Temperature-Dependent Effects on Development, Mortality, and Growth of *Hippodamia convergens* (Coleoptera: Coccinellidae)

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ABSTRACT Insect natural enemies selected for specific traits such as faster developmental times, higher survivorship, increased fecundity, and larger body size might be considered during production of biological control agents in certain situations. For instance, traits related to developmental rates may be selected for if genetically based variation exists within temperature-dependent responses. We compared preimaginal development, mortality, and size of *Hippodamia convergens* Guérin-Méneville at 4 constant temperatures (18, 22, 26, and 30°C). Total preimaginal development ranged from 51 d at 18°C to 14 d at 30°C. Developmental times were significantly different among isofemale lines of field-collected *H. convergens* from Oregon at all temperatures tested (18, 22, 26, and 30°C). Variation within female lines was significant only at 26°C. The lower developmental thresholds for egg, larval, and pupal stages were 9.9, 13.7, and 14.5°C, respectively. Degree-day (DD) requirements for development were 58.8, 166.7, and 52.6 for eggs, larvae, and pupae, respectively. Total preimaginal development required 231 DD above a temperature threshold of 13.6°C. Degree-day requirements for 14 field-collected female lines varied from 223 to 273, whereas the lower threshold for development ranged from 13.1 to 13.8°C. Mortality decreased with increasing temperatures. At the lower temperature (18°C), higher mortality occurred during the 4th instar and pupa. Pupal and adult weights differed across temperatures. Heavier pupae and adult beetles were reared at 22°C. Also, wings were larger among beetles reared at 22°C. The development, mortality, and size measurements provide data for establishing suitable rearing conditions for future studies on the ecology of *H. convergens.*

KEY WORDS *Hippodamia convergens,* developmental threshold, degree-days, weights, mortality

THE CONVERGENT LADY beetle, *Hippodamia convergens* Guérin-Méneville, is one of the most abundant and widespread species within the genus *Hippodamia* in North America (Gordon 1985). Although the species is polyphagous, it has preference for aphids and constitutes an important component in the suppression of aphid populations (Hagen 1962). In common with other coccinellids, *H. convergens* exhibits variable development rates depending on the ambient temperature (Miller 1992). Such studies on temperature-dependent development are important in understanding the dynamics of predator–prey relationships. Moreover, they contribute to enhance the efficiency of mass rearing, provide a quantitative basis for predicting development and activity in pest management programs, and are used in models to estimate insect growth, development, and reproduction (Gutierrez et al. 1981).

Early ecological studies on *H. convergens* development under field conditions were conducted by Clausen (1915) in California, and in Florida by Miller and Thompson (1927). Nielson and Currie (1960) studied the biology of the species in Arizona when fed spotted alfalfa aphids, *Therioaphis maculata* (Buckton). Subsequently, temperature-dependent effects on the convergent lady beetle were investigated. Butler and Dickerson (1972) reported the development of *H. convergens* at different temperatures. Later, Obrycki and Tauber (1982) and Michels and Behle (1991) examined the thermal requirements for populations of the convergent lady beetle collected in New York and Texas, respectively. These data were used by Miller (1992) to compare the development of *H. convergens* from different geographic areas in the United States.

Temperature, as well as food and population density, affects adult size. The effect of temperature on adult growth for Coccinellidae has been examined by Mills (1981). However, no studies have reported the effect of temperature on *H. convergens* larval and adult size.

In the current article we examined the effect of temperature on various developmental parameters for *H. convergens* when fed pea aphid, *Acyrthosiphon pisum* (Harris). Our 1st objective was to document the developmental biology of *H. convergens* fed pea aphids at 4 constant temperatures to determine the range of variation in thermal requirements occurring among and within isofemale lines. Our 2nd objective was to determine the effect of temperature on *H. convergens* larval and adult size.

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Table 1. Developmental days (means ± SE) for F_1 offspring of 10 field-collected *H. convergens* reared at 4 constant temperatures

Female	*n*[a]	°C				r^2[b]	Dth[c]	DD[d]
		18	22	26	30			
A	40	48.7 ± 2.5	28.4 ± 2.1	17.6 ± 0.6	13.8 ± 0.8	0.98	13.6 ± 0.2	225.8 ± 5.1
B	43	50.7 ± 2.8	28.0 ± 0.7	17.8 ± 0.6	14.2 ± 0.4	0.99	13.5 ± 0.2	231.2 ± 3.7
C	38	48.0 ± 2.2	27.8 ± 0.6	16.7 ± 0.8	14.1 ± 0.6	0.97	13.2 ± 0.4	228.7 ± 7.6
D	24	50.5 ± 1.0	27.8 ± 0.4	17.5 ± 0.3	14.4 ± 0.6	0.99	13.2 ± 0.3	236.8 ± 6.0
E	15	52.6 ± 1.5	28.4 ± 0.5	NA	15.0 ± 0.7	0.99	13.2 ± 0.3	251.6 ± 5.8
F	39	50.6 ± 2.9	27.0 ± 1.6	17.1 ± 0.9	14.1 ± 0.4	0.97	13.8 ± 0.3	223.2 ± 7.0
G	20	54.7 ± 1.1	28.6 ± 0.7	18.7 ± 1.3	14.5 ± 0.3	0.99	13.7 ± 0.2	236.1 ± 3.6
H	11	NA	28.0 ± 1.0	18.0 ± 0.7	14.9 ± 1.1	0.97	13.2 ± 0.5	260.6 ± 14
I	12	52.0 ± 2.8	28.5 ± 0.8	NA	14.1 ± 0.5	0.99	13.8 ± 0.3	229.0 ± 5.7
J	22	51.0 ± 1.2	27.8 ± 0.8	18.0 ± 0.0	13.9 ± 0.4	0.99	13.8 ± 0.2	224.9 ± 3.5
All[e]	316	51.3 ± 3.3	28.7 ± 1.3	17.5 ± 0.9	14.3 ± 0.6	0.97	13.6 ± 0.1	230.9 ± 2.3

NA, data not available.

[a] Total number of individuals that completed development at all 4 temperatures.

[b] Regression of developmental times and temperatures.

[c] Lower developmental threshold.

[d] Degree-day requirements.

[e] Data includes all field-collected females.

Materials and Methods

Insects. Adults of *H. convergens* were collected in the vicinity of Corvallis, Benton County, OR. Field-collected females were held individually at room temperature in 30-ml plastic creamers with cardboard lids and fed daily with pea aphid, *A. pisum*, cultured on fava bean, *Vicia fabae* L. Pea aphids were reared as described by James and Lighthart (1990).

Thermal Requirements and Mortality. Egg masses ($n > 5$) from each female were collected and placed into 1 of 4 constant temperatures (18, 22, 26, or 30°C) and held at a photoperiod of 16:8 (L:D) h and 50–70% RH within 24 h of oviposition. A temperature range from 18 to 30°C was used because the preimaginal development rate for *H. convergens* is not linear above temperatures of 30°C (Obrycki and Tauber 1982, Miller 1992). The lowest temperature, 18°C, was selected because Miller (1992) reported no larval survival beyond the 3rd instar at 13°C and high mortality (83%) at 17°C. Eggs were checked for larval eclosion every 12 h. After egg hatch, a minimum of 5 neonates from each female were placed under each temperature ($n > 20$ first instars per female, at all temperatures). Larvae were fed daily with pea aphids. Larvae in the lower temperatures (18 and 22°C) were monitored once a day, whereas larvae in the higher temperatures (26 and 30°C) were monitored twice a day. Larval survival and times of molting, pupation, and adult emergence were recorded.

Size. Fourth instars and pupae were weighed within 12 h after molt. Adults were weighed to the nearest 0.1 mg within 12 h after emergence. Wing areas were measured using a Zidas (Carl Zeiss, Thornwood, NY) digital board. The area of the hind wings is expressed in square millimeters and was obtained for 173 individuals.

Statistical Analysis. Differences in developmental times within and among isofemale lines were determined using analysis of variance (ANOVA) (Abacus Concepts 1989). Also, differences in larval, pupal, and adult weights, and wing areas across temperatures were tested using ANOVA. Multiple comparisons were done using Tukey Compromise tests ($\alpha = 0.05$). Linear regression models comparing developmental rate (y, 1/d) to temperature (x) were used to estimate the lower developmental threshold and the degree-day requirements for each isofemale line. The lower developmental threshold was determined as the x-intercept of the linear equation, and the degree-day requirements were determined as the inverse of the slope. Estimates for the standard error of the 2 parameters were calculated as described by Campbell et al. (1974). Predicted days of development were obtained from the formula $y = k/(T\text{-}t)$, where k represents the degree-day requirements, T is the temperature, and t is the developmental threshold.

Results

Thermal Requirements and Mortality. The total preimaginal development time for *H. convergens* ranged from 14 d at 30°C to 51 d at 18°C (Table 1). Developmental times from egg to adult varied significantly among the isofemale lines at 18 ($F = 6.8$; df = 12, 47; $P < 0.001$), 22 ($F = 3.8$; df = 17, 91; $P < 0.001$), 26 ($F = 6.8$; df = 7, 32; $P < 0.001$), and 30°C ($F = 2.5$; df = 11, 51; $P = 0.01$) (Table 1). At 18°C, average developmental times for individual female lines ranged from 48 to 54.7 d, whereas at 22°C, developmental times ranged from 27 to 28.5 d. At 26°C, developmental times for different female lines ranged from 16.7 to 18.7 d and from 13.8 to 15 d at 30°C. Variation within isofemale lines occurred only at the 26°C temperature ($F = 4.0$; df = 14, 32; $P < 0.001$). This observed variation in developmental times among isofemale lines may allow for artificial selection of lady beetles for faster developmental rates (Rodriguez-Saona 1994).

Between 18 and 30°C, the preimaginal developmental rate was linearly related to temperature. The lower threshold for egg, larval, and pupal development were 9.9, 13.7, and 14.5°C, respectively, and required 58.8,

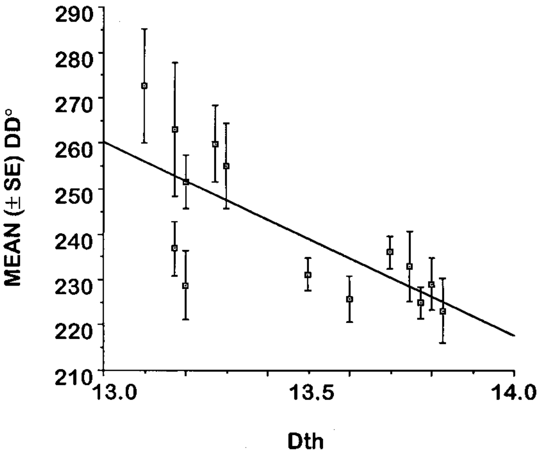

Fig. 1. Degree-days required for complete development (from oviposition to adult emergence) versus the threshold temperature (Dth) for 14 field-collected isofemale lines ($y = 809.6 - 42.3x$ [SE = 11.5]; $F = 13.6$; df = 1, 12; $P = 0.003$; $r^2 = 0.53$).

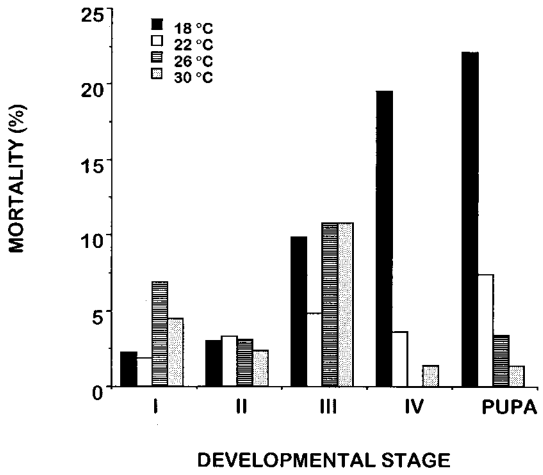

Fig. 2. Stage-specific mortality of *H. convergens* under 4 constant temperatures and held at a photoperiod of 16:8 (L:D) h and 50–70% RH.

166.7, and 52.6 DD for development. The lower threshold for total preimaginal (egg to adult) development was 13.6°C, and the thermal constant was 231 DD (Table 1).

Degree-day requirements and developmental thresholds were calculated for various field-collected females in Oregon (Fig. 1). There was a significant negative relationship between the lower development threshold and the degree-day requirements for the different female lines. The total degree-days for development decreased as the lower temperature threshold for development increased ($r^2 = 0.53$; $F = 13.58$; df = 1, 12; $P = 0.003$). Among our isofemale lines, developmental thresholds ranged from 13.2 to 13.8°C (Table 1). Degree-day requirements ranged from 223 to 261. Predicted development times at 18°C ranged from 47.4 d for a female characterized by degree-day requirement of 229 above a threshold of 13.2°C, to 55.5 d for a female characterized by a degree-day requirement of 236 above a threshold of 13.7°C. These data demonstrate the existence of significant variation in developmental rates based on isofemale lines.

Mortality of *H. convergens* decreased with increasing temperatures (Fig. 2). Mortality from eclosion of the 1st instar to adult emergence was 46.4, 19.3, 22.2, and 19.1% at 18, 22, 26, and 30°C, respectively. Larval mortality ranged from 24% at 18°C to 18% at 30°C. Pupal mortality ranged from 22% at 18°C to 1.4% at 30°C. At low temperatures (18°C), the highest mortality occurred among 4th instars and pupae (Fig. 2).

Size. Weights of 4th instars were not significantly different across temperatures ($F = 2.52$; df = 3, 267; $P = 0.06$) (Fig. 3A). However, significant differences in weights were obtained for pupae ($F = 42.4$; df = 3, 267; $P < 0.001$) and adults ($F = 34.5$; df = 3, 267; $P < 0.001$) of lady beetles reared at different temperatures (Fig. 3 B and C). Pupae in the 22°C treatment were 3.1, 15.6, and 17.5% heavier than those reared at 18, 26, and 30°C, respectively. Adults reared at 22°C were 4.9, 16.4, and 18.1% bigger than beetles reared at 18, 26, and 30°C, respectively.

Wing area is an index of body size ($r^2 = 0.65$, $n = 272$), and is less variable than live weights which vary because of water content (C.R., unpublished data). Temperature significantly affected wing areas ($F = 10.8$; df = 3, 165; $P < 0.001$) (Fig. 4). Beetles reared at 22°C had larger wings than beetles reared at higher temperatures (26 or 30°C). Females had significantly larger wing areas than males ($F = 104.7$; df = 1, 165; $P < 0.001$) (Fig. 4). However, the effects of temperature on wing area did not vary by sex. There was no significant interaction between sex and temperature ($F = 1.5$; df = 3, 195; $P = 0.21$).

Discussion

The duration of development of *H. convergens* reared at a constant temperature for different geographic locations and diet regimes has been reported (Palmer 1914, Clausen 1915, Miller and Thompson 1927, Nielson and Currie 1960). More recently, temperature-dependent studies have been conducted (Butler and Dickerson 1972, Obrycki and Tauber 1982, Michels and Behle 1991, Miller 1992). Total developmental times for a population of *H. convergens* from Texas ranged from 29 d at 20°C to 14 d at 30°C (Michels and Behle 1991). Total developmental times for a population of *H. convergens* from New York were 60.1 d at 15.6°C to 12.9 d at 29.4°C (Obrycki and Tauber 1982). Total developmental times for a population of *H. convergens* from Arizona and Oregon were 51.9 and 50.1 d at 17°C to 11.5 and 11.4 d at 33°C, respectively (Miller 1992). Miller (1992) compared *H. convergens* development for populations from New York, Texas, Arizona,, and Oregon. He concluded that the species exhibits a constancy across geographically separated

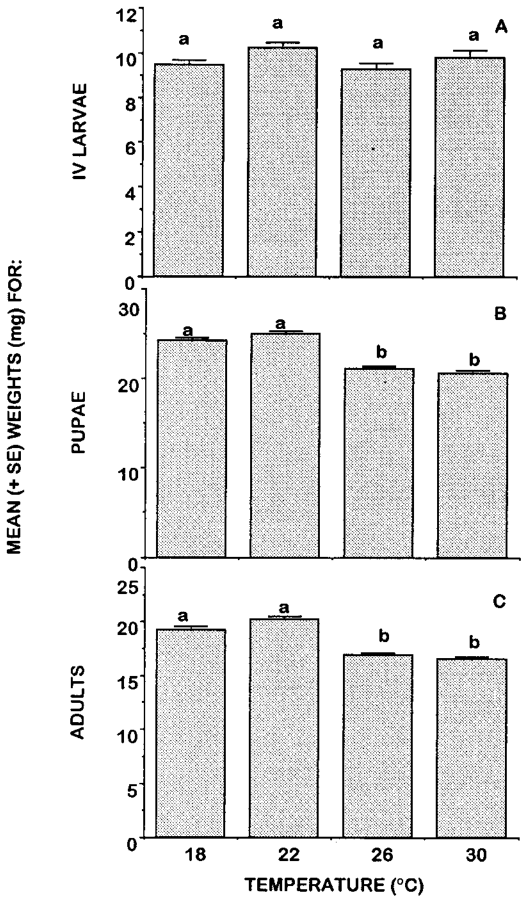

Fig. 3. Weights of *H. convergens* fed pea aphids at 4 constant temperatures, all at a photoperiod of 16:8 (L: D) h, and 50–70% RH. Bars represent standard errors. Columns with same letters are not significantly different at $\alpha = 0.05$ (Tukey compromise test).

populations in the traits of developmental threshold and degree-day requirements. Compared with his values, our calculated values were very similar. Our lower developmental threshold for egg, larva, pupa, and egg-to-adult differed only by 1.2, 2.6,1.3, and 1.1°C, respectively, and the degree-day requirements by 18, 42, 0, and 3, respectively. One aspect of the explanation for these small differences between studies is the number of constant temperatures used in the studies and resulting x-intercept values from regression analysis.

Degree-day requirements for *H. convergens* development decrease as the lower temperature threshold increases (Fig. 1). Frazer and McGregor (1992) found a similar relationship for different Coccinellidae egg development. Honek (1996) suggested that the negative relationship might be a result of an adaptation to temperature fluctuations. Furthermore, individuals with low developmental thresholds may be better suited for use in biological control because they can develop faster under cooler temperatures. Bernal and Gonzales (1993) suggested that parasitoids of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), with lower developmental threshold would have greater population densities following the winter season and thus have a greater potential as effective biological control agents. Rodriguez-Saona and Miller (1995) found that lines of *H. convergens* selected for fast developmental rate have a higher intrinsic rate of increase and number of generations per year than unselected lines.

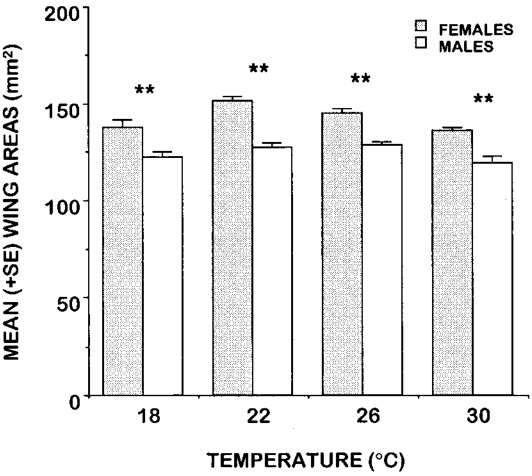

Fig. 4. Wing areas of *H. convergens* females and males reared at 4 constant temperatures, all at a photoperiod of 16:8 (L: D) h, and 50–70% RH and fed pea aphids. Bars represent standard errors. **, significant difference ($P = 0.01$) between males and females.

We have shown variation in developmental times and thermal requirements among *H. convergens* isofemale lines (Table 1). Existence of genetic variability in the thermal requirements for development among predatory insect populations has been noted. Tauber et al. (1987) reported that *Chrysopa oculata* Say from 5 widespread populations (southern Canada to montane Mexico) exhibited remarkable similarities in their thermal requirements for nondiapause development. However, despite these similarities, they indicated that degree-days required by *C. oculata* for total preimaginal development differed by ≈88 DD and the lower developmental threshold varied by 1.2°C. Similarly, Miller (1992) found consistent thermal requirements for 4 widely separated populations of *H. convergens* from North America.

Mortality of *H. convergens* increases at low temperatures (Fig. 2). Obrycki and Tauber (1982) and Michels and Behle (1991) reported no development to the adult stage at 13 and 15°C, respectively. Miller (1992) reported high mortality (83%) at 17°C. Obrycki and Tauber (1982) also reported that high mortality at the lower temperatures occurs at later stages of development.

Hippodamia convergens reared at different temperatures vary in body size (Figs. 3 and 4). Orr and Obrycki (1990) also found significant differences in the size of *H. parenthesis* (Say) when reared at different temperatures. They reported that individuals reared at 26 and 30°C were significantly smaller than those reared at 18 or 22°C. Evidence for size differences among beetles can be attributed to their variation in feeding rates, which vary depending on rearing temperatures (Honek 1996). Honek (1996) suggested that the developmental rate is apparently more accelerated than feeding, and beetles are not able to eat as much food per unit of physiological time at high temperatures compared with low temperatures. Our results suggest that this developmental effect on consumption is critical during the development of the last instar (4th), where a larva consumes ≈⅔ of its required food to develop (Nielson and Currie 1960). As a result, weights of recently molted 4th instars were not different across temperatures; however, final pupal and adult weights differed significantly (Fig. 3). In addition, female *H. convergens* were larger than males. Smith (1966), who reported that females of different Coccinellidae species are heavier and larger than males, supports our results.

In conclusion, our results provide data for establishing suitable conditions for rearing *H. convergens* and that isofemale-based cultures may exhibit divergent characteristics. For instance, mass culture methods could be enhanced by setting temperature conditions for either rapid development, maximum survival, or high fecundity. Also, family lines could be developed for traits of superior survival or rapid development at low temperatures.

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