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Survivorship and fertility schedules of two phytophagous lady beetle species, *Epilachna vigintioctopunctata* and *E. enneasticta*, under Laboratory Conditions in a Sumatran Highland, Indonesia

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ABSTRACT **Survivorship and fertility schedules of two phytophagous lady beetle species, *Epilachna vigintioctopunctata* (hereafter abbreviated as EV) and *E. enneasticta* (EN), were studied under laboratory conditions in a Sumatran highland (Sukarami, 928 m altitude), Indonesia. In the study area, both species commonly occur together on the same solanaceous host plants such as egg plant and a weed, *Solanum torvum*. EV frequently reached a high density to deplete the plants, while EN remained at low levels. Duration of immature stages was 32.1 days (EV) and 35.3 days (EN). The mean longevity of EV (125.7 days and 90.8 for males and females, respectively) was much shorter than that of EN (149.6 and 124.4). Females of both species laid eggs until day 120 (EV) and 158 (EN) after emergence. Compared to EV, EN had a lower fertility (472.7 eggs per female vs. 787.2) and longer mean length of generation (*T*) (92.6 days vs. 72.9). The intrinsic rate of increase (*r*) of EV (0.082) was higher than that of EN (0.059), resulting from the faster developmental times (immature stages and female pre-reproductive period) and the larger fertility of EV than those of EN. The different *r*-values between the two species corresponded to the difference in the density levels in the field. We also compared the demographic traits of EV populations between the highland (present study) and lowland (previous study in Padang), and found that the former had longer developmental times than those of the latter but both had similar magnitude of fecundities. The *r*-value of the former was much smaller than that of the latter because of the longer developmental times due to lower temperature condition.**

Key words: Epilachna, Coccinellidae, survivorship and fertility schedules, West Sumatra, tropical highland, Indonesia

INTRODUCTION

In previous articles, we reported that two species of phytophagous lady beetles (Coccinellidae: Epilachninae), *Epilachna vigintioctopunctata* (Fabricius) (hereafter referred to as EV) and *E. enneasticta* Mulsant (EN), were common in Java and Sumatra. EV occurs at high densities on solanaceous crops such as egg plant, potato and weeds from an altitude of 0 to 1400 m (Katakura et al. 1988, 2001). While, EN is a low density species of the same plants as EV and is restricted to cooler highlands (400-1400 m). EN frequently occurs together with EV at much lower density. From 1991 to 2000, we studied field population dynamics of the two species on a Sumatran highland (Sukarami, altitude 928 m), where the two species coexisted on a solanaceous weed, *Solanum torvum*. EV frequently reached a high density to deplete the plants, while EN remained at low levels during the study period (Nakamura et al. 2001). Survivorship and mortality schedules have been studied under laboratory conditions for many species in order to estimate the life table parameters, *e.g.*, intrinsic rate of natural increase *r* and the mean length of generation *T*, which are vital for inter- and intraspecific comparisons of demographic characteristics (*e.g.*, Birch et al. 1963; Dingle & Baldwin, 1983). To date we have studied the demographic traits of the two species as follows: EV populations in lowlands, Padang (40 km southwest of Sukarami, altitude 80 m) in the field (Nakamura et al. 1990, 2001) and under laboratory conditions (Abbas et al. 1985) and Bogor (west Java, 260 m) in the field (Nakamura et al. 2001) and under laboratory conditions (Nakamura et al. 1995), and EN populations in the highlands, Kayu Jao (central Sumatra, altitude 1250 m) (Nakano et al. 1997) and Cibodas (20 km from Bogor, altitude 1425m) (Nakamura et al. 1995) only under laboratory conditions. Nakano et al. (2001) compared survivorship and fertility schedules of four high density species and two low density species, including EV and EN cited above under laboratory conditions in Sumatra and Java. These articles clarified that, first, Indonesian epilachnine species, both high and low density species, showed more prolonged longevity and fertility schedules than the temperate species, including Japanese species. With the prolonged schedules, the Indonesian species are obviously well adapted for living in tropical environments like Padang (Nakamura et al. 1984; Abbas et al. 1985; Inoue et al. 1993). Second, comparing the Indonesian high and low density species, the latter exhibited a longer duration of immature stages, longer adult longevity, a smaller *r*-value (intrinsic rate of increase) and larger *T*-value (mean length of generation time) (Nakano et al. 2001). In this article, we (1) report the survivorship and fertility schedules with calculation of *r*-values of EV and EN in Sukarami under laboratory conditions, and discuss the difference in the schedules and *r*-values between the two species in relation to their density levels in the field, and (2) compare the survivorship and reproductive schedules and *r*-values of EV populations between highland (present study in Sukarami) and lowland (previous study in Padang) and then clarify the role of temperature in determining difference in the demographic traits between the two locations.

MATERIALS AND METHODS

The present study was conducted from August 1992 to February 1993 in Sukarami Research Institute for Food Crops (SARIF), Sukarami, Province of West Sumatra, Indonesia. Sukarami is on a highland (928 m altitude) about 40 km northeast of Padang (capital of the province), and is very wet with drizzling rain almost everyday. The average values over 22 years (1960-1982) were: annual rainfall of 2917 mm, monthly rainfall fluctuated from 145 mm (July) to 340 mm (November) and mean monthly temperature from 20.8 °C to 21.4. All experiments were carried out under relatively constant temperatures (21.0 °C to 21.5) and natural day length (12L/12D) with daily replacement of the food plant leaves of *S. torvum*.

Experiment 1. Developmental times of the immature stages. Adults of EV and EN were collected from *S. torvum* in the experimental fields of SARIF and were mass-reared with *S. torvum* leaves in plastic cups in the laboratory to obtain eggs. The food plants were checked daily for eggs. Each egg mass was isolated in a plastic cup (13 cm in diameter and 5 cm in depth) and fresh *S. torvum* leaves were put into the cup just before hatching. Ten first instar larvae selected from an egg mass were reared to adulthood. Dates of oviposition, hatching and larval molt were recorded daily to determine the developmental period. Ten cups were used for this experiment.

Experiment 2. Survivorship and fertility schedules. A pair of newly emerged (within two days) male and female adults of EV and EN were confined to the same plastic cups as used in Experiment 1. The number of eggs deposited and the dates of oviposition and adult death were daily recorded. Ten pairs for each species were reared.

Estimation of the parameters. Although sex ratio was not recorded in this observation, a 1:1 ratio was reported for EV in Padang (Abbas et al. 1985) and EN in Kayu Jao near Sukarami (Nakano et al. 1997). Our long-term field study of population dynamics in Sukarami also confirmed the unity of the sex ratio of both species (Nakamura et al. 2001; Hasan et al. in preparation). On the basis of the expected 1:1 sex ratio, the age-specific fertility in these figures is equivalent to m_x x 2 (m_x is usually defined as the number of living females born per female per unit time; Southwood, 1978). The reproductive value is given by $\frac{V_x}{V_0} = \frac{e^{rx}}{l_x}\sum_{l=x}^{\infty} e^{-rl} l_t m_t{}^{\Delta t}$, where Δt is interval used for measuring l_x and m_x (Δt =1 day in this case) (Fisher, 1930). The intrinsic rate of natural increase (*r*) was determined by solving the equation $\sum e^{-rt} ltmt = 1$ for *r*, where *t* is age in days (Birch, 1948). We use the life table for both the immature and adult stages in the calculation of *r*. However, in both the present and previous studies eggs, larvae, and pupae rarely died on *S. torvum* leaves unless we had mishandled them (Nakamura et al. 1984, 1995; Abbas et al. 1985; Nakano et al. 1997). Thus, we assumed no deaths in the immature stages in practice. Net reproductive rate (R_0) is the average number of female eggs produced per female adult (=$\sum lxmx$). The fertility, total number of eggs produced per female, is twice the values of R_0. The mean length of generation (*T*) was derived from $T = \log \frac{R_0}{r}$.

Statistical procedures. Wilcoxon rank-sum test and Steel-Dwass multiple comparison were used to compare mean values of the $l_x m_x$ parameters between the two species and among the populations of the same species.

RESULTS

Developmental times of immature stages

Table 1 shows that the mean duration of successive immature stages, except L3 and pupa, of EV was significantly shorter than that of EN (Wilcoxcon rank-sum test, P<0.01 for egg, and P<0.05 for L1, L2 and L4). The overall duration of these stages of EV (32.1 days) was significantly shorter than that of EN (35.3) (P<0.01).

Egg mass size

Figure 1 shows the frequency distribution of egg mass size of EV and EN. The mean egg mass size of EV (24.8, n=317) was significantly larger than that of EN (21.2, n=223) (Wilcoxon rank-sum test, P<0.001).

Table 1. Mean duration of immature stages (in days) of *Epilachna vigintioctopunctata* and *E. enneasticta* under laboratory conditions in Sukarami, West Sumatra, Indonesia. Data are shown as mean ± standard deviation (n=10). ** and * refer to significant difference at 1% and 5% levels, respectively (Wilcoxon rank-sum test).

Species/stage	Egg**	L1*	L2*	L3	L4*	Pupa	Total**
E. vigintioctopunctata	5.7 ± 0.5	4.7 ± 0.5	4.8 ± 0.4	5.0 ± 0.7	6.5 ± 0.5	5.4 ± 0.5	32.1 ± 1.3
E. enneasticta	6.4 ± 0.5	5.3 ± 0.5	5.2 ± 0.5	5.1 ± 0.3	7.2 ± 0.6	6.1 ± 0.9	35.3 ± 1.5

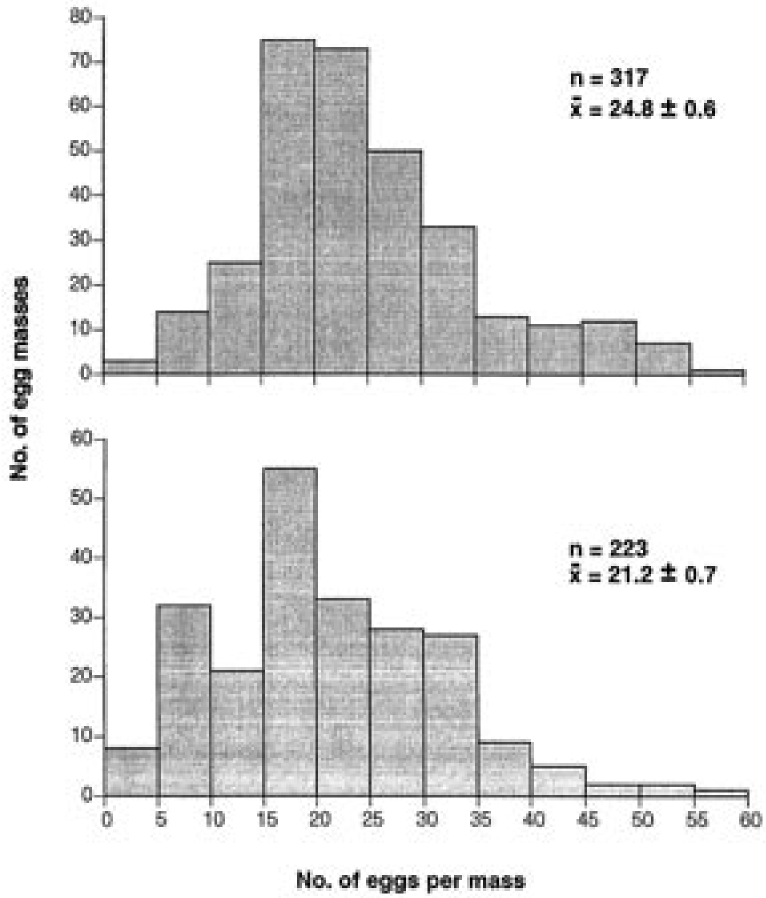

Fig. 1. Frequency distributions of *E. vigintioctopunctata* (top) and *E. enneasticta* (below) egg mass size. The number of egg masses examined (n) and the means ($\bar{x}$) with standard deviations are shown.

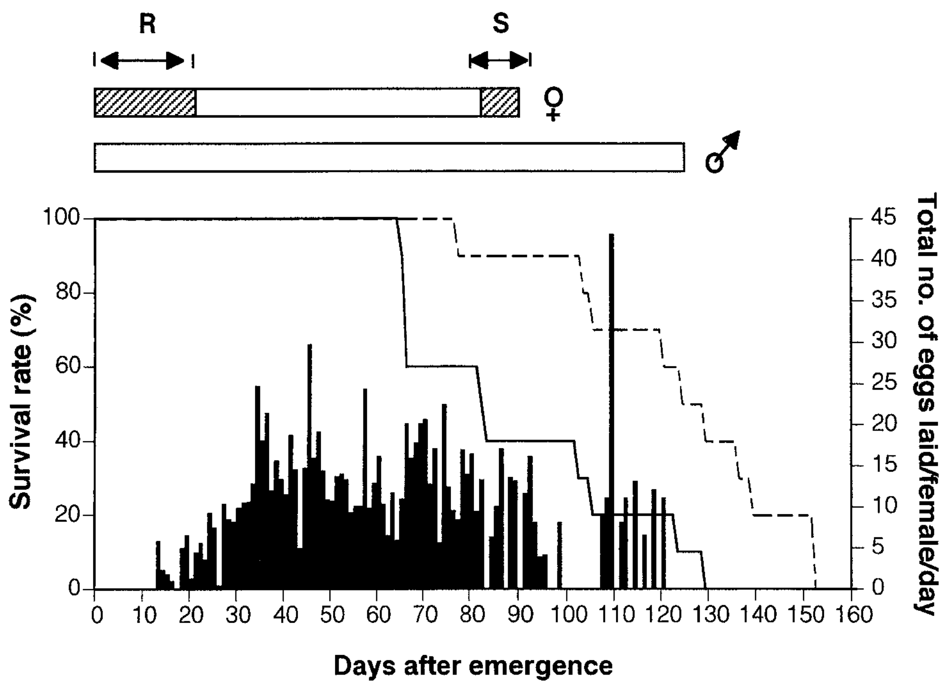

Fig. 2. Survivorship and fertility schedules of *E. vigintioctopunctata* under laboratory conditions. Solid and dotted lines refer to survivorship curves for females and males, respectively. The histograms show the number of eggs laid per female per day. Two horizontal bars depict the average longevity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

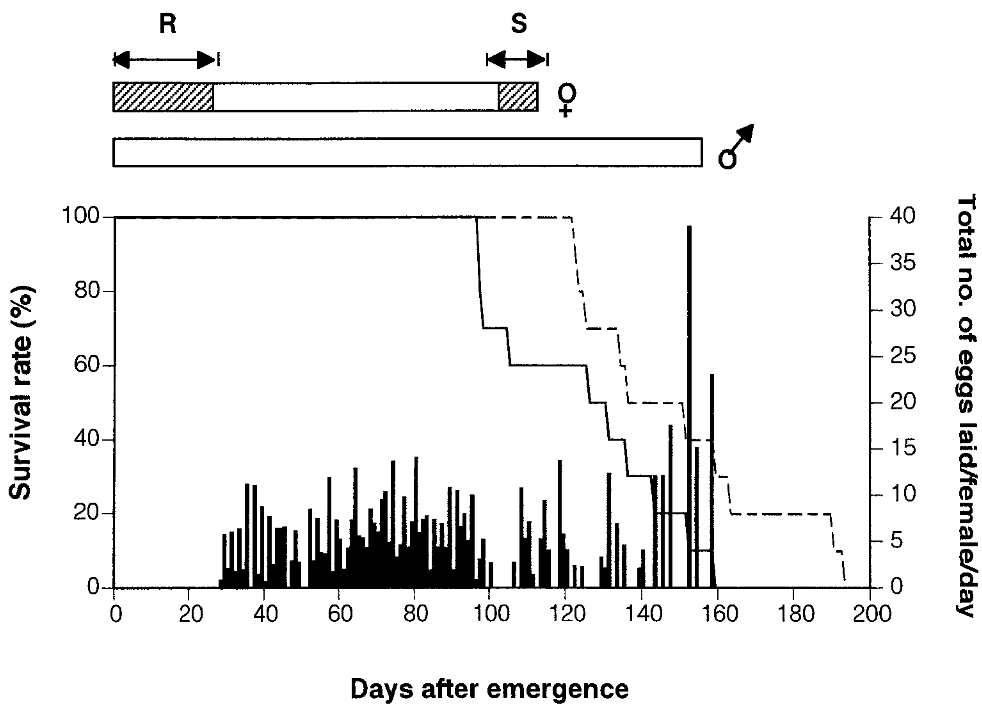

Fig. 3. Survivorship and fertility schedules of *E. enneasticta* under laboratory conditions. Explanations as in Fig. 2.

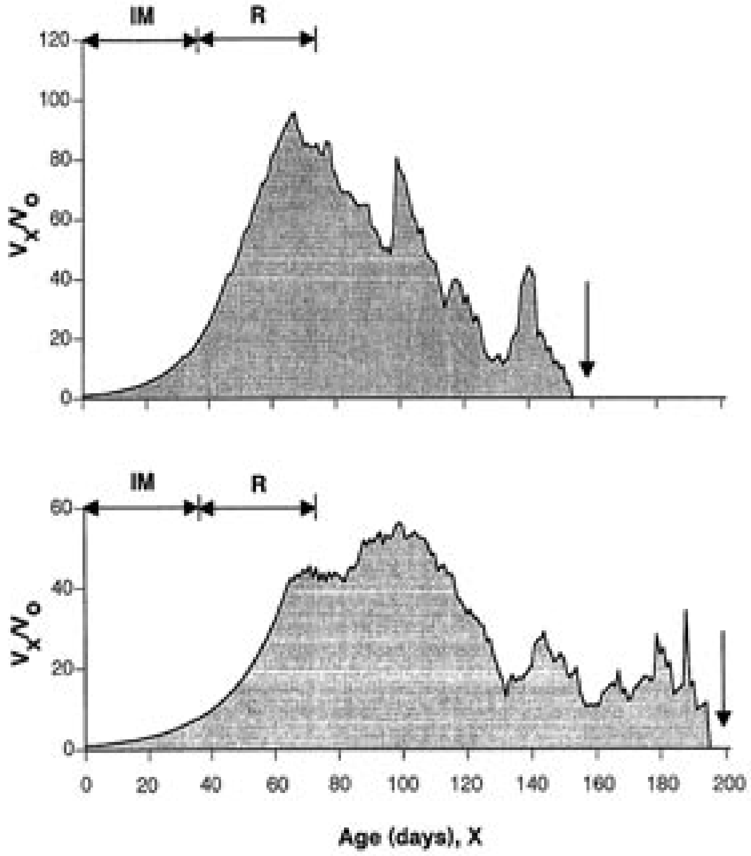

Fig. 4. Reproductive function ($l_x m_x$, top) and reproductive value ($\frac{V_x}{V_0}$, bottom) plotted against age after oviposition for *E. vigintioctopunctata* (top) and *E. enneasticta* (bottom) under laboratory conditions. *IM*: duration of the immature stages. *R*: mean duration of the pre-reproductive period. Vertical arrows show the death of females.

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. Table 2 summarizes the longevity, pre- and post-reproductive periods, fertility, intrinsic rate of natural increase (r), and mean length of generation (T) of the two species.

a. Longevity, pre- and post-reproductive periods

Males lived longer than females in both species: 125.7 days (male) and 90.8 days (female) for EV (P<0.01), and 149.6 (male) and 124.4 (female) for EN (n.s.). The mean longevity of EV was longer than that of EN for both sexes (n. s. for male, and P<0.05 for female). The length of the pre-reproductive period varied considerably for EV (13-32 days) and for EN (28–39 days). The mean value for EV was shorter than that for EN (21.5 days vs. 31.3, P<0.05). The mean value of the post-reproductive period for EV was shorter than that for EN (8.0 days vs. 9.5, n. s.). The mean value of the pre-reproductive period was much longer than that of the post-reproductive period in both species (P<0.0001 for EV and P<0.05 for EN).

b. Age specific fertility

The shape of the histogram giving age-specific fertility shows that females of both species laid eggs continuously at a rather constant rate until around 100th day after emergence, and then daily fertility rate became variable due to the decrease in number of females alive and increased oviposition intervals (Figs. 2 and 3).

c. Reproductive value

The reproductive value of EV and EN reached a peak at 66.1 days (*i.e.*, 34.0 days after the start of the female's adult life) and 98.3 days (*i.e.*, 63.0 days), respectively, and then the value dropped gradually with a few peaks until near the end of the female's life span in both species (Fig. 4).

d. Intrinsic rate of natural increase r

The derived r-value was 0.082 (EV) and 0.059 (EN) per capita per day (Table 2).

e. Net reproductive rate (R_o), fertility and mean length of generation (T)

The R_0 (=$\sum l_x m_x$) was 393.6 (EV) and 236.4 (EN). The fertility, total number of eggs produced per female (= R_0[x]2) was 787.2 (EV) and 472.7 (EN) (P<0.05) (Table 2). The mean length of generation T was 72.9 days (EV) and 92.6 (EN) (Table 2).

DISCUSSION

Comparison of demographic traits between EV and EN in Sukarami

Table 2 summarizes the demographic traits of EV and EN collected and reared in Sukarami. As mentioned in the Results, EN had significantly longer duration of immature stages, longer male longevity, longer female longevity, and longer pre-reproductive period (Figs. 2, 3 and 4). Fertility of EN was only 60% of EV, which is attributed to both smaller egg mass size and larger total number of the masses laid per female (Fig. 1). The T-value of EN was 1.3 times larger than EV, resulting from the slow development of immature stages and older female age at first reproduction. The r-value of EN was 70% of EV, which is attributed to the lower fertility and larger T-value (Figs, 2, 3 and 4). A population study in *S. torvum* fields in Sukarami showed that EV populations sometimes reached high densities while co-occurring EN populations remained at low levels (Nakamura et al. 2001). Life tables compiled in this field study revealed that the magnitudes of mortalities of EV and EN were almost same in both adult stage and the whole immature stages (eggs, larvae and pupae) (Nakamura et al. in preparation), which indicates that the mortalities in the field were not responsible for the low density status of EN in Sukarami. The present study indicates that the difference in the r-values between the two species corresponded to the different density levels of the them in the field. Adults of EV had active and strong dispersal power by flight (Nakamura et al. 1988, 1990), which is one of pest traits. While adults of EN were sedentary, and remained on the food plants even when artificially disturbed. Nakano et al. (2001) reported that the demographic traits under laboratory conditions of *E. pytho*, a low density species feeding on wild cucurbits, showed the following common traits: (1) living only at higher elevations, (2) long immature stage, (3) long adult longevity and female pre-reproductive period, (4) small r and large T, and (5) sedentary nature of adults, which are shared with EN in Sukarami.

Comparison of demographic traits of EV between highland (Sukarami) and lowlands (Padang)

EV collected from the fields in Sukarami (928 m altitude) and Padang (40 km southwest of Sukarami, 80 m altitude, Abbas et al. 1985) were reared under room temperatures in the same sites (21.0–21.5 °C and 24–27, respectively). Table 2 summarizes the demographic traits of the two population. We do not use previous data for other

Table 2. Survivorship and fertility schedules of *Epilachna vigintioctopunctata* and *E. enneasticta* reared with *Solanum torvum* (Solanaceae) under laboratory conditions in the present and previous studies. Data are shown as mean ± standard error (range). Means with different letters in the same raw are significantly different (Wilcoxon rank-sum test and Steel-Dwass multiple comparison test, P = 0.05).

Species	*E. vigintioctopunctata*		*E. enneasticta*
Origin (Elevation, m)	Sukarami, West Sumatra (928)	Padang, West Sumatra (80)	Sukarami, West Sumatra (928)
Rearing temperature (°C)	21.0 – 21.5	24.0 – 32.0	21.0 – 21.5
No. of replications	10	10	10
Longevity (in days) Male	125.7 ± 7.4 (79–154)[a]	87.3 ± 1.4 (80–94)[b]	149.6 ± 7.2 (122–193)[c]
Female	90.8 ± 7.8 (67–132)[a]	57.7 ± 3.5 (43–81)[b]	124.4 ± 7.9 (97–159)[c]
Larval period (in days)	32.1 ± 0.4[a]	23.2 ± 0.3[b]	35.3 ± 0.5[c]
Pre-reproductive period (in days)	21.5 ± 2.4 (13–32)[a]	11.0 ± 0.7 (8–15)[b]	31.3 ± 1.1 (28–39)[c]
Post-reproductive period (in days)	8.0 ± 1.4 (3–16)[a]	2.3 ± 0.6 (1–7)[b]	9.5 ± 3.7 (1–35)[a]
Fertility (Total no. of eggs laid per female)	787.2 ± 77.3 (440–1114)[a]	770.7 ± 47.8 (590–1115)[a]	472.7 ± 65.9 (158–850)[c]
Intrinsic rate of natural increase (per capita per day), r	0.082	0.125	0.059
Mean length of generation (in days), T	72.9	47.6	92.6
Reference	Present study	Abbas et al. 1985	Present study

populations (see Introduciton), because they were reared under room temperature higher than in the original sites, which might have resulted in a shorter developmental time and an anomaly in survival and reproduction. The duration of immature stages of EV in Sukarami (32.1 days) was 1.4–1.5 times longer than that in Padang (23.2) (Steel-Dwass multiple test, P=0.05). Longevity of male (125.7 days) was longer than that of female (90.8) in Sukarami, as in Padang. The longevity of both sexes in Sukarami was also 1.4–2.1 times longer than that in Padang (male 87.3 days, P=0.05; female 57.7, P=0.05). Pre- and post-reproductive periods in Sukarami (21.5 days and 8.0) were again 2.0–3.5 times longer than that in Padang (11.0 days and 2.3) (P=0.05). Pre-reproductive period was longer than post-reproductive period in both populations. The fertility of EV in Sukarami (787.2) was similar to that in Padang (770.7) (n. s.). The r-value in Sukarami (0.082) was much smaller than that in Padang (0.125), due to longer duration of the immature stages and female pre-reproductive period. The r-values depend mainly on age at first reproduction rather than on fertility (*e.g.*, Krebs, 1994). The T-value in EV in Sukarami (72.9 days) was 1.5–1.6 times larger than in Padang (47.6). It is well known that longer developmental times and longevity are found under lower rearing temperatures in many insects, even if the materials examined were collected from the same locality. Kahono *et al*. (2001) compared diapause and tolerance to extreme temperatures among EV populations in tropical (Bogor), subtropical (Okinawa, Japan) and temperate (Hiroshima, Japan) regions. They mentioned that EV in Bogor was least tolerant to both heat and cold. It is worth determining the responses of EV populations (*e.g.*, Padang and Sukarami) in development and fertility to different temperatures.

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