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Special Collection: Asian Longhorned Beetle

# Validating a variable-instar, climate-based phenology model for the Asian longhorned beetle (Coleoptera: Cerambycidae) using field data from South Carolina

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The Asian longhorned beetle, *Anoplophora glabripennis* (ALB, Coleoptera: Cerambycidae), is a federally regulated invasive species capable of infesting several different genera of hardwood trees. Accurate knowledge of ALB's phenology is critical for the effective implementation of management and eradication plans. We updated the ALBLT prediction model and used empirical data collected in South Carolina, USA to validate ALBLT v. 2.0. The new model largely agreed with ALB life stages found in field collections, except for late instars and pupae. We also ran the model at 8 other potentially high-risk cities in the contiguous United States with latitudes ranging from 28°N (Tampa, FL) to 41°N (Chicago, IL) to predict how long a single ALB generation might take to develop in these environments. Model predictions ranged from a 2–3-yr lifecycle in Chicago to a potential life cycle of < 1 yr in Tampa. These predictions can help inform managers and invasive species specialists should ALB be found in new environments, and these data can aid in developing an adequate management and eradication plan.

*Key words: Anoplophora glabripennis*, forest health, invasive species, management, prediction modeling

## Introduction

Invasive species are widely regarded as one of the greatest threats to the health and sustainability of natural ecosystems worldwide (Liebhold et al. 1995, Holmes et al. 2009, Lovett et al. 2016, Diagne et al. 2021). Capable of causing significant damage to native ecosystems and costing billions of dollars in lost profits and management costs (Liebhold et al. 1995, Holmes et al. 2009, Moser et al. 2009, Diagne et al. 2021, Mayfield et al. 2021), effective management of invasive species is necessary to protect and conserve these ecosystems (Flint 2012, Mayfield et al. 2021). To that end, the 4 main elements of invasive species management are prevention, detection, control/management, and restoration, and each requires accurate knowledge of the target species' biology to function effectively, but hands-on field research is rarely suitable for the rapid response and quick control of a situation necessary to prevent invasives from spreading (Flint 2012). Predictive modeling is a valuable tool for invasive species management, as it can equip managers with information both before an invasion is introduced and after the infestation is established (Flint 2012). Predictive models have been used to aid land managers in making management decisions for both flora and fauna (Cook et al. 2019, Zhang et al. 2023, Mori et al. 2024). However, models are never perfect, and new information and empirical data should always be used to test model performance and improve model predictions.

The Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky, hereafter ALB) is a wood-boring beetle invasive in Europe and North America (Cavey et al. 1998, Hu et al. 2009, Dodds and Orwig 2011). Native to China and Korea, breeding populations of ALB have been found in 10 European countries, 1 Canadian province, and 6 US states (Haack et al. 2010, Coyle et al. 2021, USDA APHIS 2023a). ALB was first discovered in North America in 1996 in New York, and while many populations have been successfully eradicated, 4 active infestations remain (USDA APHIS 2023b). ALB is a polyphagous wood-boring beetle with a strong preference for *Acer* in North America (Ludwig et al. 2002, Haack et al. 2006, Dodds et al. 2014, Coyle et al. 2021, Turgeon et al. 2022). After

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hatching from eggs laid under the bark of their host trees, ALB's first 3 instars are spent feeding on the cambium layer of the tree, after which the larva tunnels deeper into the sapwood and heartwood, where it feeds until pupation. After pupating, the adult beetle will chew a 10–15-mm diameter exit hole to emerge from the host tree, feed on leaf petioles and juvenile bark, and find a mate (Haack et al. 2010). ALB is typically introduced to new landscapes as a stow-away in solid wood packing material (e.g., crates and wooden pallets) and may also move within regions through the movement of firewood (Fleming et al. 2003, Carter et al. 2010, Haack et al. 2010, Javal et al. 2019).

Prior to 2020, the range that ALB's invasive populations inhabited tended to be high in latitude, stretching from Finland (60°N) at the northern edge of its range down to Ohio, USA (39°N). This range was extended further south in 2020 with the discovery of an established population of ALB in Hollywood, South Carolina, USA (32°N; Coyle et al. 2021). But ALB has the potential to survive even further south given that its native range extends to the higher elevations of Hainan province of China (19°N) (Zhang et al. 2022), the latitudinal North American equivalent of southern Mexico. Models have been used to predict the potential distribution and spread of ALB throughout its invasive and native range (Lu and Russell 2005, Schatz et al. 2013, 2016, Gourley and Lou 2014, Trotter et al. 2018, Huang et al. 2020, Zhang et al. 2022) but have not been used to predict ALB phenology with comparable frequency (Faccoli et al. 2014, Trotter and Keena 2016). This often leaves management agencies without precise phenology information, which can render surveying and management methods that require strict timing ineffective (Flint 2012, Finch et al. 2021, Venette et al. 2021).

Despite ALB's extensive native range, little field research has been conducted on the beetle's phenology, and past work has focused on northern parts of this range (Roden et al. 2008, Feng et al. 2014, Straw et al. 2015, Liu et al. 2016); thus, the population in South Carolina provides an opportunity to examine ALB phenology at a lower latitude. Several laboratory studies have been conducted to determine ALB's development rate under various temperatures (Keena 2002, 2006, Keena and Moore 2010, Sánchez and Keena 2013) and these data were used to create a predictive model and risk map for the conterminous United States (Trotter and Keena 2016, Kappel et al. 2017). These studies predicted that while most ALB in northern regions generally develops in 2–3 yr, ALB in the southeastern United States had the potential to reach adulthood in as few as 8 mo (Trotter and Keena 2016, Kappel et al. 2017). This would be a substantial increase in development rate compared to other infestations in North America and would have major implications for the management programs involved in eradication efforts. As the current model has been validated only using data from northern regions, the South Carolina population provided a unique opportunity to evaluate the model and validate it with field data from a lower-latitude population. Two years of field sampling showed a clear univoltine life cycle for ALB in South Carolina (Schmitt et al. 2024). Thus, our objectives were to (i) assess the model's predictive accuracy of ALB's development rate and generation times for South Carolina using field-collected validation data and (ii) use the updated model to make predictions about ALB's development rate and generation times for 8 at-risk locations in the continental United States.

## Methods

The phenology model used in this study is an updated version of the ALBLT model described in Trotter and Keena (2016). The updated version (ALBLT version 2.0, and hereon referred to as simply "the phenology model") is an agent-based simulation of beetle development created in MATLAB® (Mathworks® R2019a Update 9; https://www.mathworks.com/) in which the development of multiple individual beetles is simulated through time at rates determined by life-stage-specific requirements and the accumulation of heating degree days. The life stage for each beetle in the simulation is tracked daily, and individuals are transitioned from one life stage to the next based on the accumulation of specified heat requirements. Variation in heating degree day requirements for both individual beetles and individual life stages is added based on a random normal distribution that mimics the variation among individuals observed in both natural and laboratory-reared populations. The parameters that define the heat requirements for each of the life stages are based on laboratory studies (Keena 2006, Keena and Moore 2010, Sánchez and Keena 2013) and validated using both laboratory and field studies from the native range of ALB (Yan and Qin 1992, Yang et al. 2000, Smith et al. 2004, Haack et al. 2006) as described in Trotter and Keena (2016). Simulations are run for multiple years, with adults in the simulation replaced by eggs based on the phenological timing of reproduction, such that phenological development over multiple generations is simulated in the absence of population growth or mortality.

Within this study, simulations were run for 400 years using 400 beetles. In a univoltine system, this would yield 160,000 beetles; however, due to multivoltinism and the failure of some individuals to complete development in the allotted period, the total number of beetles yielded by the simulation is lower. The simulations were run using standard parameters as described in Trotter and Keena (2016): eggs were started on ordinal date 230; flight season was ended on ordinal date 345; and a pupal hold was included (as described in Schmitt et al. 2024). For more information on the exact parameters used in this model, see Trotter and Keena (2016).

ALBLT version 2.0 uses the same model structure and core model (ALBLT version 1) as described in Trotter and Keena (2016). Changes in version 2 include (i) additional graphics outputs, (ii) automated retrieval of GHCN data from the National Oceanic and Atmospheric Administration National Centers for Environmental Information via https://www.ncei.noaa.gov/products/land-based-station/global-historical-climatology-network-daily, (iii) tools to average daily minimum and maximum values for a specified year range and improve missing data management (i.e., tactics to maintain model continuity when GHCN data are unavailable), (iv) data management and options to run multiple locations (gives the model the ability to run simulations on multiple locations concurrently), and (v) automated calculation and formatting of heating degree day values based on GHCN temperature records. Daily heating degree days were calculated using a double-sine method based on Allen (1976).

The performance of the model was evaluated in South Carolina by comparing the projected timing of life stages generated by the model using a weather station in Charleston, South Carolina (32°N, Station ID USW00013880, 1980-2010) with monthly field assessments of ALB development within the ALB infestation in Hollywood, SC. A recent study using 1,009 ALB eggs, larvae, and pupae collected from SC, showed that most individuals had a univoltine life cycle with the possibility of some individuals either completing development in < 1 yr, or in about 1.5 yr (Schmitt et al. 2024).

To further explore the potential application of the phenology model, we ran the model using temperature data from 8 additional locations in the continental United States: Chicago, IL (41°N, Station ID USW00094846), Salt Lake City, UT (40°N, Station ID USW00024127), Bowling Green, KY (37°N, Station ID

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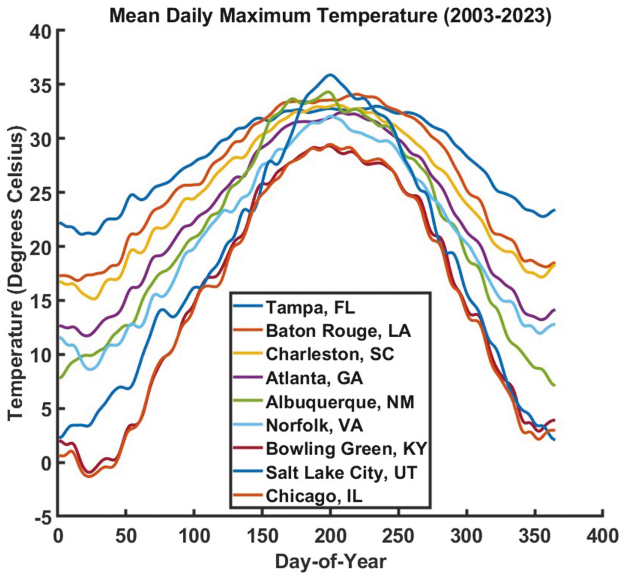


**Fig. 1.** Mean daily maximum temperature (2003–2023) from the locations used in this study. Data obtained from the National Oceanic and Atmospheric Administration (https://www.noaa.gov/).

USC00330862), Norfolk, VA (36°N, Station ID USW00013737), Albuquerque, NM (35°N, Station ID USW00023050), Atlanta, GA (33°N, Station ID USW00013874), Baton Rouge, LA (30°N, Station ID USW00013970), and Tampa, FL (28°N, Station ID USW00012842). These locations were chosen to capture a variety of latitudes in areas with a high percent host tree basal area (Kappel et al. 2017), a high risk of invasion (e.g., near a large port, airport, or other urban area), and the availability of continuous temperature records from 1 January 2003 to 1 January 2023 (Fig. 1).

## Results

Monthly population samples collected in the field over the course of 2 yr (Schmitt et al. 2024) suggest the timing of the phenology model generally agrees with field observations for most life stages (Fig. 2). The timing for the presence of eggs (late May to August), instars 1 through 4 (early June to late November), and sclerotizing adults (May) agrees well, though the timing and abundance of both fifth instars and pupae are shifted suggesting the cues that govern the timing and duration of pupation in southern populations are not as well understood.

The model predicted that ALB in Chicago (Fig. 3a) and Salt Lake City (Fig. 3b) could complete development in ~1–3 yr; beetles in Bowling Green (Fig. 3c), Norfolk (Fig. 3d), and Albuquerque (Fig. 3e) could complete development in ~1–2 yr; beetles in Atlanta (Fig. 3f), Charleston (Fig. 3g), and Baton Rouge (Fig. 3h) could complete development in ~0.5–1.5 yr, and beetles in Tampa (Fig. 3i) could take only 4 mo to 1 yr to fully develop. Charleston and Baton Rouge have the most clustered results, with most beetles in each location (58.1% and 61.0%, respectively; Table 1) predicted to complete development in exactly 1 yr (Fig. 3). The next highest cluster is in Chicago, where 43.1% of beetles are predicted to develop in exactly 2 yr, followed by Atlanta, with 35.0% of beetles predicted to develop in exactly 1 yr (Table 1).

Overall, ALB in cities at lower latitudes (with warmer climates) are predicted to take less time to develop (i.e., have a shorter development time, Table 1), except for Bowling Green, Norfolk, and Albuquerque, which all take approximately the same amount of time to develop (Table 1, Fig. 3). Tampa, with the lowest latitude, has the shortest predicted development time of the cities, with the longest predicted development period (i.e., the time it takes for 100% of the beetles in a generation to complete development, 13 mo; Table 1) shorter than beetles in Baton Rouge, the next most southern city, by nearly 7 mo. Tampa also has the most continuous development completion predicted, with beetles potentially completing development monthly from the fourth to thirteenth month, whereas the rest of the cities have adult beetles predicted to finish development in clumps around the 6-mo, 1-yr, 1.5-yr, 2-yr, and 3-yr marks (Fig. 3, Table 1).

## Discussion

Simple degree-day models are still commonly used to predict flight seasons and general development patterns (Smith et al. 2004, Faccoli et al. 2014), but these models do not always make highly precise predictions and may omit more nuanced or complex factors, such as variation in degree day requirements between instars, or the timing of diapause periods (Nielsen et al. 2016, Rebaudo and Rabhi 2018), and the cues that regulate shifts between life stage. The agent-based life-table model evaluated and used here, however, offers some opportunities to include more complex factors with effects that vary among individuals in the population, while using a structure that is conceptually simple (Trotter and Keena 2016). This method of modeling has been successfully utilized to determine the phenology of lepidopterans and heteropterans (Chen et al. 2011, Nealis and Règniére 2014, Nielsen et al. 2016), and this increased accuracy allows researchers and managers to survey and apply management methods more effectively.

This phenology model was able to reasonably predict the development rate of ALB in South Carolina, though questions remain. For example, while the model captures the general timing of fifth instars and pupation, the abundance of the stages during the field season (Schmitt et al. 2024) is not well represented by the model. Several factors may play a role here and merit further investigation. Past research has shown that the timing of pupation (Keena and Moore 2010, Trotter and Keena 2016) in ALB is a highly variable trait that may contribute to its climatic plasticity. Cues governing pupation in temperate climates have worked well in past infestations (Trotter and Keena 2016), but in the semi-tropical landscape of South Carolina, mediating factors including solar exposure of trees (infested host trees are often in closed-canopy swamps), tree condition, and the potential temperature fluctuations induced by the movement of water through the trunk likely alters the temperature profile experienced by the beetle (Vermunt et al. 2012, Kappel et al. 2017). While work is underway to collect this information, published data on the role of the canopy and trunk in mediating the temperatures directly experienced by the beetle is not yet available. Past work by Keena and Moore (2010) suggested a 2-degree reduction in temperatures to account for the wood may be suitable, and results in Trotter and Keena (2016) agreed. In this study, however, a more substantial adjustment of 4°C seems to fit well and may suggest an increasing role of temperature mediation (at least for high temperatures) may be appropriate in warmer climates. Moving forward, incorporating a more accurate temperature regime into the model should be a priority, as this tactic has paid dividends with other forest pests (e.g., Powell 1967, Hofmann et al. 2024).

Our model predicted that ALB in Charleston would take around 1 yr to develop to adulthood, which was consistent with 1-yr life cycle shown by field data collected in the Hollywood, SC area (Schmitt et al. 2024). The similarity in the model output and field-collected

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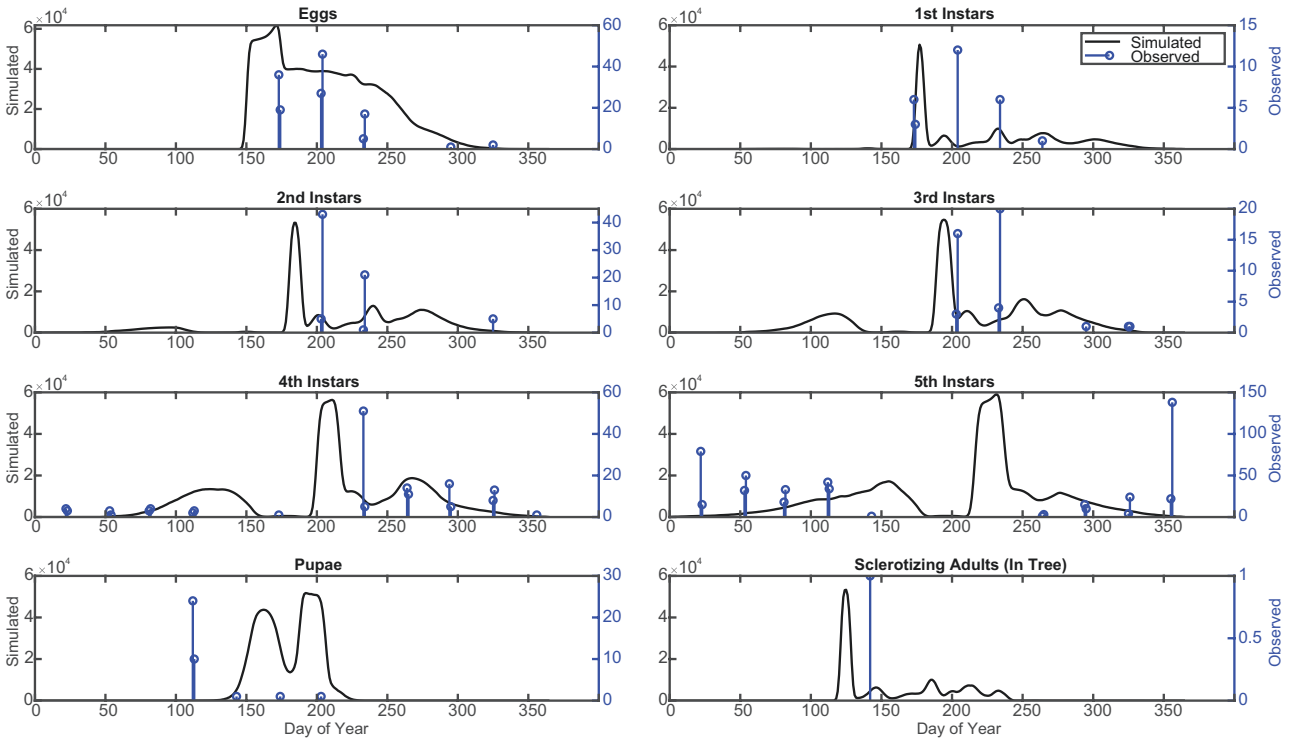


**Fig. 2.** Simulated predictions of ALB phenology (solid black line) compared with observed occurrence (vertical, straight blue lines/circles) for different beetle life stages using data from South Carolina, USA. The observed occurrence data was collected from the ALB quarantine zone in South Carolina monthly from August 2021 to July 2023 (Schmitt et al. 2024). Observed counts are the total of 2 mo worth of collections. The simulated data line represents the model output after incorporating the SC data.

data indicate that the model, despite being originally designed and validated using laboratory data and empirical data from ALB's native range in China and from northern US populations, is making reliable predictions in a more southern climate. This will be beneficial should ALB be found in other parts of North America, as the model is already reasonably accurate.

The model also predicted that a small percentage of the population may develop in as few as 4 to 5 mo, a considerable jump in development rate compared to northern populations. The possibility of ALB developing in < 1 yr is noteworthy because no other infestations in the United States have been found to develop in this short period (Trotter and Keena 2016). The potential for increased reproduction rates and resulting population spread could make ALB management a much greater challenge, especially in the southeastern United States where management agencies are already facing more difficult conditions due to the large number of swamps and wetlands where heavy machinery used in most eradication operations cannot be utilized (Ratcliff 2022). It is unknown, however, whether generations that take < 1 yr to develop will be able to persist in the population or will be re-synchronized to a yearly cycle by the pupation hold that ALB undergoes in cold weather.

Although the agreement between field observations and the model output is far less clear-cut when compared with field data, there is evidence that ALB could have populations that complete their life cycle in < 1 yr and other populations that revert to the more widely seen year-long cycle. The presence of eggs in November 2021 and October 2022 (Schmitt et al. 2024) does match the timing of an egg laid in May or June taking 5–6 mo, or 18 mo, to develop to adulthood and lay eggs of its own. It is impossible to say if either of these scenarios is occuring without additional research, especially because these unusually timed eggs do not seem to persist in the population, as there were no first instars present during or immediately after the months these eggs were found (Schmitt et al. 2024). More research on larval development, especially during the fall, is needed to determine if the model's prediction of ALB developing in < 1 yr is possible. To dispel the uncertainty around these predictions, continued evaluation of the model's accuracy at a wider variety of latitudes and ecosystems would be ideal, but because the South Carolina population is the furthest south ALB has been found in North America, it is currently the only available opportunity for collecting field data at lower latitudes.

Overall, the latitude of the cities is a major determinant of how quickly beetles are predicted to develop. Although this pattern breaks slightly with the 3 cities most similar in latitude (Bowling Green, Norfolk, and Albuquerque), it holds true for the northernmost and southernmost locations (Fig. 3). Tampa, the location furthest south, has an even more abrupt decrease in development time compared to the rest of the cities. Although Florida has a lower basal area of host trees at risk than the rest of the Southeast (Kappel et al. 2017), it also has the potential for very fast beetle growth, with the longest predicted development of only 13 mo. Not only is this fast, but the continuous timing of development, with beetles maturing to adulthood every month, also has the potential to morph into a continuous year-round emergence of adults. This rate of growth and constant presence of adults would almost certainly lead to faster reproduction, population growth, and spread of beetles, and even in an area with relatively few host trees would make it much more difficult to manage and eradicate an infestation.

ALB development in warmer areas also raises the question of whether the pupal hold ALB has maintained is obligate. Research is limited on this topic, and what exists does not reach a strong consensus. One study indicated that ALB required a period of chilling

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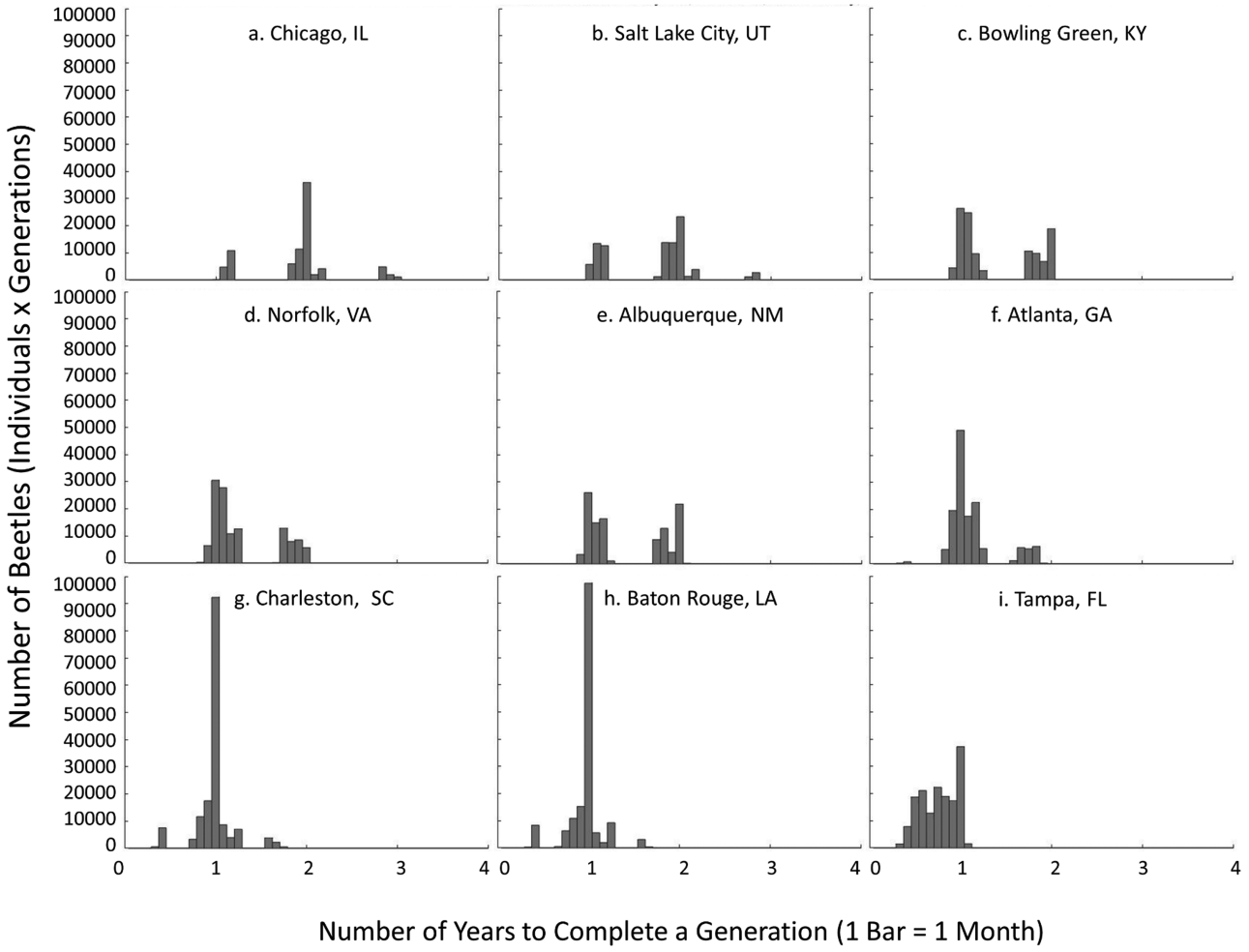


**Fig. 3.** Model outputs displaying histograms of the number of years ALB populations take to develop in 9 locations throughout the United States. Locations are ordered from highest latitude to lowest.

for a larva to pupate, but research was not able to determine the minimum dormancy time a larvae needed before it was able to pupate and was not able to determine the maximum temperature at which ALB would enter into this dormancy period (Torson et al. 2021). Another study indicated that ALB were capable of pupating without this chilling period when reared at a continuous 20°C, but chilling was required at higher rearing temperatures (Keena and Moore 2010). More research is needed to determine whether this dormant period is obligate for ALB and, if not, what temperature threshold is required to bypass it, as this information is critical to understanding how development will change in warmer locations and is highly relevant to ALB population prediction model development.

These predictions also become potentially more concerning when taking climate change into account, as states like South Carolina—that have both an abundance of hosts and an already accelerated beetle development rate compared to northern populations—experience increased temperatures. For management programs tasked with quarantining, controlling, and eradicating infestations, faster spread will mean more difficult, labor-intensive, and costly work. This increased risk makes it especially important for federal and state ALB management programs to be able to predict where new populations of ALB may occur, and how fast they will be able to grow in those locations both now and in the future. The global use of solid wood packing material for shipping leaves ports at risk for introductions of wood-boring beetles (Greenwood et al. 2023), and despite phytosanitary treatment of wood and inspection of material at entry ports, the constant influx of nonnative beetles means that new populations of invasive species will always be a concern (Haack 2006, Wu et al. 2017).

ALB is not the only invasive species that can benefit from this type of phenology model. Management programs for other forest pests will also be improved by the introduction of agent-based phenology models. Even the emerald ash borer (*Agrilus planipennis* Fairmaire), one of the most devastating invasive insects in North America (Herms and McCullough 2014, Klooster et al. 2018), has had surprisingly little research conducted on its phenology until recently (Lyons et al. 2005, Lyons and Jones 2006, Bohannon et al. 2022), and phenology modeling of this species is similarly limited to simple degree day models (Discua Duarte 2013). Without specific, location-tailored phenology knowledge, management programs must contend with imprecise targeting of life stages, and subsequently less effective control of pest species negatively impacting North America's forests. This model will help improve others around the world, as it provides evidence for the accuracy and versatility of agent-based phenology models. It is vital for management agencies to have accurate phenological information on invasive species in as wide a range of conditions as possible so they can prepare for and effectively manage new and current infestations.

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**Table 1.** Percent of ALB population predicted to complete development during each month for 9 cities in North America.

| Month | Chicago | Salt Lake City | Bowling Green | Norfolk | Albuquerque | Atlanta | Charleston | Baton Rouge | Tampa |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 2 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 3 | 0% | 0% | 0% | 0% | 0% | 0% | * | 0% | 0% |
| 4 | 0% | 0% | 0% | * | * | 0.20% | 0.39% | 0.22% | 0.95% |
| 5 | 0% | 0% | 0% | 0.01% | 0.01% | 0.55% | 4.76% | 5.31% | 4.96% |
| 6 | 0% | 0% | 0% | * | 0% | 0% | 0% | 0% | 11.81% |
| 7 | 0% | 0% | 0% | 0.01% | 0% | 0% | 0% | 0.01% | 13.18% |
| 8 | 0% | 0% | 0% | * | 0% | 0% | 0.05% | 0.34% | 8.00% |
| 9 | 0% | 0% | 0% | 0% | 0% | 0.06% | 2.15% | 3.90% | 14.02% |
| 10 | 0% | 0% | 0.05% | 0.23% | 0.06% | 3.71% | 7.37% | 6.87% | 11.96% |
| 11 | 0% | 0.04% | 3.75% | 5.22% | 3.08% | 14.09% | 10.92% | 9.68% | 10.92% |
| 12 | 0.24% | 6.01% | 23.14% | 24.87% | 23.69% | 34.95% | 58.10% | 60.98% | 23.18% |
| 13 | 5.62% | 14.52% | 21.91% | 22.29% | 13.68% | 12.73% | 5.36% | 3.57% | 1.02% |
| 14 | 12.89% | 13.54% | 8.39% | 8.85% | 14.77% | 15.76% | 2.43% | 1.23% | 0% |
| 15 | 0.05% | 0.13% | 2.87% | 10.17% | 0.97% | 4.08% | 4.38% | 5.64% | 0% |
| 16 | * | 0% | 0.01% | 0.01% | 0.03% | * | 0% | 0% | 0% |
| 17 | 0% | 0% | * | 0% | * | 0% | 0% | 0% | 0% |
| 18 | 0% | 0% | 0% | 0% | 0.01% | 0% | 0% | * | 0% |
| 19 | 0% | 0% | 0% | 0% | * | 0.84% | 2.39% | 1.95% | 0% |
| 20 | 0% | 0% | 0.01% | 0.15% | 0.01% | 4.22% | 1.37% | 0.27% | 0% |
| 21 | 0.02% | 1.38% | 9.29% | 10.40% | 7.97% | 3.91% | 0.36% | * | 0% |
| 22 | 7.22% | 14.79% | 8.58% | 6.37% | 11.64% | 4.70% | 0% | 0% | 0% |
| 23 | 13.47% | 14.83% | 5.79% | 6.88% | 3.97% | 0.18% | 0% | 0% | 0% |
| 24 | 43.10% | 24.79% | 16.19% | 4.54% | 19.90% | 0% | 0% | 0% | 0% |
| 25 | 2.42% | 1.50% | * | 0% | 0.24% | 0% | 0% | 0% | 0% |
| 26 | 5.19% | 4.24% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 27 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 28 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 29 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 30 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 31 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 32 | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 33 | 0.06% | 1.30% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 34 | 5.91% | 2.93% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 35 | 2.37% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| 36 | 1.43% | 0% | 0% | 0% | 0% | 0% | 0% | 0% | 0% |
| **Totals** | **100%** | **100%** | **100%** | **100%** | **100%** | **100%** | **100%** | **100%** | **100%** |

* indicates < 0.01%.

## Conclusions

Based on validation data from the South Carolina ALB population, the phenology model has continued to make reasonable predictions in the southern United States. ALB between 40 and 41°N (Chicago and Salt Lake City) are predicted to develop in 1–3 yr; ALB from 35 to 37°N (Bowling Green, Norfolk, and Albuquerque) in 1–2 yr; ALB between 30 and 33°N (Atlanta, Charleston, and Baton Rouge), are predicted to have a predominantly univoltine life cycle, with a small percentage developing in 4–5 mo and 1 yr and 8–9 mo; and ALB in Tampa (28°N) are predicted to develop in 1 yr or less. This has major implications for management programs in the southern United States, as faster development may lead to faster population growth and more difficult eradication of beetle populations. In addition, as climate change increases temperatures, both new and already established populations could see an increase in development rate. Since the beetle's native range extends much further south than South Carolina, ALB can survive warmer temperatures than they currently experience, leaving all of the southern United States and most of Mexico at risk for new infestations.

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## Author contributions

Lena R. Schmitt (Formal analysis [equal], Investigation [equal], Methodology [equal], Writing—original draft [equal], Writing—review & editing [equal]), Talbot Trotter (Conceptualization [equal], Formal analysis [equal], Investigation [equal], Methodology [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal]), and David Coyle (Conceptualization [equal], Funding acquisition [equal], Project administration [equal], Resources [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal])

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