

Temperature and Prey Density on Bionomics of *Coccinella septempunctata* (Coleoptera: Coccinellidae) Feeding on *Aphis gossypii* (Homoptera: Aphididae) on Cotton

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ABSTRACT Life history parameters of *Coccinella septempunctata* L. feeding on *Aphis gossypii* Glover on *Gossypium hirsutum* L. were determined in 2 experiments. The 1st experiment addressed the effect of temperature (15, 20, 25, 30, and 35 ± 0.5°C) on *C. septempunctata* bionomics supplied with unlimited food. The 2nd experiment addressed the effect of food quantity on the beetle's bionomics at 25°C. Relationships of life cycle parameters with abiotic and biotic factors were described by mathematical equations. *C. septempunctata* developed most rapidly at 35°C, with a preimaginal period of 10.8 d. Survival from egg to adult was highest at 25°C (47%). Oviposition was greatest at 25°C, with a lifetime oviposition of 287.4 eggs per female and a mean oviposition rate during the reproductive period of 22.4 eggs per female per day. Threshold temperatures for development of the respective stages ranged from 10.9 to 13.9°C, with 12.6°C for the entire life span. The thermal constant was 42.0, 103.7, 63.6, and 302.9 DD for eggs, larvae, pupae, and adults, respectively. Over the range of prey densities tested, a 3.5-fold increase in prey density resulted in a 2-fold reduction in larval development time and a 3-fold increase in larval survival. A 2-fold increase in prey density brought about a 2-fold increase in lifetime oviposition and mean oviposition rate.

KEY WORDS *Coccinella septempunctata*, *Aphis gossypii*, bionomics, temperature, prey density

SEVENSPOTTED LADY BEETLE, *Coccinella septempunctata* L., is a key predator of cotton aphid (*Aphis gossypii* Glover) at the seedling stage of cotton (*Gossypium hirsutum* L.) in the North China cotton region (Beijing University 1984). Biological control of the cotton aphid is a priority for integrated cotton pest management to avoid early season application of insecticides, thus laying a foundation for biological control throughout the season (Xia et al. 1996). Development of biological control for cotton aphid requires insight into the bionomics of *C. septempunctata* under different climatic conditions, notably temperature and different prey densities.

Effects of temperature on *C. septempunctata* bionomics have been studied with several aphid species as food, such as turnip aphid, *Lipaphis erysimi* Katt. (Sethi and Atwal 1964, Singh and Malhotra 1979, Rhamhalinghan 1987, Zhu 1987); pea aphid, *Acyrthosiphon pisum* (Harris) (Butler 1982, Frazer and McGregor 1992); black bean aphid, *Aphis fabae* Scopol (Hodek 1958); and Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Michels and Flanders 1992). The impact of prey supply on *C. septempunctata* bionomics has been investigated with pea aphid (Pandey et al. 1984, Evans and Dixon 1986). No further information is available on the effect of prey supply on the

bionomics of *C. septempunctata*. Nothing is known in this respect with regard to *A. gossypii* on cotton.

The objective of this study was to determine the effect of temperature and prey density on life history parameters of *C. septempunctata* feeding on *A. gossypii* on cotton. The study was undertaken to provide basic data for a quantitative analysis of biological control of *A. gossypii* with *C. septempunctata* in cotton-wheat intercropping in the North China cotton region, using simulation modeling as an analytical and explorative tool.

Materials and Methods

This study was carried out at the China Cotton Research Institute (CCRI), Anyang, Henan province (36.07° N latitude and 114.22° E longitude), in 1993. Two experiments were conducted. The 1st experiment studied the effect of temperature on the bionomics of *C. septempunctata*. Five temperatures were set: 15, 20, 25, 30, and 35 ± 0.5°C. Coccinellids were fed on excess *A. gossypii*. The 2nd experiment studied the effect of food quantity on the beetle's bionomics, which was done at a constant temperature of 25°C. Six levels of prey density were supplied for each predator stage (Table 1). All experiments were conducted in a Multi-Unit-Chamber (Messrs. Brabender, KSE-S 6-125/RN, Germany) at 70-90% RH and a photoperiod of 14:10 (L:D) h.

A laboratory colony was started with *C. septempunctata* pupae collected from winter wheat *Triticum aes-*

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Table 1. Number of young *A. gossypii* adults offered daily to individual *C. septempunctata* to determine effect of food supply on bionomics at a constant temperature of 25°C

| Predatory stage | Level of prey density | | | | | |
|-----------------|-----------------------|----|-----|-----|-----|-----|
| | I | II | III | IV | V | VI |
| First instar | 10 | 15 | 20 | 25 | 30 | 35 |
| Second instar | 15 | 20 | 25 | 30 | 35 | 40 |
| Third instar | 20 | 30 | 40 | 50 | 60 | 80 |
| Fourth instar | 40 | 60 | 80 | 100 | 120 | 150 |
| Adults | 50 | 80 | 110 | 140 | 170 | 200 |

tivum (L.) in mid-May. The pupae were maintained in glass petri dishes (15 cm diameter and 2.5 cm deep) at 25°C for emergence. Newly emerged adults were paired (female + male), held in plastic containers (10 cm diameter and 8 cm deep) at 25°C, and fed with excess aphids obtained from field-grown cotton for oviposition. Eggs were used for rearing experiments.

In the 1st experiment, ≈62–95 freshly laid eggs were kept in glass petri dishes for each temperature. They were observed for hatching every 24 h at 15 and 20°C, and every 12 h at 25, 30, and 35°C. At each temperature, 53–71 newly hatched larvae were individually kept in plastic containers (6 cm diameter and 8 cm deep) and supplied with excess aphids of mixed instars. Molting and mortality were monitored at time intervals of 24 h at the 2 lower temperatures and 12 h at the 3 higher temperatures. Each day, aphids were added and cotton leaves were replaced. Newly emerged adults were transferred to larger glass containers (10 cm diameter and 15 cm high) after copulation had been observed. The eggs that were produced in these containers were counted and removed every 12 h at 15 and 20°C, and every 6 h at 25, 30, and 35°C. Observations ended after death of the females.

In the 2nd experiment, 30–35 newly hatched larvae were individually reared at each level of prey density and supplied daily with different amounts of young *A. gossypii* adults according to their developmental stage (Table 1). The procedure of observations was the same as in the 1st experiment.

In both experiments, we estimated the following life cycle parameters: development time of each larval instar, duration of all larval stages together, pupal stage duration, and total preimaginal period (the time from egg to emerged adult); duration of the preoviposition period, oviposition period, and oviposition plus post-oviposition period as well as total adult longevity; entire life span (from birth to death); lifetime oviposition; and the mean oviposition rate during the reproductive period (number of eggs laid per female per day). All parameters were compared among treatments of temperature or prey density, using the general linear model (GLM) procedure of SAS (SAS Institute 1993–1995).

Developmental rate (R_d , d^{-1}) of each life stage was computed as the reciprocal of the stage duration in both experiments. The Logan et al. (1976) model was used to describe the relationship between temperature (T , °C) and the developmental rate:

$$R_d = a_1 \{ \exp [a_2(T - T_1)] - \exp [a_2(T_u - T_1) - (T_u - T)/a_3] \}, \quad [1]$$

where T_1 is the lower threshold temperature (°C); T_u is the upper lethal temperature (°C); and a_1 , a_2 , and a_3 are coefficients. The upper lethal temperature was assumed to be the same for all life stages: 38°C as estimated in growth chambers by Sethi and Atwal (1964). The lower threshold temperature of each life stage was determined by linear regression, excluding the data for the higher temperature where the relationship becomes nonlinear (see Kawauchi 1982). The equation used was

$$T = b_1 + b_2 R_d, \quad [2]$$

where T is temperature (°C) and b_1 and b_2 are regression coefficients representing the threshold temperature (°C) and the duration of the stage, expressed in degree-days, respectively. The relationship between the developmental rate and prey density was described with a negative exponential saturation curve:

$$R_d = c_1 + c_2 [1 - \exp(-c_3 D_a / c_2)], \quad [3]$$

where D_a denotes the aphid density; and c_1 , c_2 , and c_3 are coefficients.

Mortality and fecundity in the adult stage are not only temperature- but also age-dependent. Twenty age classes were distinguished to describe the age dependency of fecundity and mortality according to the method of Rabbinge (1976). The duration of each age class was determined by dividing the maximum life span by the total number of age classes. The maximum life span was defined as the mean life span plus 3 standard deviations. The relative mortality rate (R_m , d^{-1}) of each life stage and each adult age class was computed as

$$R_m = (\ln N_t - \ln N_{t+\Delta t}) / \Delta t, \quad [4]$$

where N_t is the number of insects at time t , $N_{t+\Delta t}$ is the number of insects at time $t+\Delta t$, and Δt is the time interval between observations (i.e., duration of a life stage or an age class). The relationship between temperature and the relative mortality rate was described with a parabola

$$R_m = d_1 + d_2 T + d_3 T^2, \quad [5]$$

where d_1 , d_2 and d_3 are coefficients. A negative exponential decay equation was used to describe the response of the relative mortality rate to prey density (D_a):

$$R_m = e_1 \exp(-e_2 D_a), \quad [6]$$

where e_1 and e_2 are coefficients.

Weibull's (1951) model was used to describe the relationship among temperature and lifetime oviposition (A), mean oviposition rate during the reproductive period (B), and the mean oviposition rate of each adult age class (C). This model has the form

$$Y = f_2 / f_1 f_3 [(T - T_1) / f_1]^{f_2 - 1} \exp \{ -[(T - T_1) / f_1]^{f_2} \}, \quad [7]$$

where Y stands for A, B, or C; T and T_1 have the same meaning as in equation 1; and f_1 , f_2 , and f_3 are coefficients. Equation 3 was used to describe the response of lifetime oviposition and the mean oviposition rate to prey density. An equation modified from Bieri et al. (1983) was used to describe the relationship between the mean oviposition rate (R_q) and adult age class (q):

$$R_q = g_1 q / (g_2)^q, \quad [8]$$

where g_1 and g_2 are coefficients.

Model equations were selected to provide a biologically appropriate shape, minimum root mean square error and maximum coefficient of determination (r^2). All parameters in nonlinear models or equations were estimated iteratively by minimization of the sum of squared residuals, using the Levenberg-Marquardt algorithm (Slide Write Plus for Windows 1983–1993).

Results

Effect of Temperature

Development. The time to complete preimaginal development decreased with temperature from 69 d at 15°C to 11 d at 35°C (Table 2). Longevity of the adult decreased with temperature from 38 d at 20°C to 14 d at 35°C (Table 2).

Relationships between temperature and the developmental rate (R_d) were in all life stages adequately described using the Logan et al. (1976) equation (Fig. 1). Root mean square error ranged from 0.018 to 0.034 d^{-1} for eggs through the 3rd larval instars, and from 0.0013 to 0.0094 d^{-1} for the 4th larval instars through the oviposition plus postoviposition adults. All r^2 -values exceeded 0.97. The highest development rates were found at 35°C (Fig. 1), only a few degrees below the lethal temperature of 38°C.

Survival. Survival of all preadult stages (except for the 2nd instar) increased with temperature up to 25°C and then decreased (Table 2). The highest survival during the preadult period (47%) at 25°C was ≈ 3 times that at 15°C (16%) and 2 times that at 35°C (26%) (Table 2). No adults survived to the oviposition phase at 15°C.

A parabola satisfactorily described the relationship between temperature and the relative mortality rate (R_m) of each preoviposition stage (Fig. 2). Root mean square error ranged from 0.0016 to 0.0042 d^{-1} for eggs through the 2nd larval instars, and from 0.00034 to 0.00095 d^{-1} for the 3rd larval instars through the preoviposition adults. The r^2 ranged from 0.97 to 0.99. In most cases, the relative mortality rate was fairly low at 20–25°C but slightly higher at 15 and 30°C, and much higher at 35°C (Fig. 2). The relationship between temperature and the relative mortality rate of each adult age class was also adequately described by a parabola (Table 3). As shown in Fig. 3, the relative mortality rate increased with adult age at all 4 temperatures, and it also increased with temperature in each adult age class.

Oviposition. Lifetime oviposition and mean oviposition rate were highest at 25°C but lowest at 15 and

Table 2. Effect of temperature on life history parameters (mean \pm SE) of *C. septempunctata* feeding on *A. gossypii* on cotton

| | Temp (°C) | | | |
|-----------------------------------|----------------------------|----------------------------|----------------------------|----------------------------|
| | 15 | 20 | 25 | 30 |
| Egg developmental time, d | 9.3 \pm 0.13 (89, 71.9)a | 5.8 \pm 0.05 (64, 82.8)b | 3.0 \pm 0.02 (77, 88.3)c | 2.3 \pm 0.03 (62, 85.5)d |
| Larval developmental time, d | | | | |
| First instar | 9.1 \pm 0.20 (64, 51.6)a | 4.6 \pm 0.13 (53, 73.6)b | 2.0 \pm 0.06 (68, 85.3)c | 1.4 \pm 0.04 (53, 83.0)d |
| Second instar | 7.5 \pm 0.34 (33, 81.8)a | 3.2 \pm 0.09 (39, 89.7)b | 2.1 \pm 0.05 (58, 89.7)c | 1.2 \pm 0.06 (44, 93.2)d |
| Third instar | 8.3 \pm 0.16 (27, 88.9)a | 4.5 \pm 0.13 (35, 91.4)b | 2.0 \pm 0.08 (52, 92.3)c | 1.4 \pm 0.05 (41, 90.2)d |
| Fourth instar | 14.5 \pm 0.3 (24, 83.3)a | 7.4 \pm 0.17 (32, 87.5)b | 3.6 \pm 0.11 (48, 89.6)c | 2.3 \pm 0.06 (37, 89.2)d |
| Total larval period | 38.7 \pm 0.5 (20, 31.3)a | 19.3 \pm 0.3 (28, 52.5)b | 9.7 \pm 0.16 (43, 63.2)c | 6.2 \pm 0.07 (33, 62.3)d |
| Pupal developmental time, d | 16.4 \pm 0.3 (20, 70.0)a | 10.1 \pm 0.2 (28, 85.7)b | 5.7 \pm 0.11 (43, 83.7)c | 3.6 \pm 0.08 (33, 78.8)d |
| Age at emergence, d | 68.8 \pm 0.6 (14, 15.7)a | 25.1 \pm 0.2 (24, 37.5)b | 18.3 \pm 0.2 (36, 46.7)c | 12.3 \pm 0.1 (26, 41.9)d |
| Adults, d ^a | | | | |
| Pre-oviposition | 33.4 \pm 1.5 (7)a | 16.7 \pm 0.9 (13, 76.9)b | 11.1 \pm 0.7 (17, 89.5)c | 7.8 \pm 0.51 (15, 73.3)d |
| Oviposition plus post-oviposition | — | 21.4 \pm 1.9 (10)a | 15.6 \pm 1.6 (17)b | 11.6 \pm 1.4 (11)b |
| Entire adult period | — | 37.6 \pm 2.1 (10)a | 27.1 \pm 1.6 (17)b | 19.3 \pm 1.4 (11)c |
| Total life span, d | — | 72.6 \pm 2.0 (10)a | 45.3 \pm 1.6 (17)b | 31.4 \pm 1.5 (11)c |
| Oviposition per female | — | 191.6 \pm 21 (10)b | 287.4 \pm 24 (17)a | 207.3 \pm 17 (11)b |
| Oviposition per female per day | — | 11.1 \pm 1.1 (10)b | 22.4 \pm 1.6 (17)a | 20.5 \pm 1.2 (11)a |

Means in each row followed by the same letter in a row are not significant ($P < 0.05$, GLM) in ANOVA (LSD). The first value in parentheses is the number of beetles tested, and the second is the percentage survival to the next stage.
^a Only females were taken into account.

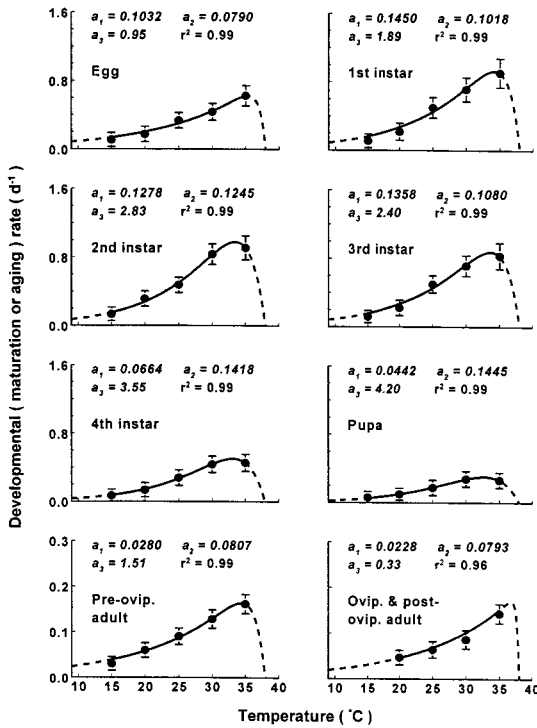


Fig. 1. Relationship between temperature and the rate of development (maturation or aging) of *C. septempunctata* feeding on *A. gossypii* on cotton. Bars represent observation means with 95% CL. Fitted lines are Logan curves (equation 1) with the indicated parameter values. The lower threshold temperatures (T_l) are presented in Table 5, and the upper lethal temperature (T_u) is in all cases 38°C.

35°C (Table 2). Lifetime oviposition increased with temperature from 191.6 eggs per female at 20°C to 287.4 eggs per female at 25°C and then decreased down to 54.1 eggs per female at 35°C. The mean oviposition rate (20.5–22.4 eggs per female per day) at 25–30°C was 2 times as large as at 20 and 35°C (Table 2).

Weibull's (1951) model adequately described the relationship of lifetime oviposition and mean oviposition rate with temperature (Fig. 4). Root mean square error was 46.2 eggs per female for lifetime oviposition (Fig. 4A) and 3.3 eggs per female per day for the mean oviposition rate (Fig. 4B); r^2 was 0.99 for both. Lifetime oviposition and the mean oviposition had an optimum around 25°C (Fig. 4). The relationships between temperature and oviposition rate for each adult age class were satisfactorily described by Weibull's (1951) model (Table 4). As shown in Fig. 5, the relationship between the mean oviposition rate of each age class (R_q) and adult age was well described by equation 8 at all 4 temperatures. Root mean square error was 1.1, 3.1, 8.5, and 4.1 eggs per female per day for 20 through 35°C, respectively; r^2 ranged from 0.96 to 0.99.

Threshold Temperature. Threshold temperatures ranged from 12.9 to 13.9°C for the 1st larval instars

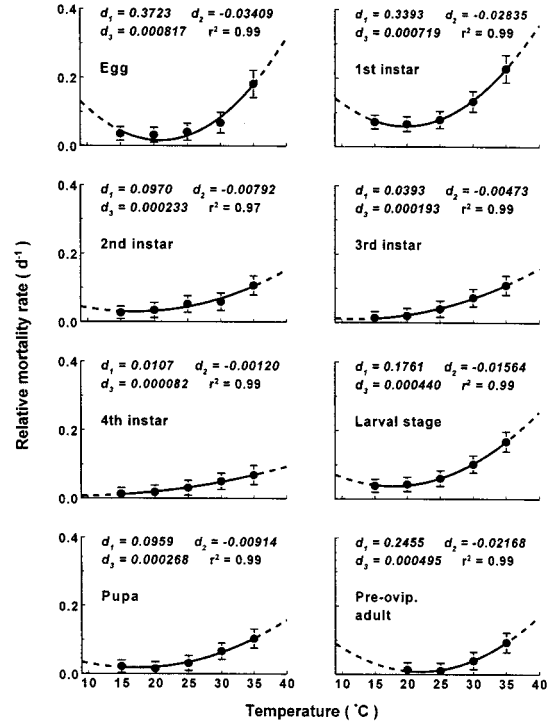


Fig. 2. Relationship between temperature and the relative mortality rate of *C. septempunctata* feeding on *A. gossypii* on cotton. Bars represent observation means with 95% CL. Fitted lines are defined by equation 5 and the indicated parameter values.

through pupae and from 10.9 to 11.5°C for the eggs and adults, with 12.6°C for the entire life span (Table 5). The thermal constant for the adult stage was 302.9 DD, which accounted for >50% of 546.3 DD for the total life span (Table 5).

Effect of Prey Density

Development. Development time of the larval stages of *C. septempunctata* decreased substantially with prey density from level I to level IV and then

Table 3. Relationship between temperature and relative mortality rate of different age classes of *C. septempunctata* adults feeding on *A. gossypii* on cotton, based on equation 5

| Age class | d_1 | d_2 | d_3 | RMSE | r^2 |
|-----------|-------|---------|---------|--------|-------|
| 1 | 0.034 | -0.0028 | 0.00007 | 0.0002 | 0.98 |
| 2 | 0.116 | -0.0091 | 0.00020 | 0.0007 | 0.98 |
| 3 | 0.094 | -0.0070 | 0.00019 | 0.0013 | 0.98 |
| 4 | 0.680 | -0.0553 | 0.00118 | 0.0058 | 0.99 |
| 5 | 0.670 | -0.0533 | 0.00118 | 0.0067 | 0.99 |
| 6 | 1.468 | -0.1172 | 0.00249 | 0.0161 | 0.99 |
| 7 | 1.504 | -0.1213 | 0.00268 | 0.0248 | 0.99 |
| 8 | 1.807 | -0.0750 | 0.00132 | 0.0339 | 0.98 |
| 9 | 2.256 | -0.1791 | 0.00392 | 0.0289 | 0.99 |
| 10 | 2.788 | -0.2217 | 0.00484 | 0.0603 | 0.99 |
| 11 | 3.836 | -0.3095 | 0.00672 | 0.0796 | 0.99 |
| 12 | 5.358 | -0.4202 | 0.00887 | 0.0753 | 0.99 |

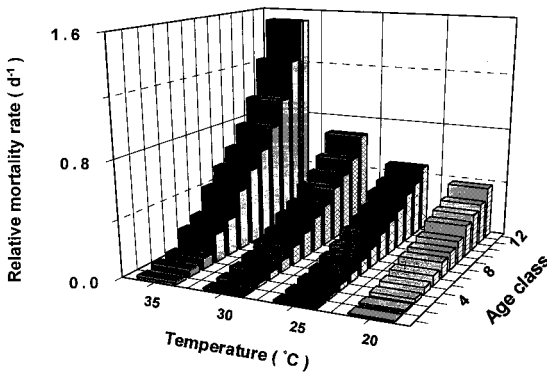


Fig. 3. Age class-dependent relative mortality rate of *C. septempunctata* adults feeding on *A. gossypii* on cotton at 4 temperatures.

decreased slightly with further increase of prey density (Table 6). Over the range of prey densities tested, an average 3.5-fold increase in prey density resulted in a 2-fold decrease in larval developmental time (Tables 1 and 6). Duration of the pupal stage only slightly decreased with prey density (Table 6). The adult life span decreased sharply with prey density up to level III and then decreased slightly (Table 6). The response of the developmental rate (R_d) to prey density was well described by equation 3 for the 1st through 4th instar (Fig. 6A). Root mean square error ranged from 0.0041 to 0.0183 d⁻¹, and all r^2 exceeded 0.97. The developmental rate of all larval stages increased with prey density, approaching an asymptote at higher prey densities (Fig. 6A).

Survival. Survival of all preadult stages increased with prey density and was greatest at the highest prey density (Table 6). A 3.5-fold increase in prey density from prey density level I to IV brought about a 3-fold increase in survival from the 1st instar to the adult stage (Table 6). Equation 6 satisfactorily described the relationship between prey density and the relative mortality rate (R_m) of each larval stage (Fig. 6B). Root mean square error ranged from 0.00075 to 0.00291 d⁻¹, and r^2 from 0.92 to 0.95.

Oviposition. Lifetime oviposition and mean oviposition rate increased monotonically with prey density

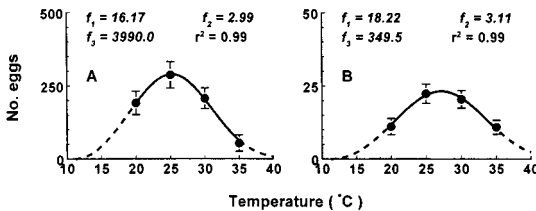


Fig. 4. Relationship between temperature and (A) lifetime oviposition per female and (B) mean oviposition rate (eggs per female per day) of *C. septempunctata*, feeding on *A. gossypii* on cotton. Bars represent observation means with 95% CL. Fitted lines are Weibull curves (equation 7), with the indicated parameter values. The lower temperature (T_1) is 11 °C (Table 5).

Table 4. Relationship between temperature and mean oviposition rate of 9 age classes of *C. septempunctata* adults feeding on *A. gossypii* on cotton, based on equation 7

| Age class ^a | f_1 | f_2 | f_3 | RMSE | r^2 |
|------------------------|-------|-------|-------|------|-------|
| 1 | 18.6 | 2.81 | 443.9 | 11.1 | 0.95 |
| 2 | 19.4 | 3.19 | 558.7 | 6.9 | 0.99 |
| 3 | 19.7 | 2.94 | 453.0 | 6.5 | 0.98 |
| 4 | 19.7 | 3.07 | 310.2 | 4.3 | 0.98 |
| 5 | 18.9 | 3.68 | 214.2 | 2.8 | 0.99 |
| 6 | 18.4 | 3.87 | 136.0 | 1.6 | 0.99 |
| 7 | 18.8 | 4.33 | 97.7 | 2.3 | 0.95 |
| 8 | 19.1 | 4.39 | 62.7 | 1.2 | 0.94 |
| 9 | 15.3 | 3.88 | 20.7 | 0.1 | 0.99 |

^a No eggs were laid in age classes 10–12.

(Table 6). A 2.5-fold increase in prey density from density level I to VI led to a doubling of lifetime oviposition and mean oviposition rate (Tables 1 and 6). Equation 3 adequately described the response of lifetime oviposition and mean oviposition rate to prey density (Fig. 7). Root mean square error was 39.0 eggs per female for the lifetime oviposition (Fig. 7A) and 0.7 eggs per female per day for the mean oviposition rate (Fig. 7B); r^2 was 0.99 for both. Lifetime oviposition and the mean oviposition rate increased with prey density, reaching a plateau at the higher prey densities (Fig. 7).

Discussion

Coccinella septempunctata attains its most rapid development at 35 °C (Hodek 1958, Sethi and Atwal 1964, Singh and Malhotra 1979, Kawauchi 1982, Zhu 1987). High temperature, however, exerts a deleterious effect through increased respiration cost (Mills 1981), resulting in a reduction of survival and oviposition (Table 2). This may be the major cause for the seven-spotted lady beetle to aestivate or enter diapause in the North China cotton region during summer (Qin

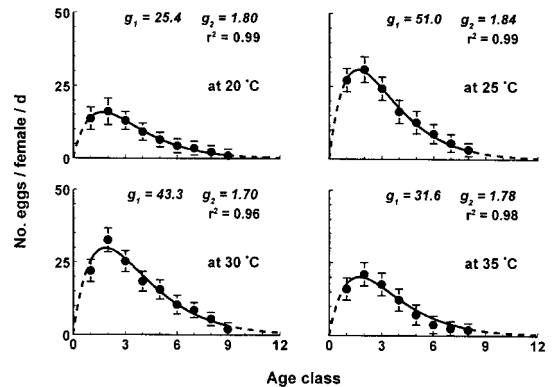


Fig. 5. Relationship between adult age class and the mean oviposition rate (eggs per female per day) of *C. septempunctata* feeding on *A. gossypii* on cotton at 4 temperatures. Bars represent observation means with 95% CL. Fitted lines are defined by equation 8 and the indicated parameter values.

Table 5. Threshold temperature and thermal constant (mean ± SE) of *C. septempunctata* feeding on *A. gossypii* on cotton

| Stage and period | Threshold temp (°C) | Thermal constant (D°) | r ² |
|--|---------------------|-----------------------|----------------|
| Eggs | 11.5 ± 1.4 | 42.0 ± 4.2 | 0.98 |
| First instar | 13.8 ± 1.2 | 22.8 ± 2.4 | 0.98 |
| Second instar | 13.6 ± 1.7 | 20.4 ± 2.5 | 0.96 |
| Third instar | 13.6 ± 1.3 | 23.1 ± 4.3 | 0.98 |
| Fourth instar | 13.9 ± 1.3 | 38.0 ± 6.2 | 0.98 |
| Total larval period | 13.7 ± 1.2 | 103.7 ± 11 | 0.98 |
| Pupae | 12.9 ± 1.6 | 63.6 ± 8.6 | 0.97 |
| Pre-oviposition adults | 10.9 ± 0.6 | 151.9 ± 7 | 0.99 |
| Oviposition plus post-oviposition adults | 11.1 ± 1.0 | 166.1 ± 24 | 0.99 |
| Total adult period | 12.4 ± 1.5 | 302.9 ± 28 | 0.98 |
| Entire life span | 12.6 ± 0.5 | 546.3 ± 15 | 0.99 |

1978). As shown in Fig. 8, the rate of preimaginal development (R_d) of the sevenspotted lady beetle differs little among populations from different parts of the world: China (this study), Europe (Hodek 1958), India (Sethi and Atwal 1964), and Japan (Sakurai et al. 1991). Only at high temperature, there is a noticeable difference. Likewise, there is little difference among distant populations of *C. septempunctata* in the relationship between survival and temperature, except near the upper temperature limit (Hodek 1973).

Coccinella septempunctata had greater survival and oviposition at 20–30°C than at 10 and 35°C, indicating that the life performance of the beetle is best at intermediate temperatures, which are predominant in the North China cotton region in May and in September, but not during the height of summer, which is substantially hotter. *C. septempunctata* is an effective biological control agent of *A. gossypii*, especially at the seedling stage of cotton (May and June; Beijing University 1984, Xia et al. 1996), when temperatures favor its bionomics, whereas aphid populations may still be small enough to control.

A linear relationship of the developmental rate, survival, and oviposition with prey density is commonly observed in predatory arthropods (Beddington et al. 1976). The current study, however, indicates that developmental rate, relative mortality rate, lifetime oviposition, and mean oviposition rate of *C. septempunctata* are nonlinearly related to prey density (Figs. 6 and 7). Such nonlinearity was also observed in other coccinellid species, such as *Adalia bipunctata* (F.) feeding on *A. pisum* (Mills 1981), and *Cheilomenes lunata* (F.) feeding on *A. craccivora* (Ofuya and Ak-ingbohunge 1988).

The 2 experiments presented in this article overlap when they investigate life performance at 25°C and maximum prey supply. The only difference is that in the temperature experiment the beetles were fed an excess of mixed stages of *A. gossypii*, whereas in the prey supply experiment the beetles were fed young adult aphids, which, according to Chen et al. (1980) and Sinha et al. (1982), are the less preferred prey. Our results are in agreement, because the development time from hatch to pupa was 1 d shorter on the

Table 6. Effect of prey density on life history parameters (mean ± SE) of *C. septempunctata* fed on *A. gossypii* on cotton at 25°C.

| | Level of prey supply | | | | | |
|-----------------------------------|----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|--|
| | I | II | III | IV | V | VI |
| Larval development time, d | | | | | | |
| First instar | 4.2 ± 0.28 (35)a [71.4] | 3.8 ± 0.15 (30)a [76.7] | 3.3 ± 0.14 (30)b [80.0] | 2.9 ± 0.11 (30)bc [83.3] | 2.7 ± 0.11 (30)c [86.7] | 2.6 ± 0.10 (30)c [90.0] |
| Second instar | 3.2 ± 0.33 (25)a [68.0] | 2.7 ± 0.19 (23)b [73.9] | 2.4 ± 0.14 (24)bc [79.2] | 2.2 ± 0.08 (25)cd [85.0] | 2.0 ± 0.10 (26)cd [88.5] | 1.8 ± 0.08 (27) ^d [92.6] |
| Third instar | 3.6 ± 0.14 (17)a [76.5] | 3.1 ± 0.12 (17)b [82.4] | 2.6 ± 0.12 (19)c [84.2] | 2.2 ± 0.10 (22)d [86.4] | 2.1 ± 0.07 (23)d [91.3] | 2.0 ± 0.05 (25) ^d [92.0] |
| Fourth instar | 7.0 ± 0.21 (13)a [61.5] | 6.0 ± 0.25 (14)b [71.4] | 5.4 ± 0.17 (16)c [75.0] | 4.6 ± 0.21 (19)d [79.0] | 4.4 ± 0.20 (21)d [85.7] | 4.2 ± 0.15 (23)d [87.0] |
| Total larval period | 18.1 ± 0.5 (8)a [22.9] | 15.7 ± 0.5 (10)b [33.3] | 13.8 ± 0.4 (12)c [40.0] | 11.9 ± 0.3 (15)d [50.0] | 11.3 ± 0.3 (18)de [60.0] | 10.6 ± 0.2 (20)e [66.7] |
| Pupal developmental time, d | 6.5 ± 0.42 (8)a [62.5] | 5.9 ± 0.32 (10)ab [80.0] | 5.7 ± 0.23 (12)b [83.3] | 5.4 ± 0.23 (15)b [93.3] | 5.3 ± 0.19 (18)b [88.9] | 5.2 ± 0.18 (20)b [95.0] |
| Adults, d ^a | | | | | | |
| Pre-oviposition | 35.8 ± 1.7 (4)a | 24.9 ± 1.6 (7)b | 16.4 ± 0.9 (7)c | 14.5 ± 0.7 (8)cd | 12.9 ± 0.6 (9)d | 12.7 ± 0.6 (10)d |
| Oviposition plus post-oviposition | — | 34.6 ± 2.6 (5)a | 24.2 ± 2.0 (5)b | 20.2 ± 1.9 (6)bc | 17.7 ± 1.2 (7)c | 16.1 ± 1.1 (8)c |
| Total adult period | — | 59.5 ± 3.7 (5)a | 40.6 ± 2.2 (6)bc | 34.6 ± 2.2 (6)bc | 30.6 ± 1.4 (7)c | 28.7 ± 1.5 (8)c |
| Oviposition per female | — | 137.5 ± 16 (5)a | 225.0 ± 13 (5)a | 243.9 ± 14 (6)a | 266.1 ± 19 (7)a | 272.5 ± 16 (8)a |
| Oviposition per female per day | — | 5.2 ± 1.22 (5)d | 11.9 ± 1.0 (5)c | 15.8 ± 1.6 (13)bc | 18.6 ± 1.5 (7)ab | 20.1 ± 1.4 (8)a |

Means in each row followed by the same letter in a row are not significantly different ($P < 0.05$, GLM) in ANOVA (LSD). Values in parentheses is the number of beetles tested. Values in square brackets are percentage survival to the next stage.
^a Only females were taken into account.

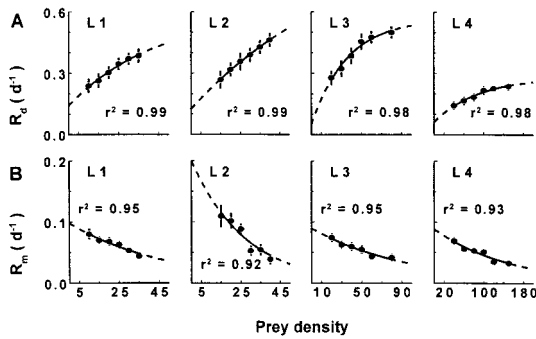


Fig. 6. Effect of prey density on (A) developmental rate (R_d), and (B) relative mortality rate (R_m) of the 1st through 4th instar (L1 to L4) of *C. septempunctata* feeding on *A. gossypii* on cotton. Bars represent observation means with 95% CL. The development response is described by equation 3 and the mortality response by equation 6.

younger prey (9.7 ± 0.16 d) than on the adult prey (10.6 ± 0.2 d).

Temperature and food quantity are 2 major factors affecting *C. septempunctata* population dynamics in the North China cotton region. In some years, development and reproduction of the seven-spotted lady beetle in wheat are enhanced by favorable temperatures and abundant prey, especially *Sitobion avenae* (F.). This results in large beetle populations that immigrate for the greater part to (monoculture) cotton and provide for biological control of *A. gossypii*. In years in which temperatures in April and May fall substantially below the beetle's optimum, development is prolonged, mortality increased, and reproduction reduced, such that even if cereal aphids are abundant, the beetle abundance is significantly lowered and its impact on the cotton aphid is reduced. Effective control of cotton aphid in cotton monoculture is, therefore, most likely if temperature and wheat aphid density favors the bionomics of seven-spotted lady beetles in wheat during April and May.

Results of this study provide a basis for a further analysis of factors regulating population dynamics of *A. gossypii* on cotton in fields, using simulation modeling of the spatiotemporal population interaction between *A. gossypii* and natural enemies as an analytical

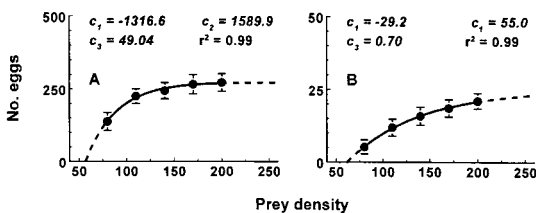


Fig. 7. Effect of prey density on (A) lifetime oviposition per female, and (B) mean oviposition rate (eggs per female per day) of *C. septempunctata* feeding on *A. gossypii* on cotton. Bars represent observation means with 95% CL. Fitted lines are defined by equation 3 and the indicated parameter values.

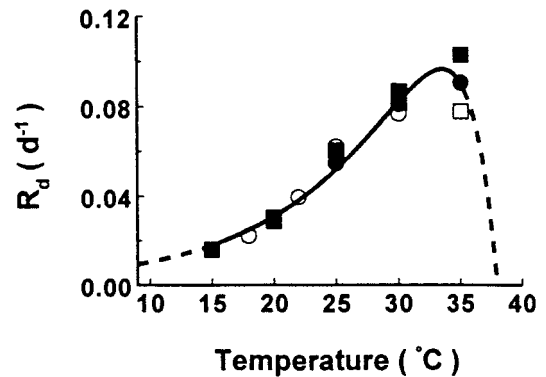


Fig. 8. Comparison of developmental rates (R_d) to the adult stage of *C. septempunctata* in originating from China (●) (this study), Japan (○) (Sakurai et al. 1991), Europe (■) (Hodek 1958), and India (□) (Sethi and Atwal 1964).

and explorative tool. When scaling up our results to the field situation, some translation problems need to be overcome. Particular attention needs to be paid to relating prey consumption in the field situation, and its possible effects on life performance of *C. septempunctata*, to the effects of prey supply on development, survival, and reproduction as reported here. It is now possible to calculate predation rates under field conditions, using functional responses that were established under the same experimental laboratory conditions as used in the experiments presented here (Xia 1997). To do so, predator search rates were converted to units of area per unit time. As a consequence of this, prey intake under our experimental conditions and under field conditions can both be reliably calculated. This calculation provides the linkage that is required to scale up to the field level. The validity of the fitted responses of development, survival and reproduction to changes in temperature, as presented in Figs. 1–6 is in principle restricted to the temperature range tested. To allow judgment of the potential appropriateness of extrapolations outside this range, which we do not recommend, the fitted curves are presented, hatched, outside the validity range.

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