Development and Life Table of *Acalymma vittatum* (Coleoptera: Chrysomelidae), a Vector of *Erwinia tracheiphila* in Cucurbits

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ABSTRACT *Acalymma vittatum* (F.) is a cucurbit herbivore specialist and the vector of *Erwinia tracheiphila* (E. F. Smith) Holland, the causal agent of bacterial wilt in cucurbits. We determined the temperature-dependent development, survivorship, longevity, sex ratio, and fecundity of this vector. Egg-to adult development was modeled as $y = e^{(0.225 \times T)} - e^{[0.225 \times 36.017 - (36.017 - T)/4.425]}$, which suggests a maximum development rate of 4.29%/d at 32°C. Linear extrapolations suggest a lower threshold of 13°C and 432 DD needed for *A. vittatum* development. Survivorship of immature stages, which ranged from 60% at 27°C to 4% at 33°C, was strongly influenced by temperature, and no beetles survived to the adult stage at 36°C. Sex ratios did not deviate from 1:1. Adults were long-lived, with continuous egg production, which ranged from 0 to 4 eggs/female/d, after an 8-d preovipositional period at 27°C. Life table statistics were generated using these data. Together, these phenology models and life table information can be used to further develop integrated pest management programs for both *A. vittatum* and *E. tracheiphila* in cucurbits.

KEY WORDS *Acalymma vittatum*, *Erwinia tracheiphila*, temperature-dependent development, survivorship, fecundity

The striped cucumber beetle, *Acalymma vittatum* (F.), a specialist herbivore of cucurbitaceae, is a serious insect pest of fresh market cucurbits. Adult feeding during early plant growth can cause significant stand reduction (Brewer et al. 1987), and rind-feeding by adults or immatures later in the season renders crops unmarketable and may serve as routes of entry for fungal pathogens. Larval feeding also impacts root development (Ellers-Kirk et al. 2000) and has been correlated with fusarium wilt (Latin and Reed 1985) and viral transmission (Coudriet et al. 1979). This species, however, is considered most significant because of its association with the bacterial pathogen *Erwinia tracheiphila* (E. F. Smith) Holland, the causal agent of bacterial wilt (Rand and Enlows 1916, Garcia-Salazar et al. 2000a, b). *E. tracheiphila* is dependent on *A. vittatum* for transmission and overwintering (Fleischer et al. 1999). Feeding by "male pioneers" results in volatile cues, apparently produced by the males and by plants induced by male feeding, which attracts conspecifics (Smyth and Hoffmann 2002, 2003). Aggregation behavior or concentrated feeding is a key component for bacterial wilt epidemiology (Brust 1997b, Fleischer et al. 1999). Variation in susceptibility exists among cultivars because of beetle behavior (Brust and Rane 1995) and host plant factors (Brust 1997a), but levels of host plant resistance have not been high enough to manage this disease.

Disease management, therefore, relies on vector management. Relationships exist between beetle density, behavior, and bacterial wilt incidence. Yao et al. (1996) developed regressions of the area under the disease progress curve against beetle density soon after immigration. Disease development is also strongly influenced by inoculum dose (Lukezic et al. 1996), which may reflect interactions between frass deposition and wounding (Brust 1997a). Cultural methods can manage the problem in machine-harvested, short-season processing pickles that have high plant populations, but the vector/disease complex presents very difficult risks for long-season cucurbit crops that are grown at much lower plant populations.

Studies directed at management have considered rhizobacteria (Zehnder et al. 1997), plastic mulch (Necibi et al. 1992, Ellers-Kirk et al. 2000), microbial metabolites (Reed et al. 1986, Johnson et al. 1993), trap crops (Pair 1997), host plant resistance (Brust and Rane 1995), entomophagous nematodes (Reed et al. 1986, Ellers-Kirk et al. 2000), and kairomonal baits (Fleischer and Kirk 1994, Brust and Foster 1995). Current disease management relies mainly on vector control directed at adults, to stop pathogen transmission, through the use of systemic and foliar insecticides (Yao et al. 1996, Fleischer et al. 1998). Larval control is also feasible. Necibi et al. (1992) showed that growing muskmelons under a black plastic mulch/drip irrigation system reduced diabroticite pressure, and Ellers-Kirk et al. (2000) reduced larval

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survival 57% with the properly timed introduction of entomopathogenic nematodes through the drip lines.

Integration of these management options to reduce pest pressure and minimize disease at a farm or landscape scale needs to consider the ecological relationships of *A. vittatum.* Houser and Balduf (1925) wrote of the biology of *Diabrotica (=A.) vittatum*, and Bach (1980a, b, 1981) discussed how host plant density, diversity, and growth form affect the population dynamics of *A. vittatum* as a specialist herbivore. Although phenology models exist for related species (Elliott et al. 1990, Davis et al. 1996, Avila et al. 2002), we were unable to find phenology models or fecundity and survival rates in the literature. Reed et al. (1984), Cuthbert et al. (1968), and Howe and Zdarkova (1971) discussed laboratory rearing, and Reed et al. (1984) compared different cucurbit cultivars as hosts, but these authors did not provide the information necessary for the development of life table statistics or estimates of rates of development, survivorship, fecundity, preoviposition period, and sex ratio. Information to develop phenology models is also incomplete. Radin and Drummond (1994) attempted to develop a degree-day model from field colonization data. They tried to estimate a lower developmental threshold using the mean accumulated degree-days in Maine (starting with 1 April) at the time of initial beetle colonization (which was assumed to be equal to initial emergence of overwintered adults) over a range of randomly selected lower developmental thresholds, but they were unable to meet the assumptions of a degree-day model with this method. The authors did find the thresholds for mating and oviposition activity to be 13 and 10°C, respectively. *A. vittatum* seek hosts at temperatures above 12°C. We have been unable to find upper developmental thresholds, or developmental rate models, in the literature.

Here we determine the temperature-dependent development, survivorship, sex ratio, and fecundity of *A. vittatum* under laboratory conditions, as well as determine lower and upper developmental temperatures to generate a functional life table and degree-day model.

Materials and Methods

Temperature-dependent Development. Time required for egg to adult development was determined as a function of temperature. To estimate egg-to-adult development, two cohorts of 100 *A. vittatum* eggs (<24 h old) collected from an established laboratory colony reared on the same host as described below (see Ellers-Kirk 1996 for colony-rearing methods) were placed on separate rayon/cellulose gauze pads moistened with water. Two 15.5-liter Rubbermaid storage boxes (=flats) were filled with 5 liters of Metro Mix 250 (W. R. Grace, Marysville, OH) potting soil and seeded with 30 *Cucurbita maxima* variety Blue Hubbard squash. Once the squash reached the cotyledon stage, one gauze pad was placed, egg side down, onto the surface of the potting soil in each flat. The gauze was moistened, and netting was placed over each flat. The two flats were held at 18, 24, 27, 30, 33, or 36°C. Data from both flats for the same temperature were collected simultaneously, but not all temperatures were run concurrently. All other variables, including a 16:8 (light:dark) photophase and 60% RH, were held constant. Food, in the form of *C. maxima* seedlings, and water were added as needed. Daily observations of adult emergence were made. On emergence, adults were collected and sexed. Sampling continued until 5 consecutive days passed with no emergence.

Developmental time in days was plotted as a function of temperature to determine how an increase in temperature affected immature development. The developmental rate (DR) was calculated as $DR = (1/d) \times 100$, where d is the days for median development. Median developmental rate was regressed as a linear function of temperature <33°C (because development was not completed at 36°C) using SAS (SAS Institute 1989) to estimate the lower threshold temperature for *A. vittatum* development. A nonlinear model of median developmental rate, using modification 1 of the Logan model as described in Lactin et al. (1995), was used to estimate rates at high and low temperatures. The predicted percent development per day (rate) was calculated as $y = e^{(a \times T)} - e^{[a \times Tmax - (Tmax - T)/d]}$ where a, Tmax, and d are parameters solved with nonlinear regression. Rate (y) is the predicted value and T is observed temperature. Parameters for the nonlinear curve were determined with nonlinear regression in SAS.

Stage-specific Development, Survivorship, Sex Ratio, Fecundity, and Life Table Statistics. Stage-specific development was determined using 24 *A. vittatum* eggs (<24 h old) from a laboratory colony that were reared individually in 50-ml polystyrene beakers. These beakers were placed on a tray in a growth chamber at a constant temperature of 27°C, 16:8 (light: dark) photophase, and 60% RH. Each beaker was lined with moistened germination paper to provide moisture and covered with parafilm. Food, in the form of *C. maxima* seedlings and roots, was provided as needed. Cage conditions changed as the individual's life stage warranted: Egg and larval stages were held with a host plant seedling on moist germination paper, and the pupal stage was kept in the same environment with the seedling removed until emergence as an adult. Individuals were monitored daily and a change in life stage or death was recorded.

Data on adult female survivorship and fecundity of *A. vittatum* were also collected at 27°C, 16:8 (light: dark) photophase, and 60% RH. Newly emerged adults reared as described for the egg-to-adult survivorship study above were separated into 25 mating groups (two males to one female) and held in 1-liter cylindrical containers covered by a clear, cylindrical Plexiglas tube with a piece of screening on top. A rayon/cellulose gauze pad moistened with water was placed on the bottom of the container in a 15-ml petri plate lid to provide moisture and a oviposition substrate. Beetles were allowed to feed on a *C. maxima* fruit disk, which was placed on the gauze and changed according to need. New males were added when

needed to keep two viable males with the female at all times. All mating groups were examined every other day to determine female survivorship rate and egg deposition. This was done by removing all three beetles from the container with an aspirator, removing the gauze pad and fruit disk so that the eggs could be counted, checking the petri plate lid and sides of the container for eggs and removing these eggs when present, adding a new moistened gauze pad and fruit disk, and reintroducing the beetles. This was continued until death of the female.

Together, these data were used to estimate stage-specific development, fecundity, sex ratio, and adult female survivorship at a single temperature. The percent of the total developmental time spent in each life stage was calculated by dividing the median number of days in a particular life stage by the median number of days needed to complete the egg-to-adult portion of the life cycle, multiplied by 100. The actual median days for egg-adult development is reported. Degree-days for each surviving individual at each life stage at 27°C were calculated by subtracting the estimate of the lower developmental threshold temperature from 27°C and multiplying by the median number of days necessary for completion of that particular life stage.

Egg-to-adult survivorship and sex ratio at different temperatures were determined using the data collected in the temperature-dependent development section described above. Survivorship was estimated as the total adults emerging for each sex, divided by the number of eggs initially added, and multiplied by 100. Sex ratio was tested for conformation to a 1:1 ratio with χ^2. The mean number of eggs per day and the number of females alive in the cohort on that date were plotted against the days from adult eclosion at 27°C. Mean cumulative fecundity expresses the proportion of eggs that can be oviposited by one adult female over her life span. Survivorship and fecundity rate were expressed as a life table, and life table statistics (gross and net reproductive rate, birth and death rate, and intrinsic rate of increase) were calculated as in Carey (1993). Fecundity, based on female birth rate, was calculated by multiplying the total number of eggs by 0.5, assuming a 1:1 sex ratio.

Results

Temperature-dependent Development. Temperature affected the growth rate of *A. vittatum* (Fig. 1A). At the low temperature (18°C), *A. vittatum* required 72 d to develop from egg to adult, whereas at the highest temperature, where there was survival (33°C), development took 24 d. There was no emergence of adults at 36°C. Developmental rate (the inverse of development time) did not exceed 4.2% per day. Linear regression was used to fit a line to the median development rate with the data from 36°C not used in the regression (Fig. 1B). Development rate (y) could be expressed as a linear function of temperature (T) as $y = 0.02T - 0.26$, which extrapolates to a lower development threshold temperature for *A. vittatum* development of 13°C. This provides a basis for the development of degree-day models. A nonlinear fit, which includes data from the 18–36°C temperature range (Fig. 1C), was calculated as $y = e^{(0.225 \times T)} - e^{[0.225 \times 36.017 - (36.017 - T)/4.425]}$. The model suggests a maximum development rate of 4.29%/d at 32°C, which is close to the observed maximum rate of 4.2%/d at 33°C.

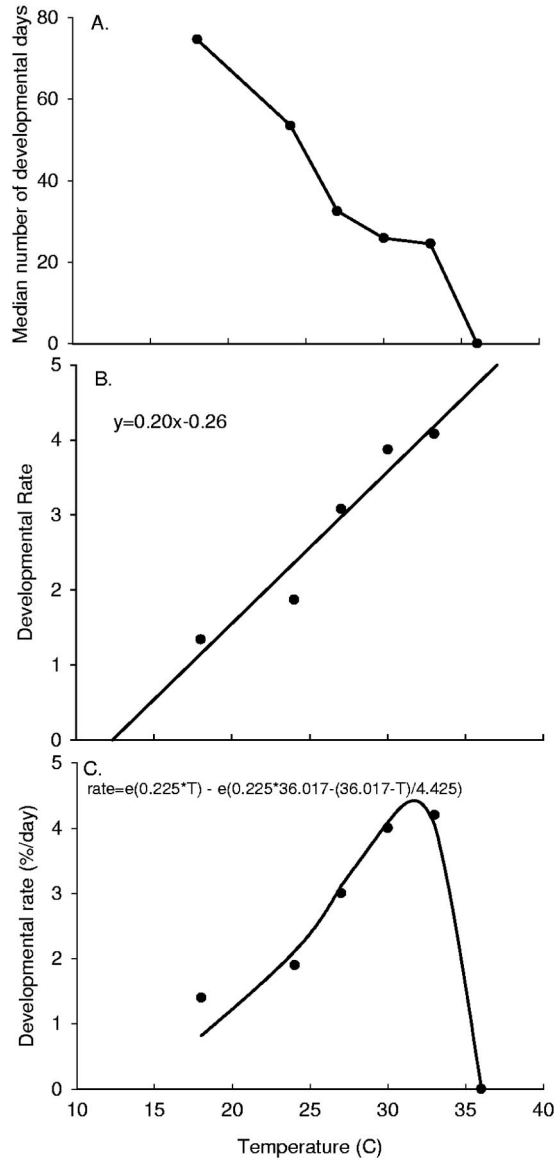

Fig. 1. Egg-to-adult temperature dependent development of *A. vittatum* reared on *C. maxima* variety Blue Hubbard squash. (A) Median days to development. (B) Linear model of development rate extrapolated to a lower threshold. (C) Logan nonlinear model of development rate.

The percent of time spent in specific life stages was determined at a single temperature (27°C) that had the highest survival rate and was close to the temperature for maximum developmental rate. Of the three subterranean immature life stages, the majority of time (71%) is spent in the larval stage (Table 1). *A.*

Table 1. Stage-specific development rate of *A. vittatum* at 27°C

Life stage	Median days (SE)	Median degree-days (SE)[a]	Percent of total median development time	*N*
Egg to meonate	5 (0.14)	70 (1.82)	16.13	24
Neonate to pupae	22 (0.79)	308 (11.08)	70.97	12
Pupae to adult	6.5 (0.48)	91 (6.70)	20.97	4
Egg to adult	31 (0.41)	434 (5.72)	—	4

[a] Degree-days developed using a base temperature of 13°C derived from Fig. 1B.

vittatum was in the soil for a total of 31 median days at 27°C. Degree-days for time spent in these life stages in the laboratory were calculated at 27°C to make these data more applicable to integrated pest management (IPM) programs (Table 1).

Stage-specific Development, Survivorship, Sex Ratio, and Fecundity. Temperature had a strong effect on the survivorship of the soil-dwelling life stages of *A. vittatum* (Table 2). Survival ranged from 60% at 27°C to 4% at 33°C. No beetles survived to the adult stage at 36°C. Temperature, however, did not influence sex ratio. Sex ratio at all five temperatures was not significantly different from a 1:1 ratio (Table 2).

Once reaching the adult life stage, *A. vittatum* were long-lived. Eighty percent of the adult females monitored at 27°C survived for 59 d before a steady decline in adult survivorship was seen (Fig. 2A). Beetles seemed to die in clusters spread out over time, with the final female dying 126 d after adult eclosion.

Combining the survivorship of a particular day with the day just proceeding it, dividing that number by two, and multiplying by 100 yielded a daily female survivorship rate (Fig. 2A). Egg survivorship was high (100%). After egg eclosion, a laboratory-reared cohort of *A. vittatum* was subject to the highest rate of mortality as immatures before adult eclosion. The total survivorship curve (egg to adult death) took ≈160 d to complete at 27°C.

Oviposition occurred throughout the long adult life (Fig. 2B) and ranged from 0 to 4 eggs/female/day. The only time that egg production was 0 was during the 8-d preoviposition period and just after a large proportion of cohort mortality (Fig. 2A and B). Spikes in the rate of oviposition usually occurred just before female mortality. This was especially obvious toward the end of the cohort's life cycle (Fig. 2A and B). The mean cumulative fecundity of a single female with an adult life span of ≈80 d approached 125 eggs.

Table 2. Temperature-dependent egg to adult survivorship and sex ratio of *A. vittatum*

Temperature (°C)	Survivorship				χ^2
	Males	Females	Total	Percent	
18	43	44	87	44	0.011ns
24	49	64	113	57	2.009ns
27	62	58	120	60	0.133ns
30	35	41	76	38	0.474ns
33	6	2	8	4	1.000ns
36	0	0	0	0	na
Total	195	209	404	34	0.491ns

ns, not significantly different from a 1:1 sex ratio; na, not available.

Life Table Statistics. Life table statistics of *A. vittatum* at 27°C showed that the mean age of reproduction was 67.9 d, and the net reproductive rate was 12.2 females/newborn female. The intrinsic rate of birth and the intrinsic rate of death showed that there will be 0.061 births and 0.018 deaths, respectively, for every individual in the population. The intrinsic rate of increase for this population of *A. vittatum* at 27°C was 0.043.

Discussion

Inferences about population dynamics of insects are often derived from laboratory measurements of temperature and stage-specific development, survivorship, sex ratio, and oviposition (Carey 1993). It was our goal to determine the phenology, survivorship, sex

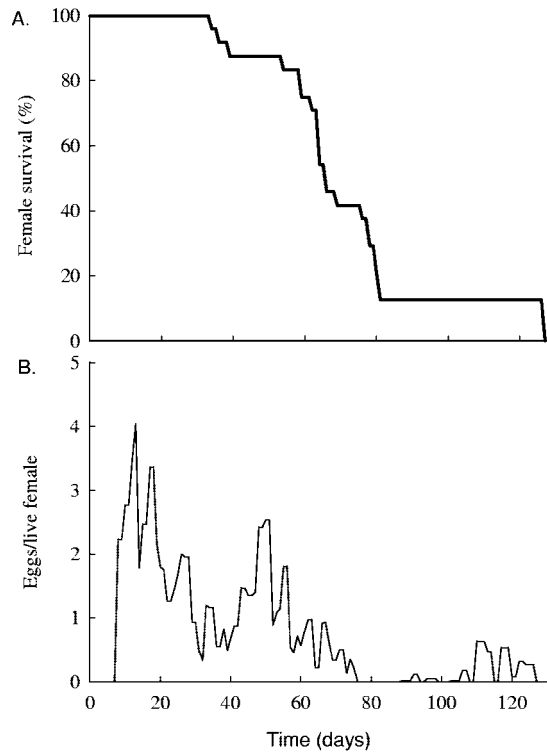

Fig. 2. *Acalymma vittatum* adult female survivorship (top) and fecundity (bottom) at 27°C when reared on *C. maxima* variety Blue Hubbard squash.

ratio, and fecundity of *A. vittatum* under laboratory conditions to develop a better understanding of the insect life cycle and phenology for field use.

Temperature strongly influenced both developmental rate and survivorship of *A. vittatum.* As the upper developmental threshold is neared, the developmental rate increases but survivorship declines rapidly (Fig. 1A; Table 2). This may help provide a mechanism to explain how black plastic mulch used in cucurbit production contributes to *A. vittatum* larval mortality (Necibi et al. 1992, Ellers-Kirk et al. 2000). Black plastic mulch will increase soil temperatures, with the rate and depth of increase influenced by soil and moisture conditions, and these soil conditions may, in turn, influence larval behavior. Soil temperature collected over an hour at 15 sites in Centre Co., PA, showed that the mean ambient temperature (23.1°C) was slightly cooler than the mean temperature under plastic mulch (26°C) and 5 cm under the soil (26.4°C) (C.E.-K., S.J.F., and D. deMackiewicz, unpublished data). Further studies could improve *A. vittatum* management with mulches or other environmental modifications by focusing on their influence on immature development and survivorship.

Acalymma vittatum mortality was high during the subterranean stages (Table 2). This observation shows that this could be a viable target stage for beetle control. *A. vittatum* immigrate into cucumber crops in the early summer as adults, but survivorship to the F1 and F2 generations may be controlled by increasing mortality during the larval and pupal stages. In an IPM program, it may be possible to integrate sampling programs (Burkness and Hutchison 1998, Brust and Foster 1999), trap crops or volatile cues (Pair 1997, Smyth and Hoffmann 2003), insecticides for the control of the immigrating adults, and biological and cultural controls such as entomopathogenic nematodes and plastic mulch (Ellers-Kirk et al. 2000) for the control of the larval and pupal stages of the F1 and F2 generations. The phenology models presented here can be validated in the field and applied to these feral populations of *A. vittatum* to improve the accuracy of timing of control measures (Table 1) and possibly to help differentiate among immigrants and F1 adults.

Female *A. vittatum* are long-lived (Fig. 2A and B) and lay ≈125 eggs/individual over their lifetime when reared at 27°C. When applied to the field, this information will help to understand how a feral *A. vittatum* population grows and changes over time and, with further research, will help to better time control measures. Because the rate of development of bacterial wilt in cucurbits is dependent on the dose of *E. tracheiphila* (Lukezic et al. 1996) and because the dose is directly related to the number of beetles available to feed on these plants (Yao et al. 1996, Fleischer et al. 1999), having an estimate of the F1 and F2 generations of *A. vittatum* will be an important management tool. The data presented here will help to build models for both the phenology and density of *A. vittatum* population dynamics.

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