

Developmental Rate Estimation and Life Table Analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae)

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ABSTRACT Egg and nymphal development were studied under constant temperatures for the newly introduced pest species, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae). Development was assessed at seven constant temperatures (15–35°C). Development to adult was completed at temperatures between 17 and 33°C, with egg hatch also occurring at 15°C. The relationship between temperature and developmental rate was evaluated using three developmental models. Of the models evaluated, the Briere-1 model was the best fit for the empirical data of egg and total development and for providing accurate values for the temperature threshold. Application of the linear degree-day model estimated 537.63 DD are needed for total development (egg to imaginal ecdysis). An additional 147.65 DD are needed for the preoviposition period of the female. Reproductive parameters were evaluated at 25°C and indicate a median number of 28 eggs per egg mass. Oviposition occurred at 4.32-d intervals, and a female can continue to oviposit throughout its lifespan. *H. halys* is univoltine in New Jersey and Pennsylvania, but if it spreads to warmer climates in the United States, it could have multiple generations per year.

KEY WORDS development rate, nonlinear model, stink bug, invasive species

Halyomorpha halys (Stål) (Hemiptera: Pentatomidae) is an Asian stink bug species that was accidentally introduced into North America in Allentown, PA, around 1996 (Hoebeck and Carter 2003). *H. halys* is highly polyphagous, with >300 reported host plants, including many agricultural crops, particularly fruits and vegetables important for fresh market sales (Hoffman 1931, Hoebeck and Carter 2003). In Japan, Korea, and China, *H. halys* is an occasional pest of soybeans and tree fruit, including apples, citrus, and pear. Since its establishment in the United States, *H. halys* has been collected from multiple mid-Atlantic and New England states, as well as from Oregon and California (unpublished data).

Stink bugs are increasingly serious pests in many agricultural crops, including tree fruit, because of reductions in broad-spectrum insecticide use, including organophosphates, which previously controlled stink bugs in many crops (Willrich et al. 2003, Snodgrass et al. 2005). Although it is uncertain what level of economic or ecological impact *Halyomorpha halys* will ultimately have in the United States, economic losses resulting from *H. halys* feeding injury have occurred in commercially grown apples, peaches, and pears in New Jersey and Pennsylvania beginning in 2006. Therefore, it is important to understand the development and reproductive parameters of *H. halys* as a possible emerging pest.

In Asia, *H. halys* overwinters as an adult and produces offspring by midsummer on host plants where the majority of the feeding damage occurs (Hoffman 1931). Many stink bug pest species like *Acrosternum* sp., *Nezara* sp., and *Euschistus* sp. exhibit similar behaviors (McPherson and McPherson 2000). The study reported here determined the developmental biology of the New Jersey population of *H. halys* under controlled conditions. The relationship between temperature and developmental rate typically increases from a minimum threshold until the optimum temperature, at which point it rapidly declines (Logan et al. 1976, Lactin et al. 1995). Comparisons between biological models have been done for Acari, Homoptera, Coleoptera, Hymenoptera, and others to aid in understanding specific developmental characteristics for insects (Lactin et al. 1995, Briere et al. 1999, Sánchez-Ramos and Castañera 2001, Roy et al. 2002, Kontodimas et al. 2004, Arbab et al. 2006). To examine the developmental rate of *H. halys*, we chose models that predicted the minimum and maximum temperature thresholds (Campbell et al. 1974, Logan et al. 1976, Lactin et al. 1995, Briere et al. 1999, Roy et al. 2002). For this, we evaluated the linear degree-day model and the nonlinear Briere-1 and Lactin-2 models as descriptors of both egg and total development.

As *H. halys* expands its range in North America and increases in population density, developmental rate studies are a necessary first step to understanding its biology and ecology. Life table analysis for the New

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Jersey and Pennsylvania populations will help provide the necessary components for population models and the development of integrated pest management (IPM) programs, should the need arise. This study presents the first laboratory data on developmental rates and life table parameters of *H. halys* in the United States under constant temperatures.

Materials and Methods

Laboratory Colony. *Halyomorpha halys* adults ($N \approx 200$) were initially collected in September 2003 at the Rodale Organic Tree Center in Allentown, PA, to establish a laboratory colony. Each year, the colony is supplemented with individuals ($N \approx 200$) collected from the same location in August and September. Colony individuals are maintained on green bean (*Phaseolus vulgaris* L.), Spanish peanut (*Arachis hypogaea* L.), corn (*Zea mays* L.), and water under room temperature at a 16 L:8 D photoperiod (maintained with fluorescent lighting) (Niva and Takeda 2003) in BugDorm2 cages (BioQuip, Rancho Dominguez, CA). Green beans were grown without insecticides in the Rutgers University Entomology Greenhouses and fertilized weekly (1.0 tlb/gal; Miracle Grow, Marcusville, OH). Pest insects in the greenhouse were controlled using horticultural oil (AllSeasons; Bonide Products, Oriskany, NY) at 1.0 tlb/gal water. When green beans were not available, organically grown green beans were purchased from local markets. Water was replaced every other day, food was replaced twice weekly, and nymphal cages were replaced as needed. Developmental rate and fecundity studies using colony members began in March 2004 and continued until March 2006. Voucher specimens are deposited at the collections of Department of Entomology, Rutgers University (New Brunswick, NJ).

Effect of Temperature on Development of *H. halys*. The effect of temperature on developmental time was examined at eight temperatures, 15, 17, 20, 25, 27, 30, 33, and 35°C, at 16 L:8 D and 65–75% RH. A long-day photoperiod was used to maintain nondiapausing conditions (Niva and Takeda 2003) inside environmental chambers (Precision Scientific, Winchester, VA) at $\pm 1^\circ\text{C}$ of the set temperature. Temperature and relative humidity were recorded using a Hobo LCD Data Logger (Onset Computers, Pocasset, MA). Individual 235-ml cardboard containers (Sweetheart Jazz, Owing Mills, MD) with the lid replaced with organdy mesh for ventilation were used for rearing stink bugs throughout the study. A moist dental wick, piece of green bean, and a Spanish peanut were placed into each container. For each temperature replicate, five egg masses oviposited within 24 h were randomly chosen from the colony and placed individually into rearing containers.

Development was evaluated under constant conditions in two ways. For the first temperature experiment, 24 h after egg hatch, or when first instars began moving away from the egg mass, 10 first instars were randomly selected from each of the five egg masses and placed into the individual rearing containers. Dur-

ing the second experiment, cohorts were separated after the molt to the second instar, and 10 second instars from each egg mass were randomly chosen. This was done to evaluate any benefits such as reduced mortality that could be gained during first-instar aggregation. A total of 800 *H. halys* eggs were used with each nymph labeled according to the egg mass from which it had emerged (adapted from Rings and Brooks 1958). Individuals were checked every 24 h for development or mortality. Water was replaced every other day, and food was provided twice weekly. Development was documented by the presence of exuvia and nymphal characteristics as outlined in Hoebeck and Carter (2003). At the final molt to adult, all individuals were sexed.

Data Analysis and Developmental Rate Models. For the purpose of evaluating the regression models, data from both developmental experiments were combined. Data were subjected to the general linear model (GLM) for equality of variance, followed by Tukey's test for mean separation $P < 0.05$ (version 9.1; SAS Institute, Cary, NC). Developmental parameters, including degree-days, were estimated for egg development (time from oviposition to hatch) and for total development (oviposition to imaginal ecdysis). We compared three developmental models for their fit to the empirical data and definition of the biological parameters, T_o and T_m , where T_o is the minimum temperature threshold and T_m is the maximum temperature threshold. The linear regression model ($y = y_o + bx$; where y_o is the y-intercept and b is the slope of the line) using mean developmental rate (1/d) estimated minimum temperature threshold as $T_o = -y_o/b$ and estimated DD requirements ($DD = 1/b$) (Campbell et al. 1974). The linear regression model does not calculate T_m and may not provide the most accurate prediction of T_o because only temperatures within the linear portion of the development curve may be used. Thus, two nonlinear models, the Lactin-2 and Briere-1, were evaluated for their ability to predict T_o and T_m (Lactin et al. 1995, Briere et al. 1999). The Lactin-2 model is described as:

$$r(T) = e^{\rho T} - e[\rho T_m - (T_m - T)/\Delta] + \lambda$$

where $r(T)$ is the developmental rate (1/d) at temperature T ; T_m is the maximum lethal temperature; and ρ , Δ , and λ are fitted parameters. The Briere-1 model is described as:

$$r(T) = aT(T - T_o)(T_m - T)^{1/2}$$

where a is an empirical constant. Parameters were defined using the iterative function of PROC NLIN (version 9.1; SAS Institute) according to the Marquardt method. Models were compared by the residual sum of squares (RSS) and the calculated Akaike Information Criterion (AIC) for goodness-of-fit (Briere et al. 1999, Roy et al. 2002, Arbab et al. 2006, Zamani et al. 2007). The Briere and Lactin models differ in the number of parameters, which can lead to better fit to the empirical data. The AIC is defined as:

$$\text{AIC} = n \ln(\text{SSE}/n) + 2p$$

Table 1. Mean developmental time (days \pm SE) and survivorship of *H. halys* at constant temperature

Temperature	Egg ^a	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Total	Percent survival
15°C	22.00 \pm 0.00a	—	—	—	—	—	—	0.00
17°C	17.20 \pm 0.08b	17.01 \pm 0.16a	30.36 \pm 1.53a	22.40 \pm 4.02a	23.00 \pm 1.08a	28.00 \pm 0.00a	121.50 \pm 0.50a	2.00
20°C	11.50 \pm 0.05c	9.34 \pm 0.08b	16.25 \pm 0.23b	11.78 \pm 0.29b	13.66 \pm 0.31b	20.16 \pm 0.36b	81.16 \pm 0.80b	62.00
25°C	6.10 \pm 0.03d	4.82 \pm 0.10c	9.62 \pm 0.21c	7.08 \pm 0.22c	7.38 \pm 0.28c	10.44 \pm 0.28c	44.92 \pm 0.80c	61.00
27°C	4.87 \pm 0.10e	4.25 \pm 0.05d	7.64 \pm 0.19d	5.49 \pm 0.21d	5.90 \pm 0.18c	7.81 \pm 0.28d	35.81 \pm 0.52d	52.50
30°C	3.00 \pm 0.00g	3.70 \pm 0.05e	7.05 \pm 0.13d	6.11 \pm 0.28cd	6.11 \pm 0.23c	8.47 \pm 0.28cd	33.39 \pm 0.50e	51.00
33°C	4.00 \pm 0.00f	3.01 \pm 0.01f	7.47 \pm 0.23d	7.45 \pm 0.53c	7.20 \pm 0.40c	10.60 \pm 0.81c	37.80 \pm 0.86f	5.00
35°C	—	—	—	—	—	—	—	0.00

^a Means within a column followed by different letters are significantly different ($P < 0.05$).

where n = the number of observations, \ln = the natural log, SSE = the model sum of squares term, and p = the number of parameters. This evaluation is parameter independent, permitting the Briere and Lactin models to be compared. The model with the smallest RSS and AIC values is considered the best fit (Zamani et al. 2007).

Mean stage-specific mortality of each nymphal stage was calculated as $[d_x/l_x]$, where d_x = the number of individuals dying stage x and l_x = the number of individual alive at the beginning of stage x . Mean generational mortality was calculated at each temperature as $[d_x/l_o]$, where l_o = the starting number of individuals (Wittmeyer and Coudron 2001).

Life Table Analysis. Fecundity and fertility parameters for *H. halys* were evaluated at the optimal developmental temperature to construct a time-specific life table (Rings and Brooks 1958, Canerday 1965, Medeiros et al. 2000, Legaspi and Legaspi 2005). Incubators (Precision Scientific, Winchester, VA) were maintained at $25 \pm 1^\circ\text{C}$, 16 L:8 D, and 65–75% RH. Rearing conditions were similar to the developmental study, except 710-ml translucent plastic containers were used that were lined with a 9-cm filter paper (Fisher, Atlanta, GA) at the bottom and organdy mesh replaced the lid. Newly emerging adults, within 24 h since imaginal ecdysis, from the laboratory colony were sexed and placed under the controlled conditions. Twenty-two females were paired individually with a male of similar age, and six females without access to a male were observed every 24 h for oviposition and mortality (Rings and Brooks 1958). Egg masses were removed daily, labeled according to the female identifier, and placed in the incubator until hatching. The number of emerging first instars was counted and subsequently verified by counting the number of egg breakers present on the egg mass using a stereomicroscope (MZ8; Leica, Wetzlar, Germany). Males were rotated weekly between containers to reduce effects caused by male fitness. When a male died, it was replaced with another male of similar age. Data were recorded until the end of the life of the female.

Mean total fecundity, egg hatch, preoviposition period, and female longevity were recorded. Degree-day accumulations for the preoviposition period were calculated as $DD = (25^\circ\text{C} - \text{lower developmental threshold}) \times (\text{days spent in development})$ (Cullen and

Zalom 2000). Fecundity was defined as the number of eggs laid over the lifespan of the female, and fertility was the ability to produce at least one fertile egg mass. Age-dependant fecundity was calculated by dividing the age of the females into 7-d intervals and calculating the mean number of egg masses oviposited during that week (Medeiros et al. 2000). Preoviposition period and female life span were compared with the unmated females.

Life table parameters were estimated for net reproductive rate ($R_o = \sum l_x m_x$), intrinsic rate of increase ($r_m = (\ln[R_o])/T$), finite rate of increase ($\lambda = e^{r_m}$), mean generation time [$T = \sum (l_x m_x) / \sum (l_x m_x)$], and doubling time ($DT = \ln 2 / r_m$), where l_x is the proportion of individuals alive at age x , and m_x is the number of female offspring produced per female in the age interval x (Carey 1993). Eggs were not reared to adult, and a 1:1 sex ratio was assumed (Wittmeyer and Coudron 2001, Legaspi and Legaspi 2005). Reproductive parameters were adjusted using the number of first instars that hatched and not the number of eggs oviposited (Wittmeyer and Coudron 2001, Legaspi and Legaspi 2005).

Results

Effect of Temperature on Development of *H. halys*.

Egg development time was significantly impacted by temperature ($F = 4933.75$; $df = 6, 624$; $P < 0.0001$) and occurred from 15 to 33°C. Incubation was longest at 15°C (22 d) and shortest at 30°C (3 d; Table 1). Mean developmental time was 22.00, 17.20, 11.50, 6.10, 4.87, 3.00, and 4.00 d for 15, 17, 20, 25, 27, 30, and 33°C, respectively. High mortality (50%) occurred at 15°C. No egg development occurred at 35°C (Table 1).

Development of *H. halys* first-instar nymphs to imaginal ecdysis successfully occurred between 17 and 33°C (Table 1). Total developmental time (egg incubation to adult) was longest at 17°C and shortest at 30°C and was also significantly impacted by temperature ($F = 424.40$; $df = 5, 222$; $P < 0.001$). When the two experiments were combined, the mean developmental time from egg to imaginal ecdysis was 121.50, 81.16, 44.92, 35.81, 33.40, and 37.80 d for 17, 20, 25, 27, 30, and 33°C, respectively. Development time from egg to adult ecdysis was associated with increasing temperature up to 30°C. Of the temperatures where development to adult was completed, there was

Table 2. Stage-specific (d_x/l_x) (100) and generational mortality (d_x/l_o) (100) of *H. halys* developmental stages

Temperature	Egg	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Generational
15°C	50.00	100.00	0.00	0.00	0.00	0.00	100.00
17°C	2.00	35.71	80.95	50.00	16.67	40.00	97.00
20°C	1.00	9.09	16.67	5.00	4.00	15.28	39.00
25°C	0.00	6.00	13.83	18.52	4.55	3.17	39.00
27°C	0.00	0.00	16.25	14.93	10.53	17.65	47.50
30°C	0.00	6.00	12.77	9.76	16.22	17.74	49.00
33°C	5.00	15.79	45.00	50.00	31.82	66.67	95.00
35°C	100.00	0.00	0.00	0.00	0.00	0.00	100.00

a significant difference in total developmental time at each temperature ($P < 0.05$), with development being shortest at 30°C ($33.39 \pm 0.50^\circ\text{C}$). Development to adult did not occur at either temperature extreme (15 and 35°C). The duration of the first nymphal stage was typically the shortest for all temperatures; development during the fifth stadium was the longest. Development time was shorter and survival higher at 25°C (61%) than the upper threshold range (27–33°C) and should be considered the optimal temperature for *H. halys* development. Mean stage-specific mortality (d_x/l_x) of the nymphal instars was lowest during the fourth instar (Table 2). Generational mortality (d_x/l_o) was lowest at 20 and 25°C and extremely high at 17 (97%) and 33°C (95%). High mortality throughout development at 17°C resulted in only two surviving adults, both of which were males (Table 1). At 15°C, development past the first instar did not occur (Table 2).

Mortality of the first instars decreased when they were allowed to aggregate at all temperatures, although there was no significant difference between replicates ($P = 0.54$; Table 3). There was no significant difference in the number of individuals surviving to the adult stage ($P = 0.75$), but total development was shorter at each temperature when the first instars were allowed to aggregate (Table 3).

Developmental Rate Models. A linear regression model was first applied to the egg incubation and total

development by plotting development rate (1/d) against temperatures 15–30°C (Egg development: $y = 0.019x - 0.271$, $R^2 = 0.90$; total development: $y = 0.002x - 0.024$, $R^2 = 0.97$). The linear regression model was not a good fit for the data at all temperatures because development rate decreased after the peak at 30°C (Fig. 1). The inverse of the slope of the linear line is used to calculate the accumulated DD requirements for insect development. Using the data for 15–30°C, the accumulated DD for egg and total development were 53.30 and 537.63 DD, respectively.

The Briere-1 nonlinear model provided a good estimation of parameters for the egg incubation period as $T_o = 13.94$ and $T_m = 37.73$. The Lactin-2 model did not converge on the data for egg development and was not included in the analysis. Both the Lactin-2 and Briere-1 nonlinear models provided estimation of the parameters for total development of *H. halys*. Temperature thresholds for total development were calculated as $T_o = 14.17$ and 15.00 and $T_m = 35.76$ and 43.53 by the Briere and Lactin-2 models, respectively.

Life Table Analysis. At 25°C, *H. halys* females exhibited a 13.35 ± 0.72 -d preoviposition period. Each egg mass contained a median number of 28 eggs (mean = 26.08 ± 0.31), and a mean interval of 4.32 ± 0.41 d was needed between oviposition events (Table 4). Twenty females laid at least one viable egg mass during the study, which was a fertility rate of 90.90%.

Table 3. Effect of 1st instar aggregation on developmental time and survival to the next instar of *H. halys*

Temperature	Experiment ^a	Egg ^b		First instar		Second instar		Third instar		Fourth instar		Fifth instar		Total development	
		Mean	Survival	Mean	Survival	Mean	Survival	Mean	Survival	Mean	Survival	Mean	Survival	Mean	Survival
15°C	1	22.00	$n = 50$	—	$n = 0$	—	—	—	—	—	—	—	—	$n = 0$	
	2	—	$n = 0$	—	—	—	—	—	—	—	—	—	—	$n = 0$	
17°C	1	16.60b	$n = 50$	16.71	$n = 21$	27.50b	$n = 6$	22.40	$n = 5$	23.00	$n = 4$	28.00	$n = 2$	121.50	$n = 2$
	2	17.80a	$n = 50$	17.16	$n = 43$	33.80a	$n = 5$	—	$n = 0$	—	—	—	—	$n = 0$	
20°C	1	12.00a	$n = 50$	10.00a	$n = 41$	16.76a	$n = 38$	11.36	$n = 38$	13.88	$n = 35$	20.59	$n = 32$	83.68a	$n = 32$
	2	11.00b	$n = 50$	8.80b	$n = 50$	15.75b	$n = 38$	12.18	$n = 38$	13.44	$n = 38$	19370	$n = 30$	78.46b	$n = 30$
25°C	1	6.20a	$n = 50$	5.75a	$n = 44$	9.97	$n = 38$	7.54a	$n = 37$	8.11a	$n = 35$	11.12a	$n = 33$	47.97a	$n = 33$
	2	6.00b	$n = 50$	4.00b	$n = 50$	9.30	$n = 43$	6.48b	$n = 29$	6.46b	$n = 28$	9.64b	$n = 28$	41.32b	$n = 28$
27°C	1 ^c	4.00b	$n = 30$	4.00b	$n = 30$	9.30a	$n = 20$	6.77a	$n = 17$	6.43	$n = 14$	8.92a	$n = 13$	38.92a	$n = 13$
	2	5.40a	$n = 50$	4.40a	$n = 50$	6.94b	$n = 47$	4.95b	$n = 40$	5.70	$n = 37$	7.31b	$n = 29$	34.42b	$n = 29$
30°C	1	3.00	$n = 50$	3.36b	$n = 44$	7.03	$n = 37$	7.57a	$n = 30$	6.43	$n = 21$	8.84	$n = 19$	35.05a	$n = 19$
	2	3.00	$n = 50$	4.00a	$n = 50$	7.07	$n = 45$	5.11b	$n = 44$	5.95	$n = 41$	8.25	$n = 32$	32.41b	$n = 32$
33°C	1	4.00	$n = 50$	3.03	$n = 35$	6.95b	$n = 22$	7.33	$n = 15$	7.60	$n = 10$	11.67	$n = 3$	38.33	$n = 3$
	2	4.00	$n = 45$	3.00	$n = 22$	8.00a	$n = 7$	7.71	$n = 5$	6.40	$n = 2$	9.00	$n = 2$	37.00	$n = 2$
35°C	1	—	$n = 0$	—	—	—	—	—	—	—	—	—	—	$n = 0$	
	2	—	$n = 0$	—	—	—	—	—	—	—	—	—	—	$n = 0$	

^a Experiment 1, the first instars were not allowed to aggregate >24 h; experiment 2, the first instars were allowed to aggregate until molt to the second instar.

^b Means within a column for each temperature followed by a different letter are significantly different ($P < 0.05$); n signifies the no. of individuals surviving indicated life stage.

^c Initial no. for this replicate was 30.

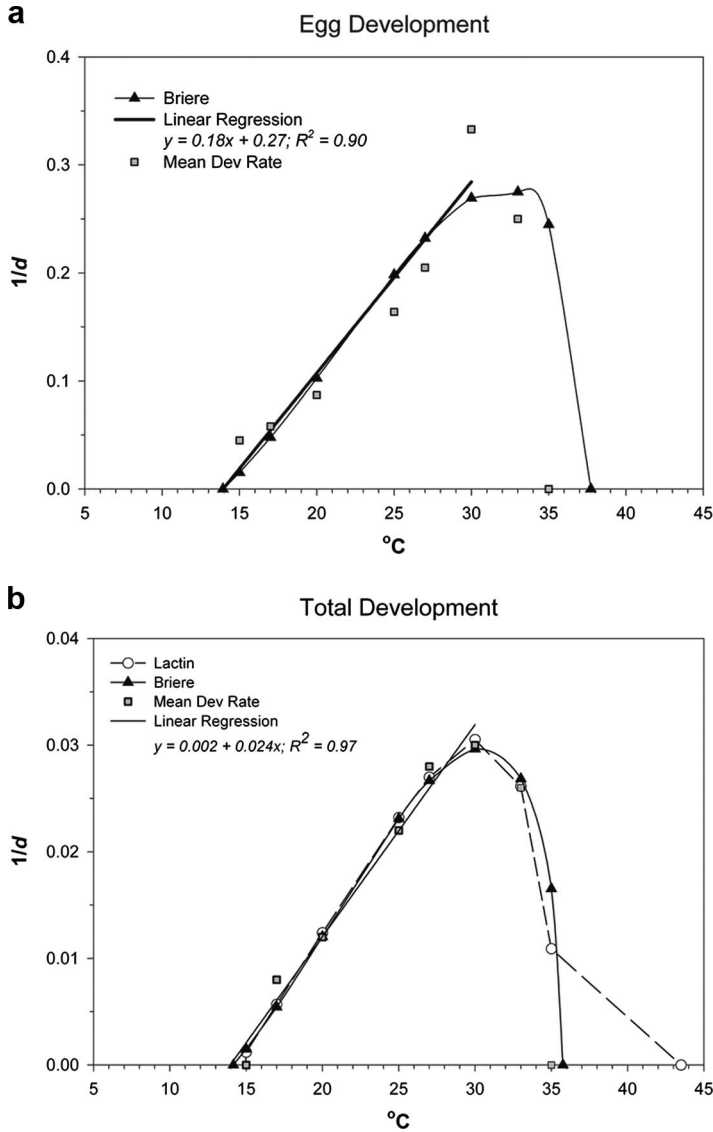


Fig. 1. (a) Fit of nonlinear developmental models for *H. halys* egg development. (b) Fit of nonlinear developmental models for total development (egg to imaginal ecdysis) of *H. halys*.

Table 4. Reproductive parameters for mated *H. halys* females at 25°C

Variable	Mean mated females (\pm SE)	Mean females ovipositing more than one egg mass (\pm SE)
Preoviposition period	13.35 (\pm 0.72)	12.44 (\pm 0.49)
Oviposition interval	4.32 (\pm 0.41)	4.83 (\pm 0.22)
Number of egg masses ^a	8.00 (\pm 0.19)	9.33 (\pm 1.04)
Number oviposited	26.08 (\pm 0.31)	
Number hatched ^b	21.30 (\pm 0.48)	
Total no. of eggs ^a	212.25 (\pm 31.04)	243.78 (\pm 27.48)

^a Per female.

^b Per egg mass.

Few mating events were directly observed because of *H. halys*' short copulatory duration and the limited time of each observation. The total mean number of eggs produced over a lifetime was 212.25 ± 31.04 or 8.00 ± 0.19 egg masses. Female fertility affected the number of egg masses oviposited. Females that produced more than one egg mass oviposited an average of 243.78 ± 27.48 eggs or 9.33 ± 1.04 egg masses over her lifespan. Mean age-specific fecundity peaked during the second and third week postecdysis with females producing a maximum of 1.36 ± 0.20 egg masses per week (Fig. 2). Fertility also increased with female age. The first egg mass produced was the least fertile, 61% increasing to 80% thereafter, and remained constant for the remainder of the lifespan.

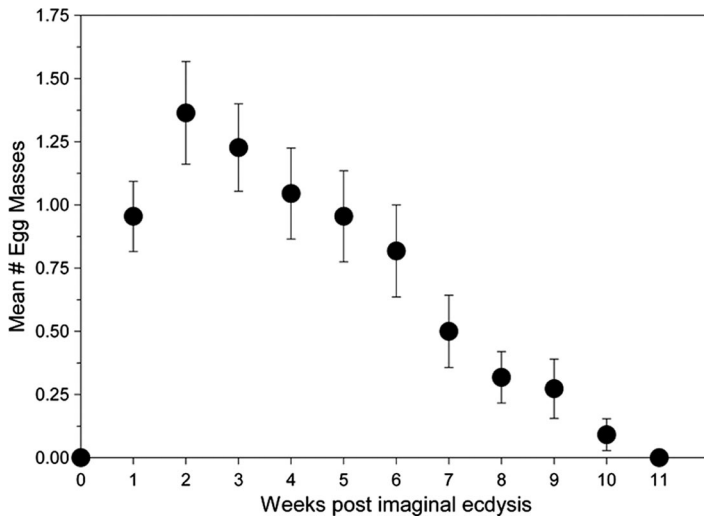


Fig. 2. Weekly average (\pm SE) age-specific oviposition rates of *H. halys* at 25°C.

All the virgin females observed produced unfertilized egg masses but not on a specific interval. The preoviposition periods for mated (13.35 ± 0.72 d) and virgin females (18.17 ± 2.93 d) were significantly different at $P < 0.05$. Based on the lower temperature threshold calculated by the Briere model, degree-day accumulations from imaginal ecdysis until the first oviposition event (preoviposition period) were calculated to be 147.65 DD.

Using a mean development calculated at 25°C of 47.97 d and assuming a 1:1 sex ratio, 159.90 female eggs were produced per female. The life table parameters at 25°C, $R_0 = 60.02$, $T = 56.59$, and $r_m = 0.07$ were adjusted to account for the number of first instars emerging.

Discussion

Developmental rate studies provide biological information that can be used in many ways, especially for understanding seasonality and population dynamics of a species. This is the first extensive laboratory study under controlled conditions for the U.S. population of *H. halys*. Preliminary observations of the northeastern U.S. population indicated total developmental time of a cohort as 42.25 d at room temperature, data that are consistent with our study of mean development time at 25°C to be 41.32 d when first-instar aggregation was permitted (Hoebeck and Carter 2003). Field development observed in southern China was estimated at 27 d, and it was estimated at 37–45 d in northern Japan (Hoffman 1931, Saito et al. 1964). Aggregation during the first instar did not have a significant effect on survivorship to adult. There is some suggestion that the pentatomid first instars increase humidity regulation during aggregation or feed on the egg chorion during the aggregation and obtain symbionts that may provide physiological benefits (Hirose et al. 2006). We showed that the aggregation of first instars significantly reduced nymphal and total

development time in *H. halys*, although the cause was not studied.

Most previous studies on pentatomid development have been restricted to linear models. Linear regression was applied to *H. halys* development for a comparison of temperature threshold estimations to other studies and to calculate degree-day requirements. Application of the Briere-1 and Lactin-2 models, however, provided a better fit to the temperature dependent development of *H. halys* and allowed more accurate prediction of the temperature threshold. However, the calculation of maximum threshold temperature by the Lactin-2 model of $T_m = 43.53^\circ\text{C}$ is unrealistic because development of *H. halys* did not occur at 35°C, suggesting that the Briere-1 model is the best fit for the empirical data for total development of *H. halys*. That the Briere-1 model is the most appropriate model to use for *H. halys* development is supported by AIC analysis ($\text{AIC} = -10,019.68$). Furthermore, the Lactin-2 model for egg development did not converge and was an unreliable model for development of *H. halys*.

The minimum temperature threshold is important not only for determining degree-day accumulations and adult emergence but also for overwintering survival and range expansion. Temperature threshold can limit the potential geographic range of *H. halys* in the United States. Its current distribution in the northeastern United States indicates that *H. halys* is able to survive colder winter temperatures than the southern green stink bug, *Nezara viridula*, which is abundant in warm habitats. Similarly, in its native Japan, *H. halys* has a higher winter survival rate than *N. viridula*, presumably because of *H. halys*' lower temperature threshold and choice of overwintering habitat (Kiritani 2006). The T_o for *H. halys* egg development in Japanese provinces ranges from 9.9 to 15.1°C, with 12.2°C being the most reported. The reported T_o for total development in Japan ranges from 11.1 to 12.9°C (Kiritani 1997). In our study, the temperature thresh-

old estimated was higher than reported in Japan. This suggests a possible origin from a warmer climate; the range of *H. halys* in Asia includes subtropical regions of China and India. Based on its distribution in Asia and similarities with the temperature thresholds of native stink bugs, *H. halys* should be able to increase its current distribution into areas of economically important agroecosystems in the southern United States.

Fertility and fecundity parameters for *H. halys* were estimated at 25°C (optimum developmental temperature) for use in calculating a simple life table. A high proportion (90.90%) of *H. halys* females were fertile, and of those females ovipositing more than one egg mass, an average of 243.78 ± 27.48 eggs per female were oviposited. Each egg mass contained a median number of 28 eggs, consistent with previous reports and having ovarioles in multiples of seven (Hoffman 1931, Kawada and Kimura 1983, Hoebeck and Carter 2003, Bernon 2004). For all females, egg masses averaged a hatch rate of 81.60%. This is lower than observed hatch rates of field populations (A.L.N., unpublished data). Artificial mating conditions could account for the lower hatch rate in the laboratory, and egg masses of overwintering females may result in a higher hatch rate (Rings and Brooks 1958). The pre-oviposition period for *H. halys* in this study averaged 13.35 ± 0.72 d, with an average 212.25 ± 31.04 eggs/female. Kawada and Kimura (1983) reported a pre-oviposition period of 14–15 d for Japanese *H. halys* and an average of 486.6 eggs/female. Rearing conditions, developmental length, geographic variation, and other variables could account for this substantial difference between the numbers of eggs produced by a female (Rings and Brooks 1958, Kawada and Kimura 1983). Without primary egg parasitoids, *H. halys* has the potential to increase in population densities faster than native species. In the absence of species-specific natural enemies and with expanded host diversity in the United States, including host plants native to Asia plus an abundance of European and North American varieties in the same families, it is likely that *H. halys* could become an economic concern in many cropping systems if it continues to increase in density and distribution. Life table analysis on *H. halys* will be important in future modeling efforts and development of biological control programs.

Although *H. halys* is not a highly damaging pest in Asia, we predict it will become an important addition to the phytophagous stink bug complex in the United States. The reduction in the amount of broad-spectrum insecticides previously used to control tree fruit pests and the increased planting of *Bacillus thuringiensis* (Bt)-modified cotton has increased the incidence of pest stink bugs in these crops and may lead to increased economic losses (Willrich et al. 2003, Lesky et al. 2005, Snodgrass et al. 2005). Stink bug pests are often managed as a complex in agroecosystems because of similarities in host feeding and development. The primary factor for incorporating *H. halys* into any IPM program for stink bugs will be the number of generations per year and the peak of the filial adult population, which is the most damaging stage.

Nonlinear regression estimates that 537.63 DD are needed to complete development, with an additional 147.65 DD until oviposition starts. In central New Jersey and Pennsylvania, *H. halys* is univoltine, with a peak in the population in late July or early August. It is likely that if *H. halys*' distribution spreads south, the number of generations per year will increase. *H. halys* is known to be multivoltine in semitropical climates, such as the Canton province of southern China, where up to six generations per year have been reported (Hoffman 1931). However, other environmental factors such as photoperiod length also determine the number generations per year. Maintenance of a long photoperiod and warm temperatures during nymphal development are necessary to prevent physiological changes signaling diapause development in *H. halys* (Niva and Takeda 2002).

The developmental rate, temperature threshold, degree-day requirements, and fecundity of *H. halys* are similar to native pest pentatomid species and will not limit its distribution as expands its range in the upcoming years. Based on the similarities in temperature thresholds and host plant ranges of native species, we predict that, over time, *H. halys*' distribution in the United States will resemble that of other phytophagous species with similar host ranges, such as *N. viridula*, *Acrosternum hilare*, and *Euschistus* sp. As a result, IPM programs should be modified to incorporate *H. halys* in the regions where it becomes established.

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References Cited

- Arbab, A., D. Kontodimas, and A. Sahragard. 2006. Estimating development of *Aphis pomi* (DeGeer) (Homoptera: Aphididae) using linear and nonlinear model. *Environ. Entomol.* 35: 1208–1215.
- Bernon, G. 2004. Biology of *Halyomorpha halys*, The brown marmorated stink bug (BMSB). Final report. (<http://cphst.aphis.usda.gov/docs/BernonfinalreportT3P01.pdf>).
- Briere, J., P. Pracros, A. LeRoux, and J. Pierre. 1999. A novel rate model of temperature-dependent development for arthropods. *Environ. Entomol.* 28: 22–29.
- Campbell, A., B. Frazer, N. Gilbert, A. Guitierrez, and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. *J. Appl. Ecol.* 11: 431–438.
- Canerday, T. D. 1965. On the biology of the harlequin bug, *Murgantia histrionica* (Hemiptera: Pentatomidae). *Ann. Entomol. Soc. Am.* 58: 931–932.
- Carey, J. R. 1993. Applied demography for biologists with the special emphasis on insects. Oxford University Press, New York.
- Cullen, E. M., and F. G. Zalom. 2000. Phenology-based field monitoring for consperse stink bug (Hemiptera: Pentatomidae) in processing tomatoes. *Environ. Entomol.* 29: 560–567.

- Hirose, E., A. Panizzi, J. de Souza, A. Cattelan, and J. Aldrich. 2006. Bacteria in the gut of southern green stink bug (Heteroptera: Pentatomidae). *Ann. Entomol. Soc. Am.* 99: 91–95.
- Hoebeck, E. R., and M. E. Carter. 2003. *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae): a polyphagous plant pest from Asia newly detected in North America. *Proc. Entomol. Soc. Wash.* 105: 225–237.
- Hoffman, W. E. 1931. A pentatomid pest of growing beans in South China. *Pek. Nat. Hist. Bull.* 5: 25–26.
- Kawada, H., and C. Kitamura. 1983. The reproductive behavior of the brown marmorated stink bug, *Halyomorpha mista* Uhler (Heteroptera: Pentatomidae): observation of mating behavior and multiple copulation. *Appl. Entomol. Zool.* 18: 234–242.
- Kiritani, K. 1997. The low development threshold temperature and the thermal constant in insects, mites, and nematodes in Japan. *Misc. Publ. Natl. Inst. Agro-Environ. Sci.* 21: 1–72.
- Kiritani, K. 2006. Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. *Popul. Ecol.* 48: 5–12.
- Kontodimas, D. C., P. A. Eliopoulos, G. J. Stathas, and L. P. Economou. 2004. Comparative temperature-dependent development of *Nephus includens* (Kirsch) and *Nephus bisignatus* (Boheman) (Coleoptera: Coccinellidae) preying on *Planococcus citri* (Risso) (Homoptera: Pseudococcidae): evaluation of a linear and various non-linear models using specific criteria. *Environ. Entomol.* 33: 1–11.
- Lactin, D., N. J. Holliday, D. L. Johnson, and R. Craigen. 1995. Improved rate model of temperature-dependent development by arthropods. *Environ. Entomol.* 24: 68–75.
- Legaspi, J. C., and B. C. Legaspi, Jr. 2005. Life table analysis for *Podisus maculiventris* immatures and female adults under four constant temperatures. *Environ. Entomol.* 34: 990–998.
- Leskey, T. C., and H. W. Hogmire. 2005. Monitoring stink bugs (Hemiptera: Pentatomidae) in mid-Atlantic apple and peach orchards. *J. Econ. Entomol.* 98: 143–153.
- Logan, J. A., D. J. Wollkind, S. C. Hoyt, and L. K. Tangioshio. 1976. An analytic model for description of temperatures dependent rate phenomena in arthropods. *Environ. Entomol.* 5: 1133–1140.
- McPherson, J. E., and R. M. McPherson. 2000. Stink bugs of economic importance in America north of Mexico. CRC, Boca Raton, FL.
- Medeiros, R. S., R. S. Ramalho, W. P. Lemos, and J. C. Zanuncio. 2000. Age-dependent fecundity and life-fertility tables for *Podisus nigrispinus* (Dallas) (Het., Pentatomidae). *J. Appl. Entomol.* 124: 319–324.
- Niva, C. C., and M. Takeda. 2003. Effects of photoperiod, temperature and melatonin on nymphal development, polyphenism and reproduction in *Halyomorpha halys* (Heteroptera: Pentatomidae). *Zool. Sci.* 20: 963–970.
- Rings, R. W., and R. F. Brooks. 1958. Bionomics of the one-spot stink bug in Ohio. *Ohio Agric. Exp. Stn. Res. Circ.* 50: 1–16.
- Roy, M., J. Brodeur, and C. Cloutier. 2002. Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcDanieli* (Acarina: Tetranychidae). *Environ. Entomol.* 31: 177–187.
- Saito, Y., S. Saito, Y. Ohmorio, and K. Yamada. 1964. Studies on bionomics of the bean bugs occurring in mountain regions, with particular reference to that of *Halyomorpha picus* and the insecticidal test in laboratory and field. *Jap. J. Sanitary Zool.* 15: 7–16.
- Sánchez-Ramos, I., and P. Castañera. 2001. Development and survival of *Tyrophagus putrescentiae* (Acari: Acaridae) at constant temperatures. *Environ. Entomol.* 30: 1082–1089.
- Snodgrass, G. L., J. J. Adamczyk, and J. Gore. 2005. Toxicity of insecticides in a glass-vial bioassay to adult brown, green and southern green stink bugs (Heteroptera: Pentatomidae). *J. Econ. Entomol.* 98: 177–181.
- Willrich, M., B. Leonard, and D. Cook. 2003. Laboratory and field evaluation of insecticide toxicity to stink bugs (Heteroptera: Pentatomidae). *J. Cotton Sci.* 7: 156–163.
- Wittmeyer, J. L., and T. A. Coudron. 2001. Life table parameters, reproductive rate, intrinsic rate of increase and estimated cost of rearing *Podisus maculiventris* (Heteroptera: Pentatomidae) on an artificial diet. *J. Econ. Entomol.* 94: 1344–1352.
- Zamani, A. A., A. Talebi, Y. Fathipour, and V. Baniamiri. 2007. Effect of temperature on life history of *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Braconidae), two parasitoids of *Aphis gossypii* and *Myzus persica* (Homoptera: Aphididae). *Environ. Entomol.* 36: 263–271.

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