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A Study of the Effect of Spatial Distribution on Mortality  
of the Immatures, and Associated Predators of the  
Phytophagous Lady Beetle, *Epilachna*  
*vigintioctomaculata* (Coleoptera:  
Coccinellidae)

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**Abstract** We investigated the effect of spatial distribution pattern on the immature of *Epilachna vigintioctomaculata*, employing two distinctly different spatial distribution patterns (clumped and uniform), and examined the associated predator fauna in an experimental study site in the field. Mortality was higher in the uniform distribution as compared to the clumped one in 1992 and 1993. The dominant predators were spiders, ants, and other predators were Coccinellids, bugs and mantis. Predator numbers showed a decrease with a decrease in prey population. Egg mass sizes varied widely with an average of ca. 27. Since prey distribution was the major difference between the two fields, and predation was the major mortality factor, predation probably acted with varying intensities on the different spatial distribution patterns.

**Key words:** spatial distribution pattern; survival; *Epilachna vigintioctomaculata*; predators.

### Introduction

It has long been noted that many insect populations are aggregated in space (e.g. STILING, 1987; CAPPUCINO, 1988). Obviously this tends to affect their spatial distribution patterns. Authors have theoretically argued that spatial distribution patterns can profoundly affect the extent of interaction between animals (e.g. IVES & MAY, 1985). While there has been ample examination of the theoretical importance of this phenomena, few empirical, and particularly few field studies (but see TURCHIN & KAREIVA, 1989; IVES, 1991) have been carried out to test these theories for specific insect species.

In gregarious species, in general, the female adults lay their eggs in a mass. Basically, the egg mass size may determine the degree of clumpness, and the newly hatched larvae remain aggregated during a certain developmental period. However, they disperse slowly thereafter, and the clumped distribution of the larvae tends towards an uniform distribution. Therefore, a change of spatial distribution with the advance of larval age may affect survivals.

In a field study of natural populations of *Epilachna vigintioctomaculata*

MOTSCHULSKY, MORIMOTO *et al.* (1976) found a positive relationship between aggregation size and mortality of the immatures. To investigate this dependency, we carried out field experiments to document the survivorship of the immatures in two extremely different spatial distribution patterns by using the phytophagous lady beetle, *Epilachna vigintioctomaculata* (*Ev*). This species is one of the gregarious insects, and the newly hatched larvae form a strong aggregation. However, the aggregation is maintained only in the first larval stadium and the larvae disperse slowly thereafter (MORIMOTO, 1967). Newly hatched larvae that were isolated did not suffer higher mortalities (MORIMOTO, 1965). However, even the full grown larvae maintain a clumped distribution which results from the original egg mass (MORIMOTO *et al.*; unpublished). Therefore, this species is suitable material for comparing survivals in extremely different spatial distribution patterns.

We also examined the mortality factors regulating *Ev* populations, especially the natural enemy fauna associated with the *Ev* in the experimental fields. The study was extended to the range of egg mass sizes because difference in egg mass size may be responsible for the different spatial distribution patterns in the field populations.

## Materials and Methods

### *Natural history of the experimental system*

In the study area, Shinshu University experimental farm, the phytophagous lady beetle, *Epilachna vigintioctomaculata* is a serious pest of potato plants. Both the larvae and the adults feed on the same host plant. Usually it has one generation a year, hibernates as adults and breeds on potato leaves in spring. The newly emerged adults which appear from late June to early July, disperse to various vegetables, e.g. egg plant, tomato, and beans, and feed on these crops until they enter into hibernation in October.

### *Census and experimental methods*

#### *Spatial distribution effect on mortality of immatures*

Field studies were conducted in 1992 and 1993 at the same sites on potato fields in the university campus. In each study, we compared, in terms of mortality of immatures, two different models of spatial distribution pattern (clumped and uniform) of *Ev*, with two replications of each distribution pattern in both years. We created the two extreme distribution patterns. By using these two very different spatial distribution patterns, we hoped that the effect of the distribution patterns on mortality could be more clearly observed. Figure 1 shows the field layout of infestation in the two spatial distribution patterns. Two potato fields were established, each with a total plant number of 54, and a

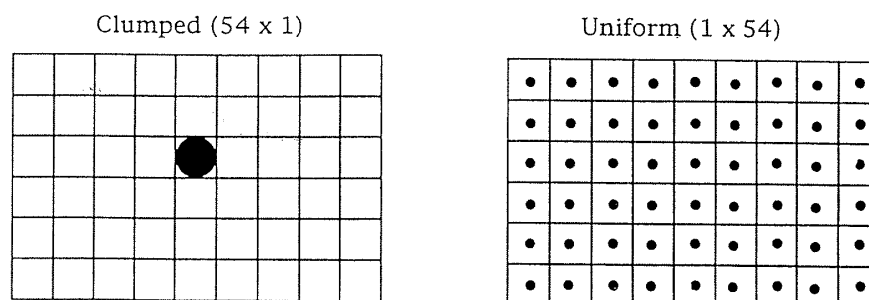


Fig. 1. Field layout of the two different spatial distribution patterns of the infested newly hatched larvae. Indicated in parentheses with each distribution pattern is the number of infested newly hatched larvae and total number of plants infested. Each square represents a plant.

planting distance of 0.5 m, adequate to allow inter-plant dispersion of the larvae. A plant represented one quadrat. Adult *Ev* were collected from neighbouring potato fields and reared in plastic containers (15 cm in diameter, 9 cm in depth) lined with paper to serve as oviposition substrates at 25°C under 16hr/8hr light/dark cycle in the laboratory. Daily observations were then to collect any eggs that had been laid. The larvae thus hatched served as material for infestation of the fields. In both distribution patterns, infestation of newly hatched larvae was carried out on the back of a single detached leaf using a fine brush, and subsequently affixing the leaf with the help of pins to the underside of a leaf. In the clumped distribution field, infestation was done on the centermost plant with 54 individuals put together, while in the uniform distribution field, it was done one larva per plant. To ensure unhindered dispersal onto adjacent plants, infestation was done after the canopies had overlapped. In the uniform distribution, a few newly hatched larvae were unable to establish on the plant and died on the first day after infestation, so extra ones were added. The plants were then examined daily for counts of the larvae on each plant to the pupal stage. Sources of overestimation are the presence of newly hatched larvae in the field, especially at locations close to the infestation point, and the presence of adults in the field which could cause more eggs and therefore larvae to be added to those infested. To avoid this, the field were carefully cleared of all larvae and adults before infestation. In addition to this, daily, we inspected and removed all adult *Ev* that were noticed.

#### *Survey of natural enemy species*

To follow the population changes and composition of the natural enemies associated with *Ev* in the different spatial distribution patterns, we carefully examined each entire field and recorded the number and species of natural enemies observed at 2-day intervals in the morning. To determine if the numbers of the natural enemies showed a dependency on the decline of *Ev*, we

calculated the standard correlation coefficient between the total numbers of natural enemies and *Ev* numbers. The survey was conducted in both distribution patterns in 1992 and 1993.

### *Egg mass sizes*

In 1992 and 1993, 788 egg masses were collected from the neighbouring potato fields, and the number of eggs per mass was examined in the laboratory.

## Results

### *Spatial distribution pattern and survivorship of immatures*

Survivorship curves were drawn for 1992 and 1993 to depict the mortality differences between the two spatial distribution patterns (clumped and uniform). The curves for both experimental years showed the maintenance of a higher population by the clumped distribution as compared to the uniform distribution over the entire study period of experimentation (Fig. 2).

Table 1 shows the mortality for both years for the two distribution patterns at the various developmental stages of the immatures. The total mortalities in the clumped and uniform distributions in 1992 were 76.9% and 94.4%, respectively. Those mortalities in 1993 were 59.3% and 96.3%, respectively. There was a significant difference in total mortality between the clumped and uniform distribution (*G* test,  $P < 0.05$ ) in both years. For both years, and in both distribution patterns, mortality was higher in early larval stadia than that

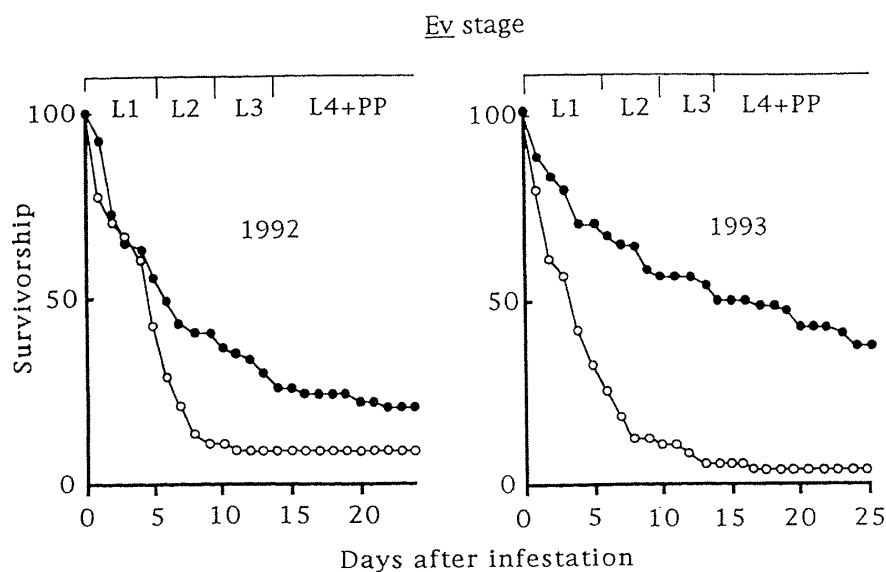


Fig. 2. Survivorship curves of immatures under clumped (●—●) and uniform (○—○) distribution patterns in 1992 and 1993. L1-L4; 1st to 4th larval stadia, PP; prepupa.

Table 1. The relationship between spatial distribution pattern (clumped and uniform) of *E. vigintioctomaculata* and the mortality of immatures.

Stage of immature	1992				1993			
	Clumped		Uniform		Clumped		Uniform	
	N	M	N	M	N	M	N	M
L1	28	51.9	38	70.4	18	33.3	40	74.1
L2	7	13.0	11	20.4	6	11.1	8	14.8
L3	5	9.3	0	0	3	5.6	3	5.6
L4+PP	3	3.6	2	3.7	5	9.3	1	1.9
TOTAL	43	79.6	51	94.4	32	59.3	52	96.3

N: Number of individuals died, M: Mortality (%), L1-L4: 1st to 4th larval stadia, PP: prepura. The difference between the distributions in terms of total mortality was significant (*G* test,  $P < 0.05$ ) both in 1992 and 1993.

Table 2. Total numbers of each of the major predators observed during the course of the experiment.

Year	Spatial distribution pattern of <i>Ev</i>	Predator types				
		Spiders	Ants	Coccinellids	Bugs	Mantis
1992	clumped	188(29.7)	147(23.2)	65(10.3)	66(10.4)	0(0)
	uniform	228(34.3)	152(22.9)	61(9.1)	52(7.8)	0(0)
1993	clumped	452(40.4)	489(43.7)	41(3.7)	21(1.9)	39(3.5)
	uniform	329(45.1)	317(43.5)	17(2.3)	8(1.1)	37(5.1)

Percent values in terms of total predator numbers in the field are in parenthesis.

in the other immature stages. In particular, mortality in the 1st larval stadium accounted for more than half of the total mortality, even in the clumped distribution, whilst in the uniform distribution in 1992 and 1993, it accounted for 70.4% and 74.1% of the total mortality, respectively.

### Natural enemy

No evidence of parasitoid or disease presence was noticed, but many kinds of predators were observed in both distribution pattern fields. Among the predators, various species of spiders, ants, Coccinellids, bugs and mantises were observed. However, mantises were not found in 1992.

Table 2 shows the total numbers of the known predators observed on the various census days in the distribution pattern fields. Spiders and ants were generally the most abundant predator types in the distribution pattern fields in both years.

Figure 3 shows changes of the total number of predators observed in the clumped and uniform distribution patterns in 1992 and 1993. In 1992, the

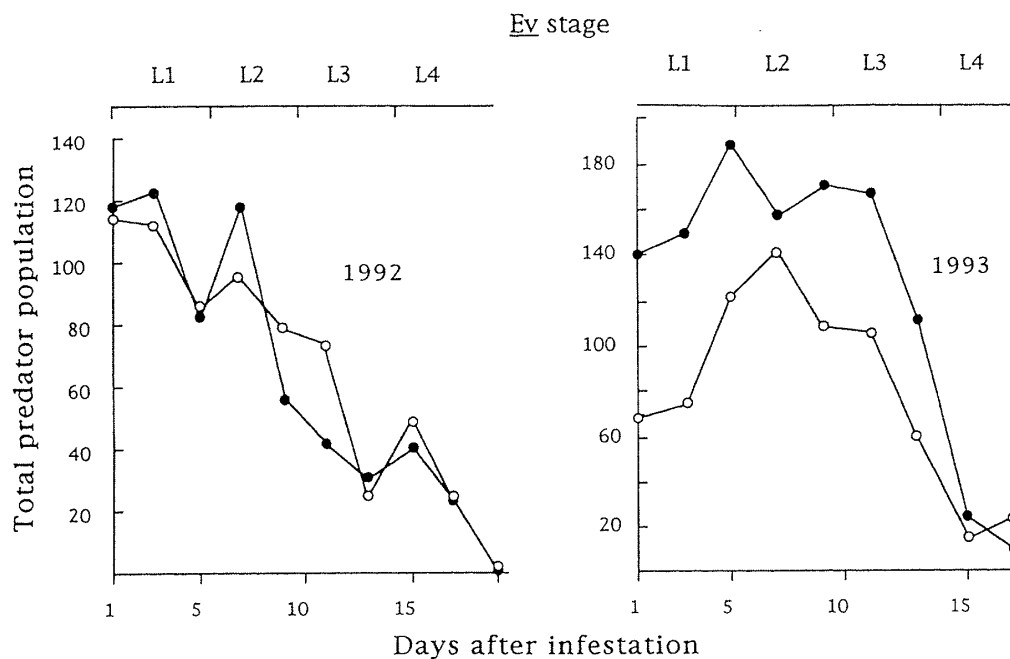


Fig. 3. Changes in the total number of predators observed in the clumped (●—●) and uniform (○—○) distribution patterns in 1992 and 1993. L1-L4; 1st to 4th larval stadia.

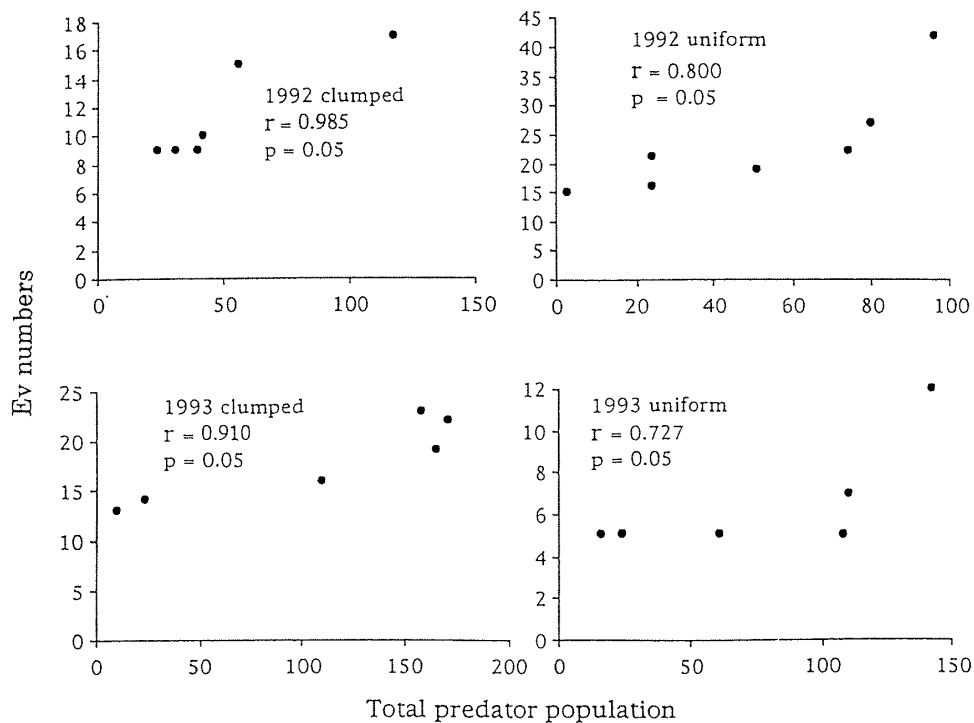


Fig. 4. The relationship between the *Ev* numbers and total number of predators.

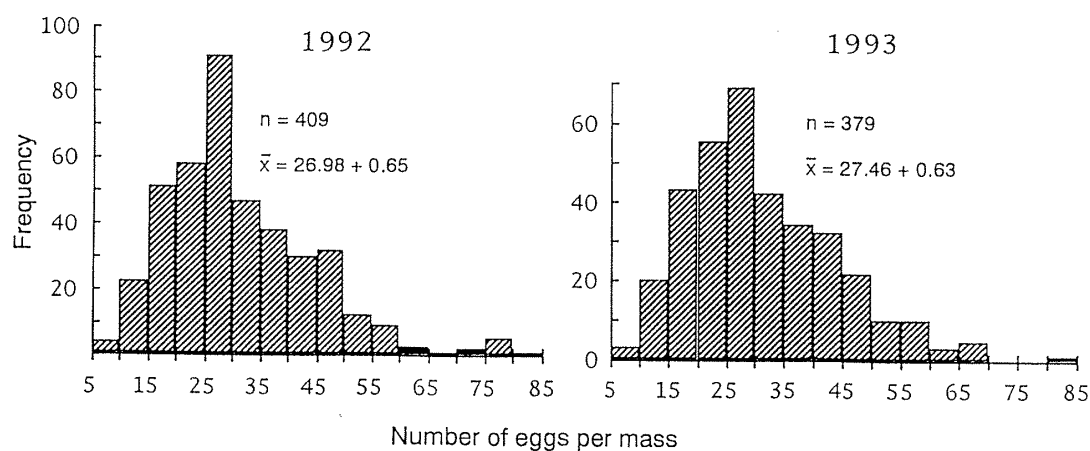


Fig. 5. Frequency distribution of the egg mass size. The number of masses observed ( $n$ ) and values of means ( $\bar{x}$ ) with 95% confidence limits (S.E.) are given in each figure.

predator population was generally high in the early larval stadia, whilst in 1993, there was an initial increase during the period corresponding to the 1st larval stadium. The predator population then declined in both years as the larval age advanced. Generally, the total predator populations were similar in the two distribution patterns in 1992, but in 1993 the clumped distribution had higher numbers. Figure 4 shows the relationship between the *Ev* numbers and total number of predators in terms of the standard correlation coefficient. The total number of predators increased significantly with increasing *Ev* numbers: 1992 clumped,  $r=0.985$  ( $P<0.05$ ); 1992 uniform,  $r=0.800$  ( $P<0.05$ ); 1993 clumped,  $r=0.910$  ( $P<0.05$ ); 1993 uniform  $r=0.727$  ( $P<0.05$ ). By the time of *Ev* adult emergence, no predator could be found in either census field.

#### *Egg mass size*

Figure 5 shows the eggs per mass in both years. The egg mass sizes ranged from 3 to 76 with an average of ca. 27, and the most commonly observed sizes were in the class 21 to 25. The distribution of egg mass size was close to a log-normal distribution in both years.

### Discussion

Populations of phytophagous insects are commonly found to be aggregated on their host-plants (e.g. TAYLOR *et al.*, 1978; STANTON, 1983). The causes of aggregation vary, but one of the more notable causes is that aggregation may be a simple consequence of eggs being laid in batches. That is, if females deposit their eggs in a mass randomly on the host plants, the resulting distribution of eggs will be contagious (ATKINSON & SHORROCKS, 1984). Furthermore,

insects clump together to engage in cooperative feeding (e.g. GHENT, 1960), to mate, and to reduce predation risk (TURCHIN & KAREIVA, 1989). Larval aggregation of *Ev* has not been associated with cooperative feeding and mating (MORIMOTO, 1965). This is because isolating the larvae in the 1st stadium only slightly protracted the larval development, and no effect of the egg mass size on larval mortality was found (MORIMOTO, 1967). Theoretically, the phenomenon of clumping can greatly influence the dynamics of interactions between organisms (e.g. HANSKI, 1981; IVES & MAY, 1985). A high local density, such as occurs in the clumped distribution, in the presence of inadequate resources is expected to induce high mortality. But in the present study, mortality was higher in the uniform distribution than in the clumped one. This suggests that a factor other than competition for resources is responsible for the differential mortalities between the two distribution patterns. Acceleration of larval development by clumping may contribute to reduce the risk of being attacked by natural enemies because of the shortening of the early larval stages. We observed in the present study that the most common predators of the *Ev* larvae were spiders and ants. In studies using *Ev*, IWAO (1971) also recorded spiders and Coccinellids, and MORIMOTO *et al.* (unpublished) observed spiders and ants as the major predators of the larval stages.

Therefore it is postulated that the main factor responsible for the differential mortality between the distribution patterns is predation, that is, the mode of action of the predators on the larvae in the different distribution patterns is different. Predators could play a dominant role in the regulation of some insect populations (NAKAMURA & OHGUSHI, 1981). It is also known that predation is sometimes responsible for causing differential mortality in prey situations where spatial variability exists (e.g. HEADS & LAWTON, 1983; REEVE & MURDOCK, 1985).

From the results of the present study, it is clear that the mortality of *Ev* was due to neither intraspecific competition for food nor parasitism/disease. So predation was considered to be a major mortality factor on *Ev* larvae. In fact, the population densities of the predators corresponded to the *Ev* population density (Fig. 4). In the field, the infested larval aggregation size in the clumped distribution was larger than that of an average egg mass. Therefore, larval dispersion in the clumped distribution started earlier than that in smaller larval aggregation size (ADU-GYAMFI & MORIMOTO; unpublished) because a larger larval aggregation affects speed of utilization of resource and accelerates larval development. However, the 1st stadium larvae in the clumped distribution still remained aggregated on an infested plant leaf.

The present study indicates that very different spatial distribution patterns of immature *Ev* in the field result in different mortality rates, which may be due to different modes of predation. However, to clearly tie predation to the



observed differential mortality between the two spatial distribution patterns, further studies are needed to determine how much predation contributes to the total mortality and how the predators' mode of attack depends on the distribution pattern.

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