Thermal Requirements for Development of *Hippodamia convergens* (Coleoptera: Coccinellidae)[1]

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ABSTRACT

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Preimaginal development of *Hippodamia convergens* Guérin-Méneville from the Ithaca, N.Y., area (~42°N) requires an accumulated 230 degree-days over a threshold of 12°C. The optimal temperature for development of *H. convergens*, the temperature with fastest development and lowest mortality, is 29°C. Above 17°C, the rates of development were faster for the population of *H. convergens* from New York than for a population from Arizona (~32°N). As is the case for three other multivoltine predacious coccinellids in the Ithaca area, thermal requirements for development and food availability act to regulate the voltinism of *H. convergens* by influencing development and reproduction.

Widely distributed species show intraspecific variation in their responses to many of the environmental factors that regulate seasonal development (see Danilevskii 1965, Masaki 1978, Tauber and Tauber 1978, Beck 1980). Among the developmental responses that vary geographically are the critical photoperiod for diapause induction, thermal requirements for postdiapause development, dietary requirements for diapause induction and termination, and thermal requirements for nondiapause growth and development (see Tauber and Tauber 1981a).

A thorough understanding of the phenology of a species requires both an examination of geographically separated populations and comparative studies of sympatric species (Tauber and Tauber 1978). Such studies provide explanations for the variation in voltinism of widely distributed species (Masaki 1978, Tauber and Tauber 1978, 1981a) and make it possible to predict seasonal growth, development, and reproduction of locally adapted populations. Also, this approach is a prerequisite for understanding population dynamics of insect pests and beneficial species and for effective insect pest management (see Tauber and Tauber 1976a)

As part of a study of the seasonal cycles of predacious coccinellids (Obrycki and Tauber 1978, 1979, 1981), we examined the thermal requirements for development and survival of *Hippodamia convergens* Guérin-Méneville, a widely distributed North American species. Aspects of its seasonal phenology that have been studied include voltinism of different populations, seasonal migration, and the influence of diet on reproduction and diapause induction (see Hagen 1962, Hagen and Sluss 1966, Stewart et al. 1967, Lees 1980).

The development of *H. convergens* has been examined under field conditions in California (Clausen 1915), New York (Pack 1925), and Arizona (Neilson and Currie 1960). Also, a population from Kansas was studied under fluctuating temperatures (Simpson and Burkhardt 1960). Butler and Dickerson (1972) reared a population from Arizona under a range of constant temperatures and determined the thermal requirements for preimaginal development.

In this report we present the thermal requirements for development of *H. convergens* from Ithaca, N.Y., and we compare them with those of *H. convergens* from Arizona (Butler and Dickerson 1972).

Materials and Methods

Adult *Hippodamia convergens*, collected during the summer and autumn in the Ithaca, N.Y., area, were maintained at LD 16:8, 24° ± 1°C. These adults were provided with water, a Wheast-protein food mixture, and a constant supply of *Acyrthosiphon pisum* (Harris) (pea aphids) and *Myzus persicae* (Sulzer) (green peach aphids). All tests used first-generation offspring from field-collected adults.

At least five different females were used as egg sources for each replicate at each constant temperature (Table 1); three to eight individuals were reared from each egg cluster laid by a female. On the day of hatching, we transferred the 1st instars to individual vials. The larvae were fed *A. pisum* and checked daily for ecdysis.

Developmental times (days) were recorded for each preimaginal life stage (ecdysis to ecdysis) and for total development. If an individual died, data for life stages before death were not used in calculating developmental times. The 4th instar included the prepupa, an immobile stage preceding the pupal ecdysis. Statistical analysis followed Obrycki and Tauber (1978); in all analysis of variance (ANOVA) tests between replicates and for linearity we used a 0.05 level of significance.

To describe the temperature-developmental rate relationship, we used two empirically calculated values: *t*—the lower theoretical threshold for development, estimated by extrapolating the linear portion of the temperature-developmental rate curve, and *K*—the thermal constant, calculated as 1/slope of the temperature-developmental rate equation. We calculated SEs for the *t* and *K* values by the method described by Campbell et al. (1974) and Neuenschwander (1975), modified for replicated data (Tauber et al. unpublished data).

The method of thermal summation we used is based on the linear portion of the temperature-developmental rate relationship for a middle range of temperatures (see Morris and Fulton 1970, Campbell et al. 1974). Several other theoretically based models of this relationship have been developed (e.g., Stinner et al. 1974, Logan et al.

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Table 1.—Development of *H. convergens* from Ithaca, N.Y., (~42°N) under constant temperatures (± 1°C; LD 16:8)

	Developmental times (days; mean of replicate means ± SE)					
Stage	15.6°C	18.3°C	21.1°C	24.0°C	26.7°C	29.4°C
Egg	8.3 ± 0.3	5.5 ± 0.2	4.1 ± 0.7	3.4 ± 0.4	2.8 ± 0.3	2.3 ± 0.2
1st Instar	8.4 ± 1.5	4.9 ± 0.6	3.4 ± 0.3	2.9 ± 0.2	2.2 ± 0.2	1.9 ± 0.1
2nd Instar	6.5 ± 0.6	3.9 ± 0.3	2.4 ± 0.3	1.9 ± 0.1	1.7 ± 0.1	1.1 ± 0.1
3rd Instar	7.0 ± 0.6	4.5 ± 0.1	2.8 ± 0.5	2.2 ± 0.4	1.8 ± 0.1	1.5 ± 0.5
4th Instar and prepupa	16.4 ± 1.4	9.3 ± 0.6	6.0 ± 0.2	4.6 ± 0.1	3.5 ± 0.2	3.2 ± 0.4
Pupa	13.5 ± 1.4	8.8 ± 0.6	6.2 ± 0.4	4.8 ± 0.2	3.8 ± 0.2	3.0 ± 0.1
Total development	60.1 ± 2.7	36.8 ± 2.0	24.9 ± 1.6	19.8 ± 0.9	15.8 ± 0.6	12.9 ± 0.6
No. in each replicate[a]	(6, 7, 12, 8)	(25, 18, 24, 19)	(25, 23, 25, 18)	(26, 20, 24, 21)	(27, 22, 26)	(20, 22, 16)

[a] Number of individuals that completed development at each temperature.

1976) to describe development over a wider range of temperatures. For many insects, however, linearly derived *t* and *K* values provide an accurate basis for predicting development in the field (e.g., see Tauber and Tauber 1976b, Wright and Laing 1978, Johnson et al. 1979).

Ideally, comparative studies examining intraspecific variation should be done under identical experimental conditions. In this study of *H. convergens*, comparisons between New York and Arizona populations are valid because our methods were very similar to those of Butler and Dickerson (1972); that is, the range of temperatures at which development was examined overlap, and similar larval diets were used. Butler and Dickerson (1972) fed their larvae both *A. pisum* and *Aphis gossypii* Glover (cotton aphids); we used *A. pisum*.

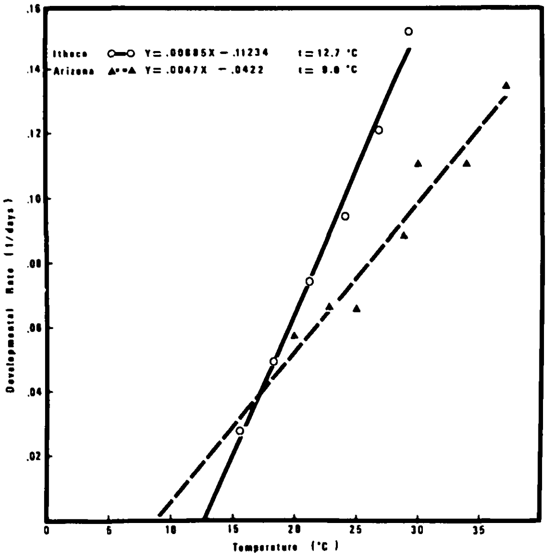

FIG. 1.—Larval (1st- through 4th-instar) developmental rates for *H. convergens* from Ithaca, N.Y. (~42°N) (_________) and Tucson, Ariz. (~32°N) (-----). Intercepts on abscissa are the lower theoretical thresholds for development. (*t*). The regression line for the population from Arizona is from Butler and Dickerson (1972).

Results

Between 15.6 and 29.4°C, the rate of development (1/developmental time in Table 1) for each life stage (except the second and third instars) as well as for total development of *H. convergens* was linearly related to temperature (see Fig. 2). The developmental rate for both the second and third instars was linearly related to temperature between 15.6 and 26.7°C.

Mortality of *H. convergens* decreased with increasing temperatures (Table 2). Eggs at 10°C shriveled and darkened after 30 days; no hatching was observed. At 12.8°C, all individuals died by the 3rd instar. At temperatures from 15.6 to 26.7°C, mortality was generally highest in the 4th-instar/prepupal stage (Table 2).

Theoretical thresholds for development (*t*) for *H. convergens* life stages fell between 10.3 (egg) and 12.5°C (4th instar/prepupa) (Table 3). Total development re-

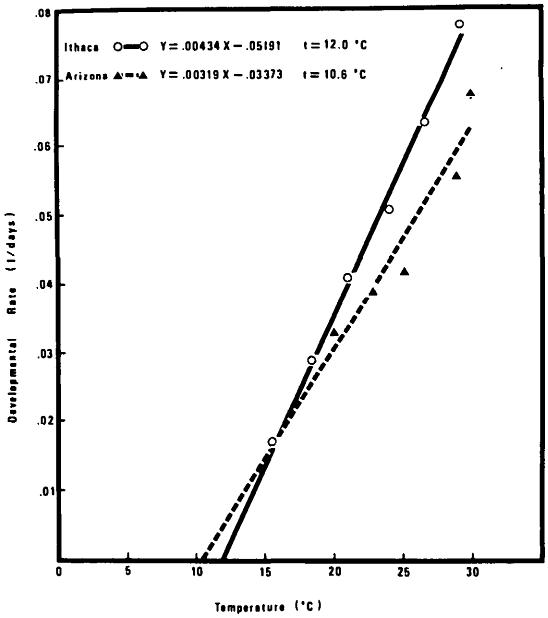

FIG. 2.—Developmental rates for *H. convergens* from Ithaca, N.Y. (~42°N) (____________) and Tucson, Ariz. (~32°N) (-----) (from oviposition to adult emergence). Intercepts on the abscissa are the lower theoretical thresholds for development. (*t*). The regression line for the population from Arizona was calculated from data given by Butler and Dickerson (1972).

quired 230 degree-days (K) above 12°C (t). The 100% mortality at 12.8°C (Table 2) indicates that the theoretical lower developmental threshold of 12°C closely approximates the actual lower threshold for complete development of *H. convergens*. The t and K values for total larval development (1st through 4th instar) of the Ithaca population were calculated to be 12.7°C and 113 degree-days respectively.

By using the developmental data of Butler and Dickerson (1972) for temperatures from 20 to 30°C, we calculated the theoretical threshold (t) and thermal constant (K) for total preimaginal development of their *H. convergens* population from Arizona to be 10.6°C and 313 degree-days. Larval development (1st through 4th instar; data from 20 to 37.2°C) of this population requires an accumulated 213 degree-days above 9.0°C (Table 3). We considered the egg developmental rate to be linearly related to temperatures from 20 to 28.9°C; the calculated t and K values are 10.5°C and 44.4 degree-days, respectively.

Discussion

Thermal Requirements for Development of H. convergens

In their study of the development of *H. convergens* from the Manhattan, Kans., area (~39°N) under fluctuating temperatures ($\bar{x}$ = 26.1°C), Simpson and Burkhardt (1960) reported a total developmental time (from oviposition to adult) of 14 to 18 days ($\bar{x}$ = 16.9 days). This value and the developmental times for each instar are very similar to those of the Ithaca population at 26.7°C. The total developmental time of a California population of *H. convergens* at 23°C was 23 days (Hagen 1962); this value lies between the developmental times we observed at 21.1 and 24°C (Table 1).

The only published study of *H. convergens* with sufficient data to calculate t and K values is that by Butler and Dickerson (1972). Their population from the Tucson, Ariz., area (~32°N), and ours from Ithaca, N.Y. (~42°N) show considerable geographic variation in postembryonic development. The Ithaca population has higher t and lower K values for larval, pupal, and total development (Table 3) and consistently faster rates of larval and total development at temperatures above ~17°C (Fig. 1 and 2). The t and K values for egg development of the two populations were similar.

A cause for the observed developmental differences between the Ithaca and Tucson populations could be differences in rearing procedures and aphid diets. For example, nutrition could effect survival, developmental rates, or adult size. However, in comparing the developmental rates of the two *H. convergens* populations, it appears unlikely that nutrition or rearing conditions could cause more rapid development at higher temperatures and slower development at lower temperatures for the Ithaca population. We conclude that the differences in developmental rates reflect geographic variation that attunes development to local conditions.

Recently, Gutierrez et al. (1981) gave thermal thresholds and degree-day summations for *H. convergens* development, stating that they used Butler and Dickerson's (1972) results to derive their values. However, the values given by Gutierrez et al. (1981) differ from those we calculated from Butler and Dickerson's (1972) data and regression equations. These differences are not easily resolved, because: (1) Gutierrez et al. (1981) did not specify the methods they used to calculate the developmental thresholds and degree-day summations, and (2) data that they cite as originating from Butler and Dickerson (1972) do not occur in the paper (see Table 1, bottom portion in Gutierrez et al. [1981]). Elsewhere in their paper, Gutierrez et al. refer to these results as the "Butler-Hamilton data," and no information is provided as to the source.

In many insect species, populations from higher latitudes develop more rapidly than populations from lower latitudes (e.g. Bigelow 1960, Masaki 1967, Holzapfel and Bradshaw 1976). The geographic differences could be the result of four forms of variation: (a) variation in t alone, (b) variation in K alone, (c) variation in t and K, and (d) no variation in either t or K. Three of these possibilities have been demonstrated. Variation in K alone occurs in the pupal development of *Hyphantria cunea* (Morris and Fulton 1970, Morris 1971) and in the cereal leaf beetle parasitoid *Tetrastichus julis* (Nechols et al. 1980). Variation in both t and K occurs in certain aphids and their parasites (Campbell et al. 1974, Campbell and Mackauer 1975) and in *Chrysopa carnea* (Tauber and

Table 2.—Mortality of *H. convergens* from Ithaca, N.Y., (~42°N) under constant temperatures (± 1°C; LD 16:8)

Mortality (%)	Stage	10.0°C	12.8°C	15.6°C	18.3°C	21.1°C	24.0°C	26.7°C	29.4°C
Total[a]		100 (>100)	100 (40)	68 ± 7 (72)	28 ± 17 (36)	14 ± 8 (15)	10 ± 11 (10)	6 ± 4 (5)	1 ± 3 (1)
Stage-specific[b]	Egg	100%	—	—	—	—	—	—	—
	1st Instar	—	75%	9.6%	8.3%	33%	10%	20%	100%
	2nd Instar	—	20%	5.5%	11.1%	—	10%	20%	—
	3rd Instar	—	5%	5.5%	11.1%	20%	20%	—	—
	4th Instar and prepupa	—	—	57.5%	50%	20%	50%	40%	—
	Pupa	—	—	21.9%	19.4%	27%	10%	20%	—

[a] Mean of replicate percentages ± SD. Values in parentheses indicate number dead.

[b] Number that died during life stage per total number that died at given temperature.

Table 3.—Thermal requirements for development of *H. convergens* from Ithaca, N.Y., (~42°N) and Tucson, Ariz. (~32°N)

	Ithaca area		Tucson area[a]	
Stage	*t* (°C) ± SE	*K* ± SE	*t* (°C)	*K*
Egg	10.3 ± 1.2	44.2 ± 2.1	10.5	44.4
1st Instar	11.2 ± 1.0	34.9 ± 1.4		
2nd Instar	11.7 ± 1.4	24.2 ± 1.8		
3rd Instar	11.9 ± 1.0	26.8 ± 1.4		
4th Instar and prepupa	12.5 ± 0.9	52.2 ± 1.9	7.3[b]	22.0[b]
Total larval development	12.7 ± 0.9	113.1 ± 4.2	9.0	212.8
Pupa	12.0 ± 1.2	54.4 ± 2.6	9.5	69.0
Total development	12.0 ± 0.7	230.3 ± 6.8	10.6[c]	313.2[c]

[a] Data from Butler and Dickerson (1972).

[b] Prepupal development only.

[c] Total developmental time calculated as sum of average preimaginal developmental times.

Tauber 1978). In contrast, no significant variation was found in the nondiapause development of *H. cunea* from Canada, Japan, and Slovakia (Morris and Fulton 1970), the univoltine coccinellid *Coccinella septempunctata* L. (c.f. Bodenheimer 1943, Hodek 1973, Obrycki and Tauber 1981), several species of Lepidoptera (Danilevskii 1965), and *Chrysopa downesi* from eastern and western North America (Tauber and Tauber 1981b).

Thus, *H. convergens* falls into the third category; both *t* and *K* values of the Ithaca population differ from those of the Arizona population. The high *t* values of the Ithaca population presumably retard development during unseasonably warm periods in early spring, whereas its low *K* values allow rapid development during the short reproductive season.

It is clear that the relationship between latitude and thermal requirements for insect development is not a simple one. The particular form of geographic variation in *t* and *K* that a species expresses reflects its overall phenological adaptations (e.g., voltinism, diapause characteristics) and the characteristics of its locality (Tauber and Tauber 1978).

Geographic variation in the phenology of economically important insects presents an additonal problem for the accurate prediction of the seasonal occurrence of pests and beneficial species in insect pest management systems [e.g., *H. cunea* (Morris 1971), *Ostrinia nubilalis* (Beck and Apple 1961), *Leptinotarsa decemlineata* (Hsaio 1982), *C. carnea* Tauber and Tauber 1978), *T. julis* (Nechols et al. 1980)]. These examples and our present study illustrate the need to determine developmental rates for populations throughout the range of the species.

Interspecific Comparisons of Thermal Requirements

H. convergens is one of a group of primarily aphidophagous coccinellids commonly found in the Ithaca, N.Y., area (Pack 1925). We have determined the thermal requirements for development of four of these species (Table 4). The *t* value for total development of *H. convergens* is similar to the values for *C. transversoguttata* and *C. septempunctata*, but higher than those for *A. bipunctata* and *C. maculata* (Table 4). The *K* value for total development of *H. convergens* is higher than that for the two *Coccinella* spp., but similar to *C. maculata* and lower than *A. bipunctata* (Table 4). Thus, early in the season *H. convergens* could begin development at about the same time as *C. septempunctata* and *C. transversoguttata*, whereas, during midseason its developmental rate would be similar to *C. maculata*.

Table 4.—Developmental thresholds (*t*) and thermal constants (*K*) for preimaginal development of five coccinellid species from the Ithaca, N.Y., area (~42°N)

Species	*t* (°C) ± SE	*K* ± SE
Adalia bipunctata[a]	9.0 ± 0.9	262.8 ± 9.0
Coleomegilla maculata[b]	11.3 ± 0.6	235.8 ± 0.7
Coccinella septempunctata[a]	12.1 ± 0.4	196.8 ± 4.4
Coccinella transversoguttata[a]	12.2 ± 1.3	218.2 ± 14.5
Hippodamia convergens	12.0 ± 0.7	230.3 ± 6.8

[a] Obrycki and Tauber (1981).

[b] Obrycki and Tauber (1978).

The thermal characteristics of these five coccinellids influence the temporal occurrence of the species and also determine the maximal number of generations per year in any one area (Obrycki and Tauber 1981). Annual variation in temperature and food availability interact to determine the number of generations actually produced each year, and the degree of importance of these two factors varies geographically. Hagen (1962) concluded that prey availability influences the voltinism of *H. convergens* populations more than abiotic factors. He based this conclusion on the observation that, in California populations, food availability appears to influence voltinism by inducing an aestival diapause (Hagen 1962). However, aestival diapause does not occur in *H. convergens* in New York (Pack 1925, Obrycki and Tauber, unpublished data), where prey availability and temperature influence growth and development directly, and may result in two to three generations each year.

Seasonal synchrony between entomophagous species and their hosts or prey are strongly influenced by their thermal adaptations. Campbell et al. (1974) and Campbell and Mackauer (1975) observed higher *t* and *K* values for several aphid parasites than for their aphid hosts.

They proposed that the higher thermal requirements for development of the aphid parasites have two effects: early in the season, the higher *t* values prevent the emergence of parasites before the appearance of their hosts, whereas the higher *K* values ensure that a continual minimal number of hosts is available. A similar pattern appears to exist between the five coccinellids (Table 4) and two of their common aphid prey, *M. persicae* and *A. pisum*. *M. persicae* has a *t* of 4°C and a *K* of 74.2 degree-days for development of a reproductive adult (Whalon and Smilowitz 1979), and *A. pisum* has a *t* of 5.5°C and a *K* of 110 to 119 degree-days for total development (Campbell and Mackauer 1975). These *t* and *K* values are much lower than those of the coccinellids we studied (Table 4). However, before the significance of the differences between the coccinellids and their prey can be determined, it will be necessary to investigate aspects of the species' seasonal activity (e.g., diapause termination, postdiapause development, and the role of alternative food sources) in field populations.

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