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Research

A Variable-Instar Climate-Driven Individual Beetle-Based Phenology Model for the Invasive Asian Longhorned Beetle (Coleoptera: Cerambycidae)

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Abstract

Efforts to manage and eradicate invasive species can benefit from an improved understanding of the physiology, biology, and behavior of the target species, and ongoing efforts to eradicate the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) highlight the roles this information may play. Here, we present a climate-driven phenology model for *A. glabripennis* that provides simulated life-tables for populations of individual beetles under variable climatic conditions that takes into account the variable number of instars beetles may undergo as larvae. Phenology parameters in the model are based on a synthesis of published data and studies of *A. glabripennis*, and the model output was evaluated using a laboratory-reared population maintained under varying temperatures mimicking those typical of Central Park in New York City. The model was stable under variations in population size, simulation length, and the Julian dates used to initiate individual beetles within the population. Comparison of model results with previously published field-based phenology studies in native and invasive populations indicates both this new phenology model, and the previously published heating-degree-day model show good agreement in the prediction of the beginning of the flight season for adults. However, the phenology model described here avoids underpredicting the cumulative emergence of adults through the season, in addition to providing tables of life stages and estimations of voltinism for local populations. This information can play a key role in evaluating risk by predicting the potential for population growth, and may facilitate the optimization of management and eradication efforts.

Key words: simulation, population structure, heating degree days, voltinism

Managing nonnative species that pose a threat to the ecology and economics of an introduced environment is a complex challenge that can benefit from a sound understanding of the biology, behavior, and population dynamics of the target species. The Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) is an excellent example of this issue. Prior to its detection in the United States in Brooklyn, NY, in 1996 (Poland et al. 1998), only limited research had been conducted in the beetle's native range in China and the Korean peninsula, driven primarily by its identification as a pest of introduced tree species in parts of the Three North Shelter Forest Program in China (Yan and Qin 1992). Since the detection of a breeding population of beetles in Brooklyn, NY, additional populations have been found in four other states in the United States along with populations in Canada, France, Germany, Italy, the United Kingdom, the Netherlands, Austria, Switzerland, Japan, and Finland, making this a species of global concern and highlighting the need to understand the phenology and population structure of the beetle under varying climatic conditions.

Although biological knowledge of this species has expanded greatly since the Brooklyn detection, including the development of a heating-degree-day model for adult emergence described by Smith et al. (2004), there are still knowledge gaps that limit our understanding of the basic biology driving the invasion dynamics of the beetle, and filling these may assist the development of management and eradication program strategies. For example, the European and Mediterranean Plant Protection Organization (EPPO) requirement for the declaration of eradication states "*A. glabripennis* can be considered eradicated when the following condition is fulfilled: no findings of *A. glabripennis* for two complete life cycles of the pest with a minimum of 4 years of annual monitoring and sampling in the regulated area." (EPPO 2013). However, limited data are available on the time required for beetles to complete development (referred to hereafter simply as patterns of voltinism, for simplicity). Several previous studies have indicated the beetle is typically univoltine, with a minority of the population completing development in 2 yr (Yan and Qin 1992; Li and Wu 1993; Gao et al. 1997; Lingafelter and

Hoebeke 2002; Haack et al. 2006, 2010; Hu et al. 2009; Sánchez and Keena 2013). However available data on voltinism are limited, and many statements regarding beetle voltinism are based on work by Hua et al. (1992), summarized by Lingafelter and Hoebeke (2002), and Li and Wu (1993) as summarized by Hu et al. (2009). Using surveys of larvae in trees, Hua et al (1992) found that 80–95% of the population was expected to complete development in a single year, with older overwintering instars suggesting a semivoltine component of the population. Similarly, Li and Wu (1993) found that in Inner Mongolia a single generation takes 2 yr to complete development, but in Shandong Province, about 90% of the beetles in a population complete development in a single year. As discussed by Hu et al. (2009), it is likely that patterns of voltinism are likely to vary with changes in climate. A recent paper by Straw et al. (2015), that assessed a population of Asian longhorned beetle under eradication in the United Kingdom, has expanded the range of observed voltinisms with the finding that most of the surveyed beetles required 3 yr to complete development. As new infestations are found, there is a need to rapidly determine the potential for population growth; however, at this time tools to predict voltinism or timing of beetle life-stages and instars in a population are not available. One of the primary reasons for these knowledge gaps, succinctly stated by Gao et al. (1997) is that, with the exception of adults, the life stages of the beetle take place inside trees. Because generation time and population structure play heavy roles in determining population growth rates, phenology models for this species are needed to describe these patterns in both known and newly identified populations (Faccoli et al. 2015, Straw et al. 2015).

Sources of data on the development of the Asian longhorned beetle in host material include several field-based and laboratory studies conducted within the beetle's native range in China (Yan and Qin 1992, Yang et al. 2000, Smith et al. 2004, Haack et al. 2006), as well as exotic populations in Cornuda, Italy (Faccoli et al. 2015) and Paddock Wood in the United Kingdom (Straw et al. 2015). Currently, the best tool available for evaluating the phenology of beetle populations is the heating-degree-day model (hereafter simply degree-day model) developed by Smith et al. (2004). Based on intensive field surveys carried out in the beetle's native range in China, this model provides a tool to predict both the timing of first emergence and the accumulation of adult beetles through the growing season. A recent study by Faccoli et al. (2015) of a reproducing population in Italy has provided good support for the model's identification of the first day of beetle emergence. However, once adult emergence started in the population studied by Faccoli et al. (2015), it progressed more quickly than predicted by the degree-day model, suggesting additional tools are needed to continue to improve our understanding of the beetle's phenology. However, as previously noted, the development of beetles within trees precludes following individual beetles through full development, and limits most surveys to snap-shots in time of population structure from which phenology and voltinism can be inferred.

Laboratory studies can fill some of these knowledge gaps. By rearing beetles in artificial diet and tracking the development of individual beetles through each instar and life stage (Keena 2006, Keena and Moore 2010, Sánchez and Keena 2013) under controlled conditions more detail about the number and requirements of various beetle life stages can be evaluated. Using a population of laboratory reared beetles maintained in a quarantine facility, Keena and Moore (2010) were able to document the heat requirements for individual beetle instars and pupae, and found that larvae must complete a minimum of five instars and reach a critical weight of 500 mg to proceed to pupation. Other laboratory based studies conducted by Keena (2006) and Sánchez and Keena (2013) have identified the requirements for eggs and emerging adults (respectively). Constant temperature experiments, however, rarely represent natural patterns. Field studies by both Haack et al. (2006) and Faccoli et al. (2015) found that beetles typically overwinter as eggs or larvae. This indicates beetles, once they reach a suitable size and instar for pupation, may proceed to pupate, or, if it is too late in the growing season to complete development, may remain as larvae through the fall and into the winter. Unfortunately, the specific cues (threshold temperature, time spent at decreasing temperatures, etc.) that trigger this postponement of pupation are not known.

Because field studies are limited in their ability to track the development of individual beetles through time, and laboratory conditions rarely mimic natural conditions, the development of a phenology model for this species must depend on the use of both sources of information. Here we seek to synthesize available data and observations on the phenology of the Asian longhorned beetle to develop a consolidated phenology model applicable to known infestations, as well as regions of the landscape considered at-risk to invasion. By synthesizing this information, it is possible to both identify continuing gaps in knowledge, and provide tools to improve our understanding of the biology of the beetle, and management approaches suited to that biology.

Currently, eradication programs are based on the visual identification of infested trees by surveys for visible oviposition scars and exit holes, and the destruction of infested trees by chipping. Due to this approach, surveys of the landscape for beetles and beetle damage is an expensive, time-consuming, and costly endeavor and tools that can optimize or prioritize survey efforts could benefit eradication programs. The challenges of conducting large-scale ground-based surveys has also prompted the push to develop additional survey tools including pheromone-baited traps (Nehme et al. 2013, Meng et al 2014, Nehme et al. 2014) as well as efforts to improve their efficacy (Crook et al. 2014). The use of these traps, which are effective only for the mobile adults, require periodic trap-checks and maintenance of the lures. Consequently, there is a benefit to limiting the deployment of traps both spatially and temporally to focus on the adult flight season.

Knowledge of the timing of the adult flight season could also have bearing on protocols used to remove trees. For example, disturbing standing infested trees by felling creates the opportunity to encourage beetles that might otherwise have remained in the infested natal canopy to take flight, creating a potential but unquantified risk for population spread. However, leaving the tree in place until after the flight season ends misses the opportunity to remove beetles from the population before they emerge from the tree. Balancing the potential for spread by dispersal with the potential for population growth by the continued presence of an infested tree will require an improved understanding of both the phenology of the insect as it relates to local climates, as well as its behavior, population dynamics, and potential for population growth.

Here, we seek to compile and expand on past work to develop a phenology model based on allowing individual beetles to progress through each of the life-stages and instars at rates dictated by local temperatures, and following the patterns observed by both field and laboratory studies, such as the lack of overwintering pupae. This approach offers the opportunity to consolidate available information on the life-history of the Asian longhorned beetle, and extend this information to identify the timing of key life-stages in beetle populations such as flight times and voltinism in a testable way. Using an individual beetle-based approach also provides an opportunity to allow extensive flexibility in the model, and offers the opportunity to modify it as new information is developed.

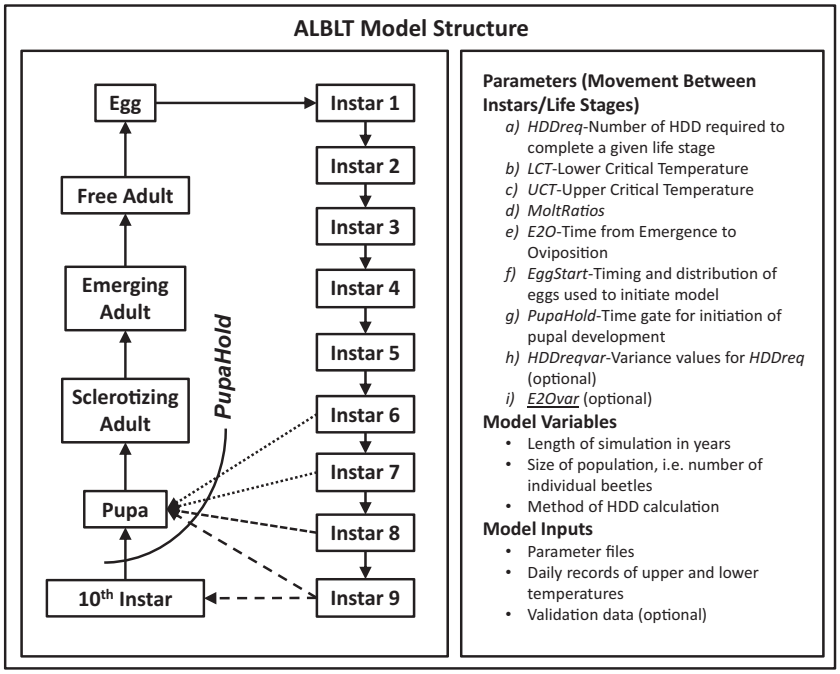

Fig. 1. The panel on the left shows the general flow of the individual beetles through the simulated phenology model. Arrows between instars denote movement of individuals between instars/life stages based on the parameters listed in the right panel. The line marked with the variable *Pupalhold* represents the temperature gate that can prevent beetles progressing to pupation in the fall.

Materials and Methods

General Model Structure and Overview

An individual-beetle-based Asian Longhorned Beetle Life-Table [ALBLT] model (hereafter simply "phenology model" for simplicity) was built for the Asian longhorned beetle using MATLAB R2013b (8.2.0.701) (code available in Supplemental Appendix [online only]). This model carries individual beetles through (up to) 16 steps in the beetle's life history including egg, instars 1–11, pupa, sclerotizing adult (time between eclosion and initiation of chewing to exit the tree), emerging adult (time spent chewing out of tree), and free (emerged) adult (Fig. 1). The model is initiated with a population of eggs and subsequent instars/life stages develop at rates driven by the accumulation of heating degree days (Allen 1976) based on the lower and upper critical temperatures specific to each instar/life stage. Use of heating degree days has a long history of application in estimating the physiological age of poikilothermic organisms including many insects (Allen 1976, Bernhardt and Shepard 1978). Within the simulation, the beetles are treated as a fixed population such that each individual adult beetle is ultimately replaced with an individual egg. Population growth and mortality are not considered within this model, as the goal of this model is to provide a life-table for the beetle to estimate population phenology, voltinism, and flight seasons for adults rather than simulating population dynamics.

The beetle population in the phenology model is represented by a matrix of size $i \times s \times g$, in which i represents the number of individual beetles, s represents each of the possible 16 beetle instar/life-stages, and g represents the number of generations. Values within the matrix indicate the cumulative Julian date (JD) on which an individual beetle has completed a specified instar/life-stage. The population is initiated with a population of eggs using start dates based on either a list of dates provided by the user, or by using a probability distribution of start dates based on parameters selected by the user. These parameters are set using the parameter *EggStart* (note that variables used in the model are denoted in the text by italics). Initially the egg start dates used in the model were based on a normal distribution (mean Julian date = 230, standard deviation = 24 d), however later analyses indicated the simulation was not sensitive to variation in start dates, making the parameter irrelevant within these analyses. Once initiated each beetle proceeds through each life-stage and instar at a rate dictated by daily minimum and maximum temperatures and the resulting accumulation of heating degree days (Allen 1976). Each beetle life-stage and instar has unique requirements for the accumulation of heating degree days (*HDDreq*), as well as unique upper and lower critical temperatures for development (*UCT*, *LCT*, respectively). Heating degree days are calculated using the modified sine wave method and the six temperature cases described by Allen (1976), which do not assume that temperature fluctuations are symmetrical through time (i.e. minimum temperature on day T is not assumed to be the same as the minimum temperature on day T + 1). Calculations are carried out using a custom script hddAllen.m available in the Supplemental Appendix (online only). The Julian date on which an individual beetle completes an instar/life stage is determined simply by

$$JD_{i,s,g} = JD_{i,s-1,g} + D_{i,s,g}$$

where $JD_{i,s,g}$ is the Julian day on which individual beetle i of generation g completed instar/life-stage s, $JD_{i,s-1}$ is the date on which individual i completed the prior instar/life stage, and $D_{i,s,g}$ is the number of elapsed days required to accumulate the required number of heating degree days for instar/life-stage s, with a start date represented by $JD_{i,s-1}$. Numbers of days required for each beetle are determined by calculating the daily accumulated heating degree days for each day in the simulation using *UCT* and *LCT* values for each of the instars/life-stages.

Although the phenology model includes utilities to calculate heating degree day values using alternate methods, the modified sine wave method provides a robust estimate of heat accumulation, and so the outputs shown here are limited to this method. Additional methods allowing higher temporal resolution such as those discussed by Reicosky et al. (1989) are computationally intensive, but may have utility and merit further exploration; however, their application is beyond the scope and focus of this paper.

Previous research has shown there is plasticity in the number of instars the Asian longhorned beetle may go through prior to pupation, with individuals passing through at least 5, and in very rare occasions under laboratory conditions, as many as 22 instars (Keena and Moore 2010). To accommodate this variation, beetles in the simulation can develop through up to 11 instars, and beetles are allowed to progress from any instar between the 5th and the 10th (inclusive) directly to pupae based on instar-specific probabilities derived from data used in Keena and Moore (2010). The assigned probability for each beetle is considered an independent event, such that the probability of a beetle progressing to pupation does not influence the probability of pupation for any other beetle. These probabilities are incorporated into the model using the variable *MoltRatios*, their logical role in the model is indicated by the dashed lines in Fig. 1, and the parameters used are provided in Table 1. Within the phenology model, beetles were limited to a maximum of 11 instars for three reasons. First, beetles that progressed beyond the 11th instar were typically those held at constant temperatures $\geq 35\,^{\circ}C$, a condition which is atypical of the deciduous extra-tropical systems that would be expected to host the beetle. Second, few beetles that progressed beyond this instar survived to become adults (Keena and Moore 2010). Third, these late instars have been documented for only seven beetles, and this population was too small to statistically determine the *LCT* and *UCT*. Because of the omission of these rare (~2%) individuals, it is important to note that the output from the model may not capture extremely long voltinism rates expressed by rare individuals. Similarly, these upper temperature limits for beetle development suggest the model may not be suitable for application in tropical systems.

Parameters of Beetle Development

The model uses seven sets of required parameters including the number of heating degree days required for the completion of each of each instar/life stage (*HDDreq*), the upper and lower critical temperatures for development (*UCT* and *LCT*, respectively), the probability of molting from any instar between 5 and 10 (inclusive) to pupae (*MoltRatios*), the time from the emergence of an adult to oviposition (*E2O*), a table of egg start times (or a probability distribution for the start dates) for the first generation of eggs (*EggStart*) used to initiate the model (Fig. 1), and a time-and-temperature gate used to identify the time in the growing season beyond which beetle larvae will not progress to pupation (*PupaHold*). The values used for these parameters are provided below, and are loaded into the model as formatted text or Microsoft Excel files. Copies of these files are provided in the Supplemental Appendix (online only).

The original parameter estimates for the required number of heating degree days (*HDDreq*) and lower critical temperature (*LCT*) were obtained from Keena and Moore (2010). This source provided parameter estimates for instars 1–8, a separate category labeled the ultimate instar (defined as the instar preceding pupation), and pupae. Although *HDDreq* and *LCT* were well parameterized in Keena and Moore (2010), there were limited data available to identify the upper critical temperature thresholds, though Keena and Moore (2010) found that development was severely limited above $30\,^{\circ}C$ and that the lethal temperature was somewhere between 35 and $40\,^{\circ}C$. Based on this information, the upper critical temperature (*UCT*) for all instars and life stages was set to $30\,^{\circ}C$ with the exception of the first instar for which the UCT was set to $40\,^{\circ}C$ based on Table 1 in Keena and Moore (2010). Values for *HDDreq*, *UCT*, and *LCT* for eggs were obtained from Keena (2006). Following pupation, beetles continue through three additional life stages. The first two of these are the time spent as a sclerotizing adult and an emerging adult, as described by Sánchez and Keena (2013). The parameters for *HDDreq*, *UCT*, and *LCT* for these two within-tree stages were obtained from Table 1 in Sánchez and Keena (2013). Time from adult emergence to oviposition (the free adult stage indicated by the parameter *E2O*) was set to the minimum observed rate of 16 d, as described in Keena (2006). Although temperature is known to play a role in determining ovipositional behavior (Keena 2006) for the Asian longhorned beetle, the inclusion of long emergence to oviposition rates in the simulation due to low temperatures late in the year creates the unrealistic potential for adults to oviposit in winter. This set rate is used with the recognition that this has the potential to result in a slight bias toward shorter voltinism rates than might occur for this subset of the population under natural conditions. The phenology model uses this first day of oviposition as the time point at which to transition adults to eggs for the initiation of the next generation. Collectively, the parameters from the sources described above are referred to within this analysis as the original parameters, and are listed in Table 2.

Although these original parameters provide a starting point for estimating the phenology of the Asian longhorned beetle, we recognize that the use of a pooled ultimate instar category as described in Keena and Moore (2010) may overgeneralize the development of the beetles. To expand the phenology model to include later instars the data originally used in Keena and Moore (2010) were recalculated using alternate criteria for inclusion. First, only those beetles that completed development were included in the analyses. Second,

Table 1. Values for the parameters *UCT* and *MoltRatios* for each life stage, and specified times for *E20* and *PupalHold* used in the model

Beetle life stage/Instar	*UCT*	*Molt Ratios*
Eggs	34	0
1st Instars	40	0
2nd Instars	30	0
3rd Instars	30	0
4th Instars	30	0
5th Instars	30	0.002695418
6th Instars	30	0.078167116
7th Instars	30	0.283018868
8th Instars	30	0.544474394
9th Instars	30	0.684636119
10th Instars	30[a]	0.916442049
11th Instars	30[a]	1
Pupae	30	1
Sclerotizing adult	30	1
Emerging (chewing) adult	30	1
Individual parameter values	Specified times (d)	
E20	16	
PupaHold	14	

[a] When the original data are used, the values for 10th and 11th instars are replaced with zeros, as these instars are not included in the original data from Keena and Moore (2010).

Table 2. Parameters for *HDDreq* and *LCT* for each life stage or instar used in the phenology model for each of the three scenarios used in developing it

Beetle life stage/ Instar	Original		Recalculated		Modified	
	HDDreq	*LCT*	*HDDreq*	*LCT*	*HDDreq*	*LCT*
Eggs	248.39	12.00	248.39	12.00	248.39	12.00
1st Instars	78.30	9.66	66.28	11.10	66.28	11.10
2nd Instars	111.70	10.32	92.77	11.75	92.77	11.75
3rd Instars	153.00	10.11	119.36	13.06	119.36	13.06
4th Instars	250.60	9.10	243.88	8.74	243.88	8.74
5th Instars	284.80	9.81	282.96	9.52	282.96	9.52
6th Instars	279.20	12.67	300.70	11.33	300.70	11.33
7th Instars	315.90	13.30	374.40	11.54	374.40	11.54
8th Instars	365.80	12.06	418.61	11.02	418.61	11.02
9th Instars	711.80	12.26	410.13	9.81	410.13	9.81
10th Instars	0.00	0.00	1081.76	−3.47	256.01	11.61
11th Instars	0.00	0.00	251.04	18.22	251.04	18.22
Pupae	255.70	10.10	262.86	9.78	262.86	9.78
Scleritizing adult	124.20	−1.20	124.20	−1.20	124.20	−1.20
Emerging (chewing) adult	132.40	−6.50	132.40	−6.50	132.40	−6.50

only those beetles held at constant temperatures (i.e. not transitioned to secondary temperatures during the original experiment, see Keena and Moore (2010) for additional information) were included. Third, parameters were estimated for instars up to and including instar 11, without the use of an ultimate instar category. These same data were used to recalculate the parameters for beetle pupae, and are hereafter referred to as the recalculated parameters (Table 1).

The temperature gate that prevents larvae from overwintering as pupae is incorporated in the model as a set date, beyond which the initiation of the pupal life-stage is put on hold (*PupaHold*). The date is defined as the number of days after the peak summer temperature, within these analyses, a 14 d gate was introduced that prevents larvae that have completed the development of an instar ≥ 5 from molting to pupa if more than 2 wk has passed since the maximum summer temperature. Development is held until temperatures begin to increase again in the spring and exceed the lower critical temperature necessary for continued development.

In addition to the seven sets of required parameters, the model also includes two optional parameters including the addition of variation in *HDDreq*, and variation in the number of days between adult beetle emergence from the tree and oviposition (*E2Ovar*). Because populations are maintained at a constant size, the oviposition date represents the date on which an adult beetle transitions to an egg. Though variance estimates are available for these parameters from their respective published sources, variance in these parameters was not included within these analyses in order to facilitate comparisons among locations by generating location-typical distributions of voltinism.

Model Validation

To evaluate the performance of the phenology model, results of the model were compared with a validation data set based on 184 beetles reared at temperatures that varied weekly to reflect the annual variation in temperature typical of Central Park in New York City, NY. This population was initiated using 31 pairs of laboratory-reared adults from the eighth laboratory generation of the Chicago, IL, population (Keena 2006). Pairs were put together the day that they were first provided *Acer saccharum* Marshall twigs for feeding, 4 d after their emergence; mating likely did not occur until about 2 wk later since adult beetles must first go through a period of maturation feeding. Pairs were then maintained in rearing jars with 3–7 cm diameter by 20 cm long *A. saccharum* bolts for oviposition. Oviposition pits chewed by the females were labeled daily, and bolts were replaced weekly. A total of 1,982 eggs were removed from under the bark 2–3 d after each bolt was removed from the rearing jar. Eggs were placed individually in the wells of a 24-well tissue culture plate and held in a water box in the same environmental chamber that held the adults.

Of the eggs laid, 1,193 larvae hatched, of which 406 were placed in artificial diet in 100- by 15-mm square petri dishes and monitored for molts. Larvae were monitored daily when chamber temperatures were >15 °C and one to three times per week at lower temperatures. When a molt was observed the larva was removed, weighed, the head capsule was saved, and the beetle was returned to a different corner of the same dish. Larvae were moved to new dishes of diet as the diet became unsuitable (dried out, indications of fungal growth, completely tunneled, etc.), or every 6 wk. If a larva appeared to be dead the date was recorded and the larva was held for 2 d to ensure that it was not simply inactive, as can be the case when a molt is impending. Larvae that died were removed from the study. As larvae prepared to pupate (shortened, becoming limp, with clearing behind the head), they were moved to a 50-ml container with a piece of damp paper towel to maintain moisture and held in a darkened water box in the study chamber until adult emergence. This procedure yielded 184 beetles that completed development from egg to adult, referred to hereafter as the validation data. Key milestones in the phenology of individual beetles in the validation data are provided in the Supplemental Material (online only). Other aspects of adult and larval rearing methods and artificial diet (AG2) mirror those described by Keena and Moore (2010).

To allow comparison between the phenology model and the validation data, the phenology model was run using the same temperature profile used to rear the validation beetles, and was initiated with 184 beetles with egg start dates that mirrored those of the validation data to ensure equivalent starting conditions. The timing and proportions of the population in each instar between the simulated population and the validation population was compared graphically.

User-Defined Variables and Options

In addition to the values used to define the required number of heating degree days, upper critical temperatures, and lower critical temperatures for each of the beetle stages and instars (*HDDreq*, *UCT*, and *LCT*, respectively) the phenology model includes user-defined model parameters. These include the length of the simulation (number of years the simulation runs), the population size (number of beetles used in the simulation driven by the number of eggs used to initiate the model), and the method of HDD calculation. ALBLT includes methods for calculating heating degree days including single triangulation and double sine (Allen 1976, Zalom et al. 1983). Evaluations of the sensitivity of the model to variation in the population size, simulation length, and timing of egg start dates are described below. Within the analyses discussed within this report data were presented based on the use of the double sine method, as this has been shown to be a robust estimation of heating degree days (Allen 1976).

Climate Data Inputs and Sources

The accumulation of heating degree days and associated development of the beetles is driven within the phenology model by daily minimum and maximum temperature normals. Data for locations within the United States were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NCEI) Climate Data Online (CDO) website (www.ncdc.noaa.gov/cdo-web/, accessed 31 March 2016) and were based on 30-yr averages (normals). Daily temperature normals in Italy, China, and Canada were based on daily values for the available periods of record for stations 00016098, 00052889, and 006158733, respectively, in the Global Historical Climatology Network (GHCN), also accessible through NOAA NCEI CDO. Temperature records for Paddock Wood were obtained from the British Atmospheric Data Centre (BADC) database. Temperatures representative of the newly identified infestation in Vantaa, Finland, were obtained from the GHCN network for the Helsinki Airport. Temperature data were loaded into the model as formatted text files or Microsoft Excel files. The expected temperature unit for the phenology model is degrees Celsius, though data in degrees Fahrenheit can be loaded and converted within the model when necessary. An example temperature data for New York City, NY, are provided in the Supplemental Appendix (online only).

Model Stability

The sensitivity and stability of the phenology model was assessed by running the model with varying population sizes (2 to 1,000 beetles for 400 yr using a Julian egg start date of 230), simulation lengths (2 to 1,000 yr using 400 beetles and a Julian egg start date of 230), and egg start dates (day 1 to 365, using 400 beetles with a simulation length of 400 yr), using the temperature normals for New York, NY. The output for each of these runs included the proportion of the population that completed development with a specified voltinism (Fig. 2). In each panel, the individual lines represent a specific voltinism, for example, the upper dashed line represents the portion of the population that completed development in 24 mo. The lack of crossing lines shows that as population size, simulation length, and egg-start date varied, the proportion of the population completing development in 24 mo remained consistent. The variation evident in the early portions of the graph represent stochasticity that would be expected in short simulations and small populations. Stability occurs around 100 yr and 100 beetles. To balance stability with computational requirements, the simulations described in the results section were run for 400 yr with 400 beetles. As Fig. 3C shows, start dates do not effect model results, though a start date of 230 was used for consistency.

Results and Discussion

Model Validation and Parameter Selection

Initial comparisons of both the simulated and validation beetle populations indicated the model effectively captured variation in the timing and proportions of beetle instars from egg through instar 9 (i.e. the ultimate Instar as described by Keena and Moore 2010) when the original parameters were used (Fig. 3A). The simulation did not capture the development of 10th and 11th instars, as those instars and their parameters were missing from the simulation (this was achieved computationally by forcing the individuals through these instars in a single day; Table 1). Despite the absence of these instars, the model captured the timing of the emergence of adults well for both the univoltine and semivoltine portions of the population. These findings are in agreement with Gao et al. (1997) and Yan and Qin (1992) in that beetle development may require 2 yr. However, the pattern differs in that prior studies suggested the majority of beetles complete development in 1 yr, whereas here, the semivoltine beetles make up the majority of the population in both the simulation results, as well as the experimentally reared beetles used to build the validation data set.

As described in the methods, the original parameters lacked information for instars 9–11. Running the phenology model using the recalculated parameters allows for the inclusion of these instars and produces the output shown in **Fig. 3B**. As the figure shows, the simulation now captures the segments of the population that developed through these late instars. Like the output resulting from the use of the original parameters, the phenology model captures the timing of adult emergence, as well as the ratios of both the univoltine and semivoltine portions of the population. The lack of a difference between the results generated by the original and recalculated parameters is likely the result of the use of the "ultimate instar" category described by Keena and Moore (2010) that compiled the time spent in instars 9 through 11. Although these instars were not individually described, the time spent in them is still included due to the use of the pooled "ultimate instar" category and so convergence would be expected between the data sets at pupation, with some variance driven by the probabilities of beetles progressing through these late instars.

Although the recalculated LCT parameters for instars 1 through 8 remained stable when compared with the original parameters, the newly calculated parameters for instars 9–11 yielded values for the *HDDreq* and *LCT* for instar 10 that deviated substantially from the values calculated for other instars (Table 1). With any phenological analysis (particularly when sample sizes are limited) there is always the potential to have atypical patterns driven by a few individuals in the population. In the case of these beetles however, an overview of the data does not suggest that this pattern is driven by a few beetles with extreme values. However, in the interest of evaluating the potential role these extreme values may play in the model, the simulation was run with these extreme values replaced with values based on the averages of the other 10 instars (modified parameters, Table 1). These changes made little difference to the timing of beetle development and results are highly similar to those produced by the recalculated parameters. Based on this limited impact, and in the absence of a biological or empirical rational for using the original data with its pooled late instars, the following analyses and comparisons are made using the recalculated parameters.

As noted by Haack et al. (2006) and Faccoli et al. (2015), populations of the beetle overwinter as eggs or larvae, suggesting a temperature gate prevents beetles from progressing to pupae in the fall. Within this phenology model this is accomplished through the use of a temperature-and-time gate. To evaluate the impact of this development gate, the simulation was run without it (Fig. 3C), with results showing that in the absence of a gate, the proportion of the population with a univoltine generation time is overestimated. An assessment of variations in the pupal gate suggest that a 14 d gate yields development and voltinism patterns for adults that match the empirical patterns found in the validation data. Periods substantially longer than this resulted in overestimates of the proportion of the population with a univoltine life-history, periods substantially shorter can overestimate the beetles with semivoltine life-histories. Based on these data, and in the absence of additional biological information, the model was set to a 14 d pupal gate, though additional research on this issue may help continue to refine the model.

Comparison of Model with Published Beetle Phenology Studies

Life history studies of the Asian longhorned beetle have been carried out in numerous field locations, including the beetle's native range in Liu Hua, near Lanzhou in Gansu Province, China (Smith et al. 2004), and two nonnative populations near Cornuda, Italy (Faccoli et al 2015), and Paddock Wood in the United Kingdom (Straw et al. 2015). Each of these studies was able to sample and/or survey a reproducing beetle population under field conditions at ambient temperatures, and these studies provided an opportunity to compare the findings of the Asian longhorned beetle phenology model described here, with population patterns found in multiple real-world locations.

Lanzhou, China, Asian Longhorned Beetle Population

Within the beetle's native range in China, Smith et al. (2004) found that adult beetles were detectable on the landscape once ~500 heating degree days (10°C base) had accumulated, and that the proportion of the emerged beetles could be modeled based on the continued accumulation of heating degree days. Based on the temperature normals for Lanzhou, China, the phenology model indicates the first beetles are likely to appear on May 30th, which is consistent with the first detection of adult beetles on June 2 by Smith et al. (2004) in the year 2000. This agreement highlights a more subtle consistency between the Smith et al. (2004) model and the laboratory-derived data used to parameterize the Asian longhorned beetle phenology model. Based on the observation by both Faccoli et al. (2015) and Haack et al. (2006) that beetles overwinter as larvae, the first adults to emerge in the summer should be the individuals that were ready to pupate at the end of the prior growing season and were gated by decreasing temperatures. Keena and Moore (2010) found pupae require about 254 heating degree days (with a 10.1 °C base), and Sánchez and Keena (2013) found that sclerotizing adults and emerging adults chewing through the wood of the host require 124 and 132 heating degree days (respectively) to complete, though with base temperatures of −1.2 and −6.5 °C under laboratory conditions. Thus, the ~500 degree days necessary for adult emergence documented by Smith et al. (2004) captures quite closely the cumulative heat requirements for the development of pupae and sclerotizing and emerging adults found in laboratory studies.

In addition to documenting the timing of beetle detections, Smith et al. (2004) assessed the accumulation of adult beetles over the growing season (equation 2 in Smith et al. 2004). The upper and lower confidence bounds of this model are shown with dashed lines on the panels of Fig. 4. The accumulation of adults predicted by the phenology model (solid line) is in general agreement with that predicted by the Smith et al. model for the beetles near Lanzhou China, though the phenology model predicts a rapid pulse of adult emergence at the beginning of the summer as a result of the backlog of late instar larvae entering the winter. The smoother and more gradual arrival of adults in the system observed by Smith et al. (2004) may be the result of variation in the microclimatic conditions experienced by the beetles due to shading, tree size, topographic position, etc., that would be expected in a natural landscape. Keena and Moore (2010) discussed the potential role the wood of the host tree may play in buffering thermal conditions experienced by the larvae, and previous authors including Hu et al. (2009) have suggested inter- and intraspecific variation in host quality may influence development rates. While the phenology model described here is in agreement with the laboratory population reared for model validation as well as the patterns found in the field by Smith et al. (2004), additional work is needed to refine the simulated patterns of emergence described by this model and characterize the role these additional factors play in patterns of beetle phenology.

In addition to estimating first emergence and the accumulation of adults through the growing season, the phenology model described here offers an opportunity to evaluate the patterns of voltinism for a population based on the heat requirements for each of the beetle's instars and life stages. Previous studies in China have indicated that populations of Asian longhorned beetle are likely to be a combination of univoltine and semivoltine, with the majority of the population developing in 1 yr (Hua et al. 1992, Yan and Qin 1992, Gao et al. 1997, Yang et al. 2000, Haack et al. 2006, Haack et al. 2010). The ALBLT phenology model agrees with the prediction of polyvoltinism (Fig. 5A); however, two patterns emerge that differ from previous findings. First, the study by Hua et al. (1992) found that ~80–95% of the beetle population was univoltine. Similarly, information available in the abstract for Yang et al. (2000) found that 90% of the beetles were univoltine, while 10% were semivoltine. Here, the phenology model suggests the opposite pattern, with the bulk of the population expressing a semivoltine life-history. The phenology model also suggests a small portion of the population may undergo a 3-yr life-cycle. While this third, slower developing portion of the population has not been confirmed in the field, the agreement with both the validation data (Fig. 2) and the timing of emergence described by Smith et al. (2004) suggests the potential for this third population component cannot be eliminated.

Asian Longhorned Beetle Near Cornuda, Italy

While there is consistency between field data and the phenology model for a native population in China, the need for the phenology model is driven largely by the beetle's establishment in novel environments and the need to evaluate patterns of beetle phenology under nonnative conditions. A study by Faccoli et al. (2015) took advantage of one of these populations by assessing the patterns of beetle development and emergence in a reproducing population near Cornuda, Italy. This study found adults emerging from trees at an earlier calendar date than had been observed in China, with emergence starting on May 22nd in 2011. This calendar date, however, is in agreement with the Smith et al. (2004) 500 degree-day physiological date for this location. Although first emergence was well predicted by the degree day model (Smith et al. 2004), the data presented by Faccoli et al. (2015) seems to indicate beetle populations emerged more quickly than were predicted once emergence had started (Fig. 3 in Faccoli et al. 2015). It is worth noting that the phenology model described here is consistent with both the estimated first date of emergence as well as the more rapid emergence of adults (Fig. 5G), though only for the first half of the adult emergence season. Although temperature differences between Cornuda, Italy, and Lanzhou, China, were substantial enough to produce a change in the timing of first emergence and the accumulation of adults, patterns of voltinism between these populations are similar, suggesting (all other factors being equal) population growth rates at these locations may also be similar.

Asian Longhorned Beetle Near Paddock Wood, England

In 2012, Straw et al. (2015) documented the population structure of a reproducing population of Asian longhorned beetle at Paddock Wood in Kent in the United Kingdom. By dissecting infested trees they were able to collect more than 450 live and dead larvae and document their size distribution. Their findings suggested that

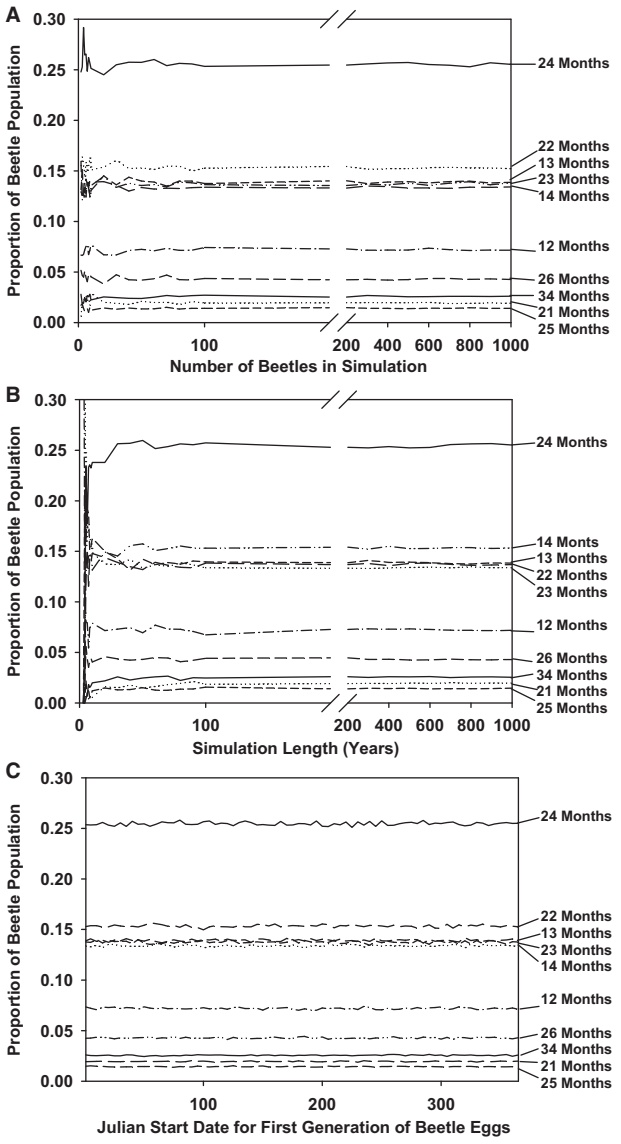

Fig. 2. Patterns of voltinism, represented by lines indicating the proportion of the beetle population that completes development in a given number of months, are shown with variations in numbers of beetles in the simulation (**A**), simulation lengths (**B**), and start dates used for the eggs to initiate the phenology model (**C**). The lack of intersecting lines shows that the phenology model exhibits stability with variation in these parameters.

beetles in this location undergo a 3-yr life cycle based on a dichotomous distribution of larval sizes in early-to-mid summer. This generation time is longer than has been previously described, though is consistent with the cooler conditions at Paddock Wood. Using weather data from the same area, the phenology model also indicates a substantial portion of the population requires 3 yr to develop (Fig. 5H), although the model also indicates beetles may develop in as few as 2 yr, or as many as 4, with 3 yr being the dominant voltinism. The phenology model also indicates there may be portions of the population that take up to 8 yr to develop; however, this assumes that the beetles would be able to survive predation, plant defenses, and a stochastic environment for an extended time period. Without information on survival at these time scales, it is not possible to determine whether this long-lived cohort is biologically feasible.

Straw et al. (2015) also found adults emerged later in the season than previously described populations, with the bulk of emergence occurring in August. Using weather data from the same location used in Straw et al. (2015) in the ALBLT phenology model indicates emergence might first occur 2 wk earlier, in mid-July. Although this difference of 2 wk may seem large it is important to note that the estimated emergence dates at Paddock Wood were based on estimating the seasonality of adult emergence using callous growth associated with exit holes. Based on the inherent limits in dating precision using this approach, the identification of emergence to within 2 wk by Straw et al. (2015) seems very successful.

The patterns of voltinism described by Straw et al. (2015), and supported by the phenology model highlight the unique nature of this population growing at lower temperatures. This is evident when the emergence patterns predicted by the Smith et al. heating degree day model are applied to this location. Although the date of first emergence remains accurate, the accumulation of beetles through the season is skewed downward, and the model does not capture either the timing or the proportions of emergence as shown by the dotted lines.

Cold Weather Beetle Populations

The recent finding of a reproducing beetle population near Helsinki, Finland, offers an opportunity to further explore the utility of this modeling approach. Temperatures in Helsinki are substantially lower than they are in previously described populations. Although average minimum temperatures at this location regularly drop below -10°C, beetles are clearly able to survive and develop, perhaps facilitated by the freeze tolerance of larvae described by Roden et al. (2008). At this location, the phenology model indicates the most rapidly growing portion of the population would develop in 3 yr, with portions of the population requiring 4, 5, and 6 yr to develop, and these long generation times may result in extremely slow population growth.

Flight Seasons in Breeding Beetle Populations in North America

The Asian longhorned beetle is known to have established in at least five general areas in North America. These locations include the eradicated populations in Chicago, IL, parts of New York, NY, Jersey City, NJ, and Boston, MA, as well as populations under eradication in Toronto, Canada, New York, NY, Bethel, OH, and Worcester, MA. Patterns of voltinism and population development for these populations are similar in some respects to the population near Lanzhou, China (Figs. 4 and 5), with the exception of Worcester, MA, where lower temperatures may result in generally longer generation times than are found at the other locations. The effect of the variations in the voltinism patterns shown by these populations on the potential for population growth remains to be evaluated.

In conclusion, the Asian Longhorned Beetle Life-Table phenology model described here was able to accurately predict the timing of beetle development in a laboratory environment, and is in agreement with phenology studies carried out in naturalized settings in China (Smith et al. 2004), Italy (Faccoli et al. 2015), and The United Kingdom (Straw et al. 2015). Using a combination of field and laboratory data, it is possible to produce estimated life tables and patterns of voltinism for the Asian longhorned beetle for invaded areas, though additional opportunities to evaluate the accuracy of the model should be taken advantage of as they occur. Although the model also accurately predicts first emergence, the complexity of the

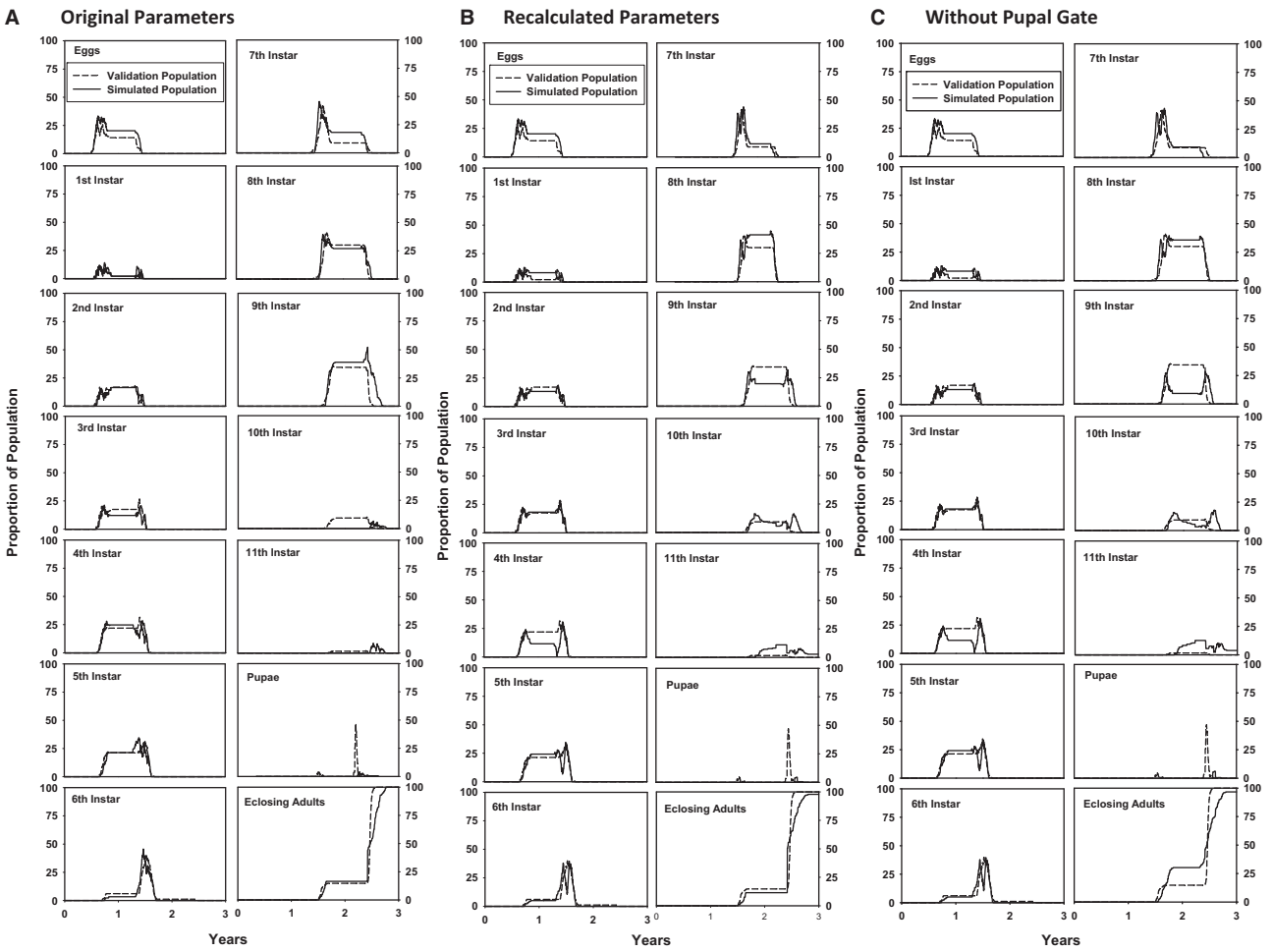

Fig. 3. Panels represent the number of individuals in the validation data set (dashed line), and the simulated data set (solid line) passing through each of the beetle stages/instars. Figure (**A**) provides the results based on the use of the original parameters in which instars 10 and 11 are absent in the model. Figure (**B**) displays the phenology model output based on the recalculated parameters, which includes 11 instars. Figure (**C**) shows the projected development of beetles in the absence of a temperature gate to prevent overwintering pupae, sclerotizing adults, and emerging adults.

model makes the use of the equally accurate and easier to calculate degree day model developed by Smith et al. (2004) a simpler tool when this parameter is the only parameter of interest.

Many previous authors have noted the apparently slow growth and spread of Asian longhorned beetle populations. Using the phenology parameters available, the current phenology model suggests that even in the beetle's native range, population times may range from 1 to 3 yr, with even longer times at cooler temperatures. This generation time may help explain the slow growth of populations, particularly in areas such as Worcester, MA, where the population seems to have remained geographically limited despite having been present and undetected for 10 yr (Sawyer et al. 2010). By this same logic, the reproducing population of beetles near Bethel, OH, may represent a more serious threat, as this population is also large and has a shorter average generation time, and therefore a greater potential for rapid population growth.

The discovery of a reproducing population in Finland provides tremendous information about the potential range of the beetle by documenting its ability to survive and reproduce in a cool climate. However, as the phenology model indicates, populations in locations like Helsinki may experience extremely long generation times and correspondingly slow population growth. The extended time beetle larvae spent in the tree may also subject the beetles to increased risk of mortality by predation or other mortality agents. Consequently, while the establishment of these populations highlights the general threat the beetle poses to the ecology of many regions, it seems likely that the relative scale of the threat may vary.

Although the phenology model described here improves our ability to estimate potential risk of population growth by the beetle, and helps to identify patterns such as accumulated adult emergence that may inform eradication efforts, there are limits to the model. Two key limits include the need to quantitatively incorporate the thermal buffering properties of the wood, and the need to identify sources of variation in development time such as host quality. An additional issue that remains to be addressed is the potential effect rearing insects under constant temperatures may have in developing estimates of thermal development requirements, as discussed by Manel and Debouzie (1997) and Gramig et al. (2015). However, in the case of the Asian longhorned beetle phenology model described here, the use of parameters derived from insects reared at constant temperatures provided good agreement with both the insects reared under artificially varying temperatures (i.e. the validation data), and

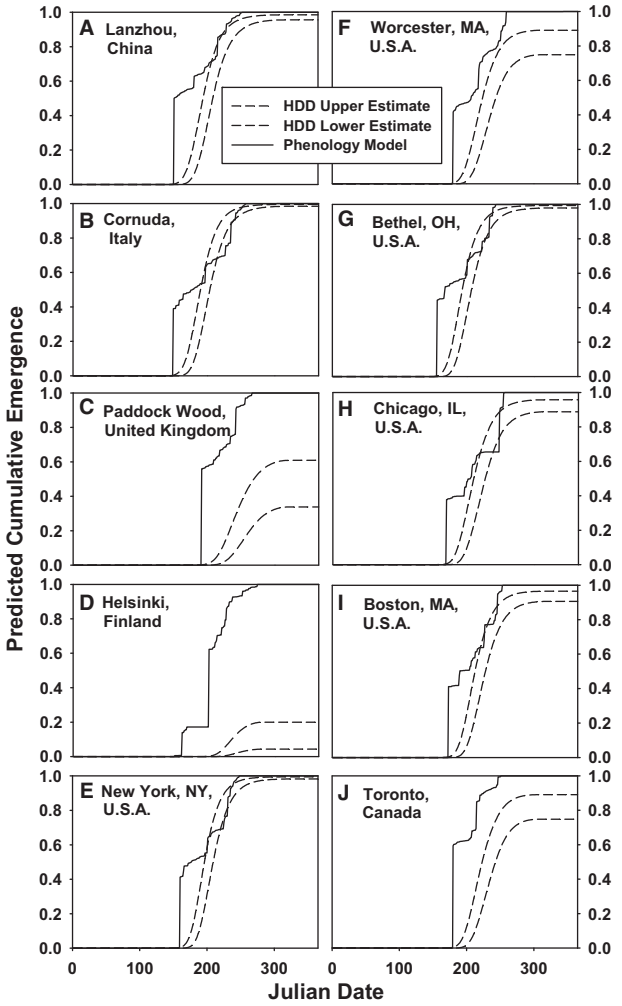

Fig. 4. (**A–J**) Panels show the patterns of cumulative adult emergence over the growing season for populations at 10 locations known to have reproducing populations of the Asian longhorned beetle. The dotted lines denote the upper and lower confidence bounds calculated using the degree day model described by Smith et al. (2004). The solid lines represent the predicted cumulative adult emergence based on the described phenology model. Note the abrupt initiation of emergence that is likely driven by a lack of variation in the simulated system.

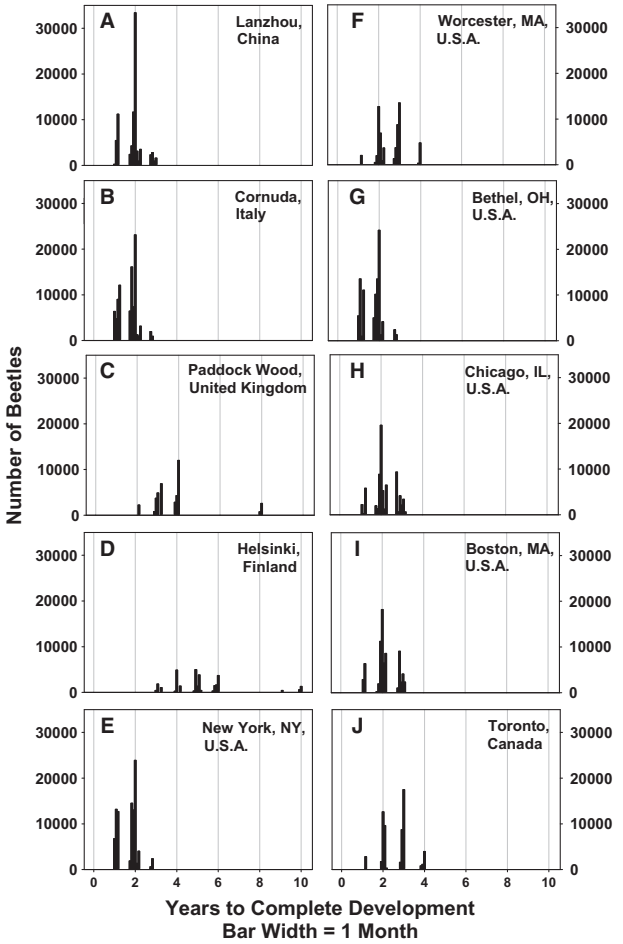

Fig. 5. (**A–J**) Panels show the distribution of voltinisms for populations at 10 locations known to have reproducing populations of the Asian longhorned beetle, based on the described phenology model.

populations in both native and introduced field environments. Similarly, expanding phenology studies to incorporate this variation may not be feasible with species such as the Asian longhorned beetle that are under eradication. As such, once trees are identified as infested they are rapidly removed and destroyed by chipping, precluding the opportunity to follow undisturbed populations through time. This problem is further compounded by the increasing rarity of infested trees as eradication programs proceed.

With the continued growth and expanding reach of international trade, the threat posed to ecological systems by the introduction of nonnative species can be expected to continue to increase. While prevention is by far the best strategy, the logistical limitations imposed by the sheer quantity of imports makes continued introductions likely. With these introductions comes the need to rapidly evaluate potential risks and develop the tools needed to manage them. Here, we have developed a phenologically based model that can be used to identify key population parameters including the emergence period for adults and generation time, parameters that can play a role in structuring eradication programs. By taking a flexible, individual beetle based modeling approach, the phenology model can be readily modified as new information becomes available, and can also be modified for use with other organisms.

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