RATES OF DEVELOPMENT OF A KENTUCKY POPULATION OF *GEOCORIS ULIGINOSUS*[1,2]

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Abstract: The effect of temperature on rate of development of eggs and nymphs of a population of *Geocoris uliginosus* (Say) from Kentucky (~38°N) was investigated at five constant temperatures, 15, 21, 24, 27, and 30°C (± 0.5°C). Successful development occurred at all temperatures except 15°C. The relationship between temperature and rate of development was expressed as a linear thermal unit model for each stage and for total development (i.e., egg to adult). Total development required 279.7 degree-days (DD) above a threshold of 18°C. Rates of development were faster for the Kentucky population than for a population from Texas (~32°N). Significant differences in threshold temperatures (T_o) and mean thermal unit requirements (K) were most striking in the egg stage (Kentucky: T_o = 16.6°C, K = 87.9 DD; Texas: T_o = 15.2°C, K = 116.1 DD).

Key Words: *Geocoris uliginosus,* temperature, development, predator.

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Geocoris uliginosus (Say) is a common predator found in both uncultivated and cultivated areas in the United States east of the Rocky Mountains from the Gulf Coast to Canada (Crocker and Whitcomb 1980, Readio and Sweet 1982). As a predator, *G. uliginosus* has been shown to have a broad host range that includes such insect pests as *Heliothis zea* (Boddie) (Whitcomb and Bell 1964), *H. virescens* (Fabricius) (McDaniel and Sterling 1979), *Pseudoplusia includens* (Walker) (Richman et al. 1980), and *Nezara viridula* Linnaeus (Crocker and Whitcomb 1980), as well as many other non-pest insects (Crocker and Whitcomb 1980). Knowledge of the feeding habits of *G. uliginosus* is important to understanding the mortality that may be inflicted on a particular pest population by this predator. However, this knowledge alone is not sufficient to understand the role of *G. uliginosus* in pest population dynamics. Information on other aspects of the biology of this predator is also required.

The biology of *G. uliginosus* was investigated by Davis (1981), who examined the effect of temperature on the development, survival, reproduction, and longevity of a population of *G. uliginosus* from Central Texas. Among populations of the same species from different geographical locations, biological rates such as those measured by Davis (1981) may differ, and this may result in a modification of the seasonal phenology and biology of a species from one geographical location to another (e.g., Obrycki and Tauber 1982). In the present study, we investigated the effect of five constant temperatures on the developmental rates of *G. uliginosus* from Kentucky and compared these rates to those found by Davis (1981).

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MATERIALS AND METHODS

Developmental periods for eggs and nymphs of *G. uliginosus* were measured at the following constant temperatures: 15 (12L:12D), 21 (12L:12D), 24, (12L:12D), 27 (15L:9D), and 30°C (15L:9D) (all ± 0.5°C). The F_1 progeny of field-collected adults were used. The adults were collected during April, May, July, and August, 1983, from red clover, *Trifolium pratense* Linnaeus, alfalfa, *Medicago sativa* Linnaeus, and soybean, *Glycine max* Linnaeus (Merrill), at the University of Kentucky Spindletop Research Farm near Lexington, KY. The field-collected adults were held as male-female pairs in petri dishes at 21°C (12L:12D). Moisture and food requirements of the adults were met by providing them with green bean *(Phaseolus vulgaris* Linnaeus) sections and *H. virescens* eggs. A small ball of absorbent cotton served as an ovipositional substrate.

Cotton balls containing eggs deposited during a 24 h period were removed from the petri dish, and the numbers of eggs were counted and recorded. A total of 18 females contributed eggs which were then reared at the appropriate temperatures. Numbers of females (of the original 18) supplying eggs at 15, 21, 24, 27 and 30°C were 14 females (102 eggs), 17 females (152 eggs), 13 females (138 eggs), 11 females (131 eggs), and 11 females (116 eggs), respectively. Upon emergence, nymphs were placed individually in 30 ml plastic cups with paper lids. Green bean sections and *H. virescens* eggs were provided as food.

Development was monitored daily. The date and time of each egg hatch and nymphal molt, as indicated by the presence of exuvia, were estimated as the midpoint of the period (i.e., between observations) during which the biological event of interest occurred.

To express the relationship between development and temperature, the reciprocal of the developmental time, in days, was regressed on temperature using a linear least squares technique (Steel and Torrie 1960). Temperature thresholds (T_o) for each stage were determined by extrapolation of the regression line to the abscissa. Mean thermal unit requirements (K) for each stage were calculated by taking the mean (across all temperatures) of K_t which was calculated by the following equation.

$$K_t = (T - T_o)*D_t$$

where T = 21, 24, 27, 27, or 30°C; T_o = temperature threshold for a particular stage; D_t = mean developmental time (in days) for a particular stage at temperature T. Only the developmental times of those nymphs that had completed development (i.e., became adults) were used in the calculation of the thermal units required for total nymphal development. Also, duration of development at each temperature was compared between males and females. Student's t-test was used to test for significant differences. Slopes of the regressions of mean developmental time on temperature for the Texas population and the Kentucky population were compared and tested for homogeneity (Steel and Torrie 1960).

RESULTS AND DISCUSSION

Geocoris uliginosus successfully completed development at 21, 24, 27, and 30°C (Table 1). At 15°C, only 1 egg hatched, although eyespot formation was evident on

Table 1. Mean (± SD) developmental time (d) of *Geocoris uliginosus* eggs and nymphs at each constant temperature.

	Temperature (°C)				
Stage	15	21	24	27	30
Egg	70.97	17.83 ± 1.17	12.58 ± 1.11	9.45 ± 0.52	6.12 ± 0.81
(n)*	(1)	(103)	(97)	(85)	(61)
Nymphal Instars					
First	–	14.11 ± 2.30	9.35 ± 1.65	6.23 ± 1.28	4.25 ± 1.40
(n)		(39)	(48)	(62)	(42)
Second	–	9.29 ± 3.15	5.75 ± 1.73	4.53 ± 1.40	3.19 ± 1.04
(n)		(28)	(34)	(55)	(32)
Third	–	8.64 ± 2.51	5.98 ± 1.67	4.28 ± 1.35	3.02 ± 0.80
(n)		(20)	(30)	(54)	(32)
Fourth	–	11.30 ± 2.40	6.43 ± 1.53	4.00 ± 0.96	2.76 ± 0.97
(n)		(14)	(28)	(50)	(31)
Fifth	–	15.39 ± 1.22	10.12 ± 1.54	6.56 ± 1.07	4.28 ± 1.04
(n)		(9)	(27)	(48)	(28)
Total Nymphal	–	58.22 ± 6.10	37.33 ± 3.02	25.35 ± 1.92	17.36 ± 1.15
(n)		(9)	(27)	(48)	(28)
Complete	–	74.66 ± 6.13	50.03 ± 3.20	34.66 ± 2.02	23.55 ± 1.10
(n)		(9)	(27)	(48)	(28)
Male	–	78.12 ± 7.07	51.46 ± 3.21	35.67 ± 2.10	23.88 ± 1.17
(n)		(4)	(15)	(22)	(14)
Female	–	71.89 ± 4.01	48.25 ± 2.21	33.81 ± 1.54	23.22 ± 0.95
(n)		(5)	(12)	(26)	(14)

* Number of individuals completing stage.

the embryos within most of the eggs. The individual that hatched at 15°C died within 24 h after hatching. The mean time required for development during the egg stage ranged from 6.1 d (30°C) to 17.8 d (21°C). Duration of the total nymphal period ranged from 17.4 d (30°C) to 58.2 d (21°C) (Table 1). Survival from egg to adult ranged from 5.9% (21°C) to 36.6% (27°C). Mortality during nymphal development was highest in the first instar at all temperatures.

Females developed significantly more rapidly than males at 24°C (females 48.3 d, males 51.5 d, $t_{df=26} = 2.93$, $P < 0.05$) and 27°C (females 33.8 d, males 35.7 d, $t_{df=47} = 3.53$, $P < 0.05$). Differences in duration of development at 21°C and 30°C were not significant ($P > 0.10$). This may in part be due to limited sample sizes. Davis (1981) recorded slightly longer development times for male *G. uliginosus* than for females. Regression equations for the reciprocal developmental times on temperature for each life stage, and values for T_o and K are given in Table 2. The T_o values for egg hatch, total nymphal development, and complete development (i.e., egg to adult), 16.6, 18.2, and 18.0°C, respectively, were significantly different from each other ($P < 0.05$) (Table 2). These values of T_o appear to be reasonable because development was arrested at 15°C in our experiments (Table 1). The K value for egg hatch was 87.8 degree-days (DD) above 16.6°C, while those for total nymphal and egg plus nymphal development were 220.5 D above 18.2°C, and 279.7 DD above 18.0°C, respectively (Table 2).

Table 2. Linear thermal unit models, threshold temperatures (T_o), and mean thermal unit requirement (K) for development of each stage of *Geocoris uliginosus* (See text for discussion of calculation of T_o and K).

Stage	Kentucky			Texas*		
	Equation† R^2	T_o(°C)	K(DD)	Equation† R^2	T_o(°C)	K(DD)
Egg	$y = 0.11t - 0.19$ $R^2 = 0.84$	16.61	87.86	$y = 0.009t - 0.14$ $R^2 = 0.89$	15.2	116.10
Nymphal Instars						
First	$y = 0.020t - 0.37$ $R^2 = 0.67$	18.20	49.93	$y = 0.018t - 0.33$ $R^2 = 0.94$	18.3	64.00
Second	$y = 0.022t - 0.34$ $R^2 = 0.38$	15.40	50.43	$y = 0.024t - 0.42$ $R^2 = 0.85$	17.5	42.60
Third	$y = 0.027t - 0.46$ $R^2 = 0.42$	17.00	39.62	$y = 0.026t - 0.47$ $R^2 = 0.94$	18.2	38.50
Fourth	$y = 0.036t - 0.69$ $R^2 = 0.54$	19.20	28.30	$y = 0.026t - 0.50$ $R^2 = 0.96$	19.3	38.50
Fifth	$y = 0.22t - 0.42$ $R^2 = 0.63$	19.30	42.78	$y = 0.018t - 0.34$ $R^2 = 0.96$	19.0	55.60
Total Nymphal	$y = 0.005t - 0.09$ $R^2 = 0.93$	18.20	220.49	$y = 0.004t - 0.08$ $R^2 = 0.94$	19.5	206.90
Complete	$y = 0.03t - 0.061$ $R^2 = 0.94$	18.00	279.68	$y = 0.003t - 0.05$ $R^2 = 0.93$	17.7	335.10

* Values from Davis (1981).

† y = reciprocal of mean developmental times; t = temperature; R^2 = coefficient of correlation.

The range of temperatures at which successful development occurred and the T_0 values calculated in this study differed from those of Davis (1981). He reported that successful development occurred between 23.9 and 37.8°C and noted limited egg hatch with poor first instar survival at 21.1°C. The T_0 value for the egg stage was higher for the Kentucky population than for the Texas population (16.6 and 15.2°C, respectively; Table 2), whereas the T_0 value for total nymphal development was lower for the Kentucky population (Kentucky: 18.2°C; Texas: 19.5°C; Table 2). Thus, the T_0 values for complete development were very similar, i.e., 18°C (Kentucky) and 17.7°C (Texas). The thermal unit requirement (K) for complete development above threshold temperatures was lower for the Kentucky population than that for the Texas population, i.e., 279.7 DD and 335.1 DD, respectively (Table 2). Much of this difference was attributable to differences in the K values of the egg stage (Table 2). Testing for homogeneity of regression showed the slopes of the regression lines for the Texas versus the Kentucky population to be significantly different ($P < 0.05$) for nymphal development and development during the egg stage. Slopes of the regressions of total developmental time on temperature also differed between the Texas and Kentucky populations ($0.05 < P < 0.10$).

The T_0 values in our study and that of Davis (1981) were calculated in a similar manner (i.e., extrapolation of the regression line to the abscissa); however, the values used as dependent variables in the regression equations differed. For each temperature regime, Davis (1981) used the reciprocal of the mean developmental times as the dependent variable, rather than the reciprocals of the developmental times for each individual; the latter were used in the present study. This probably affected the correlation coefficients (i.e., our approach should give lower coefficient values), but it should have little or no effect on the T_0 values.

Differences between the range of temperatures for development and T_0 values found in this study and that of Davis (1981) may have been due to any of several reasons. One possibility is that developmental rates of populations of *G. uliginosus* from different geographical locations may differ. The *G. uliginosus* used in this study came from a population located at ca. 38°N latitude (Kentucky) while those used by Davis (1981) were collected from ca. 32°N latitude (Texas). The seasonal average temperature regime for 38°N latitude (Kentucky) is ca. 5°C cooler than that for the 32°N latitude (Texas) (Anonymous 1982a, 1982b). The temperature ranges for successful development, and T_0 and K values for both populations appeared to reflect adaptation to the seasonal temperature regimes characteristic of those latitudes.

The differences in developmental rates between Kentucky and Texas populations also may have been due in part to laboratory adaptation. In the present study, the individuals were the F_1 progeny of field-collected females, and therefore, laboratory adaptation was minimal. In the study of Davis (1981), the individuals used in the experiments had been maintained in laboratory culture at 32°C (14L:10D) for 12 - 15 generations, and although field-collected individuals were periodically added to the culture, some laboratory adaptation may have occurred. The survivorship of *G. uliginosus* eggs and nymphs in Davis' study (1981) lend further support to this hypothesis because survivorship was greater at 32.2, 35, and 37.8°C than at lower temperatures. In our study, the highest nymphal mortality occurred at 21°C, the temperature at which field-collected adults were maintained. Thus, lab adaptation apparently was not a factor in the present study.

Obrycki and Tauber (1982) studied the developmental rates of *Hippodamia convergens* Guerin-Meneville from New York and compared their results with those obtained by Butler and Dickerson (1972) who studied an Arizona population of that species. They found that both T_0 and K values for egg development were similar for the two populations, but that those values differed for larval, pupal, and total development. The New York population had higher T_0 and lower K values, which Obrycki and Tauber (1982) suggested were adaptive characteristics. They presumed that the higher T_0 values of the New York population retarded development during unusually warm periods in early spring and lower K values allowed rapid development during the short growing season in New York. Similarly, the higher T_0 and lower K values associated with the egg stage of the Kentucky population of *G. uliginosus* may serve to synchronize the insect's development with favorable seasonal temperatures. The lower thermal unit requirement for complete development, due mainly to differences in the K values of the egg stage, may allow more rapid development during the shorter growing season in Kentucky as compared with Texas.

CONCLUSIONS

The rates of development and the thermal unit requirements for development of *G. uliginosus* eggs and nymphs determined in this study appeared to reflect adaptation to geographical location, although adaptation to laboratory conditions also may have had some influence. If laboratory adaptation is assumed to be minimal, then the apparent adaptation to geographical location may influence the phenology and biology of a species. For the Kentucky and Texas populations, the differences in developmental rates may be manifested in the time of first appearance of *G. uliginosus* in the spring and the number of generations that develop during a growing season. For the Kentucky population, ca. 2 generations may occur from 1 January through 31 October, assuming a preovipositional period of ca. 70 DD above 18°C (Braman and Yeargan, unpublished data) and ca. 782 DD above 18°C occurring between 1 January and October 31, inclusive (Anonymous 1982a). There are ca. 3 - 4 generations possible from 1 January through 31 October, inclusive, for the Texas population, assuming a preovipositional period of 46.2 DD above 17.7°C (calculated from Davis 1981) and ca. 1400 DD above 17.7°C occuring between 1 January and 31 October, inclusive (Anonymous 1982b). Such differences in phenology and number of generations per year may be important in determining the timing and impact of populations of *G. uliginosus* on prey population dynamics.

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