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POPULATION STUDY OF THE LARGE 28-SPOTTED LADYBIRD, *EPILACHNA VIGINTIOCTOMACULATA* (COLEOPTERA: COCCINELLIDAE)

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INTRODUCTION

Epilachna (=*Henosepilachna*) *vigintioctomaculata*-complex (Hv-complex), a series of closely related phytophagous ladybirds, has attracted much attention in Japan to the process of speciation and comparative demography because of its remarkable variations in both external morphology and biology (KATAKURA, 1981; NAKAMURA, 1983). The complex includes a wide variety of groups from pest species (*E. vigintioctomaculata*, or Evm) to non-pest species feeding on wild plants such as thistles (*E. pustulosa* and *E. niponica*) and blue cohosh (*E. yasutomii*).

The large 28-spotted lady beetle, *E. vigintioctomaculata*, is a serious pest of solanaceous crops like potato and eggplant in the northern part of Japan. Many studies have been conducted on the ecology of Evm: TAKAHASHI (1932), IWAO (1954), YASUE (1963) and SIMBO (1978) on geographical distribution; KATAKURA (1976, 1982) on phenology; IWATA (1953) and IWAO (1956, 1968) on spatial distribution pattern on food plants; IWATA (1955) and IWAO et al. (1963) on adult dispersal. Review articles are available on food preference (KATAKURA et al., 1977; also see HOSHIKAWA, 1983a, b) and reproductive isolation mechanisms (KATAKURA and NAKANO, 1986). However, no detailed study has been done on the population dynamics of Evm except IWAO's excellent field research in 1971.

In 1981 and 1982, a field population of Evm in Kanazawa, Japan was studied by marking-recapture of adults and construction of a life table. NAKAMURA (1983) summarized the results of this study, comparing the demographic traits of Evm with those of closely related non-pest species and other pest epilachnine species of *E. vigintioctopunctata*. Without repeating the general discussion previously presented, this article documents in detail adult population parameters such as daily survival rate, longevity, sex ratio and multiplication rate per generation and constructs a life table.

MATERIALS AND METHODS

Study site

A small potato field (20×20 m) was selected as the study site in a hilly region at

Yuwaku (about 200 m above sea level) and 15 km SE of Kanazawa city. Kanazawa (N36°33', E136°39') is located on the Japan Sea in the central part of the main island of Japan. The meteorological data at Shibahara (0.7 km SW of the study site) recorded by Shibahara Junior High School and preserved by the Kanazawa Meteorological Station for the period 1959–1968 showed that the mean annual temperature was 13.3°C with the mean monthly temperatures of June, July and August 20.0, 24.6 and 25.7, respectively. The mean annual rainfall was 3079.1 mm.

The study field, surrounded by a secondary forest, contained 210 potato plants planted in 14 rows, each of which consisted of 6–25 plants. The nearest potato field (Site A) was 150 m southward and was the only other potato field within a 400 m radius.

The routine census

1. Marking and recapture of adults. Censuses were carried out at 3–7 day intervals from 9 June to 30 July 1981, using the following procedure. All the beetles found were marked individually with lacquer and were immediately released on the same plant. The adult population parameters such as survival rate and total number of residents were estimated using the JOLLY (1965)–SEBER (1973) method.

2. Collection of adults. In 1982, overwintered adults were collected twice (5 and 9 June) in the study field and in Site A to examine their winter survival rate and sex ratio. To compare the sex ratio, overwintered and new adults were collected from potato fields in several localities around Kanazawa (Araya, Joriki, Teratsu, Kumabashiri and Ichihara in Table 1).

3. Rearing of 4th instar larvae. In late June of 1982, more than 500 4th (final) instar larvae were gathered from the study field and were bred to emergence of new adults in the laboratory to estimate the sex ratio of new adults (see footnote 3 in Table 1 and the section below concerning the estimation of parasitism by wasps).

4. Construction of life table. Eggs were laid in batches on the undersurface of the host plant leaves. All egg masses were counted and labeled to prevent double counting. The total number of eggs laid was obtained by adding these data. The number of eggs hatched was assessed by counting the empty shells which remained after hatching. Eggs unhatched and shriveled were categorized as "hatching failures". Egg cannibalism by adults and larvae was occasionally observed but could not be counted. IWAO (1971) also recorded egg cannibalism by adults, but the percentage of eggs killed by this factor was not estimated. The size of larvae in their early instars was so small that they could not be counted accurately; hence only 3rd and 4th instar larvae were counted. Their number at the medial age of their instar (N_{L3} and N_{L4}) was derived by S_{L3}/L_{L3} and S_{L4}/L_{L4}, where S_{L3} and S_{L4} are the areas enclosed by the seasonal prevalence curve of 3rd and 4th instars and time axis (Fig. 2), and L_{L3} and L_{L4} are the mean durations of the 3rd and 4th instars, respectively (SOUTHWOOD and JEPSON, 1962). L_{L3} was 3 days and L_{L4} 7 days at room temperature (see below), and these values were used to derive N_{L3} and N_{L4}. All pupae were labeled to prevent double counting. Numbers of larvae and pupae attacked by parasitic wasps were assessed by a direct count of the corpses which darkened and remained on the host plants. Laboratory rearing of 4th instar larvae collected from the study field in late June of 1982 also indicated the extent of parasitism by the wasp. The author tried to estimate the total number of newly emerged adults by direct counting of pupal exuviae. Regrettably this estimate was found to be greatly underestimated (only 465 exuviae were collected). Since marking-recapture of adult beetles was carried out continuously throughout the season, the total number of newly emerged adults marked was used as the estimate of the total of those newly emerged, though this value was again apparently underestimated.

Results and Discussion

I. Ecology of adults

1. Estimation of adult population size, $\hat{N}_i$ and seasonal fluctuations in the number of each developmental stage. Figure 1 shows the fluctuations in the numbers of overwintered and new adults estimated by the Jolly-Seber method ($\hat{N}_i$) and of those actually observed (n_i). Overwintered adults appeared in the potato field in early June. Figure 2 shows the seasonal fluctuations in the numbers of each developmental stage of Evm. Egg laying began soon after the arrival of the overwintered adults and peaked in late June. New adults began to emerge in early July, with a peak in mid July. A 2nd peak oj oviposition occurred in late July and was brought about by the new adults (Fig. 2). Potatoes are usually harvested in late June to mid July in Kanazawa, but the host plants

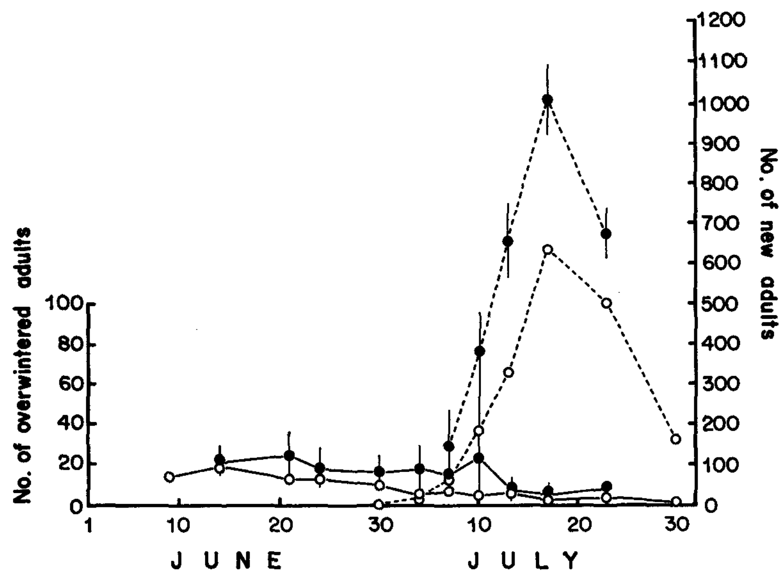

Fig. 1. Seasonal fluctuations in the numbers of overwintered (solid line) and new adults (broken line) of *E. vigintioctomaculata*. (○) no. beetles observed, (●), no. beetles estimated by the Jolly-Seber method. Vertical lines show the 95% confidence limits.

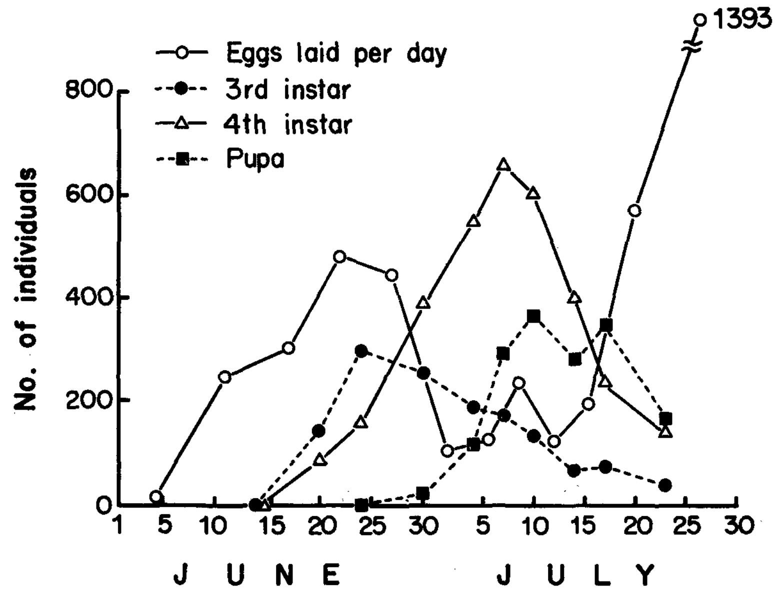

Fig. 2. Seasonal fluctuations in the numbers of each developmental stage of *E. vigintiocto-maculata.*

in the study field were left unharvested until the end of July when they were completely eaten out by adults and larvae of Evm.

Maki et al. (1964) indicated that the critical photoperiod promoting ovarian development of new adult Evm was 14–15 hours in Morioka (N39°42', E141°90'). In Kanazawa, the day length in the emergence period of Evm (from late June to mid July) was about 14.5 hours. Since the critical photoperiod generally becomes longer at lower altitudes (Danilevskii, 1961), and Kanazawa is located five degrees latitudinally southward of Morioka, the photoperiod regime of Kanazawa may have permitted the new adults, especially those emerging earlier, to oviposit in the study site, but the 2nd generation was not produced due to a severe food shortage, as mentioned below.

The sampling ratio ($n_i/\hat{N}_i$) averaged 70.0% and 55.5% for overwintered and new adults, respectively. Marking ratio was derived by the proportion of marked individuals to the whole population. In the overwintered adults, the ratio rapidly rose soon after the start of the study, reaching 1.0 in the 5th census, while in the new adults, it increased more slowly because of their mass emergence: around 0.3 in mid July, and approaching 0.9–1.0 in the late July when the number of beetles decreased.

2. *Sex ratio.* Table 1 summarizes the sex ratio derived in the following ways: (1) the total number of males and females marked during the study period; (2) the adults collected in Site A and the five neighboring localities; and (3) laboratory rearing of 4th instar larvae collected in the study field. All the results clearly showed the same trend, i.e., the sex ratio was female-biased in overwintered adults, although newly emerged adults showed no significant deviation from the expected 1 : 1 sex ratio, indi-

Table 1. Sex ratio of adult *E. vigintioctomaculata* derived from individuals collected in the study field and its neighboring areas

Generation	Locality	Distance from the study site (elevation, m)	Date of collection	No. examined		% female	χ^2-value
				Female	Male		
Overwintered adult	Study site[1]	(200)	7 June–4 July, 1981	22	4	84.6	12.46 ***[4]
	Ditto	Ditto	5 and 9 June, 1982	31 (3)[2]	24	56.4	0.89 n.s.
	Site A	0.15 km S (200)	9 June, 1982	33 (2)	21	61.1	2.67 n.s.
	Araya	1.0 km S (180)	31 May, 1977	42	33	56.0	1.08 n.s.
	Joriki	3.5 km SW (200)	1 June, 1977	14	7	66.7	2.33 n.s.
	Teratsu	4.0 km SW (200)	1 June, 1977	52	10	83.9	28.45 ***
	Kumabashiri	4.5 km SW (200)	1 June, 1977	36	27	57.1	1.29 n.s.
	Total			230	126	64.6	30.38 ***
New adult	Study site[1]	(200)	4–23 July, 1981	796	768	50.9	0.50 n.s.
	Ditto[3]	Ditto	Late June, 1982	243	268	47.6	1.22 n.s.
	Ichihara	22.5 km SW (280)	29 July, 1977	23	22	51.1	0.02 n.s.
	Total			1062	1058	50.1	0.01 n.s.

1) Total number of individuals marked during the routine census.
2) Total number of individuals bearing a 1981 mark.
3) Bred in the laboratory from 4th instar larvae collected in the field.
4) Statistically significant at 0.1% level.

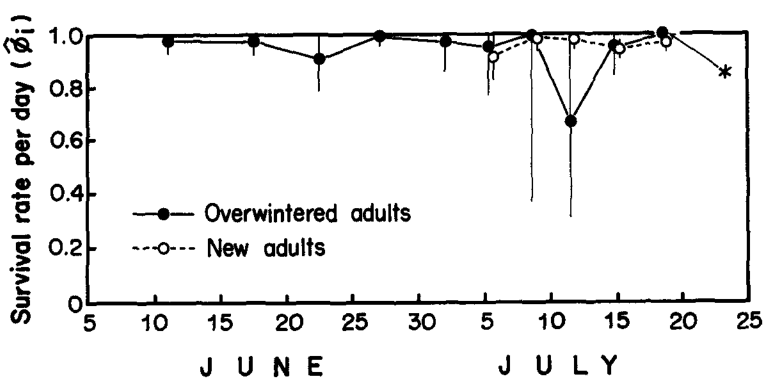

Fig. 3. Seasonal fluctuations in the residence rate of adult *E. vigintioctomaculata* estimated by the JOLLY-SEBER method. In the calculation, only females were used for overwintered adults and both sexes for new adults. Vertical lines show the 95% confidence limits (*, no standard error was derived).

cating the males suffered a higher winter mortality than females as claimed by IWAO (1971). In 1981, overwintered adults in the study field showed an extremely female-biased sex ratio (84.6%), but the cause of this remains unknown.

3. *Daily rate of residence,* $\hat{\phi}_i$. Since the study site was small, though overwintered adults are extremely sluggish and rarely move across a foodless space after they arrive in a potato field from the hibernation quarter (IWATA, 1955; IWAO et al., 1963; IWAO, 1971), the term "residence" instead of "survival" is used for values of $\hat{\phi}_i$ derived by JOLLY's formula. Figure 3 shows the seasonal fluctuations of $\hat{\phi}_i$, indicating the value was constantly high at around 0.95 in both overwintered and new adult generations, except for its sudden drop in overwintered adults between 10 and 13 July. The values of $\hat{\phi}_i$ declined toward the end of the study period as a result of host plant death by defoliation, but Jolly's method could not provide the estimates of $\hat{\phi}_i$ for the last two censuses taken. In Kyoto, the survival rate of overwintered adults showed a similar seasonal trend to that of the present study, staying at a high level (0.965–1.0 per day) until mid June and thereafter rapidly declining toward early July (IWAO et al., 1963).

4. *Length of residence time,* L_A. The values of L_A were derived from $(1-\phi_m)^{-1}$,

Table 2. The mean residence rate per day (ϕ_m), mean length of residence time (L_A, in days), the total sum of adult beetles resident during the study preriod (N_G), and multiplication rate per generation (MP).

Generation	Sex	ϕ_m	$L_A=\frac{1}{1-\phi_m}$	N_G	MP
Overwintered adult	Female	0.957	23.1	27.2	17.9(=487.7/27.2)
	Male	—	—	—*	
New adult	Female	0.935	15.3	487.7	
	Male	0.948	19.1	377.6	

* Not estimated.

Table 3. The minimum lengths of residence (L_m, in days) of adult *E. vigintioctomaculata* derived from the distribution of intervals between the first and last captures.

Generation	Sex	No. examined	L_m (Mean±95% confidence limits)
Overwintered adult	Female	22	20.5±7.1
	Male	4	11.4±18.2
	Total	26	19.8±6.2
New adult	Female	129	7.9±1.1
	Male	75	9.4±1.5
	Total	204	8.5±0.9

* Individuals which emerged from 4 to 7 July were used for calculation.

where ϕ_m is the mean of $\hat{\phi}_i$ weighted by $\hat{N}_i$. L_A was 23.1 (overwintered female), 15.3 (new female) and 19.1 days (new male), respectively (Table 2). L_A for new adults would be overestimated because the lower $\hat{\phi}_i$ values at the end of the study period were not included in the calculation of ϕ_m, as mentioned above. The minimum length of residence (L_m) was derived from the distribution of intervals between the first and last captures (Table 3). Individuals captured only once were treated conveniently as 0 days. L_m was around 20.5 (female, $n=22$) and 11.4 days (male, $n=4$) in the overwintered generation, and 7.9 (female, $n=129$) and 9.4 days (male, $n=75$) in new adults. In the calculation of L_m for new adults, individuals marked on 4 and 7 July were counted. If all the new adults were included in the calculation, L_m would be much shorter. The maximum value of L_m (in days) was as follows:

Sex	Generation	
	Overwintered	New
Male	33	26
Female	53	26

Percentage of individuals that were captured only once was 15.4 and 18.1 for overwintered and new generations, respectively.

5. *Total number of resident beetles for the study period*, N_G. Since we carried out an intensive mark-recapture procedure, the total sum of adults marked can be regarded as minimum estimates of N_G: 22 females and 4 males in overwintered and 796 females and 768 males in new adults (Table 1). Table 2 presents N_G, derived by S_{Ni}/L_A, where S_{Ni} is the area enclosed by the seasonal abundance curve of adults ($\hat{N}_i$) and the time axis (Fig. 1). However, as mentioned, the values of N_G in Table 2 were apparently underestimated as a result of the overestimated ϕ_m.

6. *Multiplication rate per generation, MP*. The multiplication rate per generation (*MP*) is defined as the number of newly-emerged females produced per overwintered female (*MP* was referred to as reproductive rate (*R*) in previous articles, NAKAMURA and OHGUSHI, 1979, 1981; NAKAMURA, 1983). The *MP* value was roughly estimated as 36.3 (=796/22, Table 1) or 17.9 (487.7/27.2, Table 2). The latter value must be largely

underestimated because the number of new females (487.7) was underestimated.

7. Recovery of marked beetles the following spring. Among the new adults marked in the summer of 1981 (796 females and 768 males), only three females were recovered in the study area and two females in Site A the following spring. This low recovery rate can be explained by: (1) The adult emergence occurred en masse, so that a substantial portion of the new adults left the potatoes without being marked, as suggested by the low marking ratio of the new adults. (2) The new adults tended to move to other fields searching for food plants or to go into aestivation nearby, because potato plants were no longer available by mid July (IWAO, 1971). Even taking into account the dilution of marked beetles from the study field, referred to in (2), the survival rate of Evm between the summer and the following spring might be a few %, which is as low as that of Evm in Kyoto (1.5–3%, IWAO, 1971) and allied pest, *E. vigintioctopunctata* (1.6–3.8%, NAKAMURA, 1976), and much less than that of non-pest species (>50% in *E. niponica*, NAKAMURA and OHGUSHI, 1979).

II. Ecology of immature stages

1. Developmental times of the immature stages. The duration of successive immature stages (in days) was confirmed in the laboratory as follows:

Egg	Larva				Pupa	Total
	1 st	2 nd	3 rd	4 th		
6	4	3	3	7	6	29

2. The distribution pattern of each stage in the potato field. IWAO's (1968) regression method based on mean(m)-mean crowding($\overset{*}{m}$) relationship was used to analyze the spatial distribution pattern of each developmental stage on the potato plants. When plotting $\overset{*}{m}$ against m, the relation can generally be fitted to a linear regression: $\overset{*}{m}=\alpha+\beta m$, where α is the intercept on $\overset{*}{m}$-axis, and β the regression coefficient. α indicates the basic component of distribution or the mean crowding expected when the mean density becomes negligible. β shows the distribution pattern of basic components: $\beta=1$ in random distributions, $\beta>1$ in aggregated distributions, and $0<\beta<1$ in uniform distributions. In this article, each individual potato plant is taken as a quadrat unit for calculating m and $\overset{*}{m}$. The spatial distribution of number of individual eggs per potato plant indicates that groups of eggs with an average of 26.8 ($=\alpha+1$) were distributed in clumps on each plant ($\beta=2.79$) (Fig. 4, far left). The aggregated distribution might have been due to some heterogeneity in the size and quality of host plants and/or female tendency to oviposit more than one egg mass in a visit. The spatial distribution of eggs in potato fields was studied by two authors: IWATA (1953) claimed that the eggs were distributed aggregatively on each plant due to the heterogeneity of plants and the non-random movements of ovipositing females, but IWAO (1968) showed that a group of eggs was distributed randomly on each plant ($\alpha=37.5$, $\beta=1$). Third instar larvae also

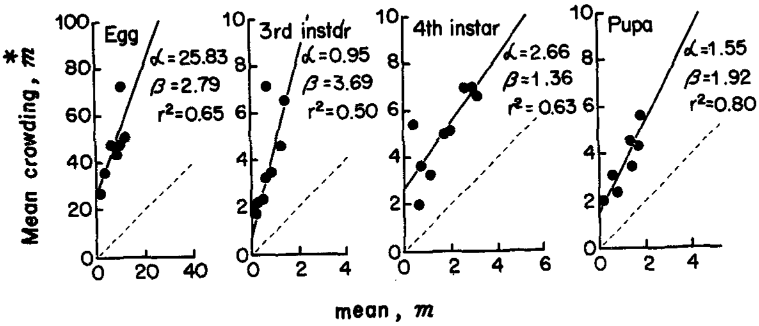

Fig. 4. Distribution pattern of immature stage of *E. vigintioctomaculata* in a potato field analyzed by the relation of mean crowding ($\overset{*}{m}$) to mean density (m).

Table 4. Life table for *E. vigintioctomaculata* in the potato field. *LX*: ‰ survival in terms of eggs.

Age class	No. of individuals	No. dying	% dying	*LX*
Overwintered adult Fecundity (No. of eggs/female)	26(22♀♀+4♂♂) [384.9]			
Egg	8468			1000.0
Larva hatched	5842	2626	31.0	689.9
3rd instar	2047	3795	65.0	241.7
4th instar	1863	184(3)*	9.0	220.0
Pupa	1061	802(19)*	43.0	125.3
New adult	1564(796♀♀+768♂♂)**			184.7

* No. killed by the parasitic wasp, *Watanabeia afissae*.
** Total no. marked.

were distributed aggregatively on plants but the mean colony size decreased to 1.95, as a result of the dispersal of the larvae from egg masses during development (Fig. 4, second from left). In 4th instar and pupa, the clump size again became larger (3.66 and 2.55) but the distributions of the clumps per plant were less aggregative than 3rd instar.

3. *Life table.* A life table (Table 4) was constructed to summarize the mortality processes in the immature stages of Evm. The survivorship curve of Evm with those of allied species was presented in a previous article (Fig. 2 in NAKAMURA, 1983). Eggs oviposited until 10 July were considered to have been laid by overwintered females and were used as the starting point of the life table (8,468 eggs in Table 4), because new adults began to oviposit on day 12–13 of their adult life (MAKI et al., 1964), and in the study field new adults were found on 4 July for the first time.

(1) Egg

The size of egg masses varied widely, ranging from 6 to 84 with a mean of 34.93 (Fig. 5). IWAO (1971) reported the mean egg mass size of Evm in Kyoto was 28. The mean egg mass size of Evm was as large as that of the pest species *E. vigintioctopunctata* (38.9, NAKAMURA, 1976) and much larger than that of closely related non-pest species *E. niponica*: 17.2 in Asiu, Kyoto (NAKAMURA and OHGUSHI, 1981) and 26.4 in Yuwaku,

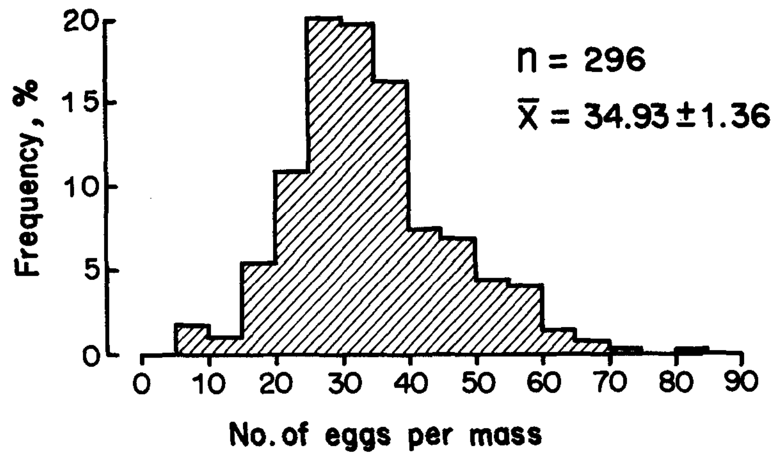

Fig. 5. Frequency distribution of the size of egg masses of *E. vigintioctomaculata*. *n*: no. of masses examined. $\bar{x}$: mean±95% confidence limits.

Kanazawa (NAKAMURA, 1983).

No direct measurement of the fecundity was practicable in the field, but it was assessed indirectly as follows:

$$\text{Mean fecundity} = \frac{\text{Total no. of eggs laid in the study field}}{\text{Total no. of overwintered resident females in the study field}}$$

Since eggs were counted by successive thorough searches of all the host plants using labels to prevent double counting and the adult population was intensively marked, the estimated value would be reasonably accurate. The mean fecundity thus derived was 311.3 (8,468/27.2, see N_G of overwintered females in Table 2 for the denominator) and 384.9 (=8,468/22, Table 4).

The egg mortality became higher as the season advanced because the potatoes were severely damaged by late instars and newly emerged adults: 22.0% and 37.1% for the eggs laid from 1 to 14 June and from 15 June to 10 July, respectively, with an average of 31.0% for the entire oviposition period of overwintered adults. After 10 July, a total of 10,846 eggs were laid mainly by new adults (Fig. 2). The mortality of 2,487 of these laid from 10 to 17 July reached 55%. No estimate was made for 8,359 eggs laid from 17 to 23 July, however, the mortality must have been much higher because of the extreme depletion of food. No parasitic wasps were found in the egg stage.

(2) Larva and pupa

Except for death from parasitism by wasps, no actual causes of larval and pupal mortality were quantified, though some arthropod predators such as coccinellids, mantids, and spiders may be suspect. Fourth instars and pupae were attacked by the wasp, *Watanabeia afissae* WATANABE (Proctotrupidae). The extent of parasitism was low: only 3 out of 2,047 3rd instars (0.15%) and 19 out of 1,863 4th instars (1.02%) were killed by this means. The low parasitism was confirmed by the laboratory rearing of the 4th instars collected in the study site in late June of 1982: only eight larvae out of

527 (1.5%) were parasitized. The wasp was found attacking 3rd and 4th instars of *E. niponica* feeding on thistles in a valley 1 km south of the present study site. The rate of parasitism in *E. niponica* again was very low (NAKAMURA, 1983). In Kyoto, no parasitic wasp was reported in any stage of Evm's life cycle (IWAO, 1971).

Major mortality factors in the larval stages are probably food shortage due to overcrowding, though the extent of this was not quantified. Late instar larvae and new adults were vigorous feeders and they occurred at high density in the study field, so that the potatoes were severely damaged in late June, and most of them were skeletonized by mid July. Under such circumstances, smaller larvae which occurred in the latter period would have a high mortality due to starvation. Table 4 shows that 18.5% of eggs laid by overwintered adults reached the adult stage in the present study. IWAO (1971) reported that about 30% of the larvae that hatched out later than mid June inevitably died due to the shortage of food and only 15% of the eggs laid successfully emerged as adults. Besides the damage caused by larvae and new adults of Evm, the shortage of food may be the result of the dying off or harvesting of the potatoes in late June to early July. At this period even a small difference in the timing of food deprivation and availability of alternative food nearby could exert a great influence on the percentage of successful emergences (IWAO, 1971).

SUMMARY

In 1981 and 1982, a population study of the large 28-spotted ladybird, *Epilachna vigintioctomaculata* was conducted in a potato field at Yuwaku, Kanazawa, Japan by mark-recapture of adults and construction of a life table

1. Overwintered adults appeared in the study field in early June. Emergence of new adults began in early July, and peaked in mid July. Egg laying peaked in late June and in late July. The 1st peak was formed by the overwintered females and the 2nd one by the new females. The 2nd generation was not produced because the potatoes were completely depleted by late instars and new adults, and no alternative food plant was available.

2. The sex ratio was female-biased in overwintered adults, but newly emerged adults showed a 1 : 1 sex ratio, indicating the males suffered a higher winter mortality than females.

3. The daily rate of residence derived by JOLLY's formula was constantly high, around 0.95, in both overwintered and new adults until mid July and then declined toward late July.

4. Length of residence time was 23.1 (overwintered female), 15.3 (new female) and 19.1 days (new male).

5. IWAO's (1968) regression method based on mean (m)-mean crowding ($\mathring{m}$) relationship was used to analyze the spatial distribution pattern of each developmental stage on the potato plants.

6. The mean number of eggs laid per overwintered female in the field was 311.3.

7. Mortality of eggs laid by overwintered females was 31.0%. The major mortality factor in the larval stages appears to be food shortage due to overcrowding. The extent of the parasitism by the wasp, *Watanabeia afissae* WATANABE (Proctotrupidae) was low: only 0.15% for 3rd instars and 1.02% for 4th instars. Among the eggs laid by overwintered adults, 18.5% reached the adult stage.

8. The multiplication rate per generation, defined as the number of newly-emerged females produced per overwintered female, was 376.3.

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オオニジュウヤホシテントウの個体群動態

中 村 浩 二

1981年から1982年にかけて金沢市郊外（湯涌）のジャガイモ畑で，オオニジュウヤホシテントウ (*Epilachna vigintioctomaculata* MOTSCHULSKY) の個体群動態を成虫の標識再捕と生命表作成により調査した．

1．越冬成虫は6月上旬に出現し，産卵ピークは6月下旬にみられた．新成虫の羽化は7月上旬から始まり7月中旬ピークに達した．新成虫による産卵ピークが7月下旬にみられたが，ジャガイモが老齢幼虫と新成虫により食いつくされ，代替食草もなかったので第2世代は羽化しなかった．

2．越冬成虫の性比は雌に偏っていたが，新成虫では1：1であったので，羽化してから翌春までの雄の生存率が雌より低いと考えられた．

3．JOLLY 法により推定した日当り生存率（調査地内滞留率）は6月中旬まで高かった（≒0.95）がその後低下した．

4．滞留日数（調査地内）は，23.1（雌越冬成虫），15.3（雌新成虫），19.1日（雄新成虫）であった．

5．IWAO (1968) の m–$\mathring{m}$ 回帰法を用いて食草上での卵，3齢および4齢幼虫，サナギの空間分布を解析した．

6．雌越冬成虫1匹あたりの実現産卵数（ジャガイモに産みつけられた総産卵数を出現した雌越冬成虫総数で割った数）は，311.3であった．

7．越冬成虫により産卵された卵の死亡率は，31.0%であった．幼虫期の主な死亡要因は餌不足による餓死であった．寄生蜂 *Watanabeia afissae* WATANABE (Procto trupidae) による死亡率は3齢幼虫の0.15%，4齢幼虫の1.02%にすぎなかった．産みつけられた卵のうち18.5%が新成虫として羽化した．

8．雌越冬成虫1匹あたりの雌新成虫羽化数は，36.3匹であった．