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## Effects of body size and plant structure on the movement ability of a predaceous stinkbug, *Podisus maculiventris* (Heteroptera: Pentatomidae)

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**Abstract** The movement ability of individuals has become increasingly important to a variety of ecological questions. In this study, I investigate how plant structure and changes in body size through development affect the movement ability of a predaceous stinkbug, *Podisus maculiventris*, on three species of goldenrod (*Solidago* spp.) representing a wide range of surface complexities. I adapt existing techniques for quantifying movement in two dimensions to the study of movement on natural plant structures in three dimensions. These experiments indicate that plant structure and insect size are significant factors affecting the movement ability of *P. maculiventris*. Changes in movement ability due to factors of ontogeny and different habitat structures suggest that the scale of an individual's ambit or ecological sphere of influence may vary within its lifespan. Considering the influence of ontogeny and habitat structure on movement ability may be useful to investigations of population dynamics, foraging behavior, and pest management.

**Key words** Movement · Body size · Ontogeny · Plant structure · Foraging

### Introduction

A consideration of spatial dynamics has become increasingly important for understanding many ecological processes. At the organismal level, spatial dynamics can be studied as the movement behavior of individuals. An individual's ability to move within its habitat may have a strong influence on its population dynamics and foraging behavior. The study of movement ability throughout ontogeny and in a variety of habitats is especially important for gauging changes in the spatial scale at which an individual interacts with its environment. A better under-

standing of the factors influencing movement ability is useful for determining an appropriate scale for further ecological investigations.

Habitat structure affects insect movement at a variety of spatial scales, ranging from landscape-level effects on *Elodes* spp. beetles (Coleoptera: Tenebrionidae) (Johnson et al. 1992; Wiens et al. 1993) and grasshoppers (Orthoptera: Acrididae) (With 1994b) to the smaller-scale effects of plant architecture and surface texture on ladybird beetles (Coleoptera: Coccinellidae) (Grevstad and Klepetka 1992; Frazer and McGregor 1994), lacewing larvae (Neuroptera: Chrysopidae) (Treacy et al. 1987; Clark and Messina 1998), minute pirate bugs (Hemiptera: Anthocoridae) (Eigenbrode et al. 1996) and hymenopteran parasitoids (Keller 1987). Movement ability may also depend on the size of the individual (Treacy et al. 1987; With 1994a, 1994b), as a direct result of greater stride length at larger sizes (Reavey 1993), or because greater stride length allows an individual to interact with its environment at a different scale of habitat structure with lower perceived complexity (Treacy et al. 1987; With 1994a; Weiss and Murphy 1988). In cases where the size of an individual changes markedly over the course of development, a particular scale of habitat structure may be expected to affect some instars more than others.

This study examines how the plant structure of three goldenrod species (*Solidago rugosa*, *S. altissima*, and *S. juncea*) influences the intraplant movement of a predatory stinkbug, *Podisus maculiventris* (Heteroptera: Pentatomidae), in the course of its nymphal development. I use the term "surface complexity" to describe plant structure on the scale of plant surfaces including some combination of the density, length, and form of plant trichomes, and the physical character or texture of the plant surface (e.g., waxiness, roughness). I ask the specific questions:

1. What is the relationship between movement ability and body size over the course of development?
2. How is movement ability within a given size class influenced by differences in plant surface complexity?

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### 3. Are differences in plant surface complexity less relevant for larger size classes?

I hypothesize that the movement ability of *P. maculiventris* is inhibited in a manner dependent on both individual size and plant surface complexity, with the specific predictions: (1) movement ability will be greater for later instars, (2) movement ability within a given instar will be more inhibited by greater plant surface complexity, and (3) differences in movement ability caused by differences in habitat structure on the scale of plant surface complexity will be less relevant for individuals with larger body sizes.

To test these predictions in the arena of natural plant structure, I extend existing methods for recording movement behavior in two dimensions (e.g., Turchin 1998) to three dimensions. In this paper, I describe a method that uses a series of photographs as a template for recording insect movement on plant structures. With this method, it is possible to track an individual's movement and record its path, displacement, and duration in three dimensions.

## Materials and methods

### Species and natural history

*P. maculiventris* is a member of the asopine subfamily of pentatomids, unique among the stinkbugs for their obligately predaceous habit (Schaefer 1996). It is a generalist both in terms of its wide habitat range and catholic diet (Evans 1980, 1982). In old-field communities near Cornell University, *P. maculiventris* forage for soft-bodied prey on a wide variety of plants, including the goldenrods *S. rugosa*, *S. altissima*, and *S. juncea*. While similar in gross architectural features, these goldenrod species present a wide range of surface complexities: *S. rugosa* has rugose leaf and stem surface textures with long tomentose trichomes in high densities, while *S. juncea* is smooth and waxy on leaf and stem surfaces, and *S. altissima* is intermediate in trichome density and length.

In the course of development, *P. maculiventris* individuals experience an approximately tenfold increase in body size through five nymphal instars and the adult stage (Decoursey and Esselbaugh 1962). Because its development is paurometabolous, this increase in body size occurs without fundamental changes in body plan. Although the first instar is non-predaceous, all stages from the second instar to the adult actively forage on the plant surface. These natural history characteristics allow an ecologically meaningful comparison of *P. maculiventris* movement abilities at different life stages on a variety of plant surfaces.

### Rearing

A colony of 100–200 *P. maculiventris* individuals was maintained in a laboratory growth chamber at 17–23°C with photoperiod 16 h light:8 h dark from 22 May to 28 August 1998. The majority of these bugs were the progeny of wild stock adults collected by J. Aldrich in pheromone-baited traps between 30 March and 4 April 1998 at the Insect Physiology Laboratory (USDA, Agricultural Research Service) in Beltsville, Maryland, United States. This colony was supplemented with a small number of individuals (two adults and seven nymphs) collected by sweepnetting in old fields near Cornell University. Eggs and nymphs were reared in 0.2-l styrofoam containers, covered with plastic Petri dish covers. Water was provided daily via a cotton plug. Adults were kept in two cylindrical wire mesh cages (30.5 cm height×20.3 cm diameter). All predaceous instars were fed an ad libitum diet (30 mg per 2nd instar nymph, 40 mg per 3rd instar nymph, 60 mg per 4th in-

star nymph, 80 mg per 5th instar nymph, 100 mg per adult) of frozen field-collected chrysomelid larvae (*Trirhabda* spp.) and mealworms (*Tenebrio molitor* larvae) in an approximately 1:1 ratio by mass each day. These methods are a synthesis of those used by Mukerji and LeRoux (1965), Evans (1980), and Aldrich et al. (1984).

### Stride length measurements

To test the assumption that stride length scales linearly with body size, I measured the body length and stride length of individuals from each foraging developmental stage. Body length was measured from the anterior tip of the head to the posterior tip of the abdomen, using a micrometer. Stride length was recorded by placing individuals within a circular "corral" of wet india ink and allowing them to walk out. I measured the pattern of stride lengths to determine the stride of the right and left prothoracic, mesothoracic, and metathoracic legs. These six stride measurements were averaged to a single mean stride length for each individual. Measurements were not repeated on the same individual at different developmental stages. All measurements were made between 16 June and 16 July 1998.

### Experiment on body size and plant structure effects

To test the effect of body size and plant structure on movement, I used an orthogonal, repeated measures experimental design in which each of 12 *P. maculiventris* individuals (6 from each of two egg clusters, drawn from each of two rearing cages) were tested on each of three plant species at each of three successive developmental stages, from the 2nd instar to the 4th instar. These instars were chosen because they show an approximately two-fold increase in body size (2nd instar, mean=2.37 mm, SD=0.19,  $n=12$ ; 3rd instar, mean=3.93 mm, SD=0.33,  $n=13$ ; 4th instar, mean=5.36 mm, SD=0.40,  $n=14$ ). Personal observations in previous work suggested that individuals with these body sizes are most affected by structures at the scale of plant surface complexity. During these experiments, individuals were maintained in separate containers to minimize the possibility of damage or cannibalism. Individuals were starved for 18–24 h before each experimental trial to standardize hunger levels.

Each plant species was represented by six ramets transplanted from old fields near Cornell University. Plants 50–60 cm in height with minimal herbivore damage were selected from distant locations in a field so that the likelihood of selecting genetically clonal plants was minimized. These plants were transplanted in the early morning and immediately potted and watered in 20.3-cm round pots with Scot's Metro Mix potting soil to minimize the effects of transplant shock. All transplants were given at least 2 days to recover before they were used in experimental trials. These plants were maintained in a climate-controlled greenhouse throughout these experiments. In order to minimize intraplant structural variation and temporal variation across trials, the rapidly growing top 10–15 cm of each plant was removed before trials began. Subsequent regrowth was removed before each trial.

On each trial day, two or three *P. maculiventris* were randomly selected from the pool of available individuals. At the beginning of the day, a randomization program selected the order in which each individual encountered the three plant species. Individuals were run in alternating turns so that no individual participated in consecutive trials, and each individual participated in trials throughout the day. This procedure sought to minimize any effects of order of encounter of plant species, temperature, and the time of day.

For each experimental trial, an individual was placed on the plant stem 15 cm from the top of the plant. Each trial consisted of a 12 min observation period during which the movement path and time spent resting was recorded. To provide a template for recording insect movement over plant structures, each plant was represented in a series of photographs (2–4 per plant) at a scale suffi-

cient to show leaf and stem structure (approximately 15–20 cm of stem per 12.7 cm×17.8 cm print) prior to these experiments. Plastic overhead transparencies were placed over these photographs and the individual's position and path were recorded on the transparency at 30 s intervals. Total elapsed times and resting times were recorded on a split timer digital stopwatch. Resting was defined as a period of no displacement, including rotations about an axis and antennal probing behavior. After the completion of each trial, I measured the recorded movement path on the experimental plant, by referencing the photo transparency. These measurements were made using callipers to approximate the recorded path in straight-line steps between plant landmarks such as stem-leaf nodes and leaf tips. Although these measurements were a series of straight-line approximations, the movement of *P. maculiventris* as constrained by *Solidago* spp. architecture seems to be well approximated by these measurements.

Time of day and temperature were recorded for each trial. All trials were conducted in a climate-controlled greenhouse at 23.6–30.8°C from 1100 to 1630 hours each day between 26 July and 10 August 1998. Trial temperatures were generally similar across instars (2nd instar, mean=26.8°C, SD=1.68; 3rd instar, mean=25.5°C, SD=1.12; 4th instar, mean=25.6°C, SD=1.38) and across plant species (*S. rugosa*, mean=26.4, SD=1.52; *S. altissima*, mean=25.8, SD=1.46; *S. juncea*, mean=26.0, SD=1.64). Trials were restarted in the instance of timer malfunction ( $n=2$ ), and aborted if an individual molted during its trial ( $n=3$ ), or if the trial individual walked off the plant ( $n=1$ ).

Movement time (min) for each trial was calculated as the total elapsed time minus the time spent resting. Movement rate (cm min<sup>-1</sup>) was calculated as the total displacement divided by the movement time. Because these movement rate data were averaged over the time spent moving, trials with very low moving times (<1.5 min,  $n=21$ ) were excluded from analyses in order to reduce the effects of measurement errors.

#### Data analysis and statistics

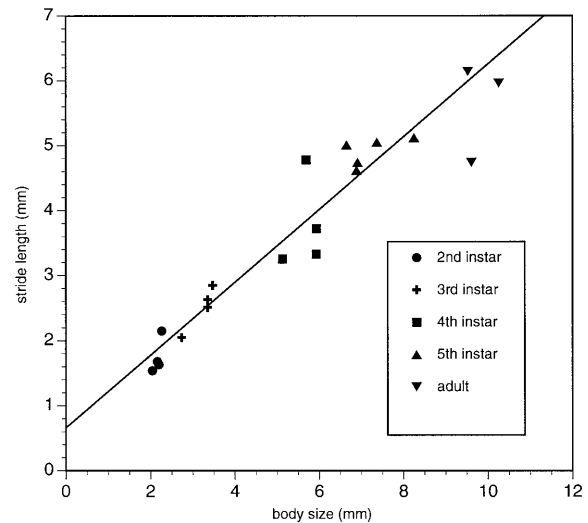
These data were analyzed with a mixed model repeated-measures analysis of variance (ANOVA) using the SAS software MIXED procedure (SAS Institute 1997). The MIXED procedure was selected for its capacity to handle unbalanced data (SAS Institute 1997) resulting from aborted and excluded trials. Developmental stage (instar), plant species, and egg cluster of origin were fixed factors in this analysis. This design included three *P. maculiventris* instars (2nd, 3rd, and 4th), and three plant species (*S. rugosa*, *S. altissima*, and *S. juncea*). While egg cluster of origin was not a factor of primary interest, two levels (one from each cage) were included in this analysis to provide some indication of possible genotypic or early environmental effects. Possible interaction effects between plant species and instar were also tested for.

Like all repeated measures designs, this experiment is based on the untestable assumption of independence between measures in a temporal series. In this design, the order of plant encounter was randomized within each measurement day, and molting occurred between measurement days, so that some effects of a previous trial (e.g., accumulated plant waxes in tarsi) were minimized and other effects (e.g., learning) were randomly controlled.

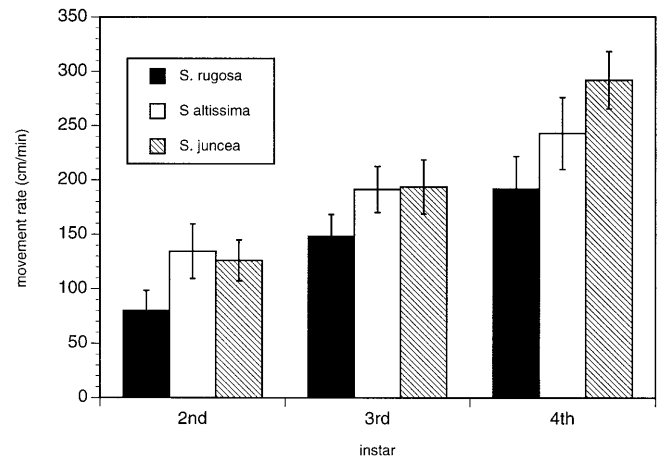
## Results

The results of the stride length and body length measurements are shown in Fig. 1. These experiments indicate a linear relationship between stride length (SL) and body length (BL) (2nd instar,  $n=4$ , 3rd instar,  $n=4$ , 4th instar,  $n=4$ , 5th instar,  $n=5$ ; adult,  $n=3$ ,  $SL=0.55BL+0.66$ ,  $r^2=0.943$ , SE of slope=0.032).

The results of the movement rate experiments are shown in Fig. 2. I investigated the effect of instar on



**Fig. 1** Body size vs. stride length relationship in *Podisus maculiventris* 2nd instars through adult (linear regression  $SL=0.55BL+0.66$ ,  $r^2=0.943$ , SE of slope=0.032)



**Fig. 2** Movement rate of *P. maculiventris* on three species of goldenrod at three stages of nymphal development. Columns represent least squared mean movement rate. Error bars represent  $\pm 1$  SE

movement rate to test the prediction that movement rate increases with increasing size. The least squared mean (lsmean) rate of movement on all plant species for each instar increased with each succeeding instar (Table 1) and instar was a significant factor in the overall analysis (Table 2). For analyses across plant species, there were significant differences for the movement rates of all possible pairs of instars (2 vs. 3;  $df=44$ ,  $P=0.0002$ ; 2 vs. 4,  $df=44$ ,  $P=0.0001$ ; 3 vs. 4,  $df=44$ ,  $P=0.0023$ ). For analyses within plant species, instar was a significant factor for all species (Table 2). Egg cluster of origin was an insignificant factor in these analyses. On all plant species tested, the movement rate of *P. maculiventris* was greater for larger, later instars than for earlier, smaller instars.

I analyzed the effect of plant species in these experiments to investigate the prediction that plant surface

**Table 1** Least squared mean (*lsmean*) movement rates of *Podisus maculiventris* on three species of goldenrod and for three nymphal instars

	Lsmean rate (cm min <sup>-1</sup> )±SE	df	P
2nd instar	113.5±14.8	44	0.0001
3rd instar	177.6±15.3	44	0.0001
4th instar	242.2±19.5	44	0.0001
<i>Solidago rugosa</i>	139.9±16.0	44	0.0001
<i>S. altissima</i>	189.5±17.63	44	0.0001
<i>S. juncea</i>	203.9±16.1	44	0.0001

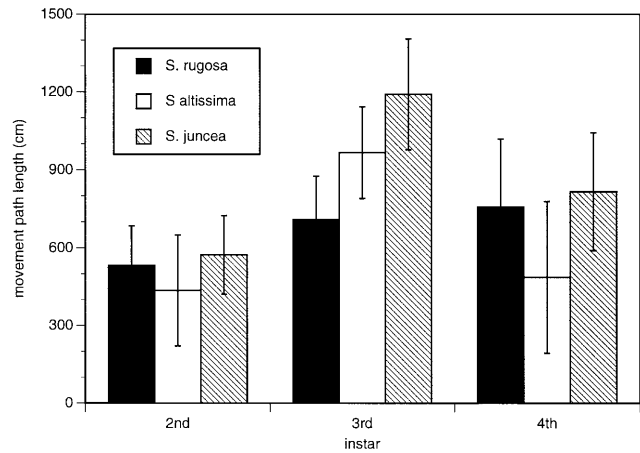
**Table 2** Mixed model repeated-measures ANOVA of *P. maculiventris* movement rates on three species of goldenrod at three stages of nymphal development

Effect	Within species	Within instar	df	P
Instar	–	–	44	0.0001**
Instar	<i>S. rugosa</i>	–	44	0.0012**
Instar	<i>S. altissima</i>	–	44	0.0209*
Instar	<i>S. juncea</i>	–	44	0.0001**
Species	–	–	44	0.0017**
Species	–	2nd	44	0.0607
Species	–	3rd	44	0.1572
Species	–	4th	44	0.0324*

\* $P < 0.05$ , \*\* $P < 0.005$

complexity influences the movement ability of *P. maculiventris*. The least squared mean movement rate for all instars was lower on plant species with greater surface complexity (Table 1) and plant species was a significant factor in the overall analysis (Table 2). Differences in the movement rate of *P. maculiventris* on these three species of goldenrod were not less significant in the 4th instar; to the contrary, for analyses within each instar, the effect of plant species was only significant in the 4th instar, and nearly significant in the 2nd instar (Table 2). The rank order of the movement rates within each instar was similar but not identical: the least squared mean movement rate of *P. maculiventris* was lowest on *S. rugosa* for all instars in these experiments and the relative movement rate of *P. maculiventris* on *S. altissima* and *S. juncea* varied between instars. The interaction effect of instar×plant species was not significant ( $df=44$ ,  $P=0.66$ ).

In these experiments, I used movement rate as a measurement of movement ability on different plant species. While movement rate was useful for investigating the mechanistic relationship between a moving insect and the plant, the total length of the movement path was a useful measurement of foraging range. I analyzed these data in a similar mixed model repeated measures ANOVA to provide insights into how movement rate translates into a foraging range. The results of these analyses are shown in Fig. 3. Instar was the only significant factor in the overall analysis ( $df=44$ ,  $P=0.0019$ ). The patterns of least squared mean path lengths within each instar were similar to the patterns for movement rate. However, in comparisons between instars, the

**Fig. 3** Total movement path length of *P. maculiventris* on three species of goldenrod at three stages of nymphal development. Columns represent the least squared mean total movement path lengths of individuals in a 12-min observation. Error bars represent  $\pm 1$  SE

least squared mean path length for 4th instar individuals was less than that of 3rd instars (4th instar,  $lsmean=703.40$  cm vs. 3rd instar,  $lsmean=958.45$  cm). This difference was not statistically significant ( $df=44$ ,  $P=0.1109$ ).

## Discussion

The results of these experiments indicate that the movement ability of *P. maculiventris* on *S. rugosa*, *S. altissima*, and *S. juncea* is dependent on both the size of the individual insect and the plant species. While a number of studies have suggested that plant structure affects the foraging behavior of insect predators (Dixon 1959; Frazer and McGregor 1994; Grevstad and Kepletka 1992; Wiedenmann and O'Neill 1992), the additional consideration of ontogeny may be an important component in understanding movement (With 1994a).

These results do not support the hypothesis that plant surface complexity is less relevant for larger *P. maculiventris* instars. *P. maculiventris* 4th instar nymphs are certainly affected by plant structure, although further experiments in different systems, with an increased range of body sizes may yield a more general understanding of scale effects on movement ability. It is important to note that while I tested the effect of plant structure on movement rate, these experiments were not able to conclusively discriminate between the contribution of plant structure on the scale of gross plant architecture (e.g., leaf number, leaf size) and on the scale of surface complexity. This distinction for a mechanistic understanding of plant structure effects on insect movement. In my observations of *P. maculiventris* movement behavior, it seemed that the primary mechanism of movement inhibition was mechanical impediment by surface complexity. These observations are supported by results reported

here (Table 1, Fig. 2) indicating that movement rate is greater on species with lower surface complexity. Further tests, perhaps with a series of conspecific plant mutants that vary in surface complexity, will be useful to separate the contribution of structure at the scale of gross plant architecture.

Studies of movement ability may be relevant to applied questions in ecology. With increasing interest in the use of *P. maculiventris* as an augmentative release agent for the control of Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) and other agricultural pests (Hough-Goldstein 1998), a better understanding of the ontogenetic and environmental factors that influence foraging and dispersal could be useful to the development of pest management strategies (Lachance and Cloutier 1997). Plant structure and insect ontogeny may influence the performance of *P. maculiventris* as a biocontrol agent in specific systems.

Changes in movement ability associated with body size and different habitat structures suggest that the scale of an individual's ambit may vary within its lifespan. These observations could be useful to indicate a reasonable spatial scale at which to begin studies of ecological interactions. Ontogenetic and environmental factors may be important in understanding many movement processes. In particular, the changes in movement ability *P. maculiventris* experiences throughout its ontogeny could influence its dispersal and foraging abilities at different stages of development.

The movement rate of *P. maculiventris* on these three goldenrod species provides some insight into the general movement behavior of *P. maculiventris*. The addition of path length data to this analysis provides a more complete description of the factors influencing movement behavior. It is interesting to note that the movement rate of *P. maculiventris* increases from the 3rd instar to the 4th instar while the total path length decreases. This is possible because the mean moving time decreased (and the resting time increased) from the 3rd to the 4th instar. This suggests that the foraging range of *P. maculiventris* actually decreases between the 3rd and 4th instars, although its movement rate while foraging increases. These changes could indicate an ontogenetic shift in the foraging behavior of *P. maculiventris* individuals along a gradient from active searching towards more sedentary ambush.

Changes in foraging ability caused by differences in plant structure suggest that interactions between searching insect predators and their prey may also involve an interaction between the predator and the plant. These interactions could represent a common tritrophic system (Kareiva and Sahakian 1990; Wiedenmann and O'Neill 1992; Carter et al. 1984). The implications of these findings are uncertain but intriguing; plants with high structural complexity may represent dispersal barriers or unfavorable foraging patches for *P. maculiventris* and may provide refuges for prey species. Changes in ontogeny could alter this perceived landscape. Because the effects of individual size operate simultaneously with the effects

of plant species, a heterogeneous environment allows both temporal and spatial variation in the movement ability of an individual.

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## References

- Aldrich JR, Kochansky JP, Abrams CB (1984) Attractant for a beneficial insect and its parasitoids: pheromone of the predatory spined soldier bug *Podisus maculiventris* (Hemiptera: Pentatomidae). *Environ Entomol* 13:1031–1036
- Carter MC, Sutherland D, Dixon AFG (1984) Plant structure and the searching efficiency of coccinellid larvae. *Oecologia* 63: 395–397
- Clark TL, Messina FJ (1998) Foraging behavior of lacewing larvae (Neuroptera: Chrysopidae) on plants with divergent architectures. *J Insect Behav* 11:303–317
- DeCoursey RM, Esselbaugh CO (1962) Descriptions of the nymphal stages of some North American Pentatomidae (Hemiptera-Heteroptera). *Ann Entomol Soc Am* 55:323–340
- Dixon AFG (1959) An experimental study of the searching behavior of the predatory coccinellid beetle *Adalia decempunctata* (L.). *J Anim Ecol* 28:259–281
- Eigenbrode SD, Castagnola T, Roux M-B, Steljes L (1996) Mobility of three generalist predators is greater on cabbage with glossy leaf wax than on cabbage with a wax bloom. *Entomol Exp Appl* 81:335–343
- Evans EW (1980) Lifeways of predatory stinkbugs: feeding and reproductive patterns of a generalist and a specialist (Pentatomidae: *Podisus maculiventris* and *Perillus circumcinctus*). Dissertation, Cornell University
- Evans EW (1982) Feeding specialization in predatory insects: hunting and attack behavior of two stinkbug species (Hemiptera: Pentatomidae). *Am Midl Nat* 108:96–104
- Frazer BD, McGregor RR (1994) Searching behavior of adult female Coccinellidae (Coleoptera) on stem and leaf models. *Can Entomol* 126:389–399
- Grevstad FS, Klepetka BW (1992) The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia* 92:399–404
- Hough-Goldstein J (1998) Use of predatory pentatomids in integrated management of the Colorado potato beetle (Coleoptera: Chrysomelidae). In: Coll M, Ruberson JR (eds) *Predatory Heteroptera: their ecology and use in biological control* (Thomas Say Publications in Entomology: Proceedings). Entomological Society of America, Lanham, pp 209–223
- Johnson AR, Milne BT, Wiens JA (1992) Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements. *Ecology* 73:1968–1983
- Kareiva P, Sahakian R (1990) Tritrophic effects of a simple architectural mutation in pea plants. *Nature* 345:433–434
- Keller MA (1987) Influence of leaf surfaces on movements by the hymenopterous parasitoid *Trichogramma exiguum*. *Entomol Exp Appl* 43:55–59
- Lachance S, Cloutier C (1997) Factors affecting dispersal of *Perillus bioculatus* (Hemiptera: Pentatomidae), a predator of the Colorado potato beetle (Coleoptera: Chrysomelidae). *Environ Entomol* 26:946–954

- Mukerji MK, LeRoux EJ (1965) Laboratory rearing of a Quebec strain of the pentatomid predator, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae). *Phytoprotection* 46:40–60
- Reavey D (1993) Why body size matters to caterpillars. In: Stamp NE, Casey TM (eds) *Caterpillars: ecological and evolutionary constraints on foraging*. Chapman Hall, New York, pp 248–279
- SAS Institute (1997) *SAS/SYSTAT user's guide*. SAS Institute, Cary
- Schaefer CW (1996) Bright bugs and bright beetles: asopine pentatomids (Hemiptera: Heteroptera) and their prey. In: Alomar O, Wiedenmann RN (eds) *Zoophytophagous Heteroptera* (Thomas Say Publications in Entomology). Entomological Society of America, Lanham, pp 18–56
- Treacy MF, Benedict JH, Lopez JD, Morrison RK (1987) Functional response of a predator (Neuroptera: Chrysopidae) to bollworm (Lepidoptera: Noctuidae) eggs on smoothleaf, hirsute, and pilose cottons. *J Econ Entomol* 80:376–379
- Turchin P (1998) *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer, Sunderland
- Weiss SB, Murphy DD (1988) Fractal geometry and caterpillar dispersal: how many inches can an inchworm inch? *Funct Ecol* 2:116–118
- Wiedenmann RN, O'Neill RJ (1992) Searching strategy of the predator *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae). *Environ Entomol* 21:1–9
- Wiens JA, Crist TO, Milne BT (1993) On quantifying insect movements. *Environ Entomol* 22:709–715
- With KA (1994a) Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. *Funct Ecol* 8:477–485
- With KA (1994b) Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecol* 9:25–36