View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by DigitalCommons@University of Nebraska

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Publications from USDA-ARS / UNL Faculty

U.S. Department of Agriculture: Agricultural Research Service, Lincoln, Nebraska

1995

Life History of Innnature *Lyctocoris campestris* (Hemiptera: Anthocoridae): Effects of Constant Temperatures and Relative Humidities

Megha N. Parajulee
Texas A&M University

Thomas W. Phillips
USDA-ARS

James E. Throne
USDA-ARS, Manhattan, KS, james.throne@ars.usda.gov

Erik V. Nordheim
University of Wisconsin-Madison

Follow this and additional works at: https://digitalcommons.unl.edu/usdaarsfacpub

Parajulee, Megha N.; Phillips, Thomas W.; Throne, James E.; and Nordheim, Erik V., "Life History of Innnature *Lyctocoris campestris* (Hemiptera: Anthocoridae): Effects of Constant Temperatures and Relative Humidities" (1995). *Publications from USDA-ARS / UNL Faculty*. 1995.
https://digitalcommons.unl.edu/usdaarsfacpub/1995

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Agricultural Research Service, Lincoln, Nebraska at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Publications from USDA-ARS / UNL Faculty by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Life History of Immature *Lyctocoris campestris* (Hemiptera: Anthocoridae): Effects of Constant Temperatures and Relative Humidities

MEGHA N. PARAJULEE,[1] THOMAS W. PHILLIPS,[2] JAMES E. THRONE,[3] AND ERIK V. NORDHEIM[4]

Stored-Product Insects Research Unit, USDA–ARS, Department of Entomology, University of Wisconsin, Madison, WI 53706

Environ. Entomol. 24(4): 889–897 (1995)

ABSTRACT Life history of immature *Lyctocoris campestris* (F.), a predator of stored-product insects, was investigated at 17, 21, 25, and 29°C and ≈43, ≈58, and ≈75% RH in the laboratory. Most life history traits of *L. campestris* were influenced by temperature, but none of the traits was influenced by relative humidity. The egg incubation period was ≈7 d at 25–29°C, but increased sharply at temperatures <25°C. An equation was developed to predict egg incubation period over a range of temperatures. Egg hatch rate did not vary with temperatures nor with the relative humidities. The mean hatch rate ranged from 78 to 86% across different temperatures summed across 3 relative humidities. The instar-specific nymphal development also varied with temperature. The 2nd stadium was the shortest followed by the 3rd, 1st, and the 4th, and the 5th stadium was the longest across all 4 temperatures. However, the ratios of duration of nymphal stadia remained constant across all 4 temperatures tested. Total nymphal durations were 20.5, 27.6, 40.1, and 66.2 d at 29, 25, 21, and 17°C, respectively; all 4 were significantly different from one another. The relationships between temperature and instar-specific nymphal durations and total nymphal durations were described by the same equation for both females and males; total nymphal durations did not vary with sex. Nymphal survival rates ranged from 0.60 to 1.00 and did not vary significantly with temperature or relative humidity. Sex ratio (proportion of males) of emerging adults ranged from 0.40 to 0.70, but did not differ from 1:1. These life history data are reported in a manner useful for developing a computer model for simulating *L. campestris* population dynamics.

KEY WORDS stored-products, biological control, modeling, population dynamics, larger pirate bug, predator

THE LARGER PIRATE BUG, *Lyctocoris campestris* (F.), is a predator being evaluated for potential as a biological control agent of moth and beetle pests of stored grain (Parajulee and Phillips 1993, 1994, 1995a, b; Parajulee et al. 1994). Because of the growing interest in the use of natural enemies in stored-product pest management systems, and the realization of the predatory potential of *L. campestris*, detailed biological studies have been undertaken. Parajulee and Phillips (1992) described rearing techniques and general biology of *L. campestris* in the laboratory. Laboratory studies showed that *L. campestris* can use all immature stages of a wide range of prey species and also the adults of some of the beetle species (Parajulee and Phillips 1993). Parajulee et al. (1994) gave a detailed account of *L. campestris* predator–prey interactions in which predator sex, prey species, and experimental habitat influenced the predatory response. However, little quantitative information is available for constructing a population dynamics model to evaluate the biological control potential of *L. campestris* under different environmental conditions. Life history data are needed to develop models that simulate predator–prey population dynamics and such models can be used in optimizing pest management strategies (Ruesink 1976). A necessary 1st step in developing a population growth model is to establish the relationship between environmental conditions and the life history traits of the insect (for example, Throne 1989). The purpose of this study was to collect life history data for *L. campestris* reared under different constant temperature and relative humidity regimes that would normally occur in grain storages. Specific objectives of this experiment were to determine the duration of immature development, instar-specific survivorship, and the sex ratio of

[1] Current address: Department of Entomology, Texas A&M University, College Station, TX 77843.
[2] Current address: Tropical Fruit and Vegetable Research Laboratory, USDA–ARS, P.O. Box 4459, Hilo, HI 96720.
[3] U.S. Grain Marketing Research Laboratory, USDA–ARS, 1515 College Avenue, Manhattan, KS 66502.
[4] Departments of Forestry and Statistics, University of Wisconsin, Madison, WI 53706.

0046-225X/95/0889–0897$02.00/0 © 1995 Entomological Society of America

emerging adults of *L. campestris* over a range of temperatures and relative humidities. These data are then used to establish relationships between environmental conditions and immature development and survival of *L. campestris,* and data are reported in a manner useful for developing a computer model for simulating *L. campestris* population dynamics.

Materials and Methods

Biological Studies. *L. campestris* used in this study were from a laboratory colony that originated from a field collection in 1991 from a grain storage in Madison, WI (Parajulee and Phillips 1992). The experiments were conducted at 4 temperatures (17, 21, 25, and 29°C) and 3 relative humidities (≈43, ≈58, and ≈75%) in biological incubators. All the experiments were conducted at a constant photoperiod of 16:8 (L:D) h and a light intensity of 16–18 $\mu M/m^2/s$. Preliminary studies showed that *L. campestris* immatures could not complete their life cycles at 33°C and adult mortality occurred within 3 d at 35°C. Similarly, at 15°C, all the life history phenomena were normal but substantially prolonged. Development from day 1 of the egg stage to the death of the last female required ≈6 mo at 15°C (Parajulee 1994). Hence, a temperature range of 17–29°C with 2 intermediate temperatures, 21 and 25°C, was selected. Temperature in each incubator was monitored with 2 mercury thermometers and a hygrothermograph. Three relative humidities were maintained within each temperature using saturated aqueous salt solutions in clear, plastic, rectangular chambers, 27.9 by 38.1 by 15.2 cm (Model T-615, Althor, Wilton, CT). Saturated aqueous solutions of sodium chloride (NaCl), sodium bromide (NaBr), and potassium carbonate (K_2CO_3) maintained relative humidities of ≈75, ≈58, and ≈43%, respectively (Greenspan 1977). Experimental insects were maintained in plastic Petri dishes (60 by 15 mm) supported on a plastic grate (30.3 by 21.5 cm) 1.25 cm above ≈750 ml of a given saturated salt solution. The grate provided a false floor above the salt solution. Each temperature treatment (incubator) received 3 humidity chambers, hence there were 12 temperature–humidity combinations (whole plot treatments). In addition to 3 temperature recording devices per incubator, both temperature and humidity were recorded once daily in each treatment chamber using a Pen Type Thermo-Hygrometer (Model PTH-1X, Omega).

Eggs of *L. campestris* were obtained on moistened filter paper from the stock cultures following the method of Parajulee and Phillips (1992), and were incubated at all the temperature-relative humidity combinations to determine the incubation period (egg development time) and the eclosion rate (percentage of nymphs eclosed per egg batch). During incubation, no additional moisture was added to the eggs. At least 4 batches of eggs (5–50 eggs per batch) were examined for each treatment.

Immature development of *L. campestris* was monitored beginning with newly emerged 1st instars. Eggs were obtained from stock cultures and were incubated at 29 ± 1°C, 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h. Upon eclosion, newly emerged 1st-instar *L. campestris* nymphs were individually (n = 30) reared on fully grown larvae of *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) in ventilated plastic Petri dishes (60 by 15 mm) simultaneously in all 12 temperature–humidity treatments. Prey larvae were killed by freezing before presentation to eliminate possible differences in prey susceptibility and equalize availability of prey across treatments. Each bug was provided 1–2 frozen larvae every 24 h until it molted to the adult stage. A piece of filter paper (5.5 mm diameter) was placed in each Petri dish to provide footing. Individual nymphs were observed every 24 h for molting and survival.

Data Analysis. The general linear models procedure (PROC GLM, SAS Institute 1989) was used to test for differences in incubation period and eclosion rate among environmental conditions. The data were analyzed as a split-plot design with temperatures and relative humidities as classes. The data on incubation period were transformed before analysis as:

$$\frac{\text{duration}^{-0.916}-1}{-0.916}$$

to stabilize variances (Box and Cox 1964). A number of different types of equations were fit to the data for incubation period (untransformed) versus temperature and relative humidity (TableCurve 3D, Jandel, San Rafael, CA). The equations were fit to the duration of development rather than to the rate of development data (Kramer et al. 1991). Selection of an equation to describe the data was based on the magnitude and the pattern of residuals, lack-of-fit tests, and R^2 values (Draper and Smith 1981). We also ensured that the shape of the response surface was reasonable for describing the data.

The differences in instar-specific and total nymphal duration of *L. campestris* across different environmental conditions were also determined using the general linear models procedure. The data were analyzed as a split-plot design with temperatures, relative humidities, and sex as classes for each of 5 instars separately. The data were also analyzed as a split-split-plot design with temperatures, relative humidities, instar, and sex as classes for all 5 instars combined. Relative humidity was not statistically significant in any of the models. Thus, a number of different types of equations were fit to the data for instar-specific and total nymphal development time versus temperature (TableCurve 2D, Jandel); the selection of a final equation was made as mentioned previously.

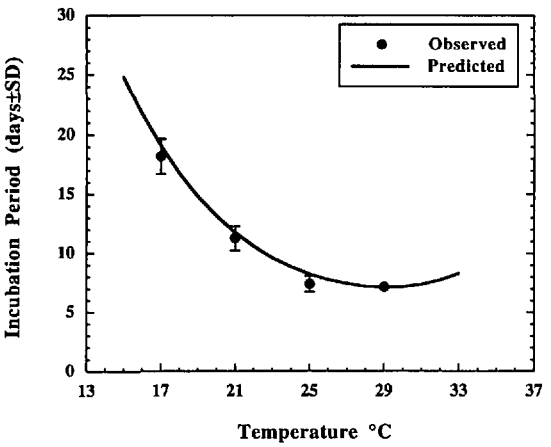

Fig. 1. Relationship between incubation period (days ± SD) and temperature (°C) for *L. campestris* eggs [ln $y = a + bx^2 + cx^3$, where x = temperature (°C) and y = incubation period (d); a = 4.5739567 ±0.0388 SE, b = −0.0092164 ±0.0002, c = 0.0002108 ± 0.0000, R^2 = 0.94; TableCurve 3D].

Instar-specific nymphal survival rate was calculated as the proportion of nymphs surviving to the next instar and the total nymphal survival rate was calculated as the proportion of nymphs reaching adulthood. The differences in nymphal survival rates were also assessed using the general linear models procedure (PROC GLM, SAS Institute 1989).

Deviation in sex ratio of the emerging adults from 1:1 and differences in sex ratios of emerging adults at each temperature–relative humidity combinations were tested using a G statistic (Sokal and Rohlf 1981).

Results

Incubation and Eclosion Rate. The general linear models procedure showed that the duration of the egg stage (incubation period) varied with both temperature (F = 87.38; df = 1, 712; P = 0.0001) and relative humidity (F = 32.98; df = 1, 712; P = 0.0001); interaction between temperature and relative humidity was also significant (F = 44.26; df = 1, 712; P = 0.0001). However, the data on incubation period were described by the equation ln $y = a + bx^2 + cx^3$, where x = temperature (°C) and y = incubation period (d), using the TableCurve 3D (Fig. 1). That is, temperature alone explained most of the variability for the data on incubation period. The discrepancy between GLM and curve fitting results are merely the result of differences in the types of model each program uses; GLM uses a linear model and the TableCurve software uses a nonlinear model. Because the egg developmental data showed a nonlinear relationship with temperatures, the parameters derived from TableCurve are considered more appropriate than those obtained from the GLM. The observed incubation period was the shortest at 29 and 25°C and was longest at 17°C (Table 1; Fig. 1). No eggs hatched above 33°C and the incubation period was fairly constant from 25 up to 29°C. The incubation period increased sharply at temperatures below 25°C. The model predicted an incubation period of ≈25 and ≈7 d at 15 and 30°C, respectively, by extrapolation. These predictions are similar to those data reported by Parajulee (1994) and Parajulee and Phillips (1992).

Eclosion rates for the treatments ranged from 70 to 90% and did not vary with temperature (P = 0.51) or relative humidity (P = 0.23) within the limits of the temperature and relative humidity tested. However, we note that the 43% RH treatments yielded slightly lower eclosion rates (70–79%) than the other 2 (84–85% and 76–91% for 58 and 75% RH, respectively), but the differences were not significant. The mean eclosion rates (summed across 3 relative humidities) were 78, 86, 80, and 83% at 17, 21, 25, and 29°C, respectively, with a grand mean of 81.6%.

Nymphal Development. Instar-specific nymphal developmental period varied with temperature, but did not vary with relative humidity (Table 1). The 2nd stadium was the shortest followed by the 3rd, 1st, and the 4th, and the 5th stadium was the longest across all 4 temperatures. The last stadium, the longest of all 5 stadia, was >3-fold longer than the shortest stadium. The ratios of duration of nymphal stadia remained constant across all 4 temperatures tested (Table 1). The total nymphal duration (from eclosion of the nymph to adult emergence or the sum of durations of 5 stadia) also varied with temperature, but not with relative humidity. Total nymphal durations were 20.5, 27.6, 40.1, and 66.2 d at 29, 25, 21, and 17°C, respectively; all 4 were significantly different from one another (F = 336.31; df = 3, 6; P = 0.0001; PROC GLM, split-plot design with protected least significant difference for mean separations). The relationships between nymphal development and temperature were described by the equation (development time)$^{0.5}$ = a + b/(temp)^2 for all instars and the total nymphal development, where a and b are parameters (see Table 2 for parameter values). The relationships between temperature and instar-specific nymphal durations and total nymphal durations were described by the same general equation for both females (Fig. 2) and males (Fig. 3). Total nymphal durations for females did not vary from that for males (F = 3.17; df = 1, 6; P = 0.125; PROC GLM, SAS Institute 1989) across all temperatures (Table 1). However, the analysis of variance (ANOVA) (split-split-plot design with temperatures, relative humidities, instar, and sex as classes) revealed that male nymphs took slightly more time than female nymphs to reach adulthood at 17°C. More importantly, significant differences in male and female nymphs at the lowest temperature regime was attributed only to the last 2 in-

Table 1. Mean ± SD duration of immature development of *L. campestris* (in days) at various temperatures and relative humidities

Stage	Temp, °C	Sex	RH, %		
			43	58	75
Egg	17		17.75 ± 2.06	18.25 ± 1.26	18.50 ± 1.29
	21		11.20 ± 1.09	11.00 ± 1.22	11.6 ± 0.89
	25		7.25 ± 0.96	7.25 ± 0.50	7.75 ± 0.50
	29		7.50 ± 0.58	7.00 ± 0.00	7.00 ± 0.00
First instar	17	Female	10.33 ± 0.77	11.17 ± 1.16	12.87 ± 1.96
		Male	11.31 ± 1.11	10.67 ± 0.89	12.41 ± 0.87
	21	Female	6.38 ± 0.50	6.88 ± 0.99	7.00 ± 0.71
		Male	6.75 ± 0.86	6.38 ± 0.72	7.26 ± 0.80
	25	Female	4.50 ± 0.51	4.27 ± 0.47	4.50 ± 0.52
		Male	4.70 ± 0.48	4.56 ± 0.70	4.57 ± 1.34
	29	Female	3.91 ± 0.51	3.33 ± 0.49	3.59 ± 0.62
		Male	3.50 ± 0.67	3.28 ± 0.47	4.45 ± 1.57
Second instar	17	Female	8.08 ± 0.51	9.33 ± 1.50	8.67 ± 1.11
		Male	8.77 ± 1.69	8.83 ± 0.94	8.29 ± 0.98
	21	Female	4.92 ± 0.49	4.75 ± 0.88	4.89 ± 0.60
		Male	5.25 ± 0.62	5.19 ± 0.75	4.95 ± 0.40
	25	Female	3.57 ± 0.65	3.82 ± 0.40	3.58 ± 0.79
		Male	3.40 ± 0.70	3.11 ± 0.58	3.64 ± 0.50
	29	Female	2.75 ± 0.87	2.53 ± 0.52	2.65 ± 0.49
		Male	2.58 ± 0.51	2.71 ± 0.47	2.45 ± 0.52
Third instar	17	Female	9.17 ± 1.80	10.50 ± 1.04	9.56 ± 1.13
		Male	10.31 ± 2.10	11.17 ± 1.03	9.18 ± 0.64
	21	Female	5.92 ± 0.64	6.75 ± 0.88	5.33 ± 0.71
		Male	5.75 ± 0.62	5.75 ± 0.77	5.27 ± 0.61
	25	Female	3.93 ± 0.47	3.73 ± 0.65	3.92 ± 0.79
		Male	4.00 ± 0.47	3.94 ± 0.54	3.64 ± 0.63
	29	Female	2.92 ± 0.67	2.80 ± 0.41	2.76 ± 0.56
		Male	2.92 ± 0.67	2.71 ± 0.47	2.91 ± 0.54
Fourth instar	17	Female	11.75 ± 1.35	13.50 ± 1.97	11.11 ± 0.78
		Male	13.77 ± 3.17	14.75 ± 1.91	11.53 ± 0.87
	21	Female	7.62 ± 0.76	7.88 ± 1.12	7.33 ± 0.71
		Male	7.42 ± 0.79	7.75 ± 1.00	7.84 ± 1.01
	25	Female	5.14 ± 0.53	5.27 ± 0.65	5.42 ± 0.51
		Male	5.40 ± 0.52	5.33 ± 0.49	5.78 ± 1.67
	29	Female	4.00 ± 0.43	3.67 ± 0.49	3.29 ± 0.59
		Male	3.92 ± 0.51	3.78 ± 0.42	4.00 ± 0.63
Fifth instar	17	Female	22.75 ± 3.57	25.33 ± 1.75	21.56 ± 2.00
		Male	24.15 ± 1.86	26.42 ± 1.78	22.00 ± 0.79
	21	Female	14.38 ± 0.77	15.25 ± 0.88	14.11 ± 0.60
		Male	14.75 ± 0.96	15.56 ± 0.81	14.89 ± 1.15
	25	Female	10.14 ± 0.53	10.00 ± 0.89	10.17 ± 0.72
		Male	10.50 ± 0.53	10.33 ± 0.48	10.71 ± 1.32
	29	Female	7.75 ± 0.75	7.53 ± 0.52	7.59 ± 0.62
		Male	7.92 ± 0.90	7.71 ± 0.61	7.73 ± 0.47
Total	17	Female	62.08 ± 7.12	69.83 ± 4.53	63.78 ± 6.07
		Male	68.31 ± 7.48	71.83 ± 4.51	63.41 ± 1.91
	21	Female	39.23 ± 2.04	41.50 ± 4.03	38.67 ± 2.29
		Male	39.91 ± 3.26	40.63 ± 2.45	40.47 ± 2.01
	25	Female	27.28 ± 1.27	27.09 ± 1.13	27.58 ± 1.50
		Male	28.00 ± 1.25	27.28 ± 1.32	28.36 ± 4.33
	29	Female	21.33 ± 2.01	19.87 ± 1.06	19.88 ± 1.17
		Male	20.83 ± 0.94	20.21 ± 0.97	21.54 ± 1.57

Duration of the egg stage varied with temperature ($F = 87.38$; df = 1, 712; $P = 0.0001$) and with relative humidity ($F = 32.98$; df = 1, 712; $P = 0.0001$); temperature × relative humidity interaction was also significant ($F = 44.26$; df = 1, 712; $P = 0.0001$) (PROC GLM on Box-Cox transformed data; SAS Institute [1989]). Overall experiment-wise ANOVA was significant (df = 401, 1,128; $P < 0.0001$) for all the nymphal stages combined where temperature ($F = 332.7$; df = 3, 6; $P = 0.0001$) and instar ($F = 2.99$; df = 4, 24; $P = 0.0001$) were significant and relative humidity ($F = 1.00$; df = 2, 6; $P = 0.4213$) was not significant. Overall ANOVAs were also significant for each nymphal stage separately (df = 23, 282; $P < 0.0001$); temperature (df = 3, 6; $P < 0.0001$) was significant and relative humidity was not significant; sex was significant for the last 2 instars only (PROC GLM, SAS Institute [1989]).

stars. Both male and female nymphs took the same amount of time to reach the 4th instar, but it took longer to reach 4th and final molts for male than for female nymphs (Table 1).

Instar-specific and total nymphal survival rates did not vary significantly with temperature or relative humidity (Table 3). Total nymphal survival rates were 0.77, 0.86, 0.88, and 0.90 at 17, 21, 25,

Table 2. Parameter values ± SEM for the best model to describe the relationships between the duration of immature development (d) of *L. campestris* and temperature (°C)

Stage	Sex	Parameters[a]				Lack-of-fit test[b]		
		Intercept	Slope	R^2	Max R^2	F	df	P
First instar	Female	1.0864 ± 0.091	667.4547 ± 36.032	0.90	0.91	1.45	2, 134	>0.10
	Male	1.1622 ± 0.093	649.7784 ± 34.825	0.90	0.90	1.72	2, 164	>0.10
Second instar	Female	0.9977 ± 0.083	558.9886 ± 32.801	0.89	0.90	2.79	2, 134	>0.05
	Male	0.9361 ± 0.085	583.6776 ± 31.850	0.89	0.89	1.43	2, 164	>0.10
Third instar	Female	1.0031 ± 0.097	618.1524 ± 38.387	0.88	0.89	3.30	2, 134	<0.03
	Male	0.9098 ± 0.095	661.6901 ± 35.158	0.89	0.90	1.11	2, 164	>0.25
Fourth instar	Female	1.2131 ± 0.089	660.5639 ± 35.561	0.91	0.92	6.80	2, 134	<0.05
	Male	1.1683 ± 0.127	722.8183 ± 47.305	0.85	0.85	1.88	2, 164	>0.10
Fifth instar	Female	1.7466 ± 0.099	892.3289 ± 39.761	0.93	0.94	2.63	2, 134	>0.05
	Male	1.7905 ± 0.088	905.8231 ± 33.436	0.95	0.95	4.07	2, 164	<0.05
Total	Female	2.7455 ± 0.141	1,541.5139 ± 55.917	0.95	0.96	2.48	2, 134	>0.05
	Male	2.7258 ± 0.136	1,593.0745 ± 50.813	0.96	0.96	0.96	2, 164	>0.25

Relationships between nymphal development and temperature were described by the equation (developmental time)$^{0.5}$ = a + b/(temp)^2 for all instars and the total nymphal development, where a and b are intercept and slope, respectively (TableCurve 2D).

[a] R^2 is the amount of variation explained by the given equation; maximum R^2 indicates the attainable amount of variation that any equation fit to the data could explain, given the pure error in the data (Draper and Smith 1981).

[b] Lack-of-fit tests for parameters at α = 0.05. Although the lack of fit were significant in 3 out of 12 cases, response surfaces that fit the data better did not seem reasonable for describing the data (see text for criteria on the selection of the final model).

and 29°C, respectively, averaged across 3 relative humidities. Similarly, the total nymphal survival rates were 0.82, 0.83, and 0.90 at 43, 58, and 75% RH, respectively, averaged across all 4 temperatures.

Sex Ratio. The sex ratio (percentage of males) of emerging adult *L. campestris* ranged from 0.40 to 0.70 at different temperature–relative humidity combinations, but was not significantly different from 1:1 for any of the temperature or relative humidity regimes tested (Fig. 4, G test, n = 5–19, P > 0.05) (Sokal and Rohlf 1981). Also, the sex ratio of emerging adults did not vary significantly with the temperature or relative humidity (Fig. 4, G test, n = 5–19, P > 0.05) (Sokal and Rohlf 1981). Sex ratios for 58 and 75% RH at 17 and 21°C apparently showed a noticeable difference compared with those for 43% RH treatments (Fig. 4), but none of these four treatments was significantly different from 43% RH treatments across all temperatures.

Discussion

Most life history traits of *L. campestris* were influenced by temperature, but none of the traits was influenced by relative humidity. Arbogast (1975) reported similar findings in another anthocorid, *Xylocoris flavipes* (Reuter), in which he found a significant effect of temperature, but virtually no effect of relative humidity on immature development. No eggs of *L. campestris* hatched at 33°C and the incubation period was longer at low temperatures (Fig. 1). *X. flavipes* can, however, complete its life cycle at 35°C, although the immature mortality is very high (Arbogast 1975). At the lower end of the temperature range, *L. campestris* egg hatch rate was >80% at 17°C and it was similar to that at higher temperatures. Parajulee and Phillips (1994) reported occurrence of *L. campestris* in flat storages of corn in Wisconsin in winter months when average grain temperatures were below 0°C.

Instar-specific nymphal development varied with temperature (Figs. 2 and 3), but showed a similar trend as that reported by Parajulee and Phillips (1992). The curvilinear relationship between temperature and instar-specific or total nymphal durations in *L. campestris* is similar to those documented in many stored-product insects, including natural enemies. Smith (1992) described the developmental rate of *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae) in relation to temperature by a nonlinear model using the Sharpe–DeMichele biophysical equation (Wagner et al. 1984). Schwartz and Burkholder (1991) reported a 4-parameter nonlinear model (Wagner et al. 1984) to describe relationships between temperature and development rate in *Sitophilus granarius* (L.). The Sharpe–DeMichele model has also been used to predict developmental times of 6 stored-product moth species (Subramanyam and Hagstrum 1993). The temperature range we tested closely approximates developmentally relevant temperatures one would encounter in the field. Hence, the relationships established between immature development and temperature at the range of 17–29°C should be appropriate to use in modeling *L. campestris* immature development.

We found no difference in total nymphal durations of *L. campestris* for the 2 sexes across all temperatures (Table 1). We are unable to generalize this finding to other anthocorids nor to any predaceous species because there is no such information on other predaceous bugs. However, there are reports that sex does not affect the duration of immature development in certain other stored-

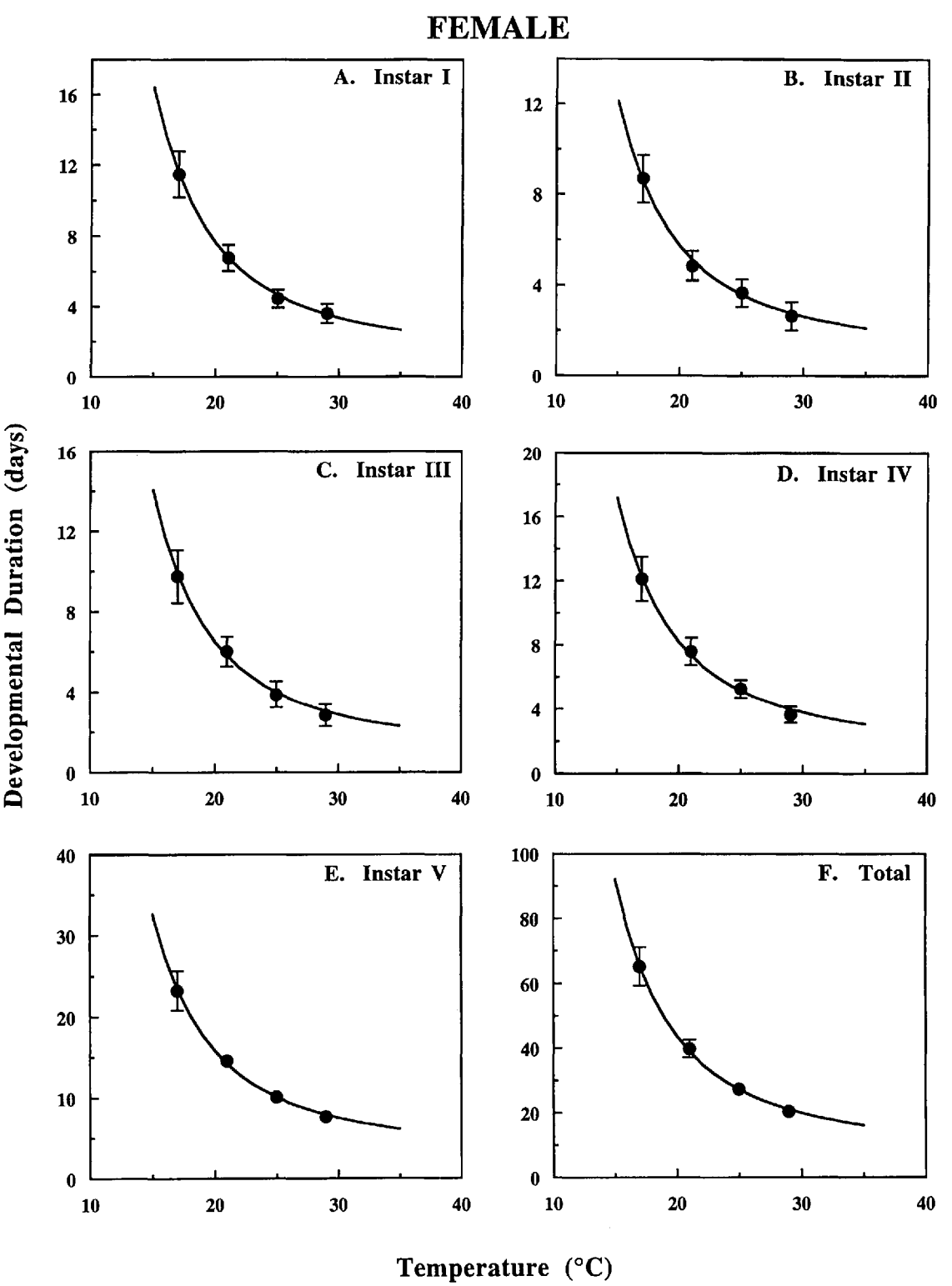

Fig. 2. Relationships between female nymphal developmental period (days) and temperature (°C) for *L. campestris* (see Table 2 for model fit and parameter values). Closed circles represent mean laboratory development times ± SD; solid line represents model prediction.

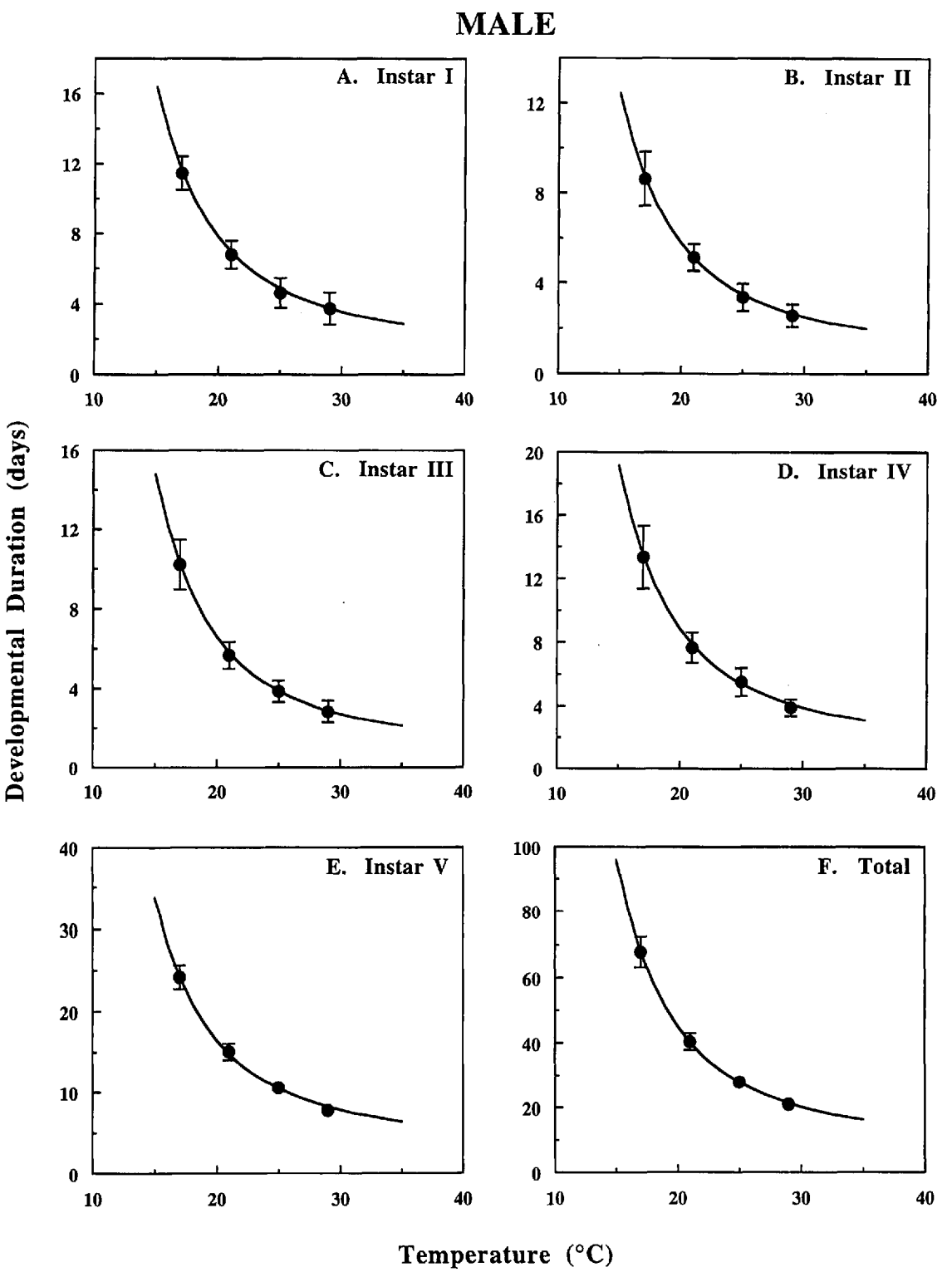

Fig. 3. Relationships between male nymphal developmental period (days) and temperature (°C) for *L. campestris* (see Table 2 for model fit and parameter values). Closed circles represent mean laboratory development times ± SD; solid line represents model prediction.

Table 3. Instar-specific nymphal survival rate (proportion of nymphs survived to the next instar) of *L. campestris* at various temperatures and relative humidities

Immature stage	Temp, °C	RH, %		
		43	58	75
First instar	17	1.00	0.97	1.00
	21	1.00	1.00	1.00
	25	0.93	1.00	0.97
	29	0.97	1.00	0.97
Second instar	17	0.93	0.86	1.00
	21	0.97	0.97	0.97
	25	0.93	1.00	1.00
	29	0.97	1.00	1.00
Third instar	17	0.96	0.84	0.93
	21	0.93	0.86	1.00
	25	0.96	1.00	1.00
	29	0.96	0.97	0.97
Fourth instar	17	1.00	0.90	0.96
	21	1.00	0.96	0.97
	25	1.00	0.97	1.00
	29	0.96	1.00	1.00
Fifth instar	17	0.93	0.95	0.96
	21	0.93	1.00	1.00
	25	0.96	1.00	0.93
	29	0.92	1.00	1.00
Total	17	0.83	0.60	0.87
	21	0.83	0.80	0.93
	25	0.80	0.97	0.90
	29	0.80	0.97	0.93

Instar-specific and total nymphal survival rates did not differ with temperature (df = 3, 6; $P > 0.10$) or relative humidity (df = 2, 6; $P > 0.10$) (PROC GLM, SAS Institute [1989]).

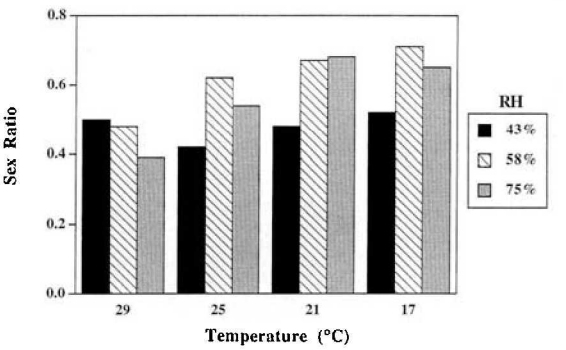

Fig. 4. The sex ratio (proportion of males) of emerging *L. campestris* adults at 4 temperatures and 3 relative humidities in the laboratory. No deviation in sex ratios from 1:1 in any temperature–relative humidity combinations tested ($P > 0.05$; *G* statistic; Sokal and Rohlf 1981).

product insects (Satomi 1960, Throne 1994). Although an ANOVA revealed that male nymphs took significantly longer time than female nymphs to reach adulthood at 17°C, significant difference between male and female nymphs was attributed only to the last 2 instars and evidence of protogyny was not apparent in *L. campestris*. Moreover, the data on immature development for both sexes fit to the same equation with similar parameter values (Table 2). Hence, we believe there is no effect of sex on the duration of *L. campestris* immature and, thus, sex may not be included as a factor when modeling *L. campestris* immature development.

Instar-specific and total nymphal survival rates of *L. campestris* were similar across all temperatures and relative humidities in our study. This indicates that *L. campestris* immatures would develop similarly in a dynamic field environment and constant laboratory environment. The immature survivorship in *L. campestris* was very high compared with that of *X. flavipes*. We found the egg hatch rate of *L. campestris* no less than 70% in any of 12 temperature–relative humidity combinations. Arbogast (1975) reported immature survivorships of <50 and 50% at 35 and 20°C with 60% RH, respectively. *X. flavipes* eggs failed to hatch at 15°C, even if eggs were transferred to 30°C after 16 d at 15°C (Press et al. 1976). *L. campestris* eggs, on the other hand, hatched in 6 d after they were transferred to 29°C after being held at 10°C for 30 d (M.N.P., unpublished data). Thus, it is apparent that the ability of *L. campestris* to survive at low temperatures is far greater than that of *X. flavipes*. The greater ability of *L. campestris* immatures to survive and complete their life cycles at lower temperature regimes suggests that this bug is adapted to cooler climates. On the other hand, *X. flavipes*, which can tolerate high temperature regimes, will be better suited to warmer regions.

A 1:1 sex ratio in our study (Fig. 4) is similar to that reported by Parajulee and Phillips (1992, 1993) for laboratory colonies. Parajulee and Phillips (1992) reported a similar sex ratio of *L. campestris* at 30°C and 60–70% RH. The sex ratio of emerging adult *L. campestris* was also similar on 8 different prey species with no significant deviation from 1:1 (Parajulee and Phillips 1993).

These results indicate that the ideal environmental conditions for *L. campestris* growth and development lie within the range of 25–29°C. The temperature range at which *L. campestris* develops is actually limiting for most temperate areas. However, major pest problems usually occur during late spring and summer. Hence, *L. campestris* could be useful in cooler climates throughout the year or during the cool parts of the year in warmer climates. This is an advantage over other natural enemies that may not be as active in cool weather. Thus, the wide adaptability of *L. campestris* could be exploited in biological control programs targeting pest species with varying spectra of environmental fluxes. Adult survivorship and fecundity data are required to understand fully the population dynamics of this bug and to determine the optimum range of environmental conditions for population growth. Once the data on *L. campestris* reproduction are available, a population growth model can be constructed. A simulation model developed in such a manner can be coupled with prey population dynamics models to develop pest management strategies involving biological control programs in stored grain.

Acknowledgments

We thank Olga Vladimirovna Andreeva (University of Wisconsin–Madison) for valuable technical assistance. We greatly appreciate the reviews of the manuscript by David K. Weaver (USDA–ARS, Savannah, GA), David B. Hogg, Daniel L. Mahr, and Daniel K. Young (all from University of Wisconsin–Madison, WI) and 2 anonymous reviewers. This research was supported by a USDA–ARS specific cooperative agreement between the Stored-Product Insects Research and Development Laboratory, Savannah, GA, and Stored-Product Insects Research Unit, Madison, WI.

References Cited

Arbogast, R. T. 1975. Population growth of *Xylocoris flavipes:* influence of temperature and humidity. Environ. Entomol. 4: 825–831.

Box, G.E.P., and D. R. Cox. 1964. An analysis of transformations. J. R. Stat. Soc. Ser. B 26: 211–243.

Draper, N. R., and H. Smith. 1981. Applied regression analysis, 2nd ed. Wiley, New York.

Greenspan, L. 1977. Humidity fixed points of binary saturated aqueous solutions. J. Res. Natl. Bur. Stand. A81: 89–96.

Kramer, D. A., R. E. Stinner, and F. P. Hain. 1991. Time versus rate in parameter estimation of nonlinear temperature-dependent development models. Environ. Entomol. 20: 484–488.

Parajulee, M. N. 1994. Life history, predatory biology, and population ecology of *Lyctocoris campestris* (F.) (Hemiptera: Anthocoridae) in stored grain. Ph.D. dissertation, University of Wisconsin, Madison.

Parajulee, M. N., and T. W. Phillips. 1992. Laboratory rearing and field observations of *Lyctocoris campestris* (Heteroptera: Anthocoridae), a predator of stored-product insects. Ann. Entomol. Soc. Am. 85: 736–743.

1993. Effects of prey species on development and reproduction of the predator *Lyctocoris campestris* (Heteroptera: Anthocoridae). Environ. Entomol. 22: 1035–1042.

1994. Monitoring field populations of *Lyctocoris campestris,* a predator of stored grain insects: assessment of different trapping designs, pp. 429–434. *In* Proceedings, Sixth International Working Conference on Stored-Product Protection, 17–23 April 1994, Canberra, Australia, CAB International, Wallingford, UK.

1995a. Survivorship and cannibalism in *Lyctocoris campestris* (Hemiptera: Anthocoridae): effects of density, prey availability, and temperature. J. Entomol. Sci. 30: 1–8.

1995b. Seasonal abundance and spatial patterns of the predator *Lyctocoris campestris* in stored corn. Entomol. Exp. Appl. 75: 33–42.

Parajulee, M. N., T. W. Phillips, and D. B. Hogg. 1994. Functional response of *Lyctocoris campestris* (F.) adults: effects of predator sex, prey species, and experimental habitat. Biol. Control 4: 80–87.

Press, J. W., B. R. Flaherty, and R. T. Arbogast. 1976. The effect of low temperature on the egg hatch and subsequent nymphal survival of the predaceous bug *Xylocoris flavipes* (Hemiptera: Anthocoridae). J. Ga. Entomol. Soc. 11: 150–153.

Ruesink, W. G. 1976. Status of the systems approach to pest management. Annu. Rev. Entomol. 21: 27–44.

SAS Institute. 1989. SAS user's guide: statistics. SAS Institute, Cary, NC.

Satomi, H. 1960. Differences in some physiological and ecological characters between two allied species of the rice weevils, *Calandra oryzae* and *C. sasakii* collected from different districts of the world. Jpn. J. Ecol. 10: 218–226.

Schwartz, B. E., and W. E. Burkholder. 1991. Development of the granary weevil (Coleoptera: Curculionidae) on barley, corn, oats, rice, and wheat. J. Econ. Entomol. 84: 1047–1052.

Smith, L. 1992. Effect of temperature on life history characteristics of *Anisopteromalus calandrae* (Hymenoptera: Pteromalidae) parasitizing maize weevil larvae in corn kernels. Environ. Entomol. 21: 877–887.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry, the principles and practice of statistics in biological research, 2nd ed. Freeman, New York.

Subramanyam, B., and D. W. Hagstrum. 1993. Predicting development times of six stored-product moth species (Lepidoptera: Pyralidae) in relation to temperature, relative humidity, and diet. Eur. J. Entomol. 90: 51–64.

Throne, J. E. 1989. Effects of noncatastrophic control technologies that alter life history parameters on insect population growth: a simulation study. Environ. Entomol. 18: 1050–1055.

1994. Life history of immature maize weevils (Coleoptera: Curculionidae) on corn stored at constant temperatures and relative humidities in the laboratory. Environ. Entomol. 23: 1459–1471.

Wagner, T. L., H. Wu, P.J.H. Sharpe, R. M. Schoolfield, and R. N. Coulson. 1984. Modeling insect developmental rates: a literature review and application of a biophysical model. Ann. Entomol. Soc. Am. 77: 208–225.

Received for publication 3 November 1994; accepted 27 April 1995.