

MIGRATION AND DISPERSAL OF *COCCINELLA SEPTEMPUNCTATA* IN UTAH ALFALFA

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Summary

The migration and dispersal of the seven-spot lady beetle, *Coccinella septempunctata*, were measured in six mark-release-recapture experiments in Utah alfalfa. Three of the six experiments measured the spatial dispersal in a 30 m radius around a 4 m radius release area. Spatial dispersal of beetles around the point of release was described with normal distributions whose variance increased linearly in time with 3.8, 1.1 and 0.34 m² per hour. The tendency to stay within the 34 m radius sample area was characterised by average residence times of respectively 12, 6 and 1.6 h.

In the other three experiments the emigration of marked beetles from sugar-sprayed plots and control plots was compared. Residence times were 20-30% longer in sugar-sprayed plots than in control plots, with mean residences of 5.3, 3.6, and 2.9 h. in the sugar-sprayed plots in the three experiments, respectively, and means of 4.4, 2.7, and 2.4 h. in the control plots. Estimates of residence time were corroborated by an analysis of the aggregation of unmarked beetles into sugar-sprayed plots. The density of unmarked beetles increased by a factor of 10-20 in the sugar sprayed plots during the first 4 to 6 hours following early morning spraying of sugar. This rapid and enormous increase in density can only be explained by increased immigration. We hypothesise that aggregation into sugar-sprayed plots is mediated by volatile compounds produced by the plant-pest-predator assembly, in response to sugar spraying.

INTRODUCTION

Biological control of field crop pests by naturally occurring enemies such as predators may be affected profoundly by the amount of enemy resource habitat in agricultural landscapes and by the spatial design of the landscape (e.g., Stern et al., 1964; van Emden, 1965; Landis & Haas, 1992; Marino & Landis, 1996; Elliot et al., 1999). The closer resource habitats are to the field crops where natural enemy impact is desired, the more likely it is that the enemies will be timely and effective (van der Werf, 1995; Landis & van der Werf, 1997; Tschamtko & Kruess 1999). The question as to how close is close enough requires an assessment of the dispersal behaviour of natural enemies in diverse landscapes and the construction of spatially explicit models to integrate the available information (Brewster & Allen, 1997; Corbett 1998; Logan et al., 1997). Knowledge on dispersal is hard to get because it requires spatially explicit studies at the field scale and beyond.

Lady beetles are a well-known and abundant group of aphid predators, and aphids in turn are an important group of pests in field crops. Lady beetles are very mobile (Frazer, 1988) and a large proportion of the resident population in a field may be replaced by immigrant individuals in a single day. Precise estimates of rates of departure and replenishment are scarce in the literature (Hodek & Honek, 1996). At the within-field scale, dispersal of lady beetles by walking has received considerable attention (e.g.

Kareiva & Odell, 1987; Xia, 1997). Lady beetles are quite apt to fly, especially under sunny and warm conditions, and short flights provide a mechanism for quick redistribution at the scale of meters and beyond. Some studies include flight in the analysis of redistribution of lady beetles (Kieckhefer & Olsen, 1974; Ives, 1981), but still too little is known to generalise on the impact of flight on ladybeetle distributions in fields.

Use of sugar sprays offers one experimental means of studying lady beetle dispersal involving flight, as researchers have demonstrated repeatedly the rapid aggregation of these predators in sugar-treated plots (Hagen, 1986; Evans & Swallow, 1993). Evans & Richards (1997), for example, found that the spraying of plots or edges in an alfalfa crop with sugar solution rapidly affected the distribution of lady beetles throughout the field. The assumed mechanism by which sugar modifies the distribution of the beetles is through a lengthening of the residence time in sugar-sprayed areas. This hypothesis is plausible because sugar itself can be used as a food resource, and because the presence of sugar on leaves may point to the presence of aphids, which excrete honeydew, a sugary waste substance (Carter & Dixon, 1984).

Studies such as those of Evans & Richards (1997) show that lady beetle distributions can be manipulated by applying sugar to bands of crop or marginal vegetation, but they do not elucidate how the redistribution process *works*. To find out more about the dynamics of the redistribution process, we designed field experiments in which the dispersal of marked and released lady beetles was monitored frequently in space and time.

MATERIAL AND METHODS

All studies were done during July 1999 in alfalfa fields on the Animal Science Farm of Utah State University, 10 km Southwest of Logan, Utah, USA. Adults of *C. septempunctata* were hand collected in barley (Expts 1-4) or alfalfa fields (Expts 5 & 6) with abundant aphids, into which the ladybeetles had aggregated. The beetles were marked with paint markers (Decocolor Opaque Paintmarker, Uchida of America Corporation, Barcode 2861702101), except in the first experiment, in which black markers (Sanford Sharpie finepoint permanent marker) were used. Beetles were kept in ventilated containers or Petri dishes at 9 °C until the next morning when they were released at sunrise, which is the coolest part of the day, minimising disturbance-induced dispersal after release.

Six experiments were conducted. Three of those (1,2, and 6 in chronological order) measured spatial dispersal, applying a circular sampling design around the release site (Fig. 1), while three other experiments (3-5) focused on the departure process of the beetles over time at given sites.

Dispersal in space: 'wagon wheel' experiments

A circular release area and 72 surrounding sampling stations (Fig. 1) were laid out in the form of a wagon wheel in the middle of a 200 x 200 m alfalfa field. The release area was 8 m in diameter, and sampling stations were located at 0, 5, 10, 15, 20, and 25 m from the edge of the release area. Sampling stations were arranged on 12 transects radiating out at 30° angles from each other from the release area. For the first, second, and sixth experiment, respectively, 1300, 1548, and 1434 *C. septempunctata* adults were marked and released at a single time.

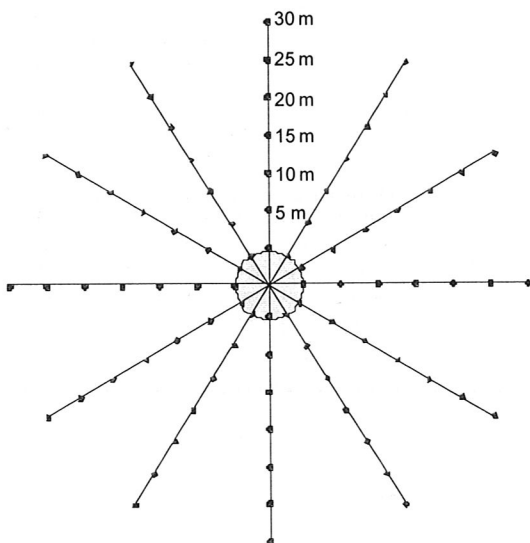


Fig. 1: Sampling design ('wagon wheel') for measuring dispersal within the field.

Sweep samples were taken at sampling stations at intervals of several hours on the day of release (Day 1) and the day after. At each sampling station on each occasion, five 180° sweeps were taken with a 39 cm diameter sweepnet. A step of 1 m was taken between subsequent sweeps. Thus, the first set of sweeps covered distances from the edge of the release area of 0 to 5 m, and so forth. Data are presented as the mean (number of marked beetles) ± standard error of the mean (SEM) of the full five sweep samples for each of the six distances ($n=12$), plus the density in the release area itself.

In the analysis of these data, we developed analytical solutions of the dispersal-departure model:

$$\frac{\partial P_{x,y,t}}{\partial t} = D \cdot \left(\frac{\partial^2 P_{x,y,t}}{\partial x^2} + \frac{\partial^2 P_{x,y,t}}{\partial y^2} \right) - \lambda P_{x,y,t}$$

where

$P_{x,y,t}$ is the density of the ladybeetles at a location (x,y) at time t (number per m^2).

$\partial P_{x,y,t} / \partial t$ is the rate of change of $P_{x,y,t}$ (number of beetles per m^2 per hour),

D is the diffusion coefficient describing lady beetle dispersal within the sample area (m^2 per hour),

λ is the *per capita* departure rate (h^{-1}), i.e., the proportion of beetles that take flight and leave the sampling area per unit time, or – equivalently – the probability per hour that a resident beetle would leave. Values of D and λ were determined by non linear curve fitting.

Effect of sugar sprays on residence time

Another set of three experiments (3, 4, and 5) was designed to quantify the departure process more precisely, and to contrast lady beetle departure in sugar-sprayed and control plots. Six sugar-sprayed and six control plots were included in each

experiment. Each plot measured 5 x 10 m, and lady beetles were released in a central area of 3 x 8 m within the plot. Sugar-sprayed plots received approximately 1.25 l of sucrose solution (150 g per l of water) applied as a fine mist to the foliage (e.g., see Evans & Richards, 1997). Sugar was sprayed soon after sunrise, and beetles were released immediately afterwards. In the third, fourth, and fifth experiment, respectively, 1678, 1200, and 1380 adults of *C. septempunctata* were marked and released (totals are for all twelve plots combined).

Beetle densities in the plots were estimated by repeated sweepnet sampling. The sampler walked on the long centre line through the plots, taking 8 sweeps in the net area. Samples were subsequently taken at 1-2 hour intervals during the first day and at 1-2 day intervals thereafter. In two of the three experiments (4 and 5), a first sweep sample was taken prior to sugar spraying. Data are presented as average number of beetles (marked or unmarked *C. septempunctata* adults) per 8 sweeps \pm SEM at each time.

Results were analysed by fitting the equation $P_t = P_0 \exp[-\lambda t]$ where P_0 is the initial number of ladybeetles (as measured in the first sweepnet sample after release). The other variables and parameters are the same as defined above.

RESULTS

Dispersal in space

Measurements of lady beetle dispersal reveal a spatial bell-shaped distribution around the point of release for each of the three experiments (Fig. 2). In each case, the spatial distribution extended in space as time progressed, and the number of beetles that were recaptured in the sample area declined rapidly. The rates of spatial extension of the distribution 'kernel', and the rates of departure differed quantitatively among the three experiments (Table 1), but the results were qualitatively similar. A likely reason for the higher rate of departure in Experiment 6, as compared to Experiments 1 and 2, is the lower aphid density in Experiment 6. This experiment was conducted in field #16 on the Animal Science Farm, and aphid densities in this field at the time of the experiment were a factor of 4 lower (12.5 ± 1.0 aphids per five standard sweeps with a sweep net) than in field #14, in which experiments 1 and 2 were conducted and where the aphid densities were, respectively, 10.8 ± 2.3 and 11.3 ± 2.1 aphids per single sweep.

Table 1. Dispersal and departure parameters, estimated from the data of the spatial mark-release experiments.

Experiment	Diffusion coefficient $D (m^2 h^{-1})$	Relative departure rate $\lambda (h^{-1})$	Residence time $1/\lambda (h)$
1	1.90	0.08	12.5
2	0.54	0.14	7.14
6	0.17	0.63	1.59

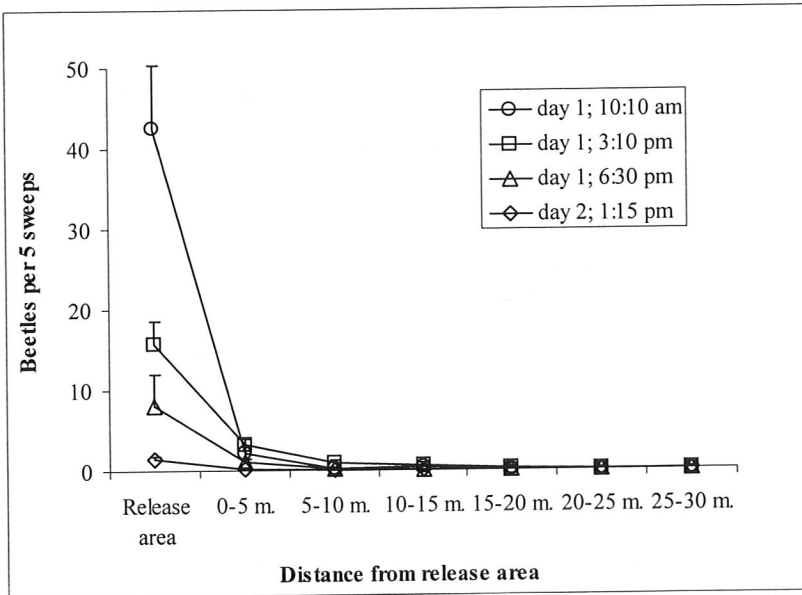


Fig. 2: Density (expressed as lady beetles per 5 sweeps) of marked and released *Coccinella septempunctata* in the release area and at six distances from the release area in the course of time in alfalfa field experiment 2.

Effect of sugar sprays on residence time and aggregation of *C. septempunctata*

The results of the "sugar spray" experiments come in two parts. The first part concerns the departure of marked beetles. The second part concerns the aggregation of unmarked beetles in sugar-sprayed plots.

The density of marked beetles declined rapidly after release in both sugar-sprayed and control plots. As in the 'wagon wheel' experiments, none of the released beetles were found in the plots after a few days (Fig. 3). Residence times ($1/\lambda$) were 20-30% longer in sugar-sprayed plots than in control plots, with mean residence times (\pm SEM) of 5.4 ± 0.64 , 3.6 ± 0.50 , and 3.0 ± 0.40 h. in the sugar-sprayed plots in experiments 2, 3, and 4, respectively, and 4.4 ± 0.51 , 2.7 ± 0.29 , and 2.4 ± 0.41 h. in the control plots. Assuming normal distributions of the fitted parameter values, the significance (one-sided p) of these differences would be 0.11, 0.04, and 0.16, respectively. Given the consistency of the difference over three experiments, the difference in residence time between sugar-sprayed and control plots should probably be considered small but real. More importantly, residence time was very short in each of the experiments, and the majority of the released beetles left the plots within twelve hours of release. This is true for both sugar-sprayed and control plots.

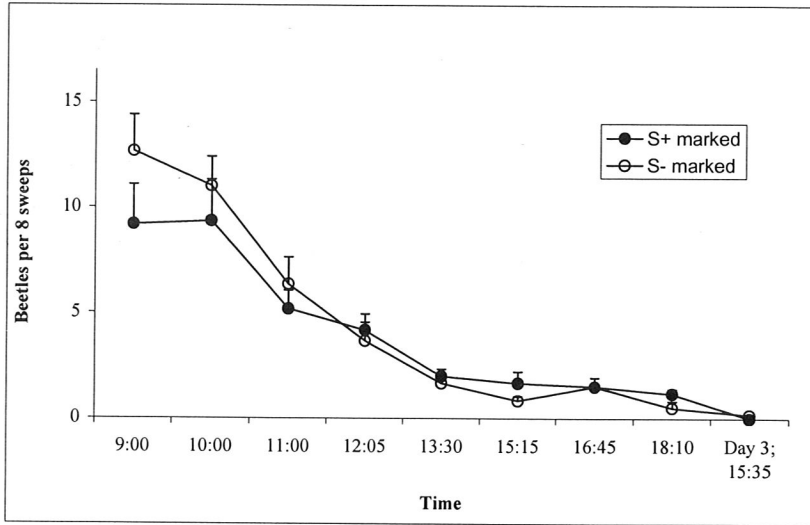


Fig. 3: Density of marked and released *Coccinella septempunctata* (expressed as lady beetles per 8 sweeps) in sugar sprayed (S+) and control (S-) alfalfa field plots in the course of time after release, in alfalfa field experiment 4 (cf. Fig. 4).

Unmarked beetles, occurring naturally in the fields, aggregated rapidly into the sugar sprayed plots in a matter of hours after release (e.g. Fig. 4). The result of this aggregation was a 10 to 20-fold increase in lady beetle density in a period of approximately 4-6 hours. A plateau ladybeetle density in the sugar sprayed plots was reached in the afternoon of the first day; afterwards the effect diminished. Residence time ($1/\lambda$) can be estimated on the basis of observations on unmarked beetles on the assumption that the aggregation process is a balance of immigration (I) and emigration (λP) according to:

$$\frac{dP}{dt} = I - \lambda P$$

where P and λ have the same meaning as above, while I is the immigration rate (beetles per m^2 per h.). The obtained estimates of λ (not shown here) confirm the estimates for ladybeetle residence time presented earlier in this paper. Hence, our results and logical reasoning indicate that increased residence is not a likely explanation for the aggregation of ladybeetles in our sugar sprayed alfalfa plots. The only alternative mechanism is increased immigration.

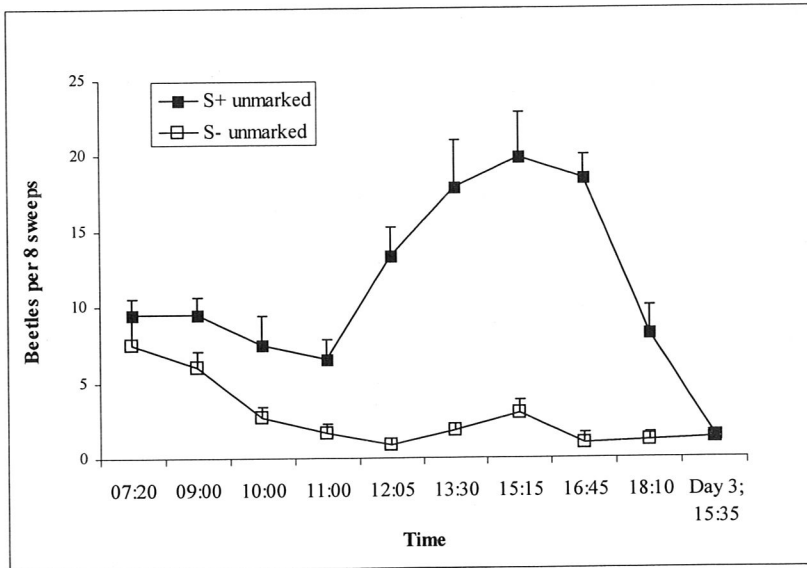


Fig. 4: Density of naturally occurring (unmarked) *Coccinella septempunctata* (expressed as lady beetles per 8 sweeps) in sugar sprayed (S+) and control (S-) alfalfa field plots in the course of time after release, in alfalfa field experiment 4 (cf. Fig. 3).

DISCUSSION

The field experiments described in this paper show that residence times of the lady beetle *C. septempunctata* in large plots of alfalfa (0.36 ha) were in the order of hours under the conditions of the study. This rapid turnover of the predator population in large areas probably reflects that few pea aphids, the primary prey of *C. septempunctata* in Utah alfalfa, were present during our experiments. In general, the tendency of predators, such as lady beetles, to stay in a resource patch increases with patch quality. Given that prey densities were low (in the order of 3-10 aphids per sweep with the sweep net) throughout our studies, it is likely that lady beetles not only quickly left the large study plots, but also rapidly emigrated from the fields in which these plots were placed. Hence, our results suggest that lady beetle populations are highly dynamic across the landscape, with substantial migration between fields, and localised dispersal within fields that is of limited importance, compared to the between-field dispersal. The tendency to emigrate when there are few prey is likely to result in predators aggregating at areas of high prey density (e.g. Evans & Youssef, 1992; Ives et al., 1993; see also Hemptinne et al., 1992).

Rapid emigration of adult ladybeetles also occurred from the study plots of alfalfa that were sprayed with sugar. This surprised us, as we had hypothesised that encounter with and consumption of sugar would lead to substantially longer residence in sugar-treated plots (e.g., see Carter & Dixon 1984). Especially surprising is the inference that the dramatic, rapid increase in lady beetle density in plots that were sprayed with sugar had to result primarily from increased beetle immigration rather than decreased emigration. Because sugar is not volatile, we are led to hypothesise that either the sugar sprayed plants or the resident lady beetles in the sugar-sprayed plots released odours that

attracted lady beetles from elsewhere. Evidence is mounting that ladybeetles are releasing and using chemical cues for intraspecific communication (Copp, 1983; Hemptinne et al., 1996; 1998; Al Abassi et al. 1998; Hamilton, 1999). This study is perhaps the first to find such strong indication of attraction under field conditions. Further research is underway to test these ideas.

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