

Thermal and Dietary Requirements for Development of *Hippodamia parenthesis* (Coleoptera: Coccinellidae)

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ABSTRACT The rate of preimaginal development of *Hippodamia parenthesis* (Say) was linearly related to temperatures from 14 to 30°C. *H. parenthesis* requires 234.8 ± 10.0 degree days (\pm SE) above a lower developmental threshold (t) of $10.8^\circ\text{C} \pm 1.1$ to complete preimaginal development. Newly emerged adults from larvae reared at 18 and 22°C weighed significantly more ($\bar{x} = 0.0095$ and 0.0099 g, respectively) than adults reared at 14, 26, and 30°C ($\bar{x} = 0.0085$, 0.0087 , and 0.0085 g, respectively). Total preimaginal development of *H. parenthesis* reared at 22°C on pea aphids, *Acyrtosiphon pisum* (Harris) (Homoptera: Aphididae), averaged 22.0 d, significantly faster than the 23.4 d required on a diet of greenbugs, *Shizaphis graminum* (Rodani) (Homoptera: Aphididae). Immature survival was approximately 90% on both aphid diets. Adults reared on *A. pisum* were significantly heavier ($\bar{x} = 0.0098$ g) and larger ($\bar{x} = 3.15$ mm wide by 5.31 mm long) than those reared on the *S. graminum* diet ($\bar{x} = 0.0068$ g and 2.88 mm wide by 4.87 mm long).

KEY WORDS Insecta, Coccinellidae, *Hippodamia parenthesis*, preimaginal development

Hippodamia parenthesis (Say) is a widely distributed, but little-studied, Nearctic aphidophagous coccinellid (Hagen 1962, Hodek 1973, Gordon 1985) found in a variety of grassy habitats and agroecosystems (see Palmer 1914, van den Bosch et al. 1959, Richerson & DeLoach 1973, Belick 1976, Kieckhefer & Elliott in press). Several 1- to 2-yr field studies examining the coccinellid fauna in a variety of agroecosystems have typically reported *H. parenthesis* in low numbers compared with other aphidophagous coccinellid species; e.g., in corn, alfalfa, and turnips in Missouri (Richerson & DeLoach 1973) and in alfalfa in California (van den Bosch et al. 1959). By contrast, *H. parenthesis* was the most abundant coccinellid species collected in 1988 in central Iowa fields of alfalfa and alfalfa mixed with brome (unpublished data). Similarly, Balduf (1926) reported that *H. parenthesis* was the most abundant coccinellid species in Illinois clover and alfalfa fields during a year with above-normal temperatures and below-normal rainfall. Because similar hot, dry conditions prevailed in Iowa during 1988, we decided to examine influence of temperature on *H. parenthesis*.

Previous temperature-development studies on *H. parenthesis* were conducted under variable conditions (Palmer 1914, Simpson & Burkhardt 1960). We determined precise thermal requirements for the development of *H. parenthesis* to establish basic biological data for the species, as well as to compare its thermal requirements with other aphidophagous coccinellid species (i.e., *Hippodamia convergens* Guerin-Meneville, *Coleomegilla maculata* (De Greer), and *Coccinella septempunctata* L.). Additionally, we determined the effects of two aphid prey (*Acyrtosiphon pisum*

(Harris) and *Shizaphis graminum* (Rodani) on *H. parenthesis* development and survival.

Materials and Methods

Hippodamia parenthesis adults were collected in June 1988 from alfalfa (*Medicago sativa* L.) (cv. Vernal) located at Iowa State University, Ames. Adults were held at $26 \pm 1^\circ\text{C}$ under a photoperiod of 16:8 (L:D) in 0.24-liter paper containers and were provided with water, *A. pisum*, and a diet supplement of a 1:1 mixture of honey and Wheat (Qualcepts Nutrients, Minneapolis). All experiments were conducted with first-generation offspring. Voucher specimens are deposited in the Iowa State University Insect Collection, Department of Entomology, Ames.

Thermal Requirements. Egg masses (4 to 12 eggs) from four to seven *H. parenthesis* females were placed at constant temperatures ($\pm 1^\circ\text{C}$): 14, 18, 22, 26, or 30°C, with a photoperiod of 16:8 (L:D). Three replicates at each temperature were conducted using 24 to 35 individuals. Eggs were checked daily for hatching; first instars were placed in individual vials plugged with cotton. Each day larvae were checked for ecdysis and given a fresh supply of *A. pisum*. Developmental times and mortality were recorded. The day after eclosion, adults were frozen and then weighed, and the overall body length and width were measured. The sex of each adult was determined by checking for the presence of the female genital plates.

Dietary Requirements. Individuals in the diet study were handled as in the temperature development study, but *H. parenthesis* larvae were reared at a photoperiod of 16:8 (L:D), 22°C on

Table 1. Comparison of the linear regression and biophysical model parameters describing the temperature-developmental rate of *H. parenthesis*

Life stage	Linear regression					Biophysical					
	t°C ± SE	°K ± SE	R ²	Model param-eters	Inhibitory temper-ature	HA	TH	HH	TL	HL	R ²
Egg	9.9 ± 2.06	42.1 ± 3.38	0.98	4	High	21,990.06	303.4 (30.4°C) ^a	728,742.4	—	—	0.99
Larval	11.0 ± 1.1	135.0 ± 5.7	0.99	4	Low	11,115.1	—	—	287.6 (14.6°C) ^b	41,667.2	0.99
Pupal	10.6 ± 1.0	57.9 ± 2.3	0.99	4	Low	12,467.64	—	—	286.0 (13.0°C) ^b	39,295.2	0.99
Total preimaginal development	10.8 ± 1.1	234.8 ± 10.0	0.99	2 ^c	—	16,552.15	—	—	—	—	0.99

^a Temperature (°C) at which the rate-controlling enzyme is half high-temperature inactive.
^b Temperature (°C) at which the rate-controlling enzyme is half low-temperature inactive.
^c No high- or low-temperature inhibition over the range of temperatures tested (14–30°C).

either *A. pisum* or *S. graminum*. Eggs from four to seven females were collected for a total of 30–35 first instars in each of three replicates.

Statistical Analysis. The relationship between mean developmental rate and temperature was determined by linear regression (SAS Institute 1985, 433–506; Wigglesworth 1972; Campbell et al. 1974) and by a biophysical model (Wagner et al. 1984). In the linear regression model, the lower theoretical threshold *t* is estimated by extrapolation, the thermal constant *K* is calculated from the equation $K = 1/m$, where *m* = slope of the regression line (Campbell et al. 1974). The biophysical model simulates development over a wide temperature range. The development rate *r* at temperature *T* is calculated as

$$r(T) = \frac{RHO25 \frac{T}{298.15} \exp\left[\frac{HA}{R} \left(\frac{1}{298.15} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{HL}{R} \left(\frac{1}{TL} - \frac{1}{T}\right)\right] + \exp\left[\frac{HH}{R} \left(\frac{1}{TH} - \frac{1}{T}\right)\right]}$$

where RHO25 = development rate at 25°C (298.15°K) assuming no enzyme inactivation, HA = enthalpy of activation of the reaction catalyzed by a rate-controlling enzyme, TL = Kelvin temperature at which the rate-controlling enzyme is half active and half low-temperature inactive, HL = change in enthalpy associated with low-temperature inactivation of the enzyme, TH = Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive, and HH = change in enthalpy associated with high-temperature inactivation of the enzyme (Table 1) (Wagner et al. 1984).

Adult weight and size from each temperature condition were analyzed by using Duncan's multiple range test (SAS Institute 1985, 113–137). Adult weight and size of *H. parenthesis* reared on *A. pisum* and *S. graminum* were analyzed by using ANOVA (SAS Institute 1985, 113–137). Adult survival data from the diet study were analyzed by using categorical data modeling (CATMOD) (SAS Institute 1985, 171–253).

Results

Thermal Requirements. The total preimaginal development time for *H. parenthesis* ranged from 11.9 ± 0.2 d at 30°C to 62.1 ± 3 d at 14°C (Table 2). Individuals reared at 14°C were significantly smaller than those reared at the four higher temperatures; however, their weight was similar to that of adults reared at 26 and 30°C.

Between 14 and 30°C, the preimaginal developmental rate was linearly related to temperature ($R^2 = 0.99$) (ANOVA test for linearity $F = 1153.59$; $df = 1, 14$; $P < 0.001$) (Table 1). The lower threshold for total preimaginal development (*t*) was estimated by extrapolation to be 10.8 ± 1.1°C, and the thermal constant (*K*) was 234.8 ± 10.0 degree

Table 2. Developmental times and adult characteristics for *H. parenthesis* reared at five constant temperatures on *A. pisum*; photoperiod of 16:8 (L:D)

	Temp, °C				
	14	18	22	26	30
	Developmental time (days ± SD)				
Life stage					
Egg	8.5 ± 0.9	5.5 ± 0.3	3.9 ± 0.1	2.5 ± 0.2	2.1 ± 0.1
Larval	38.7 ± 3.3	20.5 ± 1.6	12.8 ± 1.2	9.3 ± 0.8	7.0 ± 0.1
Pupal	14.9 ± 0.6	8.3 ± 0.4	5.3 ± 0.2	3.8 ± 0.2	2.9 ± 0.1
Total preimaginal development	62.1 ± 3.0	34.4 ± 1.7	21.9 ± 1.4	15.5 ± 0.8	11.9 ± 0.2
	Adult characteristics ^a				
Weight (g) ^a	0.0085B	0.0095A	0.0099A	0.0087B	0.0085B
Width (mm) ^a	2.93B	3.14A	3.15A	3.20A	3.15A
Length (mm) ^a	5.04B	5.30A	5.31A	5.36A	5.32A
No. 1st instars in each replicate	26, 30, 30	30, 33, 27	30, 30, 35	25, 27, 30	30, 30, 29
Total no. adults reared	28	73	88	73	75

^a Means in rows followed by the same letter are not significantly different at the *P* = 0.05 level (Duncan's multiple range test [SAS Institute 1985]).

days (DD) (Table 1). Degree days > *t*°C were 42.1 ± 3.4 > 9.9 ± 2.1 for the egg stage, 135.0 ± 5.7 > 11.0 ± 1.1 for the larval stage, and 57.9 ± 2.3 > 10.6 ± 1.0 for the pupal stage. Total preimaginal development was similarly described as a linear relationship by the biophysical model (*R*² = 0.99) (temperature range, 14–30°C) (Table 1) (Wagner et al. 1984). Egg development was best described by a four-parameter biophysical model, with high temperature inhibition observed at 30.4°C. Larval and pupal development were best described by four parameter models, with low-temperature inhibition occurring at 14.6 and 13.0°C, respectively.

Total mortality ranged from 7% at 22°C to 67% at 14°C. At 14°C, the highest mortality occurred among the first and fourth instars, 29 and 38%, respectively (Table 3). At 18°C, the highest larval mortality (40%) occurred among the fourth instars, and mortality was highest at 30°C among the second instars (50%).

Dietary Requirements. The average preimaginal developmental time period was significantly shorter for *H. parenthesis* that were fed *A. pisum* than for individuals fed *S. graminum* (\bar{x} = 22.0 versus 23.4 d) (Table 4). *H. parenthesis* adults resulting from larvae that were fed *A. pisum* were significantly heavier and larger than adults from

larvae fed *S. graminum*. Ninety percent of the *H. parenthesis* completed development on the *S. graminum* diet, whereas 92% successfully developed on *A. pisum*.

Discussion

The biophysical and linear regression models accurately describe the relationship between temperature and preimaginal developmental rate between 14 and 30°C (Fig. 1). A lack of high- and low-temperature inhibition for the total preimaginal development predicted by the biophysical model resulted in a straight line similar to the linear regression model. The high-temperature inhibitory effect present in the egg stage may have balanced the low-temperature inhibitory effects on the larval and pupal stages.

Based on a linear regression model, the preimaginal thermal responses (DD > *t*°C) of *H. parenthesis* (235 ± 10.0 > 10.8 ± 1.1) are similar to those of several previously studied Nearctic coccinellid species (e.g., *Adalia bipunctata* L., 263 ± 9 > 9.0 ± 0.9; *C. maculata*, 236 ± 0.7 > 11.3 ± 0.6; *C. septempunctata*, 197 ± 4.4 > 12.1 ± 0.4; *Coccinella transversogutata* Brown, 218 ± 14.5 > 12.2 ± 1.3; and *H. convergens*, 230 ± 6.8 > 12.0

Table 3. Number (percent) of *H. parenthesis* individuals dead by life stage for five constant temperatures; photoperiod of 16:8 (L:D)

Temp, °C	Mortality of <i>H. parenthesis</i>										Total mortality ^a	
	First instar		Second instar		Third instar		Fourth instar		Pupal stage		n	%
	n	%	n	%	n	%	n	%	n	%		
14	17	29	7	12	7	12	22	38	5	9	58	67
18	3	20	3	20	2	13	6	40	1	7	15	17
22	1	14	1	14	0	0	2	29	3	43	7	7
26	2	25	1	12	1	12	2	25	2	25	8	10
30	2	17	6	50	1	8	0	0	3	25	12	13

^a Total mortality, mortality from first instar through pupal stages; excludes egg mortality.

Table 4. Preimaginal developmental times, adult characteristics, and survival ($\bar{x} \pm SD$) of *H. parenthesis* reared on *A. pisum* and *S. graminum*; 22°C, photoperiod of 16:8 (L:D)

Aphid diet	No.	Preimaginal development, days ^a	Weight, g ^a	Width, mm ^a	Length, mm ^a	% Survival ^b
<i>A. pisum</i>	84 ^c (30, 30, 30) ^d	22.0 \pm 1.92	0.0098 \pm 2.0007	3.15 \pm 0.0458	5.31 \pm 0.0153	92
<i>S. graminum</i>	73 (30, 30, 34)	23.4 \pm 1.21	0.0068 \pm 0.0015	2.88 \pm 0.145	4.87 \pm 0.20	90
F ^e		45.43	220.31	146.39	121.88	

^a Values in the columns are significantly different (ANOVA [SAS Institute 1985]).

^b Values are not significantly different (CATMOD [SAS Institute 1985]).

^c Number of individuals that successfully completed development.

^d Number of first instars used to begin each replicate.

^e df = 1,152; $P > 0.0001$.

± 0.7 [Obrycki & Tauber 1978, 1982, 1983]). Recently Honek & Kocourek (1988) summarized the literature on lower developmental thresholds for the egg and pupal development of several aphidophagous coccinellid species. Coccinellid egg and pupal developmental threshold values ranged from 7.0 to 13.6°C and 8.7 to 13.3°C, respectively. The lower developmental thresholds for *H. parenthesis* egg (9.9°C) and pupal (10.6°C) development fall within these ranges.

The relatively higher number of *H. parenthesis* observed in 1988, a year with above-average temperatures, does not appear to be a result of high-temperature adaptations by *H. parenthesis*. Preimaginal developmental rates and survival at higher

temperatures ($>26^\circ\text{C}$) are similar to those of several other coccinellid species (e.g., *C. maculata*, *H. convergens*, and *C. septempunctata*) (Obrycki & Tauber 1978, 1982, 1983).

Hippodamia parenthesis adults have been observed in a variety of habitats preying on several aphid species, for example, *Macrosiphon solani-folii* Ashmead on potatoes (Houser et al. 1918), *Phorodon humuli* Schrank on hops (Hawley 1919), and *Therioaphis maculata* (Buckton) alfalfa (van den Bosch et al. 1959). In an experimental feeding study, Simpson & Burkhardt (1960) found that preimaginal development of *H. parenthesis* on *T. maculata* (15.0 d) was similar to that observed for *C. maculata* (17.4 d) and *H. convergens* (16.9 d).

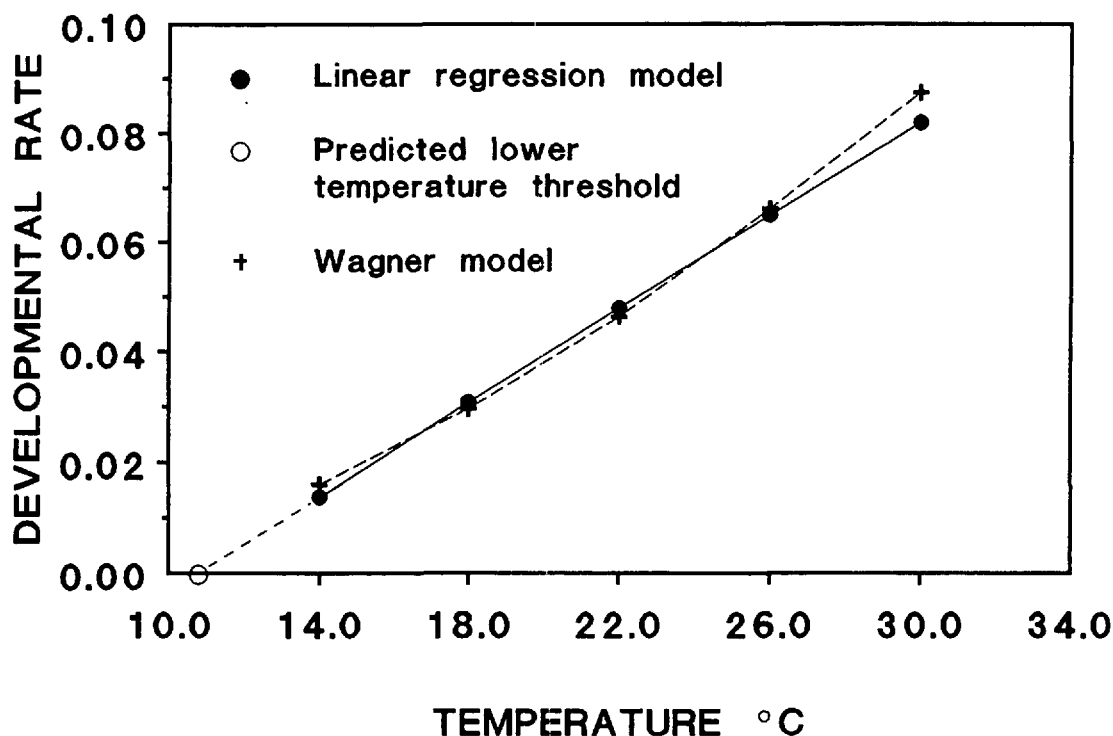


Fig. 1. Comparison of a linear regression model and a biophysical model used to describe the temperature-preimaginal developmental rate relationship of *H. parenthesis*.

Similarly, the times for *H. parenthesis* to complete development at 22°C on *A. pisum* and *S. graminum* in this study are similar to values for *C. septempunctata*, *C. maculata*, *H. convergens*, and *A. bipunctata* on *A. pisum* (see Obrycki & Tauber 1978, 1982, 1983).

From our studies, the thermal and dietary requirements of *H. parenthesis* would not account for its population variations relative to the other coccinellid species in the midwestern aphidophagous guild. In a 13-yr study in South Dakota, Kieckhefer & Elliott (in press) observed unexplained population fluctuations of a number of coccinellid species, including *H. parenthesis*. Further studies are needed on biotic and abiotic factors that influence coccinellid populations, for example, parasitism by *Dinocampus coccinellae* (Schrank) (Hymenoptera: Braconidae) (Richerson & DeLoach 1973), the effects of relative humidity (see Tauber & Tauber 1983), or the effect of rainfall on survival of early instars. Understanding the biology and ecology of aphidophagous coccinellid species will increase our ability to explain their population dynamics.

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