

Population Dynamics of a Phytophagous Lady-Beetle, *Epilachna vigintioctopunctata* (Fabricius), Living in Spatio-Temporally Heterogeneous Habitats. III. Effects of Habitat Structure on Population Dynamics

Kohji HIRANO¹⁾

Laboratory of Applied Entomology, School of Agriculture, Nagoya University, Nagoya 464, Japan

Abstract. Temporal changes in the population size of a phytophagous lady-beetle were analyzed to identify mechanisms affecting lady-beetle population dynamics at different spatial scales. The study area (15 ha) included 18 habitat patches. The major host plants were potato for first generation larvae and eggplant for second generation larvae. The habitat patches were classified into three groups according to the major host plants in each patch: P-E patches (both host plants available), P patches (potato only), and E patches (eggplant only). The winter disappearance of adults in the whole study area, and larval mortality in E patches were apparently the most important factors disturbing the overall population density. Density-dependent movement of females appeared to have the greatest stabilizing effect on the yearly fluctuation of population density. Rate of increase of female adults from the first to the second generation, R , was generally higher on eggplants in E patches than in P-E patches because the adult density of the first generation was much higher in P-E patches. The yearly fluctuation of adult density in each generation tended to be less in patches with all habitat components necessary for the full life cycle (P-E patches). However, such patches were not favorable for first generation females, as indicated by the lower rate of increase from the first to the second generation. The density and stability of lady-beetle populations is discussed in relation to habitat structure.

Key words: *Epilachna*, habitat patch, habitat structure, interpatch movement, population dynamics, regulation mechanisms.

Introduction

The habitats of most animal species are heterogeneous and discontinuous in time and space, and are split into many patches from which animals obtain essential resources by interpatch movement (Elton 1949; Southwood 1977). A habitat patch also consists of some habitat components such as food resources for feeding and reproduction, and favourable hibernation sites. It is necessary to consider such spatial habitat structures in any study of population dynamics (e.g., Gilbert and Singer 1973; Ehrlich et al. 1975), and to identify the causes of population fluctuation at different spatial scales (Iwao 1971; Nakamura and Ohgushi 1981; Hanski and Gilpin 1991). As pointed out

by Kareiva (1994), however, there have been few detailed studies from this viewpoint.

I have investigated the population dynamics of the lady-beetle, *Epilachna* (= *Henosepilachna*) *vigintioctopunctata* (Fabricius) (Coleoptera: Coccinellidae), in an area that includes 18 habitat patches. In my previous studies (Hirano 1985a, 1985b, 1993), I showed that yearly fluctuations in adult density were stable, and suggested that interpatch movements by females were the most important stabilizing factor. In the present paper, I analyze temporal changes in population sizes in relation to the spatial structure of the population, identify key factors causing fluctuation in lady-beetle populations, and show how lady-beetle numbers are influenced by habitat structure in the whole study area and within each habitat patch.

¹⁾ Present address: Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305, Japan

Materials and Methods

Study area

Population censuses were carried out from May 1976 through June 1979 in a study area of about 150,000 m². The study area, located in Fujimaki, a suburb of Nagoya City, was surrounded by wooded hills except for the south side (Fig. 1).

Small cultivated fields of host plants such as potato (*Solanum tuberosum* L.), eggplant (*S. melongena* L.), tomato (*Lycopersicon esculentum* Mill) and ground cherry (*Physalis alkekengi* L.) were distributed patchily in the study area. The first generation eggs of *E. vigintioctopunctata* were laid mainly on potato and ground cherry, and the second generation eggs were laid mainly on eggplant. The area covered with ground cherry was smaller than that covered with only 38 hills of potato. The major host plants for first and second generation larvae in this study area, therefore, were potato and eggplant, respectively. The total numbers of potato and eggplant hills in the study area were 4064 and 346 in 1976, 3136 and 352 in 1977, 3636 and 440 in 1978, and 3193 and 290 in 1979. The supply of food resources for lady-beetles was thus relatively constant throughout the study period.

The small fields were clustered in 18 habitat patches (Fig. 1), and each patch consisted of one or more small cultivated fields. The habitat patches were categorized according to the presence of the major host plants (potato and/or eggplant). Three types of patch were recognized: P-E patches with both potato and eggplant, P patches with potato only, E patches with eggplant only. Patches

ranged from 25 to 900 m² in area, and were 20–125 m away from their nearest neighboring patches. Patches no. 3 and 4 in Fig. 1 were combined for further analyses, because the distance between them was only 20 m and was without apparent barriers (e.g., tall trees or housing). Patch no. 1 in 1977–79 and patch no. 3 & 4 in 1978 had 58–107 hills and 6 hills of ground cherry as well as eggplant, respectively. The lady-beetle laid eggs on ground cherry in patch no. 1, and first generation adults emerged there. For convenience, patch no. 1 was treated as a P-E patch in 1977–79. In patch no. 3 & 4, the ground cherry was densely covered with weeds which prevented their normal growth, and was not fed on by the lady-beetle. Patch no. 3 & 4 was therefore treated as an E patch. Patch no. 17 had 5 hills of eggplant in 1977, and 1 hill of potato and 19 hills of eggplant in 1978. The five hills of eggplant in 1977 and the potato plant in 1978 were densely covered with weeds which prevented their normal growth, and were not fed on by the lady-beetle. Patch no. 17 was therefore treated as no-host patch in 1977, and an E patch in 1978.

All 18 patches were examined in 1976, and 17 patches were examined in 1977–79 (Patch no. 18 was not examined). A more detailed description of the study area is given in Hirano (1985b).

Lady beetle

The lady-beetle, *E. vigintioctopunctata*, has two generations per year. Second generation adults emerge in late July to early August, and overwinter without oviposition. Overwintered adults appear in potato fields and begin to lay eggs in early May. First generation adults emerge in late June to early July. Since the harvest time of potato coincides with this period of adult emergence, the first generation adults move on to fields of eggplants and other solanaceous crops, and oviposit mainly on eggplants in our study area.

The sex ratio, the ratio of females in the whole population, was higher than 0.5 in overwintered adults in every year. The sex ratios of first and second generation adults were both nearly 0.5 in every year.

Adult census

Adult censuses were conducted on every patch every eighth day as a rule. Adults were caught by hand from the host plants and marked individually at the time of the first capture. A detailed description of the marking and census method was given in Hirano (1981, 1985b).

Census of egg, larva and pupa

The numbers of eggs and pupae were counted every tenth

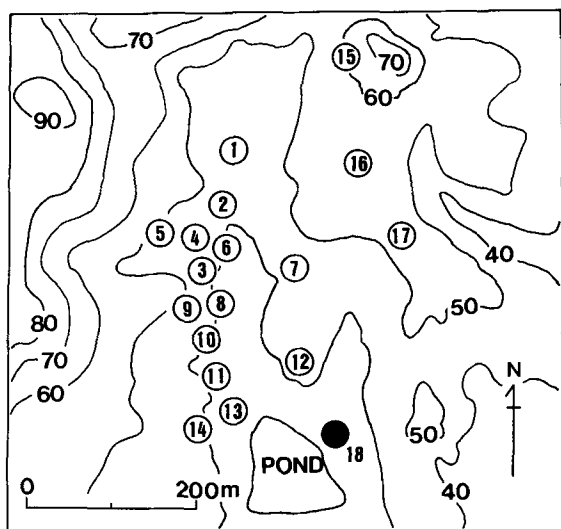


Fig. 1. Map of the study area. Circles indicate host plants patches.

day in every patch from 8 June to 1 September in 1978. The locations of egg masses and pupae were marked to avoid double counting. Ten percent of potato plants, which were fixed as a census plot, and all plants of other host species in each patch were inspected. Egg masses were collected after hatching to estimate the hatchability of eggs and the total number of the first instar larvae. Pupal exuviae were also collected in order to estimate the number of emerged adults in each patch. The parasitoid, *Pediobius foveolatus* (Crawford) (Hymenoptera: Eulophidae), was observed to attack larvae of the lady-beetle. Since larvae attacked by the parasitoid became dark and remained on the host plants for some time after dying, the larval mummies were counted, and were then removed to avoid double counting.

Census of infested leaves

As both adult and larva of *E. vigintioctopunctata* left characteristic feeding traces on leaves, it was easy to discriminate leaves infested by *E. vigintioctopunctata* from those infested by other insects. In fact, other herbivorous insects were rarely observed feeding on the leaves of solanaceous plants in the study area. Thirty-three percent of eggplant hills in each habitat patch were surveyed, and the numbers of the leaves more than 10 cm long were counted from 21 July to 19 September 1978. If more than 50% of the area of the leaf was infested by adults and larvae, it was recorded as an infested leaf. The total number of leaves in the study area was estimated as threefold of the number of leaves more than 10 cm long.

Analysis of data

The number of adults in the whole study area

The total number of adults per generation ($g=0, 1, 2$ for overwintered, first generation, and second generation adults, respectively), $\hat{N}_{T(g)}$, was estimated with the method of Nakamura and Ohgushi (1979) based on the parameters obtained by Jolly (1965) and Seber (1973) method. Detailed description of this method was given in Hirano (1985b). The total number of first generation adults that moved from potato plants to eggplants within the study area, $\hat{N}_{T(1)}$, was estimated by using the proportion of the number of adults caught on eggplant to the number caught in the whole study area (see Hirano 1993).

The number of emerging adults in each patch

The number of adults emerging on host plants x ($x=p$ and e for potato and eggplant, respectively) in k th patch ($k=1, 2, 3, \dots, 17$) in g th generation ($g=1, 2$) was estimated by two different methods: one, $\hat{N}_{b(g,k,x)}$, based on the number of pupal exuviae, and the other, $\hat{N}_{a(g,k,x)}$, based on the number of captured adults (see Appendix 1). The

number of overwintered adults which appeared in each patch was also estimated as $\hat{N}_{a(0,k,x)}$. The expression $\hat{N}_{a(1,k,e)}$ indicates the total number of first generation adults which arrived at eggplants in patch k .

Mean daily number of adults in each patch

The mean daily number of adults, $\hat{N}_{(g,k,x)}$, was used as a measure of the mean number of resident adults in each patch, that is, [the number of emerging adults] - [the number of emigrants] + [the number of immigrants] in each patch in each generation. The method of calculation is presented in Appendix 2.

The number of eggs, larvae and pupae of the second generation

In the second generation of 1978, the proportion of the total number of collected pupal exuviae to $\hat{N}_{T(2)}$ was 0.122. The proportion, 0.122, was used to obtain a measure of the total numbers of eggs, the first instar larvae and pupae in each patch as follows. The measures of the total numbers of eggs and pupae were obtained by [the total number of discovered eggs]/0.122 and [the total number of discovered pupae]/0.122 in each patch, respectively. The total number of the first instar larvae (L_1) was obtained by [the number of discovered eggs] \times [hatchability of eggs]/0.122 in each patch.

An index of the proportion of larvae attacked by the parasitoid, *Pediobius foveolatus*, was provided by [the total number of discovered larval mummies]/0.122 L_1 .

Index of yearly fluctuation of adult population density

The variances of logarithmically transformed adult densities (log of the number of adults per hill to the base 10) were used as an index of yearly fluctuation in the adult population density.

Results

Yearly fluctuations in adult population density in the whole study area

Figure 2 shows the yearly fluctuation of adult density in each generation in the whole study area. The variance of logarithms of adult density decreased drastically from the overwintered adult stage to the adult emergence of the first generation, and then increased a little from the adult emergence of the first generation to that of the second generation. The amplitudes of the yearly fluctuations of adult densities (the ratio of the highest density to the lowest density in each generation) were not large; 2.9 in overwintered adults, and 1.4 and 1.9 in the first and the second generation emerging adults, respectively. These results suggest that density-dependent regulatory pro-

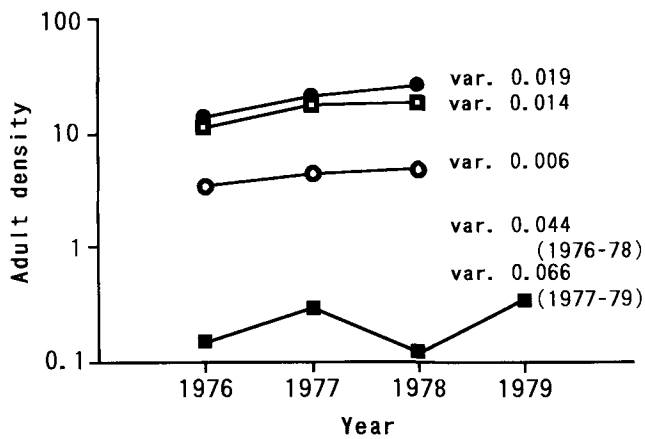


Fig. 2. Yearly fluctuations in adult density in the whole study area. ■, the number of overwintered adults per potato plant ($\hat{N}_{T(0)}/\text{plant}$); ○, the number of first generation adults emerging per potato plant ($\hat{N}_{T(1)}/\text{plant}$); □, the number of first generation adults arriving per eggplant ($\hat{N}_{T(1)}/\text{plant}$); ●, the number of second generation adults emerging per eggplant ($\hat{N}_{T(2)}/\text{plant}$); Var, Variance of logarithms of adult density.

cesses operated in the reproductive season of the lady beetle.

The variance in density increased drastically from the adult emergence of the second generation (1976-78) to the overwintered adult stage (1977-79). The disappearance of

Table 1. Mean values of population density and survival rate for each developmental stage from the first to second generation adult stages, on eggplants in P-E and E habitats.

Developmental stage	P-E habitat (8 patches)		E habitat (5 patches)	
	Mean	SD	Mean	SD
No. of first generation adults per hill ^a	24.5 ^d	15.3	9.4	8.9
No. of eggs per female	55.3	59.9	111.7	51.6
No. of eggs per hill	475.9	409.1	529.8	545.8
Proportion of hatched eggs	0.71	0.14	0.58	0.12
No. of the first instar larvae per hill	316.1	258.5	285.0	274.4
Survival rate from the first instar larvae to pupae	0.11 ^d	0.16	0.30	0.19
Proportion of adults emerged from pupa	0.75	0.19	0.74	0.18
No. of emerged adults per hill ^b	13.9	27.2	76.9	103.4
Reproductive rate from the first to second generation ^c	0.62 ^e	0.83	7.53	6.21

^a $\hat{N}_{a(1,k,e)}/\text{eggplant}$.

^b $\hat{N}_{b(2,k,e)}/\text{eggplant}$.

^c $\hat{N}_{b(2,k,e)}/\hat{N}_{a(1,k,e)}$.

^{d, e} There was a significant difference between the habitats by *t*-test on logarithms. ^d, $P < 0.05$, ^e, $P < 0.01$.

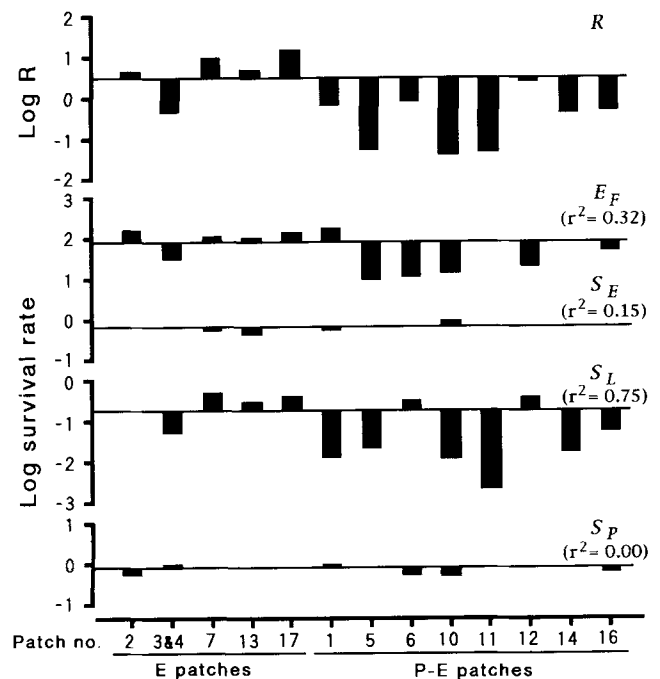


Fig. 3. Comparisons of changes in reproductive rate (R) and survival rates among different habitat patches from the first to second generation adult stages in 1978. Horizontal lines indicate the mean values for each stage. R , reproductive rate ($\hat{N}_{b(2,k,e)}/\hat{N}_{a(1,k,e)}$); E_F , the number of eggs laid per female; S_E , proportion of eggs hatched. S_L , survival rate from 1st instar to pupa; S_P , survival rate from pupa to adult emergence; r^2 , the coefficient of determination of linear regression between the survival rate (X) and reproductive rate (Y).

adults from autumn to spring was not related to the second generation adult density (Fig. 2). These results suggest disappearance of adults from autumn to spring operates as a density-independent disturbing factor in the lady-beetle population.

Key factor analysis

On the basis of life table data, Varley and Gradwell's (1960) graphical method of key-factor analysis was used to evaluate the contribution of each separate mortality to the variation of reproductive rate among different patches (Fig. 3).

In some fixed plots of potato plant the numbers of pupae found were larger than those of eggs, because larval interchange occurred among hills of the fixed plot and other hills. Thus the graphical method was only applied to the process from the first generation adults found on egg plants to the second generation emerging adults.

Figure 3 suggests that larval survival rate (S_L) was the key factor influencing the variation of R , rate of increase of female adults per generation, among patches. It also

shows that the number of eggs laid per female (E_f) was the next most important factor (Fig. 3).

R in E patches tended to be higher than those in P-E patches (Fig. 3), and the mean value of R in E patches was in fact significantly higher than that in P-E patches (Table 1).

Analysis of regulatory processes

In order to examine regulatory process in each developmental stage, and causes of the difference in R between P-E and E habitats, the data during the period of first generation adults on eggplant to second generation adults in 1978 were analyzed.

There was no significant difference in egg density between P-E and E habitats although the mean value of the first generation adult density in the P-E habitat was significantly higher than that in the E habitat (Table 1). When adult density of the first generation increased, the number of eggs per female decreased significantly (Fig. 4). These results indicate that density-dependent oviposition behavior was responsible for no significant difference in egg density between P-E and E habitats.

There was no significant correlation between egg density and proportion of hatched eggs (Fig. 5). Eggs were observed to be eaten by their adults, and by *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). The mean values of the mortality of eggs, which were due to both the cannibalism and predation, were not significantly different between the two habitats: 0.040 ± 0.057 (SD) in the P-E habitat and 0.062 ± 0.043 in E the habitat ($P > 0.05$, Mann-Whitney U -test).

The mean rate of larval survival (0.30) in the E habitat

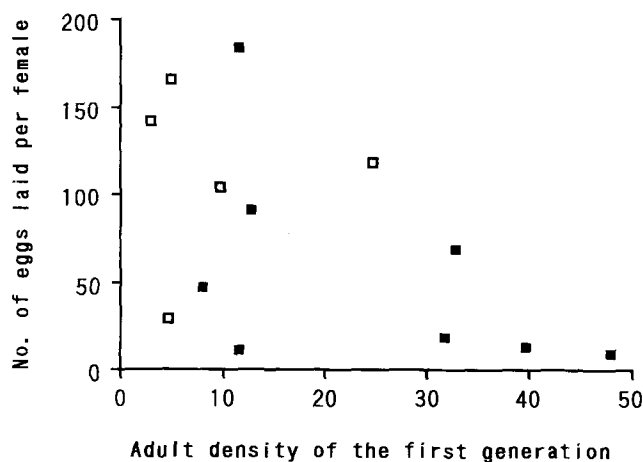


Fig. 4. Relationship between density of the first generation adult ($\hat{N}_{a(1,k,e)}$ /eggplant) and the number of eggs laid per female. ■, P-E patch; □, E patch. There was a significant negative correlation between the two variables (Kendall's rank correlation coefficient: $\tau = -0.39$, $P < 0.05$).

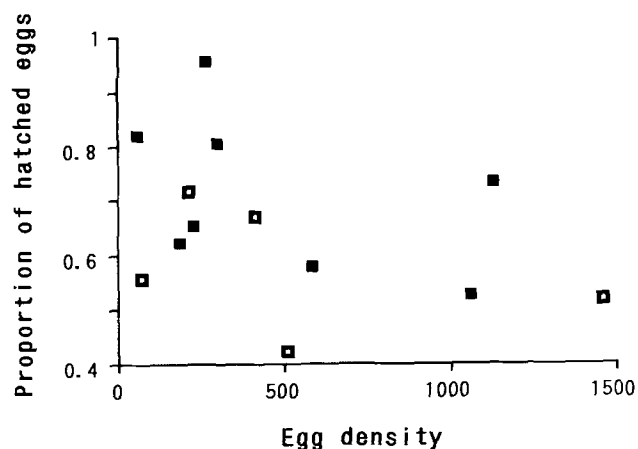


Fig. 5. Relationship between the number of eggs per eggplant and proportion of eggs hatched in the second generation. ■, P-E patch; □, E patch. There was no significant correlation between the two variables (Kendall's rank correlation, $P = 0.23$).

was significantly higher than in the P-E habitat (0.11) (Table 1). Since the relationships between larval density and the survival rate were different between the two habitats, the correlations between the two variables were examined in each habitat, separately (Fig. 6). In the P-E habitat, the larval survival rate decreased significantly when larval density increased. In contrast there was no significant correlation between the two variables in the E habitat (Fig. 6). Mean values of larval mortality due to the parasitoid, *P. foveolatus*, were not significantly different between the two habitats: 0.034 ± 0.041 (SD) in

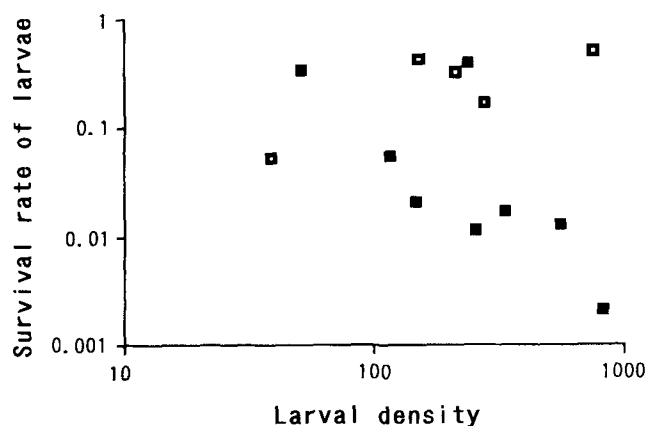


Fig. 6. Relationship between the number of the first instar larvae per eggplant and survival rate from the first instar larva to pupa in the second generation. ■, P-E patch; □, E patch. There was a significant negative correlation between the two variables in the P-E habitat (Kendall's rank correlation coefficient: $\tau = -0.64$, $P < 0.05$), and no significant correlation in the E habitat ($P = 0.39$).

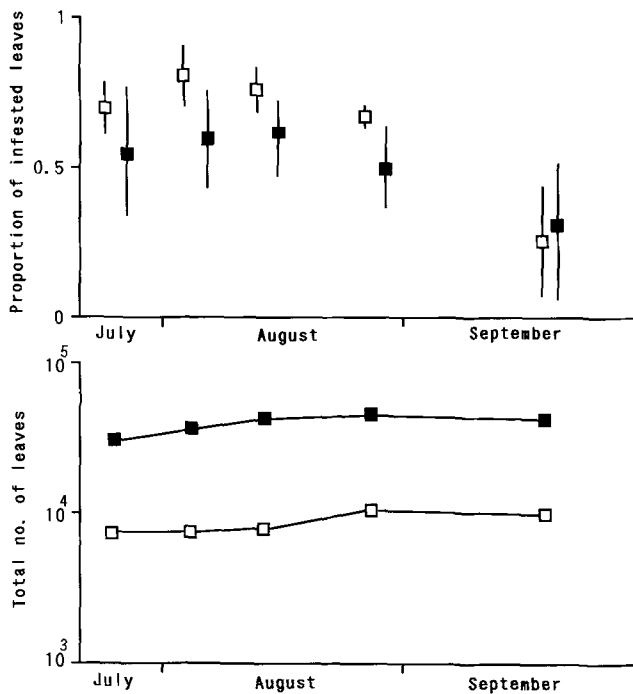


Fig. 7. Seasonal changes in eggplant condition from 21 July to 19 September 1978. Top: Proportion of leaves infested by *E. vigintioctopunctata* to total number of leaves. Bottom: total number of leaves. Vertical lines represent standard deviation. ■, P-E habitat; □, E habitat. There were significant differences in the proportion of infested leaves between the two habitats on 1 August (*t*-test on $\sin^{-1} \sqrt{x}$, $P < 0.05$) and on 26 August (Welch's *t*-test on $\sin^{-1} \sqrt{x}$, $P < 0.05$).

the P-E habitat and 0.015 ± 0.015 in the E habitat ($P > 0.05$, *t*-test on arc-sine root).

The mean proportion of infested leaves in the E habitat tended to be higher than that in the P-E habitat from 21 July to 26 August (Fig. 7). Few second generation adults emerged until 21 July. These observations suggest that the higher larval mortality in the P-E habitat was not due to food shortage in the late-instar larval stage.

There was no correlation between pupal density and the pupal survival rate (Fig. 8). The proportion of the second generation adults resident in each patch decreased significantly when density of emerging adults increased (Fig. 9).

Effect of habitat components on population fluctuations in the whole study area

Both the amount and direction of change in the density of first generation adults on eggplants were very similar between the P-E habitat and the whole study area (Fig. 10). This implies that most first generation adults, which emerged in potato plants in P-E patch, immigrated into eggplants in the same patch. However, the directions of

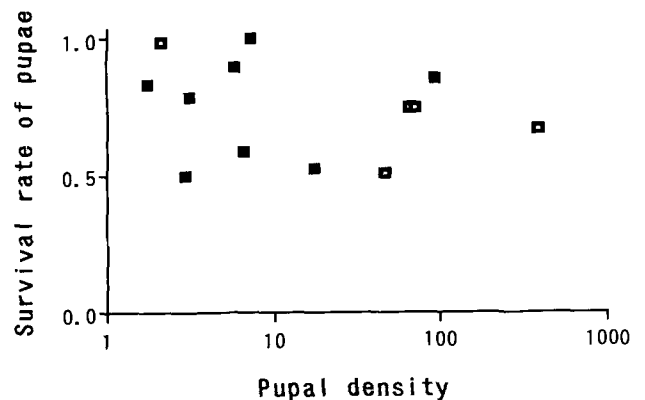


Fig. 8. Relationship between the number of pupae per eggplant and survival rate from pupa to adult emergence. ■, P-E patch; □, E patch. There was no significant correlation between the two variables (Kendall's rank correlation, $P = 0.65$).

changes in density of the second generation emerging adult in the E habitat were more similar to those in the whole study area than those in the P-E habitat. And *R* in the E habitat was much higher than that in the P-E habitat throughout the study period (Fig. 10). These results mean that the number of emerging adults of the second generation in the E habitat influenced the yearly fluctuation of adult density of the second generation in the whole study area more strongly than that in the P-E habitat did.

In 1977 and 1978, more than 50% of the second generation adults emerged in the E habitat, where the number of the first generation adults which immigrated into eggplants

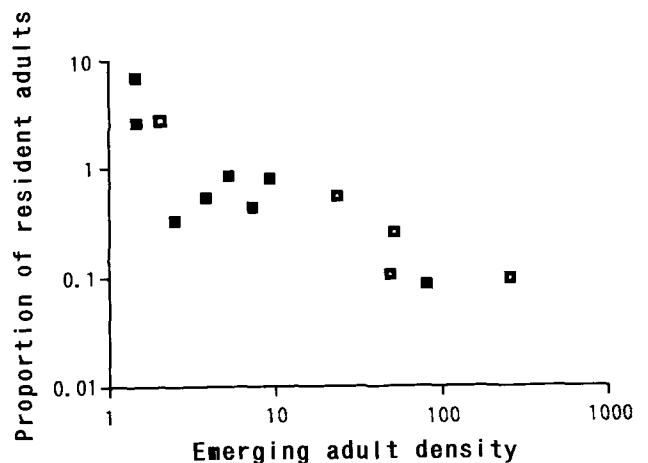


Fig. 9. Relationship between emerging adult density of the second generation ($\bar{N}_{b(2,k,e)}/\text{eggplant}$) and proportion ($\bar{N}_{(2,k,e)}/\bar{N}_{b(2,k,e)}$) of resident adults on a patch. ■, P-E patch; □, E patch. There was significant negative correlation between the two variables ($r = -0.84$, $P < 0.01$; where the proportion of resident adults was transformed into the tenth root of the proportion, and density of emerging adult log-transformed).

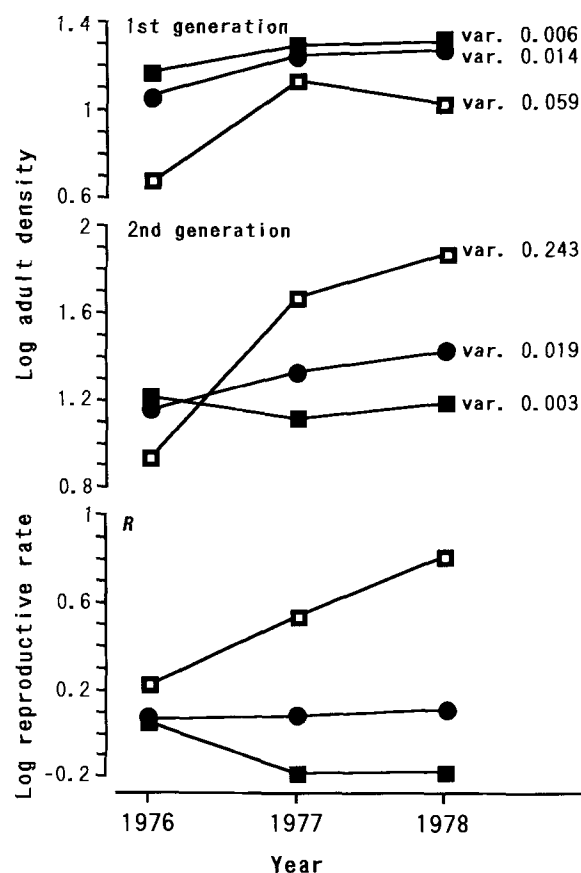


Fig. 10. Comparison of yearly changes in the number of first generation adults arriving per eggplant ($\hat{N}_{a(1,s,e)}/\text{plant}$), the number of second generation adults emerging per eggplant ($\hat{N}_{a(2,s)}/\text{plant}$), and the reproductive rate ($\hat{N}_{a(2,s)}/\hat{N}_{a(1,s,e)}$) in different habitats (s, P-E or E habitat). ●, all patches; ■, P-E habitat; □, E habitat; Var, Variance of logarithms of adult density.

was less than 20% of the total, and the number of eggplant hills was only less than 27% of the total (Table 2).

The yearly variance of logarithms in density of the first generation adults on eggplants in the E habitat was much

larger than the variance in the P-E habitat (Fig. 10). Also the yearly variance in density decreased from the first generation adult (0.006) to the second generation adult (0.003) only in the P-E habitat (Fig. 10). This suggests that density-dependent regulatory processes operated in the P-E habitat.

Effect of habitat components on population fluctuations in each patch

Overwintering adults were found frequently under the fallen leaves in groves of trees within the study area. Thus, a habitat patch close to a grove was regarded as one with favourable hibernation sites. Based on whether the habitat patch had major host plants and a favourable hibernation site as habitat components, the habitat patches in the study area were categorized into four groups (Table 3). In this table, data are presented for nine patches in which habitat components did not change during the study period (1976–1978).

Yearly variance of logarithms of overwintered adult density in P-E+OS patch was smallest in all patches (Table 3). Except for patch no. 16, the yearly variances in densities of the first generation adults which arrived on eggplant, and those of the second generation adults in P-E+OS and P-E patches were smaller than those in E patches (Table 3). These results suggest that the amplitude of the yearly fluctuation of adult density in each generation tends to be smaller in the habitat patch with habitat components necessary for completing their life cycle than in other patches.

Discussion

Regulation mechanisms and significance of interpatch movement

Larval mortality was the key factor which caused the varia-

Table 2. Changes in the numbers and proportions of first generation, second generation adults, and their host plant (eggplant) in P-E and E habitats from 1976 to 1978.

	1976		1977		1978	
	P-E	E	P-E	E	P-E	E
No. of patches	10	5	8	4	8	5
No. of first generation adults arriving at eggplants ($\hat{N}_{a(1,k,e)}$)	3297 (0.87) ^a	472 (0.13)	4792 (0.81)	1140 (0.19)	7411 (0.90)	853 (0.10)
No. of second generation adults emerging at eggplants ($\hat{N}_{a(2,k,e)}$)	3667 (0.82)	783 (0.18)	3153 (0.44)	3943 (0.56)	5042 (0.47)	5648 (0.53)
No. of eggplant hills ^b	224 (0.69)	102 (0.31)	246 (0.74)	85 (0.26)	359 (0.82)	81 (0.18)

^a The proportion of the number in each habitat to the total number in the whole study area.

^b Because the number of host plants which existed during each generation was occasionally different from the number counted in May, the numbers of eggplants during the egg stage of the first generation are given here.

Table 3. Mean values and variances of the number of adults per plant in each generation for three years (1976–78) in nine patches with constant habitat components.

Patch no.	Overwintered adults ^a		1st generation adults ^b		2nd generation adults ^c	
	Mean	Var. ^d	Mean	Var.	Mean	Var.
P-E+OS ^e						
10	0.15	0.07	49.88	0.01	28.78	0.03
12	0.41	0.09	21.11	0.03	29.21	0.04
16	0.25	0.04	6.37	0.12	7.16	0.15
P-E						
5	0.29	0.44	30.62	0.04	7.42	0.04
11	0.08	1.41	29.29	0.07	28.89	0.01
14	0.45	0.18	11.58	0.01	9.08	0.06
P+OS						
9	0.15	1.37	—	—	—	—
E						
7	—	—	18.99	0.11	88.79	0.27
13	—	—	9.60	0.13	33.90	0.14

^a No. of overwintered adults per potato plant, $\hat{N}_{a(0,k)}$ /plant.

^b No. of first generation adults arriving per eggplant in each patch, $\hat{N}_{a(1,k,e)}$ /plant.

^c No. of second generation adults emerging per eggplant in each patch, $\hat{N}_{a(2,k)}$ /plant.

^d Variance of the logarithms of adult density.

^e OS, Overwintering sites close to the habitat patch.

tion of R among patches (Fig. 3). Larval mortality was density-dependent in the P-E habitat, but density-independent in the E habitat (Fig. 6). The reason for the difference in mortality is discussed later. Interpatch variance of the logarithm of pupal density was largest in all developmental stages of the second generation (Hirano 1993). These results suggest that not only disappearance of adults during the overwintering period (Fig. 2) but also larval mortality in E habitat patches operated as the most important density-disturbing factors in the whole population.

The change in the number of eggs laid per female in each patch was the next most important factor influencing the variation of R among patches (Fig. 3). A density-dependent oviposition process of *E. vigintioctopunctata* was observed in another study area (Nakamura 1976; Hirano 1985a) as well as in the present study area. This density-dependent oviposition process seemed to be mainly due to density-dependent interpatch movement of females looking for better feeding or oviposition sites, which brought mortality during the dispersal process (Hirano 1993). This resulted in a small interpatch variance in the logarithm of second generation egg density (Hirano 1993). The density-dependent interpatch movement of females was observed in all generations (Hirano 1993). The amplitudes of the yearly fluctuations of adult density of *E. vigintioctopunctata* were very small in the study area (Fig. 2). The population density would not stabilize without any regulation mechanisms. The density-dependent movement of females seems to be the most important

mechanism to stabilize the yearly fluctuation of population density.

Some of first generation adults as well as second generation adults were observed to overwinter in the study area (Hirano 1985b). Nakamura (1976) showed, in field cage experiments, that many first generation adults did not lay eggs in the year of emergence but entered into diapause under high adult density. First generation females may cease to develop eggs in the ovary and may resorb partly developed eggs when host plants deteriorate. If the females cannot find favourable food resources to complete oviposition during the reproductive season, they would resorb eggs and diapause. Egg resorption in response to resource deterioration, therefore, would also play an important role in density-dependent oviposition process. The allied species, *E. niponica*, also has been known to adjust populations to available food resources (thistle plants) with above-mentioned processes (Ohgushi and Sawada 1985).

The rate of interpatch movements was highest in the first generation adults among all generations, and the mortality of adults tended to increase with the higher rate of interpatch movements (Hirano 1993). Since R from the first to the second generation in general was higher on eggplant in E patch than in P-E patch, the first generation females which lay eggs on eggplant in E patch would get higher fitness. This higher fitness would compensate for the mortality which interpatch movement of the first generation females must suffer.

Second generation adults must feed vigorously on host

plants to develop their fat body for overwintering (Kono 1979, 1980). Their manner of searching for favourable host plants presumably leads to the density-dependent decrease in the proportion of the second generation adults resident in each patch (Fig. 9).

Differences in R and population fluctuations between P-E and E habitats

Lower R from the first generation to the second generation in the P-E habitat than in the E habitat (Table 1) was due to (1) lower number of eggs laid per females in the P-E habitat through the density-dependent oviposition process because of higher adult density of the first generation in the P-E habitat, and (2) the higher larval mortality in the P-E habitat.

In the following, the reason of the higher larval mortality in the P-E habitat will be discussed. In P-E patches a lot of newly emerging adults of the first generation tended to move from potato plant to eggplant within the habitat patch, and fed on eggplant before reproduction. On the other hand, the number of the first generation adults which immigrated onto eggplant in E patch tended to be much smaller. Thus, leaves of eggplants in P-E patches tended to be more heavily damaged by the first generation adults than those in E patches in the early period of the reproductive season. However, the mean proportion of infested leaves in the P-E habitat was lower than that in the E habitat on 21 July, when most of the second generation adults had not yet begun to emerge (Fig. 7). This implies that many early-instar larvae died because eggplant leaves were made unfavorable by infestation with first generation adults in P-E patches. In P-E patches, eggplant leaves recovered gradually from lady-beetle infestation after many early-instar larvae died. On the other hand, the proportion of leaves infested by the larvae gradually increased in E patches because the larval mortality was lower, and late-instar larvae are vigorous feeders. Therefore shortage of food in the early-instar larval stage in the P-E habitat must have caused density-dependent larval mortality and resulted in the higher larval mortality. Shortage of food, however, did not occur in the larval stage in the E habitat. It seems to be responsible for density-independent larval mortality process in the E habitat.

Yearly variances of logarithms in density of the first and second generation adults in the P-E habitat were much smaller than those in the E habitat (Fig. 10). Also density-dependent regulatory processes were suggested in the P-E habitat from the first generation adult stage to the second generation adult stage (Fig. 10). These differences between the two habitats seem to be caused by the following two reasons. First, the number of first generation adults that immigrated onto eggplants in E patches was generally so small that a demographic stochastic process probably

operated strongly in E patch populations. In 1976 in the E habitat the density of first generation adults was much lower than in other years, and the rate of increase (R) was also much less (Fig. 10). These observations suggest that if some adults fail to reproduce in E patches with lower adult density, it can be difficult for other adults to compensate efficiently through density-dependent oviposition. Second, the density-dependent larval mortality process operated only in the P-E habitat.

Population dynamics at different spatial scales

Although yearly variances in the logarithms of adult density decreased from the first generation to the second generation in the P-E habitat (Fig. 10), the decrease in yearly variances was observed only in patch no. 11 at the patch level (Table 3). It appears that the density-dependent oviposition and larval mortality processes did not operate strongly enough to stabilize yearly fluctuations in adult density at the patch level.

Except for patch no. 16, the yearly fluctuations of adult density in the first and the second generations were smaller in each of P-E+OS and P-E patches than in E patches (Table 3). Patch no. 16 was surrounded closely by groves and isolated from other habitat patches. Thus, the larger yearly fluctuations of adult density in patch no. 16 might be due to (1) the low rate of adult immigration into the habitat patch because stabilization of density in habitat patches is related to the relative amounts of emigration and immigration, and (2) the amount of solar radiation being not enough for *E. vigintioctopunctata* to develop favorably because food crop fields were shaded by trees for some hours during daylight.

Iwao (1971) studied a population of the allied species, *E. vigintioctomaculata*, which has one generation per year, living in patchily distributed habitats. He mentioned that a complete habitat patch, which consists of all habitat components necessary for completing their life cycle, was a favorable patch for the lady-beetle, because a fairly stable population was maintained at a high level and it formed a main stock of the population in the area. Yearly fluctuations of adult density of *E. vigintioctopunctata* in each generation also tended to be more stable in P-E and P-E+OS habitat patches (Table 3). However such a complete habitat patch was not favorable for the first generation females in terms of R .

The rate of increase from overwintered adults to the first generation adults ($R=11.7-31.7$) was consistently much higher than from the first to second generation in the whole study area ($R=0.32-0.61$) (Hirano 1985b), because the numbers of overwintered adults per potato plant were much smaller than those of the first generation adults per eggplant (Fig. 2). The numbers of potato plant hills were 4.5 to 6.4 times those of eggplant hills in the study area.

On the contrary, the total numbers of the first generation adults were 19 to 32 times those of overwintered adults (Hirano 1985b). The quantity of eggplant was too small relative to the number of the first generation adults. Such difference in the relative quantity of the two host plants was generally observed in the southern part of mainland Japan where *E. vigintioctopunctata* is distributed; the ratio of potato fields to eggplant fields in area was 3.2 to 3.4 [Crop Statistics ("Sakumotsu Toukei"), 1979–83 and Horticulture Statistics ("Engei Toukei"), 1980–82]. When the relative quantity of eggplant is much less, the level of population density of second generation adults would depend on the number of first generation females that arrive at E patches and succeed in reproducing there. Also the higher the ratio of the number of P–E patches to the total number of patches is in the whole area, the more stable the yearly fluctuation of adult density of the second generation would be in the whole area.

The larval mortal process was different between P–E and E habitats. Population processes which influence population dynamics in the whole study area were also different between the two habitat types. If data were analyzed without distinguishing spatial structure within the study area, an erroneous understanding of population dynamics would result.

In the study of *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae), Hirano et al. (1995) showed that the regulation of population density is influenced by both the distance between habitat patches (or host plant fields) and the amplitude of temporal fluctuations of the quantity of food resources. These two factors were also found to be important in the present paper. When we try to identify mechanisms of population fluctuations of any animals, it is important to consider the following factors: habitat structure (e.g., the ratio of complete habitat patches to incomplete ones, the distances between habitat patches), the relative abundance of resources necessary for each generation in each habitat patch, and dispersal power and the reproductive rate per time of animals.

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Appendix 1.

$$\hat{N}_{b(g,k,x)} = \hat{N}_{T(g)} n_{b(g,k,x)} / n_{b(g)}, \quad (1)$$

where,

$n_{b(g,k,x)}$: the number of pupal exuviae collected from host plant x in patch k in generation g ;

$n_{b(g)}$: the number of pupal exuviae collected from the whole study area in generation g .

$$\hat{N}_{a(g,k,x)} = \frac{\hat{N}_{T(g)} \sum_{h=1}^2 \tau_h \sum_{j=1}^2 (\tau_j (n_{j(g,k,x)} / \hat{P}_j + n_{j+1(g,k,x)} / \hat{P}_{j+1}))}{\sum_{j=1}^2 \tau_j \sum_{h=1}^2 (\tau_h (n_{h(g)} / \hat{P}_h + n_{h+1(g)} / \hat{P}_{h+1}))}, \quad (2)$$

where,

$n_{h(g)}$: the number of adults caught in generation g in the whole study area on sample day h ($h=1, 2, 3$) which consists of three consecutive points of capture including the peak of adult number in order to maximize the value of total adult-days during the period of $h=1$ to $h=3$;

$n_{j(g,k,x)}$: the number of adults caught on host plant x in patch k in generation g on sample day j ($j=1, 2, 3$) which was given by the same method as n_h ;

\hat{P}_h, \hat{P}_j : probability of capture for adults on sample day h or j estimated by the Jolly-Seber method;

τ_h, τ_j : days elapsed between sample day h (or j) and $h+1$ (or $j+1$).

When s is described in item k in equation (1) and (2), s means either all P-E patches or all E patches in the study area.

Appendix 2.

$$\hat{N}_{(g,k,x)} = \frac{\sum_{i=1}^{t-1} \tau_i (n_{i(g,k,x)} + n_{i+1(g,k,x)})}{2\hat{P}_g \sum_{i=1}^{t-1} \tau_i}, \quad (3)$$

where,

$n_{i(g,k,x)}$: the number of adults caught on host plant x in patch k on sample day i ($i=1, 2, 3, \dots, t$) during the period of the generation g ($g=0, 1, 2$);

τ_i : days elapsed between sample i and $i+1$,

\hat{P}_g : mean probability of capture for adults during the generation g estimated by Jolly-Seber method.