# Effects of Temperature on Survival, Development, Longevity, and Fecundity of *Ophraella communa* (Coleoptera: Chrysomelidae), a Potential Biological Control Agent Against *Ambrosia artemisiifolia* (Asterales: Asteraceae)

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**ABSTRACT** *Ophraella communa* (Coleoptera: Chrysomelidae) is a leaf beetle that is unintentionally introduced in China. It is a potential biological control agent against common ragweed, *Ambrosia artemisiifolia* (Asterales: Asteraceae). The effects of temperature on the development and fecundity of *O. communa* were studied at eight constant temperature regimens (15, 20, 22, 25, 28, 30, 32, 36°C) in the laboratory. The results showed that the developmental periods for egg, larva, pupa, and entire immature stages decreased in response to the increasing temperature, with the exception of 30°C. The survival rates at different developmental stages were higher at 25 and 28°C than at other temperatures. Ovipositional period and longevity of female shortened with the increasing temperature. The highest fecundity of female was observed to be 2,712.3 eggs/female at 28°C. Life table of *O. communa* was constructed based on the data at 20–32°C. The innate capacity for increase ($r_m$), the net reproductive rate ($R_0$), and the finite rate of increase ($\lambda$) reached the maximum at 28°C, with values of 0.247, 1,773.0, and 1.280, respectively. The shortest period of a generation ($T$) was 24.6 d at 32°C, whereas the longest $T$ value was recorded as 79.3 d at 20°C. These results offer valuable insight on the establishment potential of *O. communa* in new environments with diverse temperature regimens and on its mass-rearing techniques in laboratory.

**KEY WORDS** *Ophraella communa*, *Ambrosia artemisiifolia*, development, fecundity, temperature

Common ragweed, *Ambrosia artemisiifolia* L. (Asterales: Asteraceae), is an annual harmful weed and is originally from North America (Wan et al. 2005). It is an agricultural weed, and its pollen can cause human anaphylaxis both in its native North America and in its naturalized ranges, such as southeastern Europe (Yugoslavia, Hungary), Ukraine, and southern Russia (Kovalev 1971). Common ragweed was introduced into China in the 1930s. Until now, it has been widely distributed in 14 provinces in northeastern, northern, central, eastern, and southern China (Wan et al. 2005, Ma et al. 2008). Common ragweed was listed as a quarantine agricultural pest in China in 2006 because of its agricultural importance, its notorious allergen to human health, and its impacts on biodiversity in China (Wan et al. 1995, Ministry of Agriculture of China 2006).

*Ophraella communa* LeSage (Coleoptera: Chrysomelidae) is an oligophagous leaf beetle that feeds on Asteraceae plant species including common ragweed and is originally from North America (Futuyma 1990, Palmer and Goeden 1991). *O. communa* was accidentally introduced into Japan and first discovered in Chiba Prefecture in 1996 (Takizawa et al. 1999). Thereafter, *O. communa* spread rapidly into many islands (e.g., Kyushu and Shikoku islands) in Japan (Tamura et al. 2004). Emura (1999) and Yamazaki et al. (2000) reported that *O. communa* fed almost exclusively on common ragweed and to some extent on giant ragweed (*A. trifida* L.), cockleburs (*Xanthium strumarium* L., *X. canadense* Mill, *X. italicum* Moretti), and sunflower (*Helianthus* spp.) in cage experiments in greenhouse. Thus, it was identified as a potential biological control agent against common ragweed, *A. artemisiifolia*. In China, *O. communa* was first discovered in Nanjing city, Jiangsu province, eastern China in 2001 (Meng and Li 2005). It has subsequently spread rapidly to eastern and central China, including Jiangxi, Hunan, Hubei, Anhui, Fujian, and Zhejiang provinces. It suppresses the population of common ragweed significantly in some areas invaded by common ragweed (Meng et al. 2007). At present, studies on *O. communa* are limited and mainly focus on its

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biology and the devices for its collection, storage, transport, and delivery (Welch 1978, Teshler et al. 2004, Meng and Li 2006, Zhang and Meng 2007).

Temperature is one of the critical factors that may affect the individual development and population dynamics of insects (Huffaker et al. 1999, Li 2002, McClay and Hughes 2007). Thus the optimum temperature range is necessary to be detected for mass rearing of insects (Daane et al. 2004, Huang et al. 2008). Besides, temperature is also an important factor for insect population establishment and success in the field (van Lenteren et al. 2006).

To determine the optimum temperature range for *O. communa*, its development under eight constant temperature regimens was studied in the laboratory. These temperatures were selected to represent the diverse geographical regions where the beetles could be expected to aid in the biological control of common ragweed. In addition, the population dynamics of *O. communa* under eight constant temperature regimens was analyzed by life table parameters. The results could offer valuable insights on the prospects of using this leaf beetle as a biological control agent against common ragweed covering geographically wide regions. It could also provide an optimum temperature for mass rearing of *O. communa* in laboratory and contribute to optimize the biological control programs of common ragweed in various regions.

## Materials and Methods

**Host Plants.** Seedlings of common ragweed originally grown in the nursery were individually transplanted into 15-cm-diameter plastic pots with loamy clay soil, watered every 4 d, and fertilized with N:P:K at the ratio of 13:7:15 once every 2 wk. The potted plants were maintained in an unheated greenhouse and used for experiments when they had reached a height of 50 cm.

**Insects.** *Ophraella communa* adults were collected from Linxiang county, Yueyang city, Hunan province, central China in late April 2008 and maintained on common ragweed's plants in the greenhouse of the Institute of Plant Protection, Hunan Academy of Agricultural Sciences. Pupae were collected from the greenhouse in mid-May 2008, stored in a transparent plastic box (19 by 12 by 6 cm), and kept in an air-conditioned laboratory at 26–27°C. Newly emerged adults were collected, and males and females were separately held on potted common ragweed's plants in cages (40 by 40 by 60 cm) in the same laboratory, at a density of 20 adults per plant and one plant per cage. Two-day-old adults were used for experiments.

**Development and Survivorship of Immature *O. communa*.** *Ophraella communa* adults from the above culture were paired, and each pair was placed on a potted fresh common ragweed's plant in cage (60 by 60 by 80 cm) for oviposition. The potted plants with *O. communa* eggs <12-h-old were placed in a plastic basin (50 by 30 cm), which were to absorb water from below. Plants that had at least 80 eggs were allocated randomly and placed in eight environmental chambers (PRY-450D; Ningbo Haishu Aifu Experimental Equipment, Zhejiang, China) at eight temperature regimens (15, 20, 22, 25, 28, 30, 32, and 36 ± 1°C). Five plants with eggs were used in each temperature treatment. Irrespective of the temperature, all environmental chambers were set at a relative humidity of 70 ± 5% and a photoperiod of 14 L:10 D. Eggs were checked daily until all hatched. The neonates were kept on the same common ragweed's plant until pupation. Pupae were detached from leaves, placed in an unsealed cuvette individually, and checked daily until adult emerged. Each treatment was repeated five times in the same environmental chamber, and the next cohort of eggs was placed in when all larvae in the previous treatment became pupae. Survival rates and developmental period at different developmental stages were recorded.

**Longevity and Fecundity of Leaf Beetle Adults.** Twigs of common ragweed were inserted into plastic bottles (3 cm in diameter and 5 cm in height) filled with water and with a 0.8-cm-diameter hole in the lid to hold the twig. Newly emerged *O. communa* adults at different temperature treatments were mated, and each pair was placed on such a fresh common ragweed's twig. The twigs with beetle were placed in transparent plastic boxes (19 by 12 by 6 cm) covered with mesh to prevent adult escape. These plastic boxes with *O. communa* adults and *A. artemisiifolia* twigs were placed in environmental chambers at the same temperature as their immature stages. Fresh twigs were changed daily, and the eggs of *O. communa* were counted. The observation ended until the female adult died. If the male died earlier, another newly emerged male was added. Preovipositional and ovipositional periods, longevity, and number of eggs laid per female were recorded. A total of 20 pairs were observed for each temperature treatment. Each pair was treated as one replication; thus, each treatment included 20 replications in this experiment.

**Statistical Analyses.** Data were checked for normality and homoscedasticity and, if needed, were arcsine square-root or log- transformed. The developmental periods were first transformed by the $\log_{10}(x + 1)$, and the survival rates were first transformed by arcsine square-root. Repeated-measure one-way analysis of variance (ANOVA) was conducted in comparing the overall differences of the data among treatments when significant treatment differences were indicated by a significant $F$-test at $P \leq 0.05$ (SAS Institute 2004). The Fisher protected least significant difference (LSD) test was used as a post-ANOVA test in comparing the means between treatments. Developmental rates for each life stage and total life cycle at each temperature were the reciprocals of developmental periods. Regression analyses of developmental rates versus temperature (SAS Institute 2004) were conducted for each life stage and total life cycle by pooling the data. The linear regression equation $[V = (1/K) \times T - C/K]$ was used, where $V$ is the developmental rate in days at temperature $T$ (°C), $K$ is the required heat units in degree-days (DD) in effective accumulation, and $C$ is the minimum developmental thresholds (DTs) (Ding

1980). The computational formulas of life table parameters were described as

$$R_0 = \Sigma l_x M_x$$

$$T = \Sigma l_x M_x / R_0$$

$$r_m = \ln r_0 / T$$

$$\lambda = \exp(r_m)$$

where subscript $x$ is the age in days of *O. communa*, $l_x$ is the survivorships at time $x$, and $M_x$ is the mean number of female offspring produced per female adult during the age interval $x$. $T$ is the mean generation time; $R_0$ is the net reproductive rate; and $r_m$ is the intrinsic rate of increase (Birch 1948).

Here, the life table parameters ($R_0$, $T$, $r_m$, and $\lambda$) were all computed by a computer program for age-stage, two-sex life table analysis (Chi 1994, 2008).

## Results

**Effects of Temperature on Development, Survivorship, and Sex Ratios of *O. communa*.** Egg could not hatch within 30 d at 15°C, and the mortality of first larval instars was 100% at 36°C; thus, the treatments at 15 and 36°C were omitted from the analysis. Temperatures from 20 to 32°C affected the developmental periods of egg, larva, pupa, and entire immature stages of *O. communa* significantly ($P < 0.05$). The developmental period for each stage decreased with the increasing temperature, with the exception of the treatment at 30°C. It took ≈17–20 d for an entire immature stage to develop at 28–32°C. Immature development period of *O. communa* at 20°C was approximately three times as long as that at 32°C (Table 1).

Survival rates of *O. communa* eggs, larvae, or pupae were significantly affected by temperature ($P < 0.05$). The survival rates of *O. communa* from egg to adult stages were much higher at 25 and 28°C than at other temperatures. Overall survival rate during entire immature stage varied from 9.6% at 20°C to 61.4% at 28°C (Table 1).

Female ratio of *O. communa* decreased with the increasing temperatures from 20 to 32°C (Table 1). However, the female ratios were not significantly affected by temperatures compared with the expected female ratio of 0.5 ($x^2 = 0.0023$, $x2 < x^2_{0.05} = 11.07$, df = 5, $P > 0.05$).

**Degree-Day Requirement of *O. communa*.** Among the different developmental stages of *O. communa*, the lowest threshold temperature was observed at the pupal stage (9.00°C), whereas the highest was noticed at the larval stage (15.94°C). The lowest threshold temperature for egg development was 14.06°C. The effective accumulative temperature for *O. communa* to develop from egg to adult was 307.20 DD (Table 2).

**Effects of Temperature on Adult Fecundity of *O. communa*.** Longevity, preovipositional period, ovipositional period, and number of eggs laid of female *O. communa* were significantly affected by temperature ($P < 0.05$). Preovipositional period, ovipositional period, and longevity of *O. communa* shortened with

**Table 1. Effects of temperature on the development, survival, and adult sex ratios of *O. communa***

| Temperature (°C) | Developmental period (d)[a] | | | | | Survival rate (%)[a] | | | Female ratio (%)[c] |
|---|---|---|---|---|---|---|---|---|---|
| | Egg | Larva | Pupa | Entire immature[b] | Egg | Larva | Pupa | Entire immature[b] | |
| 20 | 12.5 ± 0.1a (80) | 24.9 ± 0.3a (39) | 12.5 ± 0.17a (35) | 49.8 ± 0.7a (34) | 70.4 ± 1.7c | 14.5 ± 1.0f | 93.6 ± 5.9cd | 9.6 ± 0.9c | 0.514 ± 0.009a |
| 22 | 7.0 ± 0.0b (80) | 17.2 ± 0.1b (45) | 8.7 ± 0.1b (43) | 32.5 ± 0.2b (41) | 69.9 ± 1.1c | 57.0 ± 1.4d | 90.3 ± 1.8d | 38.4 ± 9.9b | 0.508 ± 0.355ab |
| 25 | 6.5 ± 0.1c (80) | 12.1 ± 0.1c (65) | 7.3 ± 0.1c (63) | 25.9 ± 0.3c (62) | 85.9 ± 0.9a | 66.0 ± 0.2b | 99.0 ± 1.6a | 41.1 ± 2.0b | 0.503 ± 0.007bc |
| 28 | 5.0 ± 0.0d (80) | 7.1 ± 0.1e (69) | 6.3 ± 0.0d (68) | 18.5 ± 0.2e (67) | 79.8 ± 2.1b | 79.3 ± 2.1a | 97.2 ± 2.2ab | 61.4 ± 1.4a | 0.496 ± 0.004c |
| 30 | 6.0 ± 0.0e (80) | 7.9 ± 0.1d (49) | 6.2 ± 0.0d (47) | 20.1 ± 0.2d (46) | 61.9 ± 0.6d | 60.3 ± 2.5c | 96.5 ± 2.7abc | 36.0 ± 1.8b | 0.485 ± 0.003d |
| 32 | 4.0 ± 0.0f (80) | 7.6 ± 0.1de (35) | 6.0 ± 0.0d (33) | 17.6 ± 0.3f (31) | 78.5 ± 1.2b | 51.0 ± 1.1e | 93.1 ± 1.1cd | 35.6 ± 2.6b | 0.475 ± 0.008e |
| F, df | 1756.48, 5 | 1623.86, 5 | 1126.52, 5 | 2529.41, 5 | 214.81, 5 | 1352.40, 5 | 5.60, 5 | 92.54, 5 | 28.02, 5 |
| P | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | 0.0015 | <0.0001 | <0.0001 |

[a] Mean ± SE ($n$), $n$ is no. of individuals observed. Means within the same column followed by the different letters are significantly different at $P < 0.05$ level according to ANOVA: LSD test.
[b] Entire immature refers to the developmental period of *O. communa* from egg to adult emergence.
[c] Female percentage = no. of females divided by no. of all adults emerged.

**Table 2. Linear regression analyses of the development of *O. communa* under different temperatures**

| Life stage | Regression equation[a] | $R^2$ | F | P | $C$[b] | $K$[c] |
|---|---|---|---|---|---|---|
| Egg | $V = 0.0138T - 0.1940$ | 0.77 | 1105.81 | <0.0001 | 14.06 | 72.49 |
| Larva | $V = 0.0093T - 0.1488$ | 0.89 | 1427.57 | <0.0001 | 15.94 | 107.12 |
| Pupa | $V = 0.0081T - 0.0727$ | 0.89 | 984.33 | <0.0001 | 9.00 | 123.85 |
| Entire immature[d] | $V = 0.0033T - 0.0434$ | 0.91 | 3061.49 | <0.0001 | 13.34 | 307.20 |

[a] Calculated after Ding (1980), where $V$ is the developmental rate (1/developmental period) and $T$ is the temperature (° C).
[b] $C$ is the minimum thermal threshold for development (° C).
[c] $K$ is the effective accumulative temperature with the unit of degree-days.
[d] Entire immature refers to the developmental period of *O. communa* from egg to adult emergence.

increasing temperatures from 20 to 32°C. The highest amount of oviposition was observed at 28°C, which yielded an average of 2,712.3 eggs/female. Female's fecundity decreased significantly no matter the temperature was increasing or decreasing. The lowest fecundity was 521.8 eggs/female at 20°C (Table 3).

**Effects of Temperature on Age-Related Survivorship and Fecundity of *O. communa*.** At 22−30°C, *O. communa* females laid most eggs during the early ovipositional periods and showed a significant peak. The age-related fecundity decreased sharply with age. Among them, it increased a bit at the late ovipositional period and showed a low peak at 28 and 30°C (Fig. 1). At 20°C, the age-related fecundity peaked at the early ovipositional period dropped and fluctuated during a long ovipositional period. At 32°C, the oviposition fluctuated and ended in a relatively short period (Fig. 1).

Almost all of female *O. communa* survived up to 85 d at 20°C, but survival rate decreased sharply after 110 d. At 22 and 25°C, female death was occurred around 45 and 41 d after emergence, respectively. Afterward, survival rate decreased slowly with age, and >50% individuals survived in the mid-term of the ovipositional period at 22 and 25°C. Survival rate decreased slowly only in the mid-term of the ovipositional period at 28 and 30°C. At 32°C, female death happened after the 26th day, and survival rate dropped sharply to <30% by 35 d (Fig. 1).

**Life Table Parameters of *O. communa* at Different Temperatures.** The intrinsic capacity for increase ($r_m$), the net reproductive rate ($R_0$), and the finite rate of increase ($\lambda$) reached the maximum values at 28°C, which were 0.247, 1,773.0, and 1.280, respectively. Their minimum values were observed at 20°C, which were 0.074, 344.8, and 1.077, respectively. The

$R_0$ value at 25°C ranked the second. When reared at 32°C, *O. communa* had higher $r_m$ and $\lambda$ values, but its $R_0$ value was relatively low. The mean length of a generation ($T$) decreased along with the increasing temperatures. The lowest $T$ value was 24.6 d at 32°C, and the highest was 79.3 d at 20°C (Table 4).

## Discussion

Survival, development, and fecundity of insects could be significantly affected by temperatures (Huang et al. 2008). Our experiments showed that temperature affected the survival, development, longevity, and fecundity of *O. communa*, which offer important information for mass-rearing of *O. communa* in laboratory and its release into new environment to control common ragweed.

Insects have an optimum temperature range for development (Huffaker et al. 1999), and their survival and development are significantly impacted when the temperature is below or above the range (Huang et al. 2008). The results of experiments provided such evidence that *O. communa* eggs could not hatched at 15°C, and the mortality of first larval instars reached 100% at 36°C. *O. communa* could develop at 20–32°C, but survival, development, longevity, and fecundity differed significantly. Beyond the optimum temperature range of 25–28°C, immature survival rate and fecundity decreased. Goeden and Ricker (1985) reported that individual *O. communa* could lay 667 eggs, and the ovipositional period lasted 66 d when raised on *A. psilostachya* in the laboratory. Meng and Li (2006) observed that the fecundity of *O. communa* was 295.4–312.1 eggs/female, and the ovipositional period averaged 13.2 d when reared with fresh common ragweed's leaves at 24–30°C in the laboratory.

**Table 3. Effects of temperature on the fecundity of *O. communa* females**

| Temperature (° C) | Preovipositional period (d)[a] | Ovipositional period (d)[a] | Longevity (d)[a] | No. eggs laid per female[a] |
|---|---|---|---|---|
| 20 | 60.7 ± 3.1a | 60.8 ± 4.4a | 121.5 ± 4.7a | 521.8 ± 50.8e |
| 22 | 38.4 ± 0.2b | 58.4 ± 7.6a | 96.8 ± 7.6b | 1323.2 ± 94.1c |
| 25 | 29.3 ± 0.3c | 56.7 ± 4.2a | 86.0 ± 4.1b | 1792.7 ± 115.0b |
| 28 | 21.1 ± 0.2e | 49.6 ± 4.1ab | 70.7 ± 4.0c | 2712.3 ± 99.0a |
| 30 | 23.1 ± 0.2d | 39.4 ± 3.2b | 62.5 ± 3.3c | 1496.4 ± 68.9bc |
| 32 | 19.5 ± 0.3f | 15.2 ± 2.2c | 34.2 ± 2.2d | 903.3 ± 147.2d |
| F, df | 1748.44, 5 | 10.65, 5 | 51.98, 5 | 40.42, 5 |
| P | <0.0001 | <0.0001 | <0.0001 | <0.0001 |

[a] Mean ± SE. Means within the same column followed by the different letters are statistically different at $P < 0.05$ level according to ANOVA: LSD test.
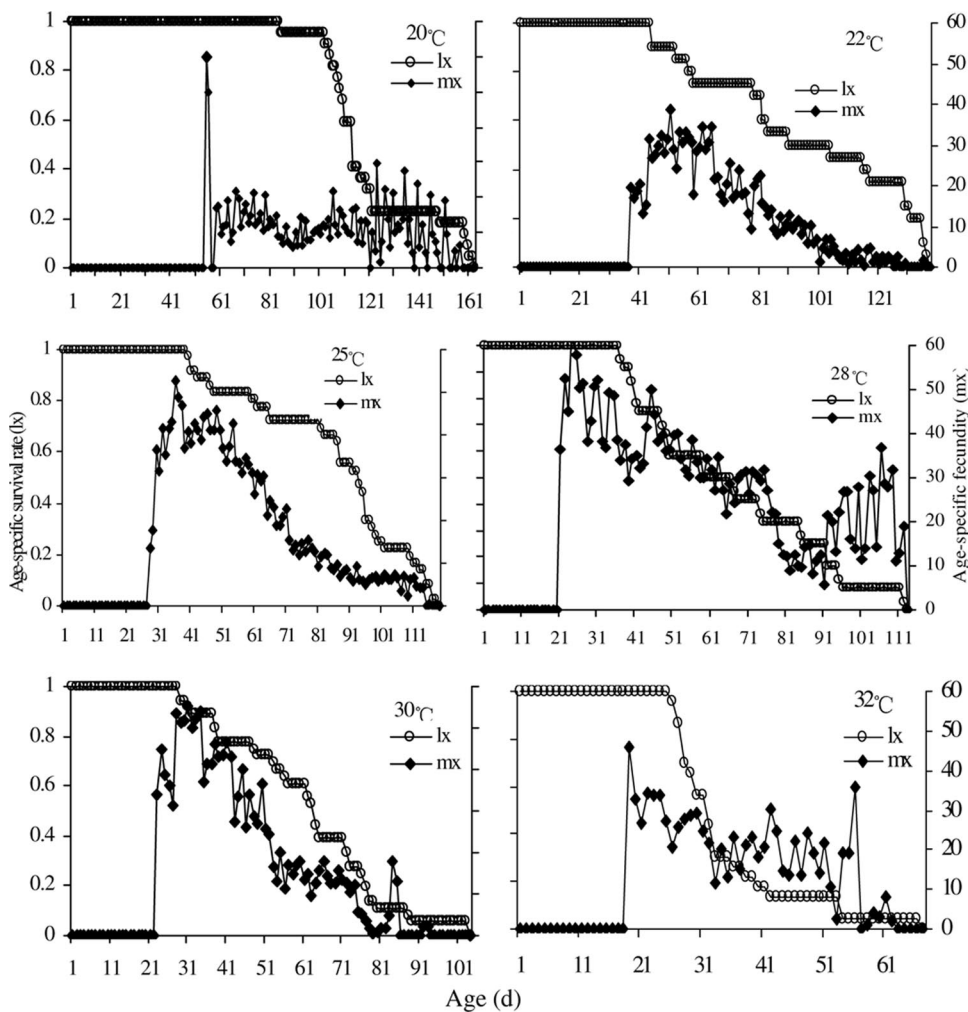
**Fig. 1.** Age-related survival rate (*lx*) and age-related fecundity (*mx*) of *O. communa* at different temperatures.

In our experiment, the fecundity of female *O. communa* was much higher. Averagely, individual paired *O. communa* female laid 1,323.2–2,712.3 eggs in a period of 39.4–58.4 d when reared on potted common ragweed's plants at 22–30°C. Compared with former reports, we conclude that the fecundity of *O. communa* was significantly affected by the host plants supplied, and the living fresh common ragweed's plant seemed more suitable for the development and subsequent oviposition of *O. communa* than the fresh dissected leaves.

Life table parameters have been widely applied to evaluate the development and reproductive potential of lady beetles, e.g., *Mecinus janthinus* and *Axinoscym-*

**Table 4.   Effects of temperature on the life table parameters of *O. communa***

| Temperature (° C) | Intrinsic rate of increase $(r_m)^a$ | Net reproduction rate $(R_o)^a$ | Generation time $(T)$ (d)$^a$ | Finite rate of increase $(\lambda)^a$ |
|---|---|---|---|---|
| 20 | 0.074 ± 0.001f | 344.8 ± 36.9d | 79.3 ± 1.0a | 1.077 ± 0.001f |
| 22 | 0.132 ± 0.002e | 1000.1 ± 119.3c | 52.5 ± 0.8b | 1.141 ± 0.002e |
| 25 | 0.181 ± 0.002d | 1485.9 ± 112.3ab | 40.3 ± 0.4c | 1.199 ± 0.002d |
| 28 | 0.247 ± 0.002a | 1773.0 ± 137.3a | 30.3 ± 0.4d | 1.280 ± 0.002a |
| 30 | 0.222 ± 0.003c | 1166.3 ± 85.76bc | 31.8 ± 0.4d | 1.249 ± 0.004c |
| 32 | 0.240 ± 0.003b | 359.6 ± 48.49d | 24.6 ± 0.6e | 1.271 ± 0.004b |
| *F*, df | 754.82, 5 | 24.10, 5 | 841.29, 5 | 691.18, 5 |
| *P* | <0.0001 | <0.0001 | <0.0001 | <0.0001 |

$^a$ Mean ± SE. Means within the same column followed by the different letters are statistically different at $P < 0.05$ level according to ANOVA: LSD test.

*nus cardilobus* (Tanigoshi and McMurtry 1977, Huang et al. 2008). Results from the literature show that $r_m$ of the beetles are not only significantly affected by temperature (Huang et al. 2008) but also by the nature of their prey/host (Tanigoshi and McMurtry 1977, Mc-Clay and Hughes 2007). The results of our experiment suggested that 25–30°C was an optimum temperature range for the population development of *O. communa*, with relatively high values of intrinsic increase rate ($r_m$), net reproduction rate ($R_0$), and finite increase rate ($\lambda$). According to these life table parameters, *O. communa* is well adapted to subtropical conditions. In fact, *O. communa* was extensively used as a biological agent for managing common ragweed in a few subtropical countries and areas, such as America, Mexico, Canada, Japan, Korea, China, and Taiwan (Palmer and Goeden 1991, Sohn et al. 2002, Tamura et al. 2004, Meng and Li 2005). The results of this experiment suggest significant potential for using *O. communa* to manage common ragweed because most of areas invaded by common ragweed belong to subtropics in China. The optimum developmental temperature range for *O. communa* largely coincides with the temperature range of the subtropical regions of China where most of the ragweed invasions are present.

Minimum thermal threshold for development and thermal constancy can provide useful information for forecasting an insect's potential distribution (Huang et al. 2008). Our results indicated that a minimum threshold temperature of 13.34°C and an effective accumulated temperature of 307.20 d-degrees were prerequisite for *O. communa* to complete a generation. It indicated that winter temperatures in subtropical regions may be unsuitable for the development of *O. communa.* The beetle might escape the adverse temperature condition in winter in subtropical regions by entering dormancy or diapause.

One necessary precondition of biological control is the co-occurrence of natural enemy with the pest. Seeds of common ragweed start germination at 6.1–6.6°C and seedlings start growth at 6–8°C (Wan et al. 1993). Thus, common ragweed's development occurs earlier than that of *O. communa* in early spring in the subtropical regions. Normally, weeds maintain a relatively high population after seeds or perennial roots germinate from the early spring season. However, insects are at low populations in the fields at the early season and expand after one or two generations of propagation. Thus, beneficial herbivorous insects should be released in the early season to suppress the weed populations. To apply *O. communa* for managing common ragweed in the early spring, mass rearing of *O. communa* under manipulated conditions is essential. The results of our experiment suggested that, to reach the highest intrinsic increase and net reproduction rates, the optimum temperature for its mass rearing is 28°C.

## Acknowledgments

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