POPULATION DYNAMICS OF A PHYTOPHAGOUS LADY-BEETLE, *HENOSEPILACHNA VIGINTIOCTOPUNCTATA* (FABRICIUS), LIVING IN SPATIO-TEMPORALLY HETEROGENEOUS HABITATS. I. ESTIMATION OF ADULT POPULATION PARAMETERS BASED ON A CAPTURE-RECAPTURE CENSUS[1]

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INTRODUCTION

The habitats of most animal species are heterogeneous and discontinuous in time and space. They usually consist of many 'patches', relatively isolated units of habitats including food and other resources. It has been pointed out, therefore, that studies on the population should be carried out with due consideration for the patchy nature of habitats according to two dimensions, time and space (e.g., HUFFAKER, 1958; GADGIL, 1971; LEVIN, 1976; SOUTHWOOD, 1977; TAYLOR and TAYLOR, 1977).

Among phytophagous lady-beetles of the genus *Henosepilachna*, field population studies from the above mentioned viewpoint have been made on *H. vigintioctomaculata* (IWAO, 1971) and *H. pustulosa* (NAKAMURA and OHGUSHI, 1979, 1981; OHGUSHI and SAWADA, 1981). Two allied species, *H. vigintioctopunctata* and *H. vigintioctomaculata*, both of which are pests of solanaceous crops such as potato plants and egg-plants, are distributed in the southern and northern parts of mainland Japan, respectively. The former species usually goes through two generations per year but the latter has one generation. *H. pustulosa* is not a pest, since it feeds mainly on thistles growing in mountainous areas, and has one generation per year. *H. pustulosa* is closely related to *H. vigintioctomaculata* and nearly sympatric with the latter in the northern part of distribution range. The spatio-temporal population dynamics of *H. vigintioctopunctata*, which is little studied so far, is needed to make a comparative study on ecological relationships among these three species and to clarify why *H. vigintioctopunctata* and *H. vigintioctomaculata* became pests of introduced crop plants.

The present paper is the first of a series of papers on the spatio-temporal dynamics of numbers in a natural population of *H. vigintioctopunctata*. The paper presents some

demographic parameters of adult beetles such as population size, sex ratio, survival rate, longevity and reproductive rate in the whole study area.

MATERIALS AND METHODS

Study Area

The study was carried out in Fujimaki, a suburb of Nagoya City, with wooded hills on all sides except to the south, from May 1976 to June 1979 (Fig. 1). Many groups consisting of one or more small cultivated fields were distributed in the area, and these were designated as 'patches'. Aside from these patches, there was no field of host plants within a distance of 1 km from the area. There are two small patches, where potato plants and egg-plants were cultivated, at 1 km to the east and 1.4 km to the northwest of the study area, respectively. No adult marked and released in the study area was recaptured at those two sites throughout the study period.

The capture-recapture census was carried out in the area (about 150000m²) including patches No. 1 to No. 18 in 1976 and pathces No. 1 to No. 17 in 1977–79. Density of adults was low in patches south of a pond (patches No. 19–No. 26). Some adults moved
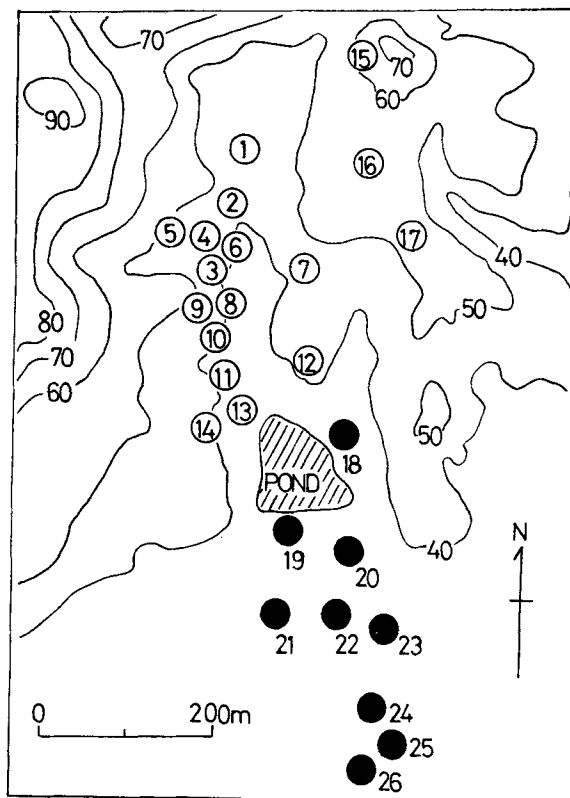

Fig. 1. Map of the study area. Circles indicate patches of host plants. The study was focused on the area of open circles. For other explanation see text.

Table 1. The number of host plants in the study area at the beginning of May.

Patch No.	1976				1977				1978				1979				Remarks
	P*	E*	T*	C*	P	E	T	C	P	E	T	C	P	E	T	C	
1	0	34	27	0	0	27	0	58	0	44	66	107	0	22	37	60	
2	3	6	14	0	15	8	6	0	0	9	9	0	0	6	10	0	
3	11	17	0	0	0	11	2	0	0	8	9	6	0	0	0	0	
4	0	5	0	0	0	5	3	0	0	4	6	0	0	0	0	0	
5	105	38	5	0	77	63	10	0	143	50	3	0	12	50	4	0	
6	0	13	11	0	0	0	0	0	13	9	5	0	12	5	7	0	
7	0	18	18	0	0	20	0	0	0	20	0	0	0	0	0	0	
8	0	0	0	0	27	0	0	0	34	0	0	0	81	0	0	0	
9	81	0	0	0	98	0	0	0	80	0	0	0	98	0	0	0	surrounded by trees
10	1949	15	88	0	1742	17	59	0	2315	28	69	0	1882	28	54	0	near the grove
11	270	22	20	0	390	25	36	0	395	28	20	0	290	26	22	0	
12	266	30	79	0	218	30	78	3	124	24	88	11	191	30	36	0	near the grove
13	0	14	4	0	0	21	5	0	0	21	8	0	0	0	0	0	
14	199	16	10	0	247	28	10	0	264	41	18	0	193	27	0	0	
15	72	35	12	0	0	30	10	0	0	0	0	0	0	0	0	0	
16	74	48	13	0	322	62	15	0	267	135	1	0	392	79	0	0	in a grove
17	0	23	0	0	0	5	0	0	1	19	5	0	42	17	6	0	in a grove
18	1034	12	36	0	—	—	—	—	—	—	—	—	—	—	—	—	
Total	4064	346	337	0	3136	352	234	61	3636	440	307	124	3193	290	176	60	
1st**	0	326	301	0	0	331	234	61	0	440	307	124	—	—	—	—	
2nd**	0	316	301	0	0	331	234	61	0	408	307	124	—	—	—	—	

* P: potato, E: egg-plant, T: tomato, C: cherry ground.

** 1st: the first generation adult stage, 2nd: the second generation adult stage. As the number of host plants which were existing during the first and/or the second generation adult stage was occasionally different from the number counted at the beginning of the census, the total number of host plants in each generation was shown. These numbers were used when adult density was calculated.

from patches north of the pond to ones south of the pond, but the reverse was rare. The numbers of host plants in the study area are shown in Table 1. The number of host plants was stable throughout the study period.

Census Method

For the adult census, every patch in the study area was examined at intervals of eight days as a rule throughout the study period. All the patches were examined within a single day. But during the peak of adult emergence, six days were needed in 1976 for the examination of all patches and two or three days in 1977–78.

All the adults taken by hand on host plants were marked individually at the time of first capture, except 29 June 1978 when only 57% of captured adults were marked. Although marking was usually done by piercing the elytra with a sewing needle (0.4 mm in diameter), teneral adults (two or three days after emergence) were marked with lacquer paints, because it was difficult to mark with the needle without injury. These beetles were marked again with the needle when they were recaptured. Neither method had any harmful effect on the survival of marked adults (HIRANO, 1981). Adults captured or recaptured were released on the same plant on which they were caught.

RESULTS

The capture-recapture data were analyzed by the method described by JOLLY (1965) and SEBER (1973). Data for both sexes were combined because there were no significant differences in survival rates and capture rates between sexes.

Seasonal Population Trends

Seasonal fluctuations of the numbers of adults actually found on host plants (n_i) on ith sample day ($i=1, 2, 3, ..., t$) and the estimated numbers of adults (N_i) which inhabited the study area from 1976 to 1978 are given in Fig. 2. Overwintered adults appeared in potato fields and began to lay eggs early in May. The first generation adults emerged late in June to early in July. The potatoes were harvested during the period of adult emergence. Then the emerged adults moved to fields of egg-plants, tomatoes and some other crops, but oviposited mainly on egg-plants. The second generation adults emerged late in July to early in August. These adults migrated to overwintering sites without oviposition around the end of August. The overwintered adults and the first generation adults are considered to be in a reproductive stage. Some adults survived till the period of emergence of the next generation, and some of them (unmarked) could not be distinguished from new adults. Therefore the estimation of adult numbers was discontinued when new adults were captured (see Fig. 2). Data on the unmarked old adults were included in the estimates of the number of new adults, but as the number of these old adults was far smaller than that of new ones, the degree of overestimation might be almost
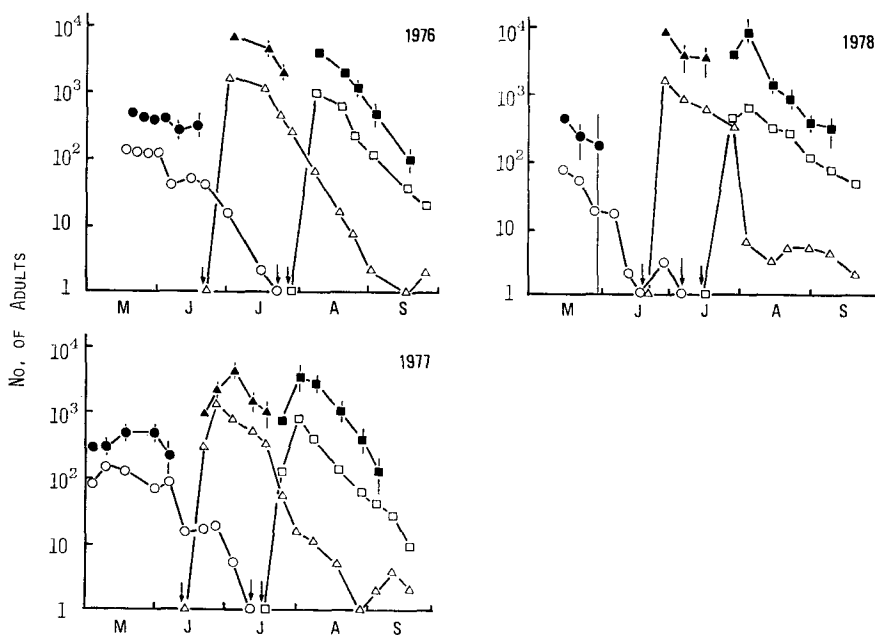
Fig 2. Fluctuations of the numbers of adults counted on each census date (open symbols) and the estimated numbers of individuals inhabiting the study area (closed symbols). Circles, triangles and squares show the numbers of overwintered, the first and the second generation adults, respectively. Vertical lines represent standard errors, and arrows represent zero.

negligible. As shown in Fig. 2, the patterns of seasonal fluctuations of adult numbers were similar throughout the study period.

Daily Survival Rate and Mean Longevity

Since emigration and death could not be separated in this study, I use terms, 'survival' and 'longevity', to mean 'residence' and 'length of resident time' within the study area, respectively.
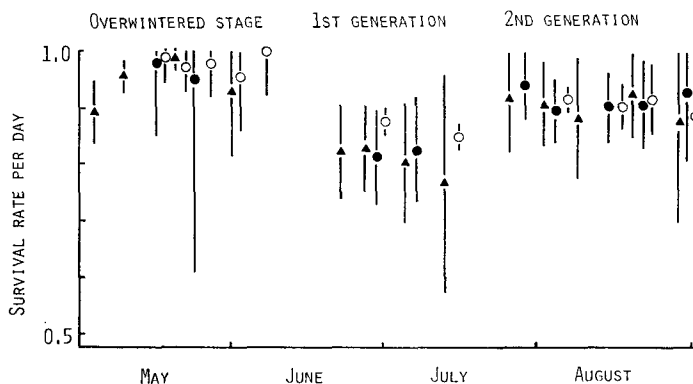

Fig. 3. Daily survival rates of adults estimated by JOLLY-SEBER model in 1976 (○), 1977 (▲) and 1978 (●) Vertical lines represent 95% confidence limits.

Table 2. Mean survival rate per day $(\hat{\phi}_m)$ and mean longevity (L) of adults during the three years.

Generation	$\hat{\phi}_m$	L (days)
Overwintered adults	0. 964	27. 8
1st generation adults	0. 825	5. 7
2nd generation adults	0. 909	11. 0

Estimated daily survival rates of adults are shown in Fig. 3, where 95% confidence limits of the survival rates were calculated by the method of NAKAMURA and OHGUSHI (1979). The values of mean survival rates per day, $\hat{\phi}_m$, and mean longevity, L, for three years are shown in Table 2. Mean longevity (L) was obtained by the equation: $L=1/(1-\hat{\phi}_m)$.

Adults of the first and second generations were seen to be caught and killed by farmers in a few patches. The number of the adults killed and the date of death were recorded, however, because the farmers agreed to keep the adults they killed in glass bottles which they gave to me every census date. The numbers of adults killed by farmers were 1.3–6.6% of the total number of adults estimated per generation $(\hat{N}_T)$, and its effect on daily mortality rates was, in most cases, less than 1%. Therefore, the effect of the number of adults killed by farmers on the whole population was considered to be negligible.

Among reproducing stages, the mean survival rate per day of overwintered adults

Table 3. Total number of marked adults (M_T), sex ratio (proportion of females), estimated number of adults emerged per generation $(\hat{N}_T)$ and the rate of female increase per generation (R).

	M_T*				$\hat{N}_T$	$\hat{N}_T$/plant**	R
	female	male	total	sex ratio			
1976							
Overwintered adults	191	151	342	0. 56	601	0. 15	
1st generation	1225	1533	2758	0. 44	13958	42. 8 (3. 43)	20. 74
2nd generation	811	932	1743	0. 47	4450	14. 1	0. 32
1977							
Overwintered adults	252	145	397	0. 63	934	0. 30	
1st generation	1530	1558	3088	0. 50	13796	41. 7 (4. 40)	11. 72
2nd generation	709	741	1450	0. 49	7096	21. 4	0. 51
1978							
Overwintered adults	81	44	125	0. 65	427	0. 12	
1st generation	1247	1205	2452	0. 51	17583	40. 0 (4. 83)	31. 68
2nd generation	786	762	1548	0. 51	10690	26. 2	0. 61
1979							
Overwintered adults	112	101	213	0. 53	1125	0. 35	

* The number of adults killed by handling were included in M_T.

** Densities (number/potato plant, in overwintered adults; number/egg-plant, in the first and the second generations; Figures in parentheses indicate number/potato plant in the first generation only.)

was much higher than that of the first generation adults (Table 2). This may be due to difference in physiological conditions between overwintered and the first generation adults. Two factors were also considered to be responsible for this difference. (a) As the number of overwintered adults per potato plant was smaller than that of the first generation adults per egg-plant (Table 3), overcrowding might have lowered adult survival rate in the first generation through dispersal (e.g., IWAO, 1971). (b) The harvest of potato plants during the adult emergence period of the first generation might have affected the survival rate, as the adults were faced with a risk of migration from the potato plants to other solanaceous plants.

Sex Ratio

The sex ratio, the ratio of females in the whole population of each generation, was calculated by using the numbers of females and males marked per generation (Table 3). The sex ratio of overwintered adults was higher than 0.5 in every year. Sex ratios of the first and second generation adults fluctuated around 0.5. In general, the sex ratios of the first and second generations seemed to be nearly 0.5.

Total Number of Adults Emerged per Generation and Rate of Increase of Female Adults per Generation in the Whole Study Area

The total number of adults emerged per generation, $\hat{N}_T$, was estimated with the method described by NAKAMURA and OHGUSHI (1979):

$$\hat{N}_T = \hat{N}_1 + \sum_{i=1}^{t-1} \left(\frac{\hat{\phi}_i \ln \hat{\phi}_i}{1-\hat{\phi}_1} \hat{N}_T - \frac{\ln \hat{\phi}_i}{1-\hat{\phi}_i} \hat{N}_{i+1} \right)$$

where

$\hat{N}_{i+1}$: the number of adults on the $i+1$th sample day $(i=1, 2, 3, ..., t)$ estimated by JOLLY-SEBER method,

$\hat{\phi}_i$: JOLLY-SEBER survival rate between the ith and $i+1$th sample days,

$\hat{N}_1$: the estimated number of adults on the first sample day, i.e., the number of adults captured in the first sample (n_i) divided by average sampling ratio during the period of the generation.

Total numbers estimated by the above equation are shown in Table 3 together with the rate of increase of adult females per generation (R). As the sex ratio was about 0.5 in the first and second generations, the rate of increase was calculated simply by dividing $\hat{N}_T$ of the latter generation by $\hat{N}_T$ of the former. However, as the sex ratio of overwintered adults was biased to females, the rate of increase from overwintered adutts to the first generation adults was calculated as follows; $\hat{N}_{T(1)} \times 0.5/(\hat{N}_{T(0)} \times$ sex ratio of overwintered adults shown in Table 3). Here, $\hat{N}_{T(0)}$ and $\hat{N}_{T(1)}$ are $\hat{N}_T$ of overwintered adults and the first generation adults, respectively. Adult densities per host plant were also shown in Table 3. Here, the number of potato plants (shown in Table 1) was used to calculate density of overwintered adults and the first generation adults. The

number of egg-plants was used for the first and second geneartion adults. $\hat{N}_T$ per potato plant in the first generation (shown in parentheses in Table 3) was used in calculating the amplitudes of the yearly fluctuation of adult densities. The amplitude was expressed as the ratio of the highest density to the lowest density in each generation.

The amplitudes of the yearly fluctuations of adult densties were not large; e.g., 2.9 in overwintered adults, and 1.4 and 1.9 in the first and the second generation adults, respectively (Fig. 2, Table 3).

Density of overwintered adults (0.12–0.35) was much lower than that of the first or the second generation adults (40.0–42.8 and 14.1–26.2, respectively). The rate of increase (R) from overwintered adults to the first generation adults was consistently higher than R from the first to the second generation. The higher the adult density, the lower the rate of increase tended to be (Table 3). These results suggest a density effect on the rate of increase (R). However the density dependent decrease in the reproductive rate was not necessarily attributed to starvation. In order to find out whether starvation is important, the numbers of egg-plant leaves more than 10 cm long were counted in the whole study area from 1977 to 1978. If more than 50% of the area of a leaf had been damaged by the adult beetles and the larvae, it was regarded as a damaged leaf. The mean ratios and the standard deviations of damaged leaves per patch in the whole study area on 5 August, 1977 and 1 August, 1978, around the peak of emergence of the second generation adults, were as follows: 0.24±0.09 in 1977 and 0.63±0.18 in 1978. In 1977, the ratio of damaged leaves was lower but the rate of increase (R) was lower than that in 1978.

Hibernation

Throughout the study period, 10 of females which had been marked and released in the previous year were recaptured in the following year. No males were recaptured. Four of those females were the first generation adults. One female which was first captured on 9 August, 1977 was recaptured on 9 August, 1978; i.e., it survived for one year. Although adults of the first generation as well as those of the second generation were able to overwinter, diapause in these first generation adults did not seem to be evoked simply by the influence of day-length (see DISCUSSION). The number of recaptured overwintered adults which were marked in the previous year was significantly smaller than the number expected from average marking ratio during the period of the second generation of the previous year, under the assumption that there was no immigration into the study area during periods of the pre- and post-diapause (χ^2-test; $p<0.005$). In the field cage experiments, there was no difference in the overwintering rate between marked and unmarked adults (HIRANO, unpublished). Therefore, the discrepancy between the number of recaptured adults and its expected value suggests the population interchange between the study area and other sites during periods of the pre- and post-diapause movement.

DISCUSSION

NAKAMURA (1976a) and NAKAMURA and OHGUSHI (1979, 1981) wrote that the fluctuation of the population density of *H. vigintioctopunctata* was violent as compared with *H. pustulosa*, because the former species lacked an effective regulation mechanism and therefore frequently reached a density level at which severe starvation occurs. It was shown, however, that the population of this species was rather stable in my study area throughout the study period (Fig. 2, Table 3). This difference may be explained as follows. In NAKAMURA's (1976a) study, the fluctuations in population density were studied in a restricted site, namely, a single patch in the environment. In contrast, my study area consists of many patches of host plants, among which frequent inter-patch dispersal takes place (HIRANO, unpublished). The number of host plants in his study area approximates the number on patch No. 12 in my study area. Although the beetles seriously injured host plants in some patches throughout the whole area, more than one third of egg-plant leaves remained free from attack even at the height of the infestation. The population density in the whole study area was thus stable without food depletion, although the fluctuations in some patches were violent (HIRANO, unpublished).

IWAO (1971) suggested that the number of *H. vigintioctomaculata* in each subpopulation tended to be stabilized by population interchanges among patches and density-dependent adult mortality (possibly losses involved in dispersal process). NAKAMURA and OHGUSHI (1981) showed that the stabilization of population size of *H. pustulosa* was attained through density-dependent regulatory processes operating in inter-patch dispersal and in oviposition. Other field experiments of *H. vigintioctopunctata* showed that the number of eggs laid per female and the females remaining in a patch tended to decrease with increasing adult density (HIRANO, 1985). The beetle density seems to be stabilized through density dependent change in fecundity and adult dispersal, probably including mortality during dispersal.

CLARK et al. (1967) showed that relatively long distances among host trees (that is, a relatively low density of host plants) were responsible for the stabilization of psyllid numbers at high mean levels. Dispersal power of insects, the distances between habitats (patches), and the structure within the habitat would have important effects on the stabilization and the level of population numbers.

YASUE and KAWADA (1964) showed that, in Okayama (34°41' N), located at about the same latitude with Nagoya (35°10' N), some adults of *H. vigintioctopunctata* entered into diapause at less than 15 h day-length at 25°C and all entered diapause at day-lengths less than 13 h at 25°C. Diapause was determined in the first 5 days after adult emergence (KONO, 1980). Since the day-length is 14.9 h on 10 July and 14.7 h on 20 July (including 0.5 h of periods of dawn and dusk) at Nagoya, some of the first generation adults may enter into diapause. In fact, some of the first generation adults were recaptured in the following spring. However, not only the day-length but also adult density can affect the ratio of diapausing adults in the first generation. NAKAMURA (1976b) showed, in

field cage experiments, that many of the first generation adults did not lay eggs in the year of emergence but entered into diapause when the adult density was more than 32 individuals per egg-plant. He also showed that all the adults which laid eggs in the year of emergence died before autumn; i.e., the completion of oviposition led to death, whereas high density interaction led to diapause instead of oviposition. In some species other than phytophagous lady beetles, diapause has also been observed to be evoked by food conditions or overcrowding even under temperature and photoperiod conditions preventing the diapause (e.g., LEES, 1953; DANILEVSKII, 1961; IWAO, 1962; KISHINO and SATO; 1975). Therefore, some of the marked females of the first generation recaptured in the following year are probably those individuals that entered into diapause after overcrowding and/or by feeding on heavily infested leaves even under a long photoperiodic condition.

SUMMARY

1. The population processes of the lady-beetle, *Henosepilachna vigintioctopunctata* (F.), were studied from the spring of 1976 to 1979 in an area (about 150,000 m²) including 17 patches of host plants.

2. Amplitudes of yearly fluctuations of adult densities were 2.9 for overwintered adults, and 1.4 and 1.9 for the first and the second generation adults, respectively.

3. The higher the adult density, the lower the rate of increase of the number of adult females to the next generation. However, the density dependent decrease in the reproductive rate was not caused by starvation.

4. The patchy nature of the farmland habitats seemed to have effects on the stabilization of population numbers.

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生息地が不均質で不連続な環境におけるニジュウヤホシテントウの個体群動態の研究
I. 標識再捕法にもとづく成虫個体群のパラメーターの推定

平 野 耕 治

1. 食草がパッチ状に分布している約 15 ha の地域（名古屋市名東区藤巻町）でニジュウヤホシテントウ個体群の調査を1976年から1979年の春にかけて行った．

2. 調査期間を通じて，成虫密度の変動幅は，越冬成虫で 2.9 倍，第 1 世代成虫で 1.4 倍，第 2 世代成虫で 1.9 倍といずれも大きくなかった．

3. 成虫密度が高いほど世代間増加率は低い傾向がみられた．しかし，これは餌不足によって生じたものではなかった．

4. 食草がパッチ状に分布する環境は個体数変動の安定化に大きな影響をもつと考えられた．