

HUNGER, MOVEMENT, AND PREDATION OF *COCCINELLA CALIFORNICA* ON PEA APHIDS IN THE LABORATORY AND IN THE FIELD

B. D. FRAZER and B. GILL

Research Station, Agriculture Canada, Vancouver, British Columbia V6T 1X2

Abstract

Can. Ent. 113: 1025-1033 (1981)

Hunger and abundance of adult *Coccinella californica* (Mannerheim) preying on pea aphids, *Acyrtosiphon pisum* (Harris), on alfalfa, *Medicago sativa* L., were assessed in the field. There was no consistent relationship between abundance or hunger and aphid density. The field beetles encountered in sampling were 4 times hungrier at each observed aphid density than expected from a simulation model of the predation that is driven by hunger. Laboratory studies revealed a circadian rhythm of beetle activity that was modified by hunger. An index of predatory potential (number of beetles times average hunger) was found to be a better indicator of impact of the beetles than absolute numbers of all coccinellids or hunger separately. It is suggested that the beetles encountered in simply walking through a field produce the most useful index of numbers of hungry beetles. This census must be done daily however because of the high vagility of adult coccinellids.

Introduction

Holling (1966) showed the importance of predator hunger on the searching behaviour of a predator and the resulting predation rate on the prey. Frazer and Gilbert (1976), using Holling's approach and variable life table simulation modeling, accounted for the population dynamics of the pea aphid, *Acyrtosiphon pisum* (Harris), in the field by including the effects of temperature on predator hunger and searching.

Sampling for coccinellids was a major problem. The sampling methods and calibration of them were labour-intensive. By using known numbers of coccinellids in field cages we found no more than 20%. The majority were immobile at the shadowed bases of the plants. The ones found were usually very active which made them easier to see. If relative numbers of active coccinellids found, rather than calibrated estimates adjusted for activity, could be used, we would save much work and the method would be more useable for integrated pest management. Tamaki and Long (1978) used Bombosch's (1963) method of estimating predatory potential from predator numbers and maximum voracity and related it to changes in aphid numbers but did not include temperature. Here we report on the effects of hunger and time of day on coccinellid activity in the laboratory; show why predator potential is a more practical and useful parameter than numbers or maximum voracity in estimating impact of coccinellids.

Materials and Methods

The hunger of adult *Coccinella californica* (Mannerheim) was determined by weighing them, allowing them to feed to satiation for 30-40 min on pea aphids, then reweighing them. Hunger is defined as the weight gain of the beetles. Hunger was determined for each sex of beetle separately. Single beetles were weighed with a Mettler ME30 to $\pm 1 \mu\text{g}$. Groups of 20 or more were weighed on a top loading balance to $\pm 10 \text{ mg}$.

Hunger curve. The hunger of groups (15-20) of beetles of known sex was determined by feeding to satiation and starving for various time intervals up to 48 h at 22°C. A beetle was considered satiated when a hand-offered aphid contacting the mouthparts was ignored. Different individuals were used for each period of starvation, and no water was provided. Data from females were excluded if they oviposited during fasting or feeding.

Field data. Sampling methods for pea aphids in alfalfa were the same as in Frazer and Gilbert (1976). Aphids were sampled from individual stems and the number of stems with aphids and without aphids was recorded. The average number of aphids per stem, the average number of aphids per infested stem (crowding), and the probability of a stem not being occupied (P-zero) were calculated. The number of stems sampled on each occasion varied from 60 to 200. Larger samples were taken when the density was low. Four plots were used during the study but the timing of agricultural operations, watering, cutting, and weeding were staggered in time over the four plots. This insured long periods when each plot could be used without disturbance from cultural practices.

Numbers of adult coccinellids was assessed almost daily in each plot by walking along the rows of alfalfa at 1400 h. Relative abundance was expressed as numbers per person-minute of walking. The average of the temperatures at the start and the end of the counting period was recorded. During each counting period, up to 40 beetles were collected, and returned to the laboratory, where their hunger was determined. The results from the first 4 days, when beetles were weighed individually, were used to estimate variation and sample sizes needed to show desired differences. Those beetles were restarved for 17 h at 22°C and reweighed after eating.

Predator influx study. In another study (Frazer *et al.*, this series) parts of each plot were caged with 6×6×2 m high cages. Caging induces rapid increases in aphid numbers. After one study, the cage was removed leaving a patch with a very dense aphid population. The aphids and coccinellids were sampled and the beetles' hunger determined each day until the aphid density in the patch returned to that in the rest of the field. The patch and an equivalent section of open field were then suction-sampled and the aphidophagous fauna counted.

Hunger and activity. Individual, laboratory-reared, female, adult *C. californica* were fed until satiated and placed in 2 cm diameter plastic Petri dishes provided with a 1 cm-square filter paper moistened with water. Groups of from 35 to 49 beetles were placed in a controlled environment room at 21.9°±0.5°, 65 R.H.%, and continuous illumination (3500 lux).

An automated camera took two pictures of the beetles 30 sec apart every 30 min. A stop watch and thermometer were placed within the field of the camera. Groups of beetles were starved for up to 24 h while the camera operated. Seventeen different groups of beetles were used, beginning at different times of day. From the film (Pl. I), the number of beetles that moved between the time the two pictures were taken and the temperature and the time interval were recorded. A beetle was considered to be moving if any displacement of the body or appendages was detectable by comparing the two pictures.

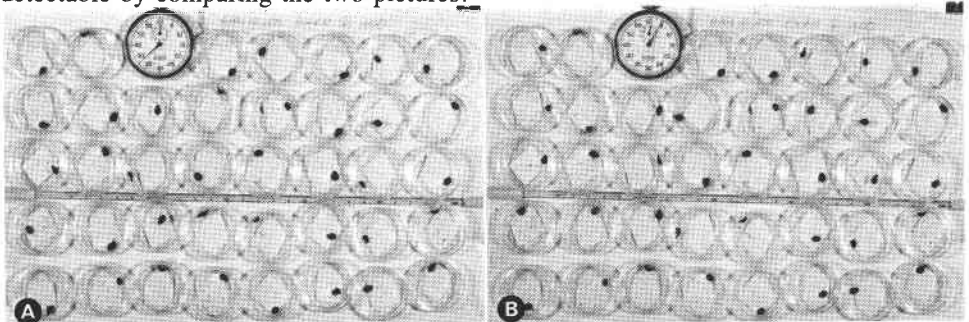


PLATE I.

The proportion, Q , of beetles that did not move was converted to an instantaneous probability, P , of movement by: $P = (-\ln Q/t)$. Because the interval is arbitrary and varied by 1-2 sec, the data were converted to the instantaneous rate. In the 17 runs, 700 pairs of photographs were compared.

Results and Discussion

Hunger curve. Hunger versus starvation time (Fig. 1) is of the form found by Holling (1966) for a mantid and by Frazer and Gilbert (1976) for *C. trifasciata*. Average estimated maximum consumption of females after 48 h of starvation was 4.33 ± 0.295 mg while that for males was 2.85 ± 0.169 mg. Starvation times longer than 20 h did not appreciably increase consumption.

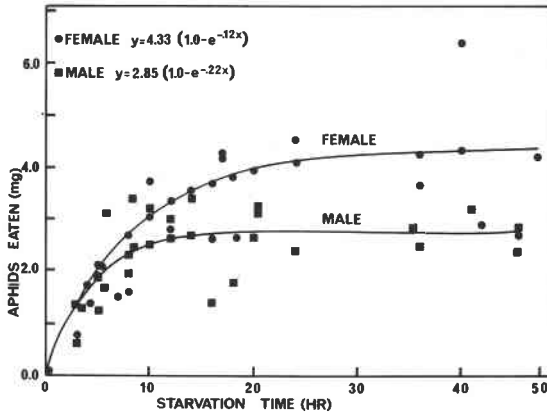


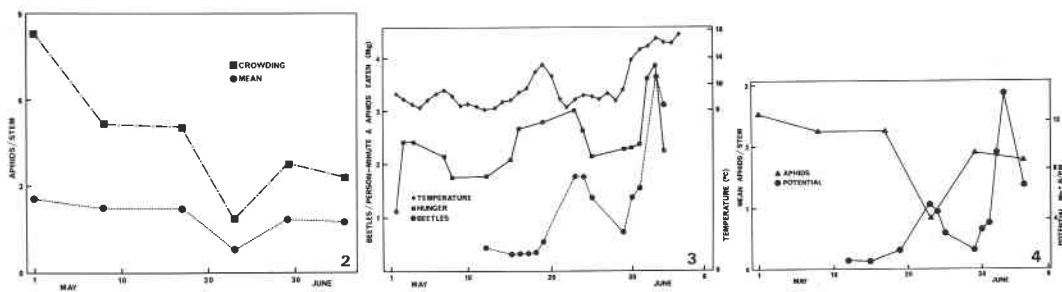
FIG. 1. Hunger curves of male and female *Coccinella californica*.

Hunger in the field. Males weighed less and ate less than females (Table I) as expected from the hunger curve. Comparing their weights when first caught and their weights after 17 h of starvation indicates that average hunger in the field during the first 4 days of the study was about equivalent to that after 17 h of fasting. Despite these similarities, however, the amount eaten after the enforced 17 h fast exceeded that eaten when first collected by 50%. This difference is probably a result of the difference in activity and feeding rates between the laboratory and nature. In the laboratory the aphids are eaten all at once; in nature, eating is spread over a longer time of intermittent searching and eating.

Field plots. The results from only one field and from one period (1 May - 6 June 1978) of alfalfa growth are shown (Figs. 2-4; Table II) but data from all fields and periods are used in subsequent analyses. These data were selected because they show the range of variation in the estimates and exemplify the relationships between the aphids and beetles that are analyzed later. Aphid density (Fig. 2) decreased over

Table I. Initial body weights and amounts of aphids eaten (\pm S.E.) by male and female *Coccinella californica*, collected in the field during the preliminary study to assess the method

Weights (mg)	Males ($n = 26$)	Females ($n = 53$)
Initial	20.8 ± 0.63	26.3 ± 0.74
Amount eaten	1.37 ± 0.186	2.13 ± 0.232
After 17 h starvation	20.2 ± 0.62	25.2 ± 0.77
Amount eaten	2.53 ± 0.179	3.47 ± 0.211



FIGS. 2-4. 2, average pea aphid density and average crowding on alfalfa in 1978. 3, average air temperature, relative density of adult *Coccinella californica* on alfalfa, and their average pea aphid consumption in 1978. 4, average pea aphid density and predatory potential (see text) of adult *Coccinella californica* on alfalfa in 1978.

the period of the example and aphid crowding decreased proportionately more. Predation when effective in either reducing the rate of increase or causing a decrease in aphid density is signalled by a change in age distribution and crowding of the aphids. These predators scatter the families of aphids and are most effective in capturing the youngest instars (Wratten 1973; Frazer and Gilbert 1976; Dixon 1959). The decline in aphid density and crowding between 17 May and 23 May also shows this effect on age distribution (Table II). Reduced beetle density thereafter was followed by an increase in aphid density by 29 May (Fig. 4) and recovery of the age-distribution (Table II).

Beetle hunger and numbers (Fig. 3) followed the aphid density (Fig. 4); the more numerous the aphids the more numerous and hungrier the beetles were. It seems paradoxical that the beetles are hungrier when their prey are more abundant. The increase in beetle numbers if due to the arrival and retention of immigrants from areas of low aphid availability could account for this with the residents of the field being satiated and not being picked up in samples. Multiplying beetle numbers by hunger to yield an index of predatory potential (Tamaki and Long 1978) more clearly shows the impact of the beetles on the aphids (Fig. 4). The numbers of beetles alone, using data from all fields, are not related to aphid density (Fig. 8). However, the predatory potential (Fig. 7) appears to be negatively correlated to aphid density. The state of the aphid population, whether increasing, decreasing or constant, would affect the hunger and density of beetles (Figs. 3-5) as the past experience and origin of the beetles determines hunger. Pooling fields in different states of aphid density and beetle flux would make for a complex relationship.

Predator influx study. The cage used to promote a high aphid density was removed on 28 May. By 1400 h, 29 May, the coccinellids and other predators (Table III; Fig. 5a) had found the abundant aphid population (Fig. 5c). The aphid density declined to that in the open field by 8 June. The hunger of the beetles in the island of high aphid density (Fig. 5b) was always less than the hunger of those in the

Table II. Proportions of pea aphids that are young (1 + 2 instar) and those older found in samples

Date	% younger	% older
May 17	89	11
May 23	28	72
May 29	77	23
June 5	44	56
7 year average	65	35

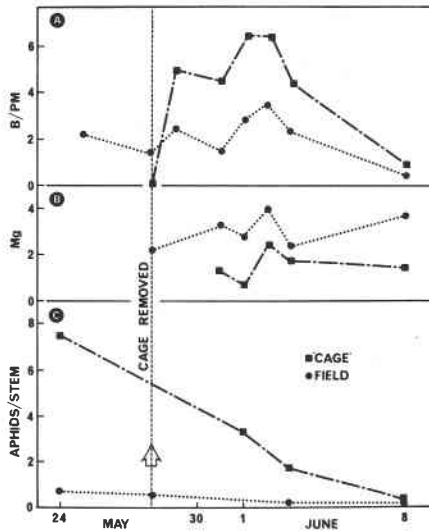


FIG. 5. Average relative density of *Coccinella californica* (beetles seen per person-minute of search). Average pea aphid consumption of those beetles, B, and average pea aphid density, C, in a field of alfalfa and in a previously caged area in 1978.

field until the aphid density of the island returned to that in the field. Comparing numbers and hunger of the beetles in the island with those in the field is a comparison between immigrants and residents respectively. The aphid density in the field and the beetle measurements are almost constant while those in the caged area are highly responsive to each other. The numbers and hunger of the beetles decline with the decreasing aphid availability.

Table III. Numbers of aphid predators in suction samples from 6 m row of alfalfa from the open field and a previously caged section

Predator	Field	"Cage"
Adult coccinellids	1	9
Adult neuroptera	3	6
Larval neuroptera	3	5
Adult <i>Orius</i>	14	27

Expected hunger levels. A simulation model of the searching behaviour of the beetles was used to predict hunger levels at various prey densities and dispersions to compare observed hunger to that which would occur if beetles do not leave but experience constant aphid availability. The hunger curve of *C. californica* (Fig. 1) was used instead of that of *C. trifasciata* used in the previous model (Frazer and Gilbert 1976). It is assumed that the other search parameters are similar for the two species. Because hunger has an overriding effect on all parameters, the effects of the assumption are probably not excessive. The model was run for 15 male and 15 female coccinellids individually for predetermined densities and dispersions (P-zero) of aphids. The model was run twice for each set of conditions. The first, using an arbitrary initial hunger and the second, using the average hunger resulting from 100 quips¹ of simulation from the first runs. The result is average expected hunger levels

¹A quip is a quarter instar period of the pea aphid and equals $6.5 \cdot D^{\circ}$ above a developmental threshold of 4.0°C .

of beetles searching at the different levels of constant aphid availability (Fig. 6). The sex ratio greatly alters the average hunger because of the difference in consumption between males and females. Measurements of field hunger were therefore corrected to a 50:50 sex ratio so as to compare expected observed hunger.

Average hunger observed in the field (Fig. 7) is 4 times greater than expected from the simulations (Fig. 6). For the 61 field samples, observed hunger averaged 80% of the maximum of the hunger curve (Fig. 1) while expected rates averaged only 20% of the maximum. The model uses absolute numbers of beetles corrected for temperature and activity to predict the predation rate and from it average hunger. The walking count method of sampling estimates only the numbers of very hungry coccinellids. This fourfold difference is also what we found between total numbers of coccinellids known to be present in a cage and the numbers we observed. If these non-active beetles presumably with low hunger in the field were included in the estimate of average hunger, the field estimate would be the same as that predicted.

Hunger and activity. Excluding preliminary runs, the data comprise 512 estimates of instantaneous rates of movement from the photograph (Pl. I), P, each with a temperature, duration of starvation from start of the run, TS, and time of day the measurement was taken, TD. These data were sorted first by increasing TS and then resorted by TD. TS was grouped into starvation times of intervals of $\frac{1}{2}$ h and TD by intervals of 1 h. Average rates per interval were then computed. The number of rates of movement for each interval of time varied from 3 to 22 but averaged 10 for TS times and 15 for TD times.

The instantaneous rate of movement, P, was highest at the beginning of each trial and decreased to a minimum after 12 h of starvation and then increased to another maximum (Fig. 9b). When the same data were plotted against the time of day (Fig. 9a), two minima, 0800 h and 2400 h and two maxima, 1200 h and 3600 h occurred. It appears that activity is affected both by a circadian rhythm (Fig. 9a) and by hunger (Fig. 9b) but the two are interacting. A curvilinear regression programme was used to separate the effects of TS and TD upon P. A number of

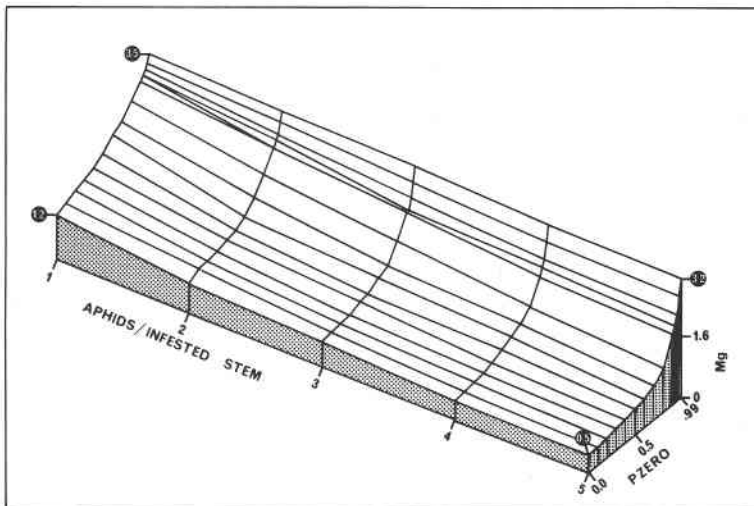
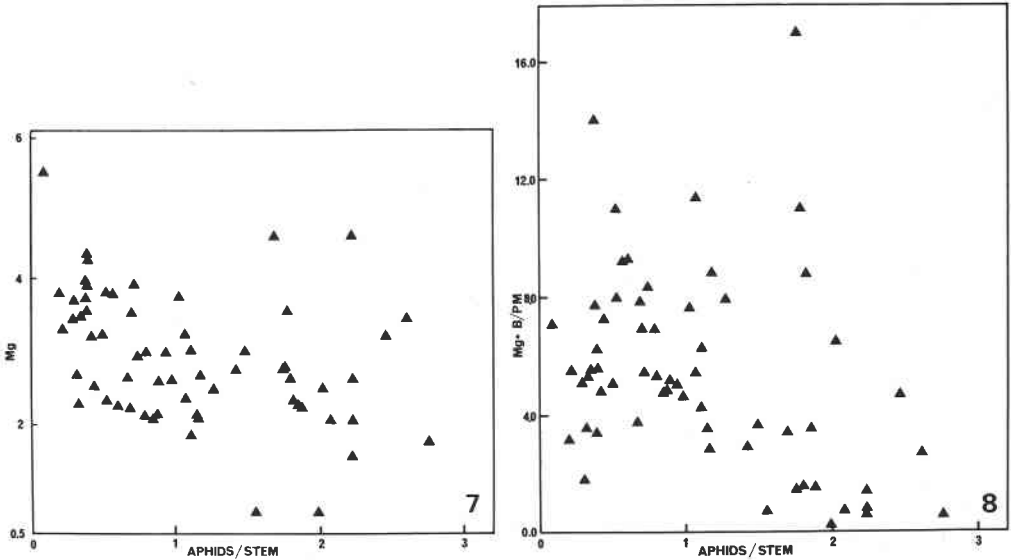


Fig. 6. Expected (see text) average hunger as consumption of pea aphids, by *Coccinella californica* when searching for pea aphids at various densities and dispersions. P-zero is the proportion of alfalfa plants in the simulated arena that have no aphids.



FIGS. 7-8. 7, average hunger of *Coccinella californica* from alfalfa in 1978 versus the pea aphid density at the time they were collected. 8, predatory potential (see text) of *Coccinella californica* from alfalfa in 1978 versus the pea aphid density at the time they were sampled.

periodic regression models were tried: The simplest model that fit the data well was: $P = b_1 + b_2 \cos (T + b_3) + (b_4 + b_5 \cos [T + b_{10}]) Z^2$ where $Z = \tan (b_6 + b_7 \cos (T + b_8) TS + b_9)$ and $T = 2\pi TD/24$. The fitted constants and their standard deviations are:

- | | |
|-----------------------------|----------------------------|
| $b_1 = 0.0140 \pm 0.00127$ | $b_6 = 0.185 \pm .0601$ |
| $b_2 = 0.0124 \pm .00141$ | $b_7 = 0.0145 \pm 0.0112$ |
| $b_3 = -9.63 \pm .521$ | $b_8 = -12.2 \pm 2.47$ |
| $b_4 = 0.00181 \pm 0.00125$ | $b_9 = -2.46 \pm 0.796$ |
| $b_5 = -0.0141 \pm 0.00311$ | $b_{10} = -8.30 \pm 0.491$ |

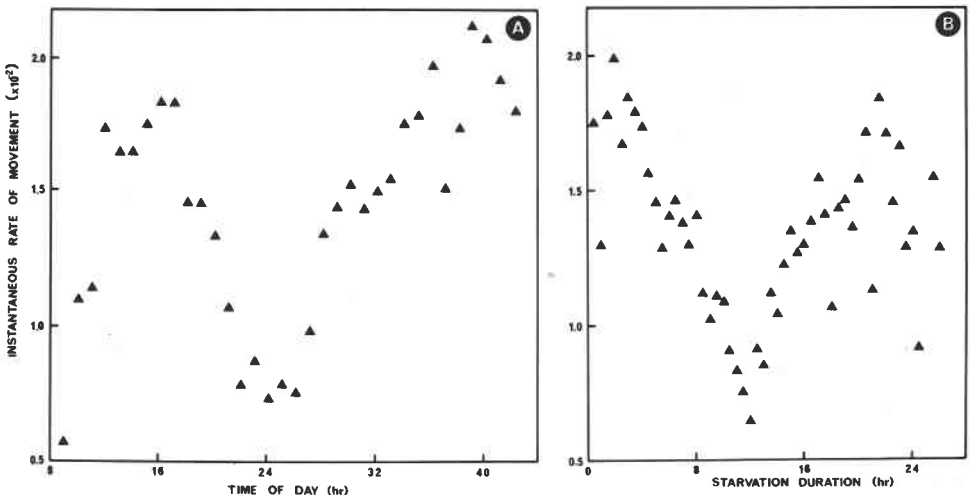


FIG. 9. Instantaneous rate of movement of female adult *Coccinella californica* versus time of day (48 h clock), A, and versus the number of hours the beetles had been starved, B.

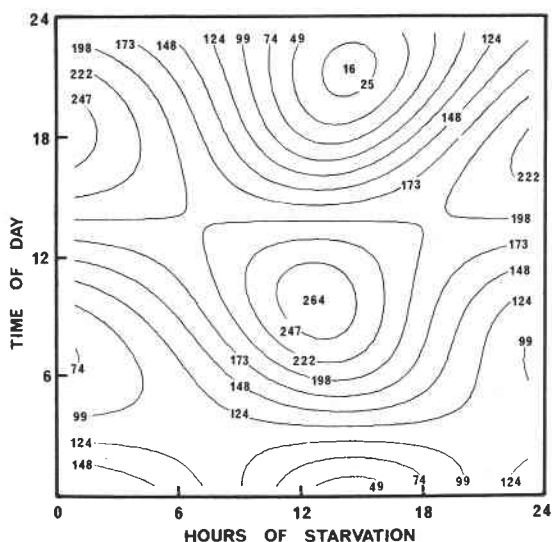


FIG. 10. A contour map of the instantaneous rate of movement, P , of female adult *Coccinella californica* plotted on a grid of hours of starvation and time of day. P is represented as elevations and its values are to be multiplied by 10^{-4} .

The coefficient of multiple determination (R)² was significant (1%) but the equation only accounts for 32% of the variation in the rate of movement. This equation was used to generate a surface of P as a function of TD and TS (Fig. 10). Movement had two maxima: when the beetles were starved between 1000 h and 1400 h and when the time of day was between 0800 h and 1200 h, and when not starved between 1800 h and 2200 h.

We usually sampled for beetles from 1400 h to 1600 h which netted us the most beetles but Fig. 10 suggests that if they were resident beetles they would be more active several hours earlier. Therefore as before the beetles we counted were mainly immigrants, some of which would remain in the field for several more days (Ives, this series) if successful in capturing aphids and then form part of the pool of inactive satiated residents.

Conclusions

Beetles encountered in sampling are mainly hungry; satiated beetles are not encountered. When aphid density is increasing and beetle numbers are increasing, the beetles are predominantly immigrants. Ives (this series), and the increase in beetles in the island of high aphid density when the cage was removed, demonstrate the high vagility of these predators. As a consequence of this opportunism, they can respond to local outbreaks rapidly. The beetles' numerical response and functional response to the aphids is mediated by their hunger. Their searching rate is set not only by hunger but also temperature and circadian rhythm of activity. Hunger of groups of field-caught beetles is easy to measure and when multiplied by numbers of beetles encountered in simply walking into a field, is a good index of the predatory potential of that population (Figs. 4, 8). It is not necessary to determine the abundance of satiated beetles.

Population is used advisedly. The high vagility of the beetles with respect to the small plots we used means that the fields are but a small fraction of the habitat of the actual population. This demands that estimates of beetle numbers and hunger be made as often as once per day. Perhaps large commercial fields would not

demand this. Ives (this series) showed that even when aphids are abundant, few beetles remain more than 4 days in the field. Kieckhefer and Olson (1974) marked and released almost 4 million *Hippodamia convergens* into fields and they dispersed independently of weather, availability of food, and relative numbers of other predators present. The significance of their behaviour and resultant use of the aphid resource is dealt with in other papers of this series.

Acknowledgments

We thank Nikon of Canada Incorp. for the loan of photographic equipment and the technical assistance of C. Booty, R. Dixon, P. Lee, L. Mack, S. MacFarlane, B. Milligan, V. Nealis, C. Sprout, and K. Wellington. We also thank Don Pearce for the agricultural operations.

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