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SHORT COMMUNICATION

Leaf overlap and the ability of ladybird beetles to search among plants

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Introduction

Several experiments have shown that aspects of plant morphology can influence the way in which insect predators and parasitoids search for herbivorous prey (Rabb & Bradley, 1968; Belcher & Thurston, 1982; Shah, 1982). These are important results because they demonstrate how a plant, by modifying its morphology, might better take advantage of the natural enemies that attack its herbivores (Obrycki *et al.*, 1983). However, all of the experiments documenting the effects of plant structure on the foraging behaviour of insect predators have been restricted to within-plant searching patterns. In contrast, our work with insect predators has emphasized between-plant searching patterns; in particular, we have examined the manner in which ladybird beetles move between plants and the consequences of variations in this movement for predator effectiveness (Kareiva & Odell, 1987). Using mathematical models and direct observations, we have found that the turning behaviour of coccinellids as they move through the vegetation is critical to their searching success, especially if they are seeking widely scattered patches of prey. This line of reasoning suggests that vegetation structure may significantly alter predator–prey interactions simply by modifying a predator's movement trajectories. In particular, one of the keys to rapid predator aggregation at patches of prey is extended linear movement in the absence of prey (Andersen & Kareiva, 1988; Kareiva & Andersen, 1988). By moving in a straight path, a predator is more likely to search a greater area than it would if it frequently changed directions (i.e. turned around and went back along the same path). The value of extended linear movements for predators seeking patchy prey has been pointed out by several experimental biologists (e.g. Fleschner, 1950; Banks, 1957; Chandler, 1969) and is one component of a stereotyped behaviour known as 'area restricted search' (Murdie & Hassell, 1973). Predators engaging in area restricted search follow linear routes when they are seeking but not encountering prey, and then switch to frequent turning behaviour after encountering prey (Curio, 1976). Since numerous predators engage in area restricted search, it is possible that they possess an innate tendency to continue moving in the same direction until prey are encountered. This tendency towards 'straight line' movement is probably often frustrated by physical irregularities such as tangled vegetation and debris. In this note we report an experiment designed to test whether something as simple as the degree of leaf overlap can significantly affect the tendency of ladybird beetles (Coleoptera: Coccinellidae) to keep moving in the same direction when not encountering prey.

Methods and Results

To test the effects of vegetation structure on ladybird beetle movement we arranged commercial bean plants (*Phaseolus vulgaris* L) in two 1.5 m diameter circles. We used a circular arrangement so that when ladybird beetles were randomly positioned on the plants, there would be no consistent bias with respect to external stimuli such as the sun. The two circles were

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established inside a well-ventilated glasshouse at the University of Washington. The bean plants were of identical size and age. However in one circle, which we call the 'highway treatment', overlapping leaves of adjacent plants were taped together (with two small pieces of tape per plant) so that they formed an almost continuous plane of leaf surface. In the other circle, plants did not have their leaves taped together and are thus referred to as the 'gap treatment'. Even without having their leaves taped, there was still considerable leaf overlap among bean plants in the so-called gap treatment; thus laydbird beetles could move among different plants in the gap treatment without venturing onto stems, although presumably not as conveniently as they could in the highway treatment. Plants in both treatments had most of their lower leaves removed to simplify their structure and to make observation easier.

For our experiment we used lab-reared adult *Hippodamia convergens* L that had no prior experience of searching bean plants, but had been allowed to forage on commercial peas (*Pisum sativum* L) and rosebay willowherb (*Epilobium augustifolium* L). Each beetle was observed in both the highway and gap circles in succession with the order of the treatments and position on each circle randomly assigned. Individual beetles were observed once in both treatments and then never used again in the experiment. After gently placing a beetle on a bean leaf, we recorded its position at 20 s intervals. The experiments were continued for either 5 min or until the beetle left the ring of bean plants. The experiments were performed on 10, 11 and 18 July in 1987. Although we attempted to observe thirty different beetles in both treatments, we recorded only twenty-eight observations in the gap treatment and twenty-one in the highway treatment (because we discarded beetles that abandoned the bean plants without starting to search the foliage).

The movement of ladybird beetles differed significantly between the highway and gap treatments (Fig. 1). First of all, beetles moved further around the circle of beans in the highway than in the gap treatment: the mean net displacement per minute was 0.82 m (SE=0.89) in the highway treatment, but only 0.22 m (SE=0.21) in the gap treatment. These represent highly significant differences when tested with a one-way analysis of variance, using the log $(x+1)$ transformation to normalize the data and homogenize variances (F[1, 47]=7.54, P=0.0085). One reason beetles travelled greater distances in the highway treatment was that they reversed direction less often in that treatment than where the leaves were not connected by tape. To quantify reversal frequency we defined a move as a change in position recorded over a 20 s interval. If during successive 20 s intervals the change in

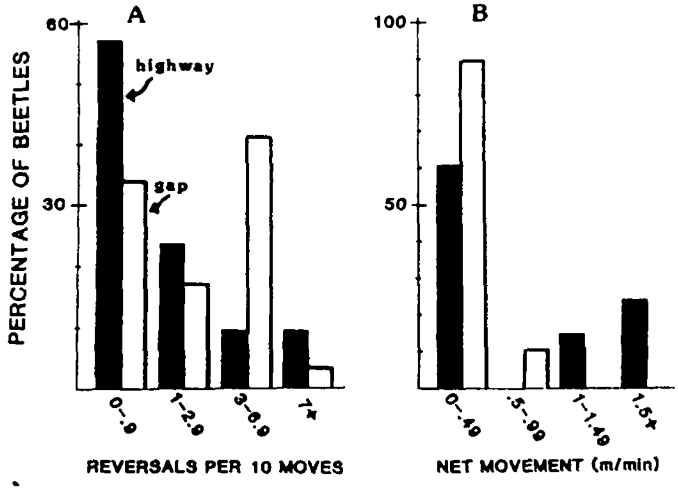

FIG. 1. The effect of leaf overlap on the movement patterns of adult *Hippodamia convergens* L while searching a circle of bean plants. The sample sizes are n=28 beetles for the gap treatment (low leaf overlap) and n=21 for the highway treatment (high leaf overlap). Graph A contrasts the frequency of direction reversals, whereas graph B contrasts the net displacements attained in the two leaf overlap treatments.

position first goes in one direction, then in the opposite direction, we call that event a reversal. The maximum number of reversals per ten moves as measured by this procedure is nine (since there cannot be a reversal on the first move). On average beetles in the gap treatment reversed their direction 1½ times more often than beetles in the highway treatment: 2.7 (SE=0.24) as opposed to 1.8 (SE=0.31) reversals per ten moves (significant at the $P<0.01$ level when tested using a Kolomogorov-Smirnov test).

Discussion

Simply by increasing the degree of overlap among leaves of adjacent plants, we substantially altered the rate at which ladybird beetles travelled through bean vegetation (as measured by net displacement per unit time). Both common sense and mathematical models suggest that the rate at which predators search vegetation for insect prey will markedly influence the effectiveness of those predators. Thus our experiment hints that subtle changes in vegetation structure could produce dramatic changes in the character of insect predator–prey interactions. Our experiment is, however, too contrived to stand on its own. Our point is not to draw conclusions, but to stimulate similar manipulations of foliage structure in more natural settings.

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