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ADULT POPULATION PARAMETERS AND LIFE TABLES OF AN EPILACHNINE BEETLE (COLEOPTERA: COCCINELLIDAE) FEEDING ON BITTER CUCUMBER IN SUMATRA

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INTRODUCTION

In Indonesia, some epilachnine beetles are serious pests of crops such as potato, eggplant and squash (KALSHOVEN, 1981). Although some basic information has been gathered on the ecology of temperate epilachnines (e.g. KATAKURA, 1981 and NAKAMURA, 1983 for Japanese species; NICHOLS and KOGAN, 1972 for the Mexican bean beetle, *Epilachna varivestis*; SCHAEFFER, 1983 for a world list of natural enemies of epilachnines), few quantitative studies have been carried out on the Indonesian species, despite their economic importance.

Since 1980 we have studied the population dynamics of some epilachnine beetles in the Province of Sumatera Barat, Indonesia (NAKAMURA et al., 1983). This article describes a field study of one "species", which is closely similar to *Epilachna sparsa* DIEKE (1947) and feeds on bitter cucumber *Momordica charantia*. The "species" was studied by mark-recapture of adults and by the construction of life tables. The preceding article showed that the species is characterized by more prolonged longevity and fertility schedules under laboratory conditions than temperate species, including Japanese epilachnines (NAKAMURA et al., 1984). The present article aims, firstly, to give basic knowledge of the population dynamics helpful for developing effective control measures against the pests, and secondly, to compare demographic characteristics of tropical and temperate species, because some information is available for Japanese epilachnines (NAKAMURA, 1976a, b, 1983; NAKAMURA and OHGUSHI, 1979, 1981, 1983; IWAO, 1971).

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Materials and Methods

Study Species

The identification of Indonesian epilachnine species has been in great confusion, firstly because the Indonesian Archipelago is rich, not only in the number of epilachnine species, but also in the intraspecific variability in populations from the same, or different, locations (Dieke, 1947), and secondly because no critical taxonomic studies have been done on these beetles since the work of Dieke, (de Gunst, 1957; Kalshoven, 1981).

The species feeding on bitter cucumber is closely similar to *Epilachna* (=*Henosepilachna*) *sparsa* recorded by Dieke (1947). The "species" was referred to as *Henosepilachna sparsa* like "species C" in our tentative list of the Epilachninae of Sumatera Barat (Nakamura et al., 1983). The species is quite common at altitudes from 0 to 2000 m, and it feeds exclusively on bitter cucumber *Momordica charantia.* The adults of "sp. C" have 28 or fewer spots, with many "non-persistent" spots (cf. Dieke, 1947). The larvae have a yellow body color and their spines are yellow to the tip. These facts suggest that "sp. C" may be identical to *Epilahna implicata* mentioned by de Gunst (1957) and Kalshoven (1981).

Study Site

The study was carried out in the garden of the Sumatra Nature Study Laboratory. Andalas University at Ulu Gadut, Padang (140 m altitude above the sea). The regular census was repeated three times in 1982: 22 March to 26 May (Period 1), 26 July to 27 September (Period 2), and 14 October to 30 December (Period 3). The mean monthly air temperature of Padang fluctuated only between 26.7 (September to December) and 27.5°C (May) and the annual rainfall was 4172 mm, according to the meteorological data from 1879 to 1941 (Rika-Nenpyo, 1983). The meteorological data at Bandar Buat (6 km WSW of the study site) recorded by the Sukarami Research Institute

Fig. 1. Meteorological data observed at Bandar Buat, 6 km WSW of the study site. Broken line and histogram show mean temperature and total amount of rainfall per 10 day period, respectively.

for Food Crops is available for the study period (Fig. 1).

Host Plant

The bitter cucumber is known as "pario" (Sumatera Barat) and "paria" (Java) in local languages and its fruits are used as human food. In Padang, it is not cultivated in large fields, but is found sporadically in gardens. No bitter cucumbers have occurred within a few kilometers of the study site since 1980. At the start of each census, 3, 2 and 3 flower pots were each sown with 2 bitter cucumber seeds, and placed under a rack (250 cm in length, 100 cm in width, and 100 cm in height) in Periods 1, 2 and 3, respectively. The bitter cucumber plants grew rapidly, began to climb up the rack on day 7, and flowered one week after that. The life span of the plant normally extends from 3 to 6 months without serious damage by pests, but the plants used in this study were completely eaten by adults and larvae of "sp. C" by the end of each study period.

Routine Census

The censuses were carried out, at 3 or 4 day intervals, using the following procedure. All the beetles found were marked individually with lacquer and they were immediately released on the same plant. The adult population parameters, such as survival rate and total number of residents were estimated by using the JOLLY (1965)-SEBER (1973) method. Eggs were laid in batches on the stems, flowers and undersurface of the leaves of the host plants. All egg masses were counted and labelled 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 were still present after hatching. Eggs attacked by parasitic wasps developed black spots and then became dark. The eggs which remained unhatched and shrivelled were categorized as "failure to hatch" in the life tables (Table 2). Egg cannibalism by adults and larvae was observed sometimes, but this could not be counted. The size of larvae in their early instars was so small that they could not be counted accurately. Hence only 4th instar larvae were counted. The number of 4th instar larvae at the medial age of their instar (N_{L4}) was derived by S_{L4}/L_{L4}, where S_{L4} is the area enclosed by the seasonal prevalence curve and time axis (Fig. 2, below), and L_{L4} is the mean duration of the 4th instar (SOUTHWOOD and JEPSON, 1962). L_{L4} was 4.9 days at room temperature (NAKAMURA et al., 1984), and this value was used to derive N_{L4}. All pupae were labelled to prevent double counting. Numbers of larvae and pupae attacked by parasitic wasps were assessed by a direct count of corpses which became dark and remained on the host plants. The total number of newly emerged adults was estimated by direct counting of pupal exuviae.

RESULTS

I. Ecology of Adults

1. Estimation of population size, $\hat{N}_i$ *and the seasonal fluctuations in the number of each* *developmental stages.* Figure 2 (above) shows the fluctuations in the numbers of adults estimated by the Jolly-Seber method ($\hat{N}_i$) and of those actually observed (n_i). The variances of $\hat{N}_i$ could not be estimated for Periods 2 and 3, because no beetle which was marked on the previous census times was recaptured on a few census times. Within two weeks after planting the seeds, adults of "sp. C" had colonized the plants. Since no bitter cucumber was found near the study site and the presence of the host plants at the study site was discontinuous, adults found in the early stage of each Period must have been immigrants from the surrounding areas, at least, a few kilometers away. Fig. 2 (below) shows the fluctuations in the number of eggs, 4th instars and pupae. In Period 1 the census was started after some beetles had arrived and laid eggs on the host plants (Fig. 2, above). The sampling ratio $\left(\frac{n_i}{\hat{N}_i}\right)$ averaged 54.1. 54.8 and 74.4% for Periods 1, 2 and 3, respectively. Egg laying peaked at the very beginning of Period 2, but no adults were found at that time. This discrepancy may be explained by the following facts. Firstly, adults of "sp. C" are so active that they frequently drop off plants or fly away, when the host plant is approached or slightly disturbed. Secondly, the residence rate of adults was not high at the beginning of each Period (Fig. 3), so that some adults which oviposited might have left the host plants without being captured. In Periods 1 and 2, new adults emerged within one month after the colonization of adults, and the second peak of emergence was seen one month after that, soon followed by host plants' death due to defoliation. The duration of immature stages from egg to adult emergence

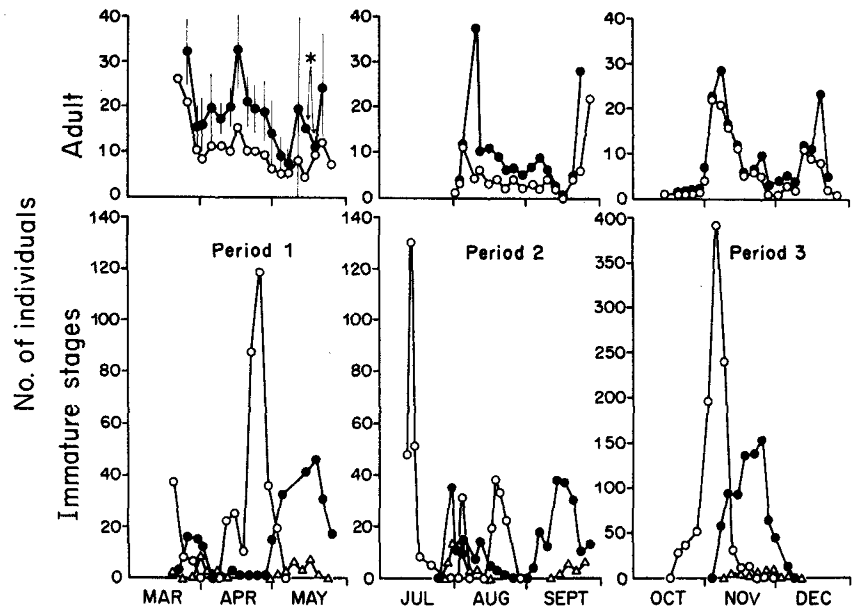

Fig. 2. Seasonal fluctuations in the numbers of each developmental stage of Epilachna "sp. C". Above: adult. (-○-) no. beetles observed, (-●-), no. beetles estimated by the Jolly-Seber method. Vertical lines show the standard error (*, no standard error was derived). Below: immature stages. (-○-), no. eggs laid per day, (-●-), no. 4th instar larvae, (-△-), no. new pupae per day.

was 22.5 days (NAKAMURA et al., 1984). In Period 3, the peak of adult emergence was seen only once because the initial egg number was so large that the food plants were killed by the larvae and new adults of the first generation (see also, Table 2). Marking ratio, i.e. the proportion of marked individuals to the whole population fluctuated from 0 to 1 with an average of 0.59, 0.57 and 0.53 for Periods 1, 2, and 3, respectively.

2. *Sex ratio.* The total number of males and females marked in each study period was as follows:

Period	Female	Male	Total	Value of χ^2
1	54	43	97	1.24
2	26	25	51	0.02
3	41	36	77	0.32
Total	121	104	225	1.28

This clearly shows that the sex ratio of the "sp. C" was 1 : 1. We could not separate newly emerged beetles from immigrants by appearance, because the elytra of the former became hard within one or two days after emergence. NAKAMURA et al. (1984) indicated that newly emerged adults of "sp. C" showed no significant deviation from the expected 1 : 1 sex ratio under laboratory conditions.

3. *Daily rate of residence,* $\hat{\phi}_i$. Since the study site was small and the beetles had a much higher flying activity than epilachnine species which one of the authors (K. N.) studied in Japan, we used a term "residence" instead of "survival" for values of $\hat{\phi}_i$ derived by JOLLY's formula. The three Periods had a common trend in the change of $\hat{\phi}_i$ with time: the value of this was lower and fluctuated more violently during the early census times (especially for Periods 2 and 3) than during later census times. The values of $\hat{\phi}_i$ declined at the end of the Periods as a result of host plants' death by defoliation (Fig. 3).

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

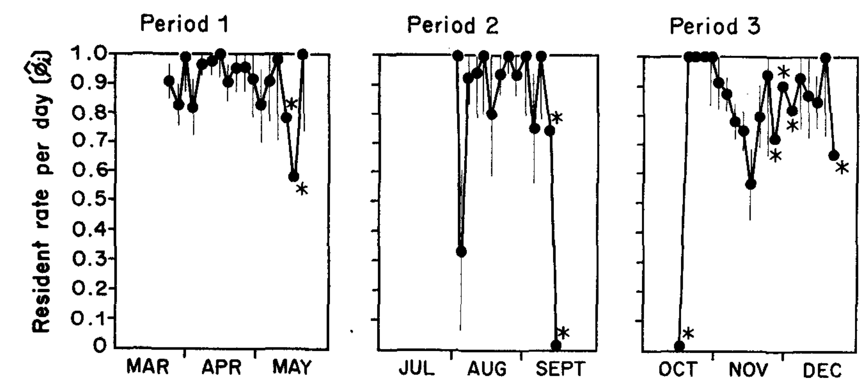

Fig. 3. Seasonal fluctuations in the residence rate of adult *Epilachna* "sp. C" estimated by the JOLLY-SEBER method. Vertical lines show the standard error (*, no standard error was derived).

ϕ_m is the mean of $\hat{\phi}_i$ weighted by $\hat{N}_i$. L_A was 10.3, 11.1 and 6.3 days for Periods 1, 2, and 3, respectively (Table 1). The minimum length of residence time (L_m) was derived from the distribution of intervals between the first and last captures (The individuals which were captured only once were treated conveniently as 0 days). L_m was around 4.5 days and no significant difference was detected between the sexes and between the Periods, except between the females of Period 1 and 3 (Fig. 4). The maximum value of L_m (in days) was as follows:

Sex	Period 1	Period 2	Period 3
Male	51	30	19
Female	48	30	16

Figure 4 also shows that between 40–80% of the beetles were captured only once.

5. *Total number of resident beetles for each 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 (Table 1). N_G can be estimated by S_{Ni}/L_A, where S_{Ni} is the area enclosed by seasonal abundance curve of adults ($\hat{N}_i$) and time axis (Fig. 2). Table 1 also presents N_G*, a corrected estimate of N_G derived by T. Inoue (unpublished; for details see

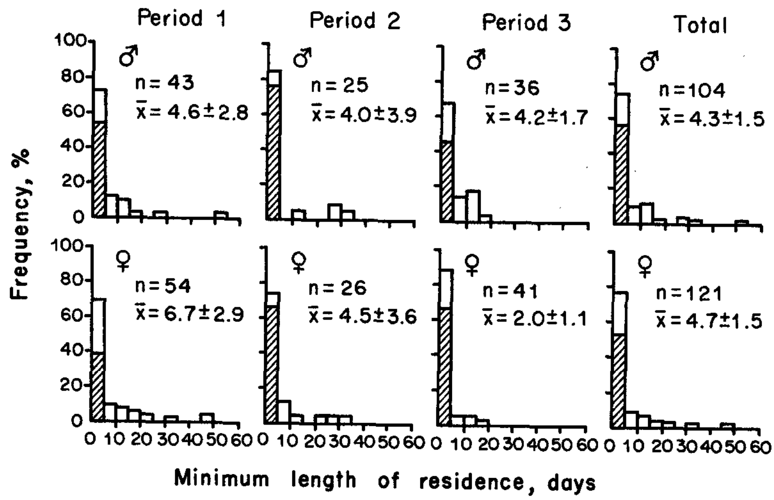

Fig. 4. Frequency distribution of the minimum lengths of residence of adult beetles. *n*: number of individuals. $\bar{X}$: mean $\pm 95\%$ confidence limits. Shaded area shows the beetles which were caught only once.

Table 1. Estimates of mean survival rate per day (ϕ_m), mean length of residence (L), and total sum of the beetles resident per study period (N_G, N_G*).

Period	ϕ_m	$L=\frac{1}{1-\phi_m}$	N_G	N_G*	Total no. marked
1	0.903	10.3	106.0	140.3	97
2	0.910	11.1	39.9	43.3	51
3	0.840	6.3	88.9	102.3	77

NAKAMURA and OHGUSHI, 1979). The values of N_G and N_G* demonstrate that most of resident beetles could be marked, although they were apparently underestimated for Period 2.

II. Life Tables and Survivorship Curves

To summarize the mortality processes in the immature stages of "sp. C", we constructed life tables (Table 2) and drew survivorship curves (Fig. 6).

1. Egg. The size of egg masses varied widely, ranging from 7 to 108, with a mean of 49.6 for all the Periods (Fig. 5). The mean size (with $\pm$95% confidence limits), calculated separately for Periods 1–3, was 47.8$\pm$8.2, 44.6$\pm$9.9 and 51.8$\pm$4.7. There was no significant difference between these means. The mean egg mass size of "sp. C" was much larger than that of related species: 23.0 and 28.1 for two Sumatran species, *Epilachna sparsa* like "sp. A" and "sp. D", feeding on solanaceous and cuccurbitaeous plants under laboratory conditions; while that of "sp. C" was 45.6 (NAKAMURA *et al.*, 1984; ABBAS, *et al.*, in preparation), coupled with 38.6 and 34.9 for two Japanese pest species, *E. vigintioctopunctata* and *E. vigintioctomaculata*, under field conditions (NAKAMURA 1976a, 1983). The egg mortality was 17.8, 50.4 and 53.9% in the 3 Periods. A parasitic wasp, *Tetrastichus* sp. B was important as a mortality factor of eggs, accounting for 48.2% $\left(\frac{138}{285}\right)$, 41.1% $\left(\frac{148}{360}\right)$ and 64.2% $\left(\frac{1240}{1929}\right)$ of the deaths during the egg stage.

2. Larva and pupa. Mortality factors were unkonwn for 1st to 3rd instar larvae, except that a few 3rd instars were found parasitized by wasps. Major mortality factors during the 4th instar to adult emergence were parasitic wasps and food shortage from overcrowding. Fourth instars were attacked by two species of wasps, *Tetrastichus* sp. C and *Pediobius foveolatus*, both of which belong to the Eulophidae, but the relative contribution of these wasps to the mortality could not be separated. The wasps were important as mortality factors of the 4th instar, i.e. 19.4%, 1.2% and 6.3% of the larvae were

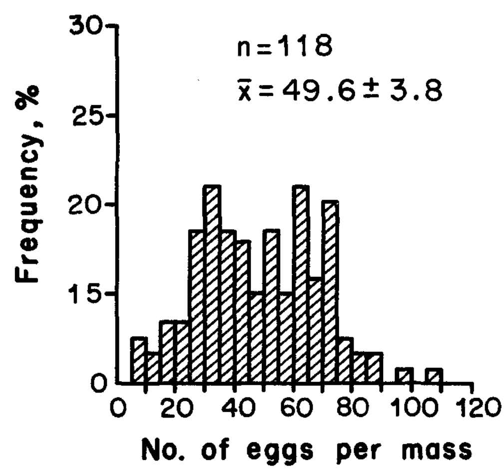

Fig. 5. Frequency distribution of the size of egg masses of *Epilachna* "sp. C". *n*: no. of masses examined. $\bar{X}$: mean $\pm$95% confidence limits.

Table 2. Life table for *Epilachna* "sp. C" in Padang, Sumatra in 1982. L_X: ‰ survival in terms of eggs.

Age class	Mortality factors	Period 1 (Mar.–May, 1982) No.	No. dying	% dying	L_X	Period 2 (July–Sept., 1982) No.	No. dying	% dying	L_X	Period 3 (Oct.–Dec., 1982) No.	No. dying	% dying	L_X
Egg		1610			1000	714			1000	3586			1000
	Parasitic wasp (*Tetrastichus* sp. B)		138	8.6			148	20.7			1240	34.6	
	Failure to hatch		54	3.4			19	2.7			0	0.0	
	Disappearence		93	5.8			193	27.0			689	19.3	
	Total		285	17.8			360	50.4			1929	53.9	
Larva hatched		1326			823.1	354			495.8	1657			462.1
	Unknown		1135	85.6			186	52.5			1132	68.3	
4th instar larva		191			118.6	168			235.2	525			146.4
	Parasitic wasps (*Tetrastichus* sp. C *Pediobius foveolatus*)		37	19.4			2	1.2			33	6.3	
	Unknown		31	16.2			0	0.0			399	76.0	
	Total		68	35.6			2	1.2			432	82.3	
Pupa		123			76.4	167			233.9	93			25.9
	Parasitic wasp (*Pediobius foveolatus*)		32	26.0			41	24.6			55	59.1	
	Dead (dried up)		17	13.8			0	0.0			0	0.0	
	Disappearence		17	13.8			50	29.9			21	22.6	
	Total		66	53.6			91	54.5			76	81.7	
New adult		57			35.4	76			106.4	17			4.7

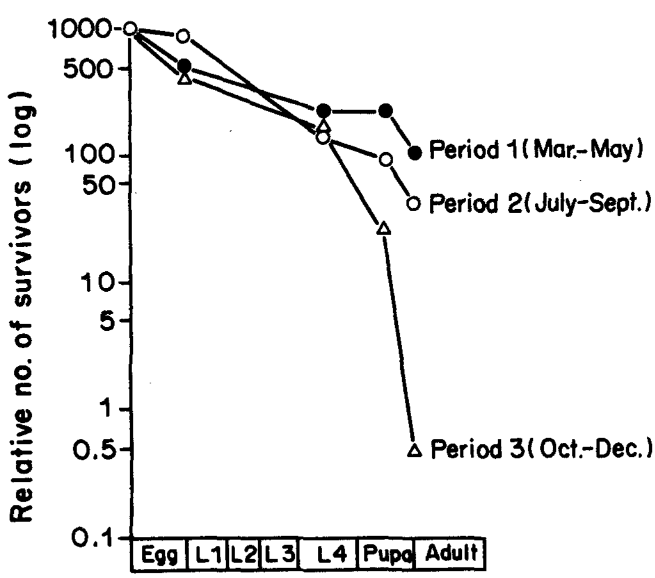

Fig. 6. Survivorship curves for *Epilachna* "sp. C".

were killed by the wasps in Periods 1–3 respectively. This made up 54.4% $\left(\frac{37}{68}\right)$, 100% $\left(\frac{2}{2}\right)$ and 7.6% $\left(\frac{33}{432}\right)$ of the deaths during the instar. Pupae were attacked only by *Pediobius foveolatus*. The extent of parasitism in this stage was larger and more persistent than that in 4th instar, i.e., 26.0%, 24.6% and 59.1%, for Periods 1–3 respectively. This was equal to 48.5% $\left(\frac{32}{66}\right)$, 45.1% $\left(\frac{41}{91}\right)$ and 72.4% $\left(\frac{55}{76}\right)$ of individuals which died during the pupal stage. Parasitic wasps caused a high mortality in egg, 4th instar, and pupal stages, but no simple density-dependent relationship was detected between this mortality and the number of individuals present. In contrast, the host plants were completely defoliated at the end of all Periods, so that death from starvation occurred in a density-dependent manner: Figure 6 shows that in Period 3, when the initial number of eggs was largest, the slope of the survivorship curve was much steeper than those of Periods 1 and 2 (in Period 2, only 4 host plants were used instead of 6 as in Periods 1 and 3, so the number of each developmental stage should be multiplied by $\frac{6}{4}$ for comparison). Figure 6 also shows that mortality was lowest in Period 2, when egg number was smallest (1071 eggs per 6 plants). Mortality increased between pupa and adult emergence (especially in Period 3) probably because pupae dropped with defoliated leaves and suffered a higher mortality on the ground.

Discussion

The 28-spotted lady beetle *Epilachna* (=*Henosepilachna*) *vigintioctopunctata* (henceforth abbreviated as Hvp) is most closely related to "sp. C" among Japanese species (Dieke, 1947; Nakamura, 1983). Hvp is a pest of solanaceous crops in the south-western part of Japan. Nakamura (1976a) carried out life table studies on Hvp in a suburb of Kyoto from 1970–1972. Overwintered adults of Hvp laid their eggs mainly in potato fields, and new adults of the first generation emerged in late June-early July. Egg mortality was 27% and was mainly due to failure to hatch and cannibalism by larvae, while food shortage was the main cause of death during larval stages, as occurred in "sp. C". Total mortality from egg to adult emergence was 90%. After the potatoes were harvested, new adults moved to eggplants and other solanaceous crops, where a 2nd generation emerged in August. These entered hibernation by the end of September. In the 2nd generation, egg and total mortality was higher than the first generation, ranging from 40–60% and 94–99.7%, respectively. The number of new adults which immigrated from potato was so large that eggs were subject to adult cannibalism and larvae to serious food shortage. Thus, "sp. C" and Hvp exhibited similar demographic traits as pest of crops, but the two were quite different in the diversity and levels of parasitism. "Sp. C" had three species of parasites, which killed a substantial portion of individuals in egg, larval and pupal stages (Table 2). In contrast, Hvp had no egg parasite and only a small percentage of 4th instar larvae and pupae were attacked by *Pediobius foveolatus*, i.e. in the first generation, no 4th instars and pupae were killed by the wasp on potato, and only 0.4–6.9% of 4th instars and 0–1.5% of pupae were attacked on egg plants. In the 2nd generation parasitism by *P. foveolatus* was again at low level, i.e. 2.5–5.0% of 4th instars and pupae were attacked, except in 1972, when the number of larvae was extremely small and 26.7% of the 4th instars were killed. HIRANO (1984) studied Hvp populations in Nagoya, central Japan, from 1976 to 1979, and confirmed the low level of parasitism by *P. foveolatus*. He found no egg parasitism and few parasitized larvae in the 1st generation on both potato and eggplant, and only 2% of individuals, in terms of initial number of eggs, were parasitized in the 4th instar during the 2nd generation.

NAKAMURA et al. (1984) studied survivorship and fertility schedules under laboratory conditions, and showed that the mean longevity of "sp. C" was as long as 70.5 and 63.8 days for male and female, respectively. After a long pre-reproductive period (18.9 days), the females laid eggs at a nearly constant rate and fertility increased even at the end of the life. Therefore the reproductive value (FISHER, 1930) of the "sp. C" had no clear peak, but had a plateau with small peaks which spanned nearly 40 days; the highest peak value was attained on day 56 of the females' adult life (NAKAMURA et al., 1984, Figs. 2 and 4). This prolonged reproductive schedule and the high power of dispersal of "sp. C" were no doubt advantageous for exploiting bitter cucumber, which is available throughout the year, but is rather patchily distributed in space.

SUMMARY

The population dynamics of an epilachnine beetle, which is closely related to *Epilachna sparsa* DIEKE (henceforth called "sp. C") and feeds on bitter cucumber *Momordica charantia*, was studied by mark-recapture of adults and the construction of life tables. The study was repeated three times, i.e., March–May, July–September and October–December in 1982, in Padang, Sumatra, Indonesia. After the establishment of the host plants, adults of "sp. C" soon colonized, and each study period ended in the death of the plants due to defoliation by the larvae and adults. The estimated mean length of residence of adults ranged from 6–11 days, but this was probably much shorter than the actual longevity, because the adults were so active that they flew away, or dropped off the plants, when they were approached or slightly disturbed. Life tables indicated that egg mortality ranged from 17.8–53.9%, and a parasitic wasp *Tetrastichus* sp. B made up 41.1–64.2% of egg mortality. Two wasps, *Tetrastichus* sp. C and *Pediobius foveolatus* killed 1.2–19.4% (7.6–100%)* of 4th instars and only the latter species attacked the pupae, killing 24.6–59.1% (45.1–72.4%). Parasitism and starvation by overcrowding contributed most to the total mortality from egg to adult emergence, which ranged from 89.4–99.5%. "Sp. C" had a higher diversity and level of parasitism than the Japanese species, *E. vigintioctopunctata*. The high dispersal power of "sp. C", coupled with the prolonged

* The figures in parentheses refer to percentage in terms of number of the deaths in each stage.

l_x–m_x schedules shown under laboratory conditions, was advantageous for exploiting the food plant which was available throughout the year, but was rather patchily distributed in space.

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ニガウリを食草とするスマトラ産エピラクナ1種の個体群動態
——成虫のマーキングと生命表による調査——

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スマトラ島パダン市においてニガウリ *Momordica charantia* を食草とするエピラクナ *Epilachna* sp. C を1982年3-5月，7-9月，10-12月の3回にわたり調査した．本種は日本にいるニジュウヤホシテントウ *Epilachna vigintioctopunctata* と非常に近縁である．毎回同じ場所にニガウリを栽培し，飛来または羽化する成虫には個体識別マークをつけ，卵から羽化までの生命表を作製した．食草を設置するとすぐに成虫が飛来し大量に産卵するので約2カ月後には幼虫，新成虫によって食草は食いつくされ枯死した．成虫の性比は1：1で，ニジュウヤホシテントウに較べてはるかに敏感でヒトが近づくと飛去したり落下しやすい．従って食草上での滞留日数の推定値6.3-11.1日よりも“真の寿命”はずっと長いだろう．生命表によれば，卵の死亡率は17.8-53.9%，寄生蜂 *Tetrastichus* sp. B は卵期の死亡の41.1-64.2%を占めた． 4令幼虫には2種の寄生蜂 *Tetrastichus* sp. C と *Pediobius foveolatus* がつき1.2-19.4% (7.6-100%)，サナギには *P. foveolatus* のみがみられ，24.6-59.1% (45.1-72.4%) の個体が死亡した（カッコ内は令期内死亡に占める割合）．結局，卵から羽化までの全死亡率は89.4-99.5%で寄生蜂とエサのくいつくしによる餓死が重要な死亡要因であった．ニジュウヤホシテントウに較べて寄生蜂による死亡の重要性が大きいことがわかった．食草のニガウリは一年中みられるが，非常に小面積にしかも一箇所では短期間しか栽培されない．本種が強い分散力をもち，長寿命でしかも平均した産卵能力を長い期間にわたってもち続けていることはパッチ状に分布する食草を利用するうえで有利な特性といえよう．