

Effects of structural heterogeneity of a laboratory arena on the movement patterns of adult *Eriopis connexa* and *Hippodamia variegata* (Coleoptera: Coccinellidae)

AUDREY A. GREZ and PAULA VILLAGRÁN

Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Casilla 2, Correo 15, La Granja, Santiago, Chile;
e-mail: agrez@uchile.cl

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Abstract. We asked if the structural heterogeneity of a laboratory arena differentially affected the abandonment of the plot, residence time, locomotory rate, pause duration and turning rate of adult *Eriopis connexa* and *Hippodamia variegata* (Coleoptera: Coccinellidae). We simulated an increase in heterogeneity by distributing vertically-oriented toothpicks in a circular arena: one control (without toothpicks), one uniform plot (toothpicks every 1 cm) and one random plot (randomly distributed toothpicks). No food was provided inside the arena. Coccinellids were released individually in the centre of each plot and their movement was videotaped. Fewer *H. variegata* adults left the plots as these become more heterogeneous. *E. connexa* did not discriminate between plots in their residence time, but *H. variegata* remained longer in the uniform and longest in the random plots. *H. variegata* only stayed longer than *E. connexa* in the random plots. This resulted because adults of *H. variegata* were stationary for longer periods, moved more slowly and less linearly and explored a higher number of toothpicks than adults of *E. connexa* in more heterogeneous environments. Thus, the physical structure of the environment differentially affects the movement patterns of insects. *Eriopis connexa* seems to be less sensitive to structural heterogeneity than *H. variegata*.

INTRODUCTION

Environments vary in structural heterogeneity. One way that organisms perceive and track the structural heterogeneity of environments is through their movement behaviour (Wiens et al., 1997; With et al., 1997). As the environment changes in structure, the resident organisms may also change their movement pattern. Different species, or even different life stages of the same species, may perceive the environment in different ways, altering their movement patterns accordingly (With, 1994). Animal movement may determine the dynamics and spatial distribution of entire populations and communities (Wiens et al., 1993a; Turchin 1998), as well as the outcome of many individual ecological processes such as searching for food, oviposition sites, mates or shelter (e.g., Jones, 1977).

The effect of the spatial distribution of biotic elements such as food resources or natural enemies on movement behaviour has been extensively studied, both theoretical and empirically (e.g. Ginsberg, 1986; Krakauer & Rodríguez-Girones, 1995). Nevertheless, the physical structure of the environment may modify this behaviour. Certain elements within the environment may facilitate movement, while others may interfere with this process (With, 1994; Ims, 1995; Wiens et al., 1997). This may be more important for ground moving animals than for flying ones. For instance, bare ground increases the speed of movement of the tenebrionid beetle, *Eleodes obsoleta*, compared with individuals in patches of grass (Wiens et al., 1997).

Coccinellids are important natural enemies of pest species, particularly aphids, and have been used frequently as biological control agents (Obrycki & Kring, 1998). They spend most of their time searching for patches of aphids or scanning the environment, using visual and olfactory cues for orientation (Bell, 1991; Ferran & Dixon, 1993; Lambin et al., 1996). They show area-restricted search in prey patches, but when prey are not available they assume an extensive searching behaviour, turning less frequently and moving more rapidly (Carter & Dixon, 1982;

Ferran & Dixon, 1993). However, their searching behaviour (i.e., extensive vs. intensive search) may be influenced by the complexity of the substrate (e.g., plant architecture or the presence of trichomes, Obrycki & Kring, 1998), and not just by the presence of prey.

In this note, we experimentally analyse whether the structural heterogeneity of a laboratory arena, an artificial setting, differentially affects the movement patterns of the adults of two coccinellid species: *Eriopis connexa* (Germ.) and *Hippodamia variegata* (Goeze). In order to identify the isolated effect of structural heterogeneity on the movement patterns of these coccinellid species, we excluded most other factors that also affect their movement in the environment (e.g., for a review see Ferran & Dixon, 1993).

MATERIAL AND METHODS

Eriopis connexa is a neotropical species native to Chile, whereas *H. variegata* was introduced to Chile for the biological control of cereal aphids (Zúñiga et al., 1986). Both species are quite common, slightly elongated in shape and are 4–6 mm long.

We simulated three kinds of environments with increasing structural heterogeneity by setting 277 toothpicks, 1 cm high, in a white circular area 20 cm in diameter (i.e., plot): one control plot (without toothpicks), one uniform plot (toothpicks distributed every 1 cm), and one random plot (toothpicks randomly distributed) (Fig. 1). Toothpicks were supposed to alter coccinellid movement and may mimic a potential unit of foraging (e.g., a grass stick). The random plot was assumed to be more heterogeneous than the uniform one as random positions of toothpicks should result in a lower probability of finding any one of them. The average (variance) nearest distance between toothpicks was 1.00 cm (0), and 0.61 cm (0.20) for the uniform and random plots, respectively.

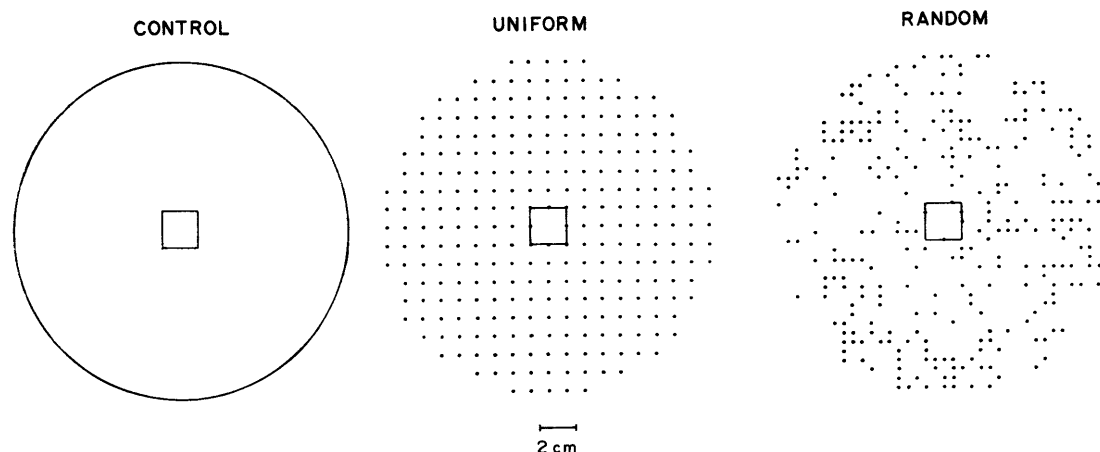


Fig. 1. Control, uniform, and random plots simulated with toothpicks. Each filled circle represents a toothpick. The square in the centre of each plot is the area where the insects were released.

Coccinellids were collected from alfalfa crops and were kept overnight in the laboratory, with no food available. For testing the effect of structural heterogeneity on movement behaviour, coccinellids were released individually in the centre of each experimental plot (in a release area 4 cm²) (Fig. 1). Their movements were videotaped with a VHS-C Panasonic NV-S750PN camera for up to 300 s or the exit of the insect from the plot. The tracks were reproduced in transparencies, identifying the position of the insect every 5 s (Wiens et al., 1993b). We used fixed-time intervals to define moves following Kareiva & Shigesada (1983). This time interval was selected because, although within approximately 5 s coccinellids reached the edge and abandoned the control plot (setting the highest time interval possible), in the other two treatments coccinellids stayed longer (sometimes more than 300 s), and with a frequency of 5 s we obtained a high number of consecutive movements (up to 60).

All experiments were carried out between 1300 and 1700 hr in a closed room, with artificial lighting. Temperatures varied between 22.4°C and 29.9°C. As these different temperatures may affect the movement patterns of insects (Ferran & Dixon, 1993), experiments for different treatments and species were interspersed in time, taking the possible effect of temperature as an experimental random error. Different individuals were used in each experiment, with a total of 48 individuals per species recorded (i.e., 16 in each treatment). The response variables analysed were: (a) percentage of insects that abandoned the plot before 300 s (usually insects stopped moving before that time period); (b) residence time inside the plot (s); (c) stop duration: percentage of the total time of each experiment that the insect remained stationary (this variable was measured for discriminating whether the residence time was due to constant move-

ment of the insect inside the plot or to long stationary periods); (d) locomotory rate (mm/s): Σ displacement distance every 5 s / total time inside the plot; (e) turning rate (deg/5 s): turning angles were measured between successive moves; this variable evaluates the linearity of movements; (f) number of toothpicks explored by coccinellids in the uniform and random plots. The percentage of insects that abandoned the plot before 300 s was analysed by χ^2 tests, variables b), c), d), and e) were analysed using a two factor MANOVA and post hoc Tukey HSD tests. Finally, the number of toothpicks explored by coccinellids was analysed using a two-way ANOVA.

RESULTS

Two out of 98 experimental individuals flew away from

TABLE 1. Percentage of individuals of *E. connexa* and *H. variegata* that abandoned the experimental plots before 300 s ($n = 16$ for each treatment and each species). Superscript letters indicate significant differences.

	Control	Uniform	Random	χ^2	<i>P</i>
<i>E. connexa</i>	100 ^a	87.5 ^a	81.3 ^a	3.3	> 0.05
<i>H. variegata</i>	100 ^a	68.8 ^b	25.0 ^c	13.6	< 0.05

patches and were not considered in the analysis as we were interested in the effect of spatial heterogeneity on the walking movements of adult coccinellids. Structural heterogeneity differentially affected the percentage of individuals that left a plot (Table 1). All individuals from both species abandoned the control plot before 8 s, but fewer individuals exited the plot in the other two treatments. This pattern was more evident in *H. varie-*

TABLE 2. Results of MANOVA on effects of species and structural heterogeneity treatments for residence time, stop duration, locomotory rate and turning rate of adult coccinellids *E. connexa* and *H. variegata*.

	Species		Structural heterogeneity		Species \times heterogeneity	
	<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>	<i>F</i> (df)	<i>P</i>
Wilks' lambda	0.81 (4,87)	0.001	0.45 (8,174)	< 0.0001	0.82 (8,174)	0.0238
Residence time	14.49 (1,90)	0.0003	22.25 (2,90)	< 0.0001	6.23 (2,90)	0.0029
Stop duration	8.75 (1,90)	0.004	18.20 (2,90)	< 0.0001	5.97 (2,90)	0.0037
Locomotory rate	15.55 (1,90)	0.0002	46.57 (2,90)	< 0.0001	6.48 (2,90)	0.0024
Turning rate	8.50 (1,90)	0.0045	8.82 (2,90)	0.0003	2.73 (2,90)	0.0703

gata, where a significantly lower number of individuals left the uniform and random plots, compared to the control plot and to *E. connexa* (Table 1). While the residence time of *E. connexa* was not significantly affected by heterogeneity, *H. variegata* remained longer in the uniform than in the control plot and longest in the random plot (Table 2, Fig. 2a). Moreover, *H. variegata* remained longer than *E. connexa* only in the random plot (Table 2, Fig. 2a). In the uniform and random plots, *H. variegata* remained stationary for longer periods of time than in the control plots. *H. variegata* had longer stationary periods, and moved significantly slower than *E. connexa* in the random plot (Table 2, Figs. 2b). Both species displayed a lower locomotory rate in the uniform and random plots, and *H. variegata* moved significantly slower than *E. connexa* in the random plot, but not in the others (Table 2, Fig. 2c). *H. variegata* had a higher turning rate in more heterogeneous plots and also when compared to *E. connexa*. This was particularly so in the random plot, whereas *E. connexa* maintained the same turning rate in the three treatments (Table 2, Fig. 2d).

In the uniform and random plots, both species not only walked on the ground but also climbed the toothpicks, probably searching for food. *H. variegata* explored more toothpicks than *E. connexa* [$F(1,60) = 12.67, P < 0.0001$], but each species explored the same number of toothpicks in the uniform and random plots [$F(1,60) = 0.007, P = 0.93$].

DISCUSSION

The structural heterogeneity of the experimental arena differentially affected the movement patterns of the experimental insects. As the arena become more heterogeneous, both species changed their movement patterns, but the change was stronger in *H. variegata*, as *E. connexa* was significantly affected by heterogeneity only in its locomotory rate, which diminished in the random plots. Changes in the movement patterns of insects related to environmental heterogeneity have been observed previously in field experiments (Crist et al., 1992; Wiens et al., 1997). Nevertheless, in field experiments many of the variables that determine the heterogeneity of an environment may covary. In our lab study, all factors other than presence and pattern of toothpicks were experimentally controlled, except for temperature which was considered as an experimental random error. Thus, the movement patterns of the coccinellids probably changed because of the variable physical structure of the arena.

The relationships between the structure of the environment and movement behaviour may depend on spatial scale (Wiens et al., 1993a) and on the life process involved (e.g., foraging, patch searching, dispersal, migration; Ims, 1995). Habitat selection by coccinellids may operate at a large scale, usually made by flying insects; thus, heterogeneity at this scale should be considered for studying this phenomenon. Food searching within habitats operates at a much finer spatial scale, usually according to the spatial distribution of resources. At this spatial scale, coccinellids usually search their food by walking. The spatial scale used in this study attempted to simulate the foraging scale of coccinellids, and at this small spatial scale their movement patterns were influenced by the physical structure of the environment.

Our results also show that the effect of environmental structural heterogeneity is species-specific. In the more heterogeneous random plots, fewer individuals of *H. variegata* left the plots and they stayed longer inside these plots due to longer stationary periods, slower and less linear movements, and a higher number of toothpicks explored, adopting a more intensive search behaviour, compared to *E. connexa*. Thus, *E. connexa* seems to be less sensitive to environmental structural heterogeneity than *H. variegata*, and therefore may have a greater potential to survey a microhabitat. This could be advantageous since

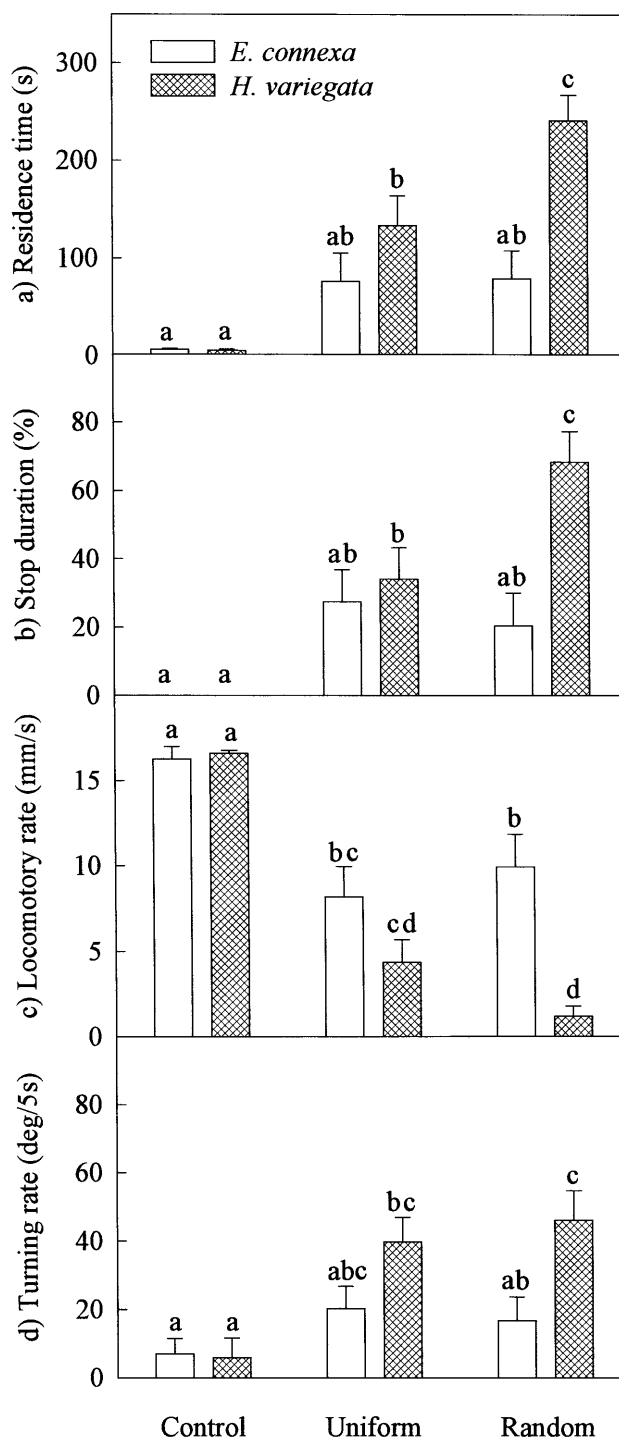


Fig. 2. Movement pattern of adults of *E. connexa* and *H. variegata* in plots with different structural heterogeneity: (a) Residence time; (b) Stop duration (% of the total time of each experiment that individuals remain stationary); (c) Locomotory rate (mm/s); and (d) Turning rate (deg/5s). Values indicate mean ± 1 SE ($n = 16$). Bars with different lowercase letters are statistically different ($P < 0.05$, Tukey HSD test).

E. connexa may aggregate more easily in rich patches of prey or quickly abandon patches of low prey density, independently of the structural heterogeneity of the environment. From this point of view, *E. connexa* may be a better agent for biological control than *H. variegata*. However, our results come from a totally artificial setting, considering only one of a long series of factors

affecting the movement of coccinellids, such as prey and host plant cues (Ferran & Dixon, 1993; Lambin et al., 1996). Therefore, these relationships should be tested in more realistic experiments in the field.

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