Development of the Teneral Adult *Anoplophora glabripennis* (Coleoptera: Cerambycidae): Time to Initiate and Completely Bore Out of Maple Wood

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ABSTRACT *Anoplophora glabripennis* (Motschulsky) is an introduced invasive pest with the potential to devastate hardwood forests in North America. Using artificial pupal chambers, we documented the time required by teneral adults at three temperatures (20, 25, and 30°C), 60–80% RH, and a photoperiod of 16:8 (L:D) h to initiate boring after eclosion and subsequently bore completely through a 7-mm (range, 3–11 mm) layer of Norway maple wood (*Acer platanoides* L.). In total, 218 laboratory-reared pupae from the Chicago, IL, or Inner Mongolia, China, populations were used in the study. Females (1.54 ± 0.03 g) weighed significantly more than males (1.12 ± 0.03 g), but the average weights of the beetles emerging in each temperature did not differ. Adult weight was positively correlated with exit hole diameter (diameter [mm] = 2.2 * weight [g] + 7.9). The rate at which beetles bored through the wood (136, 178, and 168 mm^3/d at 20, 25 and 30°C, respectively) significantly differed between temperatures but did not differ with beetle weight. Temperature had a significant effect on the time it took adults to initiate boring (7, 5, and 4 d at 20, 25, and 30°C, respectively) and subsequently to complete boring to emerge (5, 4, and 4 d at 20, 25, and 30°C, respectively). This suggests that beetles require more than a week to progress from eclosion to emergence in wood, even at summer temperatures. This information on *A. glabripennis* basic biology is critical for developing phenology models that are used to time exclusion and eradication methodologies.

KEY WORDS temperature, development, degree-days, Asian longhorned beetle, invasive species

Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae), commonly called the Asian longhorned beetle, is widely distributed in China (Lingafelter and Hoebeke 2002), and 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 *A. glabripennis* infestations discovered in North America to date are in New York City, NY (August of 1996); Chicago, IL (July of 1998); Hudson, Middlesex and Union Counties, NJ (October of 2002); Toronto, Ontario, Canada (September of 2003); Worcester, MA (August of 2008); and most recently in Bethel, OH (June of 2011) (USDA 2012). However, in 2008, after the completion of control and regulatory activities, and after confirmation surveys, *A. glabripennis* was declared eradicated in Chicago, IL, and Hudson County, NJ. Similarly, in 2011, *A. glabripennis* was declared eradicated from Islip, NY (USDA 2012).

In the United States, the USDA Animal and Plant Health Inspection Service (APHIS) implemented an eradication program by using the only currently effective method for limiting its spread, namely, the removal and destruction of all trees with signs of beetle infestation (e.g., oviposition pits or exit holes). The eradication program for *A. glabripennis* has resulted in the removal of thousands of trees and had cost state and federal agencies about US$373 million from 1997 to 2008 (Haack et al. 2010). 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, causing urban tree damage alone in excess of US$600 billion (Nowak et al. 2001).

Temperature drives insect life history processes such as development, survival, and reproduction. The response of insects to temperature is important for predicting the potential geographical range of a species and developing phenological models to predict population dynamics and temporal occurrence for control or survey programs. The effects of temperature on most of the life history of *A. glabripennis* are well known. Previous research on the effects of temperature on *A. glabripennis*, both in nature in China and in the laboratory, have focused on documenting temperature effects on larval development, activity (such as flight), stage specific survival, and fecundity (Zhou et al. 1984, Zhang et al. 1995, Keena 2006, Keena

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and Moore 2010). However, the effects of temperature on adult sclerotization and emergence have not been investigated.

In China, *A. glabripennis* is either univoltine or bivoltine, primarily determined by the climate and the timing of oviposition; eggs that are laid in the fall may not hatch until the next year (Hua et al. 1992, Yan and Qin 1992). In the United States, *A. glabripennis* females lay eggs from July to November (Lingafelter and Hoebeke 2002). First-instar larvae feed in the cambium, second and early third instars feed on phloem and outer layers of xylem, whereas late third and older instars feed in the xylem (Xiao 1980). The ultimate instar creates a chamber near the outer bark where it pupates (usually leaving ≈1 cm of xylem or phloem for the adult to bore through; M.A.K., unpublished data). Most *A. glabripennis* pass the winter in the larval stage and pupate in the spring or summer (Haack et al. 2006). Thus, most of the larval period is spent in the xylem, well protected and insulated from the outside environment. This life history makes it difficult to directly observe pupal and teneral adult development. There is a critical need for information on the basic biology of this beetle to provide the basis for predicting phenology to time exclusion and eradication methodologies. In China, it was estimated that adults spent a week in the wood before emergence (Yan and Qin 1992). In this study, we investigated the amount of time at each of three temperatures required for teneral adults to initiate boring after eclosion and subsequently completely bore through a layer of wood (i.e., simulating emergence). This information then was used to estimate the mathematical relationships between temperature and emergence rates, which will be used to develop phenological models and compare the thermal response of *A. glabripennis* with that of closely related species.

Materials and Methods

Populations and Obtaining Pupae. *Anoplophora glabripennis* pupae were reared in the USDA-Forest Service Northern Research Station Quarantine Laboratory in Ansonia, CT from two colonies: one established from adults that emerged from infested wood collected from the Ravenswood area, Chicago, IL infestation (IL: individuals from the ninth and tenth laboratory generations) and the other from large larvae imported from Inner Mongolia, China (IM: individuals from the sixth laboratory generation). All *A. glabripennis* were transported and reared under USDA permits. Voucher specimens of the *A. glabripennis* colonies were deposited at the Entomology Division, Yale Peabody Museum of Natural History, New Haven, CT. All insects were reared on artificial diet AG2 by using the methods detailed by Keena (2005) until pupation and all life stages were held in environmental chambers kept at 25°C, 60% humidity, and a photoperiod of 16:8 (L:D) h.

Pupae from both populations were subjected to three constant temperatures for these studies, 20, 25, and 30°C, with temperature fluctuations within one degree of the set value in the environmental chambers. These temperatures were selected because they occur naturally during the time that beetles pupate and emerge as adults in the field. Humidity was maintained passively using open water boxes (with 896 cm^2 of surface area) in the bottom of the 20 and 30°C chambers. The 25°C chamber has full humidity controls and did not require the open water. The humidity in the chambers averaged 80 ± 5%, 60 ± 5%, and 45 ± 5% RH at 20, 25, and 30°C, respectively.

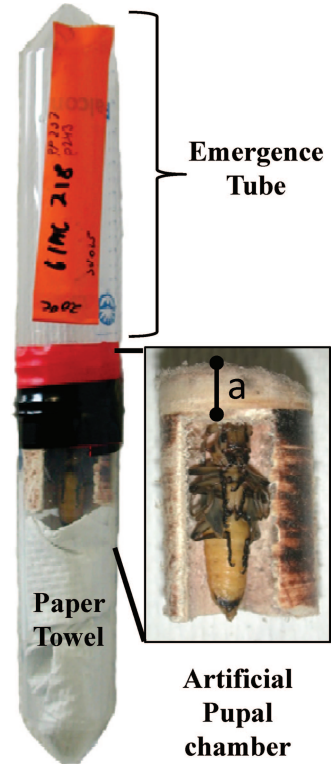

Fig. 1. Photo of the artificial pupal chamber, with inset showing the hollowed wood cylinder of Norway maple wood, and emergence tube assembly. Line *a* shows the depth of the wood plus bark that the adult had to bore through to emerge.

Experimental Setup and Data Collection

In total, 218 laboratory-reared pupae (within a few days of eclosion) from the IL or IM populations were placed in the artificial pupal chambers. Similar numbers of each sex were used from each population in each temperature treatment. The artificial pupal chamber was formed using two 50-ml centrifuge tubes (11.2-cm-long by 2.7-cm-diameter internal dimensions) held together at open ends with a specially prepared hollowed cylinder of Norway maple, *Acer platanoides* L., wood (bark included), and moistened paper towel strips packed into the distal end (3 cm) of one tube (Fig. 1). The two tubes were secured together using the wood cylinder on the inside and opaque tape on the outside, which also reduced light entry into the pupal chamber.

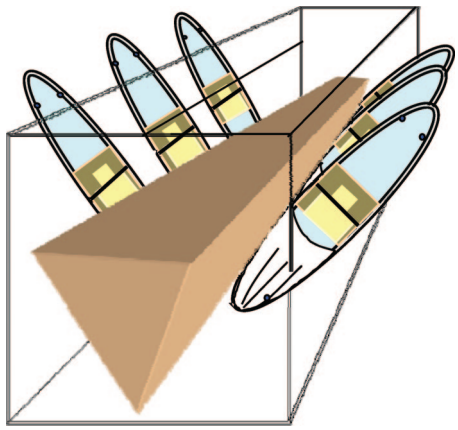

Fig. 2. Diagram of the artificial branch showing six artificial pupal chambers with emergence tubes sticking out of the box and the triangular support inside the box.

The wood cylinders were cut from fresh 10-cm-diameter Norway maple bolts of varying lengths obtained in June–September 2006. The bolts were held under cold conditions until processed to maintain the moisture content. To create the cylinder, the bolt was rough cut along the center longitudinal axis and these slabs were cut into ≈40-cm-long sections. Along the length of this rough lumber section, center marks were placed every 4.4 cm on the inner (xylem) side and a hole was countersunk to 4 cm depth in the ≈5-cm-thick section by using a 19-mm drill bit. This bolt section then was rotated bark side up and using a 32-mm keyhole saw aligned above marks centered every 4 cm on the bark side, a cylinder was cut and removed from the other side. The cylinder carefully was extracted to keep the bark intact, immediately placed in a zip lock plastic bag, and held at −20°C until use. The wood layer at the top of the cylinders was 7.13 ± 0.11 mm (range, 3–11 mm) thick, plus 1–3 mm of bark on top, that the beetles had to bore through to emerge from the artificial pupal chamber. Two small holes (1 mm diameter) were made in each 50-ml tube for air exchange and to prevent excessive moisture build-up. The pupal chamber side of the assembly was inserted at a 45° angle into a cardboard box serving as a false branch that was sealed to keep a dark interior (Fig. 2). Pupae randomly were assigned to temperatures and the boxes with the tubes were kept at 20, 25 or 30°C, 80–45% RH, and a photoperiod of 16:8 (L:D) h.

Each box was opened daily under a red light to determine when adults eclosed and later initiated boring. Adults were considered to have eclosed when the pupal skin had been completely shed. When adults began boring, wood dust was evident in the artificial pupal chamber. Adults that bored through the wood layer at the top of the cylinder were removed from the upper tube, weighed, and sexed. If the adults had not emerged by 18, 16, or 15 d at 20, 25, and 30°C, respectively, they were considered too weak to complete emergence and were removed from the study. The time for the teneral adult to initiate boring (sclerotize enough to bore wood) was calculated as the difference between the date of eclosion and the date that wood dust was seen in artificial pupal chamber. Sclerotization was not measured directly, but beetles did melanize in the first few days after eclosion, and although they had sclerotized sufficiently to bore out, may not have fully sclerotized until emergence or thereafter. The amount of wood the adult bored through to emerge was calculated as a cylindrical volume (mm^3) by using the product of the depth of wood they had bored through and the area of the exit hole. The rate of wood boring (mm^3/d) was calculated as the quotient of the wood volume bored divided by the number of days from initial boring to emergence. The time for adults to bore out of the wood was calculated as the difference between the date on which they first began boring and the date of adult emergence in the outer tube.

The lower temperature threshold (T_L) for adult sclerotization and subsequent adult boring out of the wood were estimated using linear regressions (Statistix 2008). The relationships between adult weight (g) and both exit hole diameter (mm) and rate of wood boring (mm^3/d) also were estimated using linear regressions (Statistix 2008). A restricted maximum likelihood estimation method (REML, PROC MIXED) followed by a least squares means separation test with $\alpha = 0.05$ and a Bonferroni correction (SAS Institute 1999) were used to make between temperature comparisons. This estimation method provides unbiased estimates of variance in unbalanced designs. The model for adult weights (g) and boring rate (mm^3) used temperature, population (IL or IM), and sex as fixed effects, whereas the model for developmental time (d) used temperature as a fixed effect and population as a random effect. The combined percentage failure and fungal infection rates were compared using pair-wise Pearson's χ^2 analysis (Statistix 2008) between the temperatures.

The cumulative distributions of days and degree-days to initiate boring and to complete boring to emerge out of the wood at three temperatures were calculated. The degree-days were calculated for each individual separately by subtracting the estimated T_L from the constant holding temperature, then multiplying by the number of days required to complete each phase. The data for the IM and IL populations were pooled to provide the most robust estimations of DD requirements. The cumulative proportion of individuals (P) over accumulated degree-days (DD) was described using a Gompertz function,

$$P = \exp(-\exp(-b\mathrm{DD} + a),$$

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). Predicted accumulated DD for 10, 50, 90, and 99% of individuals to complete each phase were calculated.

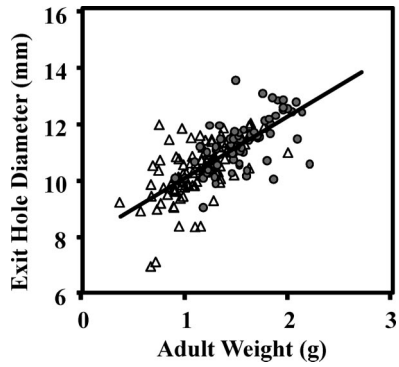

Fig. 3. Correlation between the weight (g) of beetles and the diameter (mm) of the exit hole they bored through the wood plug to emerge. Male (open triangles) and female (solid circles) weights and the linear regression line ($y = 2.1867*x + 7.9385$) are shown.

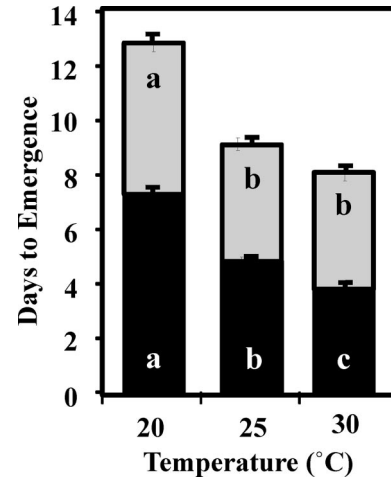

Fig. 4. Average (±SE) number of days for teneral adults (male and female combined) to initiate boring after eclosion (lower black portion of each bar) and complete boring to emerge (upper gray portion of each bar) at three temperatures. Different letters indicate significant differences separately for each developmental time frame.

Results

There was no significant difference in depth of wood the beetles had to bore through in the three temperatures ($F = 1.33$; df 183, 2; $P = 0.2674$). Although most of the adults emerged, some beetles died from fungal infections (4% at 20°C, 3% at 25°C, and 7% at 30°C), and a few were removed because they became too weak while boring to finish and emerge (1% at 20°C, 0% at 25°C, and 7% at 30°C). The combined fungal infection and failure percentages at 30°C were significantly greater than at 25°C ($\chi^2 = 7.78$, df = 1, $P = 0.0053$) and 20°C ($\chi^2 = 4.71$, df = 1, $P = 0.0300$). Females (1.56 ± 0.02 g) weighed significantly more than males (1.10 ± 0.02 g; $F = 218.6$; df 191, 1; $P < 0.0001$), and IM individuals (1.50 ± 0.2) weighed significantly more than IL individuals (1.16 ± 0.2; $F = 125.9$; df 191, 1; p, 0.0001). However, the average weight of the beetles emerging at each temperature did not differ ($F = 1.56$; df 191, 2; $P = 0.22125$). Adult weight was correlated positively with exit hole diameter (exit hole diameter = 2.07*weight (g) + 8.11; $R^2 = 0.4894$ $F = 178.4$, df = 185, 1, $P < 0.0001$) and the average diameter of the perfectly round exit holes was 10.8 ± 0.8 with a range of 5.6–13.6 mm (Fig. 3).

The rate at which beetles bored through the wood significantly differed between temperatures ($F = 6.00$; df 181, 2; $P = 0.0030$), regardless of sexes ($F = 1.32$; df 181, 1; $P = 0.2523$) or populations ($F = 0.00$; df 181, 1; $P = 0.9925$). Beetles bored (mean ± SE) 137.8 ± 8.8 mm^3/d at 20°C, 177.8 ± 8.1 mm^3/d at 25°C, and 167.0 ± 9.3 mm^3/d at 30°C; significantly faster at 25 than at 20°C. Adult weight was correlated positively ($F = 4.34$; df 185, 1; $P = 0.0387$) with the rate beetles bored out of the wood but the fit was poor (rate [mm^3/d] = 30.1 ± 14.5 * weight [g] + 121.5 ± 19.6; $R^2 = 0.0177$). The average number of days for teneral adults to initiate boring after eclosion significantly decreased with increasing temperature ($F = 5.12$; df 192, 2; $P < 0.0001$); 7.25 ± 0.39 d at 20°C, 4.77 ± 0.38 d at 25°C, and 3.80 ± 0.39 d at 30°C (Fig. 4). The average number of days to bore through the wood to emerge significantly differed between temperatures ($F = 7.22$; df 192, 2; $P = 0.0009$); beetles emerged faster at 25 and 30°C (4.35 ± 0.41, 4.36 ± 0.43) than at 20°C (5.52 ± 0.42, Fig. 4). The lower threshold temperature at which a beetle could sclerotize enough to initiate boring was estimated to be −1.2°C (eclosion to initiation of boring developmental rate (1/d) = 0.064*temperature + 0.076, $R^2 = 0.995$) and to completely bore through the wood to emerge was estimated to be −6.5°C (boring developmental rate (1/d) = 0.025*temperature + 0.16, $R^2 = 0.766$). The predicted degree-day accumulations at which 10, 50, 90, and 99% of the adults would initiate boring after eclosion and emerge after boring out of the wood along with the parameters for the calculated Gompertz curves are given in Table 1 and the actual values with the predicted fitted curves are shown in Fig. 5.

Discussion

Temperature had a significant effect on the time for adults to initiate boring after eclosion and bore through Norway maple wood to emerge; as the temperature increased the total time in the wood decreased. They spend more than a week in the wood even at summer temperatures, although there are other factors not investigated that could also affect the rate of initiation of boring or completion of boring (e.g., wood density and wood moisture content). Our findings exceed the 1 wk estimated in China (Yan and Qin 1992), but the temperatures to which those adults were exposed may have been higher than those we investigated.

The teneral adult stage involves significant increases in body weight, muscle, chemical fuel, and enzymes, as well as, changes in color and skeletal mechanical properties (Neville 1983). Based on the

Table 1. Parameter values and measures of statistical significance for predicting the relationship between proportions of *A. glabripennis* completing each phase (eclosion to initiating boring or initiating boring to emergence) and number of accumulated degree-days above the lower threshold

Phase	n^a	a ± SE	b ± SE	F	df	p	Adjusted R^2	Predicted accumulated degree-days for adults completing each phase			
								10%	50%	90%	99%
Eclosion to initiating boring	21	0.0307 ± 0.0014	3.45 ± 0.17	3686	21, 23	<0.0001	0.992	85.1	124.2	185.6	262.1
Initiating boring to emergence	26	0.0194 ± 0.0005	2.20 ± 0.07	13599	26, 28	<0.0001	0.996	70.4	132.4	229.7	351.0

[a] This *n* is the number of unique DD values (with varying proportions of the population associated with each) that were used in the calculations.

deposition of endocuticular layers in other beetles, the full skeletal tanning process may take a long time, for example, 20–40 d in *Oryctes rhinoceros* (L.) at 24–34°C (Zelazny and Neville 1972). In beetles, unlike many other insects, the number of layers deposited in a day increases, whereas the thickness of the layers decreases with increasing temperature (Zelazny and Neville 1972). As a result, the cuticle of beetles that sclerotize at higher temperatures may be thinner and less able to resist infection or withstand the rigors of boring out of the wood. This along with other factors such as, expending too much of their energy resources trying to bore out and entomopathogens generally act faster as temperature increases, may explain the higher combined fungal infection rates and failures to emerge that we observed at 30°C as opposed to the lower temperatures. This is not just a laboratory phenomenon because 3–4% of the beetles in poplars in China failed to emerge under normal summer temperatures (Zhou et al. 1993). These adverse effects on teneral adults may help to explain why the timing of pupation in *A. glabripennis* seems to be controlled by the combination of a threshold larval weight and a temperature gate that prevents adult emergence during the hottest part of the summer (Keena and Moore 2010).

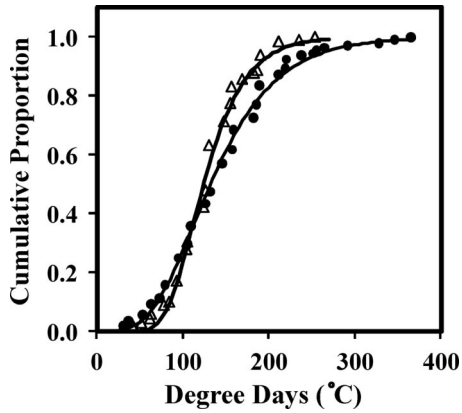

Fig. 5. Cumulative proportion of teneral *A. glabripennis* initiating boring after eclosion (open triangles) and completing boring to emerge out of the wood (black circles) over accumulated degree-days. The solid lines represent the fitted equations (Table 1).

These results can be used in a variety of ways to better define beetle behavior and population dynamics. Coupled with data on the phenology of the other beetle stages, they can be used to predict the timing of adult emergence so that eradication treatments can be appropriately timed. They can also be used to estimate when adult beetles are sexually mature after boring out of the wood. Time from eclosion to first oviposition in females or to first successful mating in males is available under a variety of environmental conditions in the laboratory (e.g., temperatures and larval hosts). Subtracting the total time in the wood from these laboratory values provides an estimate of when adults are sexually mature in nature. The relationship between the diameter of the exit hole and adult weight can be used to predict not only the size of beetles that emerged from the trees but also the fecundity of females, because female weight and fecundity are positively correlated (Keena 2002). The fecundity could then be used to assess the potential rate of population increase throughout an infested area.

Some care should be taken in directly applying these laboratory temperature relationships to the field. The thermal environment to which the teneral adult is exposed in the wood can be very different depending on location in the tree, depth within the wood, wood density, solar exposure, topographic position of the tree, and seasonality. During the day, direct solar radiation, reflected solar radiation, and thermal radiation, in addition to air temperature and wind speed, affect wood temperature. At night, stored thermal radiation continues to keep wood temperature higher than the ambient air temperature. Also, temperatures deeper in the trunk can take minutes to hours to equilibrate after external conditions have changed (Derby and Gates 1966). In *Pinus contorta* Douglas ex Loud., 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). When using the degree-day estimates from our studies to predict the phenology of this beetle at least 2°C should be added to both day and

night air temperatures or to the lower threshold when making these calculations.

Similar information on temperature effects for other stages of *A. glabripennis* (Keena 2006, Keena and Moore 2010) combined with these findings will aid in developing maps of potential geographical range and phenological models to predict the timing of all life stages. Our findings on teneral adults is particularly important for estimating the timing of adult emergence, which is critical for deployment of pheromone traps and other detection strategies available to the eradication program.

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