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Survivorship and Fertility Schedules of Two Epilachnine "Species" Feeding on Cucurbitaceous Plants under Laboratory Conditions (Coleoptera: Coccinellidae)[1,2,3]

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Two "species" of Sumatran epilachnine beetles, which are similar to *Henosepilachna sparsa* DIEKE, were reared under laboratory condition to study their survivorship and fertility schedules. The "species C" fed on bitter cucumber and "species D" on squash. The mean longevity of the males (70.5 days in sp. C and 88.6 in sp. D) was longer than that of females (63.8 days in sp. C and 63.9 in sp. D). The mean length of the pre-reproductive period (18.9 days in sp. C and 15.5 in sp. D) was longer than that of post-reproductive period (4.0 days in sp. C and 5.2 in sp. D). The females of the two species laid eggs at a nearly constant rate throughout their reproductive period. The reproductive value V_x/V_0 of the two species remained at high level for most of adult life, resulting from the prolonged survivorship and fertility schedules. The total number of eggs produced per female was 651.9 (sp. C) and 763.8 (sp. D). The intrinsic rate of natural increase r was 0.10 (sp. C) and 0.12 (sp. D) per capita per day. The demographic traits of these Sumatran species are discussed in comparison with temperate species.

INTRODUCTION

About one-fifth of described species of Coccinellidae belong to the subfamily Epilachninae. Contrary to most other coccinellids which are either insectivorous or fungivorous, all epilachnines are phytophagous, feeding on leaves of plant species belonging to Solanaceae, Cucurbitaceae, Fabaceae, etc. Abundant crops such as potato, egg plant and squash are frequently subject to serious attacks by these beetles in Indonesia, as in other regions including Japan. Although some epilachnine species occur in temperate regions, the distribution of the subfamily clearly centres in the tropics. In fact, more than fifty "species" of these beetles have been recorded from Indonesia, while only eight species occur in Japan.

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Since 1980, we have studied the population dynamics of some of these epilachnine beetles in the Province of West Sumatra. Our study consists of three parts, i.e. collection of the beetles from various localities around West Sumatra with records of their host plant, field population studies and laboratory experiments.

The present article, as the first of the series, describes the duration of successive immature stages, and the survivorship and fertility schedules of two epilachnine "species" feeding on cucurbitaceous crops under laboratory condition. The study affords an opportunity for comparison of the demographic characteristics of tropical and temperate species, because some information is available for the Japanese species (e.g. IWAO, 1971; NAKAMURA, 1976 a, b, 1983; NAKAMURA and OHGUSHI, 1979, 1981, 1983).

MATERIALS AND METHODS

As DIEKE (1947) pointed out in his revision of the epilachnine beetles, the Indonesian Archipelago is rich, not only in the number of species, but also in the intraspecific variability in populations from the same, or different localities. This has caused great confusion of the identification of Indonesian species, because no critical taxonomic studies have been carried out on these beetles since the work of DIEKE, despite their economical importance.

According to Dr. H. SASAJI (Fukui University), who kindly identified the specimens for us, the two "species" feeding on the cucurbitaceous plants were closely similar to *Henosepilachna sparsa*, recorded by DIEKE as *Epilachna sparsa*. The two "species" were referred to as *Henosepilachna sparsa* like "species C" and "species D" in our tentative list of the Epilachninae of West Sumatra (NAKAMURA et al., 1983). The two "species" are pests of cucurbitaceous crops at any altitudes from 0 to 2,000 m. "Sp. C" feeds exclusively on bitter cucumber *Momordica charantia*, and "sp. D" feeds on many kinds of crop, such as squash *Cucurbita* sp., cucumber *Cucumis sativus*, wax gourd *Benincasa cerifera* and sponge cucumber *Luffa acutangula*. The adults of "sp. C" usually have 28, or fewer, spots, with many "non-persistent" spots (cf. DIEKE, 1947). In contrast, "sp. D" is only 12 spotted, with few non-persistent spots. The larvae of "sp. D" have a yellow body color, and the tips of the spines on the back are blackish. The larvae of "sp. C" are also yellow, but their spines were yellow to the tip. A preliminary food choice experiment showed that "sp. C" and "sp. D" will feed only on the original host plants from which they were collected: "sp. C" only on bitter cucumber, and "sp. D" on squash, cucumber, sponge cucumber, etc. These facts suggest that "sp. C" may be identical to *H. implicata* mentioned by DE GUNST (1957) and KALSHOVEN (1981), and "sp. D" may be *H. dodecastigma* mentioned in KALSHOVEN (1981). Identification of the epilachnine beetles by the external appearence, such as spot-pattern and body color is difficult and often misleading (e.g. DIEKE, 1947; DE GUNST, 1957). The taxonomic status of the "species" will be studied later by examination of more reliable characteristics, especially male genitalia, and by crossings, and food choice experiments.

Experiment 1. Adults of the beetles were collected from bitter cucumber *M. charantia* ("sp. C") and from squash *Cucurbita* sp. ("sp. D") in Padang and reared in the laboratory to obtain eggs for the experiments. Each egg mass deposited was isolated in a plastic cup (13 cm in diameter and 5 cm in depth), and records were kept of hatching and of larval moults. The number of larvae reared in a cup was restricted to ten from the third instar onward to avoid overcrowding. Ten cups ("sp. C") and eleven cups ("sp.

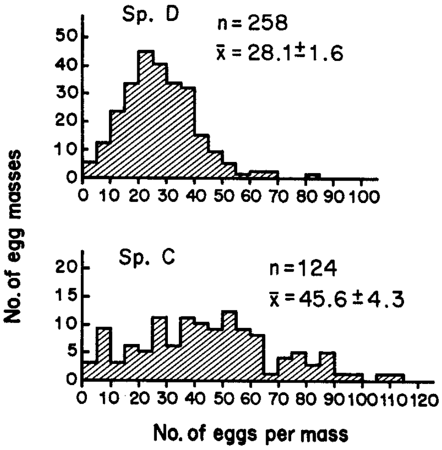

Fig. 1. Frequency distribution in the size of egg masses of *Henosepilachna* "sp. C" (bottom) and "sp. D" (top). The number of masses examined (n) and values of mean ($\bar{x}$) with 95% confidence limits are given in the figure.

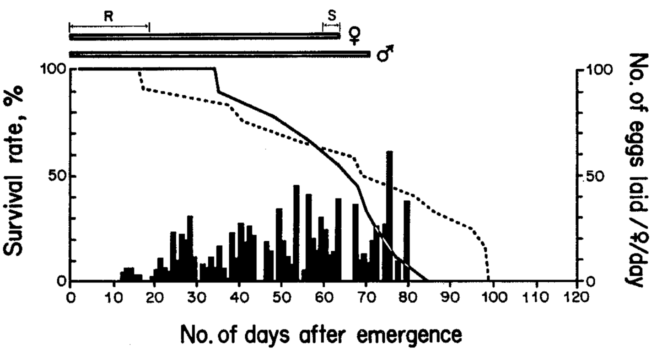

Fig. 2. Survivorship and fertility schedules of *Henosepilachna* "sp. C" under laboratory condition. Solid and dotted lines refer to survivorship curves for males and females, respectively, and the histogram shows the number of eggs laid per female per day. The horizontal bars above the figure depict the average longevity for both sexes, and R and S the average length of the pre- and post-reproductive period.

D") were used for these experiments.

Experiment 2. A pair of newly emerged adults were confined in a plastic cup of the same size to study their survivorship and fertility schedules. Nine and eleven pairs were reared for the "sp. C" and "sp. D," respectively.

All the experiments were carried out in the Sumatra Nature Study Laboratory, Andalas University in Padang under room temperatures ranging from 24 to 32°C. The mean monthly temperature of Padang fluctuated only between 26.7 (September to December) and 27.5°C (May) according to the meteorological data from 1879 to 1941 (Rika-Nenpyo, 1982). The cups were checked daily and food was changed. The study period extended from December 1981 to May 1982.

RESULTS

1. *Developmental times of the immature stages*

The duration of successive immature stages (in days) was as follows:

"Species"	Egg	I	II	III	IV	Pupa	Total
C	4.3	3.2	2.6	3.0	4.9	4.5	22.5
D	4.0	3.4	2.7	2.9	5.3	4.7	23.0

2. *Sex ratio of newly emerged adults*

Newly emerged adults of the two "species" showed no significant deviation from the expected 1 : 1 sex ratio (binomial test, $p=0.05$; 45 ♀♀ : 58 ♂♂ in "sp. C," and 44 ♀♀ : 54 ♂♂ in "sp. D").

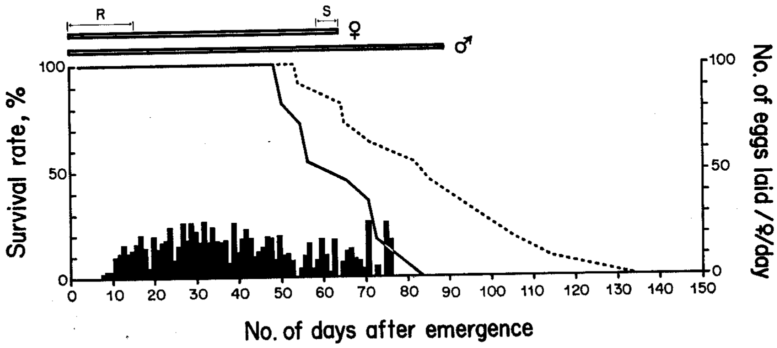

Fig. 3. Survivorship and fertility schedules of *Henosepilachna* "sp. D" under laboratory condition. Explanations as in Fig. 2.

Table 1. Comparison of survivorship and fertility schedules between the two Sumatran *Henosepilachna* "species" under laboratory conditions

Species	Sp. C		Sp. D	
Food plant	*Momordica charantia*		*Cucurbita* sp.	
No. of replications	9		11	
Longevity (in days) ♂♂	70.5± 17.5	(17– 99)*	88.6± 16.4	(55– 133)
♀♀	63.8± 11.7	(35– 84)	63.9± 7.8	(49– 83)
Pre-reproductive period (in days)	18.9± 4.7	(11– 27)	15.5± 3.7	(9– 23)
Post-reproductive period (in days)	4.0± 2.5	(1– 11)	5.2± 2.4	(2– 15)
Fertility (total no. of eggs laid per female)	651.9±309.1	(121–1,224)	763.8±204.8	(341–1,185)
Intrinsic rate of natural increase (per capita per day), *r*	0.10		0.12	
Mean length of a generation (in days), *T*	58.1		49.5	

* Average±95% confidence limits (range).

3. *Egg mass size*

Figure 1 shows the frequency distribution of egg mass size, indicating that the mean size of egg masses was 45.6 ("sp. C") and 28.1 ("sp. D"). These values were somewhat smaller than those obtained in field populations, possibly because of the limited space in the cups in which they were kept (unpublished data).

4. *Survivorship and fertility schedules*

Figures 2 and 3 show the survivorship (l_x) of female and male adults and the age-specific fertility which is expressed as the change in the number of eggs laid per female per day. Since the sex ratio of the newly emerged adults was 1: 1, the age-specific fertility in Figs. 2 and 3 is equivalent to $m_x \times 2$ (m_x is usually defined as the number of living females born per female per unit time, SOUTHWOOD, 1978). Table 1 summarizes the longevity, fecundity and two basic life history parameters r and T for both species. Table 1 shows that the mean longevity of the males (70.5 days in "sp. C" and 88.6 in "sp. D") was significantly longer than that of the females (63.8 days in "sp. C" and 63.9 in "sp. D"). The mean length of the pre-reproductive period (18.9 days in "sp.

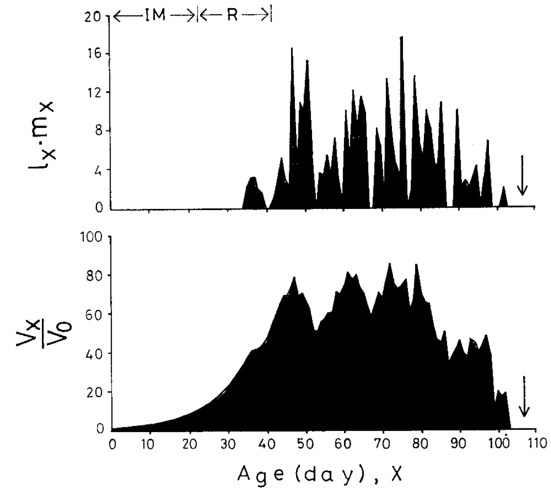

Fig. 4. Reproductive function ($l_x \cdot m_x$, top) and reproductive value (V_x/V_0, bottom) plotted against age for *Henosepilachna* "sp. D." *IM*: duration of the immature stages. *R*: mean duration of the pre-reproductive period. Vertical arrow shows the extinction of the females.

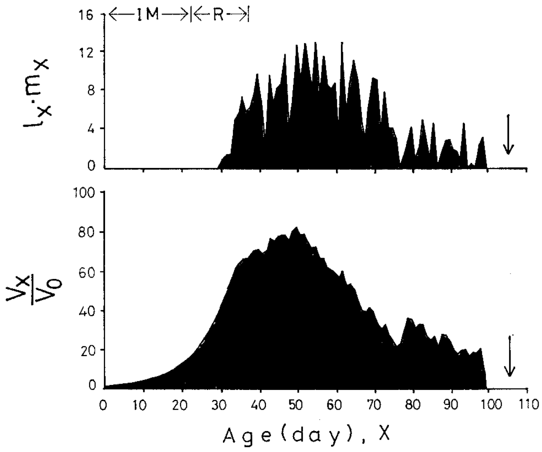

Fig. 5. Reproductive function ($l_x \cdot m_x$, top) and reproductive value (V_x/V_0, bottom) plotted against age for *Henosepilachna* "sp. D." Explanations as in Fig. 4.

C" and 15.5 in "sp. D") was much longer than that of the post-repoductive period (4.0 days in "sp. C" and 5.2 in "sp. D"). The shape of the histogram giving the age-specific fertility shows that the fertility of "sp. C" increased even at the end of the life (Fig. 2), whereas "sp. D" produced eggs at a nearly constant rate throughout its reproductive period (Fig. 3). Since the duration of the pre-reproductive period of the females varied considerably, i.e. 11–27 days in "sp. C" and 9–23 days in "sp. D," the results were examined to see whether the females with the shorter pre-reproductive period completed oviposition earlier, and whether they died earlier than those with the longer pre-reproductive period. KENDALL's rank test (τ) revealed that the females's age at first oviposition (in days) was not significantly correlated with either age at final oviposition or with age at death.

Basic population parameters, including R_0, r, T and V_x/V_0, were calculated on the basis of the l_x-m_x schedules in Figs. 2 and 3. The intrinsic rate of natural increase r is defined in a population with stable l_x-m_x schedules which is multiplying in an unlimited environment. These conditions are rarely realized in natural populations. However these parameters are very helpful in comparing demographic traits of populations between and within species (BIRCH, 1948; BIRCH et al., 1963).

The r value was determined by solving the equation $\sum e^{-rt}l_t m_t = 1$ for r, where t is age in days. For the calculation of r, the life tables of both the immature and adult stages are required. In practice, we assumed that no deaths occurred in the immature stages of the two "species," because the eggs, larvae and pupae rarely died unless we mishandled them. The r value thus derived was 0.10 and 0.12 per capita per day for "sp. C" and "sp. D," respectively.

The net reproductive rate R_0 is the average number of female eggs produced per female beetle. This is given by the expression, $R_0 = \sum l_x \cdot m_x$. Our estimates of R_0

were 332.7 ("sp. C") and 379.2 ("sp. D"). The total number of eggs produced per females was 651.9 (range 121 to 1,224) for "sp. C" and 763.8 (range 341 to 1,185) for "sp. D" (Table 1), that is twice the value of R_0.

The mean length of a generation T was derived from

$$T=\frac{log\ R_0}{r}.$$

This gave estimates of 58.1 for "sp. C" and 49.5 days for "sp. D."

The concept of reproductive value was developed by FISHER (1930) to measure the relative contribution of age x to future generations, or conversely, the diminution of future population increase by removing an individual of age x. FISHER's reproductive value is given by

$$\frac{V_x}{V_0}=\frac{e^{-rx}}{l_x}\sum_{t=x}^{\infty}e^{-rt}l_t m_t \Delta t,$$

where Δt is an interval for measuring l_t and m_t ($\Delta t=1$ in this case). The reproductive value of an individual usually increases until the age of first reproduction and then it decreases with age. However the reproductive value of the two "species" changed with age in a different manner, as shown below. The reproductive values of the "sp. C" (Fig. 4) had no clear peak, but had a plateau with small peaks which spanned nearly 40 days; the highest peak value was attained on day 79 of oviposition (it fell on day 56 and day 37 of female's adult life and of female's reproductive period, respectively). The reproductive value of "sp. D" is shown in Fig. 5, and it had a smooth peak on day 50 after oviposition (it fell on day 27 and day 12 of female's adult life and of female's reproductive period, respectively). The reproductive value remained at a relatively high level until near the end of the females's life span. Thus the two "species" showed a high reproductive value for most of their life span, resulting from the prolonged longevity and fertility schedules (Figs. 2 and 3).

DISCUSSION

Among the epilachnine beetles in Japan, *Henosepilachna vigintioctopunctata*, a notorious pest of potato and egg plant, is most closely related to the two Sumatran "species." Intensive field studies were carried out on *H. vigintioctopunctata* (NAKAMURA, 1976 a, b), but no detailed study on survival and fertility schedules under laboratory condition is so far available. The duration of the pre-reproductive period of this species was shorter than that of the Sumatran "species": 8.5 days reported by KONO (1982) and 11.3 days by YASUE and KAWADA (1964). These two studies were done under conditions of 25°C and 16L–8D which the species experiences in nature during the summer. The total number of eggs laid per female of *H. vigintioctopunctata* ranged widely, i.e. 508–1,164 (TAKAHASHI, 1932, for the overwintered and summer generation, respectively) and 588 (NAKAMURA, 1976 b, for the overwintered adults). The fecundity of the two Sumatran "species" was no higher than that of *H. vigintioctopunctata*.

The shapes of the age specific fertility curves of the two Sumatran "species" (Figs. 2 and 3) were quite different from those of temperate species, which usually have a clear peak at the beginning of the reproductive period (e.g. PEFEROEN et al., 1981 for the

Colorado potato beetle *Leptinotarsa decemlineata*; ZALUCKI, 1981 for several species of butterfly). Examples of the prolonged reproductive schedules were reported in a tropical bug and fly species: Firstly, LANDAHL and ROOT (1969) compared the l_x-m_x schedules of a milk weed bug *Oncopeltus fasciatus* from a temperate locality, and *O. unifasciatellus* from a tropical locality, and showed that the two species exhibited similar rates of development. However, the tropical species, which began ovipositing later and produced fewer eggs, had a lower value of r. Secondly, BIRCH et al. (1963) compared the l_x-m_x schedules of *Drosophila serrata* from widely separated geographic regions, and showed that the race from tropical locality had a more prolonged m_x-schedule with a less conspicuous peak, and the total number of eggs laid per female was much smaller than for the races from temperate localities. The prolonged reproductive schedules of the Sumatran epilachnine "species" no doubt have an adaptive value for living in tropical environments, where food resources are available throughout the year, but are rather patchily distributed in space.

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