ESTIMATION OF COCCINELLID NUMBERS AND MOVEMENT IN THE FIELD

P. M. IVES[1]

Institute of Animal Ecology, University of British Columbia, Vancouver V6T 1W5

Abstract

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Changes in the numbers of adults of *Coccinella californica* Mannerheim and *C. trifasciata* Mulsant in small plots of alfalfa and oats were monitored over the summers of 1974 and 1975 by mark-recapture methods. Aphid population dynamics in the plots were studied concurrently. In the second summer, movements of the beetles were also monitored by means of individual marking and sticky net traps. Approximately 1000 beetles of each species were marked in the first summer; in the second, roughly 5000 and 3000 respectively. The capture-recapture method was tested with a caged population, and was found to be feasible for estimation of the coccinellid numbers. Catch per unit effort, using visual sampling that was not dependent on marking, provided an acceptable index of numbers which could give population estimates when calibrated against mark-recapture estimates.

The number of beetles trapped on the sticky nets was primarily a function of numbers in the plots and temperature, with the two species having different relationships between temperature and flight. But for *C. californica*, the numbers trapped were also a function of aphid density in the plots; the data suggested that for *C. trifasciata* the same is probably true, but the range of densities of pea aphids was too narrow to show it. In both seasons, *C. trifasciata* was predominant in the alfalfa and *C. californica* in the oats. Plot to plot movements by overwintered beetles reflected the same apparent preference. Changes in the numbers of coccinellids in the experimental plots, and their reproductive success, are discussed in the light of these findings.

Introduction

Frazer and Gilbert (1976) studied the "functional responses" of coccinellid predators and aphid prey. They had "no satisfactory method . . . to estimate the density of predators". They therefore could not evaluate the beetles' numerical response to changes in aphid density. This paper examines the numbers of adult coccinellids in field plots of alfalfa and oats, and describes their food- and weather-related movements, which determine the extent to which they become concentrated in areas of high prey density.

Methods

The experimental plots were at two sites 0.8 km apart on the campus of the University of British Columbia. In 1974, there was one plot of oats and one of alfalfa at each site; the alfalfa plots were 18 rows × 25 m long at site 1 and 26 rows × 15 m at site 2, and the oat plots were of equivalent size. In 1975, the alfalfa plots were altered and split into two, and two new oat plots were sown at each site (Fig. 1). The aphids were sampled separately in all plots. Coccinellid numbers were estimated by the method of Jolly (1965) from capture-recapture data on animals marked in the field. Estimates of catch per unit effort were also made for comparison.

The work in 1974 was primarily concerned with perfecting marking and sampling techniques. Late that season, the method was tested by daily marking and recapturing of beetles in large ($5 \times 6 \times 2$ m high) field cages containing a known number of beetles. To minimize disturbance to the population, beetles were marked where they

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[1] Present address: CSIRO Division of Plant Industry, Cotton Research Unit, Narrabri, N.S.W. 2390, Australia.

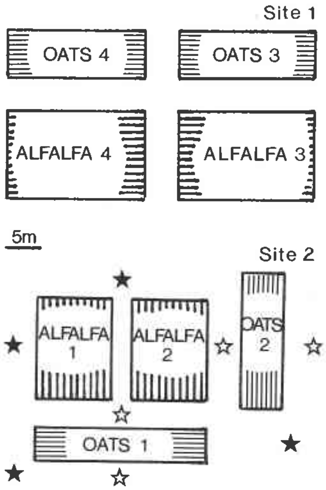

FIG. 1. Size and lay-out of experimental plots at both sites, and positions of traps (★) at site 2, in 1975. Open stars mark the two traps moved from inside to outside the site on 9 July.

were found, with one or more spots of enamel paint on their elytra, and released immediately. The problems of mark loss are considered below.

In 1974, only one colour spot was used on any particular marking occasion, the colour signifying the occasion. Initially the same colour was used for all beetles in the same site; subsequently beetles in different plots were marked with plot-specific colours. In the cage experiment, beetles were marked with one day-specific colour spot each time they were captured. In 1975, however, each beetle was marked on first capture only, with an individual 4-spot colour code. By distinguishing between left and right elytra, with two spots on each, and using 12 colours, 6084 individual colour combinations were possible. Males and females were not distinguished.

The time actually spent marking beetles considerably reduces the total number of beetles captured in any given interval, thus reducing the accuracy of the capture-recapture method. To compensate for this, periods of marking in each plot were supplemented by "walking counts". Two observers walked abreast down each side of a row of the crop, counting all visible beetles; the total number of unmarked beetles; recording the colour codes of marked beetles; and temperature.

The elytra of newly emerged adult coccinellids develop their full colour and rigidity slowly over several days, weeks, or even months (Hodek 1973). During 1975, adult beetles that were distinguishable by their paler and more flexible elytra as having emerged that season, were recorded as "new".

Marking of beetles, and regular sampling in any plot was not begun until a worthwhile number of beetles were present. In 1974, the sample frequency varied between daily and 2–4 times a week, with the same marking period often occupying 2 consecutive days (Table I). In 1975, the beetles were sampled daily, except when it was raining or very cool and overcast, when they hide among the plants and cannot be effectively sampled. No marking period lasted more than 1 h of 1 day.

In 1975, sticky traps were used to monitor the beetles' flight activity. There were six traps $2^1/_2$ m high × $1^1/_2$ m wide surrounding the plots at site 2 (Fig. 1). They were cleared daily, early in the morning. Traps set up around site 1 had to be removed as they caught bees belonging to another researcher.

Table I. Population estimates of coccinellids in the alfalfa, 1974

	C. trifasciata	*C. californica*		*C. trifasciata*
	Jolly estimate	Jolly estimate		Jolly estimate
Overwintering generation, site 1			**Overwintering generation, site 2**	
June 18 & 19	–	–	May 31	–
June 20 & 21	157	299	June 4	906
June 24	147	506	June 5	427
June 29 & 30	308	2311	June 6	464
July 1 & 2	193	1584	June 7	471
July 4 & 5	248	484	June 10	372
July 6 & 7	–	–	June 12 & 13	–
July 12 & 13	–	–	June 18	–
			June 21 & 22	–
			June 30 & July 1	–
			July 4 & 5	–
			July 6 & 7	–
			July 12 & 13	–
Second generation, site 1				
Aug. 5 & 6	–	–		
Aug. 8 & 9	915	–		
Aug. 10 & 11	264	–		
Aug. 15 & 16	210	–		
Aug. 21	176	–		
Aug. 23 & 24	–	–		
Aug. 25 & 26	–	–		
Aug. 27	–	–		

Results and Discussion — 1974

Open Field Study

Altogether about 1000 beetles of each species were marked in 1974. Events at the two sites implied totally different causes for changes in abundance of the coccinellids. At site 2, there were many *C. trifasciata*, but relatively few *C. californica* in the alfalfa when the aphids reached peak density in the second half of May. A cutting regime imposed on the alfalfa at the end of May caused aphid numbers to fall, and then remain at a much lower level than at site 1 for the rest of the season (Fig. 2). Captures of *C. californica* dwindled and recaptures ceased, only a few days after marking began. Recaptures of recently marked *C. trifasciata* continued until mid-June (Table I). By then, aphid density had dropped below 0.3/terminal (Fig. 2), the density at which Frazer and Gilbert's (1976) predation model predicts that *C. trifasciata* can catch its maintenance requirement. Aphid density never exceeded 0.6 thereafter, and very few beetles of either species were recaptured. The data suggest that while the aphid density was low, most of the beetles captured were immigrants that left again within 24 h. Extremely few second generation adults were found, so no attempt was made to mark them. Beetle reproduction in the alfalfa at site 2 had failed.

On the other hand, both species successfully produced a second generation in the alfalfa at site 1. Overwintered populations of both species were present from the first week of June until 7 July (Table I), peaking in warm weather at the end of June when aphid numbers were increasing. *C. californica* became less abundant following rain in early July and by mid-July, after 4 consecutive days of rain, few adult beetles of either species were found in the alfalfa (Table I). Either the beetles

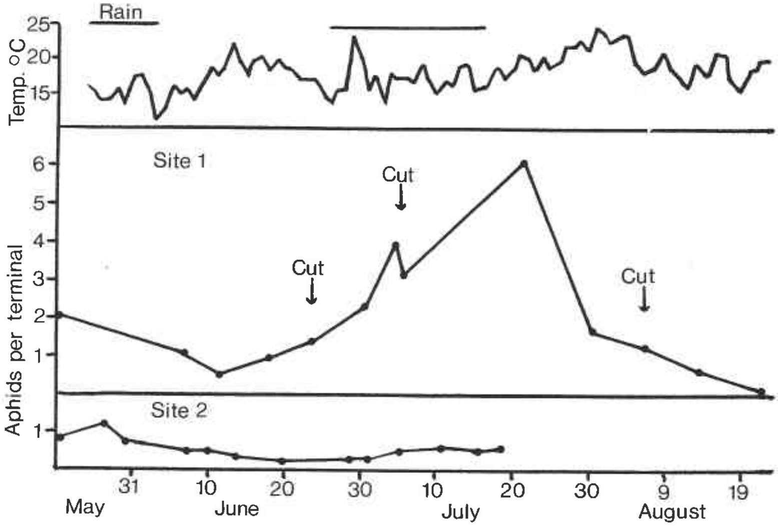

FIG. 2. Daily maximum temperature and pea aphid density, alfalfa sites 1 and 2, 1974. The arrows show when part of site 1 was cut; beetles and aphids were not sampled in the recently cut part of the field.

had died, or they had left the field while the aphid density was adequate for their needs.

Second generation beetles (many more *C. trifasciata* than *C. californica*) began emerging about the beginning of August, by which time a fungus epizootic had greatly reduced aphid density (Fig. 2). None of the marked *C. californica* was recaptured, while the new *C. trifasciata* appeared to be leaving within a few days of emergence. By 22 August, aphid density had fallen to 0.17/terminal; no *C. trifasciata* marked after that were recaptured (Table I).

By contrast, the beetles successfully reproduced in the oats at site 2, but not at site 1. In neither plot were overwintered beetles abundant, nor recaptured for very long. Out of 62 overwintered *C. californica*, and 19 *C. trifasciata*, marked in the oats at site 2, only 2 and 3 respectively were ever recaptured. Quadrat sampling in late July and early August revealed larvae on the oat plants and among the weeds between the rows. Second generation adults were subsequently marked in the oat plot. At site 1, high numbers of *C. californica* (mostly unmarked) were found in the oat plot immediately after the rainy weather early in July, when the beetles had disappeared from the alfalfa. After further rain, they too had nearly all disappeared and were all gone within a week. Altogether, 305 overwintered *C. californica* (of which 60 were recaptured in the plot at least once) and 16 overwintered *C. trifasciata* (2 recaptured) were marked at site 1. Larvae and pupae were subsequently found amongst the weeds and on the oats, but early weed growth was very rank at site 1, so the weeds were cut within 10 cm of the ground and the larvae apparently failed to survive.

Thus, although the 1974 data showed clear evidence that coccinellids were no longer recaptured when the aphid density fell below a minimum level, they also showed high losses of marked beetles when the aphid density was apparently adequate. The 1975 study was therefore designed to investigate the role of movement in the population dynamics of the beetles. But first, a check on the validity of capture–recapture was needed.

Cage Test of Jolly Estimation

The number of beetles alive in the field cages was only known accurately at the start and finish of the experiment, but it was assumed that the overall mortality was spread to give a constant survival rate. The Jolly estimates were remarkably close to the interpolated estimates (Fig. 3). This suggests that mark-recapture is a satisfactory technique for estimating beetle numbers, but population estimates in the cages were almost certainly more precise than those in the field. The weather (and so catchability of beetles) was relatively constant throughout most of the experiment. The cages were usually sampled for a more or less fixed period at the same time of day, every day. Sampling in the cages was more intensive than in the field. Thus, the sample caught was a higher proportion of the total population.

Results and Discussion — 1975

Mark Loss

In 1975, many more beetles were marked, and their individual coding made it possible to determine the proportion of all marked beetles recaptured at least once for each generation of each species (Table II, A). The 4-spot colour code allowed losses of one, two, and three marks to be assessed (Table II, B). Given that less than 5% of the recaptured beetles lost three of their four marks, it seems unlikely that the proportion losing all four paint spots was high enough to bias the results seriously. Capture records of beetles missing one and two marks were run through a computer programme which printed out the capture histories of any beetles that the beetle with the mark loss could have been. The latter was then assigned to the most recently caught possibility. Nearly half of thè beetles missing three marks were remarked with a new mark in the field and so began a new record.

Estimation of Numbers

(*a*) **Catch per unit effort.** The labour-intensive nature of mark-recapture techniques often precludes their use, so population estimates obtained by the simpler method of catch per unit effort were compared with Jolly estimates of the same populations.

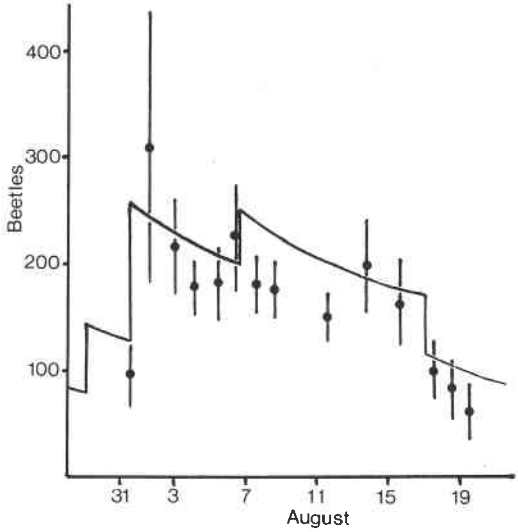

FIG. 3. Comparison of capture–recapture estimates (with standard errors) of beetle population in the cage in 1974 with numbers present. Known numbers were put in and removed on successive occasions: curves are interpolated, assuming constant mortality.

Table II. A, total numbers of adult beetles of each species marked and recaptured, and B, loss of marks by beetles in the field, 1975

		C. californica		*C. trifasciata*	
	A				
Overwintered generation	No. marked	4153		2794	
	% recaptured at least once	35.47		33.39	
Second generation	No. marked	956		380	
	% recaptured at least once	35.36		13.16	
	B				
No. of beetles lacking:	1 mark	379		135	
	2 marks	176		88	
	3 marks	53–63*		39–46*	
No. of beetles to which they were assigned as result of traceback:	1 mark	262	12 in common	95	6 in common
	2 marks	130		66	
Total beetles marked that season		5092	(1811)†	3174	(983)†
∴ proportion of marked beetles known to have lost:	1 mark	0.052	(0.145)	0.030	(0.097)
	2 marks	0.025	(0.072)	0.021	(0.067)
	3 marks	0.012	(0.035)	0.015	(0.047)

*Lower number is count if beetle with same single remaining mark seen in 2 or 3 consecutive capture periods is assumed to be same beetle. Upper number used to calculate proportion losing 3 marks.

†Nos. in parentheses show total number of beetles recaptured once or more, and numbers missing 1, 2, and 3 marks expressed as a proportion of those recaptured.

Table III. The instantaneous probability of seeing a beetle (π) in the two crops, estimated by the two methods (see text), and standard errors of the estimates, expressed as a proportion of π

Crop		π est. by method	*C. trifasciata*	*C. californica*
Alfalfa		Estimates of π adopted	.0009	.0012
Oats			.0016	.0016
Alfalfa	S.E./π	1	.0626	.0473
		2	.0658	.0494
Oats		1	.1211	.0711
		2	.1270	.0756

One person-minute was the unit of effort, so only data from the "walking counts" were used in these analyses.

Let the probability of seeing a given beetle in time $(t, t+dt)$ be πdt. If beetles may be counted more than once, the expected number seen in time T is πNT, where N = total number of beetles in the plot. But if a beetle, once seen, is not counted again, the expected number seen in time T is $N(1-e^{-\pi T})$. Here, "time" is measured in person-minutes. Estimates of π obtained by the two methods were almost identical (Table III). The values were independent of temperature and aphid density, but differed between crops. Once calibrated in this way, "walking counts" may be used to estimate coccinellid numbers in field plots of the same size.

(*b*) **Jolly estimates.** Records from alfalfa plots 1 and 2 were pooled: individual estimates for those two plots were used only for analysis of plot to plot movements. On days when the beetles were sampled by "walking counts" only, the number of beetles "released marked" (Jolly's Si) was small, leading to inaccurate estimates of beetle numbers and, consequently, to impossibly large survival rates. When the estimated survival was much greater than 1.0, and Si for one of the periods concerned was less than 20, therefore, the estimate of marked beetles was arbitrarily adjusted so that its difference from the nearest accurate value did not exceed the number of beetles marked in the interim. This small sample bias due to low values of Si was the only problem caused by releasing unmarked beetles captured in the walking counts. The only parameter estimated by the Jolly method that would be biassed by release of unmarked animals *per se* is the estimate of the number of new animals joining the population (Siniff *et al.* 1977). Estimates of this parameter were not used in this study.

(*c*) **Coccinellid numbers in alfalfa.** Although both species of beetle were found in the alfalfa, the density of *C. trifasciata* usually exceeded that of *C. californica* (Fig. 5). Until late June, beetle numbers at site 2 were roughly 3 times those at site 1, although the alfalfa area was only 1.3 times that at site 1. The lower average aphid density at site 2 (Fig. 4) parallels this difference in beetle density.

As in 1974, coccinellid reproduction in the alfalfa was more successful at site 1 than at site 2. At site 1, a measurable second generation of both species was produced in plot 3 (Fig. 5). At site 2, second generation *C. trifasciata* were extremely scarce, and although many second generation *C. californica* were caught in the alfalfa (Table IV), they probably did not emerge there. Very few larvae were observed in the alfalfa; and the large number of marked immigrants from the oat plots, found in the alfalfa during August (Table IV), further suggests that most of the second generation *C. californica* in the alfalfa were also immigrants.

(*d*) **Coccinellid numbers in oats.** As in 1974, *C. californica* was much more abundant than *C. trifasciata* in the oat plots (Fig. 6). The first *C. californica* were found in the oat plots in late May when the plants were still small, oat aphid density was low (Fig. 4), and there were no weeds. Recaptures of marked beetles began

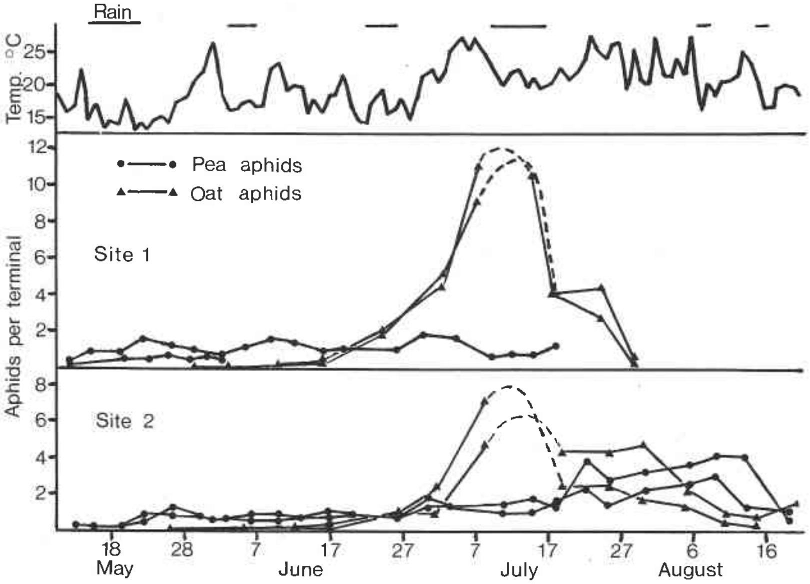

FIG. 4. Daily maximum temperature and aphid densities, 1975. Oat aphid density expressed in pea-aphid equivalents (i.e. density has been multiplied by 0.54, the relative wet wt. of oat aphids to pea aphids).

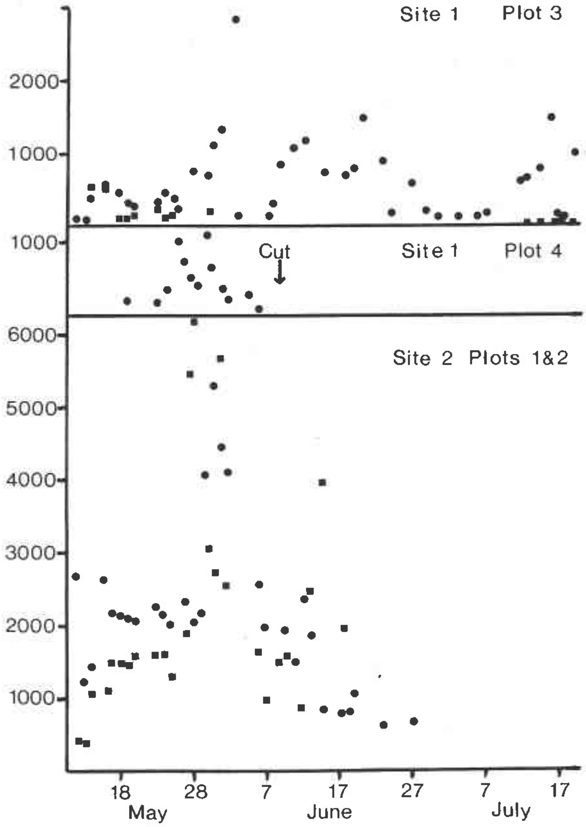

FIG. 5. Jolly estimates of populations of both species of beetles in alfalfa, 1975. ● *C. trifasciata*. ■ *C. californica*.

Table IV. Recapture information on *C. californica* marked in the alfalfa at site 2 and marked immigrants to those plots, August 1975

	Generation: 1‡	2	1	2	Both (pooled) Jolly estimate
Date	Total marked + immigrants		Ever recaptured†		
6/8	14+0	2+1	2	0	–
8/8	23+1	13+4	1	0	368
9/8	15+0	8+1	2	1	
10/8	22+1	14+2	0	0	–
11/8	15+2	13+1	0	2	2434*
12/8	23+0	15+2	1	1	4840*
13/8	12+0	7+3	1	0	828
14/8	15+0	9+1	1	2	442
15/8	41+2	19+3	0	0	–
18/8	0+0	0+2	0	0	1056*
19/8	13+1	14+2	1	0	
20/8	8+0	8+0	0	0	–
21/8	5+0	7+0	0	0	–

*Errors on these estimates even larger than usual; estimates even more suspect than usual.

†No. of beetles marked this day that were subsequently recaptured in the same plot.

‡Generation 1 is overwintered beetles.

within a few days. The four oat plots were similar in area, and average numbers of overwintered beetles in them were remarkably similar at around 250–375/plot (Fig. 6). Population estimates for *C. californica* at site 1 cease in July because few beetles were captured there after 12 July.

In all four plots, the oat aphids increased exponentially, peaking between 8 and 17 July (Fig. 4). There was a longer gap than usual between aphid samples at this period, so that actual height of the peaks cannot be determined. Non-quantitative observations of aphid abundance made during beetle sampling were therefore used to interpolate the trajectory of aphid numbers.

As in 1974, the coccinellids bred successfully in the oats at site 2, not at site 1. In this season, there was no difference in weed control at the two sites; from mid-season onwards, weeds were present at both sites, though less dense than in 1974. Larvae were recorded at both sites, but were especially conspicuous at site 1 on 11 July, when they were extremely active and abundant on the ground, as though very hungry.

Beetle Movements

(*a*) **Evidence of movements.** Catches of beetles on the flight traps, and recaptures of others in plots other than those in which they were marked, gave direct evidence of beetle movement. Altogether 1249 *C. californica*, of which 99 were marked, and 1150 *C. trifasciata*, of which 106 were marked, were caught on the flight traps between 9 May and 27 August. Two traps were moved on 9 July (Fig. 1). Fewer beetles were caught on all traps thereafter. Before 9 July, the number of each species trapped was a linear function of the numbers of that species in the plots: $y = 0.0139x - 6.745$ for *C. californica* and $y = 0.0132x - 3.443$ for *C. trifasciata*. The slopes of these regressions were virtually the same for both *C. californica* ($b = 0.0139 \pm 0.0025$ (= S.E.)) and *C. trifasciata* ($b = 0.0132 \pm 0.0028$).

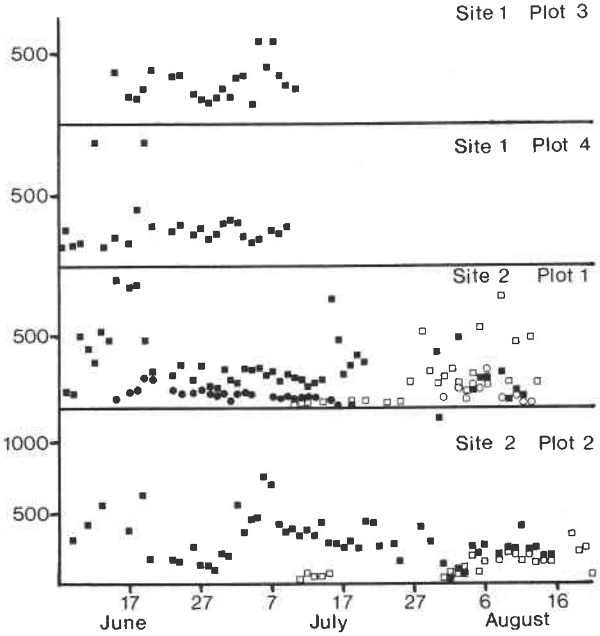

FIG. 6. Jolly estimates of populations of both species of beetle in oats, 1975. ● *C. trifasciata*. ■ *C. californica*. ■● First generation. □ ○ Second generation.

Movement of beetles between plots at the same site was considerable (Table V, B) with some beetles changing plots several times (Table V, A). Some beetles were even recaptured at the other site, 0.8 km away. A few marked beetles were recaptured elsewhere on plants other than oats and alfalfa; one 0.5 km from any release point. The *total* number of moves between particular plots could be estimated by dividing the *known* number of moves by marked beetles, by the sampling fraction; e.g., if a sample of 50 beetles, from an estimated population of 300, included 4 marked immigrants from a particular plot, then the estimated *total* immigrants from that plot was 24.

Indirect evidence of movement, from estimation of the mean length of time beetles stayed in a plot, further confirmed that there was an almost continuous flux of coccinellids in the plots. The interval between the first and last capture of a beetle in a plot, without intervening captures in other plots, was defined as a measured visit to that plot. The duration of measured visits underestimates the true visit length, because on average, only 8–18% of the marked beetles present in a plot at the time were seen in the sample. A "true" mean duration of visits was therefore estimated by adding the reciprocal of the mean proportion of marked beetles seen per day to the average measured visit length (Table VI). Even after

Table V, A. Numbers of *C. californica* (both generations pooled) known to have changed plots a given number of times

Changed plots	No. of beetles	% of total recaptured
1×	537	29.65
2×	84	4.64
3×	10	0.55
4×	3	0.17
Total i.e. ≥1×	634	35.01

Table V, B. Known and estimated total plot to plot movements of coccinellids, 1975

	C. trifasciata		*C. californica*	
	Known	Estimated	Known	Estimated
		Overwintered generation		
Number of plot changes*	289	3332	631	6998
Number of crop changes	47	412	130	1168
Number of apparent site changes	24	244	20	416
		Second generation†		
Number of plot changes*	8	–‡	87	1113
Number of crop changes	7	–	33	694
Number of apparent site changes	0	–	4	48

*This category includes both the other two.

†By the time of the second generation there were only 3 alfalfa plots so that changing plots necessarily meant changing crops, for second generation beetles in the alfalfa at site 1, unless they changed site as well.

‡No estimates possible for second generation *C. trifasciata* as there were no population estimates for their arrival plots on most of the dates they were seen there.

addition of this correction, the mean duration of visits did not exceed 15 days in alfalfa, nor 11 (by overwintered beetles) and 8 (by second-generation beetles) in oat plots. But although the overall mean durations of visits were low, there was great variation in individual visit lengths, with some beetles remaining in the plots for long periods; the maximum durations of measured visits to alfalfa and oat plots by *C. trifasciata* were 31 and 32 days respectively, and by *C. californica*, 22 and 64 days.

The flight trap catches provide evidence that the estimated mean visit duration does reflect beetles leaving the plots, rather than dying. If a fraction, p, of the beetle population leaves the plot every day, the average recorded visit length would be $1/p - 1$ (the -1 arises because marking happens only once a day for a short time, so that the visit length of any beetle remaining less than 1 day is recorded as zero). This argument assumes that all marked beetles present at the time of each day's sample are captured, so we use the estimated "true" mean visit length rather than the measured visit length. Then $1/p - 1 = 5$ to 15, or $p = 0.167$ to 0.063; i.e., 6 to 16% of overwintered beetles are estimated to leave a plot per day, on average. The number of beetles caught on flight traps, which occupied about 4.5% of the total perimeter at site 2, was on average 1% of the total number of beetles in the plots. Thus, on average, the number of beetles entering and leaving the plots, or flying near the edge without leaving the site, was 22.5% of the number of beetles in the plots. It is quite plausible, therefore, that the 6 to 16% estimated loss of beetles per day from individual plots was through emigration rather than death.

(*b*) **Causes of movement.** The beetles are more flighty at high temperatures and low aphid densities.

Table VI. Whole season mean values of $^{mi}/\hat{M}i$* and the resulting estimates of mean "true" visit duration (TVD) in days. No. of visits in parentheses

		C. trifasciata			*C. californica*		
Crop	Plot	$^{mi}/\hat{M}i$	TVD	*n*	$^{mi}/\hat{M}i$	TVD	*n*
			Overwintered				
Alfalfa	1	.076	14.9	(889)	.086	12.2	(557)
	2		14.6	(799)		12.4	(729)
	3	.113	10.8	(619)	.213	5.3	(326)
	4	.144	7.9	(344)	–	–	(95)
Oats	1	.188	7.5	(183)	.136	9.4	(804)
	2	.136	8.0	(132)	.116	10.3	(1228)
	3	–	–	(82)	.152	8.1	(514)
	4	–	–	(52)	.163	8.1	(541)
			Second generation				
Alfalfa	1	–	–	(64)	.073	–†	(81)
	2		–	(28)			(100)
	3	.031	–†	(126)	–	–	(51)
	4	–	–	–	–	–	–
Oats	1	.147	7.8	(116)	.160	7.7	(370)
	2	–	–	–	.203	6.3	(409)
	3	–	–	–	–	–	(23)
	4	–	–	–	–	–	(11)

*mi = the number of beetles marked in that plot recaptured in the *i*th sample; $\hat{M}i$ = the total number of marked beetles estimated (by the Jolly method) to be in the plot at time *i*. Calculation of correction factors for mean visit duration from this ratio is described in the text.

†Correction factors could not be calculated for these populations due to low capture and recapture rates.

During the second trapping period, after two traps were moved on 9 July, beetle numbers in the plots cannot be estimated precisely, and there were few beetles in the alfalfa. The data for the two periods were therefore analyzed separately. For both species, the data from the second period showed no particular relationships, probably for the reasons mentioned above. The remainder of this discussion, therefore, concerns 12 May to 8 July. For both species, daily maximum temperature had a significant effect on percent trapped, although the effect was much stronger for *C. trifasciata* (Fig. 7). *C. californica* appears to have a lower temperature threshold for flight than *C. trifasciata*, but the difference is not statistically significant. In the field, we consistently observed *C. californica* flying under cooler conditions than *C. trifasciata*. The trap catches, corrected for temperature by regression, were then plotted against the mean density of aphids in the plots. For *C. trifasciata*, there was no regression on aphid density; but *C. trifasciata* has a strong preference for alfalfa over oats, and the mean density of aphids in the alfalfa was relatively stable throughout the trapping periods, and never very high. For *C. californica*, there was a negative trend in the corrected trap catch with aphid density (Fig. 7).

(*c*) **Characteristics of movements.** For overwintered beetles, there were clear trends through time in the mean duration of measured visits. These trends could not be attributed to changes in the proportion of marked beetles seen in the samples. In the alfalfa, mean measured visit length declined from the start of sampling (Fig. 8). In the oats, mean duration of visits by *C. californica* increased to a peak about 21 June and then declined (Fig. 8). This peak came a month before the peak in oat

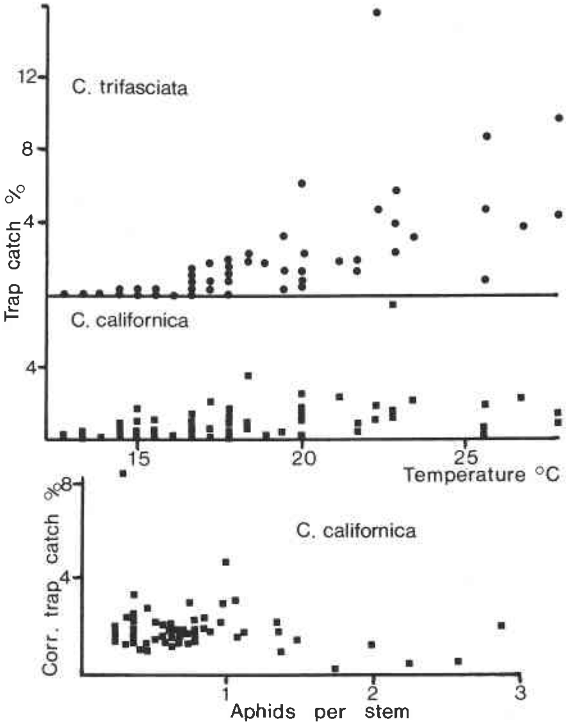

FIG. 7. Top, regression of percent caught on traps, against daily maximum temperature, for each species of beetle. Bottom, regression of trap catch of *C. californica* expressed as % of its field population and corrected for temperature, against mean aphid density in plots at site 2. The right-hand point was recorded after a hot but rainy day, so the beetles were hungrier than usual for that aphid density.

aphid density (Fig. 4). There were no such trends through time for visits by second generation beetles to any plot. The different timing of the declines in visit length in different plots makes it unlikely that they were simply due to increasing mortality; likewise the seasonal decline in total numbers of beetles caught in samples and traps, was much later than the major decline in visit length in alfalfa.

Plot to plot movements of overwintered beetles gave evidence of a preference for oats over alfalfa by *C. californica*, and the reverse for *C. trifasciata*. Movements of second generation *C. californica*, however, seemed to be influenced more by differences in aphid densities than by crop preference. The low recapture rate of second generation *C. trifasciata* meant that no conclusions about their movements or preferences were possible.

For a movement to be recorded, the beetle must move to a new plot, and remain there long enough to be recaptured. Moves may therefore reflect preferences for different crops, or responses to prey densities in either plot. If the coccinellids had no preference for one crop over another, and if prey were readily available in both crops, the numbers of within-site moves that ended in either crop would follow a Binomial distribution, with probabilities proportional to crop areas. (The proximity of the two alfalfa plots at site 2 (Fig. 1) might bias the distribution slightly at that site.) But Table VII shows that moves tended to start and finish in the same crop. *C. trifasciata* from alfalfa moved preferentially to alfalfa, and *C. californica* from oats moved preferentially to oats. Although the moves by each species from its less preferred crop were apparently random, the numbers of such moves were small (Table VII).

Moves were grouped according to the date the beetles were last captured in the plot they left. At site 1, only moves with a date of last capture (alfalfa) before 10 June were considered, because there was only one alfalfa plot at the site thereafter, the other having been cut. All 64 *C. trifasciata* that left an alfalfa plot during this

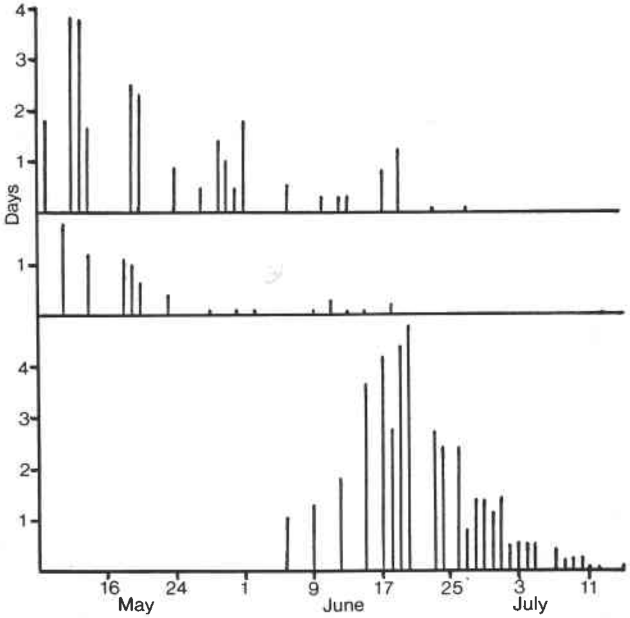

FIG. 8. Seasonal trends in mean duration (days) of measured visits by overwintered beetles. Top, *C. trifasciata* in alfalfa plot 2. Middle, *C. californica* in alfalfa plots 3 and 4. Bottom, *C. californica* in oat plots 3 and 4.

Table VII. Number of plot-to-plot moves that ended in same crop compared with expectation based on relative crop area

Moves from	at site	*p**	to same crop	Total moves	*P*	Comments
			Overwintered *C. californica*			
Alfalfa	1	.389‡	8	20	NS	Ends of moves distributed according to area of each crop
	2	.321	73	148	<.001	More moves than expected ended in same crop beetle had left
Oats	1	.440	153	161	<.001	
	2(1)†	.333	143	154	<.001	
	2(2)	.357	105	118	<.001	
			Overwintered *C. trifasciata*			
Alfalfa	1	.389‡	64	64	<.001	More moves than expected ended in same crop beetle had left
	2	.321	146	174	<.001	
Oats	1	.440	0	1	NS	–
	2(1)	.333	6	13	NS	Ends of moves distributed according to area of each crop
	2(2)	.357	4	12	NS	
			Second generation *C. californica*			
Alfalfa	1	–‡	–	–	–	
	2	.321	2	4	NS	–
Oats	1	.440	1	1	NS	–
	2(1)	.333	33	45	<.001	More moves than expected ended in same crop beetle had left
	2(2)	.357	19	31	<.01	

*Area of other plot of same crop, expressed as a proportion of total area of all other plots at the site.

†Oat plots 1 and 2 were different sizes.

‡After June 10 there was only one plot of alfalfa (plot 3) at site 1, so only moves before that date were used in this analysis.

period, but remained at site 1, were recaptured in the other alfalfa plot. In spite of a large difference in aphid density, however, with many more aphids in the alfalfa than in the oats, recaptures of *C. californica* that moved during this period were distributed randomly between the crops. At site 2 before 12 June, aphid density was much higher in alfalfa than in the oats (Fig. 4). Ninety-four percent of *C. trifasciata* moves, and 70% of *C. californica* moves, which left one alfalfa plot, ended in the other alfalfa plot. After 12 June, oat aphid density increased (Fig. 4). All but one of the remaining 45 *C. californica* that moved from alfalfa plots, and stayed at site 2, were recaptured in the oat plots. Similar numbers of *C. trifasciata* left the alfalfa plots during this time, and 71% of them went to the oats. This tendency of both species to switch from alfalfa to oats as the season progressed, paralleled the change in relative aphid densities. But the relative proportions of the two species switching through time, reflected the innate preference of *C. trifasciata* for alfalfa, and of *C. californica* for oats. The switch appears in Fig. 8 also.

At site 2, second generation adults of *C. californica* began to appear early in July (Fig. 6). Until 30 July, aphid density in at least one of the oat plots always exceeded aphid density in the alfalfa. During that time, *C. californica* moved almost entirely from oats to oats. From 30 July to 13 August, oat aphid densities declined and increasing densities of pea aphids in the alfalfa exceeded them (Fig. 4). Moves were then distributed more evenly between oats and alfalfa. After 13 August, pea aphid density fell in both alfalfa plots, while in oat plot 2, the aphids increased again. Only seven subsequent moves from oat plots ended within the site; of these, five ended in the oats. Thus, second generation *C. californica* moved preferentially to those plots with higher aphid densities.

Overall Discussion

Methodology

Releases of marked adult coccinellids by other workers have met with variable success. Kieckhefer and Olson (1974) recaptured a total of only 9 from more than 7000 locally collected *Hippodamia* spp. released in 12-ac strips of wheat, corn, and alfalfa in South Dakota. The beetles were held in the laboratory without feeding for up to 3 days, which combined with very warm temperatures, probably contributed to their dispersiveness. Kieckhefer and Olson's subsequent releases, in the next 2 years, of one and two million *Hippodamia convergens* imported from California, were no more successful, with a total of 15 recaptures at any time after 24 h.

Tamaki and Weeks (1973) released nearly 1200 marked adult coccinellids (*Coccinella transversoguttata* and *Hippodamia convergens*), with their elytra glued together with marking paint to reduce dispersal, into four 6 × 4 m plots of sugar beet. Recapture rates were much higher than Kieckhefer and Olson's: after 5 days and 1 week, approximately 20% and 10% respectively of marked beetles were found in the plots. Tamaki and Weeks concluded that ''we would have recovered almost none if the elytra had not been glued''. The present study differs from both the above in that it involved no attempt to supplement the natural population of coccinellids. It shows that high recapture rates are possible, even when there is no restriction on flight, so long as aphid densities in the area are above the level at which the beetles can catch their maintenance requirement, and some care is taken with the methods of marking and conditions of release.

No standard errors are given with the population estimates, as Roff (1973) found that unless sampling intensity is very high, standard errors estimated by Jolly's method are themselves biassed.

The techniques used ensured that the survival rate and probability of capture of the coccinellids were unaffected by marking, as required by Jolly's method. Damage resulting from marking was rare, especially in 1975, and marked beetles were neither more nor less conspicuous than unmarked ones, and searched the crop canopy in the same way. Occasionally, however, when the weather was warm and aphid density was low, a number of the beetles marked left the plot within minutes; thus they became thoroughly mixed only in the active (leaving) subpopulation, not the total population as required by Jolly's method, causing overestimation of population size on these occasions.

Although at any one time only those coccinellids that were actively searching, or sunning themselves, were available for capture, increasing hunger drives every beetle to search for prey. Female coccinellids' hunger increases faster than males', however, and they eat more overall (Frazer and Gilbert 1976), so that females may have been captured more often than males. This would underestimate population density. This is also true for the cage test of the method; Fig. 4 shows that the underestimation was trivial. Given the lower sampling intensity in the field than in the cage, the degree of underestimation there would be even less (Carothers 1973).

Thus although one, and occasionally two, of the basic assumptions of the estimation method were not met, so that an individual population estimate taken on its own cannot necessarily be trusted, this study shows that a series of such estimates can give useful information on population levels in a predator-prey interaction, especially when supported by trap catches and other data on predator movements.

Interpretation of Events in the Field

Major emigrations occurred from the alfalfa plot at site 2 in 1974, and from the oat plots at site 1 in 1975. In 1974, aphid density in the alfalfa had fallen below 0.3/terminal, the minimum density at which *C. trifasciata* can catch its maintenance requirement: *C. californica*, which has a higher maintenance requirement, left before *C. trifasciata*. In 1975, pea aphid density was always above 0.3/terminal, except once at site 2 early in the season (Fig. 4). At that time, the flight traps caught peak numbers of both species (86 *C. californica* and 85 *C. trifasciata*). This trap catch apparently included both emigrants and immigrants; the proportion of marked *C. trifasciata* in the trap catch (0.07) was much lower than the proportion of recaptures in the plot samples (0.22). The Jolly estimates (14–15 May, Fig. 6) further suggest that for both species, the influx more than compensated for the emigration. Thus, immigration and a subsequent period of cool cloudy weather, masked the beetles' numerical response to low aphid density in the alfalfa in 1975.

In the oat plots in 1975, the aphid population crash at site 1 apparently caused the coccinellid larvae to starve, and the adults to emigrate. Yet at site 2, parental generation beetles were recaptured, and larvae seen, despite a similar crash in aphid numbers, and a second generation emerged successfully. At site 2, aphids in the first sample after the crash were better distributed over the plants, with a lower proportion of first and second instars (0.25 and 0.39 in plots 1 and 2) than at site 1 (0.48 and 0.49 in plots 3 and 4), where the aphids were very clumped. These differences might explain the differences in reproductive success, since coccinellid larvae must search for prey entirely by walking, and young larvae can only catch young aphids (Frazer *et al.*, this series). Many larvae probably starved at site 1 before the very young aphids in the post-crash sample were produced.

Although there were major emigrations of coccinellids from the plots when aphid density declined suddenly or to a very low level, there was also much movement that could not be classified as a numerical response to prey density, yet which greatly influenced the outcome of the predator–prey interaction (Frazer *et al.*, this series). Do existing models of predator–prey interaction take such movement into account?

If we assume that the beetles make frequent short visits to several surrounding plots, enabling them to respond to relative aphid densities, there is a superficial resemblance to switching (Murdoch 1969; Murdoch and Marks 1973). For the overwintered beetles, however, except at very low densities of the preferred species, prey preferences override any direct response to changes in the relative density of the two prey species. For example, many *C. californica* moved from alfalfa to oats while the density of aphids in the oats was much lower than in the alfalfa. Movements of second generation *C. californica*, however, appeared to depend more on relative densities of aphids in the two crops, and may be an example of switching. But the switching model is concerned with the characteristics of such movements if they occur, rather than with whether they occur and if so, why.

Hassell *et al.* (1976) suggest that interference resulting from aggregation of predators at sites of preferred prey will lead to dispersal. Free *et al.* (1977) argue that the major form of interference in aggregated distributions of predators is not direct behavioural interference, but "pseudo-interference" which results from local exploitation of prey. Some of the small-scale numerical responses measured in this study might well result from "pseudo-interference"; but this still does not account for the changes in the amount of movement, when prey density remains adequate.

The results of this study show that the predominant controller of coccinellid movements, besides prey density, is temperature, which is ignored in most predator-prey models. Its overriding importance to the within-plot outcome of predation by *C. trifasciata* on pea aphids was stressed by Frazer and Gilbert (1976); its influence on predator movements between plots is equally important. As well as changing emigration rates, temperature has the potential to change immigration rates, but the degree to which this potential is expressed depends on factors outside the study area, such as distance from other sources of predators.

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