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Differential Mortality in Immatures between Two Different Spatial Distributions of the Phytophagous Lady Beetle, *Epilachna vigintioctomaculata*, with Reference to Arthropod Predation

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Abstract We investigated the effect of spatial distribution pattern on the immature of *Epilachna vigintioctomaculata* (*Ev*), on mortality employing two different clumped distributions (one large clump and several small clumps). We also examined the role of predators on the mortality of *Ev* immature stages with an experiment in which cages were used to eliminate natural enemies in the field. Mortality was higher in the small clumped distribution as compared to the large clumped one in 1994 and 1995. A certain degree of clumped distribution was maintained throughout the immature life of *Ev*. Overall mortality of *Ev* immature stages was significantly higher in uncaged areas than in caged areas in both distribution patterns, and the mortality due to predation (mainly by spiders and ants) was ca. 40% for each stage up to the 3rd stadium. The spatial distribution of predators was frequently close to random or slightly clumped in each of the experimental fields in both years. The cause of the differential mortality rates between the two different spatial distributions is discussed.

Key words: spatial distribution pattern; differential mortality; dispersion; *Epilachna vigintioctomaculata*; role of predators.

Introduction

ANDREWARTHA & BIRCH (1954), IWAO (1971) and HASSELL (1985) have emphasized the importance of spatial structure of animal populations on the dynamics of their numbers. Other studies have suggested that the spatial distribution pattern of prey affects the mode of action of predators (e.g. TURCHIN & KAREIVA, 1989; HASSELL, 1984). A number of studies have examined the relationship between the spatial distribution patterns of prey or host populations and the actions of predators or parasitoids. Some of these works have indicated that a clumped distribution in the prey or host population reduced the vulnerability to predators or parasitoids (e.g. CAPPUCCINO, 1987), while others have reported a positive relationship between a spatially clumped distribution and predation or parasitization rates (e.g. BURNETT, 1958; MADDEN & PIMENTEL, 1965). This discrepancy may be due to the peculiarities of the prey or predator and host or parasitoid species.

Recently, the present authors found that the mortality of the immature stages of the phytophagous lady beetle, *Epilachna vigintioctomaculata* (*Ev*) in a spatially clumped distribution was lower than that in a uniform distribution, and predator fauna was the same in both distribution fields (ADU-GYAMFI & MORIMOTO, 1997). Therefore, it is postulated that the actions of predators on the immatures of *Ev* were different in the two spatial distribution patterns. Large and small clumped distributions affect the period of dispersal of the larvae and spatial distribution pattern as well. In the present paper, we conducted further experiments to examine the effect of the degree of spatially clumped distributions (large and small clumped distributions) on the mortality of the *Ev* immature stages and to evaluate the role of predators in causing the differential mortality between the different spatial distribution patterns in the field.

Materials and Methods

Census and experimental procedures

Spatial distribution effect on mortality of Ev immature stages

Field studies were conducted in 1994 and 1995 in potato fields on the university campus. Figure 1 shows the field layout of the newly hatched larvae infested in the two different distribution patterns (large clumped and small clumped). Two potato fields were established, each containing 144 plants (12 ×12 plants) in 1994 and 100 plants (10×10 plants) in 1995. A planting distance of 0.5 m was enough to allow inter-plant dispersion of the larvae as described by ADU-GYAMFI & MORIMOTO (1997). In the large clumped distribution, infestation of the newly hatched larvae was done on one of the centermost plants with 110 and 100 clumped individuals in 1994 and 1995, respectively. In the small clumped distribution, infestation was done with 5 small clumped groups placed on 5 plants selected with a random number table. The number of individuals in each group was 22 in 1994 and 20 in 1995. The infestation of newly hatched larvae was done in a single detached leaf as described by ADU-GYAMFI & MORIMOTO (1997). To facilitate censusing on the following days, infested plants in both fields were tagged. In addition, in the field with the small clumped distribution, the infested branches within a plant were tagged. The number of larvae was recorded daily from the newly hatched larvae to the prepupal stage when the population showed no more change. At the time of daily censusing, adults immigrating from the neighbouring fields to the experimental ones were carefully eliminated.

Spatial distribution of predators

To determine whether predators clump or not towards the *Ev* infested sites,

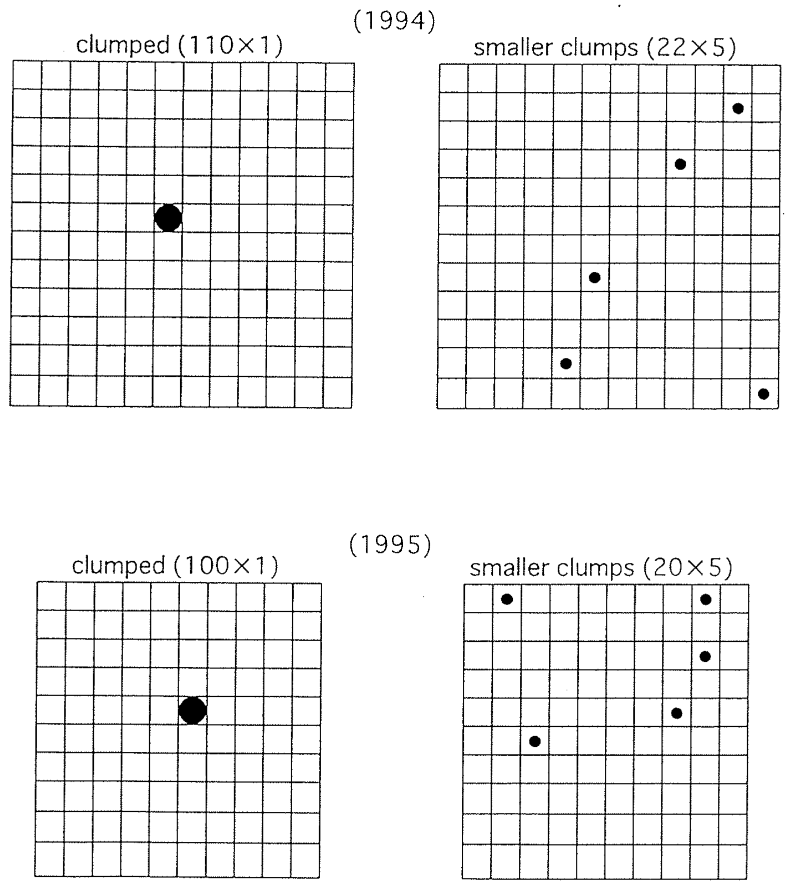

Fig. 1. Field layout of potato fields used in the experiments in 1994 and 1995. Figures in parentheses on the top of each plot indicate the number of newly hatched *Ev* larvae infested per plant and the number of plants infested.

we carefully counted the number of all predators per plant (quadrat) observed in both distribution fields at 2-day intervals in 1994 and 1995.

Evaluation of the role of predators on total mortality of Ev immature stages

As pointed out in the previous paper (ADU-GYAMFI & MORIMOTO, 1997), several types of predators were abundant in the census fields. Therefore, to evaluate the role of predators on the mortality of *Ev* immature stages, caged model experiments using cages for eliminating natural enemies were made in 1995. Therefore, to evaluate the role of predators on the mortality of *Ev* immature stages, model experiments using cages for eliminating natural enemies were made in 1995. A potato field (ca. 75 m^2) was partitioned into twelve 2.9 ×2.2 m blocks. A 1.5×1.5 m plot was situated in the center of each block. Each plot contained 25 plants (5×5, with 30 cm-intervals spacing). The 12 plots consisted of 3 replicates each of: (1) caged, large clumped distribution, (2) caged, small clumped, (3) uncaged, large clumped and (4) uncaged small clumped. The cages (1.5×1.5×1.5 m) consisted of tubular metal frames

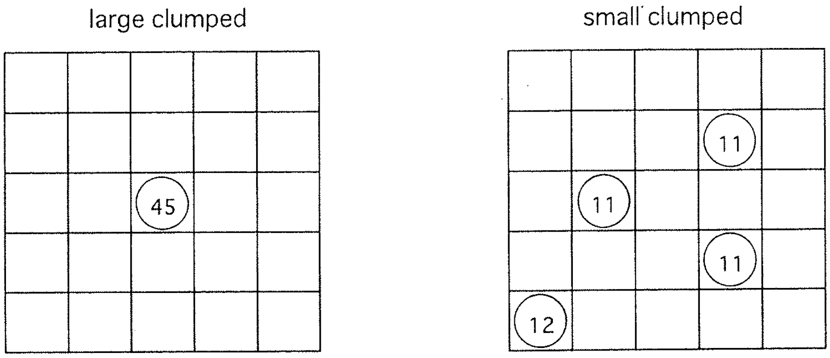

Fig. 2. Field layout of the experimental plots used in the caged and uncaged experiments in 1995. Numbers in the circles indicate the number of newly hatched *Ev* larvae infested per plant.

covered with polyester netting that extended below the soil surface to a depth of ca. 20cm. The infestation procedures were as follows (Fig. 2): in the large clumped distribution, 45 newly hatched larvae were infested in a single clump on the middle of the centermost plant, and in the small clumped distribution, 3 small groups consisting of 11 newly hatched larvae and 1 group of 12 were infested on 4 plants randomly selected with a random number table. The number of larvae was recorded daily in all 12 plots. We carefully eliminated natural enemies, especially predators found in the cages, at the time of daily censusing.

Results and Discussion

Effect of the degree of clumped distribution on mortality of Ev immature stages

Mortality of the immature stages was examined in the two distribution patterns (large clumped and small clumped) at various developmental stages up to the prepupal stage in both 1994 and 1995 (Table 1). Total mortality was significantly lower in the large clumped distribution than in the small clumped one (*G* test, $P < 0.05$). In 1994, there was higher mortality in the large clumped distribution at the 1st stadium than at the later stages, whereas high mortality was observed in the small clumped distribution during the 1st to 3rd stadia. On the other hand, in 1995, there was higher overall mortality than in 1994 in both distribution patterns. Especially in the small clumped distribution, the highest mortality was observed in the 1st stadium, and the entire population of larvae was eradicated before the end of the 3rd larval stadium. Except for a high mortality in the 2nd larval stadium in the large clumped distribution in 1995, the mortality in both distribution patterns generally decreased as the larval development advanced.

Thus, it was clear that the degree of spatially clumped distribution affected

Table 1. Effect of the two different spatial distribution patterns on mortality of *Ev.* immature on potato plants.

	1994		1995	
	Large clumped	Small clumped	Large clumped	Small clumped
Total number of infested larvae	110	110	100	100
	No. died (%)	No. died (%)	No. died (%)	No. died (%)
Stage of immature				
L1	43 (39.1)	29 (26.4)	27 (27.0)	64 (64.0)
L2	13 (11.9)	28 (25.5)	42 (42.0)	30 (30.0)
L3	10 (9.1)	20 (18.1)	11 (11.0)	6 (6.0)
L4+PP	4 (3.6)	9 (8.2)	5 (5.0)	—
Total	70 (64.6)	86 (80.9)	85 (85.0)	100 (100.0)

L1–L4: 1st–4th larval stadia; PP: prepupa.
Total mortality between the two distribution patterns was significantly different for each year (*G* test, $P<0.05$).

larval mortality. This evidence is supported by other studies of two goldenrod aphids (CAPPUCCINO, 1987).

Dispersal and change in spatial distribution during Ev immature stages

To follow changes in the spatial distribution pattern during the immature stages, the patchiness index of "mean crowding, $\overset{*}{m}/m$" (LLOYD, 1967) was employed. This index serves as a relative measure of clumped distribution (IWAO, 1968; 1971), and in the present paper, change in the $\overset{*}{m}/m$ value was also used to indicate the rate of larval dispersal in days. Figure 3 shows the change in the $\overset{*}{m}/m$ value during the *Ev* immature stages. The $\overset{*}{m}/m$ value was more than 5.0 throughout the larval life and even in the prepupal stage (except for the period when the mortality was 100%) both in the large and small clumped distributions in both years. This indicates that a clumped distribution was maintained throughout the immature life of *Ev*. The large difference in the $\overset{*}{m}/m$ value in the early larval stadia between the two distribution patterns is due to the different patterns of infestation in different numbers of quadrats. In the large clumped distribution, the $\overset{*}{m}/m$ value decreased rapidly to that of the small clumped one after the 2nd stadium. On the other hand, in the small clumped distribution, the $\overset{*}{m}/m$ value was maintained at a relatively low level from the 1 st stadium larvae to the prepupal stage. These results indicated that the larvae of early stadia dispersed earlier and faster in the large clumped distribution than in the small clumped one. IWAO (1971) observed in *Ev* larvae hatched from an egg mass in the field that dispersion movement was sluggish, and dispersion area was limited to within a few potato plants. Therefore, a certain degree of the

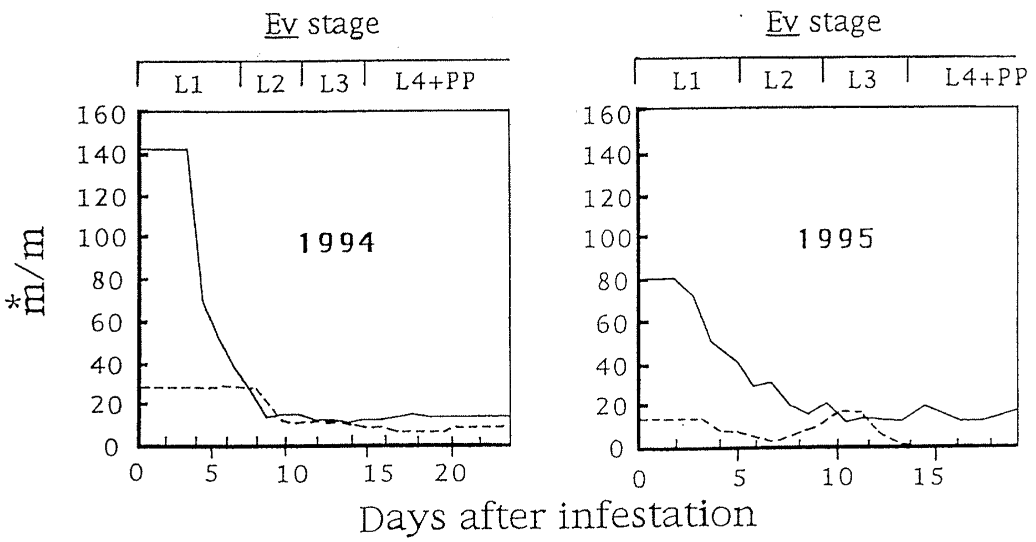

Fig. 3. Changes in the spatial distribution of *Ev* throughout the immature stage represented by $\overset{*}{m}$/m in the large clumped (———) and small clumped (--------) distributions in 1994 and 1995. L1–L4: 1st–4th larval stadia, and PP: prepupa.

clumped distribution that originated from the group of the newly hatched larvae and that was maintained throughout the immature life may largely be due to such a sluggish movement.

The role of predators on the mortality of Ev immature stages

Table 2 shows the mortality of the immature stages in the two different distribution patterns in the caged and uncaged experiments in 1995. Generally, mortality was higher in the 1st larval stadium than in other immature stages in both distribution patterns. Overall mortality of the immature stages in the uncaged experiment was significantly higher than in the caged one in both distribution patterns (*G* test, $P<0.05$). The highest mortality was observed in the small clumped distribution in the uncaged experiments, and all larvae were completely eradicated at the 3rd stadium. In the uncaged experiments, several types of predator were observed. Among them, spiders and ants were the most abundant and no evidence of parasitoid or disease presence was noticed in the experimental fields as described by ADU-GYAMFI & MORIMOTO (1997). Further, OHGUSHI & SAWADA (1985) pointed out that arthropod predation was the main factor causing high mortality in *Henosepilachna niponica*, a species closely related to *Ev*, during the immature stages. In the present paper, since mortality in the uncaged experiments was assumed to be similar to that under field conditions, we obtained an estimate of mortality due to predation by simply subtracting the mortality in the caged experiment from that in the uncaged one. The mortality due to predation, mainly by spiders and ants, was ca. 40% for each stage up to the 3rd stadium.

Table 2. The role of predators on mortality of *Ev* immature with reference to caged experiments in the field.

	Caged			Uncaged			
	Large clumped	Small clumped		Large clumped	Small clumped		
Total number of infested larvae*	135	135		135	135		
	No. died (%)	No. died (%)	Total no. died in caged expt. (%) (a)	No. died (%)	No. died (%)	Total no. died in uncaged expt. (%) (b)	Total no. died due to predation (%) (b)−(a)
Stage of immature							
L1	46 (34.0)	71 (52.6)	117	98 (72.6)	112 (83.0)	210	93 (44.3)
L2	7 (5.2)	11 (8.2)	18	14 (10.4)	17 (12.6)	31	13 (41.9)
L3	7 (5.2)	6 (4.4)	13	15 (11.1)	6 (4.4)	21	8 (38.1)
L4+PP	2 (1.5)	1 (0.7)	3	2 (1.5)	— —	2	— —
Total	62 (45.9)	89 (65.9)	151 (55.9)	129 (95.6)	135 (100.0)	264 (97.8)	113 (42.8)

L1–L4; 1st–4th stadia, PP: prepupa.

* Figures indicate the total number of infested larvae with replication of 3 of each plot (45).

Total mortality between the caged and uncaged was significantly different for each distribution pattern (*G* test, $P<0.05$)

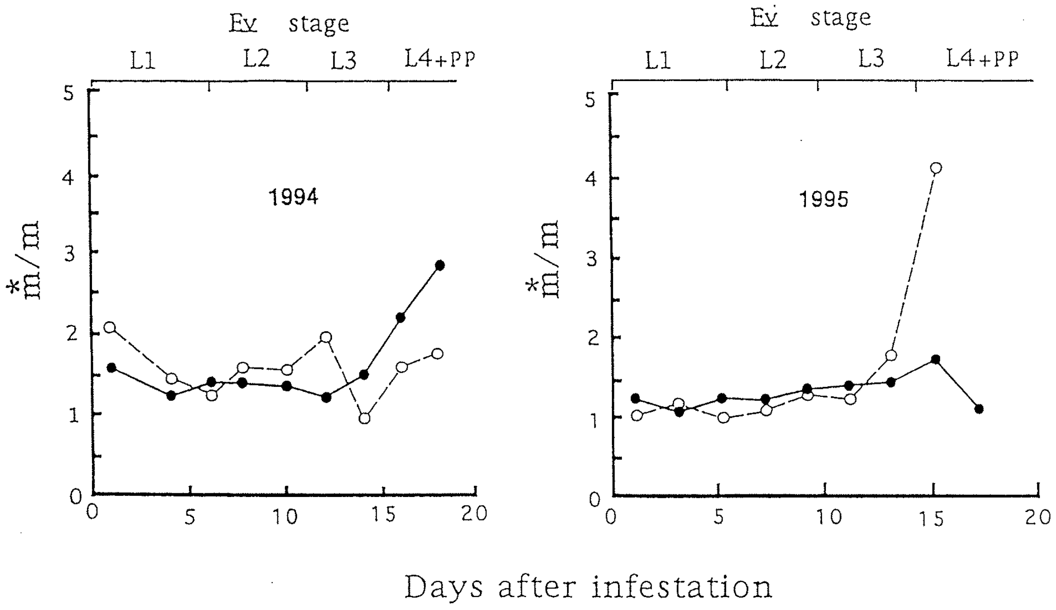

Fig. 4. Spatial distribution of predators represented by $\overset{*}{m}/m$, for large clumped (○) and small clumped (●) distribution patterns of *Ev* larvae in 1994 and 1995 measured every two days. The corresponding *Ev* immature life stages are also indicated; L1–L4: 1st–4th larval stadia, and PP: prepupa.

From the results of Tables 1 and 2, it was clear that the spatial distribution pattern affected the mortality of the immature stages, and high mortality was mainly caused by predators. This indicates that since the predators acted differently on the different spatial distribution patterns of *Ev*, the predators are responsible for the differential mortalities among the different spatial distributions in *Ev* immature stages.

Spatial distribution of predators

Figure 4 shows the spatial distribution of predators in terms of the $\overset{*}{m}/m$ index corresponding to each *Ev* immature stage in the two different distribution fields. The $\overset{*}{m}/m$ values of the predators ranged from ca. 1.0 to 2.0 during the 1st to 3rd stadia of *Ev* in both distribution fields in each year. However, high $\overset{*}{m}/m$ values were recorded in the later developmental stage of *Ev* in the small clumped (2.7 in 1994) and in the large clumped distributions (4.1 in 1995). These results indicate that the spatial distribution of predators was frequently close to random or slightly clumped in each of the experimental fields in both years, and that the predators did not clump around the prey colonies.

Mechanism causing the differential mortality in Ev immature stages between the two different spatial distribution patterns

HASSELL (1984) pointed out that denser patches of host or prey attracted parasitoids or predators, and the frequent parasitism or predation resulted in a decline in host or prey densities. On the other hand, MORRISON & STRONG (1980) and CAPPUCCINO (1987) investigated the relationship between host or prey patch density and parasitism or predation rate using generalist parasitoids or predators, and found that the patch density of host or prey had a negative effect on parasitism or predation rate. The present study revealed that there were many types of predators around *Ev* immatures in the experimental fields, and that the spatial distribution of *Ev* immatures maintained their clumped distribution throughout the immature life (Fig. 3). In addition, it revealed that the distribution of the predators was random or slightly clumped (Fig. 4). We postulated from the results of Figs. 3 and 4 that during an encounter between the prey and predators, if the consumption rate per predator was not very high because the predators are generalists, then each predator would consume a small number of prey irrespective of the degree of clumped distribution.

Therefore, it is assumed that small-sized colonies of the early larval stage in the small clumped distribution may provide more frequent encounter opportunities to the predators compared with the large-sized colonies in the large clumped distribution. This indicates a greater number of encounters and consequently a higher predation rate in the small clumped distribution than in the large clumped one. These findings and considerations appear to be able to explain the differential mortality of *Ev* immature stages between the two different distribution patterns.

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References

ADU-GYAMFI, K. & N. MORIMOTO, 1997. The effect of spatial distribution on the mortality of the immatures and associated predators of the phytophagous lady beetle, *Epilachna* vigintioctomaculata (Coleoptera: Coccinellidae). *Jpn. J. Ent.* **65**(1): 63–72.

ANDREWARTHA, H. G. & L.C. BIRCH, 1954. The distribution and abundance of animals. Chicago: University of Chicago Press.

BURNETT, T., 1958. Effect of host distribution on the reproduction of *Encarsia formosa* GAHAN (Hymenoptera: Chalcidoidea). *Canadian Entomologist*, **90:** 179–190.

CAPPUCCINO, N., 1987. Comparative population dynamics of two goldenrod aphids: spatial patterns and temporal constancy. *Ecology*, **68**: 1634–1646.

HASSELL, M. P., 1984. Parasitism in patchy environments: inverse density dependence can be stabilizing. Institute of Mathematics and its Applications. *Journal of Mathematics Applied in*

Medicine and Biology, **1**: 123–133.

——— 1985. Insect natural enemies as regulating factors. *J. Anim. Ecol.*, **54**: 323–334.

IWAO, S., 1968. A new regression method for analysing the aggregation pattern in animal populations. *Res. Popul. Ecol.*, **10**: 1–20.

——— 1971. Dynamics of numbers of the phytophagous lady beetle, *Epilachna vigintioctomaculata*, living in patchily distributed habitats. *Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970)*: 124–147.

LLOYD, M., 1967. Mean Crowding. *J. Anim. Ecol.*, **6**: 1–30.

MADDEN, J. L. & D. PIMENTEL, 1965. Density and spatial relationships between a wasp parasite and its housefly host. *Canadian Entomologist*, **97**: 1031–1037.

MORRISON, G. & D. R. STRONG, 1980. Spatial variations in host density and the intensity of parasitism: some empirical examples. *Environmental Entomology*, **9**: 149–152.

OHGUSHI, T. & H. SAWADA, 1985. Arthropod predation limits the population density of an herbivorous lady beetle, *Henosepilachna niponica* (LEWIS). *Res. Popul. Ecol.*, **27**: 351–359.

TURCHIN, P. & P. KAREIVA, 1989. Aggregation in *aphis varians*: An effective strategy for reducing predation risk. *Ecology*, **70**: 1008–1016.

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