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Population Dynamics of a Phytophagous Lady-beetle, *Epilachna vigintioctopunctata* (FABRICIUS) (Coleoptera: Coccinellidae), Living in Spatio-temporally Heterogeneous Habitats

II. Seasonal Changes in Adult Movement and Spatial Distribution of the Population

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The population process of the phytophagous lady beetle, *Epilachna vigintioctopunctata*, was studied in spatio-temporally heterogeneous habitats in order to clarify the seasonal changes in interpatch movement of adults, density effect on the movement, and the effect of the movement on the spatial distributions of the population. The population censuses were carried out for three years in an area of about 15 ha containing 18 distinguishable patches of host plants. The rate of interpatch movement of females tended to be highest in the first generation adults, moderate in the second generation adults, and lowest in the overwintered adults. The movement rate of females tended to increase incrementally with adult density. This density-dependent interpatch movement of females which accompanied mortality in the dispersal process reduced the patch variation in the densities of females and eggs, and was thought to be the most important foctor in stabilizing the yearly fluctuation of population density.

Key words: interpatch movement, density-dependent movement, food resource, mechanism stabilizing population fluctuation, regulatory process

INTRODUCTION

The habitats of most animal species are heterogeneous and discontinuous in both time and space (ELTON, 1949; IWAO, 1971a; SOUTHWOOD, 1977), and animals must often move to utilize resources essential to their survival and reproduction. Some field studies have shown that adult mortality is a key factor in the fluctuation of insect population density and that adult movement might play an important role in density-dependent regulatory processes of the population (e.g., HARCOURT, 1963, 1971; KUNO and HOKYO, 1970; IWAO, 1971a; SOUTHWOOD and READER, 1976; NAKAMURA and OHGUSHI, 1981, 1983; OHGUSHI and SAWADA, 1985). In order to clarify the role of the adult movement in insect populations, it is also important to take account of effects of adult movement on changes in spatial distribution of the populations (e.g., IWAO, 1971a).

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The population process of the lady-beetle, *Epilachna vigintioctopunctata* (Fabricius), was studied for three years in an area including 18 patches of host plants. In a previous paper (Hirano, 1985 a, 1985 b), I showed that the amplitude of the yearly fluctuation of adult density was small, and pointed out the importance of adult movement as a mechanism stabilizing population fluctuations. The present paper reports on seasonal changes in adult movement, the relationship between the movement rate and adult density, and the effect of the movement on spatial distributions of the successive developmental stages in the population.

MATERIALS AND METHODS

Study area. The population censuses were carried out from 1976 through 1978 in an area of about 150,000 m^2. 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 patchily distributed in the study area. *E. vigintioctopunctata* oviposited mainly on potato, eggplant and ground cherry. However, the area covered with ground cherry in the study area was less than that covered with only 15 eggplants. The major host were potato and eggplant. The total numbers of potato plants and eggplants in the study area were respectively 4064 and 346 in 1976, 3136 and 352 in 1977, and 3636 and 440 in 1978, a relatively constant supply of food resources.

The small fields were culstered in 18 patches shown in Fig. 1. Each patch consisted of one or more small cultivated fields. Patches ranged from 25 to 900 m^2 in area, and were 20–125 m away from the nearest one. Patches No. 3 and 4 in Fig. 1

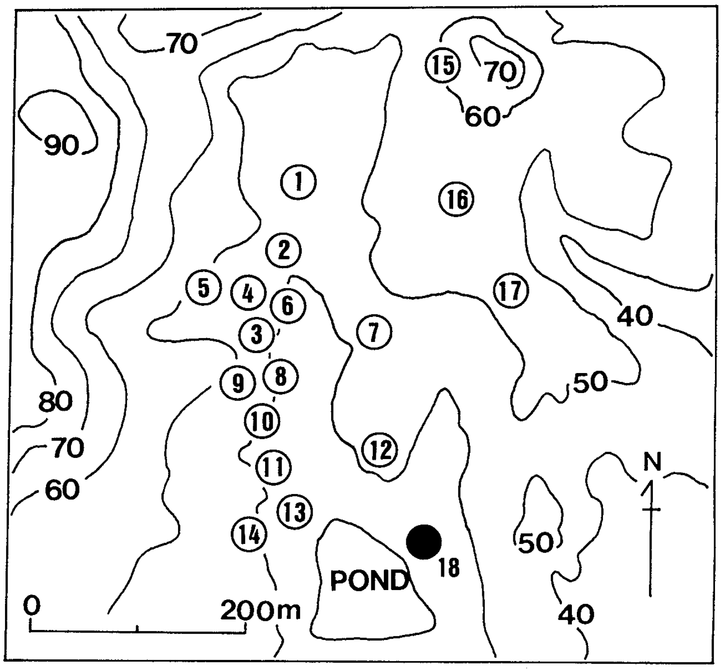

Fig. 1. Map of the study area. Circles indicate patches of host plants.

were combined to analyze data on movement, because the distance between them was only 20 m without apparent barriers (e.g., tall trees or housing). All 18 patches were examined in 1976. Patch No. 18 was not examined in 1977 and 1978. More detailed description of the study area is given in Hirano (1985 b).

Census method. E. vigintioctopunctata repeated two generations per year. The second generation adults emerged in late July to early August, and overwintered without oviposition. Overwintered adults, i.e. overwintered second generation adults, appeared in potato fields and began to lay eggs in early May. The first generation adults emerged in late June to early July. Since the harvest time of potatoes coincided with the period of adult emergence, the first generation adults moved to fields of eggplant and other solanaceous crops. They oviposited mainly on eggplant.

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, 1985 b).

The numbers of eggs and pupae were counted every tenth day in every patch from 8 June to 1 September in 1978. Locations of egg masses and pupae were marked to avoid double counting. Ten percent of potato plants and all eggplant, tomato and ground cherry in each patch were inspected. Pupal exuviae were collected to estimate the total number of emerged adults.

Analysis of data. (1) *Movement rate.* The rate of interpatch movement, $Im_{(g)}$ ($g=0$, 1, 2 for the overwintered, the first generation, and the second generation adults, respectively), was defined as $Im_{(g)}=r_b/r_c$, where r_b is the total number of individuals recaptured in patches other than the "release" patch and r_c is the total number of individuals recaptured within a month of when adult movement was most frequently observed in each generation. The potatoes were harvested during the period of emergence of the first generation adults. To clarify the effect of the potato harvest on adult movement, the rate of interpatch movement, $Im'_{(1)}$, of the first generation adults that were released on eggplant, tomato and ground cherry plants was also calculated by the same method.

(2) *Adult density in the whole study area.* The total number of adults per generation, $\hat{N}_{T(g)}$, was estimated with the method of Nakamura and Ohgushi (1979) based on parameters obtained by the Jolly (1965) and Seber (1973) methods. For the density of overwintered adults, i.e. $D_{T(0)}$, $\hat{N}_{T(0)}$ was divided by the total number of potato plants in the study area. For the density of the second generation adults, $D_{T(2)}$, $\hat{N}_{T(2)}$ was divided by the total number of eggplants. A detailed description of this method was given in Hirano (1985 b). The total number of the first generation adults which moved from potato to eggplant within the study area, $\hat{N}_{T'(1)}$, was estimated by using the number of the adults caught in the whole study area and that caught on eggplant (see Appendix 1). For the density $D_{T'(1)}$, $\hat{N}_{T'(1)}$ was divided by the total number of eggplants in the whole study area.

(3) *Number of emerging adults per plant in each patch.* The number of adults emerging on host plant x(x=p and e for potato and eggplant, respectively) in kth patch ($k=1, 2, 3, \ldots, 17$) in gth generation ($g=1, 2$), $\hat{N}_{b(g,k,\mathrm{x})}$, was estimated by using the number of pupal exuviae collected from host plant x in patch k (see Appendix 2). For the density $D_{b(g,k,\mathrm{x})}$, $\hat{N}_{b(g,k,\mathrm{x})}$ was divided by the number of potato plants in the first

generation and by the number of eggplants in the second generation.

(4) *Mean daily adult density 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 during the period of each generation. The method of calculation is presented in Appendix 3. To get the density $D_{(g,k,x)}$, $\hat{N}_{(g,k,x)}$ was divided by the number of potato plants for overwintered adults and the number of eggplants for the first and the second generations.

RESULTS

Seasonal changes in adult movements

The mean values of the rates of interpatch movements ($Im_{(g)}$) for three years are shown in Table 1. The mean value was highest in the first generation adults, moderate in the second generation adults, and lowest in the overwintered adults. The movement rates in the first generation adults ($Im_{(1)}$) were significantly higher than those in overwintered adults ($Im_{(0)}$) in both sexes. Although the movement rates in the first generation, excluding the movements from potato plants to other solanaceous plants ($Im'_{(1)}$) became lower than $Im_{(1)}$ in both sexes, they were still significantly higher than those of $Im_{(0)}$. There were no significant differences in the movement rate between the sexes within the same generation ($p>0.05$, F-test).

Figure 2 shows the frequency distribution of moving distances of adults per eight days (the period between two consecutive captures) in 1977. The moving distance of females in the first generation was largest of all generations. On the other hand, the moving distance of males in the first generation (excluding movement from potato plants to other solanaceous plants) was not significantly different from those in other generations. In the case of 1977, the rates of males resident in a field, based on data of two consecutive captures, were as follows: 0.83 in overwintered adults, 0.82 in the

Table 1. Mean value of the rates of interpatch movement in different generations of adults for three years (1976–78)

	Female			Male		
	Mean	S.D.	No. of recaptured	Mean	S.D.	No. of recaptured
$Im_{(0)}$	0.018	0.030	229	0.012	0.021	179
$Im_{(1)}$	0.330[b]	0.087	208	0.221[b]	0.036	333
$Im'_{(1)}$	0.244[a]	0.154	102	0.132[a]	0.109	197
$Im_{(2)}$	0.135	0.036	259	0.091	0.042	299

$Im_{(g)}$: the rate of interpatch movement (g=0, 1, 2 for overwintered, first and second generation adults, respectively).

$Im'_{(1)}$: the rate of interpatch movement of the first generation adults, excluding movements from potato plants to other solanaceous plants.

There were significant differences in the movement rate among generations in each sex ($p<0.01$, ANOVA on arc sin root).

[a,b] The rate was significantly higher than that in overwintered adults (a: $p<0.05$, b: $p<0.01$, Turkey's multiple comparisons on arc sin of root).

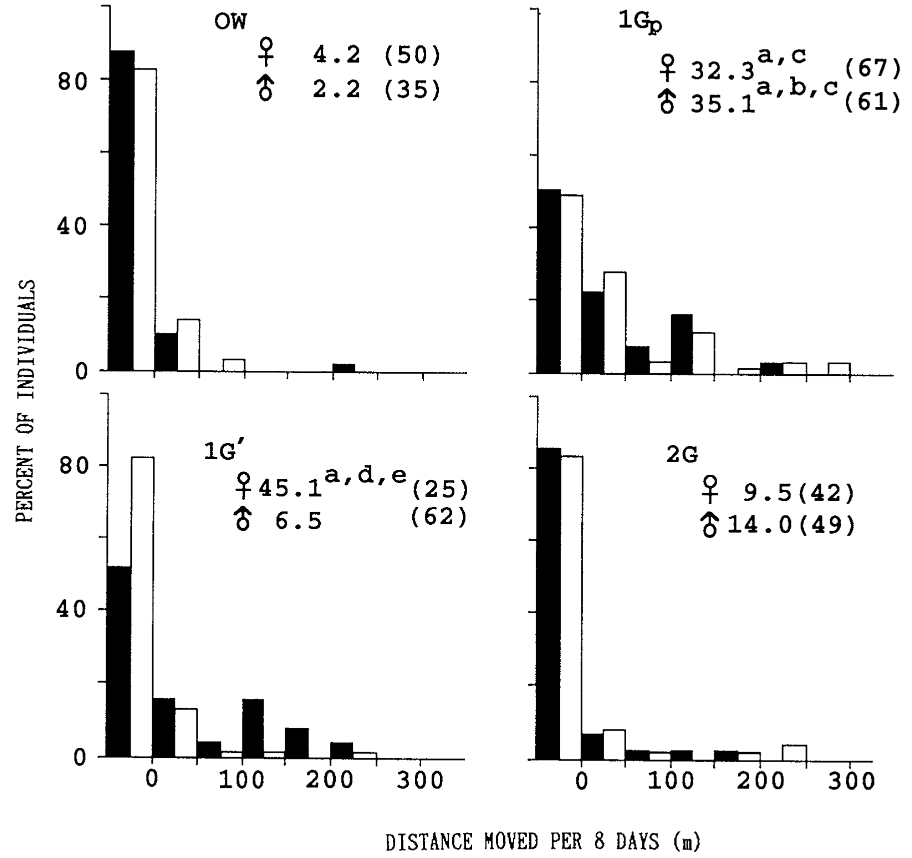

Fig. 2. Frequency distribution of moving distances per 8 days of overwintered adults (OW), the first generation adults that were released on potato plants ($1G_p$), the first generation adults that were released on host plants other than potato (1G′) and the second generation adults (2G) in 1977. The solid and open colums refer to females and males, respectively. The mean distances and the sample sizes in parentheses are given in the figure. The distances per 8 days were significantly different among the generations in each sex ($p<0.01$, Kruskal-Wallis' test). [a] The distance was significantly larger than that in OW ($p<0.01$, Scheffe's multiple comparisons based on rank sums: hereafter, abbreviated as SMCRS). [b] The distance was significantly larger than that in 1G′ ($p<0.01$, SMCRS). [c,d] The distance was significantly larger than that in 2G (c: $p<0.01$, d: $p<0.05$, SMCRS). [e] The females moved significantly farther than the males of the same generation ($p<0.01$, Mann-Whitney U-test).

first generation adults which were found on host plants except potato plants, and 0.84 in the second generation adults. The observed maximum distance of movement per eight days was 250 m in females and 300 m in males.

Relationship between adult density and movement rate

Figure 3 shows relationships between adult density and the rate of interpatch movement. The movement rate of females increased significantly with the increment of adult density in the first and second generation. On the other hand, males did not show such clear and consistent patterns.

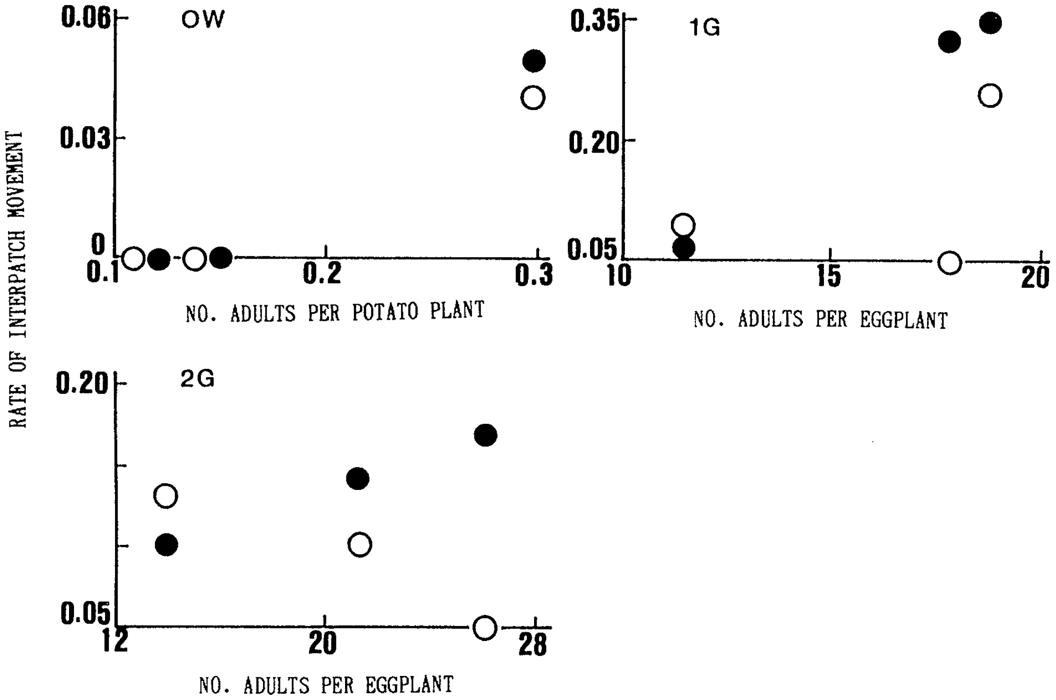

Fig. 3. Relationship between adult density and rate of interpatch movement. The open and solid circles indicate males and females, respectively. $D_{T(0)}$, $D_{T'(1)}$ and $D_{T(2)}$ were used to express the density of overwintered, first generation and second generation adults, respectively. For the rate of interpatch movement of the first generation, $Im'_{(1)}$ was used. After the rates of interpatch movement were transformed to arcsin, correlation coefficients (r) of the two variables were calculated for females. Overwintered female (OW): $r=0.988$, $p>0.05$; The first generation female (1G): $r=0.999$, $p<0.05$; The second generation female (2G): $r=0.999$, $p<0.05$. See text for explanation of parameters such as $D_{T(0)}$ and $Im'_{(1)}$.

Changes in spatial distribution of successive developmental stages among patches

Following a proposal of Iwao (1971 b), variance of the logarithmically transformed insect density (log of the number of insects per hill to the base ten) was used as an index of interpatch variation in the density. To avoid negative infinity, the value of 1/100 of mean density of a given stage was added to each density before taking the logarithm.

Figure 4 shows the changes in the variance of log density among patches for successive developmental stages. The interpatch variance in density increased from the overwintered adult stage (OW) to the adult emergence in the first generation ($N_{(1)}$). The variance in the first generation adults resident on eggplant ($A_{(1)}$) was much smaller than that of the preceding stage ($N_{(1)}$). This resulted in small variance in the second generation egg stage ($E_{(2)}$). The variance increased again from egg to pupal stage of the second generation ($P_{(2)}$). Then the variance in the second generation adults resident on eggplant ($A_{(2)}$) again decreased drastically.

DISCUSSION

The rates of interpatch movements in the first generation adults ($Im'_{(1)}$) were still significantly higher than those in the overwintered adults in both sexes even though

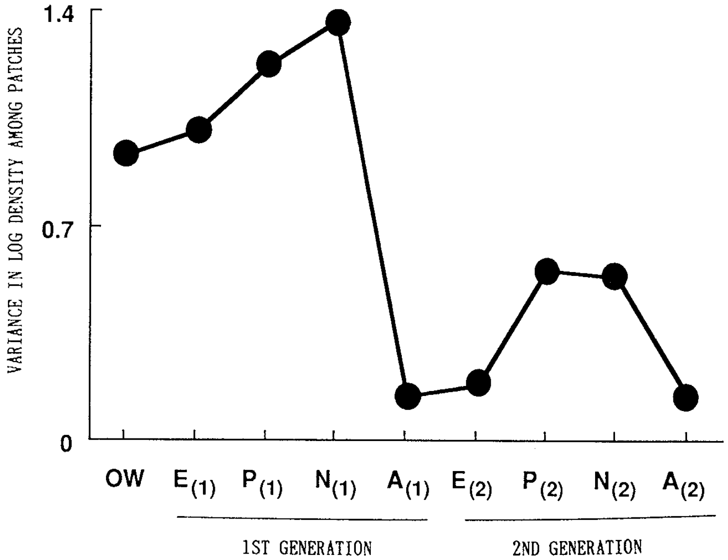

Fig. 4. Changes in interpatch variance of the logarithm of density (per plant) of the successive developmental stages from overwintered adults (OW) to the second generation adults. E: egg, P: pupa, N: emerging adult, OW and A: resident adult on host plant. The densities of egg and pupa were expressed by the number per potato plant in the first generation and per eggplant in the second generation. $D_{b(g,k,x)}$ and $D_{(g,k,x)}$ were used to express the density of emerging adults and the mean density of resident adults in each patch, respectively.

the effects of harvesting potatoes was excluded (Table 1). The values of $Im'_{(1)}$ were also demonstrated to be significantly higher than those in the second generation adults in another study area where host plants were artificially dispensed in 16 small patches (Hirano, 1985 a).

The following factors which might influence the rate of interpatch movement were examined: (1) physiological condition for movement, (2) patch size, (3) difference in main host plant (potato for overwintered adults; eggplant for the first and second generation adults), (4) adult density.

Overwintered and first generation adults were in a reproductive stage. Only the former had experienced diapause when overwintering. The second generation adults fed vigorously on eggplant to develop their fat body for overwintering. They mated and entered into diapause without oviposition. Thus there would be some physiological differences among the overwintered, first generation and second generation adults in relation to movement.

The interpatch movement of the overwintered adults was the lowest among generations (Table 1). The overwintered adults inhabited larger patches than other generation adults: mean numbers of potato plants for the overwintered adults and eggplants for other generation adults per patch were 360 and 26 in the study area, respectively. In another study area where the mean number of potato plants per patch was 25, the rates of interpatch movement of overwintered adults, whose density was low, were also very low (Hirano, 1985 a). Therefore, patch size would not be an important factor influencing the emigration rate of overwintered adults residing in a patch.

I examined whether much difference in the movement rate between overwintered and first generation adults was due to difference in main host plants. NAKAMURA et al. (1988) investigated the population of *E. vigintioctopunctata* in an eggplant field (about 120 m^2) with 91 plants in Sumatra, and showed that the maximum density of adults and the value of daily rate of residence within the study area were about 0.60 per plant and more than 0.95 during the first two months of the study period, respectively. In my study area, adult densities and the mean rates of residence were 0.12–0.30 per potato plant and 0.96 in overwintered adults, and 11.6–18.8 per eggplant and 0.825 in the first generation adults, respectively (HIRANO, 1985 b). These results suggest that when adult density was low, the rate of resident adults was high in the eggplant field as well as in the potato field.

The rate of interpatch movement of females in each generation tended to increase with increases of adult density, but that of male did not (Fig. 3). When adult density increased, the average number of eggs laid by females also decreased (NAKAMURA, 1976; HIRANO, 1985 a). These results may indicate that the rate of interpatch movement of females is determined as a function of adult density, enhancing feeding efficiency and survival rate of offspring. On the other hand, males did not show such a simple correlation between adult density and the movement rate. The movement rate of males may be influenced by feeding efficiency and probability of finding mates.

The smaller variation in density of resident adults among patches as compared with that in emerging adult density suggests density dependence of interpatch movement (Fig. 4). Interpatch movement of females was density-dependent (Fig. 3).

The amplitude of the yearly fluctuations of adult density of *E. vigintioctopunctata* was very small: the ratio of maximum to minimum density during the study period fell between 1.4 and 2.9 in each generation (HIRANO, 1985 b). The population density would not stabilized without any regulation mechanisms. Mean disappearance rates of adults per day in the study area during three years, which include death and emigration, were 0.036 in overwintered adults, 0.175 in the first generation adults, and 0.091 in the second generation adults (HIRANO, 1985 b). This indicates that the mean disappearance rate was higher in the generation when the rate of interpatch movement of adults was higher (Table 1). Taking into account the reduction of the interpatch variance of density in adult stages, therefore, it seems likely that the density-dependent movement of females accompanied with mortality in the dispersal process is the most important mechanism to stabilize the yearly fluctuation of population density.

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APPENDIX 1

$\hat{N}_{T'(1)}$ was estimated as follows.

$$\hat{N}_{T'(1)}=\frac{\hat{N}_{T(1)}\sum_{h=1}^{2}\tau_h\sum_{j=1}^{2}\left(\tau_j\left(n_{j(\mathrm{e})}/\hat{P}_j+n_{j+1(\mathrm{e})}/\hat{P}_{j+1}\right)\right)}{\sum_{j=1}^{2}\tau_j\sum_{h=1}^{2}\left(\tau_h\left(n_h/\hat{P}_h+n_{h+1}/\hat{P}_{h+1}\right)\right)}$$

where,

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

$n_{j(e)}$: the number of the first generation adults caught on eggplant in the entire study area on sample day j ($j=1, 2, 3$) (same method used as n_h),

$\hat{P}_h$, $\hat{P}_j$: probability of capture for adults on sample day h or j estimated by JOLLY-SEBER method,

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

APPENDIX 2

$\hat{N}_{b(g,k,\mathrm{x})}$ was estimated as follows.

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

where,

$n_{b(g,k,\mathrm{x})}$: 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.

APPENDIX 3

$$\hat{N}_{(g,k,\mathrm{x})}=\frac{\sum_{i=1}^{t-1}\tau_i\left(n_{i(g,k,\mathrm{x})}+n_{i+1(g,k,\mathrm{x})}\right)}{2P_g\sum_{i=1}^{t-1}\tau_i}$$

where,

$n_{i(g,k,\mathrm{x})}$: the number of adults caught on host plant x in patch k on sample day i ($i=1, 2, 3, \ldots, t$) 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.