Effects of Temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) Adult Survival, Reproduction, and Egg Hatch

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ABSTRACT *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae) is a recently introduced non-native invasive species in North America that has the potential to destroy several tree species in urban and forest habitats. Adult survival, reproduction, and egg hatch of *A. glabripennis* from two populations (Ravenswood, Chicago, IL, and Bayside, Queens, NY) were evaluated at seven constant temperatures (5, 10, 15, 20, 25, 30, and 35°C), and adult survival was evaluated at −1°C. Nonlinear regressions were used to estimate the temperature optimum and thresholds for each life history parameter. The estimated optimum temperature for median longevity was 18°C, and upper and lower thresholds were 39 and −3°C for females and 38 and −2°C for males. The estimated upper and lower thresholds for fecundity were 35 and 11°C for the New York population and 34 and 14°C for the Illinois population. The estimated optimum temperature for maximum fecundity was 23 and 24°C for the New York and Illinois populations, respectively. Both longevity and fecundity declined as temperature increased or decreased from the optimum. Oviposition was arrested at temperatures ≤10 and ≥35°C, and either eggs did not mature or were reabsorbed by females that did not oviposit at the higher temperatures. Days to first oviposition approached infinity near 10°C and declined exponentially to a minimum of 16 d at 30°C. The lower threshold for egg hatch was estimated as 10°C and the upper threshold at 32°C, and eggs would be predicted to hatch the fastest at 29°C. Maximum percentage hatch was estimated to occur at 23°C, and the estimated upper and lower thresholds were 34 and 12°C, respectively. These results indicate that summer temperatures throughout most of the lower 48 United States should support beetle survival and reproduction, although oviposition may be suspended and adult survivorship would decline when summer temperatures are sustained for full a day or more at or above 30°C, and there are no cooler locations where the beetles can retreat. In addition, although beetles may survive into the fall, they may lay fewer eggs at lower temperatures, and those eggs may not hatch until spring. These responses of *A. glabripennis* to temperature can be used for predicting the potential geographical range of this species and in developing phenological models to predict the timing of egg hatch and adult mortality, which are important for management programs.

KEY WORDS *Anoplophora glabripennis*, temperature, survival, reproduction, fecundity

Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae), referred to as Asian longhorned beetle, is widely distributed in China (Lingafelter and Hoebeke 2002) and is present in South Korea (Williams et al. 2004). In China, it is considered a major pest of several deciduous broadleaf tree species (Xiao 1992) and causes severe damage from 21 to 43° N latitude and from 100 to 127° E longitude (Yan 1985). The corresponding climatic zones in North America extend from southern Canada to southern Mexico. The only *A. glabripennis* infestations discovered in North America to date are in the New York City area (August 1996), the Chicago area (July 1998), northern New Jersey (October 2002), and the Toronto area, Ontario, Canada (September 2003) (Haack et al. 1997, Poland et al. 1998, APHIS/USDA 2005). In the United States, the USDA Animal and Plant Health Inspection Service (APHIS) has implemented an eradication program using the only currently effective method for limiting its spread: the removal and destruction of all trees with signs of beetle infestation (oviposition pits or exit holes). The eradication program for *A. glabripennis* has resulted in the removal of thousands of trees and has cost millions of dollars (Nowak et al. 2001). However, if the established populations of *A. glabripennis* are not eradicated, the beetle could potentially move into urban, suburban, and forested areas throughout the range of its known hosts and cause

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estimated losses in urban trees alone in excess of $600 billion (Nowak et al. 2001). This does not include the even greater threats to the hardwood (e.g., lumber and maple sugar) and recreational industries (e.g., fall tourism) that depend on potential host trees of *A. glabripennis.*

Temperature has profound effects on insect life history processes such as development, survival, and reproduction. The response of insects to temperature can be important in predicting the potential geographical range of a species and in developing phenological models to predict population dynamics and the timing of various stages for planning control or survey programs. Little information exists on the effects of temperature on the life history of *A. glabripennsis.* Research on *A. glabripennis* (form *nobilis*) adults in China suggests the upper and lower limits of activity to be 5 and 37°C, respectively, with normal activity from 16 to 28°C, increased activity at 28–32°C, and irregular activity at <10 and >32°C (Zhou et al. 1984). Adult emergence generally occurs anytime from May to October in China (Lingafelter and Hoebeke 2002) and is known to vary across geographic locations. Peak adult emergence has been observed to occur in July–August in Gansu Province, China (Smith et al. 2004) and Ganguo Province, China (Zhou et al. 1984). Eggs are laid beneath the bark and generally hatch during the summer, but eggs that are laid in the fall may not hatch until the next year (Yan and Qin 1992). Effects of temperature on egg hatch and larval development of *Anoplophora malasiaca* (Thomson), a closely related species, at 20, 25, and 30°C on citrus bolts were evaluated by Adachi (1994), but similar work on *A. glabripennis* has not been reported.

The purpose of this study was to determine the relationships between various life history parameters and temperature for *A. glabripennis.* Summary parameters for adult survival, reproduction, and egg hatch were calculated over a range of constant temperatures. The mathematical relationships for selected parameters were developed to facilitate use of this information in developing phenology models and to compare the thermal responses of *A. glabripennis* with closely related species reported previously.

Materials and Methods

Populations and Temperatures. Individuals were from the third to seventh laboratory generations of populations established from adults that emerged from infested branch sections obtained at eradication tree cuts in the United States and transported under permit to the USDA Forest Service quarantine facility in Ansonia, CT. The infested branch sections were obtained in February 1999 from the Ravenswood, Chicago, IL, infestation (1,450 adults, 41.58° N and 87.42° W) and April 1999 from the Bayside, Queens, NY, infestation (384 adults, 40.45° N and 73.45° W). Voucher specimens of both populations were deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT.

Eight constant temperatures were used for these studies: −1, 5, 10, 15, 20, 25, 30, and 35°C. The temperature in the environmental chambers rarely fluctuated >1° above or below the set value, and a photoperiod of 16:8 (L:D) h was used. Humidity was passively maintained by placing one or two buckets (32 by 28 by 14 cm) of water in the bottom of each chamber, depending on the size of the chamber. The only exception was the chamber at 25°C, which had full humidity controls. The humidity in the chambers averaged 80 ± 10, 85 ± 15, 70 ± 10, 80 ± 5, 60 ± 5, 45 ± 5, and 68 ± 4% RH at 5, 10, 15, 20, 25, 30, and 35°C, respectively. Actual humidity in the mating jars was likely higher than in the chamber because of the fresh host material they contained. At −1°C, humidity was maintained near saturation by placing the adult containers on grates over water in a sealed clear plastic box (36 by 24 by 16 cm). Because there were not enough chambers to run all of the temperatures simultaneously, the studies were set up over a period of 3 yr. In the first year, 15 mating pairs from each population were held at 15, 20, and 25°C (90 total pairs assessed). In the second year, 10 Illinois and 5–10 New York mating pairs were held at 30 and 35°C and 15 mating pairs from each population were held at 25°C as a control to compare between years (65 total pairs assessed). In the third year, 10 Illinois mating pairs and 5 New York individuals of each sex were held at −1, 5, and 10°C (45 total pairs assessed). In preliminary trials, no eggs were laid by pairs held at 10°C, so pairs were allowed to copulate at room temperature first to exclude the possibility that lack of oviposition was caused solely by poor mating success. A 25°C control was not set up in the third year because there were no significant differences in the dependent variables measured in the first 2 yr. Eggs laid at 25°C and excised from bolts were moved to 5 and 10°C in the second year and to 35°C in the third year to monitor hatch at temperatures at which no eggs were laid.

Mating Adults and Obtaining Eggs. Adults used in these studies came from larvae reared on artificial diet (*A. glabripennis* modification 1 or 2 with ≤0.06 g $FePO_4$ per liter; Keena 2005). Newly emerged adults were held in 50-ml plastic centrifuge tubes (with two pinholes in the lid and a piece of damp paper towel) in a tightly closed 50 by 40 by 25-cm opaque plastic box for 4 d at 25°C to allow the cuticle to fully sclerotize before they were sexed, weighed, and randomly assigned to a temperature regimen. Virgin females were moved to their assigned temperature 4 d after emergence (except in the third year) and held individually in 3.8-liter glass jars with *Acer saccharum* Marshall (sugar maple) twigs (3–7 mm diameter with leaves removed) as a food source and *A. saccharum* bolts (3–7 cm diameter and 20 cm long) with both ends waxed as an oviposition substrate. A virgin male was added to the female's jar 0–11 d later (i.e., as soon as a mate of the same strain that had been held at the same temperature became available). Males that could not be mated immediately were held at their assigned temperatures in 950-ml glass jars with fresh twigs as a food source. In the third year, virgins of both

sexes were held individually in 950-ml glass jars with twigs for 1–2 wk at 25°C before temperature treatment to allow them to complete their maturation feeding (Keena 2002) and become sexually mature (Li and Liu 1997), which would likely happen in nature before adults would be exposed to cooler temperatures. Individuals were held in the 950-ml jars with twigs at 5°C. At −1°C, individuals were placed in petri dishes (100 by 25 mm) with filter paper and held in a box as previously described. Twigs were cut fresh weekly and held in plastic bags, bolts were cut bi-weekly, and both were stored at 10°C and ≥80% RH until used for food or oviposition bolts, which were changed weekly. Folded paper towels were placed in the bottoms of the jars to collect frass and excess moisture. Two holes (1–2 mm diameter) were drilled in the plastic jar lids to allow airflow.

The oviposition bolts were replaced weekly (except at 10°C where they were replaced monthly) until a female died. Oviposition bolts held at 15–35°C and were checked daily for eggs, the date of each new oviposition pit chewed in the bark was recorded, and the pit was marked. After each female had laid her first egg, the daily marking of oviposition pits was only continued for a subsample of eight pairs in each temperature regimen until 50 eggs were obtained or the female died. All pits chewed in the bark including both pits that obviously contained eggs and those that did not were counted, and the bolt diameter was measured when the oviposition bolts were removed. After removal from the mating jars, the bolts were held at the same temperature as the mating pair to which they were exposed.

Daily marked bolts were held 14, 14, 8, 6, and 2 d at 10, 15, 20, 25, and 30°C, respectively, before the bark was stripped, and all eggs were counted and removed. This allowed all eggs to at least partially embryonate, which reduced egg mortality caused by handling. The only exceptions were bolts with eggs that were to be moved from 25 to 35°C; these were stripped the day that the bolt was removed from the jar. Eggs removed from under bark were placed individually in wells of a 24-well tissue culture plate that was held in a water box at the temperature at which the egg was laid or at the temperature to which the egg was to be moved (i.e., 5, 10, or 35°C). Eggs were checked daily for 8, 4, 6, 9, 12, 30, and 30 wk at 35, 30, 25, 20, 15, 10, and 5°C, respectively. These time periods were chosen to ensure that all eggs that could hatch at a given temperature did. Any eggs that had not hatched after the given period of time were moved to 25°C and observed for an additional 4 wk. Weekly marked bolts were held at 10°C for 1–5 wk to stockpile eggs for use in other studies and incubated at 25°C for a minimum of 4 wk to allow all the eggs to hatch before the bark was stripped off, and the number of eggs (i.e., including those that were dead, killed, or potentially viable) and larvae were counted. Any eggs that appeared viable were held as described above for 2 wk at 25°C. All eggs obtained from daily marked bolts, up to a maximum of 50 per female from the eight pairs per strain from bolts that were marked daily, were used to assess egg hatch at each temperature. All eggs laid by seven Illinois females over a 3-wk period were moved to 35°C, and two eggs from each of 15 females per strain (total of 60 eggs per temperature) were moved to 5 and 10°C to assess egg hatch at those temperatures.

Adult Survival and Reproduction. Mating pairs were checked at least twice a week (daily when bolts were marked every day) for mortality. The only exception was that individuals held at −1°C had to be warmed to 10°C to check for mortality, and this was done only once or twice a week. When females died, they were dissected, and all unlaid eggs were counted. Observations of female survival and reproduction at each temperature at which females laid eggs were used to calculate the mean number of eggs laid per week per female alive during that week. The following dependent variables were analyzed in PROC MIXED (SAS Institute 1999) using Restricted Maximum Likelihood (REML) estimation methods, which is a statistical approach to provide unbiased estimates of variance in unbalanced designs: female and male weight at 4 d, female and male longevity, days to first egg, fecundity, maximum weekly oviposition, week at which maximum oviposition occurred, and mean weekly oviposition pits per female. Females and males were analyzed separately in all cases. The model used temperature, population (New York or Illinois), and the interaction between the two as fixed effects, whereas maternal family was treated as a random effect. Year was not included in the models because there were no significant differences between years 1 and 2 at 25°C. Differences among means were determined using the Tukey-Kramer test with $\alpha = 0.05$ (SAS Institute 1999).

Median longevity was calculated for each sex at each temperature and the responses of the two sexes were separately fit according to

$$y = a(t - T_L)(T_U - t) \quad [1]$$

where y = median longevity, t = temperature (°C), a is an empirical constant, and T_L and T_U are the lower and upper temperature thresholds, respectively (Lysyk 2001). Nonlinear convergence was based on the Marquardt method (PROC NLIN; SAS Institute 1999). The values for 10°C were omitted when the model for longevity was estimated because of concerns about outlier values. The relationship between mean lifetime fecundity and temperature, and weekly numbers of oviposition pits per female and temperature were also determined for each population separately using equation 1. The optimum temperature for equation 1 can be found numerically by equating the first derivative to zero and solving for t.

The relationship between temperature (t) and mean number of days from female emergence to the first egg laid was described according to

$$y = at^b \quad [2]$$

where a and b are empirical constants, and nonlinear convergence was based on the Marquardt method (PROC NLIN; SAS Institute 1999). The percentages of

females that laid eggs and produced progeny were also calculated for each temperature.

Egg Hatch. Two dependent variables were analyzed by REML (PROC MIXED; SAS Institute 1999) to accommodate the unbalanced design: days to hatch and percent hatch for cohorts of eggs held at a range of temperatures. The model treated temperature, population, and temperature by population as fixed effects, whereas maternal family was treated as a random effect. Differences among means were determined using the Tukey-Kramer test with $\alpha = 0.05$ (SAS Institute 1999). For eggs held at 5 and 10°C and then moved to 25°C, mean number of days to hatch after being moved to 25°C was compared with that of eggs held at a constant 25°C using the same procedures and model.

To describe the relationship between temperature and mean rate of hatch for cohorts of eggs from each population, the following nonlinear model (Briere et al. 1999) was fit using the Marquardt convergence method (PROC NLIN; SAS Institute 1999):

$$y = \begin{cases} at(t - T_U)(T_L - t)^{\frac{1}{b}} & \text{for } T_U \leq t \leq T_L, \\ \text{otherwise } 0 \end{cases} \quad [3]$$

where y = rate of hatch, t = temperature (°C), T_L and T_U are the lower and upper temperature thresholds, respectively, and a and b are empirical constants. The optimum temperature for equation 3 can be found numerically by equating the first derivative to zero and using the maximum root as the solution for t (Briere et al. 1999).

The cumulative distributions of time to egg hatch at 15, 20, 25, and 30°C and degree-days to egg hatch for all eggs were calculated. The degree-days to hatch for each egg were calculated by subtracting the lower estimated threshold (equation 3 from the constant holding temperature and then multiplying by the number of days it took the egg to hatch. The cumulative proportion of eggs hatching (P) over accumulated degree-days (DD) was described using a Gompertz function:

$$P = \exp[-\exp(-bDD + a)] \quad [4]$$

in which a and b are the lag and the rate of increase, respectively (Brown and Mayer 1988; PROC NLIN and Marquardt convergence method, SAS Institute 1999).

Results

Adult Survival and Reproduction. The average weight of Illinois females (159.8 ± 10.9 mg) was significantly higher than the average weight of New York females (129.1 ± 11.1 mg; $F = 49.3$; df = 1,185; $P < 0.00001$). There was also a significant difference ($F = 24.0$; df = 1,170; $P < 0.0037$) in the average weights of males from the Illinois population (104.3 ± 4.9 mg) compared with the New York population (89.2 ± 5.1 mg). There were no significant differences in weight between beetles held at different temperatures for

Table 1. Effects of temperature on *A. glabripennis* adult survival and reproduction

Parameter	Temperature (°C)							
	−1	5	10	15	20	25	30	35
♀ Longevity (d)	21.4 ± 6.9e (15)	44.9 ± 6.9de (15)	135.6 ± 6.9a (15)	75.7 ± 4.6bc (30)	85.3 ± 4.6b (30)	78.9 ± 3.3b (60)	56.4 ± 5.1cd (25)	21.1 ± 6.9e (15)
♂ Longevity (d)	19.4 ± 13.5cd (15)	42.4 ± 13.5cd (15)	144.7 ± 13.5a (15)	101.9 ± 11.5ab (23)	127.8 ± 11.2a (27)	98.1 ± 9.0b (52)	56.5 ± 10.3c (25)	19.1 ± 12.2d (15)
Fecundity	0.0 (15)	0.0 (15)	0.0 (15)	20.9 ± 7.0c (30)	52.0 ± 7.0ab (30)	66.8 ± 5.0a (60)	41.4 ± 7.8bc (25)	0.0 (15)
Max oviposition/wk	NA	NA	NA	8.1 ± 1.4c (28)	12.3 ± 1.4bc (26)	17.3 ± 1.0a (59)	16.7 ± 1.7ab (19)	NA
Week max oviposition occurred	NA	NA	NA	6.5 ± 0.4a (28)	6.0 ± 0.4a (26)	4.4 ± 0.3b (59)	3.3 ± 0.5b (19)	NA
Time first egg laid (d)	NA	NA	NA	32.9 ± 1.8a (28)	23.6 ± 1.8b (26)	16.9 ± 1.3c (59)	16.1 ± 2.0c (19)	NA
Weekly oviposition pits chewed/♀	0.0 (15)	0.0 (15)	2.1 ± 5.4c (15)	27.7 ± 3.8b (30)	39.2 ± 3.8a (30)	37.4 ± 3.0ab (60)	28.0 ± 4.3ab (25)	12.1 ± 4.2c (15)
Percent females laying eggs	0	0	0	93	90	100	76	0
Percent females with progeny	0	0	0	57	70	93	65	0

Values are mean ± SD (*n*).

Data for New York and Illinois populations were pooled. Also, data for years 1 and 2 at 25°C were combined. Within rows, means followed by the same letter are not significantly different based on Tukey-Kramer test with $\alpha = 0.005$ (SAS Institute 1999).

NA, parameter not applicaple because no eggs were laid at these temperatures.

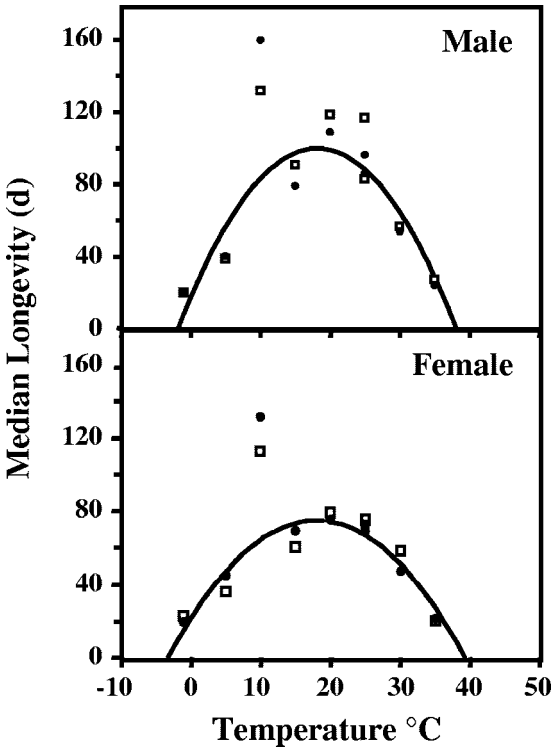

Fig. 1. Relationship between temperature and median longevity for male and female *A. glabripennis* from Illinois (□) and New York (●). The data for 10°C were outliers and not included in the model.

either sex (females: $F = 0.7$, df = 7,185, $P = 0.6781$; males: $F = 0.7$, df = 7,170, $P = 0.7109$).

The maximum longevities (Illinois and New York populations pooled) of individual females were 35, 148, 179, 152, 158, 133, 103, and 28 d and of males were 28, 61, 194, 193, 202, 177, 140, and 53 d at −1, 5, 10, 15, 20, 25, 30, and 35°C, respectively. Temperature had a significant effect on both female ($F = 32.9$, df = 7,187, $P < 0.0001$) and male longevity ($F = 24.9$, df = 7,169, $P < 0.0001$; Table 1). Population did not have a significant effect on male ($F = 0.7$, df = 1,169, $P = 0.4119$) or female longevity ($F = 0.02$, df = 1,187, $P = 0.8832$), nor did the interaction between temperature and population. Median female and male longevity, omitting the 10°C values (see discussion) were modeled reasonably well ($R^2 = 0.893$ for females and 0.823 for males) using equation 1 (Fig. 1; Table 2). Median longevity was greatest at 18°C (the estimated optimum temperature), and declined with both increasing and decreasing temperatures (Fig. 1). Male and female longevities were fit separately to equation 1 because males tended to live longer over the 5–30°C range. The estimated upper (T_U) and lower (T_L) thresholds, and optimum temperatures for longevity and the other fitted models discussed below are given in Table 2.

Once a female started laying eggs, she continued laying eggs generally until her penultimate week of life. Fecundity of *A. glabripennis* peaked (Illinois and New York populations pooled) at 25°C and declined with both increasing and decreasing temperatures (Table 1). This effect of temperature on fecundity was significant ($F = 10.3$, df = 3,135, $P < 0.0001$) and so was the effect of population ($F = 5.9$, df = 1,135, $P = 0.0165$). The percentage of females that produced progeny declined both above and below 25°C, further reducing the total reproduction at these temperatures (Table 1). Equation 1 described the relationship between mean fecundity and temperature reasonably well ($R^2 = 0.843$ for New York and 0.967 for Illinois; Table 2; Fig. 2A). Separate curves were fit for the two populations because of biologically significant differences in peak oviposition near the optimal temperature.

There were significant effects of temperature ($F = 11.8$, df = 3,124, $P < 0.0001$) and population ($F = 4.6$, df = 1,124, $P = 0.0346$) on mean maximum weekly oviposition, peaking at 25°C and declining both above and below that temperature (Table 1). The maximum weekly oviposition recorded for any female was 21, 21,

Table 2. Parameter values for two nonlinear models used to describe the relationships between temperature and selected life history values for *A. glabripennis*

Response variable	*n*	T_U	T_L	a	b	*F*	df	*P*	Adjusted R^2	Temperature range (°C)	Optimum temperature (°C)
♀ Longevity (d)[a]	16	39.21 ± 0.96	−3.29 ± 0.79	0.18 ± 0.02	—	63.79	2, 13	<0.0001	0.893	−1–35[c]	17.96
♂ Longevity (d)[a]	16	38.04 ± 1.22	−1.78 ± 0.98	0.26 ± 0.03	—	35.84	2, 13	<0.0001	0.823	−1–35[c]	18.13
New York fecundity[a]	7	35.36 ± 1.10	10.58 ± 0.96	0.32 ± 0.06	—	17.09	2, 4	0.0110	0.843	10–35	22.97
Illinois fecundity[a]	5	34.04 ± 0.68	13.80 ± 0.37	0.78 ± 0.09	—	59.63	2, 12	0.0165	0.967	15–30	23.92
Percent egg hatch[a]	12	33.76 ± 1.13	11.84 ± 1.00	0.50 ± 0.11	—	10.25	2, 5	0.0170	0.726	15–30	22.80
Weekly oviposition pits/♀[a]	14	38.22 ± 0.79	9.21 ± 0.56	0.19 ± 0.12	—	57.30	2, 11	<0.0001	0.897	10–35	23.72
Hatch rate (1/d)[b]	6	31.54 ± 1.81	9.72 ± 0.70	0.0001 ± 0.00004	4.24 ± 2.52	1081.62	4, 1	0.0228	0.997	10–35	28.82

Parameter values are means followed by SE. In the table and the models T_U = upper temperature threshold and T_L = lower temperature threshold. The temperature range used did not always include all the data points since some were above or below the thresholds based on preliminary plots.

[a] model is $y = y = a(t-T_L)(T_U-t)$, where t is the temperature (°C).

[b] model $y = \begin{cases} at(t - T_U)(T_L - t)^{\frac{1}{b}} & \text{for } T_U \le t \le T_L, \\ \text{otherwise } 0 \end{cases}$, where t is the temperature (°C).

[c] Longevity data at 10°C were omitted from the analysis because of outlier values.

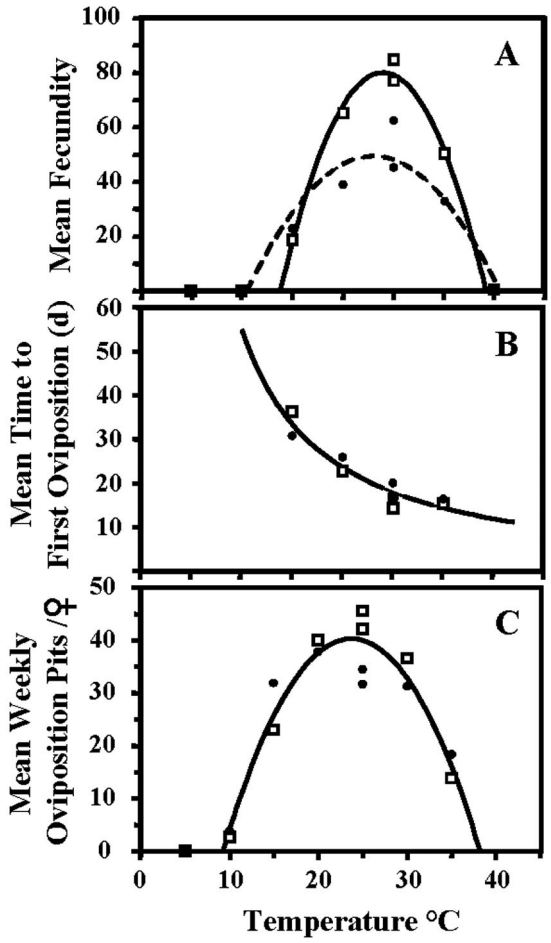

Fig. 2. Relationships between temperature and mean fecundity (A), and time to oviposition (B) and mean weekly oviposition pits chewed per female (C) for *A. glabripennis* from Illinois (□) and New York (●). The solid line in B represents the fit to the equation: time to first egg laid = $910 \pm 369 \times \text{temperature}^{-1.22 \pm 0.14}$; adjusted $R^2 = 0.894$, equation 2.

32, and 31 for Illinois females and 17, 18, 28, and 29 for New York females at 15, 20, 25, and 30°C, respectively. The week that the maximum weekly oviposition occurred was significantly affected by temperature ($F = 12.1$, df = 3,124, $P < 0.0001$) but not population ($F = 0.4$, df = 1,124, $P = 0.5120$); oviposition peaked sooner at higher than at lower temperatures (Table 1). The number of days to first oviposition (Illinois and New York populations pooled) was significantly affected by temperature ($F = 24.6$, df = 3,122, $P < 0.0001$), declining from 15 to 25°C and then remaining relatively constant (Table 1). Equation 2 described the relationship between temperature and number of days to first oviposition well with an adjusted R^2 of close to 0.9 (Fig. 2B). The average number of oviposition pits chewed weekly per female was significantly affected by temperature ($F = 20.1$, df = 5,161, $P < 0.0001$) but not by population ($F = 0.1$, df = 1,161, $P = 0.7876$), peaking between 20 and 25°C and declining both above and below those temperatures (Table 1). Equation 1 described this relationship between temperature and number of weekly oviposition pits per female well ($R^2 = 0.897$; Table 1; Fig. 2C).

At lower temperatures (5 or 10°C), females (Illinois and New York populations pooled) had fully developed eggs, averaging four and eight eggs, respectively, in their ovarioles at death. At temperatures between 15 and 25°C, there was an average of 7 mature eggs (maximum, 36 eggs) inside the females at death, and the few females that did not lay eggs had mature unlaid eggs in their ovarioles. Three of four females that did not lay eggs at 30°C and virtually all the females at 35°C had no mature eggs inside them at death (one female had one egg).

Egg Hatch. A total of 200, 380, 433, and 277 eggs from the Illinois population and 99, 261, 331, and 238 eggs from the New York population were held at 15, 20, 25, and 30°C, respectively to observe egg hatch. Thirty eggs from each population were moved to 5 and 10°C, and 102 Illinois eggs were moved to 35°C. Temperature had a significant effect ($F = 903.3$, df = 3,913, $P < 0.0001$) on mean number of days to egg hatch, but population did not ($F = 0.7$, df = 1,913, $P = 0.3982$). The number of days to egg hatch (Illinois and New York populations pooled) was lowest at 30°C and increased as temperature declined to 15°C. No eggs hatched at 5, 10, or 35°C (Table 3). Equation 3 provided an excellent fit to the hatch rate data with an adjusted $R^2 = 0.997$ (Table 2; Fig. 3A). The actual upper threshold for egg hatch could be higher because there were no data points between 30 and 35°C. The total number of days at 25°C that it took eggs to hatch after being held at 10 or 5°C for 210 d (i.e., days before and after spent at 25°C) compared with the time at a constant 25°C were not significantly different ($F = 0.01$, df = 2,361, $P = 0.9923$). In addition, some eggs

Table 3. Effects of temperature on *A. glabripennis* egg hatch

Parameter	Temperature (°C)						
	5	10	15	20	25	30	35
Time to egg hatch (d)	NA	NA	54.4 ± 0.7a (129)	25.0 ± 0.6b (321)	15.0 ± 0.6c (409)	13.3 ± 0.7c (137)	NA
Percent egg hatch	0.0 (15)	0.0 (15)	31.9 ± 6.9b (14)	52.4 ± 6.8ab (12)	63.6 ± 6.8a (15)	32.5 ± 6.6ab (13)	0.0 (7)

Values are mean ± SE (*n*).

Within rows, means followed by the same letter are not significantly different based on Tukey-Kramer test with $\alpha = 0.05$ (SAS Institute 1999). The data for the New York and Illinois populations were pooled.

NA, parameter not applicable because no eggs were laid at these temperatures.

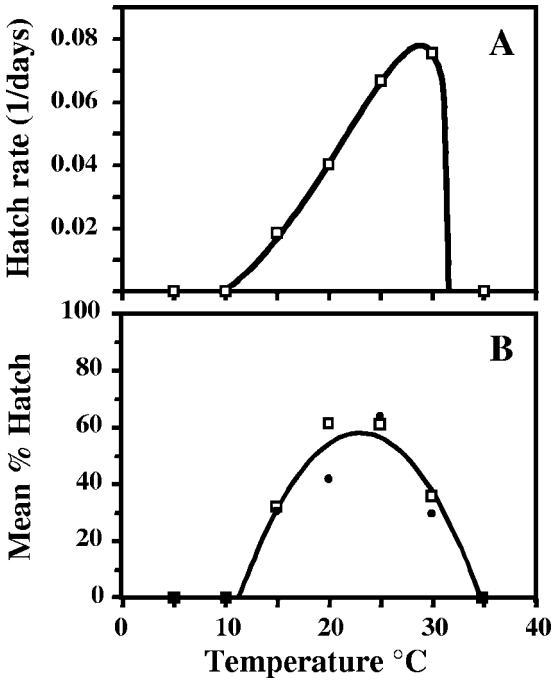

Fig. 3. Relationships between temperature and mean egg hatch rate (1/d) (A) and mean percentage egg hatch (B) for *A. glabripennis*. Results are pooled across populations in graph A (□, observed points). In B, observed points are □ for the Illinois population and ○ for the New York population.

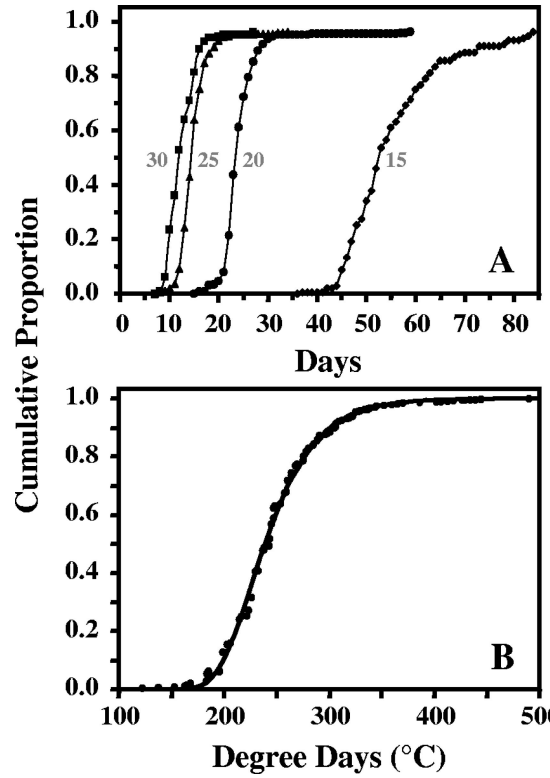

Fig. 4. Observed cumulative frequency distributions for *A. glabripennis* egg hatch times (d) at four temperatures (°C) (A). Cumulative proportion of *A. glabripennis* eggs hatching over accumulated degree-days (B). The solid line in the bottom graph represents the fit to the equation: predicted proportion hatching = $\exp[-\exp(-0.0303 \pm 0.00038 \times$ accumulated degree-days $\pm$ 6.8754 $\pm$ 0.0925]; adjusted R^2 = 0.998, equation 4.

held at 15°C that did not hatch by day 84 did hatch in an average of 8.9 ± 2.8 d when moved to 25°C. Thus, the lower threshold temperature for egg hatch may actually be higher than estimated.

Variation in the number of days to hatch at 15–30°C (Illinois and New York populations pooled) is shown in Fig. 4A. Hatch began at 37, 16, 8, and 8 d and ended at 84, 59, 38, and 27 d for eggs held at 15, 20, 25, and 30°C, respectively. Equation 4 fit the cumulative proportion versus accumulated degree-days very well (R^2 = 0.998; Fig. 4B). The predicted degree-day accumulations at which 50 and 90% of the eggs would hatch were 239 and 301 DD, respectively (Fig. 4, bottom).

The percentage of egg hatch per female was significantly affected by temperature (F = 5.7, df = 3,49, P = 0.0020) but not by population (F = 1.0, df = 3,49, P = 0.3335). Percentage hatch was highest at 25°C and declined as temperature increased or decreased (Table 3). The relationship between temperature and percentage of eggs that hatched (Illinois and New York populations pooled) was fit with lower confidence (R^2 = 0.726) by equation 1 because of uncertainty near zero at both ends of the curve (Fig. 3B; Table 2).

Discussion

Temperature had significant impacts on all the life history parameters assessed in this study. Effects of temperature on female fecundity differed between the Illinois and New York populations. However, these differences in fecundity may have been caused by the Illinois adults being heavier than New York adults, because female fecundity is positively correlated with female weight (Keena 2002). Temperature effects on longevity differed between the sexes. The mathematical relationships between temperature and the life history parameters, which provided good fits to the data, can be used to estimate the lower and upper temperature thresholds and optimum temperatures for these parameters. These relationships greatly facilitate development of phenology models and predictions of potential geographic range that are essential for effective control and eradication efforts.

Adult activity over the range of temperatures assessed was comparable with what Zhou et al. (1984) found for *A. glabripennis* (form *nobilis*) adults in China. Adults held at 15–25°C exhibited normal behaviors (feeding, mating, ovipositing and resting), which were slower at cooler temperatures. At 10°C, adults moved very slowly and fed less. Females chewed fewer pits and did not oviposit, but males were still observed mounting and copulating with females.

At 5 and −1°C, adults appeared dead, and many adults laid on the bottom of the containers upside down until warmed a few of degrees. The increase in activity at 30°C was as obvious; adults fed voraciously, moved around the jars rapidly, and often attempted to fly as soon as the lid was removed. This tendency to escape increased at 35°C, whereas reproductive behaviors decreased; females chewed fewer oviposition pits and did not oviposit. Adults held at ≥30°C were likely attempting to locate a place where the temperature was lower because *A. glabripennis* has been found to stay in shaded areas when the temperature exceeds 29°C in China (Xiao 1980).

Concomitant with the increases in activity at temperatures >20°C was a reduction in adult longevity. Higher temperatures increase metabolism and consequently reduce life span proportionately (Slansky and Scriber 1985). Higher summer temperatures in some areas where this beetle is found in China may, in part, explain the shorter average life span reported for *A. glabripennis* females in China (42.5 d by Yan and Qin 1992) compared with those reported in laboratory studies in the United States (Keena 2002, Smith et al. 2002). Adult weights, which differed between these studies, did not seem to contribute to the longevity differences because there were no indications in this study that weight and heat tolerance, as measured by longevity, were linked. Differences in humidity conditions in the reported studies could have affected adult longevity. Adult longevity can also be shortened by lower humidity, especially at low and high temperatures, as has been found for *Hylotrupes bajulus* L. (Coleoptera: Cerambycidae) (Dürr 1957). Humidity is suspected to be important in *A. glabripennis* survival because adults held in screen cages had shorter life spans compared with others held in glass jars at 25°C, likely because of increased air flow in the cages resulting in drier conditions (M. K., unpublished data). Moreover, the longer lifespan of individuals held at 10°C (Fig. 1) was most likely because of higher relative humidity in that chamber, partly because of storing the fresh twigs and bolts there until needed. Another possible explanation for the differences in reported longevity for *A. glabripennis* is that the hosts on which it feeds also can also affect longevity. The shorter adult longevities reported from China were for beetles reared on *Populus* spp. (Xiao 1992), whereas those reported from laboratories in the United States were on *A. saccharum*, *Acer platanoides* L., *Acer rubrum* L., and *Salix nigra* Marshall (Keena 2002, Smith et al. 2002). Therefore, caution should be used in applying predictions based only on temperature relationships developed in the laboratory to field conditions.

Temperature, host species, and quality can also affect the length of the precopulatory and preovipostional periods. Cerambycids of the subfamily Lamiini, of which *A. glabripennis* is a member, seem to require both precopulatory and preoviposition periods of maturation feeding averaging 6.7 and 9.0 d, respectively (Hanks 1999). Li and Liu (1997) reported that newly emerged males had mature sperm and females could copulate on emergence, but that maturation feeding increased the likelihood of copulation, was required for the development of eggs within the ovaries, and was necessary for continued vigor in males. In China, it was estimated that adults spent a week in the wood before emergence (i.e., either sclerotizing in the pupal gallery after eclosion or before chewing out) and female ovaries reached maturity ≈10 d after emergence from *Populus opera* hosts (Li and Liu 1997). When *A. glabripennis* adults that emerged from infested wood from Illinois were evaluated on *A. platanoides*, *A. rubrum*, and *S. nigra*, time to first oviposition averaged 11, 17, and 16 d, respectively (Smith et al. 2002). This suggests that in the field the precopulatory maturation feeding requirement may be partially met as the adult chews out of its host but that the precopulatory period in the laboratory may include the time from eclosion to first oviposition when the insect is reared on artificial diet. In this study, the time from eclosion to first oviposition was 17 d at the warmest temperatures, which could be the sum of, for example, 7-d precopulatory and 10-d preovipositional periods.

Increases in temperature, up to the optimum, improved reproductive efficiency, probably through increased rates of assimilation and conversion of ingested food (Haack and Slansky 1987). Oviposition sites chewed per week, fecundity, and fertility (as measured by percentage females producing progeny) in *A. glabripennis* showed this response to temperature increased from 10 to 25°C and then decreased again at higher temperatures. At lower temperatures (5 or 10°C), females laid no eggs despite having fully developed eggs in their ovarioles at death. This indicates that low temperatures arrest oviposition, because *A. glabripennis* females normally contain mature eggs, but don't begin laying eggs until after mating occurs (He and Huang 1993) or they have contact with other adults (Keena 2002). Further evidence suggesting oviposition was arrested at lower temperatures was that females chewed fewer oviposition pits. At higher constant temperatures when females failed to lay eggs (some at 30°C and all at 35°C), this was caused by a lack of egg maturation or eggs being reabsorbed within these females because no eggs were found in their ovarioles at death. There was also some evidence of genetic variation in heat sensitivity among females, particularly at 30°C. In addition, when four females that had laid eggs at 25°C were moved to 35°C for 3 d, oviposition ceased; however, the females resumed laying when returned to 25°C (M. K., unpublished data), indicating that oviposition is also arrested at higher temperatures. This pattern of reproductive response to temperature is comparable with that found for *H. bajulus* (Dürr 1957), and Adachi (1988) reported that periods of lower oviposition in *A. malasiaca* coincided with lower daily temperatures. Fecundity near the optimum temperature of 25°C was higher than that reported for *A. glabripennis* in China on *Populus* spp. (Xiao 1992) but lower than that reported in other laboratory studies on *A. platanoides* and *A. rubrum* (Smith et al. 2002). These differences

may be caused by effects of host species or quality on life span.

Temperature not only affects the number of eggs laid but has a significant impact on the percentage of the eggs that hatch. Eggs of most insect species hatch over a 15°C range of constant temperatures, and this range can be extended 3–4°C lower under fluctuating temperatures (Howe 1967). However, the percentage of eggs that hatch falls drastically within 2–3°C of the upper and lower ends of the 15°C constant temperature range (Howe 1967). *A. glabripennis* shows this pattern of fidelity to a fairly narrow range of temperatures at which eggs will hatch. There also seemed to be some genetic variation in the lower threshold for egg hatch and egg tolerance for cold temperatures. At a constant 15°C (close to the lower end of the range), there were indications of variation between families in time to hatch, egg survival, and development of eggs (some developed so slowly that they would effectively never hatch unless they were exposed to higher temperatures).

The predicted number of degree-days to 50% hatch of *A. glabripennis* eggs was 239 DD, whereas estimates for *A. malasiaca* are considerably less (184 DD) (Adachi 1988). In addition, the estimated lower threshold for *A. malasiaca* egg development was lower (i.e., 6.7°C) than for *A. glabripennis* (Adachi 1988). In using the degree-day estimates to predict egg hatch, diurnal and seasonal temperature variations in tree trucks and branches where eggs are laid should be taken into consideration. In *Pinus contorta* Douglas ex Loud., phloem temperatures on the south side of a tree were up to 33°C warmer than on the north side and up to 21°C higher than air temperature, with the largest differences occurring in the late summer and fall (Bolstad et al. 1997). Therefore, eggs that are laid in tree sections exposed to direct sunlight, especially when air temperatures are higher, could experience lethal temperatures. Daily minimum phloem temperatures for all sides of the tree averaged 2°C higher than daily air temperatures (Bolstad et al. 1997). Similar temperature differences were measured in hardwood trees; cambial temperature in aspen in April averaged 2–10°C higher than air temperatures (Derby and Gates 1966). During the day, direct solar radiation, reflected solar radiation, and thermal radiation, in addition to air temperature and wind speed, affect tree temperature. At night, thermal radiation continues to keep wood temperature higher than air temperature. Also, temperatures deeper in the trunk can take minutes to hours to respond after environmental conditions have changed (Derby and Gates 1966). When estimating time to hatch for eggs laid in trees, at least 2°C should be added to both day and night air temperatures when making these calculations. If the wood receives direct sunlight, much higher adjustments for day time air temperatures are needed.

Given the temperature effects detailed here on *A. glabripennis*, this beetle should be well adapted to the locations where it has been found. Monthly mean temperatures at Central Park, New York City, NY, were 22, 25, 24, 20, 14, and 9°C during June, July, August, September, October, and November, respectively, whereas the corresponding temperatures at Chicago O'Hare Airport, Chicago, IL, were 20, 23, 22, 18, 12, and 4°C, respectively (30-yr normals, 1961–1990, National Climatic Data Center). Maximum temperatures averaged 27, 30, 29, 25, 19, and 12°C for New York and 26, 29, 28, 24, 17, and 9°C for Illinois for the same time period. Maximum daily temperatures at both locations rarely exceed 35°C; from 2000 to 2005, maximum daily temperatures only exceeded 35°C on a total of 19 d (4 d in 2001, 7 d in 2002, and 8 d in 2005) at Central Park, New York City, NY, and 4 d (1 d in 2002 and 3 d in 2005) at Chicago O'Hare Airport, Chicago, IL (daily surface data, National Climatic Data Center). Thus, both locations experience near optimum temperatures for the beetle from June to September and, although summer temperatures >30°C may reduce adult survival, there will be few if any days that oviposition will be suspended because of temperature. In addition, beetles may survive into the fall, but because of the lower temperatures, will lay fewer eggs, and those eggs may not hatch until spring. In fact, summer temperatures throughout most of the lower 48 states should support beetle survival and reproduction, although oviposition may be suspended if the temperature is outside temperature thresholds. Also, beetles will survive for a shorter time in areas where summer temperatures are sustained for a full day or more at or above 30°C. The beetles ability to seek out locations with optimum temperatures (e.g., sunny perches when it is too cool and shady locations when it is hot) may lessen the adverse effects in both the summer and fall. These data on temperature effects on life history parameters of adults and eggs of *A. glabripennis*, combined with similar data for larvae, will aid in developing potential geographical range maps for this species and phenological models to predict the timing of life stages. Such information is critical for developing *A. glabripennis* management programs.

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