

Survivorship and Fertility Schedules of a Sumatran Phytophagous Lady Beetle, *Epilachna enneasticta* (Coleoptera, Coccinellidae) under Laboratory Conditions

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A Sumatran phytophagous lady beetle, *Epilachna enneasticta* was reared under laboratory conditions in order to study its survivorship and fertility schedules. *E. enneasticta* required 28.7 days for development of the immature stages. The mean longevity of males (90.4 days) was longer than that of females (71.4 days). The mean length of the pre-reproductive period (30.1 days) was longer than that of the post-reproductive period (2.4 days). Females laid eggs continuously at a rather constant rate throughout their reproductive period and the average number of eggs produced per female was 425.4. The intrinsic rate of natural increase r was 0.070 per capita per day. *E. enneasticta* showed half to two-thirds of the mean fecundity, twice the pre-reproductive period, and a lower intrinsic rate of natural increase than three of its sympatric species in Sumatra (*E. vigintioctopunctata*, *E. septima*, and *E. dodecastigma*).

Key words: Coccinellidae, *Epilachna enneasticta*, phytophagous lady beetle, survivorship and fertility schedules, West Sumatra

INTRODUCTION

Demography is a key to life history theory and allows us to calculate the strength of selection on life history traits under many conditions (STEARNS, 1992). Life history traits have been compared between temperate and tropical populations of single species (intraspecific comparison) as well as between those of closely related species (interspecific comparison) in various insect groups (e.g. BIRCH et al., 1963; LANDAHL and ROOT, 1969; BALDWIN and DINGLE, 1986; SHAPIRO, 1986). Survivorship and fertility schedules of phytophagous lady beetles (subfamily Epilachninae) have also been studied for five Indonesian (NAKAMURA et al., 1984, 1995; ABBAS et al., 1985) and three Australian species (RICHARDS and FILEWOOD, 1988, 1990).

One of the five Indonesian species, *Epilachna enneasticta* MULSANT is distributed at higher regions (between 400 and 1,400 m in altitude) than the other four species (KATAKURA et al., 1988, 1992). In a previous study (NAKAMURA et al., 1995) life table parameters of Javanese *E. enneasticta* were examined under higher temperature conditions than the natural habitat to enable a comparison of the parameters with those of two Javanese species living at lower regions. The present study aims to examine the survivorship and fertility schedules of *E. enneasticta* by rearing the Sumatran population under more suitable conditions.

MATERIALS AND METHODS

Experiments were carried out from October 1988 to August 1989 in the Sumatra Nature Study Laboratory of Andalas University in Padang, Central Sumatra (Province of Sumatera Barat). All rearing was carried out under relatively constant temperature (24.5 to 26°C) and natural day length (12L/12D), with a daily replacement of the food plant (*Solanum torvum* leaves).

Experiment 1. Developmental times of the immature stages. Adults of *E. enneasticta* were collected from a perennial wild shrub, *S. torvum* at Kayu Jao (1,250 m alt.), 46 km southeast of Padang. They were mass reared with the food plant in plastic boxes (22.0 × 30.5 × 6.0 cm) in the laboratory to obtain eggs. The food plant was checked daily for eggs. Each egg mass deposited was isolated in a transparent plastic cup (10 cm in diameter and 4.3 cm in depth), and fresh leaves of *S. torvum* were put into the cup just before hatching. Dates of oviposition, hatching, and larval molt were recorded daily to determine the developmental times. From the fourth stadium onward, the number of larvae reared in each cup was restricted to ten at most to avoid overcrowding. Seventy nine first stadium larvae from 4 egg masses were used for this experiment.

Experiment 2. Survivorship and fertility schedule. Recently emerged (within two days) males and females were confined in pairs in the same plastic cups as used in Experiment 1. To study the survivorship and fertility schedules, the number of eggs deposited and the dates of oviposition and adult death were recorded for 18 pairs.

RESULTS

1. *Developmental times of the immature stages*

Table 1 shows the duration of successive immature stages of *E. enneasticta*. The high mortality at the pupal stage was caused by excessive humidity in two out of eight plastic cups. The total developmental time of *E. enneasticta* in Padang was 28.7 days.

2. *Sex ratio of newly emerged adults*

Newly emerged adults (27 females, 32 males) showed no significant deviation from the expected 1:1 sex ratio ($z = 0.651$, $p > 0.5$, binomial test).

Table 1. Duration of successive immature stages (in days) of *E. enneasticta*, *E. vigintioctopunctata*, *E. septima*, and *E. dodecastigma*. Numbers in parentheses indicate number of individuals examined.

Species ^a	Egg	L1	L2	L3	L4	Pupa	Total	Reference ^b
<i>E. enneasticta</i>	5.4 (82)	4.6 (79)	3.3 (75)	3.4 (73)	6.4 (72)	5.6 (65)	28.7 (59)	♀: 28-31 ♂: 28-32 ^c
<i>E. enneasticta</i>	4.0	4.8	4.1	4.4	6.3	5.9	29.5	3
<i>E. vigintioctopunctata</i>	3.5	3.6	3.2	3.6	5.1	4.5	23.4	2
<i>E. septima</i>	4.3	3.2	2.6	3.0	4.9	4.5	22.5	1
<i>E. dodecastigma</i>	4.0	3.4	2.7	2.9	5.3	4.7	23.0	1

^a *E. vigintioctopunctata*, *E. septima*, and *E. dodecastigma* were treated as sp. A (ABBAS et al., 1985), sp. C, and sp. D (NAKAMURA et al., 1984), respectively.

^b PS: present study, 1: NAKAMURA et al. (1984), 2: ABBAS et al. (1985), 3: NAKAMURA et al. (1995).

^c Range of total developmental times.

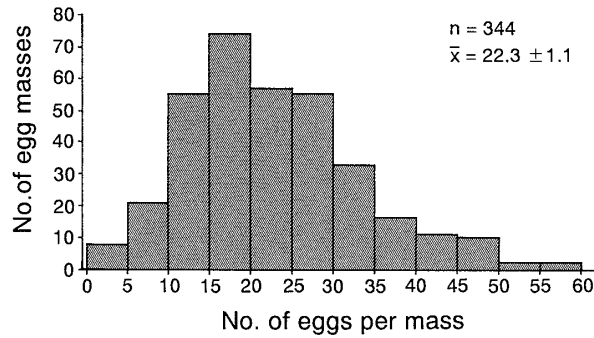


Fig. 1. Frequency distribution of *E. enneasticta* egg mass size. The number of masses examined (n) and the means (\bar{x}) with 95% confidence limits are shown.

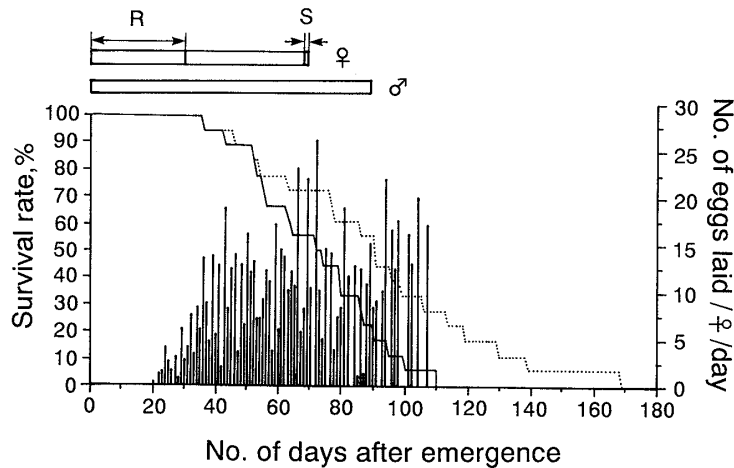


Fig. 2. Survivorship and fertility schedules of *E. enneasticta* under laboratory conditions. Solid and dotted lines refer to survivorship curves for females and males, respectively. The histogram shows the number of eggs laid per female per day. Two horizontal bars depict the average longevity for both sexes. R and S are the average length of the pre- and the post-reproductive periods, respectively.

3. Egg mass size

Figure 1 shows the frequency distribution of egg mass size. The mean size of egg masses was 22.3 ($N=344$).

4. Survivorship and fertility schedules

Figure 2 shows the survivorship (l_x ; the number of living individuals/ 18×100) 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 Fig. 2 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). The shape of the age-specific fertility shows that females produced eggs continuously at a rather constant rate throughout their long reproductive period (Fig. 2). It should be noted that females which were alive around 100 days after emergence could still oviposit as many eggs as they did during the younger period (Fig. 2). The number of eggs laid per female per day

Table 2. Survivorship and fertility schedules of four epilachnine species under laboratory conditions

Species ^a	<i>E. enneasticta</i>	<i>E. vigintioctopunctata</i>	<i>E. septima</i>	<i>E. dodecastigma</i>	
Host plant and food plants	<i>S. torvum</i>	<i>S. torvum</i>	<i>S. torvum</i>	<i>Momordica charantia</i>	<i>Cucurbita</i> sp.
Origin	W. Sumatra	W. Java	W. Sumatra	W. Sumatra	W. Sumatra
Rearing temperature	24–26.5°C	27–30°C	24–32°C	24–32°C	24–32°C
No. of replications	18	8	10	9	11
Longevity (in days)					
male	90.4 ± 17.3 (35–167) ^b	69.9 ± 13.3 (31–80)	87.6 ± 3.3 (80–94)	70.5 ± 17.5 (17–99)	88.6 ± 16.4 (55–133)
female	71.4 ± 10.4 (35–110)	73.6 ± 2.5 (69–78)	57.7 ± 8.0 (43–81)	63.8 ± 11.7 (35–84)	63.9 ± 7.8 (49–83)
Pre-reproductive period (in days)	30.1 ± 3.0 (20–43)	15.9 ± 3.7 (11–25)	11.0 ± 1.5 (8–15)	18.9 ± 4.7 (11–27)	15.5 ± 3.7 (9–23)
Post-reproductive period (in days)	2.4 ± 0.9 (1–8)	5.6 ± 2.9 (2–13)	2.3 ± 1.3 (1–7)	4.0 ± 2.5 (1–11)	5.2 ± 2.4 (2–15)
Fertility (total no. of eggs laid per female)	425.4 ± 125.3 (102–1,044)	323.6 ± 53.1 (228–412)	770.7 ± 108.2 (590–1,115)	651.9 ± 309.1 (121–1,224)	763.8 ± 204.8 (341–1,185)
Intrinsic rate of natural increase (per capita per day), <i>r</i>	0.070	0.081	0.125	0.10	0.12
Mean length of a generation (in days), <i>T</i>	76.6	62.7	47.6	58.1	49.5
Reference ^c	Present study	3	2	1	1

^a *E. vigintioctopunctata*, *E. septima*, and *E. dodecastigma* were treated as sp. A, sp. C, and sp. D, respectively, in ABBAS et al. (1985) and NAKAMURA et al. (1984).

^b Average ± 95% confidence limits (range). Although longevity, pre- and post-reproductive periods, and fertility of *E. enneasticta* in W. Java were shown by average ± SD (range) in NAKAMURA et al. (1995), they are also shown by average ± 95% confidence limits (range) in this table.

^c 1: NAKAMURA et al. (1984), 2: ABBAS et al. (1985), 3: NAKAMURA et al. (1995).

fluctuated to some extent because (1) individual females tended to oviposit at intervals of 1–3 days and (2) the number of females examined was not large. Table 2 shows the longevity, pre- and post-reproductive periods, fertility, intrinsic rate of natural increase (*r*), and mean generation length (*T*) of *E. enneasticta*.

(a) *Longevity, pre- and post-reproductive periods.* The mean longevity of the males (90.4 days) was significantly longer than that of the females (71.4 days) ($U=107.5$, $p < 0.05$ by a one tailed, MANN-WHITNEY *U*-test). The mean length of the pre-reproductive period (30.1 days) was much longer than that of the post-reproductive period (2.4 days). The duration of the pre-reproductive period of the females varied considerably, 20 to 43 days. KENDALL's rank tests revealed that the female's age at first oviposition (in days) was not significantly correlated with either age at final oviposition ($z=0.661$, $p > 0.5$) or with age at death ($z=0.859$, $p > 0.1$).

(b) *Intrinsic rate of natural increase *r*.* The *r* was determined by solving the equation $\sum e^{-rt} l_t m_t = 1$ for *r*, where *t* is age in days (BIRCH, 1948). We need the life table for both the immature and adult stages for the calculation of *r*. However, eggs, larvae, and pupae rarely died on *S. torvum* leaves (NAKAMURA et al., 1984, 1995; ABBAS et al., 1985) unless we had mishandled them. Thus, we assumed no death in the immature stages in practice. The *r* value thus derived was 0.070 per capita per day.

(c) *Net reproductive rate *R*₀ and mean generation length *T*.* The *R*₀ ($= \sum l_x m_x$) is the average number of female eggs produced per female adult. The mean length of generation *T* was derived from $T = \frac{\log R_0}{r}$. The values of *R*₀ and *T* thus derived were 213.0 (eggs per female), and 76.6 (days) (Table 2). The total number of eggs produced per female was 425.4 (Table 2), which is twice the value of *R*₀.

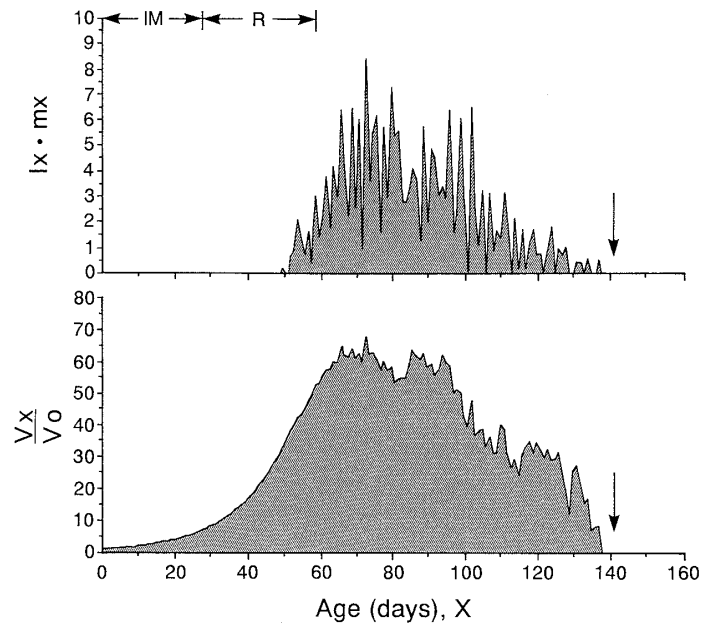


Fig. 3. Reproductive function ($l_x m_x$, top) and reproductive value ($\frac{V_x}{V_0}$, bottom) plotted against age after oviposition for *E. enneasticta* under laboratory conditions. *IM*: duration of the immature stages. *R*: mean duration of the pre-reproductive period. Vertical arrows show death of females.

(d) *Age-specific fertility and reproductive value.* FISHER'S (1930) reproductive value is given by $\frac{V_x}{V_0} = \frac{e^x}{l_x} \sum_{t=x}^{\infty} e^{-rt} l_t m_t \Delta t$, where Δt is the interval used for measuring l_x and m_x ($\Delta t = 1$ day in this case). The reproductive value of *E. enneasticta* reached a peak at 72.7 days (i.e., 44.0 days and 13.9 days after the start of the female's adult life and of her reproductive period, respectively) and then the value dropped gradually until near the end of the female's life span (Fig. 3).

DISCUSSION

In Indonesia, *E. septima* and *E. dodecastigma* are serious pests of cucurbitaceous crops (KATAKURA et al., 1988). *E. vigintioctopunctata* is also a serious pest of solanaceous crops and weeds such as egg plant, potato, and *S. torvum* (KATAKURA et al., 1988). The present species, *E. enneasticta* coexists with *E. vigintioctopunctata* on the same host plants only at higher regions in Sumatra and Java: *E. enneasticta* is distributed between 400 and 1,400 m alt., while *E. vigintioctopunctata* is found between 0 and 1,400 m (KATAKURA et al., 1988). In the coexisting range, *E. enneasticta* is always less abundant than *E. vigintioctopunctata* (KATAKURA et al., 1988).

Field population studies at Padang (less than 140 m alt.) indicated that population growth of *E. vigintioctopunctata* and that of *E. septima* on the crop plants were so rapid that the plants were often defoliated (NAKAMURA et al., 1988, 1990 for *E. vigintioctopunctata*; ABBAS and NAKAMURA, 1985 for *E. septima*). Further, adults of *E. septima*, *E. dodecastigma*, and *E. vigintioctopunctata* have such a strong dispersal ability by flight that they tend to fly away by

artificial disturbance in the routine census (NAKAMURA, personal observation). As a result, they colonized the new fields immediately after the seedlings of their host plants were planted (ABBAS and NAKAMURA, 1985; NAKAMURA et al., 1988).

Since 1990, a long-term population study of *E. enneasticta* and *E. vigintioctopunctata* on *S. torvum* has been carried out at Sukarami (980 m alt.), West Sumatra, which is 13 km north of Kayu Jao (1,250 m alt.), the collection site of the present material. The study over 4 years indicates that 1) the field population of *E. enneasticta* remained at a low level; 2) the *E. vigintioctopunctata* population was more abundant and fluctuated widely with several high peaks; 3) *E. enneasticta* was so sedentary that it remained on the food plants even when disturbed (NAKAMURA et al., unpubl.).

These field observations at Padang and Sukarami suggest that *E. enneasticta* is characterized by lower density and a weaker dispersal potential than the three species, *E. vigintioctopunctata*, *E. septima*, and *E. dodecastigma*. These differences between *E. enneasticta* and the three other species are closely related to their different survivorship and fertility schedules examined under laboratory conditions. According to NAKAMURA et al. (1984) and ABBAS et al. (1985), the above three species showed a high reproductive value for most of their life span, as a result of the prolonged survivorship and fertility schedules. Females of *E. enneasticta* also laid eggs continuously at a rather constant rate throughout their reproductive period and lived significantly longer than males (Fig. 2, Table 2). However, *E. enneasticta* exhibited the following traits which were quite different from those of the other three species: (1) the duration of the immature stage was about one week longer (Table 1); (2) the mean length of the pre-reproductive period was about twice as long (Table 2); (3) fertility was about two-thirds (Table 2); (4) the r value was smaller, and T was larger (Table 2). Slower development in the immature stage, lower fertility, a lower r value, and a resultant larger T value were also reported in Javanese *E. enneasticta* collected in Cibodas (alt. 1,425 m) and reared in Bogor (alt. 260 m), West Java (Table 2, NAKAMURA et al., 1995). Since low density and the sedentary nature of adults were observed in the field in West Java as well as in West Sumatra (NAKAMURA et al., personal observation), the common life table parameters observed in two populations seem specific to *E. enneasticta* in spite of different rearing temperatures (Table 2).

The body size of *E. enneasticta* was much larger than that of the other three species (1.08 to 1.18 times in length and 1.05 to 1.19 times in width, cf. KATAKURA et al., 1988). The allometric difference may be related to life table parameters such as longer immature period in *E. enneasticta*, which remains to be analyzed in a future study.

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