

# SEARCHING BEHAVIOUR OF ADULT FEMALE COCCINELLIDAE (COLEOPTERA) ON STEM AND LEAF MODELS

B.D. FRAZER and R.R. MCGREGOR

Agriculture Canada, 6660 NW Marine Drive, Vancouver, British Columbia, Canada V6T 1X2

## Abstract

*The Canadian Entomologist* 126: 389–399 (1994)

Behaviour of locally occurring adult females of seven species of coccinellids was assessed on wooden dowel and paper models that mimicked branching patterns and arrangements of leaf attachments to stems. Ambient temperature and hunger of the beetles were controlled. The movements up or down the main branch of the branch models when contacted from a side branch, duration of searching, and method of leaving leaf models were recorded for 20 beetles of each species.

Each species responded to the seven models with different frequencies of behaviours that reflected species-specific modifications of the taxes that lead coccinellids to the tops and terminal parts of plants. Some beetles consistently modified the pattern of responses on the models that was displayed by the species as a whole. The individual modifications could be selected for. The differences in frequencies of behaviours were judged to be sufficient to result in differences in the efficiency with which plants with different architectures were searched.

---

Frazer, B.D., et R.R. McGregor. 1994. Comportement de recherche chez des coccinelles (Coleoptera: Coccinellidae) femelles adultes mises en présence de modèles de tiges et de feuilles. *The Canadian Entomologist* 126: 389–399.

## Résumé

Le comportement de femelles adultes de sept espèces locales de Coccinellidae a été étudié sur des modèles faits de chevilles de bois et de papier imitant les ramifications des branches et l'attachement des feuilles à des tiges. La température ambiante et la faim des insectes étaient contrôlées. Les déplacements vers le haut ou vers le bas sur la branche principale des modèles à partir d'une branche latérale, de même que la durée de la recherche et la façon de quitter les modèles à feuilles ont été notés chez 20 individus de chaque espèce.

Face aux sept modèles, les espèces ont réagi selon des fréquences particulières de comportements qui reflétaient les modifications spécifiques à chaque espèce des tendances qui déterminent les Coccinellidae à se déplacer vers le haut et vers les parties terminales des plantes. Sur les modèles, certains individus avaient des comportements toujours un peu différents de ceux manifestés par l'espèce dans son ensemble. La sélection peut agir sur ces modifications individuelles. Les différences dans la fréquence des comportements ont été jugées suffisamment grandes pour modifier l'efficacité avec laquelle des plantes d'architectures différentes sont explorées.

[Traduit par la rédaction]

## Introduction

Dixon (1959) showed that positive phototaxes and negative geotaxes lead aphidophagous coccinellids to terminal parts of plants where aphids are most likely to be found. All species of aphidophagous coccinellids studied have similar behaviours (Frazer 1988). Variations in the strength of those taxes among species of coccinellids have not been studied.

Strawberry aphids [*Chaetosiphon fragaefolii* (Cockerell)] live almost exclusively on small, immature leaves that grow below an extensive canopy of large, older leaves (Dicker 1952). Immature leaves would be searched only rarely if coccinellids could not override their taxic responses. The surfaces of plant parts (glandular hairs, nectaries, and epidermal wax) add further barriers or inducements to searching (Juniper and Southwood 1986). *Coccinella septempunctata* L. larvae searching for pea aphids [*Acyrtosiphon pisum* (Harris)] on broad bean and pea plants captured fewer aphids on peas because the larvae fall

more readily from the waxy pea leaves (Carter et al. 1984). Two species of coccinellids captured more pea aphids on mutant leafless peas than they did on normal peas. The waxy leaves also resulted in more coccinellids sliding off normal plants than off leafless mutants thereby reducing overall effectiveness on the normal plants compared with the mutants (Kareiva and Sahakian 1990).

Plant characteristics that modify taxes and post-prey contact mechanisms that induce area-restricted searching cannot explain the relative numbers of different species of coccinellids on different plants because all species of coccinellids have the same responses. *Adalia bipunctata* L. is most often found on shrubs and trees whereas *Coccinella trifasciata* L. and *C. californica* (Mannerheim) are usually found on low-growing plants. In southwestern coastal British Columbia, six common species are encountered in different proportions on different crops: *C. californica* was more numerous in oat plots than *C. trifasciata* which was more numerous in adjacent alfalfa plots (Ives 1981); *Cycloneda polita* Casey is only infrequently found on crops and *C. undecimpunctata* L. is found usually in small numbers on many crops (unpublished data); *Hippodamia convergens* (Guérin-Ménéville), common throughout southern North America, is only rarely found here (Gordon 1985). The association of particular species of coccinellids with specific plant forms, thermal environments, and aphid abundances has been described (Hodek 1973; Honěk 1985; Honěk and Kocourek 1988) but species-specific behaviours of coccinellids that could contribute to these differences have not been reported.

Our working hypothesis is that differences in relative numbers of each species of coccinellids on plants are not a result of preferences but result from differential success in capturing prey by each species. The most successful species then would tend to accumulate on a plant as long as prey are available. Our interest was to quantify variations in behaviour of adult coccinellids that may result in differences in success in searching. We used models of plants, as Dixon (1959) did, to mimic the manner of attachment of leaves to petioles and the angles of attachment of petioles to stems commonly seen on plants.

### Methods and Materials

**Rearing.** Adult coccinellids (*C. californica*, *C. trifasciata*, *C. undecimpunctata*, *C. septempunctata*, *C. polita*, *A. bipunctata*, and *H. convergens*) were collected in the field. They were fed pea aphids reared on broad beans, *Vicia faba major* (L.) cv. Broad Windsor, growing in sterilized potting soil. Eggs from the field-collected adults were used to establish continuous rearings of each species. Rearing cages were supplied with forced air (Forbes et al. 1985) under lights in an environmental room maintained at  $17.9 \pm 0.3^\circ\text{C}$ . Warm and cool white fluorescent tubes provided 16 h of light per day at an intensity of  $43.3 \pm 2.3 \mu\text{E m}^{-2} \text{s}^{-1}$  of photosynthetically active radiation. Insects used in the study were at most two generations removed from wild stocks. Vagaries in rearing conditions and predation by mites precluded *C. septempunctata* and *C. polita* being available for all trials as noted in relevant sections below.

**Pre-test Procedures.** Adult females were collected from rearing cages, put individually into 3-cm-diameter plastic Petri dishes and provided with an abundance of pea aphids. Females were weighed to  $\pm 1 \mu\text{g}$  (Mettler Model ME-30) after they had stopped eating (about 1 h). Beetles were placed individually into clean Petri dishes provided with moist filter paper and placed in an environmental room used for all subsequent experiments (16 h light  $35.9 \pm 0.34 \mu\text{E m}^{-2} \text{s}^{-1}$ , and  $19.7 \pm 0.03^\circ\text{C}$ ) before being tested.

A Model PC-604 Polycorder (Omnidata International Inc., Logan, UT) was programmed to record identifying codes for the starting conditions of each run and relevant experimental values described below. Data from the Polycorder were transferred directly to a microcomputer for formatting, analyses, or transfer to a mainframe computer.

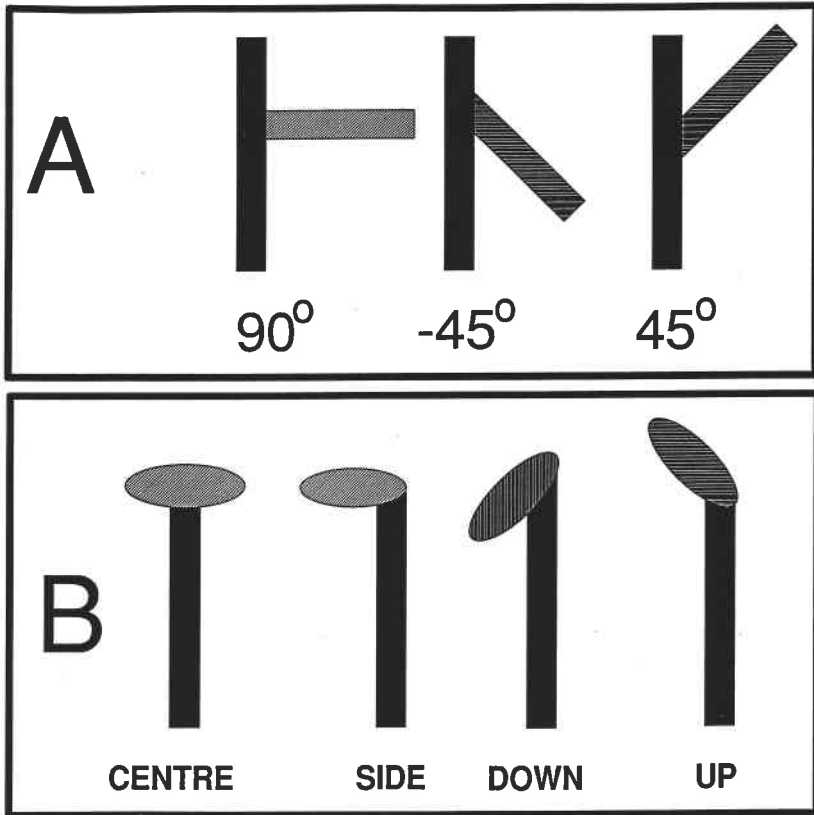


FIG. 1. Wood dowel stem (A) and leaf (B) models of plants used for coccinellid behavioural studies.

**Speed.** After at least 18 h of food deprivation, each of 80 female beetles of each species was re-weighed and placed at the bottom of an 80-cm upright wooden dowel (80 cm by 6 mm diameter), marked off every centimetre. Depriving beetles of food for 18 h engenders maximum searching activity (Frazer and Gilbert 1976). The distance a beetle moved without stopping as it ascended the dowel and the time spent moving were recorded. Individuals that stopped after a short distance were replaced at the bottom of the dowel so as to accumulate at least 80 cm of ascent. Speed of ascent of each beetle was calculated (centimetres per minute) and the duration of food deprivation, beetle identity code, and satiated weight were recorded.

**Models Simulating the Angle of Attachment of Petioles to Stems.** After 18 h of food deprivation, each beetle was placed on the tip of the side branch of each of three wooden structures (Fig. 1A) made of 6-mm-diameter softwood dowelling. Behaviour of each beetle on each model, as well as the weights when satiated and hungry, the duration of food deprivation, and the number of eggs present in the dish at the end of the food deprivation period were recorded on the Polycorder. The behaviour defined by position (top or bottom) of the adult on the side arm of the model when it encountered the upright section of each model and the direction (up or down) the adult moved on the upright was recorded for 20 beetles of each of the species except *C. septempunctata* which were not available for this test.

Each beetle was run on each model three times. Three sequences of runs (90°, 45°, -45°; 45°, -45°, 90°; -45°, 90°, 45°) were used to minimize effects of past experience (Williams

TABLE 1. Average (SE) of biological factors of six species of Coccinellidae before testing on three branch models. Pairs of values not followed by the same letter are significantly different at  $P \leq 0.05$  using Duncan's new multiple range test

Species	Weight (mg) satiated	% weight loss	Hours starved	Egg laid
<i>Coccinella californica</i>	29.8 (0.74) a	8.6 (0.01) a	21.8 (0.28) a	1.80 (0.66) a
<i>C. trifasciata</i>	20.8 (0.36) b	11.1 (0.01) b	20.6 (0.15) b	1.00 (0.38) b
<i>Hippodamia convergens</i>	23.1 (0.50) c	11.7 (0.01) b	20.7 (0.20) b	1.20 (0.48) b
<i>Cycloneda polita</i>	15.7 (0.33) d	17.4 (0.01) c	21.1 (0.21) b	2.80 (0.53) a
<i>C. undecimpunctata</i>	13.1 (0.21) e	11.3 (0.01) b	22.3 (0.25) a	0.01 (0.01) b
<i>Adalia bipunctata</i>	15.9 (0.35) d	12.9 (0.01) b	21.9 (0.34) a	2.40 (0.75) a

1949). The three sequences were run over consecutive days to minimize the effects of variations in duration of food deprivation among beetles. The sequence of nine runs was repeated for as many of the 20 beetles as possible.

**Models Simulating the Angle of Attachment of Leaves to Petioles.** Four models that simulated the manner of attachment of leaves to petioles were constructed of 6-mm dowels and 5-cm-diameter circles of Bristol board paper (Fig. 1B). Twenty females of each species (only 12 *C. septempunctata* and no *C. polita* were available) were arbitrarily selected from the rearing cage, fed to satiation, deprived of food for 5 h, and placed individually at the bottom of the upright dowel of each leaf model. The beetles almost always climbed to the paper disk immediately. The time spent actively moving on the disk was recorded. A run was terminated when a beetle walked, flew, or dropped from the disk, or if a beetle stopped moving for more than 2–3 s. The method of termination was recorded. Replications of four sequences were run as described for runs on the branching models.

**Statistical Analyses.** Small data sets were analysed using CoStat (CoHort Software, Berkeley, CA) on a microcomputer. Larger data sets were analysed using SAS (SAS Institute Inc., Cary, NC) on a VAX (Digital Equipment Corp.) mainframe.  $\chi^2$  tests for independence of two factors, one of which was species, were used to analyse frequencies of occurrence of responses on branch and leaf models. The SAS GLM module was used for multiple regression to determine relationships among numerical variables. Mention of statistical significance for single comparisons is followed by the relevant statistics or degrees of freedom and level of significance. Statistics for multiple comparisons are not included to conserve space but the level of significance used in tests was  $P \leq 0.05$  unless stated otherwise. Dummy variates (Gilbert 1973) were used as species variables in regressions when needed. Mean values in the text are followed by their standard errors. Differences between means were evaluated using Scheffé's or Duncan's new multiple range test modules of the programs when appropriate.

## Results

**Biological Variables.** The largest species weighed (*C. septempunctata* was not weighed), *C. californica*, was almost twice as heavy as the smallest species, *C. undecimpunctata*, when fully fed and the other four species were intermediate in weight (Table 1). The average durations of food deprivation differed significantly among species, but the largest difference was only 1.6 h, about 8% of the average deprivation time pooled over species and individuals.

Oviposition during the pre-trial period of food deprivation contributed to the weight loss of most females. Some females both laid and subsequently ate their eggs. Eggs present after the period of food deprivation varied from an average of about three for *C. polita* to

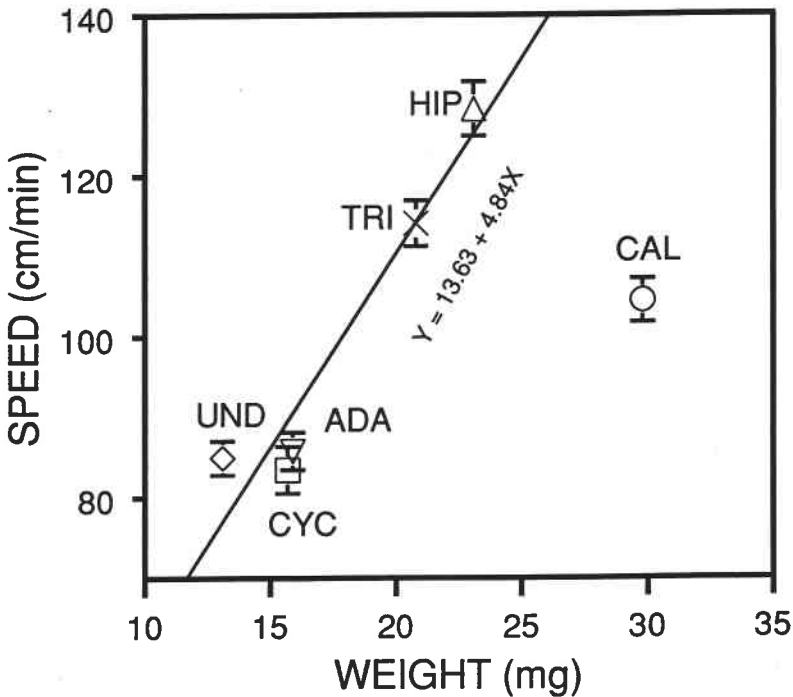


FIG. 2. Average speed ( $\pm$ SE) of ascent of adult female coccinellids versus their average weight when satiated.

almost none for *C. undecimpunctata*. The effect of oviposition was corrected for so that weight loss more accurately reflected relative hunger levels. The correction was done by regressing percentage weight loss against the number of eggs present after the food deprivation period of each species separately. The resulting equations were used to estimate the weight each beetle would have had if no eggs had been laid (the  $x$ -intercept of the line). This correction assumes, as was found earlier (Frazer and Gilbert 1976), that hunger level is not affected when eggs are laid without being consumed.

Satiated weights, corrected and uncorrected for ovipositional losses during food deprivation, and the number of eggs laid differed significantly among species (Table 1). There were no significant correlations among any of the weight or oviposition values within a species or pooled over all six species. Lack of correlations implies, but does not prove, that differences in the behaviours exhibited by beetles were due to innate qualities of the species.

**Climbing Speed on Vertical Pole.** The speed recorded for each beetle was not its maximum but the speed the beetle adopted voluntarily because all individuals moved faster up the pole when prodded with a brush. Speed of ascent increased significantly ( $r = 0.92$ ,  $P \leq 0.001$  excluding data for *C. californica*) with increased body size (estimated at fully satiated weight) up to a maximum for *H. convergens* (Fig. 2). *Coccinella californica* had great difficulty maintaining balance while climbing and tended to rotate precariously during the climb. Most *C. californica* were wider than the dowel which seemed to make it difficult for them to clasp the pole between opposing legs. *Hippodamia convergens* are also heavy but are more elongate than the oval *C. californica*.

**Behaviour on Stem Models.** For each species, a contingency table for three models by four behaviours (described from initial position and ultimate direction moved on the upright: top-up, top-down, bottom-up, bottom-down) was analysed by a  $\chi^2$  analysis of independence.

TABLE 2. Percentages of 480 runs of adult female Coccinellidae of six species pooled over three models that started on the top of the side branch and the percentage that moved up the upright section of the stem model. Values not followed by the same letter are significantly different at  $P \leq 0.05$  using Scheffé test

Species	Percentage top	Percentage up
<i>Coccinella californica</i>	88.8 (0.02) a	84.2 (0.02) a
<i>C. trifasciata</i>	95.4 (0.01) b	97.9 (0.01) b
<i>Hippodamia convergens</i>	81.3 (0.02) c	73.8 (0.01) c
<i>Cycloneda polita</i>	76.7 (0.03) d	73.8 (0.03) c
<i>C. undecimpunctata</i>	88.1 (0.01) e	84.8 (0.02) a
<i>Adalia bipunctata</i>	93.6 (0.01) f	88.0 (0.02) a

Most individuals, of all species, moved toward the upright on the upper surface of the side branch of all three models and moved up the upright when it was encountered. However, the actual proportion of individuals that elicited these (Top and/or Up) expected responses differed significantly among species (Table 2). Over 99% of the *C. trifasciata* and 84.5% of the *C. californica* elicited either the top or up behaviour or both (data not shown) regardless of the model, but in the other four species the angle of the side branch significantly affected the direction taken by beetles (Fig. 3).

**Behaviour on Leaf Models.** Almost all beetles searched only the upper edges of the paper disks and only rarely walked on the central or under surfaces of any disk.

Time searching on each model by each species (Fig. 4) was initially analysed using time of food deprivation as a covariate to remove any of its effect; it had none ( $df = 1,1780$ ,  $P = 0.23$ ). Searching time (Table 3) varied significantly among species ( $df = 5,99$ ,  $P \geq 0.0001$ ), among models ( $df = 3,291$ ,  $P \geq 0.0001$ ), and with significant interactions between models and species ( $df = 15,291$ ,  $P \geq 0.0006$ ) (Fig. 4).

Searching time on disks varied from 3- to 8-fold among individual beetles depending upon the species. The data for *A. bipunctata* are shown (Table 4) as beetles of that species had the greatest variability among individuals. Each species had its own unique pattern of responses to the leaf models and some individuals of each species significantly ( $df = 291,1790$ ,  $P \geq 0.003$ ) modified the species pattern.

The majority of *C. septempunctata*, *C. californica*, *A. bipunctata*, and *H. convergens* left the leaf models by walking down the dowel except on the model where the "petiole" was attached to the centre of the undersurface of the disk (Fig. 5). On the centre model, the majority of beetles of all six species flew off after spending significantly more time on the disk than they did on the disks of the other three models (Fig. 4). Over 65% of *C. trifasciata* flew from the centrally attached model but fewer than 35% of *C. undecimpunctata* did so (Fig. 5).

## Discussion

Our interest was to determine if there were species-specific modifications in the innate taxes of coccinellids that could confer different efficiencies by each species while searching plants with different architectures. We chose to use artificial plants because they are free from insects, mites, refuse, plant exudates, and pubescence which could alter behaviour of a searching coccinellid and would likely obscure the comparisons we were interested in.

The branch models allowed testing if the angle of attachment of a stem or petiole to a main stem affected the direction taken when the beetle reached the main stem. The artificial nature of the "stems" would not likely change the outcome as compared with a real plant. The leaf models tested the ability of beetles to escape a previously searched and unproductive "leaf" and identified the means the beetle chose to leave.

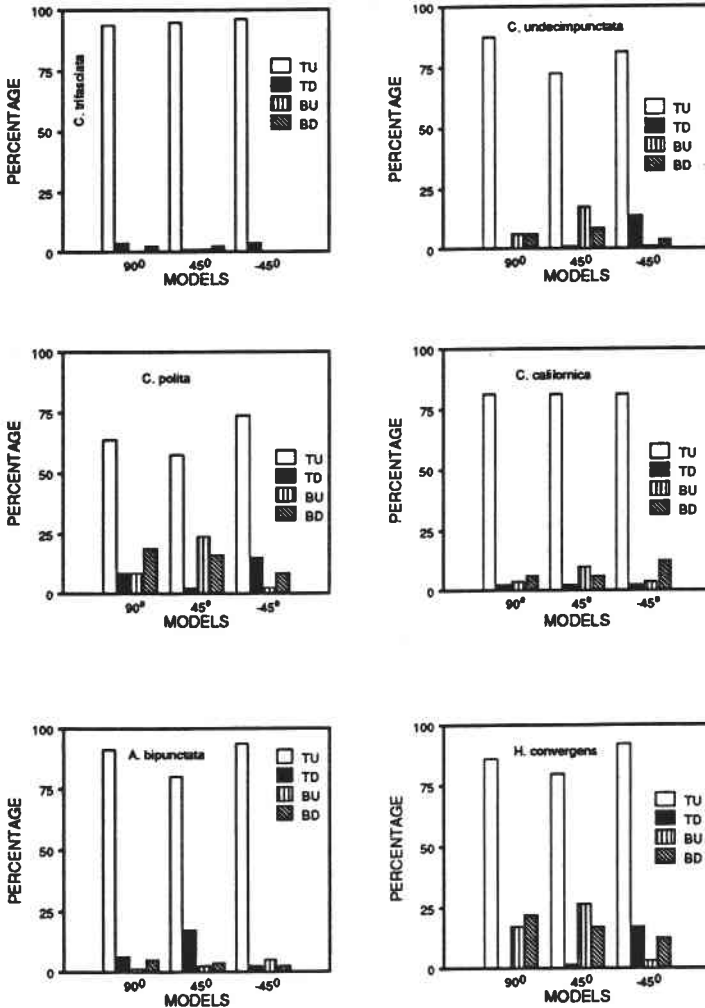


FIG. 3. Proportions of 80 adult female coccinellids of six species that moved from either the top (T) or bottom (B) of the side branch of wooden models and then subsequently moved up (U) or down (D) the main branch.

As in all earlier studies on the species used in this study, moving upward predominated on the branch models. The behaviour dominated in all species but the frequency of occurrence varied depending on plant model for all species except *C. trifasciata* and *C. californica*, which did not vary their behaviour significantly on any of the three models. Similarly, species showed up to 2-fold differences in searching times and different frequencies of the ways of leaving a leaf depending upon the species of coccinellid.

Effects of plant architecture on searching by coccinellids observed in this study, if they also occurred on natural plants, would result in considerable differences in the success of each species in finding aphids on the same plant. Leaves of cereals are attached like the SIDE and UP leaf models from which all species were able to leave most quickly and by walking. The CENTRE leaf model acted as a trap from which most individuals of all species escaped by flying after spending two to three times longer on the model. Adults of several

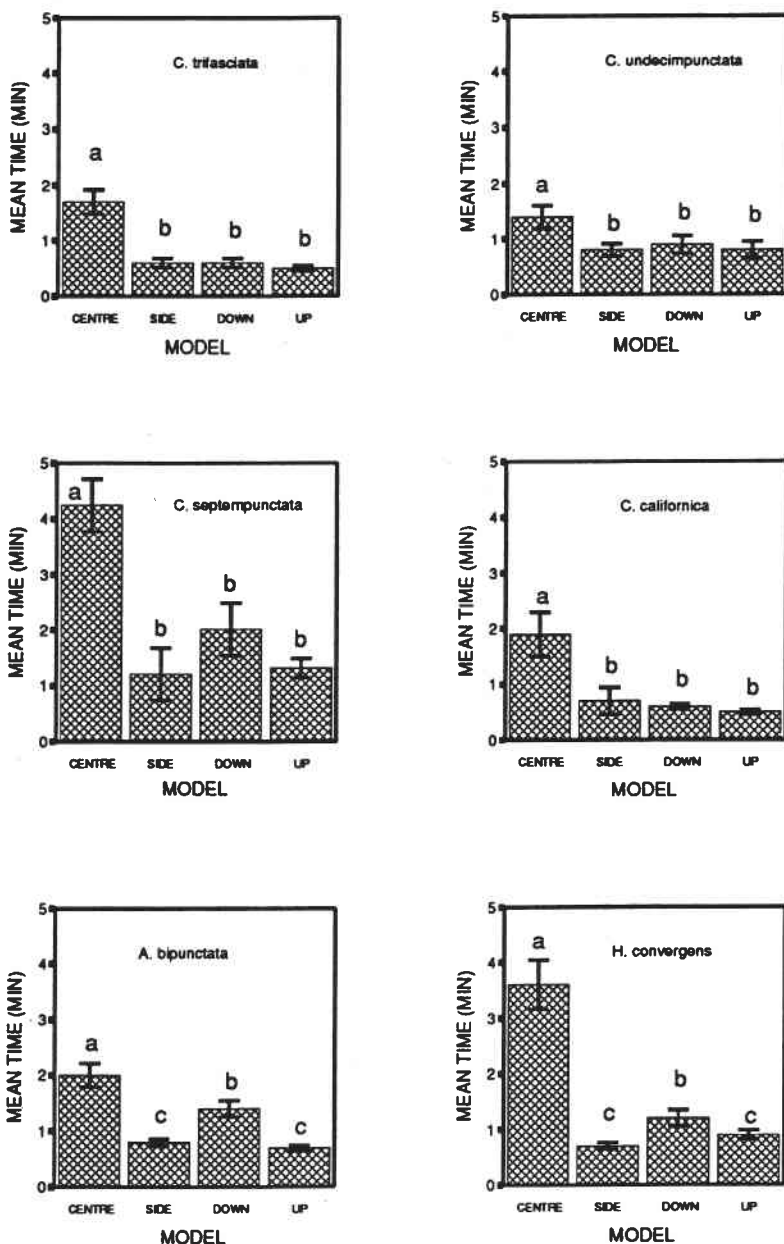


FIG. 4. Average time (minutes) spent by adult females of six species of coccinellids on each of four models that simulate the angle of attachment of leaves to petioles. Bars represent standard errors.

species of coccinellids respond to the trifoliate leaf of alfalfa as they did to the CENTRE leaf model (Frazer and Gilbert 1976). To reach the dowel of that model, or the petiole of the alfalfa, leaf beetles must move under the surface and downward. The species tested differed in their abilities to do so.



TABLE 3. Searching ( $\pm$ SE) time of six species of adult female coccinellids on paper models of leaves averaged over four models; and time on four models averaged over all species of coccinellid. Values not followed by the same letter are significantly different at  $P \leq 0.05$  by Scheffé test

Species	Time, min
<i>Coccinella septempunctata</i>	2.20 (0.236) a
<i>Hippodamia convergens</i>	1.64 (0.118) b
<i>Adalia bipunctata</i>	1.26 (0.068) c
<i>Cycloneda undecimpunctata</i>	1.15 (0.087) cd
<i>Coccinella californica</i>	0.93 (0.119) d
<i>C. trifasciata</i>	0.89 (0.064) d
Model	
Centre	1.70 (0.220) a
Down	1.09 (0.194) a
Up	0.93 (0.146) a
Side	0.89 (0.124) ab

For a coccinellid to remain satiated, as is required for oviposition, it usually must search many plants. The differences in time spent on the leaf models indicate the potential for some species to waste considerable time. That *C. californica* outnumbered *C. trifasciata* on oats and the relative numbers were reversed on alfalfa (Ives 1981) reflects the results of these two species on these models. The two species spent similar amounts of time on the leaf models but *C. trifasciata* was far more likely to fly off a leaf model sooner than *C. californica*. The less frequent flyer was trapped longer.

The results demonstrate that each species tested had a unique set of modifications to their basic taxes when confronted with different plant architectures. Those modifications would contribute to differential success of each species in finding aphids which in turn would produce different relative abundances of coccinellid species on a given plant. The variation in responses between individuals of the same species on the same model suggests that performance on these models could be used to select individuals that searched a particular model longer than average. Responses on simple plant models could be used as a means to select individuals with particular behaviours that are related to efficiency in searching for prey on a particular plant.

#### Acknowledgments

We thank John Hall for statistical and editorial advice and S. Fitzpatrick and D. Raworth for comments on an earlier draft.

TABLE 4. Average search times in minutes (SE) of individual adult female *Adalia bipunctata* spent during four runs on each of four paper leaf models. Data selected for individuals that remained on each model for the shortest and the longest times

Model	Shortest	Longest	Ratio
Centre	0.45 (0.16)	3.6 (1.90)	8.0
Side	0.36 (0.12)	1.4 (0.32)	3.8
Down	0.45 (0.10)	3.2 (1.11)	7.1
Up	0.47 (0.11)	1.4 (0.53)	3.0

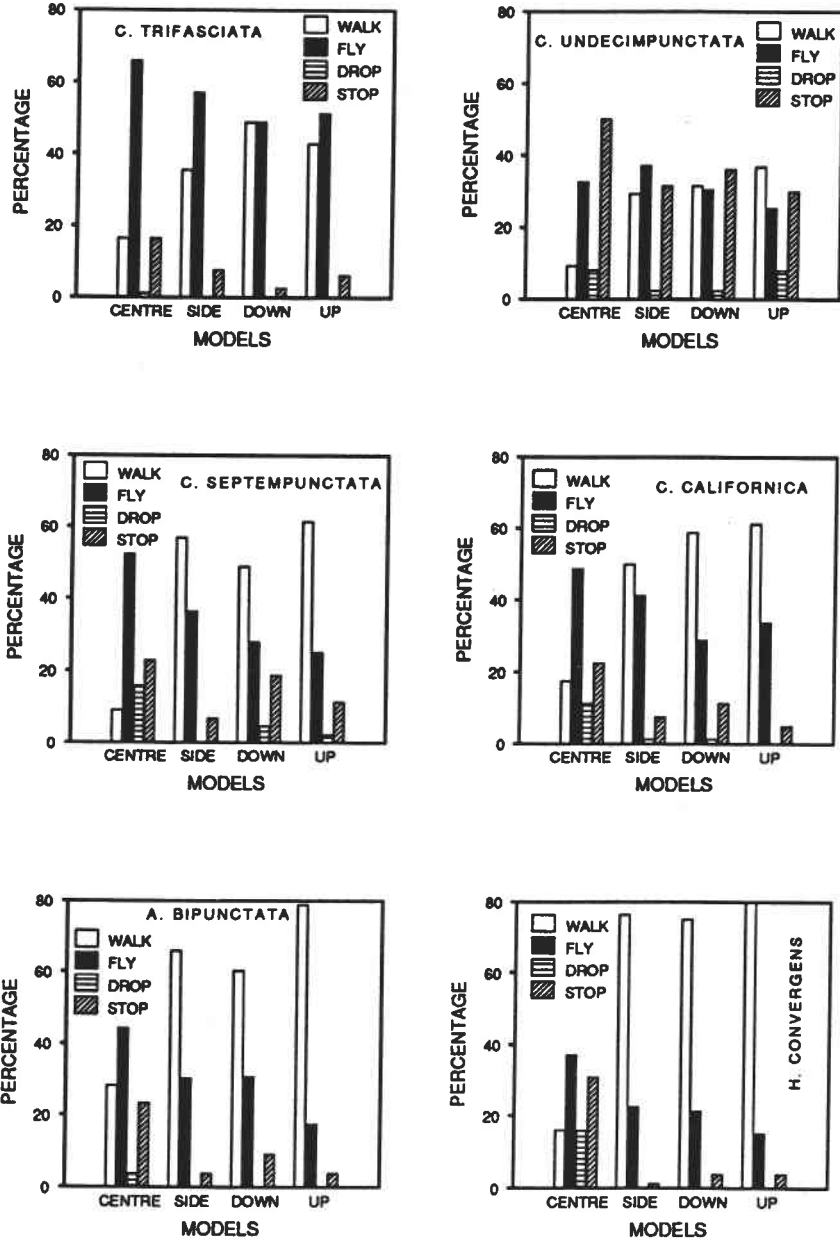


FIG. 5. Proportion of 80 adult female coccinellids of six species that ended their runs on four leaf models in various ways (see text for details).

References

Carter, M.C., D. Sutherland, and A.F.G. Dixon. 1984. Plant structure and the searching efficiency of coccinellid larvae. *Oecologia* 63: 394-397.

Dicker, G.H.L. 1952. Studies in population fluctuations of the strawberry aphid, *Pentatrichopus fragaefolii* (Cock.). 1. Enemies of the strawberry aphid. *Annual Report of the East Malling Research Station for 1951* 39: 166-168.

- 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.
- Forbes, A.R., B.D. Frazer, and C.K. Chan. 1985. Aphids. pp. 353–359 in Singh, P., and R.F. Moore (Eds.), *Handbook of Insect Rearing*, Vol. 1. Elsevier Science Publishers B.V., Amsterdam. 488 pp.
- Frazer, B.D. 1988. Coccinellidae. Chap. 9.2.1. pp. 231–247 in Minks, A.K., and P. Harrewijn (Eds.), *Aphids, their Biology, Natural Enemies and Control*, Vol. B. Elsevier Science Publishers B.V., Amsterdam. 364 pp.
- Frazer, B.D., and N. Gilbert. 1976. Coccinellids and aphids: A quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *Journal of the Entomological Society of British Columbia* **73**: 3–56.
- Gilbert, N. 1973. *Biometrical Interpretation*. Clarendon Press, Oxford. 125 pp.
- Gordon, R.D. 1985. The Coccinellidae (Coleoptera) of America North of Mexico. *Journal of the New York Entomological Society* **90**: 1–912.
- Hodek, I. 1973. *Biology of Coccinellidae*. Dr. W. Junk N.V. Publishers, The Hague, Holland. 260 pp.
- Honěk, A. 1985. Habitat preferences of aphidophagous Coccinellids [Coleoptera]. *Entomophaga* **30**: 253–264.
- Honěk, A., and F. Kocourěk. 1988. Thermal requirements for development of aphidophagous Coccinellidae (Coleoptera), Chrysopidae, Hemerobiidae (Neuroptera), and Syrphidae (Diptera): Some general trends. *Oecologia* **76**: 455–460.
- Ives, P.M. 1981. Estimation of coccinellid numbers and movement in the field. *The Canadian Entomologist* **113**: 981–997.
- Juniper, B.E., and T.R.R. Southwood (Eds.). 1986. *Insects and Plant Surfaces*. Edward Arnold Ltd., London. 360 pp.
- Kareiva, P., and R. Sahakian. 1990. Tritrophic effects of simple architectural mutation in pea plants. *Nature* **345**: 433–434.
- Williams, E.J. 1949. Experimental designs balanced for the estimation of residual effects of treatments. *Australian Journal of Scientific Research* **2**: 149–168.

(Date received: 29 June 1993; date accepted: 7 December 1993)