Title	Life Cycle Characteristics of a Population of the Phytophagous Ladybird Henosepilachna pustulosa Depending on Two Host Plants (With 19 Text-figures and 6 Tables)
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Citation	= JOURNAL OF THE FACULTY OF SCIENCE HOKKAIDO UNIVERSITY Series . ZOOLOGY, 24(3): 202-225
Issue Date	1986-03
Type	bulletin
URL	http://hdl.handle.net/2115/27697
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Life Cycle Characteristics of a Population of the Phytophagous Ladybird *Henosepilachna pustulosa* Depending on Two Host Plants

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(*With 19 Text-figures and 6 Tables*)

Introduction

Due to the remarkable variation in both morphology and biology, a series of phytophagous ladybirds belonging to *Henosepilachna vigintioctomaculata* complex has been regarded as a suitable material for the study of speciation. On the basis of various sorts of information covering morphology, food habits and their geographic variations, Katakura (1981) classified them into the following two groups: that is, group A with only one species, *H. vigintioctomaculata* (Motschulsky), and group B with three species, *H. pustulosa* (Kôno), *H. niponica* (Lewis) and *H. yasutomii* Katakura, and some populations whose specific status was unsettled. Under field conditions, *H. vigintioctomaculata* depends principally on the potato (*Solanum tuberosum* L., Solanaceae) whereas the most members of group B on several species of thistles (*Cirsium* spp., Compositae) and/or the blue cohosh (*Caulophyllum robustum* Maxim., Berberidaceae) (Katakura, 1981). Among the members of group B, *H. pustulosa* is distributed in Hokkaido except for the eastern and the southernmost parts. This species is replaced in the

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southernmost Hokkaido by the other two species of the same group, *H. niponica* and *H. yasutomii*, that are sympatrically distributed from the southernmost Hokkaido southward to middle Honshu (Katakura, 1981). *H. niponica* mainly depends on thistles, whereas *H. yasutomii* on the blue cohosh. *H. pustulosa* also depends on thistles, but what is known as the Sapporo form or the form P-III (Katakura, 1974a), distributed in the southern part of the range of *H. pustulosa*, depends not only on thistles, *Cirsium kamtschaticum* Ledeb. and its allies, but also on the blue cohosh when this plant grows together with the thistles (Katakura *et al.*, 1977). In the laboratory, it shows a high preference for the cohosh (Hoshikawa, 1984), and also a high survival ratio when reared with this plant (Kurosawa, 1953, Kimura, unpubl.). Thus, P-III shows an intermediate state of host plant utilization between *H. niponica* and *H. yasutomii* that are distributed just south to P-III, and depending respectively on thistles and the blue cohosh.

In order to know how P-III utilizes these two species of host plants, the present study was performed from July, 1977 to October, 1978 on a population of P-III depending on both host plants. Particular attention was paid to the dispersal of adults between the two host plant species and the mortality factors throughout the life cycle on each host plant. Since the 1977 survey was of preliminary nature, the results obtained in 1978 are mainly given, with some reference to those in 1977 when necessary.

Area Studied and Methods

A spot was chosen at Hokkaido National Agricultural Experiment Station in Tsukisamu, the southeastern suburbs of Sapporo city (see Katakura, 1976), in a grove composed of some broad-leaved deciduous trees and adjacent to a little stream. It covered an area of ca. 20×35 m, where ca. 100 stocks of the thistle, *C. kamtschaticum*, and ca. 70 stocks of the blue cohosh were growing (Fig. 1). The thistle stocks in the area were divided into 6 patches and further into 15 subpatches based on their patchy distribution. Similarly, the cohosh stocks were divided into 4 patches and 7 subpatches. Some thistle stocks growing on the opposite side of the stream were not included in the present study. P-III in the area depends on both species of the plants.

Each stock of host plants in the area was numbered and marked with a piece of vinyl tape. The censuses in 1978 were carried out, at 2–3 day intervals in principle, from late April to late September. Throughout the census period, all newly discovered adults were marked individually with colored felt pens or lacquer paints. The adults captured or recaptured were released on the plants on which they were caught. The numbers of eggs, newly hatched larvae, 4th instar larvae, pupae and adults on each stock of the host plants were recorded in every census for the whole study area. In order to avoid the duplication of counts, egg masses and pupae (very often pupated on the leaves of plants other than the hosts) were individually numbered and marked with labels. In making life tables, the
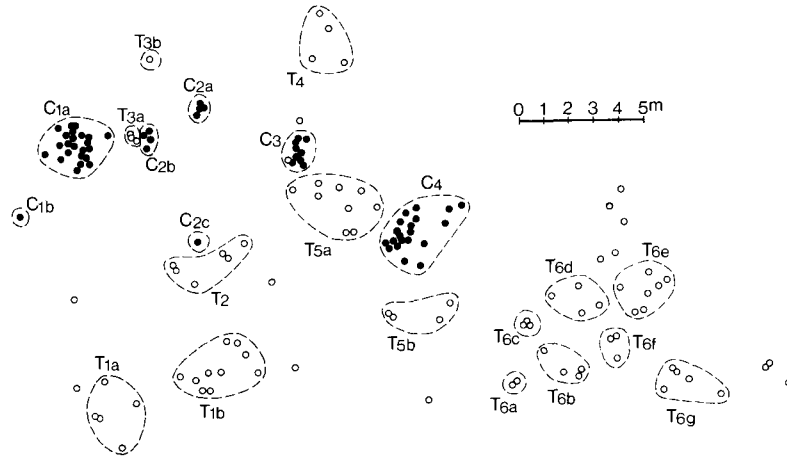
Fig. 1.   Schematic representation of the study area.   Open and solid circles indicate individual stocks of the thistle (T) and the cohosh (C), respectively.   Large broken circles indicate subpatches.

numbers of eggs, first instar larvae, pupae and adults emerged were estimated by eggs laid on, larvae hatched, 4th instar larval exuviae and pupal exuviae, respectively.   The number of 4th instar larvae was estimated by the graphical method given by Southwood and Jepson (1962) as follows: The number of the 4th instar larvae on each census date was plotted against time.   All the points were joined up and the area, in squares, below the line was measured.   This total was divided by the development time in days of the 4th instar larvae that was in the present study estimated at ca. 11 days by the interval between the peak in the number of 4th instar larvae and that of pupae; the resultant value represents the number of individuals reached the mid period of the 4th instar.

Fig. 2 shows the fluctuations of mean air temperatures in the ground of Hokkaido National Agricultural Experiment Station from April to September, 1977 and 1978.   Although the thaw in 1978 began about 2 weeks later than in 1977, the temperatures were highter in 1978 from mid June to late July, the growing period of the beetle larvae.

Results

1.   Life cycles and standing crops of host plants

1.1.   *Life cycles*: The general life cycle trends of the thistle, *C. kamtschaticum*, and the blue cohosh, *C. robustum*, in Sapporo and the vicinity were given in Katakura (1976, 1981) and Hinomizu *et al.* (1981).   The life cycles of these two host plant species in 1978 in the study area were as follows:

Most stocks of the thistle sprouted up in late April soon after the disappear-
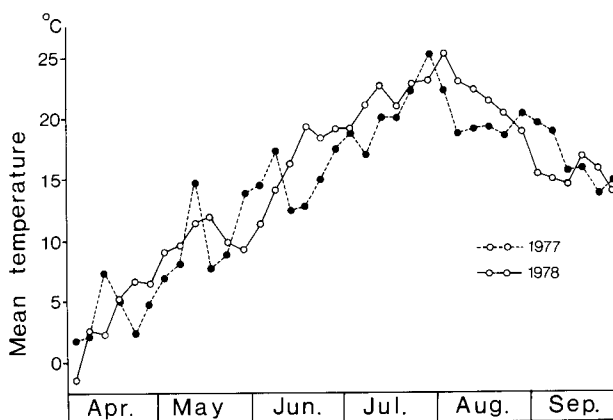
Fig. 2. Mean temperature fluctuations at Hokkaido National Agricultural Experiment Station in 1977 and 1978.

ance of the snow cover, while those of the cohosh sprouted up in early May and unfolded the leaves from mid to late May.   The thistle stocks continued growing until July, and the stems withered up by mid August, while their rosettes grew by early October.   On the other hand, the stocks of the cohosh finished growing and bloomed in early June.   All the cohosh stocks in the area were completely skeletonized by early August owing to the infestation by the beetles, although they could keep the leaves until late September if they were not fed.

1.2.   *Estimation of standing crops of the host plants*: Hinomizu *et al*. (1981) estimated the standing crops of the thistle and the blue cohosh growing in Kobetsuzawa in Sapporo.   They sampled some stocks at about 2 week intervals from May to August.   After they had measured the height (H cm), the broadest breadth (B_1 cm) and the narrowest breadth (B_2 cm) of the stocks, they reaped them and measured the dry weight of the whole (W mg) and that of the leaves (W_v mg).   The relation between the volume ($V = H \times B_1 \times B_2$ cm^3) and W based on 34 stocks of the thistle was given by

$$\log W = 0.82 \log V - 0.09 \qquad (r = 0.90)$$

and the relation between W_v and W by

$$W_v = 0.43\ W.$$

Likewise, the relations based on 41 stocks of the blue cohosh were given by

$$\log W = 0.66 \log V + 0.17 \qquad (r = 0.99),$$
$$W_v = 0.50\ W.$$

They also estimated the standing crop of the rosettes of the thistle.   The length (L cm), breadth (B cm) and dry weight (W_v mg) of a rosette leaf, based on 17 leaves, had the following relation:
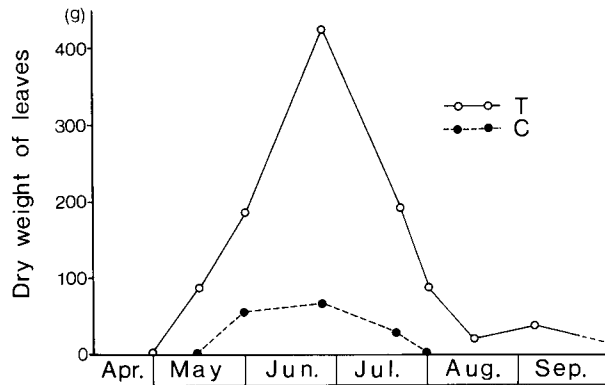
Fig. 3. Seasonal fluctuations in the standing crops of the host plants, the thistle (T) and the cohosh (C), expressed by the dry weight of leaves.

$$W_V = 1.7 \times L \times B + 50.6 \qquad (r = 0.95).$$

All these formulae were applied to the present study. Further, the consumption (C) by the beetles was empirically assessed in 6 grades by eye measurement (0: not injured, 5: entirely fed). Thus, the values of the standing crop were calculated by the following formula:

$$W_V' = W_V \times (1 - C/5).$$

As shown in Fig. 3, the standing crop of the thistle in the survey area in 1978 began to increase from early May, reached the maximum in late June, and then steeply decreased until mid August because of the feeding by the insect and withering. As the rosettes grew up from late July, the standing crop was kept constant from mid August to September. On the other hand, the standing crop of the cohosh began to increase from mid May, reached the maximum in early June and then stopped increasing. From late June it decreased owing to the feeding by the insect, and all leaves were fed up by early August.

2. Life cycle of *H. pustulosa*

The seasonal fluctuation in the number of adults and that of each developmental stage in the whole study area in 1978 are given in Figs. 4-6. Posthibernating adults were first observed on May 10. As mentioned before, the stocks of the thistle sprouted in late April while those of the cohosh in early May, but the leaves of the latter had not been unfolded yet. In mid May, therefore, adult beetles were seen mostly on young thistle leaves, although a few adults were also observed on the cohosh stocks, feeding on the stems and folded leaves. The number of individuals on the thistle reached the maximum on May 20 (Fig. 6A). Unfortunately some thistle stocks were cut down by someone on May 21, so that the number of adults abruptly decreased in late May. It slightly recovered in
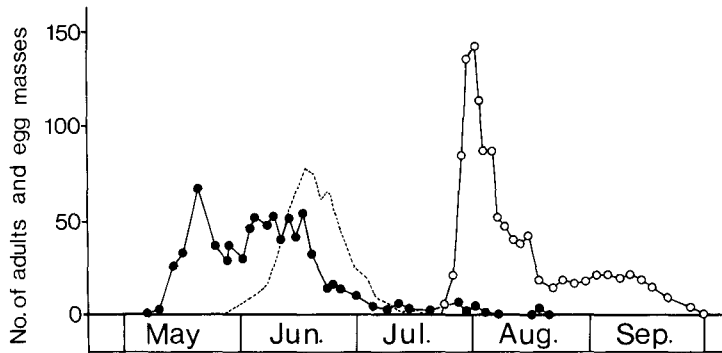
Fig. 4. Seasonal fluctuation in the number of adults. Solid and open circles show the observed numbers of posthibernating adults and newly emerged adults, respectively. The broken line indicates the fluctuation in the number of egg masses.
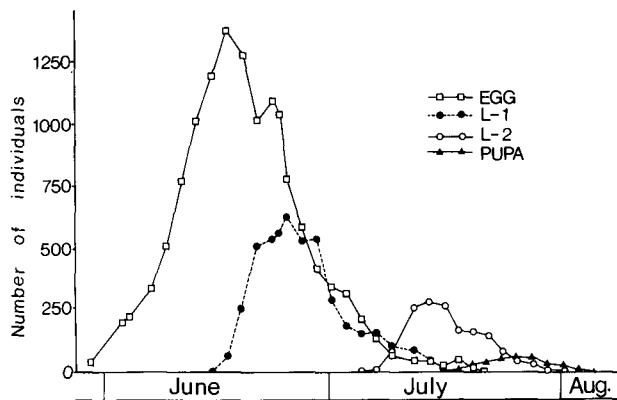

Fig. 5. Seasonal fluctuation in the number of individuals in each developmental stage. Individuals on the thistle and the cohosh combined.

early June and gradually decreased subsequently. On the other hand, most leaves of the cohosh unfolded at the end of May, so that the number of adults on this plant gradually increased and reached the maximum in mid June (Fig. 6A). Thereafter, it suddenly decreased. Most posthibernating adults disappeared in late July. Oviposition took place mainly from early June to early July with the peak of activity in mid June (Fig. 5). The peaks of the numbers of the 4th instar larvae and the pupae came in mid and late July, respectively (Fig. 5), and that of the emergence in early August (Fig. 4). The duration from the egg to the emergence was roughly estimated as 47 days. The numbers of eggs laid on the thistle and the cohosh fluctuated in a similar way (Fig. 6C), whereas the number
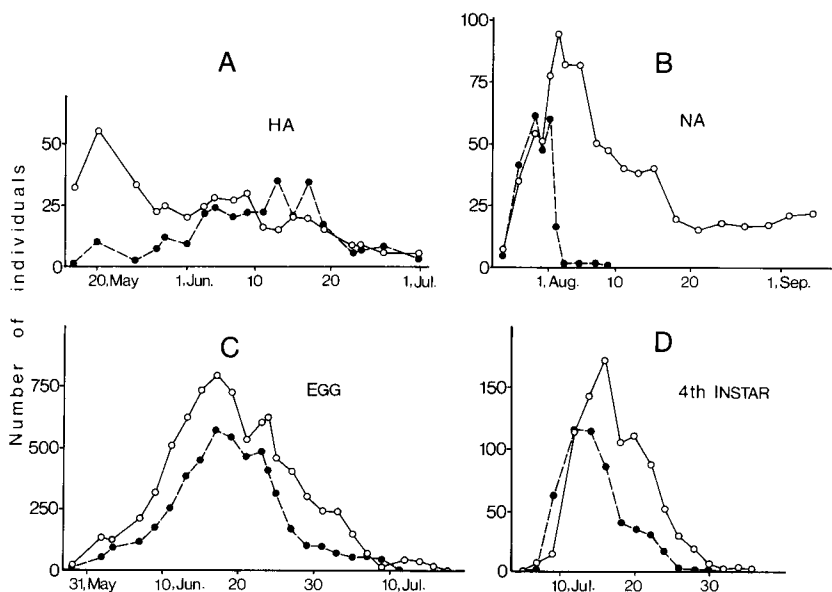
Fig. 6. Seasonal fluctuations in the numbers of posthibernating adults (HA), newly emerged adults (NA), eggs and 4th instar larvae on each host plant. Open and solid circles show the observed numbers of individuals on the thistle and the cohosh, respectively.

Table 1. The numbers of newly emerged adults per stock of the thistle and the cohosh.

	July			August		
	28th	30th	31th	1st	2nd	3rd
Thistle						
No. of adults feeding on	32	55	59	76	93	77
No. of stocks	21	27	28	35	30	24
No. of adults per stock	1.52	2.04	2.11	2.12	3.10	3.21
Cohosh						
No. of adults feeding on	30	57	47	58	16	2
No. of stocks	9	8	8	7	6	2
No. of adults per stock	3.33	7.13	5.88	8.29	2.67	1.00

of 4th instar larvae attained the maximum a little earlier on the cohosh (Fig. 6D). Newly emerged adults were first observed on July 24. The number of them on both the thistle and the cohosh suddenly increased and reached the maximum on August 2 and July 30, respectively (Fig. 6B). As shown in Table 1, they had a tendency to concentrate on a few remaining cohosh stocks. All stocks of the cohosh withered up by August 3, so that thereafter all adults fed only on the thistle (Fig. 6B). The number of newly emerged adults suddenly decreased after

reaching the maximum, down to about 20 individuals at mid August, and thereafter kept a similar level until mid September. Some adults emerged in mid summer may have entered aestivation as reported in *H. vigintioctomaculata,* another member of *H. vigintioctomaculata* complex, in Kyoto, Honshu (Iwao, 1971). Adults virtually disappeared and entered hibernation in late September.

In comparison with the result at the same study site in 1975 (Katakura, 1976), the following trends can be pointed out: 1) the appearance of posthibernating adults was delayed about one week due to the low temperature in April and the delayed thaw in 1978; 2) the beginning of oviposition was also delayed about one week; 3) the appearance of newly emerged adults was advanced about one week due to the high temperature during the developing period; 4) the peak of newly emerged adults was also advanced about 3 weeks due to the concentrated emergence and possibly also to emigration caused by the shortage of the food resource.

3. Dispersal activity in adults

3.1. *Adult dispersal*: The distance of dispersal per day is calculated for the adults captured more than once. It is calculated by

$$(x_1 + x_2 + \cdots)/(y_1 + y_2 + \cdots),$$

where $X_n (n = 1, 2, \cdots)$ are the distance of dispersal (meters) between the $(n-1)$th and (n)th recaptures, respectively, and y_n $(n = 1, 2, \cdots)$ are the interval (days) between the $(n-1)$th and (n)th recaptures. Although the distance is almost restricted within 3.0 m per day in both posthibernating adults and newly emerged adults, a striking difference is noticed between them in the frequency distribution (Fig. 7). Most individuals of posthibernating adults more or less moved per day, while new adults included many sedentary individuals. The mean distance is thus about 1 m per day in posthibernating adults, whereas 0.74 m in new adults. No difference is found between the sexes.
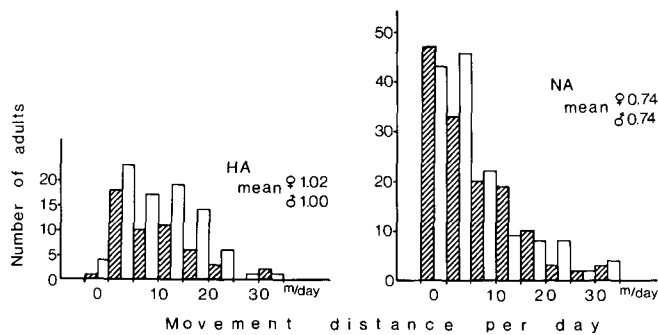

Fig. 7. Frequency distribution in the dispersal distance per day of adults. The hatched and open bars represent the numbers of females and males, respectively. HA, posthibernating adults; NA, newly emerged adults.
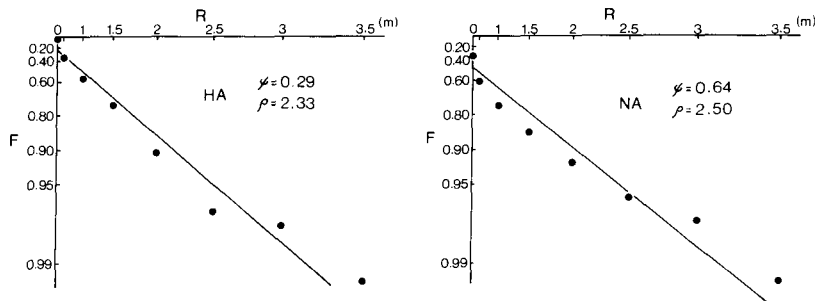
Fig. 8.   Relation between the conservatism (ϕ, phi) and the dispersal activity (ρ, rho). For the symbols R and F, see text.   HA, posthibernating adults; NA, newly emerged adults.

The dispersal activity was analysed by the method developed by Inoue (1978).   According to him, the distance and the direction from point A to point B is regarded as a vector AB when an insect moves from A to B for a unit time. The ratio of vectors whose lengths are shorter than "R" (a voluntary distance) to total vectors is shown as symbol "F".   When ln $(1-F)$ is plotted against R, they regress linearly.   The value of the intersection of the regression line and the vertical axis, ϕ (phi), indicates the conservatism for a unit time, and the reciprocal of the slope of the line, ρ (rho), indicates the degree of dispersal activity.   The dispersal activity was high in both posthibernating adults and newly emerged adults, while the conservatism of the latter seemed higher than that of the former (Fig. 8).   These results are consistent with our observation that most new adults did not move as long as the food resource existed.   The high dispersal activity may be due to the mating and oviposition behaviors in posthibernating adults, while due to the postemerging dispersal and searching for food in newly emerged adults.

3.2.   *Analysis of movement between the different species of host plants*: "Immigration ratio" (M_{TC} or M_{CT}) was calculated from the capture-and-recapture records as follows:

$$M_{TC(i)} = \frac{m_{TC(i)}}{m_{CC(i)} + m_{TC(i)}}, \quad M_{CT(i)} = \frac{m_{CT(i)}}{m_{TT(i)} + m_{CT(i)}}$$
$$(i = 2, 3, 4, \cdots)$$

where, for example, $m_{TC(i)}$ is the number of adults caught on the thistle (T) before time i and recaptured on the cohosh (C) at time i.

The seasonal fluctuations of the immigration ratios M_{TC} and M_{CT} calculated for the posthibernating adults in 1978, together with the number of adults caught, are shown in Fig. 9A.   From May 25 to June 3, when the standing crop of the cohosh was increasing, the value of the ratio M_{TC} tended to increase, but the reversed entry was seldom noticed.   From June 4 to June 17, the value of M_{TC} was
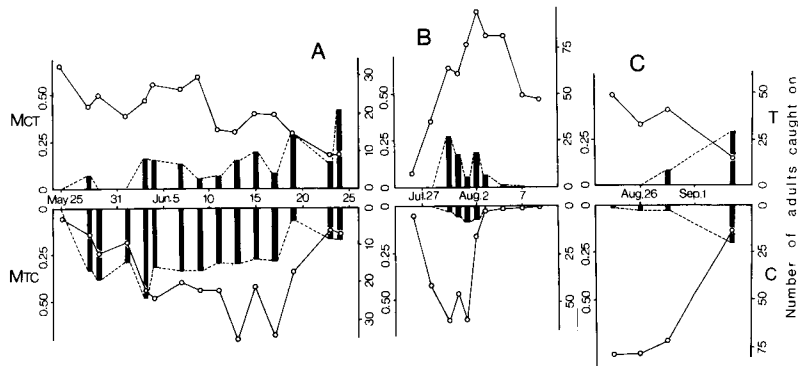
Fig. 9. Seasonal fluctuations in estimated immigration rate of posthibernating adults in 1978 (A), of newly emerged ones in 1978 (B) and of newly emerged ones in 1977 (C). The bar chart and the line graph indicate the immigration rate and the number of adults captured, respectively. For the symbols M_{TC} and M_{CT}, see text.

stable at ca. 0.30, while that of M_{CT} fluctuated between 0.05 and 0.20. Thus, although the posthibernating adults moved between the different species of host plants, their migration from the thistle to the cohosh always occurred more frequently than in the opposite direction. As a result, the number of adults feeding on the cohosh increased gradually, while that on the thistle decreased. After June 19, the number of adults decreased considerably, and the migration from the cohosh to the thistle occurred more frequently than in the opposite direction.

The seasonal fluctuations of the immigration ratios calculated for the newly emerged adults in 1978 are shown in Fig. 9B. Since all stocks of the cohosh in the area were withered up by August 3, the dispersal between the different host plant species was observed only from July 30 to August 5. The migration from the cohosh to the thistle occurred more frequently than in the opposite direction, presumably partly due to the steep decrease of the amount of the cohosh.

The immigration ratios in newly emerged adults in 1977 are shown in Fig. 9C. In 1977, some stocks of the cohosh persisted until early September, and beetles concentrated and fed on such stocks in late August. Consequent rapid decrease of the standing crop of the cohosh resulted in a parallel decrease in the number of beetles counted on the cohosh. On the other hand, after most stocks of the thistle had withered by late August, rosettes grew there, so that beetles could feed on them before they entered hibernation. Thus, both withering of the host plants and decreasing of the number of newly emerged adults were delayed in 1977 compared with those in 1978.

Fig. 10 shows the proportion of residents and emigrants in posthibernating adults and newly emerged adults in 1978. In posthibernating adults, the dispersal between the stocks of the same host plant species exceeds the dispersal between
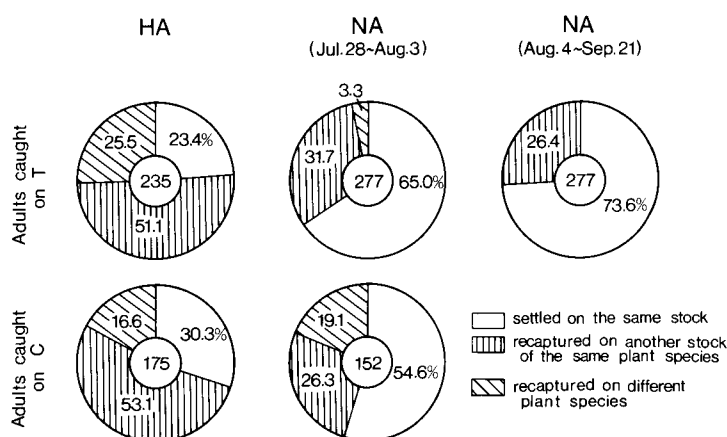
Fig. 10. Proportions of dispersal (in percents) and nondispersal. Numerals in the central circle indicate the total number of adults caught on thistle stocks (T) and cohosh stocks (C) on time i and recaptured subsequently on thistle stocks or cohosh stocks.

the different host species and nondispersal combined, the proportion of nondispersal on the cohosh was greater than that on the thistle, and the rate of migration from the thistle to the cohosh was greater than in the opposite direction. All these may indicate higher preference of posthibernating adults for the cohosh to the thistle.

Since all the cohosh stocks in the area were fed up by August 3, the phenology of newly emerged adults was divided into the following two phases in Fig. 10: the earlier phase with both the thistle and the cohosh were available and the later one with the thistle only. In the earlier phase (from July 28 to August 3), when stocks of the cohosh were being fed up one after another, the proportion of nondispersal on the cohosh was smaller than that on the thistle. The proportion of dispersal from the thistle to the cohosh was also smaller than in the opposite direction. However, there was a trend of newly emerged adults to emigrate to remaining cohosh stocks rather than to thistle stocks, when they had exhausted a cohosh stock (cf. Table 1). In the later phase (after August 4), the proportion of nondispersal became greater than in the earlier phase.

4. Oviposition process

Table 2 shows the relation between the settlement of the posthibernating adult females on each host plant and the number of eggs laid during the reproductive period (June 1-July 5). In this case, the settling days are calculated by the following method. Suppose a female was recaptured as follows:

Table 2.   Relationship between the settlement on the host
plants in posthibernating females of P-III and the
number of eggs laid on from June 1 to July 5, 1978.

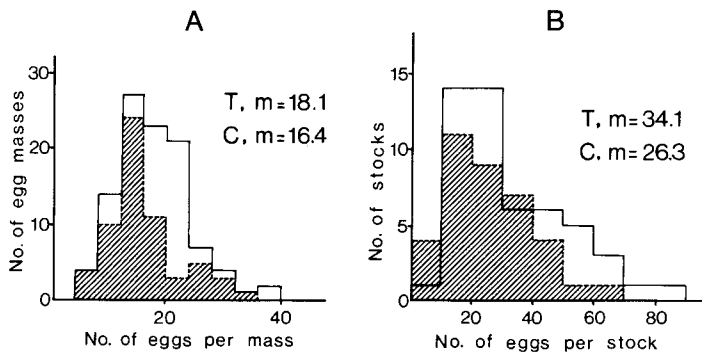|	Thistle	Cohosh
No. of females settled	42	36
Mean settled days±S.D.	3.0±2.5	3.5±3.3
No. of eggs laid	1746	985
Eggs per female	41.6	27.4
Eggs per settled day	13.8	7.8

Fig. 11.   A : Frequency distribution in size of egg masses discovered on the thistle (T)
and the cohosh (C).   B : Frequency distribution in the number of eggs per stock of each
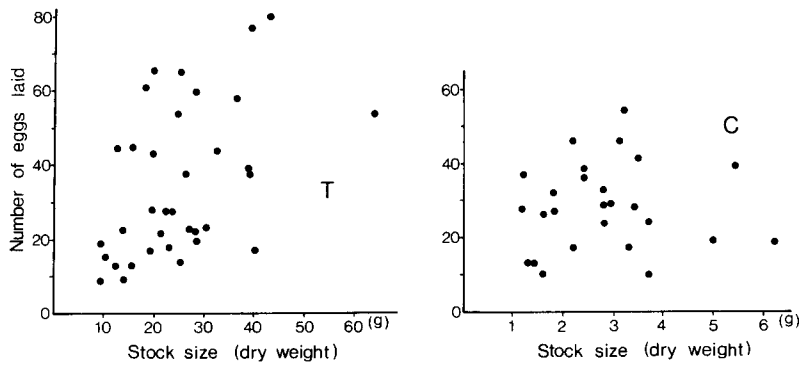host plant.

Fig. 12.   Relation between oviposition and stock size of each host plant.   Note that
the scales of the ordinate in the right and left figures are different.   T, thistle; C, cohosh.
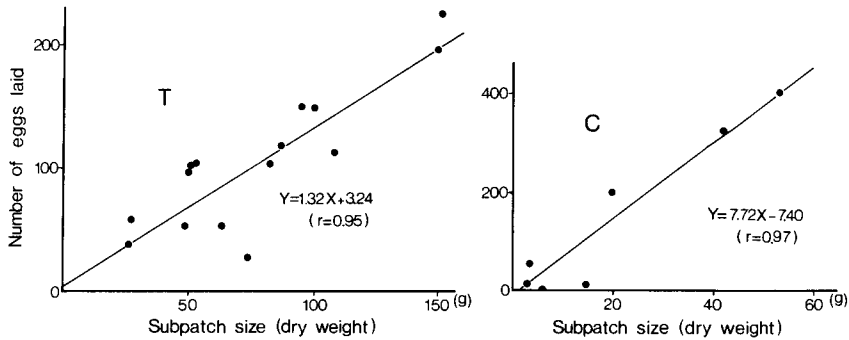
Fig. 13. Relation between oviposition and patch size of each host plant. Note that the scales of both the ordinate and the abscissa are different between the right and left figures. T, thistle; C, cohosh.

date	Jun. 4	7	9	11	13	14	16
plant	C —— C		no catch	C	T ——	T ——	T
settling days	4 days			1 day		4 days	

where the settling days of the female is estimated at 4 days on the thistle (T) and at 5 days on the cohosh (C).

The duration of settlement on the cohosh was slightly longer than on the thistle (Table 2). However, the number of eggs per egg mass on the cohosh was a little smaller than on the thistle (Fig. 11A). The number of eggs per stock of each host plant is shown in Fig. 11B. The mean number of eggs laid on one stock of the thistle and also of the cohosh was 34.1 and 26.3, respectively.

No obvious relation between the number of eggs laid and the quantity of food resource of each stock was noticed (Fig. 12). In either host plant, however, the greater the size of a subpatch was, the greater the number of laid eggs was (Fig. 13). It seems that the oviposition is not affected by the stock size, but the distribution pattern, of the host plant. It is noteworthy that the number of eggs per standing crop was overwhelmingly greater on the cohosh than on the thistle (Figs. 12, 13).

5. Life table and key-factor analysis

5.1. *Life table*: Life tables are prepared for P-III feeding on the thistle and the cohosh in the area separately (Table 3). No difference in the total mortality was found between the host plant species. However, the numbers of pupae and adults emerged may be underestimated, because it is difficult to discover individuals pupated on the underside of the leaves of undergrowths other than hosts.

As shown in Table 4, the mortality caused by the predation (including

Table 3. Life tables for P-III on the thistle (above) and the blue cohosh (below)

Stage (x)	No. of individuals alive at each stage (lx)	% survival in terms of eggs	Factors responsible for mortality (dxf)	No. of deaths during each stage (dx)	% mortality in terms of eggs	dx as % of lx (100 qx)
On the thistle						
Egg	1,862	100	Predation	711	38.2	
			Physiological death	381	20.4	
			Total	1,092	58.6	58.6
L-1	770	41.4		578	31.0	75.1
L-4	192*	10.3		132	7.1	68.8
Pupa	60	3.2		16	0.9	26.7
Adult	44	2.4				
On the cohosh						
Egg	1,000	100	Predation	73	7.3	
			Physiological death	284	28.4	
			Total	357	35.7	35.7
L-1	643	64.3		520	52.0	80.9
L-4	123*	12.3		90	9.0	73.1
Pupa	33	3.3		3	0.3	9.1
Adult	30	3.0				

* The number of individuals reached at the mid period of the stage.

Table 4. The hatchability and the mortality during egg stage. Those on the thistle and the blue cohosh are separately given.

	Thistle	Cohosh
No. of egg masses	103	61
No. of eggs	1,862	1,000
Egg mass size$\pm$S.E.	18.1$\pm$0.6	16.4$\pm$0.8
No. of eggs preyed	711	73
Mortality (%) by predation	38.2	7.3
Rate (%) of physiological death	20.5	28.4
No. of larvae hatched	770	643
Hatchability (%)	41.4	64.3
$\dfrac{\text{Larvae hatched}}{\text{Total eggs} - \text{preyed eggs}}$ (%)	70.5	69.4
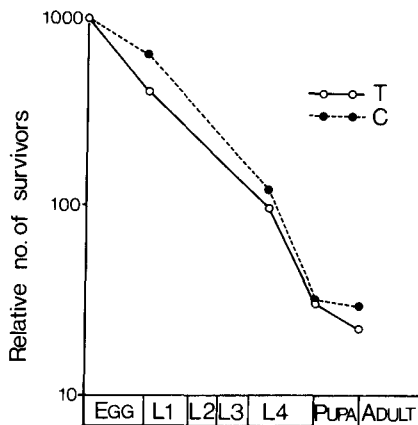
Fig. 14. Survivorship curves for P-III on the thistle (T) and the cohosh (C), respectively.

cannibalism) upon eggs was overwhelmingly higher on the thistle than on the cohosh. However, the hatchability of eggs excluding the loss by predation did not differ between the different host species. The mortality was highest in early larval stages (1st-3rd instars) on either host plant (Table 3). It attained to 75% of the total mortality on the thistle and to 81% on the cohosh. These figures may include the mortality in the early 4th instar, since the number of 4th instar larvae was estimated at the mid period of the instar by Southwood's method. The mortality in the last larval instar (4th instar) was also high, attaining 69% on the thistle and 73% on the cohosh (Table 3). The survivorship curve on the thistle is characterized by steep descents in the egg and late larval stages, while that on the cohosh mainly by a steep descent in the late larval stage (Fig. 14). The main difference in the survivorship curve between the two populations was thus the difference in mortality in the egg stage.

5.2. *Key-factor analysis*: Varley and Gradwell (1960) advocated the method analyzing "key-factor" by means of "k_i", which is defined as follows:

$$k_i = \log N_i - \log N_{i+1} \quad (i = 1, 2, \cdots, n)$$
$$K = k_1 + k_2 + \cdots + k_n$$

where N_i is the number of individuals in stage "i" and k_i is the logarithm of the

reciprocal of the survival rate between two successive developmental stages. When k_i and K are plotted against successive generations, k_i whose fluctuation pattern is most analogous to that of K is considered the "key-factor", the mortality factor most contributing to the change in the population density of inter-generations. Usually it is easy to identify the key-factor by the visual method alone. But sometimes there is no immediately obvious key-factor. In addition, the relative importance of mortalities other than the key-factor is often ignored. In order to determine the key-factor in case where it is not immediately obvious, Podoler and Rogers (1975) suggested the followng method. Their method is to plot k_i on the vertical axis against K in the horizontal axis and to calculate the regression coefficient. The k_i which gives the greatest value for the slope (b) is the key-factor. Key-factor analysis is valid to the explication of the fluctuation mechanism in the number of individuals not only over several generations but also within a generation. When life tables in several localities within a generation are made, these are applicable to the determination of the key-factor presenting the difference among the habitats (Iwao, 1971). In this case, the fluctuation pattern of K shows the difference in mortality reflecting the heterogeneity of these habitats.

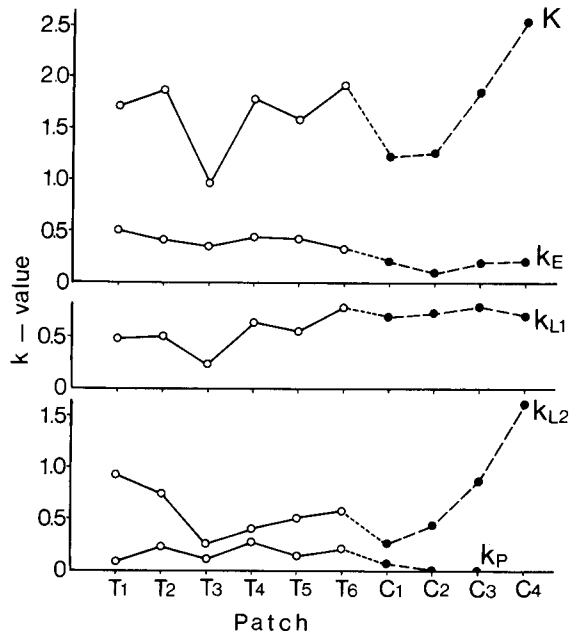In the present paper, the host plants in the area were distributed patchily, so

Fig. 15. Comparison of change in mortality expressed by k-values among different patches for the period from egg laid to adult emergence. Further explanations in text.
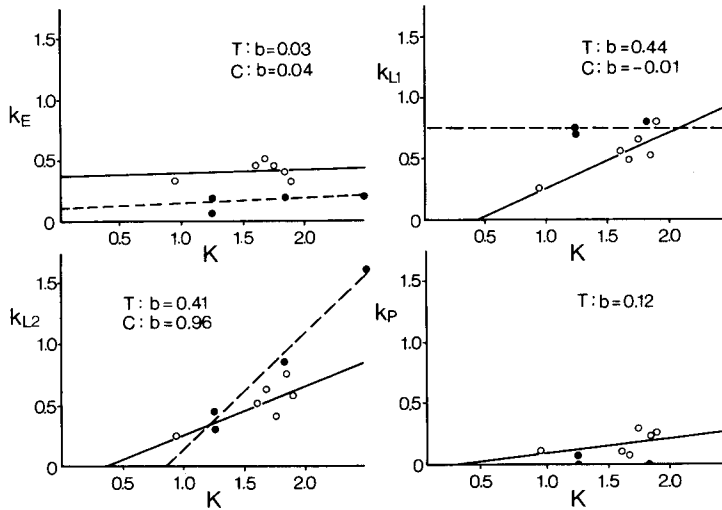
Fig. 16. Regression in k_i against K. Values of regression coefficients (b) are given in the figure. The solid line and the broken line indicate the regression line on the thistle (T) and that on the cohosh (C), respectively.

Table 5. The mean and the variance of k_i among patches

	Thistle		Cohosh	
	Mean	Var.	Mean	Var.
k_E	0.41	0.01	0.17	0.06
k_{L1}	0.53	0.07	0.73	0.00
k_{L2}	0.51	0.06	0.80	0.71
k_P	0.16	0.01	0.02	0.00

that the method mentioned above was applied to the life table data for different patches. Change in k-values and linear regression of k_i upon K are shown in Fig. 15 and Fig. 16, respectively. These results indicate that in the population depending on the thistle the key-factors are the mortalities in both early larval stage (k_{L1}) and late larval stage (k_{L2}), whereas in the population on the cohosh the key-factor is the mortality in the late larval stage alone. Further, the k-value in each developmental stage and its variance are shown in Table 5. In the population depending on the thistle, the mean values of k_{L1} and k_{L2} are great (0.53 and 0.51) and that of k_P is 0.41. The variances in k_{L1} and k_{L2} are also great (0.07 and 0.06). On the other hand, in the population on the cohosh, the mean values of k_{L2} and k_{L1} are great (0.81 and 0.73), while the variance is extremely great in k_{L2} alone.

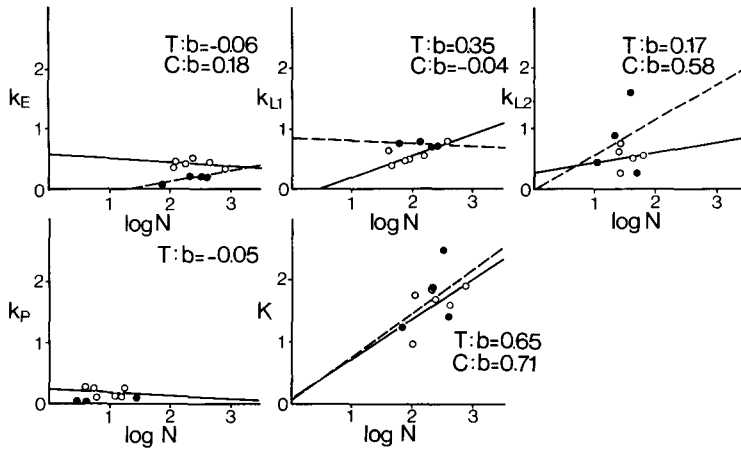From the results given above, it is clear that the mortality in the whole larval

Fig. 17. Relation between density and mortality in each stage. The solid line and the broken line indicate regression line on the thistle (T) and the cohosh (C), respectively. Values of regression coefficients (b) are given in the figure.

stage and that in the late larval stage were the strongest of all mortalities for the population depending on the thistle and for that on the cohosh, respectively, and that they contributed to the change of the number of individuals among the different patches.

5.3. *Detection of density dependence in mortality factors*: In order to detect density dependence in each mortality factor, Southwood (1966) used the slope of the regression line of k_i upon the population density log N in each stage: i.e. the closer the slope is to 1.0, the greater the density dependence of the factor is. Relations between the population density and k_i in the present case are shown in Fig. 17. In the population depending on the thistle, k_{L1} shows density dependence and k_{L2} suggests it, while no density dependence is shown in k_E and k_P. On the other hand, in the population on the cohosh, k_{L2} alone shows density dependence to a considerable degree, while no density dependence is detected in other stages.

5.4 *Mortality factors*:

1) Egg: The mortality in this stage was mainly due to predation, cannibalism and physiological death.   Nakamura and Ohgushi (1981) pointed out that the predation by polyphagous invertebrate predators was a primary cause of the mortality in this stage in *H. niponica*, another member of *H. vigintioctomaculata* complex, in Kyoto. Since the mortalities by predation and cannibalism could not be distinguished clearly, both factors were regarded as "predation" in a broad sense. Confirmed predators were the adults and larvae of an earwig, *Anechura*
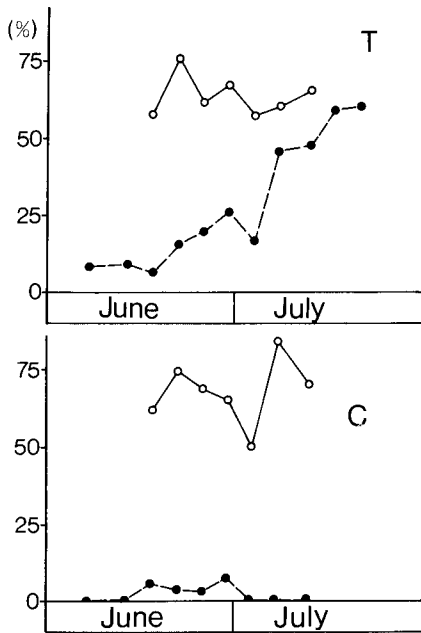
Fig. 18. Seasonal fluctuation in the hatchability and the rate of predation or cannibalism in the egg stage. Open and solid circles indicate the hatchability and the rate of predation, respectively. T, thistle; C, cohosh.

sp., the larvae of a reduviid, *Nabis apterus*, the larvae of a green lacewing, *Chrysopa* sp. and the larvae of a coccinellid, *Harmonia axyridis*, among which the first species was dominant. The eggs were also eaten by the adults and newly hatched larvae of their own species. Nakamura (1976) pointed out that cannibalism was responsible for the regulation of the population size of *H. vigintioctopunctata* (Fabr.), an affinitive species of *H. vigintioctomaculata* complex. In the present study, however, the percentage of eggs killed by cannibalism was unknown.

As mentioned earlier, the mortality by predation in the eggs laid on the thistle was higher than on the cohosh. Fig. 18 shows seasonal changes in hatchability and mortality by predation. The hatchability of eggs excluding loss by predation fluctuated almost within the range of 60–70% on either host plant. The mortality by predation on the thistle successively increased from 10% to 60%, although that on the cohosh was always below 10%. The mortality in this stage did not show any clear density dependence.

2) Early larval stage (1st–3rd instars): Although in this stage the mortality of individuals feeding on the thistle took part in the fluctuating mechanism of population size, the cause of it was unknown. Confirmed predators were the larvae of reduviids, *Nabis apterus* and *Rhynocoris leucospilus sibiricus*, and the larvae of *Harmonia axyridis*. Most predators were observed on the thistle. The mortality in the population on the thistle showed a slight density dependence, while that on the cohosh was not density dependent. Although the mortality in this stage may be due to biological factors, especially predation, non-biological factors in microhabitats could not be ignored.

3) Late larval stage (4th instar): The mortality in this stage on both host plant species took part in the fluctuation mechanism of population size. Its primary cause in particular on the cohosh was "crash", breakdown due to the depletion of the host plants. The mortality on both the thistle and the cohosh showed density dependence, and was especially high on the cohosh. Ectoparasitism by a mite and disease by mold were observed in this stage.

Table 6. Difference in mortality in pupae on the thistle, the cohosh and other
plants

	Thistle	Cohosh	Other plants
No. of pupae	30	1	62
No. of adults emerged	19	0	55
No. of pupae died	11	1	7
Mortality (%)	36.7	—	11.3

4) Pupa: The mortality in this stage was the least of all mortalities on both
the thistle and the cohosh. It is comparatively high on the thistle (Table 6),
because of the withering of the leaves where pupation took place.

Incidentally, it has been known that the larvae are infested by a tachinid,
Medina separata (Meigen), and a pointed-tailed wasp, *Watanabeia affisae*
(Watanabe), and the adults by *M. separata* and a nematomorphan. However,
any endoparasites could not be found in the course of the present study.

Concluding Remarks

On the basis of the results given above, the seasonal life cycles of the thistle
(*Cirsium kamtschaticum*), the blue cohosh (*Caulophyllum robustum*) and *Henos-
epilachna pustulosa*, form P-III, feeding on them are schematically shown in Fig.
19. The life cycle characteristics of P-III at the study area are summarized as
follows:

1) At the appearance of posthibernating adults in spring, the thistle already
unfolded the leaves but the cohosh did not yet (Fig. 19), so that the beetles first
gathered on the thistle. After the cohosh had unfolded the leaves, the posthiber-
nating adults feed on both host plant species. The migration of posthibernating
adults between the two host species was common, and the migration from the
thistle to the cohosh occurred more frequently than in the opposite direction (Figs.
9, 10).

2) The duration of settlement of posthibernating adults on the cohosh was
slightly longer than on the thistle (Table 2).

3) The egg mass size laid on the cohosh was slightly smaller than on the
thistle (Fig. 11).

4) The number of eggs per standing crop of the host plant was overwhelm-
ingly greater on the cohosh than on the thistle (Figs. 12, 13). This may have
resulted, at least partly, from the difference in the phenological properties of the
host plants. As shown in Fig. 19, the activity of oviposition peaked in mid June.
On the other hand, the standing crops of the thistle and the cohosh peaked in early
June and early July, respectively. This means that the standing crop of the
thistle increased and the number of eggs per standing crop decreased after the
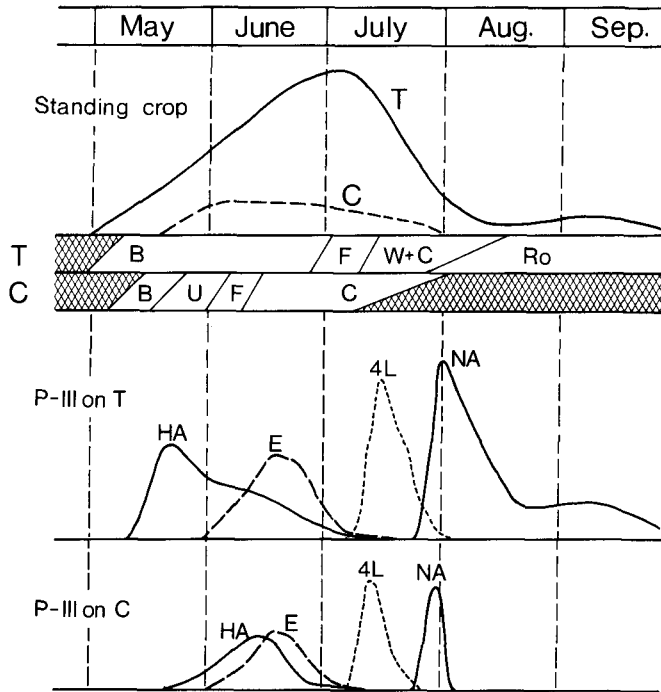prime of oviposition, whereas the number of eggs per standing crop of the cohosh

Fig. 19. Schematic life cycle trends of P-III and its host plants, the thistle (T) and the cohosh (C), in Tsukisamu in 1978.

Above : Life cycles and standing crops of the host plants.   B, sprouting of buds ; U, unfolding of leaves ; F, flowering ; W, withering ; C, consumption by insects ; Ro, rosettes.

Below : Seasonal fluctuations in the numbers of posthibernating adults (HA), egg masses (E), 4th instar larvae (4L) and newly emerged adults (NA) on each host plant.

did not decrease but somewhat increased because the food resource declined afterward due to infestation of the beetles.

5) There was no significant difference in the total mortality during the development between the population on the thistle and that on the cohosh (Table 3, Fig. 14). However, the key mortality factors were considerably different between them (Figs. 15, 16). In the population on the thistle, the key factors were the mortalities in both early and late larval stages mainly caused by the predation and death due to the depletion of the food resource, respectively. On the other hand, in the population on the cohosh associated predators were very scarce and the key factor was the mortality in the late (final) larval stage caused by the food shortage due to overexploitation.

6) New adults emerged in mid summer, when most stocks of the thistle were withered or damaged by the beetle and those of the cohosh were depleted. The

newly emerged adults fed on the remaining thistle and cohosh stocks and the thistle rosettes. The newly emerged adults tended to remain on the stocks of the cohosh as long as the leaves were available (Table 1). However, since the condition of the cohosh was declining, the migration from the cohosh to the thistle was more frequent in the newly emerged adults (Fig. 9).

7) The damage of the cohosh by P-III seemed to vary from year to year. While a part of stocks were persisted until September in 1977, all the cohosh stocks in the study area were completely skeletonized by early August in 1978. This earlier shift of the time of exhaustion was probably caused by the higher temperatures during the growing period of P-III in 1978 (Fig. 2), which apparently enhanced the larval development in the year.

Kurosawa (1953) reported for the first time that the form P-III of *H. pustulosa* fed and oviposited on the blue cohosh under field conditions at Maruyama, Sapporo (cf. Katakura, 1974 b). Rearing some larvae with the thistle and the cohosh in laboratory, he did not find any difference between the hosts in the survival ratio. A quite similar result was obtained by one of us (Kimura, unpubl.). Recently Hoshikawa (1984) examined the food preference of various forms of the *H. vigintioctomaculata* complex and found that the form P-III preferred the blue cohosh to the thistle in laboratory. The blue cohosh seems to be a very suitable food plant for P-III physiologically. Under field conditions, however, the cohosh is only fed by P-III when it grows together with thistles. No population of this form depending on the cohosh alone has ever been discovered. This suggests that the blue cohosh is not a perfect host plant ecologically. Out of the items enumerated above as the characteristics of the studied population of P-III, the items 2) to 4) seem to reflect the high preference and accessibility of P-III for the blue cohosh. On the other hand, the ecological factors which prevent the full use of the blue cohosh by P-III in nature may be as follows:

1) Phenological discrepancy: The cohosh often does not sprout, or unfold the leaves yet, when posthibernating adults of P-III appear in May. In such cases, the beetles would leave there in search for the food rather than wait for the sprouting or unfolding of the cohosh, except for the case that there are other food resources in the area where the cohosh grows.

2) Exhaustion of the stocks of the blue cohosh and resultant "crash" of the beetles: As mentioned above, the density of eggs per standing crop of the host plant is extremely higher on the cohosh than on the thistle because of the higher preference of P-III for the plant and the phenological consequence between the oviposition process of P-III and the seasonal change of the standing crop of the cohosh. Further, predators associated with the cohosh were scarce. Therefore, the populations of P-III on the cohosh tend to overcrowd especially in the late larval stage, and this overcrowding in turn results in the high mortality in the final instar larvae and the food shortage of the newly emerged adults. If some additive factors enhance the overcrowding, the population on the cohosh would easily suffer fatal damage.

The patterns of the host plant utilization by P-III are diverse. Some populations in and near Sapporo have been discovered depending on both the thistle and the blue cohosh, whereas some others depending only on the thistle. Some others partially or temporally depend on the plants other than the thistle and the blue cohosh (Katakura *et al.*, 1977). On the other hand, the phenologies of the host plants are also variable according to localities and/or years. The difference in the time of sprouting between the thistle and the cohosh may be smaller at some localities while larger in some others. Consequenly, the time and degree of the exhaustion of the blue cohosh by the ladybird may vary from year to year or from place to place. Further studies are naturally necessary to clarify the characteristics of the thistle and the blue cohosh as host plants of *H. pustulosa* and to consider the characteristics of these plants as the host plants of other members of the *H. vigintioctomaculta* complex, i.e., *H. niponica* and *H. yasutomii*.

Summary

From the summer of 1977 to the autumn of 1978, life cycle characteristics of the so-called Sapporo form (form P-III) of the phytophagous ladybird *Henosepilachna pustulosa* (Kôno) was studied at Tsukisamu, Sapporo, northern Japan, on a population depending on two species of host plants, the thistle species *Cirsium kamtschaticum* Ledeb. and the blue cohosh *Caulophyllum robustum* Maxim. On the basis of the results obtained by this study, in the present paper were described the phenological relations between P-III and its host plants, patterns of adult dispersal between and within the host plant species, oviposition processes and their relation to the standing crops of the host plants, the life table for the population on each species of the host plant, and the results of key factor analyses. In addition, the characteristics of the blue cohosh as the host plant of P-III was briefly discussed.

References

Hinomizu, H., Katakura, H., Hoshikawa, K., Kimura, T. and S. Nakano 1981. Life cycle

relations between the phytophagous ladybird *Henosepilachna pustulosa* (Kôno) and its food plants in and near Sapporo. New Entomol. **30**: 11–18. (In Japanese with English synopsis)

Hoshikawa, K. 1984. Host-race formation and speciation in the *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae) III. Geographic variation of food preference in the thistle feeder, *H. pustulosa*. Kontyû **52**: 605–614.

Inoue, T. 1978. A new regression method for analyzing animal movement patterns. Res. Popul. Ecol. **20**: 141–163.

Iwao, S. 1971. Dynamics of numbers of a phytophagous ladybeetle, *Epilachna vigintioctomaculata*, living in patchily distributed habitats. Proc. Adv. Study Inst. Dynamics Number Popul. (Oosterbeek): 129–141.

Katakura, H. 1974a. Morpholgy and distribution of the forms of *Henosepilachna vigintioctomaculata* complex in Hokkaido. Jour. Fac. Sci. Hokkaido Univ., Ser. VI, Zool. **19**: 657–680.

———— 1974b. *Henosepilachna pustulosa* feeding on *Caulophyllum thalictroides robustum* in Sapporo. Kontyû **42**: 394. (In Japanese)

———— 1976. Phenology of two sympatric phytophagous ladybirds of *Henosepilachna vigintioctomaculata* complex in and near Sapporo, northern Japan (Coleoptera: Coccinellidae). Jour. Fac. Sci. Hokkaido Univ., Ser. VI, Zool. **20**: 313–328.

———— 1981. Classification and evolution of the phytophagous ladybirds belonging to the *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae). *Ibid*. **22**: 301–378.

————, Hinomizu, H., Hoshikawa, K. and T. Kimura 1977. Problems and methods on the food habits of *Henosepilachna vigintioctomaculata* complex. Seibutsu-kyôzai **12**: 61–92. (In Japanese)

Kurosawa, T. 1953. Notes on the food-plants of *Epilachna pustulosa* Kôno (Coleoptera, Coccinellidae). Ôyô-Kontyû **9**: 12–16. (In Japanese)

Nakamura, K. 1976. Studies on the population dynamics of the 28-spotted lady beetle, *Henosepilachna vigintioctopunctata* F. I. Analysis of life tables and mortality process in the field population. Jap. J. Ecol. **26**: 49–59. (In Japanese with English summary)

———— and T. Ohgushi 1981. Studies on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (Kôno) in a cool temperate climax forest II. Life tables, key factor analysis, and detection of regulatory mechanisms. Res. Popul. Ecol. **23**: 210–231.

Podoler, H. and D. Rogers 1975. A new method for the identification of key factors from life-table data. J. Anim. Ecol. **44**: 85–114.

Southwood, T.R.E. 1966. Ecological Methods with Particular Reference to the Study of Insect Populations. 391 pp. Chapman and Hall. London.

———— and W.F. Jepson 1962. Studies on the populations of *Oscinella frit* L. (Dipt.: Chloropidae) in the oat crop. J. Anim. Ecol. **31**: 481–495.

Varley, G.C. and G.R. Gradwell 1960. Key factors in population studies. *Ibid*. **29**: 399–401.