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Temperature-Dependent Life Attributes of an Aphidophagous Ladybird, *Propylea dissecta*

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Reproductive attributes, age-specific fecundity and natality based life-tables of an aphidophagous ladybird, *Propylea dissecta* (Mulsant) were investigated at five temperatures, using aphid, *Aphis gossypii* as prey. Pre-oviposition period decreased significantly with increase in temperature up to 27°C and thereafter increased at a slower rate. Egg viability dropped significantly at temperature extremes. Females lived longer than males; however, longevity decreased significantly with increase in temperature. The predicted total fecundity and oviposition rate were 952.54 eggs and 35.15 eggs per day at 27°C predicted by a mathematical model compared to empirical estimates of 856.00 ± 30.00 eggs and 39.7 ± 2.26 eggs per day. Age-specific fecundity was triangular and temperature dependent. The peak in oviposition rate occurred earlier at higher temperatures. The highest values of net reproductive rate ($R_o = 431.1$), intrinsic rate of increase ($r_m = 0.2134 \text{ day}^{-1}$) and finite rate of increase ($\lambda = 1.2379 \text{ day}^{-1}$) were recorded at 27°C, which suggests it is the optimum temperature for the mass rearing of *P. dissecta*.

Keywords: *Propylea dissecta*, *Aphis gossypii* ladybird, temperature, aphid, age-specific fecundity, demographic analysis

INTRODUCTION

Temperature is an important factor influencing the predation, growth, development and oviposition rates of ladybirds (Coleoptera: Coccinellidae), which are important biocontrol agents of phytophagous insect pests (Hodek & Honek, 1996; Obrycki & Kring, 1998). Temperature-driven models are used to predict rates of development and oviposition (Roy *et al.*, 2002), seasonal incidence (Brière & Pracros, 1998) and suitable conditions for mass rearing of ladybirds (Orr & Obrycki, 1990; Rodriguez-Saona & Miller, 1999). Previous studies have mostly focussed on thermal requirements for development and immature

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survival (Obrycki & Tauber, 1982; Rodriguez-Saona & Miller, 1999; Roy *et al.*, 2002) and only a few on reproduction (Ponsonby & Copland, 1998; Omkar & Pervez, 2002). An energy partitioning model has been used to explain the role of temperature and age in shaping the fecundity function in insects, especially ladybirds (Kindlmann *et al.*, 2001). The model assumes that the fecundity function is shaped by senescence rather than mortality, which is supported by empirical data (Dixon & Agarwala, 2002). There are very few empirical studies on the role of temperature in shaping fecundity function in ladybirds revealing certain effects on the peak in oviposition (Ponsonby & Copland, 1998; Omkar & Pervez, 2002).

Studies on age-specific fecundity coupled with those on life table are essential as they may further enhance our understanding in fecundity functions. The intrinsic rate of natural increase and related demographic parameters are useful for predicting the potential population growth under given conditions (Ricklefs & Miller, 2000; Southwood & Henderson, 2000), but are meagerly studied in ladybirds.

Propylea dissecta (Mulsant) is a locally abundant aphidophagous ladybird in Lucknow, North India, (26.50°N, 80.54°E) where it is commonly found preying on aphid, *Aphis gossypii* (Glover), which is its essential food (Pervez, 2002; Pervez & Omkar, 2004). It has a negatively geotactic oviposition orientation, unaffected by direction of light (Omkar & Mishra, 2003), and can withstand the stress of prey deprivation by switchover from essential to alternative foods (Omkar & Pervez, 2003). Though a potent generalist predator, *P. dissecta* has largely been ignored with sporadic records of its incidence in aphid colonies (Pillai & Nair, 1986; Omkar & Pervez, 2004). It is a polymorphic species existing in three forms, *viz.* pale, typical and intermediate (Pervez, 2002), of which the pale morph is the most abundant in the field (>60% of population). Owing to the relative abundance of pale morphs and to minimize the possible effects of melanism as a variant, only adult pale morphs of *P. dissecta* were selected in the present study.

Experiments were designed to evaluate the influence of temperature on life attributes of *P. dissecta*, *viz.* pre-oviposition, fecundity, percent egg viability, longevity, age-specific fecundity and life table. A mathematical model was used to predict age-specific fecundity and the values compared with the empirical data obtained at five temperatures. Natality-based life tables were constructed to estimate various demographic parameters indicating the potential rates of increase at five temperatures.

MATERIALS AND METHODS

Stock Maintenance

Adult pale morphs of *P. dissecta* were collected from *Lagenaria vulgaris* Seringe fields in the suburbs of Lucknow, India, and used to establish a stock culture, which was kept at $27 \pm 1^\circ\text{C}$, $65 \pm 5\%$ R.H. and LD 14:10 h photoperiod in the laboratory. For the stock, groups of 20 adult beetles (sex ratio 1:1) were kept in glass jars (15.0×10.0 cm) containing moist corrugated filter paper on which the females preferred to oviposit (Pervez, 2002). The openings of the jars were covered with muslin. The adults were provided with an *ad libitum* supply of *A. gossypii* from *L. vulgaris*. The eggs were collected and reared individually from egg hatch to adult emergence in beakers (8.0×11.0 cm) above prey.

Experimental Design

Reproductive attributes of P. dissecta. A pair of newly emerged adults were sexed on the basis of black and white patches on their head and pronotum (Omkar & Pervez, 2000) and kept in a glass beaker (8.0×11.0 cm) containing *ad libitum* prey, *A. gossypii*. Thereafter, beaker was covered with muslin and kept in environmental chamber maintained at 20°C (R.H. and LD as above). The prey and host were daily replenished. Adults, on attaining sexual maturity, mated frequently and the female oviposited. The daily oviposition was recorded along with pre-oviposition, oviposition, and post-oviposition periods, fecundity,

percent egg viability and adult longevity (male and female). The experiment was repeated 10 times with one pair of ladybirds in each beaker ($n = 10$). Similar experimental setups were designed at 25, 27, 30 and 35°C. The data were subjected to one-way ANOVA and comparison of means was done using Tukey's test of significance following the statistical package MINITAB. The mean reproductive rate was calculated by taking the ratio of fecundity and oviposition period. The data were also subjected to regression analysis to describe the relationship between life attributes and temperature.

Age-specific fecundity. Age-specific fecundity trend lines were plotted using the data on daily oviposition at five temperatures. The pattern of age-specific fecundity was described using a model initially used for a predatory mite (Ydergaard *et al.*, 1997), which describes a linear function for the initial and an exponential function for the subsequent decrease in rate of oviposition:

$$F(x) = \alpha \times \exp(-\beta x)$$

where, $F(x)$ is the daily age-specific fecundity rate (eggs/day per female), x is the age in days and α and β are constants. The model was fitted by a non-linear least-square technique using the statistical package MINITAB.

Life table. On the basis of observed data (female survival and age-specific fecundity), demographic parameters, *viz.* net reproductive rate ($R_0 = \sum l_x m_x$), mean generation time ($T_c = \sum x l_x m_x / R_0$), intrinsic rate of increase ($r_m = \log_e R_0 / T_c$), finite rate of increase ($\lambda = \text{antilog}_e^{-r_m}$), and doubling time (D.T. = $\log_e 2 / r_m$), were calculated following Birch (1948). Where, x = pivotal age, l_x = number of females surviving at a particular temperature, and m_x = net fecundity at a particular temperature.

RESULTS

Reproductive Attributes of *P. dissecta*

Temperature significantly affected the reproductive attributes of *P. dissecta* (Table 1). The pre- and post-oviposition periods of *P. dissecta* decreased significantly ($F = 38.14$; $P < 0.001$ and $F = 30.03$; $P < 0.001$, respectively) with increase in temperature from 20 to 27°C and thereafter slightly increased with further increase in temperature. Oviposition period decreased significantly ($F = 60.91$; $P < 0.001$) with increase in temperature from 20 to 35°C. Fecundity ($F = 78.48$; $P < 0.001$), mean reproductive rate ($F = 37.24$; $P < 0.001$) and percent egg viability ($F = 98.71$; $P < 0.001$) increased significantly with increase in temperature from 20 to 27°C and thereafter decreased with further increase in temperature. Longevity of male ($F = 84.35$; $P < 0.001$) and female ($F = 63.62$; $P < 0.001$) ladybirds decreased significantly with increase in temperature. The relationship between life attributes and temperature has been best described using second polynomial regression equations (Table 2).

Age-Specific Fecundity

The shape of the age-specific fecundity curve in *P. dissecta* was triangular at all five temperatures (Figure 1). That is, the oviposition rate increased with reproductive age, peaked and then gradually decreased. A peak of 17.4 ± 1.95 eggs/day (range 9–30) was obtained after 25 days of reproductive age at 20°C. It was 26.8 ± 3.90 eggs/day (range 14–48) after 18 days of reproductive age at 25°C, 39.7 ± 5.45 eggs (range 16–63) after 15 days of reproductive age at 27°C, 25.9 ± 2.26 eggs (range 18–36) after 17 days of reproductive age at 30°C, and 19.8 ± 2.61 eggs (range 12–38) after 11 days of reproductive age at 35°C. The model describes a similar triangular age-specific fecundity with slightly higher values (Table 3) than those obtained empirically. Predicted and empirical estimates of oviposition rates at the peak of reproductive age of *P. dissecta* differed at all five temperatures but insignificantly ($P < 0.1$).

TABLE 1. Different bio-attributes of *P. dissecta* at five constant temperatures, using *A. gossypii* as prey

| | Temperature (°C) | | | | | F value |
|------------------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------------------------|---------|
| | 20 | 25 | 27 | 30 | 35 | |
| Pre-oviposition period (in days) | 17.90±0.60 ^d | 11.20±0.61 ^c | 8.00±0.60 ^a | 9.80±0.66 ^b | 9.90±0.66 ^b | 38.14* |
| Oviposition period (in days) | 61.10±1.99 ^e | 54.30±2.32 ^d | 50.30±2.03 ^c | 44.00±1.22 ^b | 24.40±1.07 ^a | 60.91* |
| Post- oviposition period (in days) | 15.30±0.98 ^e | 9.20±0.90 ^c | 4.10±0.66 ^a | 5.80±0.51 ^b | 11.50±0.69 ^d | 30.03* |
| Fecundity (in eggs) | 439.00±16.61 ^b | 601.30±28.22 ^c | 856.00±30.00 ^d | 646.40±23.33 ^c | 278.50±22.77 ^a | 78.48* |
| Mean Reproductive rate | 7.27±0.38 ^a | 11.09±0.28 ^b | 17.25±0.85 ^d | 14.72±0.47 ^c | 11.46±0.88 ^b | 37.24* |
| Egg viability (%) | 71.58±1.62 ^b | 87.97±1.03 ^{cd} | 96.40±0.85 ^d | 83.77±1.42 ^c | 59.78±2.16 ^a | 98.71* |
| Male longevity (in days) | 82.90±2.15 ^e | 66.20±1.72 ^d | 57.10±1.62 ^c | 52.30±1.61 ^b | 40.70±1.44 ^a | 84.35* |
| Female longevity (in days) | 94.30±2.75 ^d | 74.70±3.28 ^c | 62.40±1.93 ^b | 59.60±1.65 ^b | 45.80±1.17 ^a | 63.62* |

Values are Mean ± S.E.; *Tukey's test: range = 4.02; d.f. 4,45; Significant at the level of $P < 0.001$. Values denoted by different letters in the row are statistically different.

Life-Table

Analysis of the effect of temperature on the demographic parameters revealed that net reproductive rate (R_0), intrinsic rate of increase (r_m) and finite rate of increase (λ) were highest at 27°C (Table 4). Generation time (T_c) was longest at 20°C and shortest at 35°C.

DISCUSSION

Our results clearly indicate the effect of temperature on the life history attributes of *P. dissecta*, including age-specific fecundity and natality-based life-table, revealing its high thermal sensitivity. Of the temperatures used, 27°C appears to be the optimum temperature in terms of fecundity, intrinsic rate of increase and generation time.

The initial decrease in pre-oviposition period of *P. dissecta* with rise in temperature up to 27°C is possibly due to increase in metabolism resulting in earlier gonadal maturation. Further rise in temperature from 27 to 35°C delayed oviposition, indicating that higher temperatures adversely affect the gonadal maturation. However, in the ladybird, *Nephaspis osculatus* (Blatchley), a similar rise in temperature from 26 to 31°C resulted in decline in pre-oviposition period from 14.5 to 13.3 days (Ren *et al.*, 2002).

The reduced fecundity of *P. dissecta* at 20°C may be due to the slowing down of metabolism and/or fewer ovarioles in ladybirds reared at this temperature (Rhamhalinghan,

TABLE 2. Relationships between life attributes (Y) and temperature (X) expressed in terms of second polynomial regression equations, significant at $P < 0.001$ level

| Life attributes | Regression equation | r^2 value |
|-------------------------|------------------------------------|-------------|
| Pre-oviposition period | $Y = 87.80 - 5.22X + 0.09X^2$ | 0.718 |
| Oviposition period | $Y = 23.70 + 4.29X - 0.12X^2$ | 0.842 |
| Post-oviposition period | $Y = 119.00 - 7.96X + 0.14X^2$ | 0.686 |
| Fecundity | $Y = -4146.00 + 364.00X - 6.79X^2$ | 0.835 |
| Mean reproductive rate | $Y = -70.70 + 5.91X - 0.10X^2$ | 0.747 |
| Egg viability | $Y = -236.00 + 24.60X - 0.46X^2$ | 0.858 |
| Male longevity | $Y = 192.00 - 6.96X + 0.08X^2$ | 0.603 |
| Female longevity | $Y = 231.00 - 8.89X + 0.10X^2$ | 0.877 |

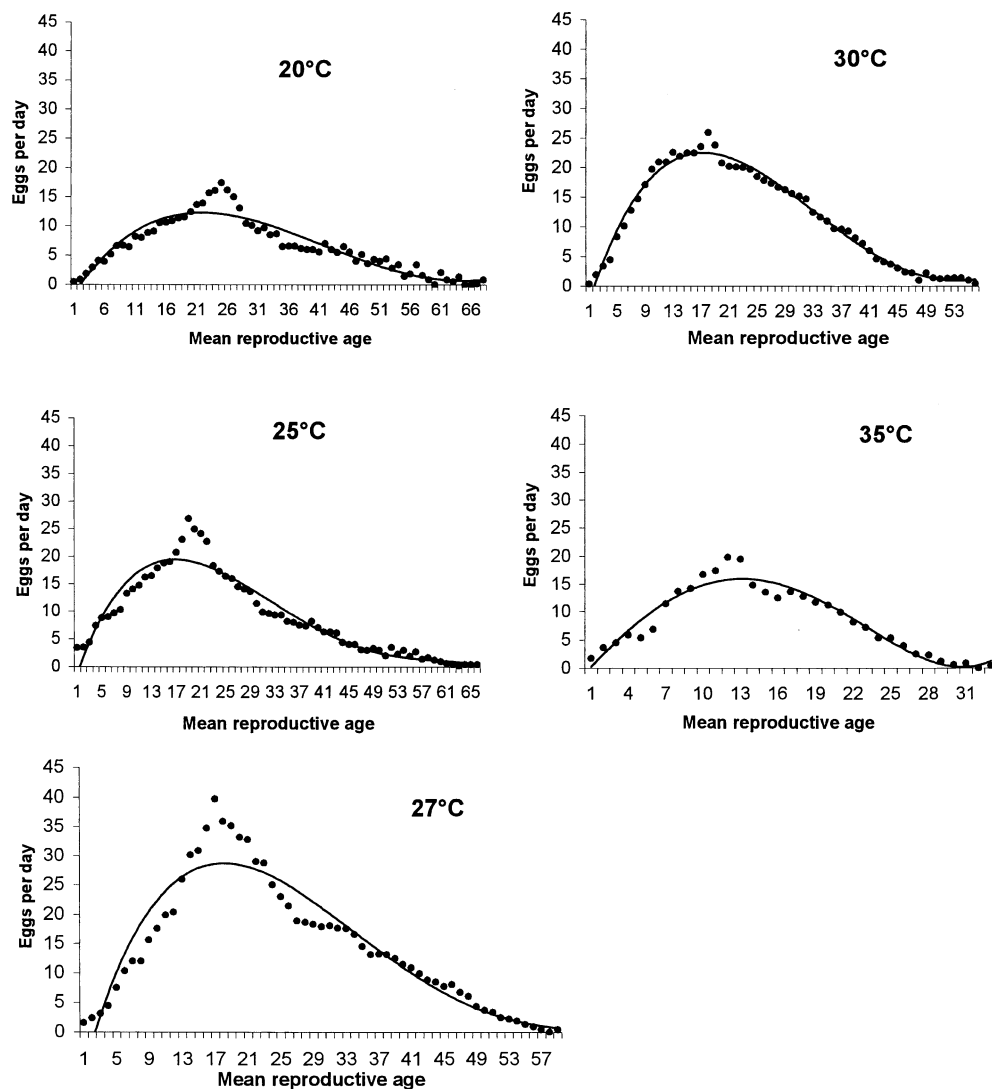


FIGURE 1. Age-specific fecundity curves of *P. dissecta* at five different temperatures, using *A. gossypii* as prey.

TABLE 3. Predicted fecundity and oviposition at the peak of reproductive age of the female *P. dissecta* (estimated from Model 1) at five temperature treatments using *A. gossypii*, as prey ($n = 10$). Regression parameters were significant at $P < 0.001$ level

| Temperature (in °C) | 20 | 25 | 27 | 30 | 35 |
|---|--------|--------|--------|--------|--------|
| α | 3.200 | 5.900 | 9.600 | 6.360 | 4.560 |
| β | 0.080 | 0.092 | 0.100 | 0.089 | 0.122 |
| r^2 | 0.89 | 0.92 | 0.95 | 0.89 | 0.91 |
| Predicted fecundity (eggs) | 487.96 | 693.32 | 952.54 | 791.43 | 305.46 |
| Predicted oviposition rate at the peak (eggs per day) | 14.70 | 23.69 | 35.15 | 26.28 | 13.75 |

TABLE 4. Demographic values of *P. dissecta* at five temperatures

| Demographic parameters | Temperature (°C) | | | | |
|--|------------------|--------|--------|--------|--------|
| | 20 | 25 | 27 | 30 | 35 |
| Net reproductive rate (R_0) | 228.64 | 320.79 | 431.15 | 341.00 | 124.11 |
| Generation time (T_c) (in days) | 42.10 | 32.50 | 28.43 | 27.50 | 22.94 |
| Intrinsic rate of Increase (r_m) (day^{-1}) | 0.1290 | 0.1776 | 0.2134 | 0.2121 | 0.2102 |
| Finite rate of increase (λ) (in day^{-1}) | 1.1377 | 1.1943 | 1.2379 | 1.2362 | 1.2339 |
| Doubling time (D.T.) (in days) | 5.37 | 3.90 | 3.25 | 3.27 | 3.30 |

1986). The reduced feeding rate observed at low temperatures may also account for the decreased fecundity (Veeravel & Baskaran, 1997). The highest fecundity at 27°C suggests efficient conversion of prey biomass into progeny by the predator at this temperature (Baumgärtner *et al.*, 1987). Temperatures above 27°C resulted in a drastic decrease in fecundity, as is also observed in *N. osculatus* (Ren *et al.*, 2002). Egg viability was also significantly reduced at temperature extremes. At 20°C, it was possibly due to inhibition of spermatogenesis or mortality of sperm in the spermathecae of female ladybirds (Ponsonby & Copland, 1998), while at 35°C the non-viable eggs appeared to be desiccated. The highest egg viability was recorded at 27°C, which indicates it is the optimum temperature for progeny production.

Females lived longer than males at all temperatures, which may be attributed to their higher voracity and increased food requirements enhancing their fitness. Increased energy expenditure in mate search (Dixon, 2000) and vulnerability to pathogenic/ parasitic attacks (Majerus & Hurst, 1997) are the possible reasons for the shorter lifespan of males.

The shape of the age-specific fecundity function of *P. dissecta* is triangular and temperature dependent. Senescence largely shapes the triangular fecundity function; that is, the decline in egg production in latter life is linked with decline in food consumption, assimilation, speed of locomotion and fertility (Dixon & Agarwala, 2002). In *P. dissecta*, there is, however, an initial increase in oviposition rate, which is absent in *C. sexmaculata* (Dixon & Agarwala, 2002).

Both the empirical and predicted shapes of age-specific fecundity reveal that young females are more efficient in converting aphid biomass into eggs than older ones. It is assumed that the probability of surviving to reproduce is much greater in early than in later life (Stearns & Koella, 1986). If this is true then young females should invest more in reproduction even at the cost of reducing their potential longevity (Williams, 1974).

The age-specific fecundity trends were almost similar in pattern at all five temperatures, though the peak occurred earlier in adult life at the higher temperatures. The peak occurred on day 25 at 20°C and day 15 at 27°C, indicating that increase in temperature shortens the time period between the onset and the peak of oviposition. As the peak in oviposition occurs earlier and the rate is greatest at 27°C, this is the optimum temperature for the rapid and effective mass rearing of this species. Though, the model predicted a slightly higher value for fecundity, it can be used in similar ecological studies to predict fecundity functions.

Besides temperature, significant influences of prey quality have been found on the life attributes of *P. dissecta* in our recent study (Pervez & Omkar, 2004). More suitable prey species (*A. gossypii* and *Aphis craccivora* Koch), when provided as food, shortened the time period between onset and peak in oviposition. In addition, the peak in oviposition occurs earlier and the oviposition rate is higher on the more suitable prey (Omkar & Mishra, unpublished data).

R_0 value of *P. dissecta* increased with temperature up to 27°C and thereafter decreased. The R_0 value for *P. dissecta* is high compared with that obtained in other ladybirds, such as, *Propylea japonica* (Thunberg) ($R_0 = 67.6$ at 25°C; Chi & Yang, 2003), *Scymnus frontalis* (Fabr.) ($R_0 = 33.1$ at 26°C; Gibson *et al.*, 1992) and *N. osculatus* ($R_0 = 33.1$ at 26°C; Ren *et*

al., 2002). High R_0 values at range of temperatures (25–35°C) are also reported for *N. includens* (Canhilar *et al.*, 2001). Generation time (T_c) decreases with increase in temperature. Although T_c was short at 35°C, the low net reproductive rate suggests that shortening was due to decreased survival of females and low net fecundity. The present study indicates that T_c is shorter in *P. dissecta* than in co-generic species, *P. japonica* (Chi & Yang, 2003).

The r_m value was greatest at 27°C. Because r_m is a composite statistic, taking into account life history parameters, such as, fecundity, survival and sex ratio (Carey, 1993), it can be used as an important criterion for evaluating the potential of biocontrol agents. The r_m -value of *P. dissecta* (0.1776) is higher than that of *P. japonica* (0.1133; Chi & Yang, 2003) at 25°C. Although this laboratory study revealed high r_m values, it may not account for field conditions. The partial life tables of two predatory ladybirds, *Coccinella septempunctata* Linnaeus and *Coleomegilla maculata* DeGeer revealed high levels of mortality amongst life stages (Obyrcki *et al.*, 1997). The reasons for this may be the complex heterospecific interactions and abiotic factors. Thus, to have a better understanding of the life tables of *P. dissecta*, similar studies are needed in field and glasshouse conditions.

Thus, it may be concluded from the laboratory experiments that: (i) the reproductive attributes of *P. dissecta* varied significantly with change in temperature, (ii) increase in temperature reduces adult longevity, (iii) age-specific fecundity is triangular and temperature-dependent, (iv) increase in temperature results in peak of oviposition occurring early in adult life and the rate of oviposition highest at 27°C, accounting for maximum net reproductive rate and intrinsic rate of natural increase occurring at this temperature.

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