n*	Distance walked (mm)	Time spend walking (%)	*n*	Turning rate (° mm^{-1})	Angular Velocity (° s^{-1})	Net speed (mm s^{-1})
(1) Control	32	551 ± 176a[a]	13 ± 4a	48	7.3 ± 0.3a	11.9 ± 1.4a	7.9 ± 0.4a
(2) Host plant only	63	1332 ± 128b	29 ± 3b	71	6.4 ± 0.2b	19.2 ± 1.6b	7.8 ± 0.2a
(3) Host plant plus host scale	74	1228 ± 117b	29 ± 2b	94	7.4 ± 0.2a	20.8 ± 1.3b	7.3 ± 0.2a
$P > F$		0.001	0.0007		0.0009	0.0003	NS[b]

[a]Means within a column with the same letter are not significantly different.
[b]NS = not significant.

600 s. In such cases, continuous data (distance walked, time spent in odour field, time walking) were excluded from analyses of variance, though other responses were included. Comparisons between measurements in odour field 1 and those in the other three fields combined were carried out, and were paired in order to compensate for the variation between individual beetles. For relative parameters, a paired *t*-test was used where data approximated to a normal distribution, while a non-parametric test (Wilcoxon's test) was used where data were skewed. Continuous data (distance walked and time in odour field) were compared using a *t*-test, assuming a null hypothesis that 25% of time or distance walked was in odour field 1. However, for ease of interpretation, data for these categories are presented as the mean value of individual odour fields. Individuals which spent all of their time in odour field 1 or in the other three fields were excluded from the analysis as no comparison could be made between their relative behaviour in the two fields. For this reason, and because of the problems mentioned earlier with the video camera, numbers of replicates vary between the different analyses. For ease of interpretation, time spent walking is presented in all data sets as a percentage but was analyzed using the original time measurements.

RESULTS AND DISCUSSION

Odourless controls revealed no significant differences in the directional response between individual fields (Table 1), indicating that there was no bias in the apparatus. This was also supported in field-by-field analyses of variance (not shown) where there were no significant

TABLE 3. Responses of *C. nigritus* to the odour of *S. tuberosum*: multiple comparisons between mean of individual odour fields ($n = 63$)

	Odour field[a]	Distance walked (mm)	Time in odour field (s)	Time spent walking (%)
S. tuberosum	1	348a[b]	88a	53a
Clean air	2 (A)	399a	140a	38a
" "	3 (O)	202b	257b	10b
" "	4 (A)	349a	124a	37a
SE		± 39	± 26	± 4
$P > F$		0.003	0.03	0.003

[a]A = fields adjacent to odour source; O = the field opposite.
[b]Means within a group with the same letter are not significantly different.

differences between parameters in any of the fields. Trials involving *S. tuberosum* odours also revealed no directional bias (Table 1). A significantly higher number of beetles orientated towards the combined odour of *A. cyanophylli* and *S. tuberosum*, exhibiting a typical upwind orientation, as shown in Figure 2(a).

Other responses (Tables 2 and 4) show that the presence of *S. tuberosum* with or without *A. cyanophylli* volatiles did modify the behaviour of *C. nigritus*. Table 2 presents a treatment-by-treatment analysis of mean totals, which shows that the presence of *S. tuberosum* or *A. cyanophylli* plus *S. tuberosum* increased the distance walked, the time spent walking and angular velocity. Net speed was not generally altered by the presence of these odours, though turning rate was significantly lower in treatment 2. An explanation of these results may be found in the mechanism of self-steered counter-turning linked to optomotor anemotaxis as postulated by (for example) Kuenen and Baker (1983), Kennedy (1986) and Preiss and Kramer (1986), where a 'central nervous turn generator' was found to induce bursts of left and right activity in lepidopteran subjects. Evidence that similar mechanisms exist in other insect groups may be found in numerous references, for example in the beetle, *Leptinotarsus decemlineata* Say (Thiery & Visser, 1986) and the aphid, *Cryptomyzus korschelti* Börner (Visser & Taanman, 1987).

In the case of *C. nigritus*, odourless conditions induced non-directional movement characterized by reduced orthokinesis. The turning rate was increased under these conditions when compared with trials involving *S. tuberosum* odours only, but was similar to that observed when beetles were exposed to a combination of *S. tuberosum* and *A. cyanophylli* volatiles (Table 2). The low angular velocity is accounted for by the reduced amount of time spent walking. A typical trace of insect movement under these conditions (Figure 2(b)) agrees with the findings of Preiss and Kramer (1986) who tested de-winged gypsy moths, and of Thiery and Visser (1986) with walking Colorado beetles, and shows relatively straight segments interspersed with irregular, left and right circling. It is interesting to note in the current study that, although beetles in all treatments frequently arrested on reaching the extreme arms of the olfactometer, not one beetle in over 200 replicates actually passed through into the tubes beyond, despite the fact that they were of sufficient diameter to allow an exit in this manner.

In the presence of *S. tuberosum* volatiles, the turning rate was significantly lower than treatments 1 and 3, while the angular velocity and time spent walking were relatively high (Tables 2 and 4). Paired analysis (Table 4) also revealed a significantly higher net speed, which, taken together with the other data, suggests relatively shallower turning at high speed such as that illustrated in Figure 2(c) (i.e. showing increased orthokinesis but decreased klinokinesis). Although no directional bias was detected in Table 1, the field-by-field analysis of variance (Table 3) indicated a difference in behaviour in the field opposite the one carrying host plant odour (odour field 3). In this field, beetles travelled a shorter distance, spent approximately twice the amount of time there compared with the fields either side of the odour source and about three times that spent in the odour field itself. The time spent walking was reduced considerably compared with odour field 1, but less so in relation to fields 2 and 4. As there is apparently no reason why the clean, humidified air in field 3 should initiate an arrestment response, it seems safe to conclude that the presence of *S. tuberosum* volatiles in field 1 increased orthokinesis in *C. nigritus*. The data in Table 3 suggest that such behaviour could also be interpreted as a repellent effect from the plant volatiles, but there was no evidence of such an effect in the first choice analysis (Table 1). Beetles were also observed to enter and move deep into the odour field without exhibiting any reluctance (see Figure 2(c)).

With the addition of volatiles from *A. cyanophylli*, the angular velocity remained relatively high (Tables 2 and 4). Paired comparisons also revealed that the distance walked, the time spent in the odour field, the turning rate and the net speed were all significantly increased in the presence of odour from *A. cyanophylli* (Table 4). These factors suggest a more directional movement (as shown in Figure 2(d)), where beetles orientated towards the mixture of volatiles from *S. tuberosum* and *A. cyanophylli* while in the odour field until the limits of the arena were reached. Since individuals did not pass through the exit tubes, they eventually turned downwind and, as inevitably occurs in such a small arena, the edge of the odour field was reached and the

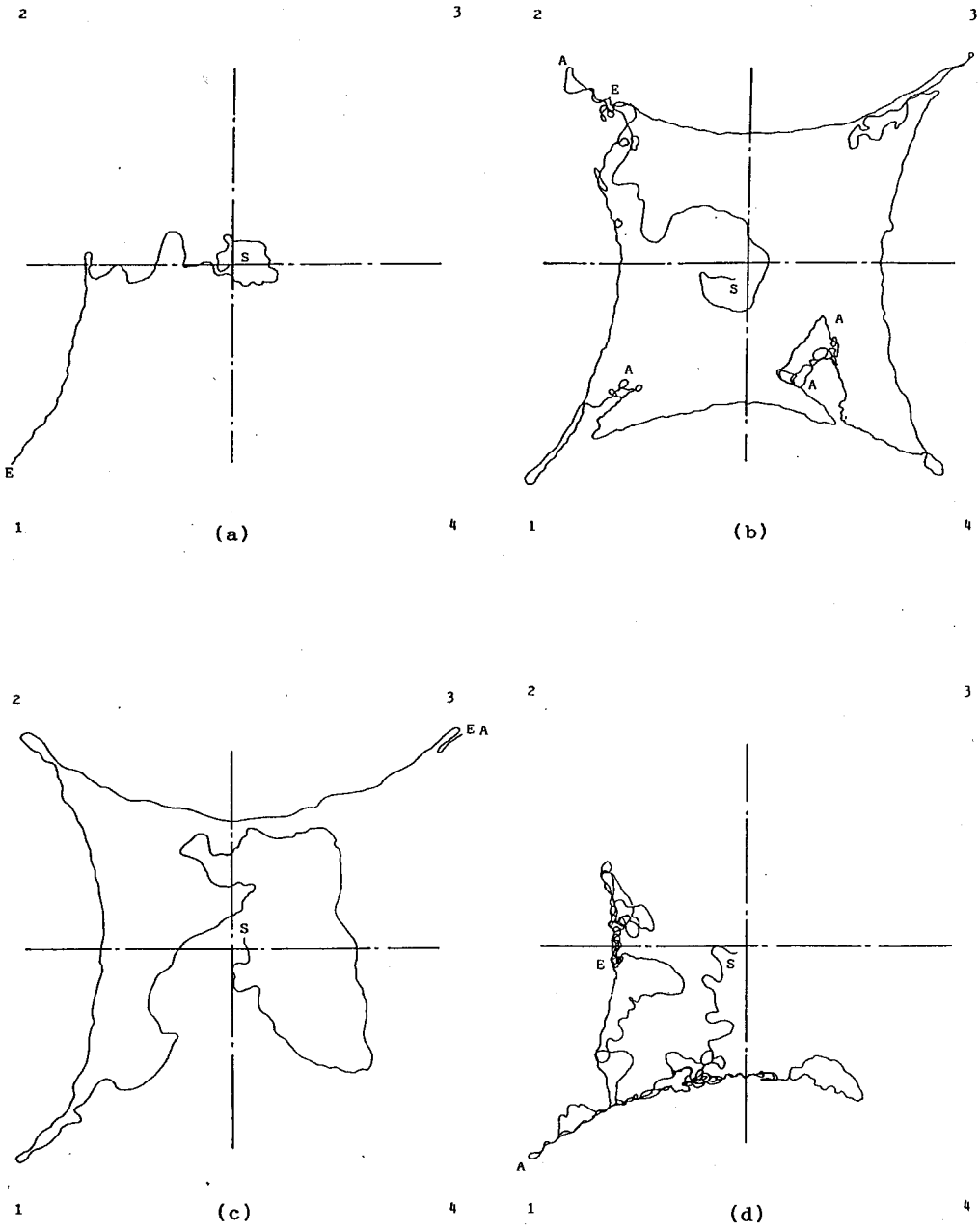

FIGURE 2. (a) The first few seconds of a trace of a beetle responding positively to odour from *S. tuberosum* and *A. cyanophylli*. (b) A typical trace of a beetle responding to clean, humidified air from all four arms of the olfactometer. (c) A typical response of a beetle to *S. tuberosum* odour only. (d) The response of a beetle to *S. tuberosum* plus *A. cyanophylli* odour. 1 = odour source; 2,3,4 = clean air; S = start of trace; E = end of trace; A = point at which the beetle arrested. Lines crossing the centre mark the odour field boundary.

TABLE 4. Responses of *C. nigritus* to odours of host plant (*S. tuberosum*) and mixture of host scale (*A. cyanophylli*) and host plant: comparisons between behaviour in odour and clean air using paired *t*-tests (means of individual fields ± SE)

Treatment	Odour field	*n*	Distance walked (mm)	Time in odour field (s)	Time spent walking (%)	Turning rate (° mm^{-1})	Angular velocity (° s^{-1})	Net speed (mm s^{-1})
S. tuberosum	1	55	501a[a]	125a	58a	6.1a	36.8a	8.4a
Clean air	2,3,4		427a	158a	34a	6.6b	22.9b	7.6b
SE			± 42	± 19	± 16	± 0.2	± 2.9	± 0.3
$P > t$			NS[b]	NS	NS	0.003	0.0001	0.01
A. cyanophylli plus *S. tuberosum*	1	68	557a	260a	51a	7.8a	33.5a	7.6a
Clean air	2,3,4		253b	113b	47a	6.9b	30.4a	7.1b
SE			± 53	± 24	± 6	± 0.4	± 3.5	± 0.2
$P > t$			0.0001	0.0001	NS	0.05	NS	0.05

[a]Means within a group with the same letter are not significantly different.
[b]NS = not significant.

cue lost. Wide reversals then replaced counter-turning due to the self-steered mechanism, and speed declined. The higher turning rate and angular velocity were accounted for by the wide reversals at the edge of the field and the upwind zig-zagging. Thus, in the presence of *S. tuberosum* with or without *A. cyanophylli* odours, *C. nigritus* exhibited a positive odour-conditioned response, though increased upwind orientation was detected only in the presence of the odour from both sources. In the light of other studies (e.g. Baker, 1986; Kennedy, 1986), this is probably due to an anemotactic response, though in this type of olfactometer where odour fields are likely to be heterogeneous (see Figure 1), the possibility of chemotaxis cannot be excluded. Since its size does not allow beetles to fly, it is also difficult to assess from this apparatus whether attraction to *A. cyanophylli* is also exhibited in flying beetles.

In summary, orthokinesis was increased in starved *C. nigritus* adults by the presence of *S. tuberosum* volatiles, although they did not exhibit a strong orientation towards them. Directional response analysis and general observations suggest that this behaviour was not caused by a repellent effect. These findings are partially in agreement with those of Obata (1986), who found that beetles were attracted to the host plant by both visual and olfactory cues, but spent less time in its presence than that of the aphid host or the aphids in addition to the host plant. In the current study, a strong directional response occurred only when *S. tuberosum* odours were supplemented by *A. cyanophylli* volatiles. Such a mechanism would keep beetles active in the favoured host habitat, thus greatly enhancing the ability of coccidophagous coccinellids to find their relatively rare and sessile prey among a forest or orchard full of suitable host plants. Aphidophagous species may, arguably, have less need for such a strategy, because there are few species of plant which do not support populations of their ephemeral and relatively common prey on summer hosts and random landings are likely to yield some prey. However, even they would find it advantageous if they could detect and orientate towards kairomones released by host plants in response to aphid feeding or semiochemicals released by the aphids themselves (e.g. aggregation or alarm pheromones). In the autumn, orientation to aphids on woody winter hosts might well be achieved by homing in on sex pheromones.

Visual orientation has not been examined in this study, though Obata (1986) found that the combination of visual and olfactory cues had a synergistic effect on the attraction of *H. axyridis* to its aphid host. Long-range vision is also thought to play a role in the aggregation behaviour of some coccinellid species (Hagen, 1962; Hodek, 1973). It is suggested, therefore, that like parasitoids, predaceous coccinellids possess a hierarchical host finding mechanism, *viz.*

(1) a long distance, olfactory and (probably) visual strategy, which operates over (at least) several metres and places the beetle in the correct habitat to find the host;
(2) a strongly directional location strategy, probably based on optomotor anemotaxis (linked to self-steered counter-turning) which singles out individual host plants bearing host insects; and
(3) switching to a general pre-location method (once the insect is in the immediate vicinity of its prey) which utilizes short-range visual cues, plant topography, plant morphology and photo- and geotaxes to place the predator at sites of high prey density.

This latter process could be aided by leaf-marking, contact chemoreception of arrestant host cues, such as honeydew and wax exuviae, and probably host odour. Such a close searching strategy would be more likely to succeed at leaf and branch level than an entirely odour-orientated one as there would be a great deal of air turbulence over and around these structures, leading to confused, and therefore unreliable, odour plumes.

In conclusion, *C. nigritus* is here considered to show a genuine attraction to *A. cyanophylli* odours when produced in conjunction with the host plant. This response can be explained in terms of the mechanism of self-steered counter-turning as postulated by other workers in this field, and is most probably driven by optomotor anemotaxis, although chemotaxis cannot be ruled out and the optomotor link has not been examined in this study. However, while the olfactometer used is a powerful tool for detecting directional responses, its size limitations and heterogeneous odour fields render it unsuitable for unambiguous diagnostic studies of some odour-conditioned

responses of coccinellids. This study adds a new dimension to predator–prey relationships amongst the Coccinellidae and shows, for the first time, that a member of this family was able to orientate towards its host using chemical cues. Future work now needs to be done to determine the nature of the attractant chemicals and whether or not they can be utilized to modify behaviour in this and other coccinellid species.

ACKNOWLEDGEMENTS

We wish to thank the UK Ministry of Agriculture, Fisheries and Food for funding the work, Dr Trudy Watt and Mr Alan Clewer for statistical advice, Dr Wilf Powell of Rothamstead Experimental station for his valuable suggestions and Dr Chris Hodgson for his critical review of the manuscript.

REFERENCES

ALLEN, D.C., KNIGHT, F.B. & FOLTZ, J.L. (1970) Invertebrate predators of the Jack-pine budworm, *Choristoneura pinus*, in Michigan. *Annals of the Entomological Society of America* **63**, 59–64.

BAKER, T.C. (1986) Pheromone-modulated movements in flying moths, in *Mechanisms in Insect Olfaction* (PAYNE, T.L., BIRCH, M.C. & KENNEDY, C.E.J., Eds) Clarendon Press, Oxford, pp. 39–48.

BORDEN, J.H. (1977) Behavioural responses of Coleoptera to pheromones, allomones and kairomones, in *Chemical Control of Insect Behaviour: Theory and Application* (SHOREY, H.H. & MCKELVEY, J.J., Jr, Eds) John Wiley and Sons, New York, NY, USA, pp. 169–198.

COLBURN, R. & ASQUITH, D. (1970) A cage used to study the finding of a host by the ladybeetle *Stethorus punctum*. *Journal of Economic Entomology* **63**, 1376–1377.

DIXON, A.F.G. (1959) An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.). *Journal of Animal Ecology* **28**, 259–281.

FLESCHNER, C.A. (1950) Studies on searching capacity of the larvae of three predators of the citrus red mite. *Hilgardia* **20**, 233–265.

HAGEN, K.S. (1962) Biology and ecology of predaceous Coccinellidae. *Annual Review of Entomology* **7**, 289–326.

HEIDARI, M. & COPLAND, M.J.W. (1992) Host finding by *Cryptolaemus montrouzieri* (Coleoptera: Coccinellidae) a predator of mealybugs (Homoptera: Pseudococcidae). *Entomophaga* **37**, 621–625.

HEIDARI, M. & COPLAND, M.J.W. (1993) Honeydew: a food or arrestant for the mealybug predator *Cryptolaemus montrouzieri*. *Entomophaga* **38**, 63–68.

HODEK, I. (1973) *Biology of the Coccinellidae*, W. Junk, The Hague.

JONES, R.L. (1986) Orientation by insect parasitoids, in *Mechanisms in Insect Olfaction* (PAYNE, T.L., BIRCH, M.C. & KENNEDY, C.E.J., Eds) Clarendon Press, Oxford, pp. 149–158.

KENNEDY, J.S. (1986) Some current issues in orientation to odour sources, in *Mechanisms in Insect Olfaction* (PAYNE, T.L., BIRCH, M.C. & KENNEDY, C.E.J., Eds) Clarendon Press, Oxford, pp. 11–26.

KUENEN, L.P.S. & BAKER, T.C. (1983) A non-anemotactic mechanism used in pheromone source location by flying moths. *Physiological Entomology* **8**, 277–289.

MARKS, R.J. (1977) Laboratory studies of plant searching behaviour by *Coccinella septempunctata* L. larvae. *Bulletin of Entomological Research* **67**, 235–241.

MUSTAPARTA, H. (1986) Allelochemical effects of pheromones: receptor responses, in *Mechanisms in Insect Olfaction* (PAYNE, T.L., BIRCH, M.C. & KENNEDY, C.E.J., Eds) Clarendon Press, Oxford, pp. 263–268.

OBATA, S. (1986) Mechanisms of prey finding in the aphidophagous ladybird beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Entomophaga* **31**, 303–311.

PAYNE, T.L., BIRCH, M.C. & KENNEDY, C.E.J. (Eds) (1986) *Mechanisms in Insect Olfaction*. Clarendon Press, Oxford.

PICKETT, J.A., WADHAMS, L.J. & WOODCOCK, C.M. (1992) The chemical ecology of aphids. *Annual Review of Entomology* **37**, 67–90.

PREISS, R. & KRAMER, E. (1986) Anemotactic orientation of gypsy moth males and its modification by the attractant pheromone (+)-disparlure during walking. *Physiological Entomology* **11**, 185–198.

TAYLOR, T.H.C. (1935) The campaign against *Aspidiotus destructor* Sign., in Fiji. *Bulletin of Entomological Research* **26**, 1–100.

THIERY, D. & VISSER, J.H. (1986) Masking of host plant odour in the olfactory orientation of the Colorado potato beetle. *Entomologia Experimentalis et Applicata* **41**, 165–172.

THOMPSON, W.R. (1951) The specificity of host relations in predacious insects. *Canadian Entomologist* **83**, 262–269.

VAN DEN MEIRACKER, R.A.F, HAMMOND, W.N.O. & ALPHEN, J.J.M. VAN (1990) The role of kairomones in prey finding by *Diomus* sp. and *Exochomus* sp., two coccinellid predators of the cassava mealybug, *Phenacoccus manihoti. Entomologia Experimentalis et Applicata* **56**, 209–217.

VARLEY, M.J., COPLAND, M.J.W., WRATTEN, S.D. & BOWIE, M.D. (1994) Parasites and predators, in *Video Techniques in Animal Ecology and Behaviour*, (WRATTEN, S.D., Ed.) Chapman & Hall, London, pp. 33–64.

VET, L.E.M., LENTEREN, J.C. VAN, HEYMANS, M. & MEELIS, E. (1983) An airflow olfactometer for measuring olfactory responses of hymenopterous parasitoids and other small insects. *Physiological Entomology* **8**, 97–106.

VINSON, S.B. (1976) Host selection by insect parasitoids. *Annual Review of Entomology* **21**, 109–132.

VISSER, J.H. & TAANMAN, J.W. (1987) Odour-conditioned anemotaxis of apterous aphids (*Cryptomyzus korschelti*) in response to host plants. *Physiological Entomology* **12**, 473–479.

WRATTEN, S.D. (1973) The effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.) as a predator of the lime aphid, *Eucallipterus tiliae* L. *Journal of Animal Ecology* **42**, 785–802.