

Temperature-Dependent Development of the Convergent Lady Beetle (Coleoptera: Coccinellidae)

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ABSTRACT Development of the convergent lady beetle, *Hippodamia convergens* Guérin-Méneville, was compared at six constant temperatures. Two populations, one from Corvallis, Oreg., and another from Tucson, Ariz., did not differ in larval survival or developmental rates. Mortality from eclosion of the first instar to adult emergence was 100, 83, 15, 18, 10, and 5% at 13, 17, 21, 25, 29, and 33°C, respectively. Development from oviposition to adult ranged from 51.9 d at 17°C to 11.4 d at 33°C. The heat-unit requirements for development from egg to adult were 228 degree-days above a developmental threshold of 12.5°C. Published data on development of *H. convergens* from Ithaca, N.Y., and Bushland, Tex., suggest a constancy in developmental requirements for the species from four widely separated regions of North America.

KEY WORDS Insecta, lady beetle, degree-day, *Hippodamia*

THE CONVERGENT LADY BEETLE, *Hippodamia convergens* Guérin-Méneville, is a prominent species in the native North American fauna of natural enemies in many agroecosystems (Hagen 1962, Belnavis 1989, Elliott & Kieckheffer 1990). Although a polyphagous predator, the convergent lady beetle exhibits a preference for aphids. The developmental biology of *H. convergens* has been studied in detail to understand its function as a biological control agent (Nielsen & Currie 1960, Butler & Dickerson 1972, Baumgaertner et al. 1981, Gutierrez et al. 1981, Obrycki & Tauber 1982, Wipperfurth et al. 1987). Data on development in relation to temperature are important to understanding the dynamics of predator-prey relationships. For instance, the conceptual model for growth, development, and reproduction of *H. convergens* (Gutierrez et al. 1981) requires data on temperature-dependent development. Also, population differences in developmental rates, if they exist, may be associated with certain climatic conditions and thereby influence population dynamics of natural enemies when imported for biological control of pests (Miller 1983).

The wide distribution of *H. convergens* makes the species an appropriate model organism for assessing geographical differences in developmental responses to temperature. Butler & Dickerson (1972) evaluated the development of *H. convergens* from Tucson, Ariz. These data were used by Gutierrez et al. (1981) in the development of a conceptual model of population biology of *H. convergens*. Obrycki & Tauber (1982) evaluated temperature-dependent growth in a population of *H. convergens* from Ithaca, N.Y. The results of these studies suggested growth rates were different between the New York and

Arizona populations. Furthermore, determination of developmental thresholds and heat-unit requirements from the Butler & Dickerson (1972) data differed from analyses by Gutierrez et al. (1981) and Obrycki & Tauber (1982). Development of *H. convergens* also has been documented from a population in Bushland, Tex. (Michels & Behle 1991).

Three questions were the basis for the present study. First, what are the values for the lower developmental threshold and degree-day requirements to complete immature development for *H. convergens* from Corvallis, Oreg.? Second, what values describe the temperature requirements for the Tucson population? Third, do populations of *H. convergens* from Corvallis, Tucson, Ithaca, and Bushland possess different characteristics of temperature-dependent growth? The answers to these questions provide data for describing the development of the convergent lady beetle.

Materials and Methods

The study was conducted during the spring and summer of 1989. Adult beetles were collected from alfalfa fields in Corvallis, Oreg., and Tucson, Ariz., during April and May. The field-collected beetles were reared at 22°C and fed the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and the oat-bird cherry aphid, *Rhopalosiphum padi* (L), to obtain egg clusters. Only F1 progeny from the field-collected adults were used in the study.

Six constant temperatures were used: 13, 17, 21, 25, 29, and 33°C. Each temperature treatment was conducted at a photoperiod of 16:8 (L:D) in

Table 1. Average time (days) for development of first generation *H. convergens* from field-collected adults from Corvallis, Oreg., and Tucson, Ariz., at six constant temperatures, 1989

Life stage	Source	Temp (°C), $\bar{x} \pm \text{SE} (n)$					
		13	17	21	25	29	33
Egg	Oregon	60 + * (23)	7.0 ± 0.0 (20)	4.5 ± 0.0 (16)	3.0 ± 0.0 (18)	2.5 ± 0.0 (26)	2.2 ± 0.0 (31)
	Arizona	60 + * (23)	6.8 ± 0.0 (26)	4.5 ± 0.0 (19)	2.8 ± 0.0 (27)	2.3 ± 0.0 (34)	2.0 ± 0.0 (24)
Instar I-IV	Oregon	36.7 + * (0)	29.0 ± 1.4 (4)	17.3 ± 0.3 (15)	10.2 ± 0.2 (14)	7.7 ± 0.2 (16)	6.4 ± 0.1 (17)
	Arizona	37.3 + * (0)	30.8 ± 0.7 (6)	18.7 ± 0.4 (19)	10.7 ± 0.2 (20)	8.3 ± 0.1 (19)	6.9 ± 0.2 (22)
Pupa	Oregon	** (0)	14.1 ± 0.8 (4)	7.0 ± 0.6 (15)	4.8 ± 0.1 (14)	3.3 ± 0.1 (16)	2.5 ± 0.1 (17)
	Arizona	** (0)	14.3 ± 0.5 (6)	6.7 ± 0.2 (19)	4.3 ± 0.1 (20)	3.2 ± 0.1 (19)	2.6 ± 0.1 (22)
Egg-Adult	Oregon	** (0)	50.1 ± 1.4 (3)	28.8 ± 0.2 (15)	18.0 ± 0.2 (13)	13.5 ± 0.1 (16)	11.4 ± 0.2 (17)
	Arizona	** (0)	51.9 ± 0.5 (6)	29.9 ± 0.5 (19)	17.8 ± 0.2 (20)	13.8 ± 0.1 (19)	11.5 ± 0.1 (22)

+, Eggs did not hatch and larvae did not complete development as of the listed number of days. *, No data available because of extended larval development or mortality.

50–70% RH. Eggs ($n = 19$ –34) were placed into one of six constant temperature cabinets within 8 h of oviposition. Eggs were checked for larval eclosion every 12 h. Larvae were reared individually in 1-oz plastic creamers with cardboard lids. Observations on larval survival and the duration of each instar were conducted every 12 h. An overabundance of fresh prey was consistently maintained. Observations on larval development were initiated for 16–23 individuals per treatment but mortality reduced this number in successive life stages. Data on developmental time were restricted to include only those individuals completing a given life stage (ie., egg, larval, and pupal). Larvae were fed the same aphid species, cultured on wheat, as the adults.

Statistical analyses were conducted by a G test for independence regarding the survival data, analysis of variance for developmental times, and linear regression for developmental threshold and degree-day requirements. Data on temperature-related developmental time obtained in this study, presented by Butler & Dickerson (1972), and from Michels & Behle (1991) were analyzed by regression using only those treatments where the relationship was linear (Stinner et al. 1974). Points, specifically those at the low and high ends of the temperature treatments, were considered to define the linear portion of the developmental-rate curve if developmental rate did not increase in proportion to an increase in temperature. The lower developmental threshold was determined as the x intercept of the linear equation. The degree-day requirements were determined as the value of the inverse of the slope of the linear equation. Standard errors for the lower developmental threshold and degree-days were obtained from the statistical program in Quatro Pro (Borland, Scotts Valley, Calif.). Predictions on days for developmental time were used to compare populations and were derived from the formula $z = a / (T - x)$, where a was the average degree-day requirements, T was the temperature, and x was the developmental threshold. Furthermore, a de-

scription of the developmental threshold and degree-day requirements for *H. convergens* was developed into a general model by combining data from all three populations. Data from Michels & Behle (1991), representing the Texas population, was not incorporated into the general model but was used to test the accuracy of estimates produced by the model.

Results and Discussion

Survival. Egg, larval, and pupal mortality did not differ between population sources ($G = 1.94$, $df = 1$, $P > 0.05$) but did differ by temperature ($G = 103.4$, $df = 1$, $P < 0.001$). Larvae eclosed from all eggs reared between 13 and 33°C. However, no larvae survived beyond the third instar at 13°C and mortality was high (83%) at 17°C. Michels & Behle (1991) observed that *H. convergens* failed to develop past the first instar at 15°C. Similarly, Orr & Obrycki (1990) noted that *Hippodamia parenthesis* (Say) exhibited relatively high mortality at 14°C. Thus, at least two species of aphidophagous coccinellids exhibit high mortality at temperatures around 13 and 14°C. In the present study mortality at the higher temperatures (21–33°C) ranged from 5–18%.

Growth and Development. The period of development for each life stage did not differ between population sources ($F = 0.04$, $df = 1$, $P > 0.05$) (Table 1). Development from eggs to adult ranged from 51.9 d at 17°C to 11.4 d at 33°C. Development of eggs, larvae, and pupae ranged between 14–19%, 56–60%, and 22–28% of the total developmental period, respectively. The time *H. convergens* spent in each life stage was in the same range of proportions to that of other aphidophagous coccinellids (Obrycki & Tauber 1981, Butler 1982).

A comparison of data from the present study to Butler & Dickerson (1972) is necessary for determining which values on development should be used to represent the Tucson population in a generalized degree-day model. The data exhib-

Table 2. Developmental threshold (D_{th}) and degree-days (DD) requirements \pm SE for first-generation *H. convergens* from field-collected adults from Corvallis, Oreg.; Ithaca, N.Y. (Obrycki & Tauber 1982); and Tucson, Ariz. Reanalysis of Butler & Dickerson (1972); AZb = author (JCM) calculations; AZo = Obrycki & Tauber (1982); AZg = Gutierrez et al. (1981)

Life stage	Variable	Source					
		N.Y.	Oreg.	Ariz. ^a	Ariz. ^b	Ariz. ^c	Ariz. ^d
Egg	D_{th}	10.3 \pm 1.2	11.3 \pm 1.1	11.7 \pm 0.9	10.7	10.5	7.4
	DD	44 \pm 2.1	45 \pm 3.0	41 \pm 2.3	44	44	29
Instar I-IV	D_{th}	12.7 \pm 0.9	13.0 \pm 0.6	12.9 \pm 0.7	7.5	9.0	8.8
	DD	113 \pm 4.2	126 \pm 5.7	136 \pm 7.3	250	212	200
Pupa	D_{th}	12.0 \pm 1.2	14.1 \pm 0.6	13.4 \pm 0.2	10.7	9.5	8.8
	DD	54 \pm 2.6	49 \pm 2.5	50 \pm 0.7	65	69	42
Egg-Adult	D_{th}	12.0 \pm 0.7	12.6 \pm 0.5	12.8 \pm 0.6	8.1	10.6	8.8
	DD	230 \pm 6.8	228 \pm 8.9	228 \pm 10.3	375	313	338
Predicted no. days, 20°C		30.8	28.8	31.7	31.5	33.3	30.2
Predicted no. days, 25°C		18.4	17.7	18.7	22.2	21.7	20.9
Predicted no. days, 30°C		13.1	12.8	13.3	17.1	16.1	15.9

Reanalysis of Butler & Dickerson (1972).

^aThis study.

^bAuthor calculations.

^cObrycki & Tauber (1982).

^dGutierrez et al. (1981).

ited similarities and differences in developmental time depending on life stage and temperature. Butler & Dickerson (1972) reported values for egg development that differed from the present study by 0% at 20–21°C, 7% at 25°C, 4% at 28.9–29°C, and 5% at 33–33.9°C. Similarly, they reported values for pupal development that differed from the present study by 3% at 20–21°C, 11% at 25°C, 9% at 28.9–29°C, and 8% at 33–33.9°C. These data suggest the two studies produced similar results. However, data on larval development in Butler & Dickerson (1972) differed from the present report by 1% at 20–21°C, 54% at 25°C, 47% at 28.9–29°C, and 41% at 33–33.9°C. The time required for *H. convergens* larval development as reported by Butler & Dickerson (1972) was consistently longer. Conditions contributing to the differences noted in larval development between the two studies of the Tucson population follow the discussion on estimates of lower developmental thresholds and degree-day requirements.

The lower temperature threshold for development of the Corvallis and current Tucson populations was determined from data on growth rates between 17 and 33°C (Table 2). Lower developmental thresholds for eggs, larvae, and pupae differed according to life stage but not population source ($F = 0.01$, $df = 1$, $P > 0.05$). Differences in the developmental threshold for eggs were 1.2–1.7°C and 1.7–2.8°C below the larval and pupal thresholds, respectively. The larval threshold for development was 0.5–1.1°C below the pupal developmental threshold.

Degree-day requirements above the developmental threshold for each life stage were not significantly different ($F = 0.12$, $df = 1$, $P > 0.05$) between population sources of the current study (Table 2). Because the accumulation of degree-

days is dependent on the estimated developmental threshold, comparison of degree-day requirements are best conducted by assessing predicted days for development at various temperatures. Data for the Corvallis and Tucson populations of the current study differed by 1–3% in predicting days for development from egg to adult at 20, 25, and 30°C. In contrast, various analyses of the Butler & Dickerson (1972) data exhibited an 11–17% difference for 25 and 30°C. Only at 20°C did the prediction of developmental time result in similar values.

An analysis determining the developmental threshold for *H. convergens* using the data from Butler & Dickerson (1972) resulted in different values from the same data by either Gutierrez et al. (1981) or Obrycki & Tauber (1982) (Table 2). Also, an analysis of the Butler & Dickerson (1972) data resulted in values different from the current assessment of *H. convergens* from Tucson. Differences in the determination of temperature-dependent developmental requirements for *H. convergens* from the Butler & Dickerson (1972) data may be attributed to at least four conditions: (1) the lower temperatures tested did not represent the low range at which *H. convergens* may develop; (2) the higher temperatures tested, while appropriate for assessing developmental dynamics, should not be included in the linear regression because these temperatures were beyond the point of maximum growth rate; (3) development at one of the midrange temperatures (25°C) does not fit a linear pattern and thus appears to be inaccurate; and (4) rearing conditions pertaining to diet, photoperiod, and relative humidity were different. Each of these points is considered in the following discussion.

Only three temperature treatments from the Butler & Dickerson (1972) data set were appro-

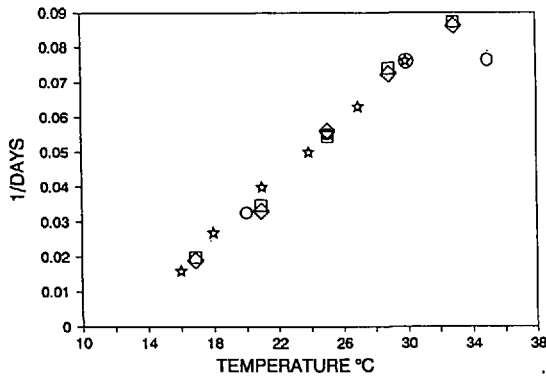


Fig. 1. Relationship between temperature and the rate of growth (1/d) for complete development of *Hipodamia convergens*. □, Corvallis, Oreg.; ◇ Tucson, Ariz.; * Ithaca, N.Y. (Obrycki & Tauber 1982); ○ Bushland, Tex. (from Michels & Behle 1991).

appropriate for the application of the linear regression analysis. Developmental rates at these temperatures were not representative of the broad range of temperatures across which *H. convergens* exhibits a highly correlated response in growth. Thus, the developmental threshold cannot be accurately estimated. Differences in general rearing conditions, in particular diet (Orr & Obrycki 1990), may affect growth rates and therefore result in different degree-day requirements for development. The diet given to larvae of *H. convergens* consisted of different prey species in some of the studies. Butler & Dickerson used the pea aphid, *Acyrtosiphon pisum* (Harris) and the cotton aphid, *Aphis gossypii* Glover while I used the Russian wheat aphid and the oat-bird cherry aphid. However, Obrycki & Tauber used the pea aphid and obtained results more similar to those reported in the present study. Therefore, differences in diet may not be the primary factor that explains differences in the existing data on larval development of *H. convergens*.

Differences in the estimation of the developmental threshold may best explain the inconsistent results between some of the studies. Esti-

mation of the developmental threshold is sensitive to the criterion of using only those temperature treatments that correlate with developmental rate in a linear fashion. Therefore, only the data presented in this study (representing populations from Corvallis, Oreg., and Tucson, Ariz.) and by Obrycki & Tauber (1982) (representing a population from Ithaca, N.Y.) were considered for developing a generalized model on temperature-dependent growth for *H. convergens*.

The major conclusion from a comparison of the development of *H. convergens* from Corvallis, Ithaca, and Tucson is that the species exhibits a constancy across geographically separated populations in the traits of developmental threshold and degree-day requirements (Fig. 1). Similar observations were made for *Chrysopa oculata* Say (Tauber et al. 1987) and the European corn borer, *Ostrinia nubilalis* Hubner (Calvin et al. 1991).

A generalized estimation of the developmental threshold and degree-day requirements for *H. convergens* is presented in Table 3. Degree-day requirements above respective thresholds for each life stage and for all life stages combined produced an average estimate of the temperature-dependent development of *H. convergens*. The data for *H. convergens* development from Texas (Michels & Behle 1991) provided an independent set of values for testing the accuracy of the generalized model. A reanalysis of the data presented by Michels & Behle (1991), which incorporated only those values in the linear section of the growth rate function, demonstrated a developmental threshold of 12.0°C and developmental requirements from egg to adult of 239 degree-days. Thus, data from four distinct regions of North America suggest that temperature-dependent growth of *H. convergens* is relatively uniform and may be characterized by a lower developmental threshold of 12.5°C with 228 degree-days required for egg-adult development.

Table 3. Values of the lower developmental threshold and degree-day requirements for predicting mean days and range \pm SE for temperature-dependent development of *H. convergens*, based on populations from Corvallis, Oreg.; Ithaca, N.Y.; and Tucson, Ariz.

Life stage	Developmental parameter		Predicted vs observed development		
	D _{th}	DD	20°C	25°C	30°C
Egg	11.1 \pm 1.0	41 \pm 2.5	4.6 vs 5 (3.9–5.5)	2.9 vs 3 (2.6–3.4)	2.2 vs 2 (1.9–2.4)
Larva	12.9 \pm 0.7	125 \pm 5.8	17.6 vs 17 (15.3–20.4)	10.3 vs 10 (9.3–11.5)	7.3 vs 8 (6.7–8.0)
Pupa	13.2 \pm 0.7	53 \pm 2.6	7.8 vs 8 (6.7–9.1)	4.5 vs 5 (4.0–5.0)	3.2 vs 3 (2.9–3.5)
Egg-Adult	12.5 \pm 0.7	228 \pm 9.4	30.4 vs 30 (26.7–34.9)	18.2 vs 18 (16.6–20.1)	13.0 vs 13 (12.0–14.1)

Observed data obtained from Michels & Behle (1991) for a population from Bushland, Tex. $n = 3$. D_{th}, Developmental threshold. DD, Degree-days.

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