Computer Model for Simulating Population Dynamics of the Predator *Lyctocoris campestris* (Heteroptera: Anthocoridae) in Stored Shelled Corn

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ABSTRACT   A computer model for simulating population dynamics of *Lyctocoris campestris* (F.), a predator of stored-product insects, was developed using data from the literature and newly collected data for adult longevity and fecundity. Immature development time and survival, adult longevity, fecundity, and cannibalism were simulated. The model was validated at ambient environmental conditions during three seasons in Wisconsin. The model accurately simulated development of the predator feeding on larvae of the Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), in the validation studies. The model will be useful in optimizing mass-rearing and augmentative releases of this predator for biological control of stored-product insect pests.

KEY WORDS   *Lyctocoris campestris*, stored products, predation, simulation model, biological control, fecundity

Lyctocoris campestris (F.) is a predator of insects in stored grain and other stored commodities. Little was known about the biology of *L. campestris* until recent studies determined its potential as a biological control agent in stored-product ecosystems. Procedures for mass rearing *L. campestris* and developmental parameters at 30°C and 60–70% RH were reported by Parajulee and Phillips (1992). Development from egg to adult takes 30 d at 30°C, and females can lay >250 eggs during a 40-d oviposition period. Both laboratory and field studies indicated that high moisture aided population increase. Adults readily fed on beetle and moth larvae that were as large as 20 mm long. Prey are immobilized within seconds of being bitten, which suggested that a venom was used to overcome prey. The bug's omnivorous feeding habits and ability to feed on large prey indicated potential for use in biological control programs.

A test of 30 species of Coleoptera, Hymenoptera, and Lepidoptera as potential prey for *L. campestris* indicated that there were few immature insects unsuitable as prey (Parajulee and Phillips 1993). However, only a few adults, all stored-product beetles, were attacked and killed by *L. campestris.* Prey species most affected nymphal survivorship and fecundity in life history studies. Both male and female *L. campestris* were able to kill up to 10 lepidopteran or coleopteran prey in 24 h in laboratory functional response studies (Parajulee et al. 1994). Rate of predation doubled when grain was not present in the search arenas, as might occur in a warehouse storage situation. Rate of predation was lower in oats than in corn or wheat (Meagher and Locke 1997). *L. campestris* is cannibalistic, and cannibalism increases with density (Parajulee and Phillips 1995). Adult longevity is reduced by ≈50–70% when water or prey are not provided (Parajulee and Phillips 1995). Duration of development and survivorship of immature stages of *L. campestris* are affected by temperature, but not relative humidity (Parajulee et al. 1995).

A computer model for simulating population dynamics of *L. campestris* would aid in determining the potential of this predator for controlling stored-product insect pests and in optimizing control programs using this predator. We report on the effects of temperature and relative humidity on adult longevity and fecundity, the development of a computer model for simulating *L. campestris* population dynamics, on studies conducted under ambient outdoor conditions to collect data to validate the model, and on the validity of the model.

Materials and Methods

Insects. *L. campestris* were from a laboratory colony initiated with insects collected from a grain storage in Dane County, WI, in 1991. Additional *L. campestris* collected from grain storages in Dane County were added to the colony each year. The colony was maintained using techniques developed by Parajulee and Phillips (1992). Indianmeal moth, *Plodia interpunc-*
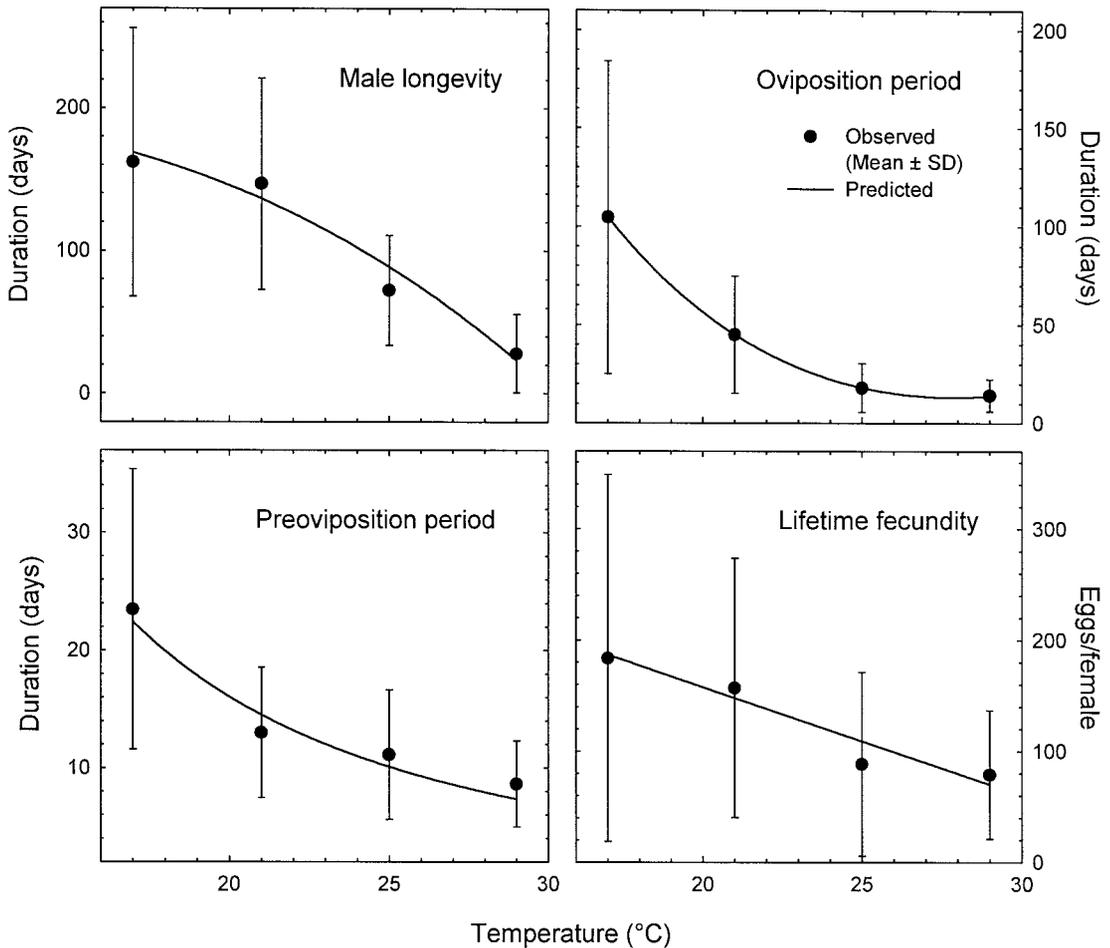
Fig. 1. Effects of temperature on life history of adult *Lyctocoris campestris*.

tella (Hübner), larvae from a laboratory colony (rearing procedures in Silhacek and Miller 1972) were used as prey. Voucher specimens of *L. campestris* were placed in the Oregon State University and University of Wisconsin-Madison insect collections.

Adult Longevity and Fecundity. Longevity and fecundity data were obtained at 12 temperature-relative humidity combinations—four temperatures (17, 21, 25, and 29°C) and three relative humidities (43, 58, and 75%)—at a photoperiod of 16:8 (L:D) h, using methods as in Parajulee and Phillips (1992). Adults used in the fecundity study at different temperature-relative humidity regimes were obtained from immatures reared at the respective regimes. Newly laid eggs from the laboratory colony were incubated at each temperature-relative humidity combination. Upon eclosion, newly emerged first instars were individually reared on fifth-instar *P. interpunctella* simultaneously in all 12 environmental conditions. Upon adult emergence, adults were confined as single mating pairs (*n* = 10–20 pairs per treatment) in individual petri dishes (100 by 15 mm) with one or two fifth-instar *P. interpunctella* as prey. *P. interpunctella* larvae used as prey

for nymphs and adults were frozen before use to kill them, and they were replaced daily. A stack of three filter papers (9-cm-diameter Whatman No. 1, Kent, UK) moistened with distilled water was provided in each petri dish for oviposition. Eggs were harvested and counted from each pair every day until the last female died. Longevity and fecundity data were analyzed using analysis of variance (PROC GLM, SAS Institute 1990). Data for male longevity and duration of female preoviposition and oviposition period were transformed ($\lambda = 0.27$, 0.03, and 0.13, respectively) before analysis using the Box-Cox transformation (Box and Cox 1964) to homogenize variances. Fecundity data were transformed before analysis using a logarithmic transformation.

Model Development. TableCurve 2D software (Jandel Scientific 1996) was used to fit equations describing the effects of temperature on development time and survivorship of immature stages using data from Parajulee et al. (1995) and on adult longevity and fecundity. We did not use the equations developed by Parajulee et al. (1995) because differences between sexes were small and there was no obvious pattern to

Table 1. Parameter values (±SEM) for equations describing the relationship between temperature (°C) or density (for cannibalism) and *L. campestris* life history

Life history process	Parameters			Fit[a]		Lack-of-fit		
	a	*b*	*c*	R^2	Max R^2	*F*	df	*P*
Egg duration[b]	39.31 ± 1.441	−0.05057 ± 0.003367	0.008074 ± 0.0005716	0.95	0.96	1.07	9, 39	0.41
Nymph 1 duration[c]	−0.7306 ± 0.1590	3458 ± 69.09	—	0.88	0.88	5.79	2, 350	<0.01
Nymph 2 duration[c]	−0.6392 ± 0.1220	2635 ± 53.45	—	0.88	0.88	3.82	2, 338	0.02
Nymph 3 duration[c]	−1.045 ± 0.1408	3126 ± 62.28	—	0.89	0.89	3.42	2, 321	0.03
Nymph 4 duration[c]	−0.9096 ± 0.1902	3890 ± 84.54	—	0.87	0.87	1.59	2, 314	0.21
Nymph 5 duration[c]	−0.8041 ± 0.2223	6999 ± 99.21	—	0.94	0.94	1.68	2, 303	0.19
Adult male longevity[d]	205.6 ± 12.90	−0.007475 ± 0.0008977	—	0.37	0.39	1.47	2, 115	0.23
Preoviposition period[c]	−0.5561 ± 1.934	6655 ± 830.8	—	0.35	0.37	1.55	2, 115	0.22
Oviposition period[e]	2066 ± 515.0	31.72 ± 10.89	−882.6 ± 245.1	0.40	0.40	0.00	1, 115	1.00
Fecundity[f]	352.3 ± 57.96	−9.727 ± 2.531	—	0.11	0.12	0.68	2, 115	0.51
Cannibalism[g]	1.051 ± 0.04453	0.01377 ± 0.001365	—	0.97	—	—	—	—

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

[b] Relationship between duration of egg development (y, in days) and temperature (x, in °C) was described by the equation $y = a + bx^{2.5} + cx^3$. In simulations, duration of the egg stage above 32°C was set equal to that at 32°C. At temperatures below 15°C, duration equalled $((((15−x)+1)*23)+23)$. Duration below 0°C was set equal to that at 0°C.

[c] Relationships between duration of nymphal development and preoviposition period (y, in days) and temperature (x, in °C) were described by the equation $y = a + b/x^2$. At temperatures below 17°C in simulations, duration equalled $((((17−x)+1)*z)+z)$, where z = 11.5, 8.6, 9.9, 12.7, and 23.5 for the first through fifth nymphal stages, respectively. Duration below 1°C was set equal to that at 1°C. For the preoviposition period, duration below 5°C was set equal to that at 5°C.

[d] Relationship between male longevity (y, in days) and temperature (x, in °C) was described by the equation $y = a + bx^3$. In simulations, male longevity above 29°C was set equal to that at 29°C. Longevity below 1°C was set equal to that at 1°C.

[e] Relationship between duration of the oviposition period (y, in days) and temperature (x, in °C) was described by the equation $y = a + bx + clnx$. In simulations, longevity below 10°C was set equal to that at 10°C and longevity above 29°C was set equal to that at 29°C.

[f] Relationship between fecundity (y, in days) and temperature (x, in °C) was described by the equation $y = a + bx$. No eggs are laid at temperatures below 15°C or above 32°C. Females laid eggs throughout their lives (Parajulee and Phillips 1993) at a constant rate.

[g] Relationship between percentage of survivorship during cannibalism (y) and density of *L. campestris* (x) was described by the equation $y = ae^{−bx}$. Parameters for the equation during the first 4 wk of the study are as listed in the table. During the rest of the study, the parameter *b* and its standard error were twice that listed in the table. Data for this equation were from Parajulee and Phillips (1995) and the equation was developed without replication in the data; hence, lack of fit parameters cannot be calculated.

these differences, so we combined sexes of immatures in the model. We chose equations based on their simplicity and based on our expectations of the effects of temperature on insect development. That is, we expected the rate of development to be slow at low temperatures, rise to an optimum, and then to slow again at high temperatures. We examined lack of fit and the maximum possible R^2 that could be achieved given pure error in the data caused by replication (Draper and Smith 1981). A time-varying distributed delay was used to simulate variation in development times, apply survivorship, and move insects through stages (Manetsch 1976). The methods for calculating *k*, the parameter that describes the shape of the curve of individuals leaving a stage over time, were as in Throne (1989). Time step in the model (*dt*) was ½₄ d, so *k* for any stage was not allowed to exceed the minimum mean development time (μ) of that stage times 12 $(=\mu/2dt)$ to ensure stability of the delay (Abkin and Wolf 1976). Sex ratio of emerging adults was 1:1 (Parajulee et al. 1995).

Survivorship for immature stages was 0.82, 0.98, 0.97, 0.95, 0.98, and 0.96 for the egg and first through fifth nymphal stages, respectively, and generally did not vary with temperature or relative humidity (Parajulee et al. 1995), except that survivorship of immature stages above 32°C equaled 0. However, in the distributed-delay model, all insects will not die in one time step if the temperature exceeds 32°C. Rather, if du-

ration of development is 3 d at a constant temperature above 32°C and survivorship is 0, then all insects will die over a 3-d period.

Cannibalism was included in the model because densities were expected to be high near the end of validation studies, although we would expect cannibalism to play a minimal role in *L. campestris* population dynamics in the field. Rates of cannibalism are based on data for a small arena and high prey density in Parajulee and Phillips (1995). In that study, five prey per day were provided. In the validation studies (described below), 20 prey were provided every 2 d for 4 wk and then 40 prey every 2 d for the rest of the study. Thus, during the first 4 wk of the validation study, there were twice as many prey available as in Parajulee and Phillips (1995) and four times as many prey during the rest of the validation study. So, we multiplied densities in Parajulee and Phillips (1995) by two and fit an equation to proportion survivorship as affected by cannibalism as a function of density. This equation was used to simulate cannibalism during the first 4 wk of the validation study. Densities were multiplied by four to develop the equation to simulate cannibalism during the rest of the validation study. We assumed that only nymphs would be cannibalized in the simulations because adults are only cannibalized when no other food is available (M.N.P., unpublished data). Survivorship of immatures in the simulations was the product of survivorship caused by environ-
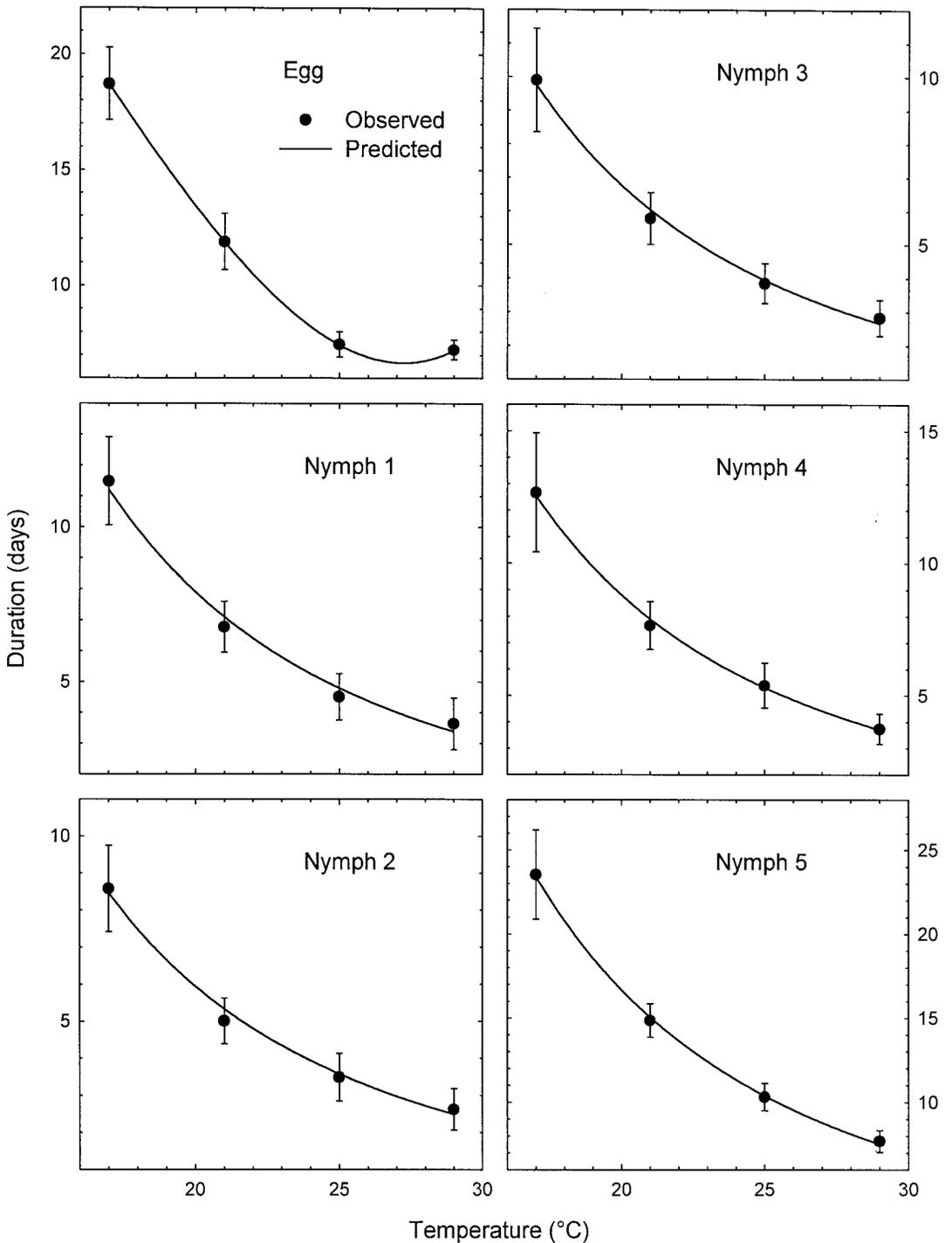
Fig. 2.   Effects of temperature on mean ± SD duration of development of immature *Lyctocoris campestris*.

mental conditions and survivorship caused by canni-balism.

Validation. Validation studies were conducted in a screened shed on the University of Wisconsin-Madi-son campus. Validation tests were set up on 26 May, 7 July, and 18 August 1994, and each test lasted 16 wk. The design for each test was the same. The bottom of each of 16 cans (≈8 liters, 24 cm diameter by 19.5 cm high) was covered to a depth of 1 cm with shelled corn (*Zea mays* L.), and five pairs of newly emerged
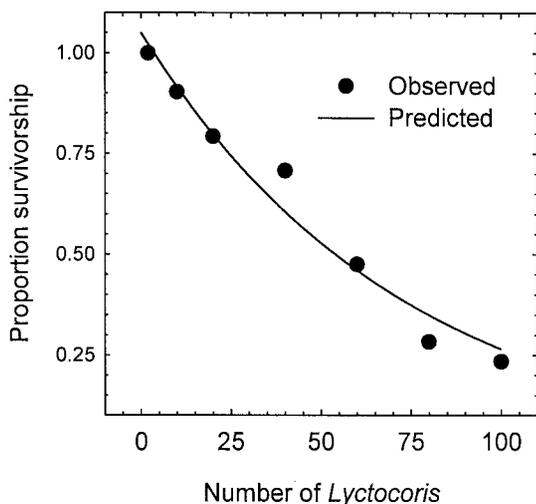
Fig. 3. Relationship between density and proportion survivorship as a result of cannibalism in *Lyctocoris campestris.*

L. campestris (0–24 h old) adults were placed in each can. Twenty frozen fifth-instar *P. interpunctella* were placed in each can as prey every other day for the first 4 wk, and then 40 larvae were placed in each can every other day for the remainder of the study. An oviposition substrate consisting of a stack of three filter papers (9-cm-diameter Whatman No. 1) moistened with distilled water was also placed in each can every other day, and all filter papers remained in the cans throughout the study. Four cans were destructively sampled every 4 wk, and all live and dead nymphs and adults in the cans were counted. Temperature and
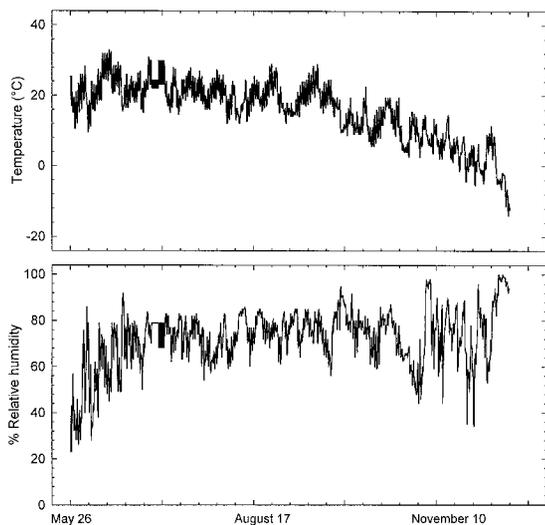

Fig. 4. Environmental conditions recorded hourly during validation tests in a screened shed in Madison, WI. Lines below the graph indicate the duration of each of the three validation studies.
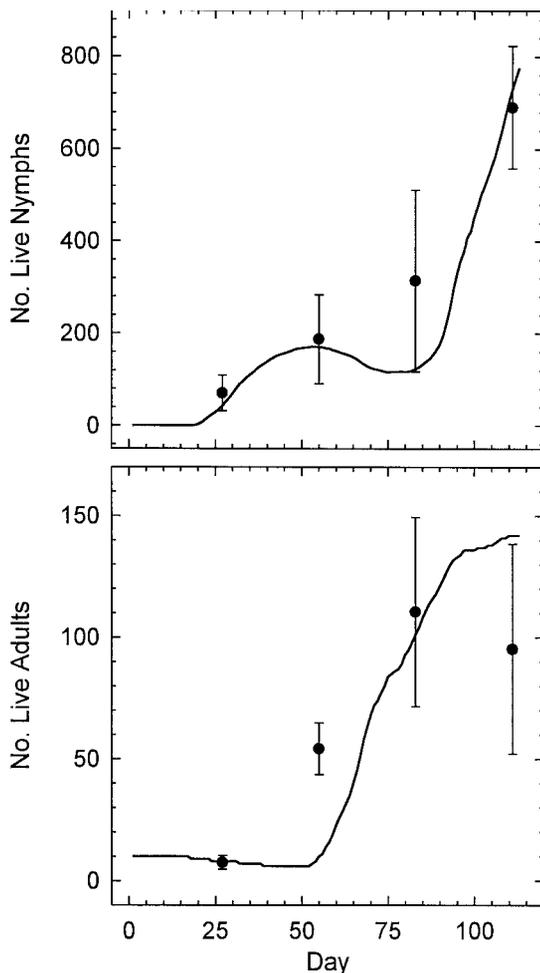

Fig. 5. Observed (circles, mean and 95% confidence intervals) and simulated (solid line) population development of *L. campestris* in the first validation test conducted from 26 May to 15 September in a screened shed in Madison, WI.

relative humidity were monitored in an uninfested can throughout the study (Datapod DP220, Omnidata International, Logan, UT).

Simulations were started with five pairs of newly emerged adults (0–24 h old). Recorded hourly temperatures from the validation study were input and used to determine population development. Our goal was for predictions to be within the 95% CL of population levels in the validation studies.

Results

Adult Longevity and Fecundity. Male longevity varied with temperature ($F = 33.8$; df = 3, 107; $P < 0.01$) (Fig. 1), but not relative humidity ($F = 1.8$; df = 2, 107; $P = 0.18$; interaction $F = 1.1$; df = 6, 107; $P = 0.39$). Duration of female preoviposition period varied with temperature ($F = 29.7$; df = 3, 111; $P < 0.01$) (Fig. 1) and relative humidity ($F = 3.9$; df = 2, 111; $P = 0.02$; interaction $F = 1.6$; df = 6, 111; $P = 0.17$). However,
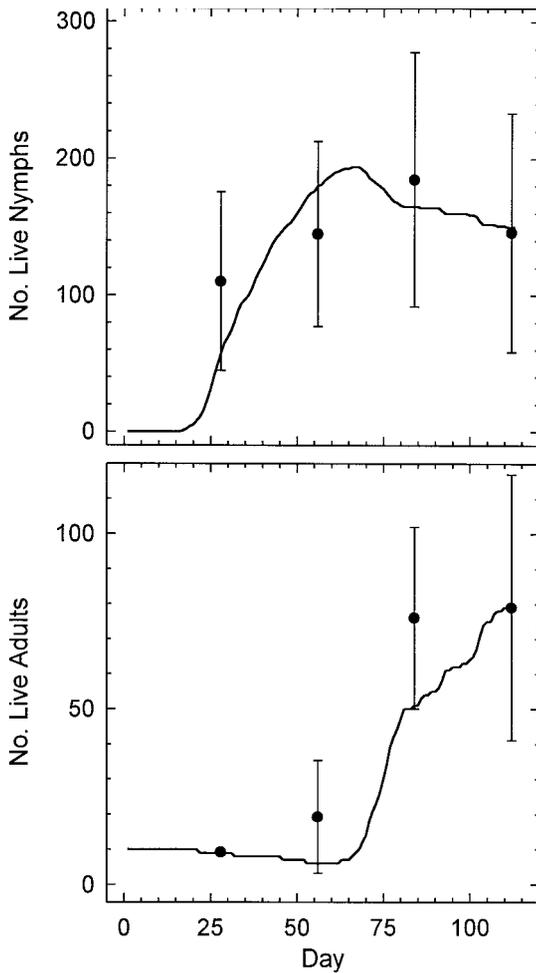
Fig. 6. Observed (circles, mean and 95% confidence intervals) and simulated (solid line) population development of *L. campestris* in the second validation test conducted from 7 July to 27 October in a screened shed in Madison, WI.
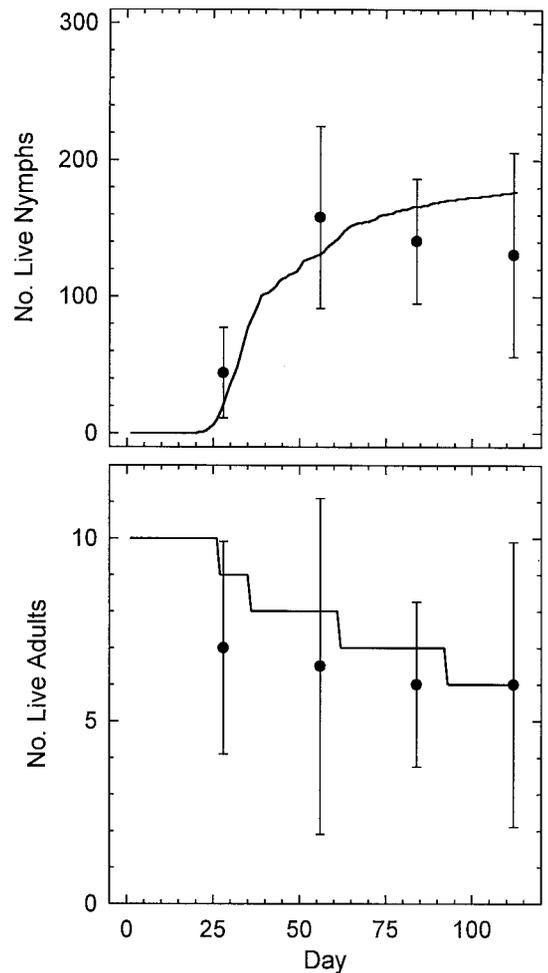
Fig. 7. Observed (circles, mean and 95% confidence intervals) and simulated (solid line) population development of *L. campestris* in the third validation test conducted from 18 August to 8 December in a screened shed in Madison, WI.

there was no obvious pattern to the relationship between duration of preoviposition period and relative humidity, therefore we did not include relative humidity in the model. Duration of female oviposition period varied with temperature ($F = 37.3$; df = 3, 111; $P < 0.01$) (Fig. 1), but not relative humidity ($F = 1.5$; df = 2, 111; $P = 0.23$; interaction $F = 1.4$; df = 6, 111; $P = 0.23$). Similarly, fecundity varied with temperature ($F = 4.5$; df = 3, 111; $P < 0.01$) (Fig. 1), but not relative humidity ($F = 1.1$; df = 2, 111; $P = 0.35$; interaction $F = 1.3$; df = 6, 111; $P = 0.25$).

Model Development. Equations for describing the effects of temperature on life history of *L. campestris* and the effects of density on mortality caused by cannibalism are presented in Table 1 (Figs. 1–3). Although lack-of-fit was significant for some equations, we used these equations because other equations that resulted in a nonsignificant lack-of-fit did not have a form that one would expect based on biological principles.

Validations. In the first validation test, which ran through the summer (26 May to 15 September), temperatures in the cans were between 9.5 and 33°C and relative humidities were between 23 and 92% (Fig. 4). Simulated number of nymphs was always within the 95% confidence intervals for observed numbers of nymphs (Fig. 5). However, simulated numbers of nymphs and adults appeared to lag slightly behind observed population levels, and simulated number of adults at the end of the study was slightly higher than the upper confidence limit for the observed data.

Population levels of both adults and nymphs were always within the 95% confidence intervals for observed numbers of nymphs and adults in the second and third validation tests (Figs. 6 and 7). The second validation test was conducted from midsummer into autumn (7 July to 27 October). Temperatures were between 2.5 and 30°C, and relative humidities were between 54 and 95% (Fig. 4). The third validation test was conducted from late summer into winter (18 Au-

gust to 8 December). Temperatures were between −14 and 29°C, and relative humidities were between 34 and 100% (Fig. 4). No adults were produced in the third validation test because of low winter temperatures. The model accurately simulated *L. campestris* population development under a series of very different environmental conditions.

Discussion

Although simulated population levels were almost always within 95% confidence intervals for observed population levels, population development may be slightly slow in the model. Simulated number of adults appeared to lag behind observed number of adults, although simulated numbers were usually within observed 95% CL. Temperatures to which the insects were actually exposed may have been slightly different than in the can in which we monitored temperature, or fluctuating temperatures in the validation studies may have affected insect development slightly differently than did constant temperatures in the laboratory studies used to collect data to develop the model (Liu et al. 1995). It is also possible that *L. campestris* that were cannibalizing other *L. campestris* in the validation studies may have developed more rapidly than *L. campestris* feeding on *Plodia*. Duration of the nymphal stage varied by 6 d, depending on prey species, in a previous study (Parajulee and Phillips 1993). As with most insects, effects of extreme temperatures on development of *L. campestris* have not been determined. We made assumptions in the model about development at extreme temperatures, and inaccuracies in those assumptions could be partly responsible for the possible time lag in the simulations. Also, rate of cannibalism may vary with temperature, particularly at extreme temperatures, but did not vary with temperature in the model.

Observed numbers of adults dropped more rapidly at the end of the first validation study than in the simulation. Again, this difference may have been a result of slightly slower development in the simulation or to inaccuracy of simulation of cannibalism at extreme temperatures (temperatures were high at the end of the first validation study). However, this may also indicate that cannibalism may not be accurately simulated in the model at high population densities. The population densities at the end of the first validation study were much higher than densities in the studies in which the cannibalism data were collected (Parajulee and Phillips 1995). These population densities would not be expected in a field situation where *L. campestris* would be able to disperse as population levels increased.

The lack of a significant effect of relative humidity in the longevity and fecundity studies was probably a result of providing moist filter papers for oviposition. In an earlier study, eggs laid in *P. interpunctella* larvae in the laboratory did not hatch if the larvae desiccated, and most *L. campestris* trapped in a field study were in portions of the grain mass with high moisture (Parajulee and Phillips 1992). Dependence on moisture for oviposition and egg hatch may be a limiting factor for use of this predator for biological control of insect pests of grain and stored commodities, but it may be possible to overcome this limitation by providing a contained source of moisture or by repeated augmentative releases of nymphs or adults.

This model is the first developed for a predator of stored-product insects. Models for simulating population development of natural enemies of stored-product insect pests are generally lacking (Throne 1995), although there has been recent work in this area (Flinn and Hagstrum 1995). Such models are useful for understanding population ecology and optimizing pest management strategies.

Lyctocoris campestris has potential for controlling insect pests in both grain storages and in warehouses and other facilities where processed commodities are stored. *L. campestris* is a general predator (Parajulee and Phillips 1993) and quite fecund (Parajulee and Phillips 1992). *L. campestris* is also able to develop at relatively low temperatures (17°C or lower, Parajulee et al. 1995), and therefore it may be suitable for use with aeration (blowing cool air through grain to lower the temperature and help control insect pests, Arthur et al. 1998) or grain chilling with refrigeration (Maier et al. 1996). Use of this simulation model should enhance efforts to optimize mass rearing and release of this species for augmentative biological control.

References Cited

Abkin, M. H., and C. Wolf. 1976. Distributed delay routines: DEL, DELS, DELF, DELLF, DELVF, DELLVF. Department of Agricultural Economics Computer Library for Agricultural Systems Simulation Document 8. Michigan State University, East Lansing.

Arthur, F. H., J. E. Throne, D. E. Maier, and M. D. Montross. 1998. Feasibility of aeration for management of maize weevil populations in corn stored in the southern United States: model simulations based on recorded weather data. Am. Entomol. 44: 118–123.

Box, G.E.P., and D. R. Cox. 1964. An analysis of transformations. Proc. R. Stat. Soc. 26: 211–252.

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

Flinn, P. W., and D. W. Hagstrum. 1995. Simulation model of *Cephalonomia waterstoni* (Hymenoptera: Bethylidae) parasitizing the rusty grain beetle (Coleoptera: Cucujidae). Environ. Entomol. 24: 1608–1615.

Jandel Scientific. 1996. TableCurve 2D automated curve fitting and equation discovery, version 4. Jandel Scientific, San Rafael, CA.

Liu, S. S., G. M. Zhang, and J. Zhu. 1995. Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. Ann. Entomol. Soc. Am. 88: 107–119.

Maier, D. E., W. H. Adams, J. E. Throne, and L. J. Mason. 1996. Temperature management of the maize weevil,

Sitophilus zeamais Motsch. (Coleoptera: Curculionidae) in three locations in the United States. J. Stored Prod. Res. 32: 255–273.

Manetsch, T. J. 1976. Time-varying distributed delays and their use in aggregative models of large systems. IEEE Trans. Syst. Man Cybern. SMC-6: 547–553.

Meagher, R. L., Jr., and L. A. Locke. 1997. Predation of Indianmeal moth larvae by *Lyctocoris campestris* (F.) (Hemiptera: Anthocoridae) in different stored commodities. J. Entomol. Sci. 32: 271–280.

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.

Parajulee, M. N., and T. W. Phillips. 1993. Effects of prey species on development and reproduction of the predator *Lyctocoris campestris* (Heteroptera: Anthocoridae). Environ. Entomol. 22: 1035–1042.

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

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

Parajulee, M. N., T. W. Phillips, J. E. Throne, and E. V. Nordheim. 1995. Life history of immature *Lyctocoris campestris* (Hemiptera: Anthocoridae): effects of constant temperatures and relative humidities. Environ. Entomol. 24: 889–897.

SAS Institute. 1990. SAS/STAT user's guide, version 6, 4th ed. SAS Institute, Cary, NC.

Silhacek, D. L., and G. L. Miller. 1972. Growth and development of the Indian meal moth, *Plodia interpunctella* (Lepidoptera: Phycitidae), under laboratory mass-rearing conditions. Ann. Entomol. Soc. Am. 65: 1084–1087.

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.

Throne, J. E. 1995. Computer modeling of the population dynamics of stored-product pests, pages 169–195. *In* D. S. Jayas, N.D.G. White, and W. E. Muir [eds.], Stored-grain ecosystems. Marcel Dekker, New York.