



Population Ecology

Phenology and voltinism of the Asian longhorned beetle (Coleoptera: Cerambycidae) in South Carolina, United States

Lena R. Schmitt¹, R. Talbot Trotter III², Crystal J. Bishop¹, Katy E. Crout¹, Scott E. Pfister³, David R. Coyle^{1,*}

¹Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA, ²USDA Forest Service, Northern Research Station, Hamden, CT, USA, ³USDA APHIS, PPQ, S&T, Forest Pest Methods Laboratory, Buzzards Bay, MA, USA
*Corresponding author, email: dcoble@clemson.edu

Disclaimer: The findings and conclusions in this publication are those of the authors, may not necessarily express APHIS' views, and should not be construed to represent any official USDA or US Government determination or policy.

Subject Editor: Melody Keena

Received on 19 August 2024; revised on 21 November 2024; accepted on 17 December 2024

A new population of the Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), an invasive species in North America since 1996, was discovered in Charleston County, South Carolina, in 2020. This population is the furthest south Asian longhorned beetle has established in North America. Previous models only estimate development time at this latitude; as such, we examined Asian longhorned beetle phenology in this novel climate. Over 24 consecutive months, we collected 153 eggs, 878 larvae, 37 pupae, and 1 unemerged adult (1,009 total specimens) from the federal quarantine zone in South Carolina and used larval head capsule width to determine development rate and voltinism. The presence of Asian longhorned beetle adults was determined via visual field observations. Asian longhorned beetle in South Carolina appears to have a synchronous univoltine life cycle, in contrast to populations in the northern United States and Canada that typically develop in 2–3 yr. This information will be useful for future model development to determine Asian longhorned beetle life cycles, for implementing novel management methods, and will aid in predictions to benefit visual survey efficacy.

Key words: *Acer*, climate, forest health, head capsule width, invasive species

Introduction

Invasive species can have a significant impact on the environment, economy, and human health and safety (Liebhold et al. 1995, Holmes et al. 2009, Lovett et al. 2016, Diagne et al. 2021). Often a consequence of international trade (Krishnankutty et al. 2020, Greenwood et al. 2023), invasive insects such as the spongy moth (*Lymantria dispar* L., Lepidoptera: Erebidiae), hemlock woolly adelgid (*Adelges tsugae* Annand, Hemiptera: Adelgidae), and emerald ash borer (*Agrilus planipennis* Fairmaire, Coleoptera: Buprestidae) are serious threats to eastern North American forests (Davidson et al. 1999, Herms and McCullough 2014, Lovett et al. 2016, Ellison et al. 2018). Invasive species cause widespread harm to ecosystems by killing or outcompeting native species (Liebhold et al. 1995, Moser et al. 2009) and can generate significant economic and ecological losses both directly by their presence, and indirectly by the

cost of management and eradication (Holmes et al. 2009). Wood-boring invasive species (e.g., the emerald ash borer) are especially harmful, causing major damage to ecosystems and costing billions of dollars in tree removals and replacements (reviewed in Herms and McCullough 2014).

Understanding the phenology of an invasive species is a critical component required for enacting effective management strategies, as knowing when different pest life stages will be present can improve everything from predictive models (e.g., Crimmins et al. 2020) to survey efficacy (Beltrà et al. 2013) to biological control (Bohannon et al. 2022). For example, empirically collected phenology data from the invasive *Halyomorpha halys* (Stal) helped improve predictive models and management strategies in Japan (Kamiyama et al. 2021), and phenology data from *Lymantria dispar asiatica* Vnukovskij and *L. d. japonica* (Motschulsky) helped inform a decision support tool

that is used to estimate potential infestation of cargo ships in an effort to prevent the spread of this invasive forest pest into North America (Gray 2016). Understanding the phenology of wood-boring species can help support and improve phytosanitary risk management approaches and help prevent the spread of invasive forest pests (Pawson et al. 2021), thus protecting potentially millions of hectares of forests globally.

The Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky, Coleoptera: Cerambycidae) is a polyphagous wood-boring beetle native to China and the Koreas, and invasive in both Europe and North America (Cavey et al. 1998, Hu et al. 2009, Dodds and Orwig 2011, Turgeon et al. 2015, Javal et al. 2019). The first established population of Asian longhorned beetle in North America was found in 1996 in New York (Haack et al. 1996). Since that first detection, additional populations have been found in Ontario, Canada, and several US states, including Illinois, Massachusetts, Ohio, New York, New Jersey, and South Carolina (Lingafelter and Hoebeke 2002, Coyle et al. 2021). Asian longhorned beetle is typically introduced to new landscapes via wood packing materials such as pallets, crates, or dunnage (Fleming et al. 2003, Haack et al. 2010), and human-mediated transport such as moving firewood has contributed to localized spread (Carter et al. 2010, Javal et al. 2019).

Asian longhorned beetle can feed on and develop in members of at least 12 tree genera, but in North America infestations are almost exclusively limited to *Acer*, *Betula*, *Fraxinus*, *Platanus*, *Populus*, *Salix*, and *Ulmus* (Ludwig et al. 2002, Haack et al. 2006, Turgeon et al. 2022), with preference given to *Acer* species (Dodds et al. 2014, Coyle et al. 2021, Turgeon et al. 2022). Trees become infested when adult females chew oviposition pits in the bark, underneath which they may insert a single egg into the cambium. A single female can lay up to 170 eggs under laboratory conditions but usually lays an average of 50–75 in the field (Keena 2002). Once the eggs hatch, roughly 3 instars are spent feeding in the cambium before larvae tunnel into the heartwood, where they continue to feed until pupation (Haack et al. 2010). After pupating, adults chew a circular exit hole 10–15 mm in diameter and exit the tree. Free-living adults feed on the thin bark of twigs and petioles and may disperse to other host trees to find mates or suitable oviposition sites (Haack et al. 2010). Adults usually stay within 600 m of their emergence point, and often reinfest the same tree in which they developed (Smith et al. 2001, 2004, Trotter and Hull-Sanders 2015, Trotter et al. 2018, Xu and Teale 2021).

Asian longhorned beetle was first discovered in South Carolina in 2020, the furthest south a population has established to date in North America (Coyle et al. 2021). Although it is uncertain how this population reached South Carolina, genetic analyses indicate the population is closely related to the population found in Ohio, suggesting it was either transported from Ohio to South Carolina on infested woody material (e.g., firewood) or was introduced to the United States via cargo originating from the same region of China as the Ohio population (Coyle et al. 2021). The infested area in South Carolina has a novel ecology and climate compared to other infestations in North America and provides a unique opportunity to examine this Asian longhorned beetle population's phenology (Coyle et al. 2021). Although several laboratory studies have investigated Asian longhorned beetle's development rate under different temperature conditions (Keena 2002, 2006, Keena and Moore 2010, Sánchez and Keena 2013), little information exists on the phenology of field-collected Asian longhorned beetle; what does exist was obtained from more northern latitudes (Roden et al. 2008, Feng et al. 2014, Liu et al. 2016). The information provided by laboratory studies has been used to build a predictive model

and maps of growth rate and risk for the United States (Trotter and Keena 2016, Kappel et al. 2017). These predictions indicate that while northern populations of Asian longhorned beetle in the United States develop in an average of 2–3 yr, Asian longhorned beetle in South Carolina could reach adulthood in as little as 8 mo (Kappel et al. 2017). Therefore, the Asian longhorned beetle infestation in South Carolina offers a unique opportunity to test the available phenology model in a novel landscape and improve our understanding of how this invasive species develops in warmer climates. As such, our objectives were to determine (i) how long it takes for Asian longhorned beetle to complete a single generation in South Carolina, (ii) if Asian longhorned beetle has a synchronous life cycle, and (iii) what time of year each instar and life stage are present.

Methods

Site Description

The South Carolina federal Asian longhorned beetle quarantine zone is currently a 197 km² (76 mi²) area covering sections of Charleston and Dorchester counties (USDA APHIS 2023, Fig. 1). Located in the coastal marsh ecoregion of South Carolina, this quarantine zone is characterized by pine and hardwood forests, with a humid, subtropical climate that features hot summers and mild winters (Griffith et al. 2002, SC DNR 2005, Griffin and Mogil 2021). The North Charleston Weather Station (KHB29 Charleston) recorded an annual high of 36°C (98°F) and low of -8°C (18°F) in 2022, with a total of 127.3 cm (50.1 inches) precipitation. 2021 had an annual high of 35°C (95°F) and low of -3°C (26°F), with a total of 149.1 cm (58.7 in) of precipitation (climate data acquired from the National Oceanic and Atmospheric Administration's annual climate report from the National Weather Service Forecast Office in Charleston, South Carolina: <https://www.weather.gov/wrh/Climate?wfo=chs>, accessed 4 Oct 2022).

Tree Selection

To track the timing of Asian longhorned beetle life stages and their development, we collected live specimens monthly from infested trees between Aug 2021 and Jul 2023. Collections were made exclusively from red maple trees (*Acer rubrum* L.) since they make up the majority (~98%) of Asian longhorned beetle's host trees in this area (Coyle et al. 2021). Trees were identified and obtained in collaboration with state and federal regulatory agencies. Highly infested red maple trees between 15 and 50 cm diameter at breast height were preferentially selected to maximize the quantity of Asian longhorned beetle obtained from tree dissections. Signs of heavy infestation vary among different stages of the Asian longhorned beetle life cycle (Fig. 2). Eggs and neonates can only be identified via the egg site chewed by their mothers, but after a few weeks of growth, larval feeding causes sap and frass to be exuded from the egg site providing additional visual cues. As the larvae grow larger and tunnel into the heartwood, the quantity of sap coming from egg sites declines, frass and sawdust discharge increases, and the bark covering the galleries begins to dry and crack. In heavily infested trees, external signs of stress such as epicormic sprouting can appear. Between 3 and 11 trees were collected each month depending on the number of recently infested tree detections and intensity of the infestations. Selected trees were cut down and the visibly infested sections were transported to the field laboratory at the USDA APHIS Facility on the College of Charleston's Stono Plantation (32°44'39.9"N, 80°10'56.0"W).



Fig. 1. Map of the federal Asian longhorned beetle quarantine zone in Charleston and Dorchester Counties, South Carolina, United States. All sampling of Asian longhorned beetle life stages occurred within this zone.

Life Stage Collection

Eggs and early instars were collected by identifying Asian longhorned beetle oviposition sites and damaged areas and peeling the bark down to the cambium layer with a draw knife, chisel, or pocketknife to locate eggs and larvae in the vascular cambium. We only collected live eggs, which were whitish in color and plump (i.e., not shriveled and dark in color). Tunneling larvae and pupae were collected by splitting the wood using an electric log splitter (Central Machinery, Calabasas, California). Logs with visible signs of Asian longhorned beetle damage were split into approximately 1-in sections, which helped ensure no section of wood large enough to hold undetected larvae remained. Collected Asian longhorned beetle specimens were preserved using 95% ethanol and transported to the Forest Health and Invasive Species Laboratory at Clemson University in Clemson,

South Carolina (34°40'12"N, 82°49'48"W). The presence of flying adults was recorded via visual field observations or specimen collections by USDA APHIS, Davey Resource Group, and Clemson University survey and research personnel.

Larval Head Capsule Measurements

In soft-bodied holometabolous species such as coleopterans, larval body size changes as individuals grow, but the size of the head capsule for each instar is set when it sclerotizes after a molt. Because of this fixed size, head capsule measurements through time tend to have a multi-modal distribution, with modes associated with specific instars, as described by Dyar's Rule (Logan et al. 1998, Calvo and Molina 2008, Delbac et al. 2010). As such, we measured head capsule width to determine larval age and the number of instars before



Fig. 2. Signs of damage made by various life stages of Asian longhorned beetle. A) An Asian longhorned beetle oviposition site, chewed into the bark by an adult female. Each pit may have a single egg laid underneath the bark. B) Three oviposition pits bleeding sap, caused by larval feeding in the cambium. C) A gallery made by a first to early third instar Asian longhorned beetle. D) A gallery made by a third or later instar Asian longhorned beetle, with a tunnel (arrow) leading deeper into the heartwood of the tree. E) Tunnels and pupal chambers dug into the heartwood of the tree by a prepupal larva (left arrow) and a pupal stage Asian longhorned beetle (right arrow). F) Asian longhorned beetle exit holes, made by adults chewing a tunnel out of the tree after pupation. Photos by L.R.S., Clemson University.

pupating (Panzavolta 2007, Calvo and Molina 2008, Delbac et al. 2010) by taking digital images of the ventral side of the head with a microscope and camera system (Motik K-400 Stereomicroscope [Motic-America, Schertz, Texas] with Canon DSLR Camera [Canon USA, Long Island, New York]) with inclusion of a digital scale bar. Images were then imported to ImageJ (Schneider et al. 2012) and the head capsule was measured (in mm) at its widest point.

HCAP Program

HCAP is a statistical program created in 1998 by a team of researchers seeking to determine the instar distribution of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) using head capsule widths (Logan et al. 1998). The program was developed using MATLAB (MathWorks 1993) and uses a combination of user input and iterative mathematics to determine the statistical modes in the head capsule

measurement data to identify and calculate the size ranges associated with each instar. The program starts by producing a histogram of input head capsule widths, then asks the user to provide a set of initial estimates of the locations of size breaks between instars. Once the user has chosen where they believe the instar peaks fall, the program uses the user-provided breaks to start an iterative process of fitting lines using multiple polynomial models to the histogram, and then graphs individual curves where the program calculates each instar distribution lies. The final output of the program is a histogram with 3 lines: a line fitted to the user's original guess, a line fitted to the best-fit line, and a parabola for each distinct instar showing the possible range of head capsule sizes. We used this program with slight alterations, namely updating the code to work with the current version of MATLAB (MathWorks 2021), set data formatting, and the addition of scripts that generate graphs that display the monthly head capsule widths on

top of the combined head capsule widths of both years to better display the changes in distribution over time. We used the preestablished parameter of 30 boxes in the histogram and chose to select 5 instars as an estimation because of the appearance of the graph and because any instars past the fifth do not greatly increase in size (Keena and Moore 2010), making any differentiation based on size difficult.

Results

Instar Determination

We collected a total of 153 eggs, 878 larvae, 37 pupae, and 1 unemerged adult over the sampling period (Table 1). The number of larvae collected varied each month, ranging from 0 (May 2022) to 139 (Dec 2022). The HCAP program determined that first instar head capsules were ≤ 1.19 mm, second instar head capsule size ranged from 1.20 to 1.64 mm, third instar from 1.65 to 2.20 mm, fourth instar from 2.21 to 4.06 mm, and fifth instar from 4.07 to 5.97 mm (Fig. 3). Using this calculation, the collections yielded 28 first, 75 second, 46 third, 148 fourth, and 521 fifth instars. First to third instars were present during and immediately after time periods when eggs were found, from Jun until Nov of both years, but were only found in relatively large numbers in Jun, Jul, and Aug (Fig. 4). Fourth and fifth instars comprised the largest proportion of the population for most of the time in which larvae were present. Fewer small larvae than large were collected, with fifth instars making up more than half of the larvae collected (Fig. 5). A small percentage of larvae reached fourth or fifth instar as early as Aug, and most of the population reached fourth or fifth instar by Sep (Fig. 4).

Head Capsule Widths and Life Cycle

Eggs were present from Jun through Nov and comprised the largest portion of the population in Jun of both years (Fig. 4). Larvae were

present year-round, except for May 2022 where the only specimen collected was a single adult that had not yet chewed a tunnel from its pupal chamber to exit the tree. From Dec through Mar of both years, larvae were the only life stage present (Fig. 4). Pupae were only collected in Apr in 2022 but were collected in Apr–Jun in 2023. No unemerged adults were collected in 2023. Adults were observed in May and Jun in 2022, and May through Jul in 2023.

The range in sizes of head capsules was almost entirely identical between the 2 yr of sampling, and a considerable difference in head capsule size ranges is evident only in Aug for each year (Fig. 5). Larval head capsule width increased in size from Jun to Dec, and then maintained size until Apr (Fig. 5). The average larval head capsule width was smallest in Jun in both 2021 and 2022 (average head capsule width of 1.52 ± 0.4 mm and 1.09 ± 0.01 mm, respectively) and largest in Jan 2022 (4.82 ± 0.05 mm) and Dec 2023 (5.01 ± 0.03 mm) (Fig. 6).

Discussion

Knowing a pest's phenology is an important tool for forest pest managers, but in many cases, it is overlooked in favor of research studying immediate eradication or management concerns. Tactics like pheromone trapping, insecticide applications, host species risk, biocontrol, and modeling distribution and spread often take precedence over investigating underlying biological mechanisms of a species, such as phenology and voltinism. However, without this information, many of these eradication methods are hampered by inexact targeting of specific life stages. Phenology research is even more important for wood-boring beetles because much of their life history is obscured while their larvae are burrowed inside trees (Haack et al. 2010, Herms and McCullough 2014). While some phenological milestones may be easy to monitor, such as flight seasons, especially of species like spongy moth that are easily captured via trapping

Table 1. Counts of Asian longhorned beetle life stages and instars for each month over 2 yr of sampling

	Eggs	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Pupae	Unemerged Adults	Totals
Aug 2021	5	0	1	4	51	0	0	0	61
Sep 2021	0	1	0	0	14	1	0	0	16
Oct 2021	0	0	0	0	16	15	0	0	31
Nov 2021	2	0	5	1	8	4	0	0	20
Dec 2021	0	0	0	0	0	22	0	0	22
Jan 2022	0	0	0	0	4	79	0	0	83
Feb 2022	0	0	0	0	3	32	0	0	35
Mar 2022	0	0	0	0	3	18	0	0	21
Apr 2022	0	0	0	0	2	42	24	0	68
May 2022	0	0	0	0	0	0	0	1	1
Jun 2022	36	6	0	0	1	0	0	0	43
Jul 2022	27	0	5	3	0	0	1	0	36
Aug 2022	17	6	21	20	5	0	0	0	69
Sep 2022	0	0	0	0	11	3	0	0	14
Oct 2022	1	0	0	1	5	10	0	0	17
Nov 2022	0	0	0	1	13	24	0	0	38
Dec 2022	0	0	0	0	1	138	0	0	139
Jan 2023	0	0	0	0	3	15	0	0	18
Feb 2023	0	0	0	0	1	50	0	0	51
Mar 2023	0	0	0	0	4	33	0	0	37
Apr 2023	0	0	0	0	3	34	10	0	47
May 2023	0	0	0	0	0	1	1	0	2
Jun 2023	19	3	0	0	0	0	1	0	23
Jul 2023	46	12	43	16	0	0	0	0	117
Totals	153	28	75	46	148	521	37	1	1,009

Instar counts were calculated using the HCAP program (Logan et al. 1998).

(Liebhold et al. 2021), more subtle changes such as timing of specific instars cannot be determined by observation alone—particularly with species whose larvae feed within trees. Phenological data are necessary to give integrated management programs from agriculture and natural resources systems precise timing on a pest life stages so they can implement effective management efforts (Ascerno 1991, MacDonald et al. 2022, Oppedisano et al. 2022), especially with increasing temperatures from climate change causing shifts in insect ranges and development rates.

While there is a great deal of information pertaining to Asian longhorned beetle's life cycle based on data from laboratory studies (e.g., Keena 2006, Keena and Moore 2010, Sánchez and Keena 2013, Torson et al. 2021) and modeling efforts (e.g., Trotter and Keena 2016, Kappel et al. 2017, Schmitt et al. 2025), few empirical

data exist that document Asian longhorned beetle phenology from field-collected individuals. Based on our results, Asian longhorned beetle in South Carolina appears to have a synchronous univoltine life cycle, as eggs laid in Jun, Jul, and Aug can reach fifth instars and are large enough to pupate the following Apr. This is a considerable increase in development rate compared to populations in northern latitudes in North America, Europe, and China, where a 2- or 3-yr life cycle is common (Hua et al. 1992, Li and Wu 1993, Straw et al. 2015, 2016). However, a univoltine life cycle does occur in more southern latitudes in Asian longhorned beetle's native range (Hua et al. 1992, Li and Wu 1993), and this is the first documented univoltine life cycle for Asian longhorned beetle in North America.

Asian longhorned beetle adult activity observed in South Carolina is similar to that recorded in southern parts of Asian longhorned beetle's native range, where adults were observed from May through Sep (Li and Wu 1993). Asian longhorned beetle adults were observed in May, Jun, and Jul during the 2 yr of this study (2021 and 2022), and in Aug and Sep in previous and subsequent years (2020, 2023, 2024; D.R.C., pers. obs.). Thus, compared to infestations in more northern latitudes, where adults are typically active later in the summer (Li and Wu 1993, Haack et al. 2006, Straw et al. 2015), Asian longhorned beetle adults in South Carolina may have extended periods of activity or a longer emergence period. While this was not captured in our sampling, additional sampling would help support or refute this notion as adult emergence periods can be highly variable. For example, in northern Italy, Asian longhorned beetle emergence occurred during a 7-wk period in 2010 (Jul–Aug), a 14-wk period in 2011 (May–Aug), and an 8-wk period in 2012 (Jun–Aug) (Faccoli et al. 2015). Collectively, these data support the idea that Asian longhorned beetle has considerable developmental plasticity, and annual variation in phenology is likely based on several environmental and biological factors.

Larval head capsule widths in our study were similar to those from a laboratory study using Asian longhorned beetle populations from the northern United States (Keena and Moore 2010)—especially for earlier instars (i.e., instars 1 and 2). However, head capsule widths of instars 3–5 from our data spanned the range of those from instars 3 to 14 in their study, and our largest head capsule widths

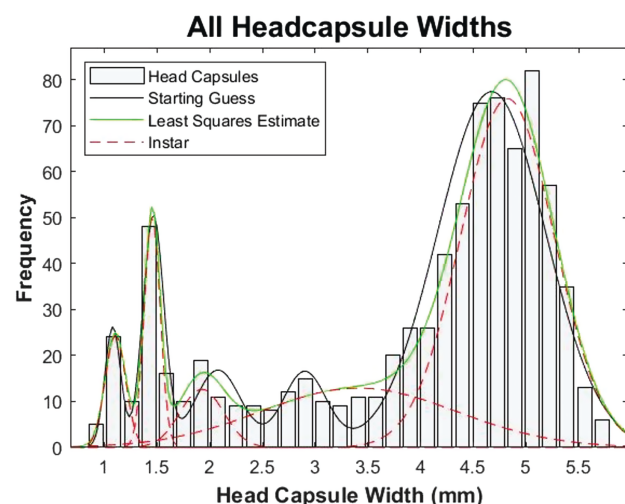


Fig. 3. Instar curves created by using the HCAP program (Logan et al. 1998) based on head capsule width. The solid black line indicates curves based on an estimation of breaks between instars; the solid gray/green line indicates curves based on the best fit as calculated by the program; the dashed lines indicate the distribution of each individual instar.

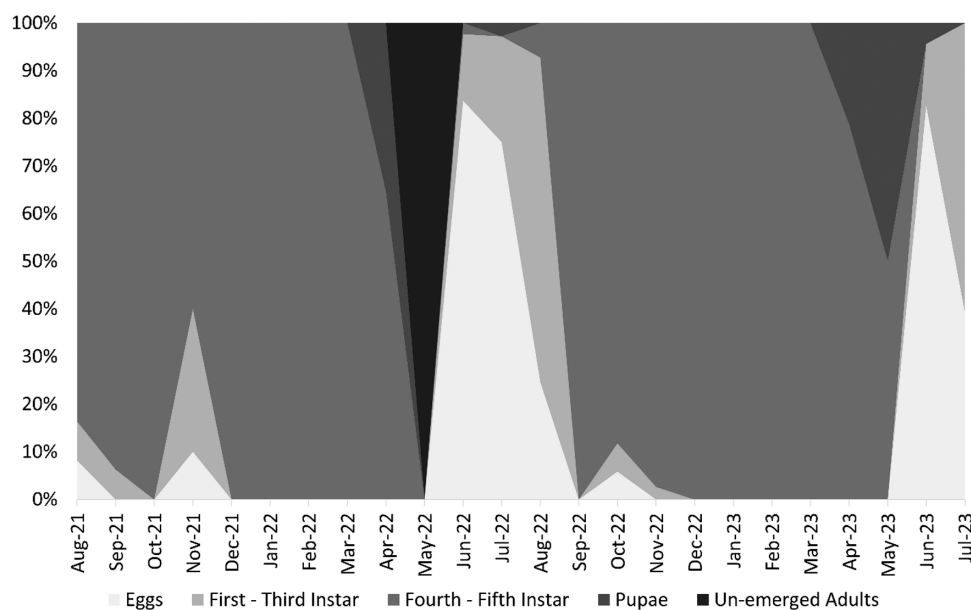


Fig. 4. Percentage of Asian longhorned beetle life stages (eggs, pupae, and unemerged adults) and larvae present split between first-third instars and fourth-fifth instars every month for 2 yr.

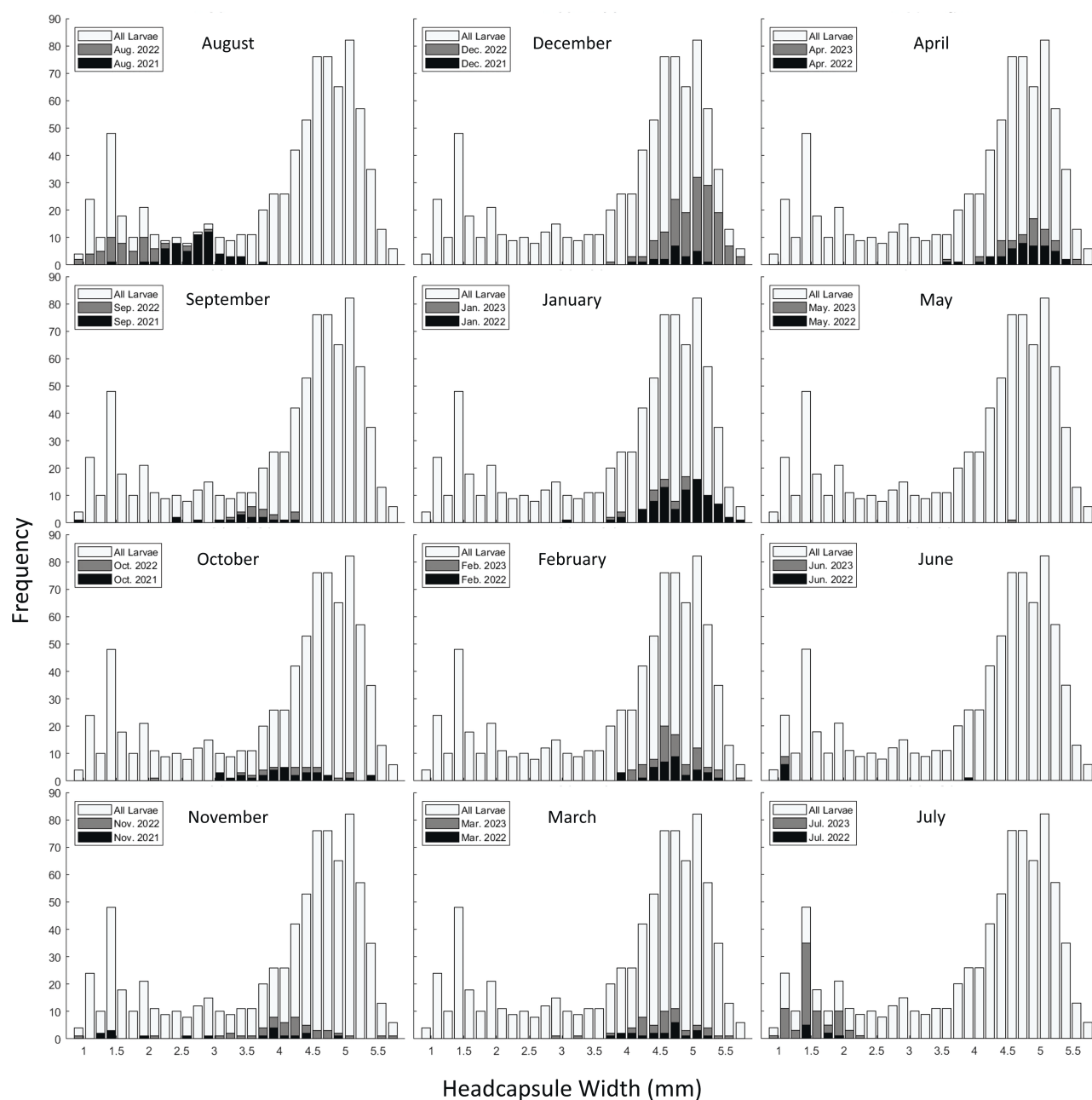


Fig. 5. Frequency distribution of Asian longhorned beetle head capsule widths for each month over the course of 2 yr. Aug 2021–May 2022 was the first (partial) generation sampled, May 2022–May 2023 was the second (full) generation sampled, and May 2023–Jul 2023 was the third (partial) generation sampled. Light gray bars represent all larvae of a particular size collected over the duration of this study, while the darker colored bars represent larvae collected during a particular year.

(nearing 6 mm) were over 0.5 mm wider than the largest measured in Keena and Moore (2010). Similarly, head capsule widths of field-collected larvae from England ranged from 0.5 to 4.5 mm, with their first and second instar head capsule widths (0.5–1.5 mm) similar to ours, while our later instar head capsule widths were overall larger than observed there (Straw et al. 2015). These data suggest that larvae in the warm South Carolina climate are growing larger, and growing faster, than those in more northern climates. Unsurprisingly, mean annual temperatures (and therefore degree-day accumulation) increase as latitude decreases (Fig. 7) while precipitation is more variable (Table 2).

The phenology model described by Trotter and Keena (2016) was built using a pupal hold, a period during which larvae pause

their development or do not progress toward pupation until they have been exposed to winter temperatures. Prior to this study, it was not known whether this pause in development would occur under the warm conditions found in South Carolina. These data also show that Asian longhorned beetle in South Carolina appears to retain a pupal hold period with little or no growth throughout the winter months, and adult emergence occurs at approximately the same time in the spring, resulting in some life stage synchrony within the population. Most Asian longhorned beetle larval growth occurs within the first 3 mo after egg hatch. Larval growth rate slows down after the fourth instar, which most did by Sep, likely because larvae are now feeding on a nutrient-poor substrate (xylem) as opposed to the relatively nitrogen-rich phloem. By Oct most individuals are in

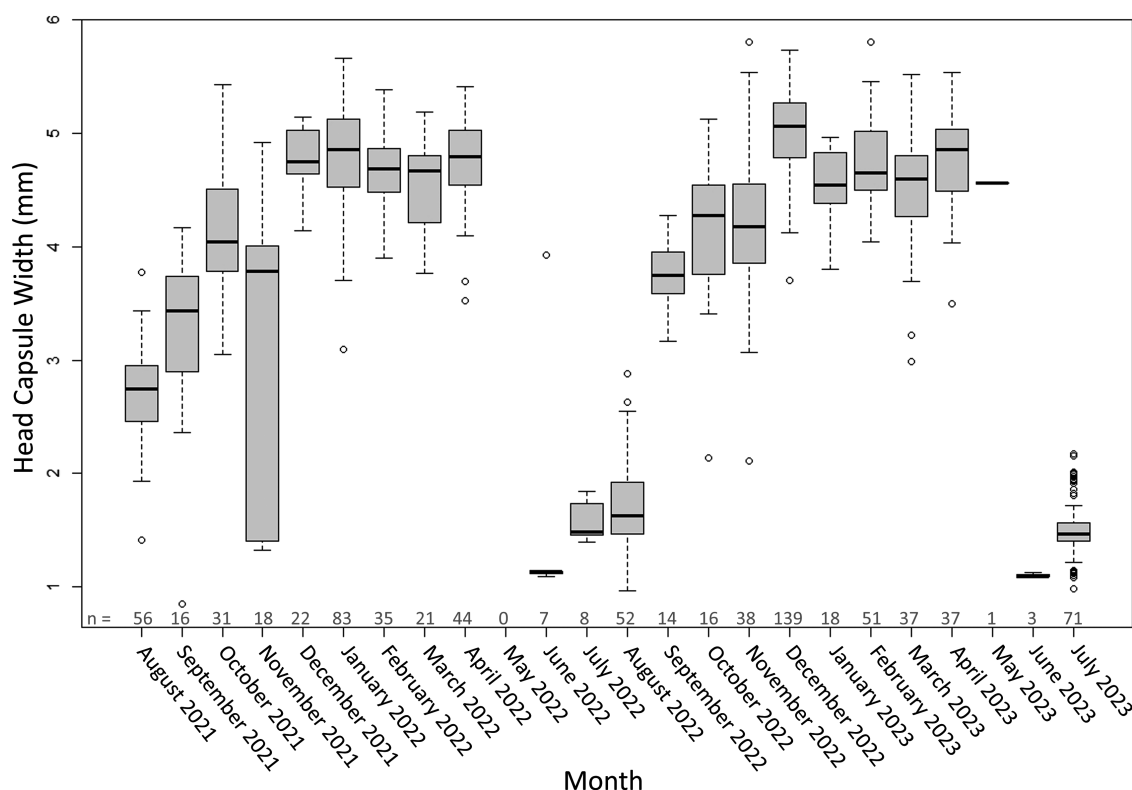


Fig. 6. Boxplots of head capsule width (mm) of Asian longhorned beetle larvae every month for 2 yr. Whiskers indicate values within 1.5x the interquartile range in either direction. Each boxplot represents all the larvae collected during a particular month.

the fifth instar, although slight growth continues until Dec (Fig. 5). It is unknown if a warmer location with milder winters will cause a pupal hold (Keena and Moore 2010, Torson et al. 2021). Without the pupal hold restricting larvae to a yearly life cycle, multiple generations per year may be possible as predicted by various modeling exercises (Trotter and Keena 2016, Kappel et al. 2017, Schmitt et al. 2025). To that end, we did find eggs and neonates present in Nov 2021—a time when fourth and fifth instars were expected. This supports models (e.g., Kappel et al. 2017) that suggest the possibility of a generation completing development in less than 1 yr. However, this variation could be caused by several scenarios, including (i) adults from the 2021 flight season that oviposited much later in the year than usual, either from long-lived adults or adults emerging from less suitable host species (which may have increased development time); (ii) eggs laid during the 2020 flight season grew unusually slowly, and took ~18 mo to develop into adults, which therefore laid their eggs several months later than their generational cohort; or (iii) eggs laid early in the 2021 flight season developed unusually quickly, and were able to gain weight fast enough to pupate before the weather cooled down and the pupal hold went into effect. The last possibility is the most concerning option (though seeming least likely, as no pupae were observed during the late summer or early fall months), since it would indicate that in an ideal climate Asian longhorned beetle would be capable of having a 6-mo life cycle. This would be a major concern for management and eradication efforts, since the slow growth and spread of Asian longhorned beetle is one of the major reasons it has been successfully controlled in many of the locations it has invaded (Haack et al. 2010). Climate change leading to a warmer habitat for Asian longhorned beetle may also contribute to the creation and perpetuation of fast-growing populations of Asian longhorned beetle. So

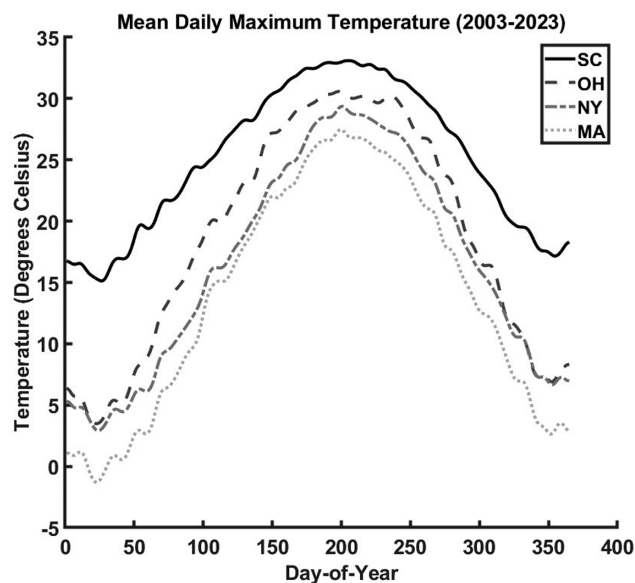


Fig. 7. Mean daily maximum temperature (2003–2023) from the 4 active Asian longhorned beetle infestations in the United States: South Carolina (Charleston, station ID USW00013880), Ohio (Cincinnati, station ID USW00093812), New York (Farmingdale, station ID USW00054787), and Massachusetts (Worcester, station ID USW00094746). Data obtained from the National Oceanic and Atmospheric Administration (<https://www.noaa.gov/>).

far, these small larvae do not appear to be persisting in the population after Nov, as no first, second, or third instars were collected in Dec of either year (Fig. 4), though more research is needed to examine this anomaly.

Table 2. Mean annual monthly precipitation (mm) for the period 2003–2023 from the 4 active Asian longhorned beetle infestations in the United States: South Carolina (Charleston, station ID USW00013880), Ohio (Cincinnati, station ID USW00093812), New York (Farmingdale, station ID USW00054787), and Massachusetts (Worcester, station ID USW00094746)

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
SC	6.92	8.52	7.58	9.30	9.55	16.30	18.25	20.26	14.53	10.99	6.90	9.63	138.73
OH	7.15	8.08	10.34	10.75	11.43	11.56	12.36	8.55	8.04	8.54	7.47	8.35	112.61
NY	5.83	5.86	7.58	9.14	7.81	9.98	8.02	9.31	8.93	10.32	7.27	9.97	100.00
MA	9.24	10.03	10.46	11.83	9.51	11.44	13.31	11.94	12.01	14.90	10.13	13.10	137.90

Data obtained from the National Oceanic and Atmospheric Administration (<https://www.noaa.gov/>).

While our data provide strong evidence of a univoltine lifecycle for Asian longhorned beetle in South Carolina, our determination of putative instars in the head capsule size data was potentially limited by the HCAP analyses, specifically by the sample size and study organism. The HCAP program was originally designed for instar determination of Scolytinae (Logan et al. 1998)—a group in which it is relatively easy to collect thousands or tens of thousands of individuals. Asian longhorned beetle differs from the scolytines in several biological ways, thus making the field collection of thousands of individuals extremely difficult and logistically challenging. Despite monthly sampling in an active infestation zone, we were only able to collect fewer than a thousand larvae over the course of 2 yr. The lower sample size made selections of the instar bound more difficult and made for much more variable results. Younger larvae, in particular, were more difficult to find, likely because visual evidence of their presence is less obvious than that of larger larvae (Fig. 2). The addition of Asian longhorned beetle's supernumerary instars also made using the program more complicated, as although we chose to select 5 instars, the variability in fifth instar size may be because it also includes instars past fifth (e.g., sixth or seventh instars) that may or may not lead to a change in the larva's size. Despite these issues, the HCAP program was able to give at least an estimate of instar size and timing.

Population modeling is also an essential tool to give management programs phenology information without requiring labor-intensive fieldwork at every new location. The ability to anticipate how an invasive insect will respond to local climates before a population is established gives management programs a significant advantage, allowing them to locate areas at high risk for invasion and negative impacts, time surveying for new detections, and have a management plan in place for a rapid response to new invasions. A phenology model has been created for Asian longhorned beetle but has only been tested using data from the beetle's native range, European infestations, and populations from the northern United States (Trotter and Keena 2016). This research can help evaluate whether this model will make reliable predictions in the southern United States.

Conclusions

Survey and management efficacy depends on accurate knowledge of Asian longhorned beetle phenology. The 4 fundamental elements of invasive species management (prevention, detection, control, and restoration) all necessitate knowledge of the species' growth rate and timing of life stages to be effective (Dix et al. 2013). Awareness of when specific life stages are present during the year can improve the accuracy of surveys (Dix et al. 2013, Oswalt et al. 2021) and can increase the effectiveness of control methods that require specific timing such as the application of some insecticides (Poland et al. 2006, Ugine et al. 2011), biocontrol strategies (e.g., Lupu 2024), and alternative methods applied in locations unsuitable for the heavy

machinery used in typical Asian longhorned beetle management strategies (Ratcliff 2022). These management options are most effective against first through third instars that have not tunneled into the heartwood, and their efficacy is also impacted by the rate of larval growth. If first through third instars are only present 3–4 mo of the year, it greatly reduces the amount of time that these management options can be successfully utilized. Because of the unknown impacts of this new climate on Asian longhorned beetle development, having accurate phenological information is necessary for both detection and management of Asian longhorned beetle. Our data show that Asian longhorned beetle populations in South Carolina exhibit a pattern in sizes and life stages consistent with a synchronous, univoltine life cycle present in the southern parts of Asian longhorned beetle's native range. This univoltine life cycle seems to be imposed by the hold in development that occurs in winter prior to pupation. The loss of this pupal hold period could lead to faster development with some potential for a multivoltine cycle. This has significant implications for management, as faster development and speed of spread could make controlling invasions of this species much more difficult. Overall, more research is needed to confirm the possibility of Asian longhorned beetle reaching adulthood in less than a year and predicting whether other areas of the United States will be at risk for a rapidly growing population.

Acknowledgments

We thank the United States Department of Agriculture's Animal and Plant Health Inspection Service (USDA APHIS), South Carolina Forestry Commission, and Clemson University Asian Longhorned Beetle Program for project support, as well as the many field personnel who helped us accomplish this research. Thanks also to the South Carolina Forestry Commission, Clemson University, and USDA personnel for their earlier reviews of this manuscript. We thank Melissa Griffin, South Carolina Department of Natural Resources, for assistance in compiling precipitation data.

Author contributions

Lena R. Schmitt (Investigation [equal], Methodology [equal], Writing—original draft [equal]), David Coyle (Conceptualization [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Supervision [equal], Writing—review & editing [equal]), Scott Pfister (Conceptualization [equal], Project administration [equal], Writing—review & editing [equal]), Katy E. Crout (Investigation [equal], Methodology [equal], Validation [equal], Writing—review & editing [equal]), Crystal J. Bishop (Investigation [equal], Methodology [equal], Writing—review & editing [equal]), and Talbot Trotter (Formal analysis [equal], Investigation [equal], Software [equal], Validation [equal], Writing—review & editing [equal])

Funding

This work was made possible, in part, by Cooperative Agreements AP21PPQS&T00C002, AP22PPQS&T00C002, and AP23PPQS&T00C004 from the United States Department of Agriculture's Animal and Plant Health Inspection Service (USDA APHIS) and an Emerging Pests Program grant (number 21-DG-11083145-008) from the USDA Forest Service and South Carolina Forestry Commission. Technical Contribution No. 7322 of the Clemson University Experiment Station. This material is based upon work supported by NIFA/USDA, under project number SC-1050622,1700622.

References Cited

- Ascerno ME. 1991. Insect phenology and integrated pest management. *Arboric. Urban For.* 17:13–15. <https://doi.org/10.48044/jauf.1991.003>
- Beltrà A, García-Marí F, Soto A. 2013. Seasonal phenology, spatial distribution, and sampling plan for the invasive mealybug *Phenacoccus peruvianus* (Hemiptera: Pseudococcidae). *J. Econ. Entomol.* 106:1486–1494. <https://doi.org/10.1603/ec13024>
- Bohannon GR, Johnson CL, Jetton RM, et al. 2022. Phenology and voltinism of emerald ash borer (Coleoptera: Buprestidae) in central North Carolina. *Environ. Entomol.* 51:1077–1085. <https://doi.org/10.1093/ee/nvac088>
- Calvo D, Molina JM. 2008. Head capsule width and instar determination for larvae of *Streblote panda* (Lepidoptera: Lasiocampidae). *Ann. Entomol. Soc. Am.* 101:881–886. <https://doi.org/10.1093/aesa/101.5.881>
- Carter M, Smith M, Harrison R. 2010. Genetic analyses of the Asian longhorned beetle (Coleoptera, Cerambycidae, *Anoplophora glabripennis*), in North America, Europe and Asia. *Biol. Invasions* 12:1165–1182. <https://doi.org/10.1007/s10530-009-9538-9>
- Cavey JF, Hoebeke ER, Passoa S, et al. 1998. A new exotic threat to North American hardwood forests: an Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae). *Proc. Entomol. Soc. Wash.* 100:373–381.
- Coyle DR, Trotter RT III, Bean MS, et al. 2021. First recorded Asian longhorned beetle (Coleoptera: Cerambycidae) infestation in the southern United States. *J. Integr. Pest Manag.* 12:1–6. <https://doi.org/10.1093/jipm/pmab007>
- Crimmins TM, Gerst KL, Huerta DG, et al. 2020. Short-term forecasts of insect phenology inform pest management. *Ann. Entomol. Soc. Am.* 113:139–148. <https://doi.org/10.1093/aesa/saz026>
- Davidson CB, Gottschalk KW, Johnson JE. 1999. Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *For. Sci.* 45:74–84. <https://doi.org/10.1093/forestscience/45.1.74>
- Delbac L, Lecharpentier P, Thiery D. 2010. Larval instars determination for the European grapevine moth (Lepidoptera: Tortricidae) based on the frequency distribution of head-capsule widths. *Crop Prot.* 29:623–630. <https://doi.org/10.1016/j.cropro.2010.01.009>
- Diagne C, Leroy B, Vaissière A, et al. 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592:571–576. <https://doi.org/10.1038/s41586-021-03405-6>
- Dix ME, Bass B, Covell SA, et al. 2013. Forest service national strategic framework for invasive species management. Washington (DC): US Department of Agriculture Forest Service, FS-1017; 36 p.
- Dodds KJ, Orwig DA. 2011. An invasive urban forest pest invades natural environments—Asian longhorned beetle in northeastern US hardwood forests. *Can. J. For. Res.* 41:1729–1742. <https://doi.org/10.1139/x11-097>
- Dodds KJ, Hull-Sanders HM, Siegert NW, et al. 2014. Colonization of three maple species by Asian longhorned beetle, *Anoplophora glabripennis*, in two mixed-hardwood forest stands. *Insects* 5:105–119. <https://doi.org/10.3390/insects5010105>
- Ellison AM, Orwig DA, Fitzpatrick MC, et al. 2018. The past, present, and future of the hemlock woolly adelgid (*Adelges tsugae*) and its ecological interactions with eastern hemlock (*Tsuga canadensis*) forests. *Insects* 9:172. <https://doi.org/10.3390/insects9040172>
- Faccoli M, Favaro R, Smith MT, et al. 2015. Life history of the Asian longhorned beetle (Coleoptera: Cerambycidae) in southern Europe. *Agric. For. Entomol.* 17:188–196. <https://doi.org/10.1111/afe.12096>
- Feng Y, Xu L, Tian B, et al. 2014. Cold hardiness of Asian longhorned beetle (Coleoptera: Cerambycidae) larvae in different populations. *Environ. Entomol.* 43:1419–1426. <https://doi.org/10.1603/EN13352>
- Fleming MR, Hoover K, Janowiak JJ, et al. 2003. Microwave irradiation of wood packing material to destroy the Asian longhorned beetle. *J. For. Prod.* 53:46–51.
- Gray DR. 2016. Risk reduction of an invasive insect by targeting surveillance efforts with the assistance of a phenology model and international maritime shipping routes and schedules. *Risk Anal.* 36:914–925. <https://doi.org/10.1111/risa.12474>
- Greenwood L, Avila MA, Coyle DR, et al. 2023. Exploring pest mitigation research and management associated with the North American wood packaging supply chain: what and where are the weak links? *Biol. Invasions* 25:2395–2421. <https://doi.org/10.1007/s10530-023-03058-8>
- Griffin M, Mogil HM. 2021. The weather and climate of South Carolina: “nothing could be finer than to be in (South) Carolina”. *Weatherwise* 74:25–34. <https://doi.org/10.1080/00431672.2021.1924043>
- Griffith GE, Omerik JM, Comstock JA, et al. 2002. Ecoregions of South Carolina. Corvallis (OR): U.S. Environ. Prot. Agency.
- Haack RA, Cavey JF, Hoebeke ER, et al. 1996. *Anoplophora glabripennis*: a new tree-infesting exotic cerambycid invades New York. *Newsl. Mich. Entomol. Soc.* 41:1–3.
- Haack RA, Bauer LS, Gao R, et al. 2006. *Anoplophora glabripennis* within-tree distribution, seasonal development, and host suitability in China and Chicago. *Great Lakes Entomol.* 39:169–183. <https://doi.org/10.22543/0090-0222.2163>
- Haack RA, Hérard F, Sun J, et al. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. *Annu. Rev. Entomol.* 55:521–546. <https://doi.org/10.1146/annurev-ento-112408-085427>
- Hermes DA, McCullough DG. 2014. Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annu. Rev. Entomol.* 59:13–30. <https://doi.org/10.1146/annurev-ento-011613-162051>
- Holmes TP, Aukema JE, Holle BV, et al. 2009. Economic impacts of invasive species in forests. *Ann. New York Acad. Sci.* 1162:18–38. <https://doi.org/10.1111/j.1749-6632.2009.04446.x>
- Hu J, Angeli S, Schuetz S, et al. 2009. Ecology and management of exotic and endemic Asian longhorned beetle *Anoplophora glabripennis*. *Agric. For. Entomol.* 11:359–375. <https://doi.org/10.1111/j.1461-9563.2009.00443.x>
- Hua L, Li S, Zhang X. 1992. Coleoptera: Cerambycidae. In: Peng J, Liu Y, editors. *Iconography of forest insects in Hunan China*. Changsha: Hunan Science and Technology Press; 60+4+147 pp.
- Javal M, Roques A, Haran J, et al. 2019. Complex invasion history of the Asian long-horned beetle: fifteen years after first detection in Europe. *J. Pest Sci.* 92:173–187. <https://doi.org/10.1007/s10340-017-0917-1>
- Kamiyama MT, Matsuura K, Yoshimura T, et al. 2021. Improving invasive species management using predictive phenology models: an example from brown marmorated stink bug (*Halyomorpha halys*) in Japan. *Pest Manag. Sci.* 77:5489–5497. <https://doi.org/10.1002/ps.6589>
- Kappel AP, Trotter RT III, Keena MA, et al. 2017. Mapping of the Asian longhorned beetle's time to maturity and risk to invasion at contiguous United States extent. *Biol. Invasions* 19:1999–2013. <https://doi.org/10.1007/s10530-017-1398-0>
- Keena MA. 2002. *Anoplophora glabripennis* (Coleoptera: Cerambycidae) fecundity and longevity under laboratory conditions: comparison of populations from New York and Illinois on *Acer saccharum*. *Environ. Entomol.* 31:490–498. <https://doi.org/10.1603/0046-225x-31.3.490>
- Keena MA. 2006. Effect of temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) adult survival, reproduction, and egg hatch. *Environ. Entomol.* 35:912–921. <https://doi.org/10.1603/0046-225x-35.4.912>
- Keena MA, Moore PM. 2010. Effects of temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) larvae and pupae. *Environ. Entomol.* 39:1323–1335. <https://doi.org/10.1603/EN09369>
- Krishnakutty SM, Bigsby K, Hastings J, et al. 2020. Predicting establishment potential of an invasive wood-boring beetle, *Trichoferus campestris* (Coleoptera: Cerambycidae) in the United States. *Ann. Entomol. Soc. Am.* 113:88–99. <https://doi.org/10.1093/aesa/saz051>

- Li W, Wu C. 1993. Species, distributions, and host plants of the longhorned beetles injuring poplars. Ch. 2. In: Integrated management of longhorned beetles damaging poplar trees. Beijing: China Forest Press; 290 p.
- Liebholt AM, MacDonald WL, Bergdahl D, et al. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. For. Sci. Monogr. 30:1–49. <https://doi.org/10.1093/forestscience/41.s1.a0001>
- Liebholt AM, Leonard D, Marra JL, et al. 2021. Area-wide management of invading gypsy moth (*Lymantria dispar*) population in the USA. In: Hendrichs J, Pereira R, Vreysen MJB, editors. Area-wide integrated pest management. Boca Raton (FL): CRC Press; p. 551–560; 1012 pages.
- Lingafelter SW, Hoebeke ER. 2002. Revision of *Anoplophora* (Coleoptera: Cerambycidae). Washington (DC): Entomological Society of Washington; 236 pp + 41 color plates.
- Liu H, Bauer LS, Zhao T, et al. 2016. Seasonal abundance and development of the Asian longhorned beetle and natural enemy prevalence in different forest types in China. Biol. Control. 103:154–164. <https://doi.org/10.1016/j.biocontrol.2016.08.010>
- Logan JA, Bentz BJ, Vandygriff JC, et al. 1998. General program for determining instar distributions from headcapsule widths: example analysis of mountain pine beetle (Coleoptera: Scolytidae) data. Environ. Entomol. 27:555–563. <https://doi.org/10.1093/ee/27.3.555>
- Lovett GM, Weiss M, Liebholt AM, et al. 2016. Nonnative forest insects and pathogens in the United States: impacts and policy options. Ecol. Appl. 26:1437–1455. <https://doi.org/10.1890/15-1176>
- Ludwig SW, Lazarus L, McCullough DG, et al. 2002. Methods to evaluate host tree suitability to the Asian longhorned beetle, *Anoplophora glabripennis*. J. Environ. Hortic. 20:175–180. <https://doi.org/10.24266/0738-2898-20.3.175>
- Lupu M. 2024. An evaluation of potential biocontrol agents for *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in South Carolina, USA [master's thesis]. [Clemson (SC)]: Clemson University; 82 p. https://tigerprints.clemson.edu/all_theses/4222
- MacDonald B, Bardack R, Westwood AR, et al. 2022. Predicting emerald ash borer adult emergence and peak flight activity in Winnipeg, Manitoba, Canada. Fron. Ecol. Evol. 10:846144. <https://doi.org/10.3389/fevo.2022.846144>
- MathWorks. 1993. MATLAB reference guide. Natick (MA): MathWorks.
- MathWorks Inc. 2021. MATLAB version: 9.11.0 (R2021b). Natick (MA): The MathWorks Inc. <https://www.mathworks.com>
- Moser WK, Barnard EL, Billings RE, et al. 2009. Impacts of nonnative invasive species on US forests and recommendations for policy and management. J. For. 107:320–327. <https://doi.org/10.1093/jof/107.6.320>
- Oppedisano T, Shrestha G, Anderson S, et al. 2022. Predicting phenology of four major hemipteran pests to enhance integrated pest management programs in potatoes in the Lower Columbia Basin. J. Econ. Entomol. 115:430–437. <https://doi.org/10.1093/jeet/toab215>
- Oswalt S, Oswalt C, Crall A, et al. 2021. Inventory and monitoring of invasive species. In: Poland TM, Patel-Weyand T, Finch DM, Miniat CF, Hayes DC, Lopez VM, editors. Invasive species in forests and rangelands of the United States: a comprehensive science synthesis for the United States forest sector. Cham (Switzerland): Springer; p. 231–241.
- Panzavolta T. 2007. Instar determination for *Pissodes castaneus* (Coleoptera: Curculionidae) using head capsule widths and lengths. Environ. Entomol. 36:1054–1058. [https://doi.org/10.1603/0046-225x\(2007\)36\[1054:idfpcc\]2.0.co;2](https://doi.org/10.1603/0046-225x(2007)36[1054:idfpcc]2.0.co;2)
- Pawson SM, Kerr JL, Kimberly MO, et al. 2021. Large-scale, multi-year, phenology modelling of forest insects in *Pinus radiata* plantations. J. Pest Sci. 94:1375–1592. <https://doi.org/10.1007/s10340-021-01328-9>
- Poland TM, Haack RA, Petrice TR, et al. 2006. Field evaluations of systemic insecticides for control of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in China. J. Econ. Entomol. 99:383–392. <https://doi.org/10.1603/0022-0493.99.2.383>
- Ratcliff AR. 2022. Alternative control methods for the eradication of the Asian longhorned beetle [*Anoplophora glabripennis* (Motschulsky)] in infested bottomland sites in South Carolina [master's thesis]. [Raleigh (NC)]: North Carolina State University. <https://www.lib.ncsu.edu/resolver/1840.20/40187>
- Roden DB, Haack RA, Keena MA, et al. 2008. Potential Northern distribution of Asian longhorned beetle in North America. In: McManus KA, Gottschalk KW, editors. Proc. 19th U.S. Department of Agriculture Interagency Research Forum on Invasive Species. Newton Square (PA): U.S. Department of Agriculture, Forest Service; p. 65–167; 100 pages.
- Sánchez V, Keena MA. 2013. Development of the teneral adult *Anoplophora glabripennis* (Coleoptera: Cerambycidae): time to initiate and completely bore out of maple wood. Environ. Entomol. 42:1–6. <https://doi.org/10.1603/EN12225>
- SC DNR. 2005. Coastal zone and marine ecoregion terrestrial and aquatic habitats. [accessed 2023 Oct 15]. dc.statelibrary.sc.gov/bitstream/handle/10827/26421/DNR_Coastal_Zone_Ecoregion_Terrestrial_and_Aquatic_Habitats_2005.pdf?sequence=1.
- Schmitt LR, Trotter III RT, Coyle DR. 2025. Validating a variable-instar, climate-based phenology model for the Asian longhorned beetle (Coleoptera: Cerambycidae) using field data from South Carolina. Environ. Entomol. <https://doi.org/10.1093/ee/nvae127>
- Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods. 9:671–675. <https://doi.org/10.1038/nmeth.2089>
- Smith MT, Bancroft J, Li G, et al. 2001. Dispersal of *Anoplophora glabripennis* (Cerambycidae). Environ. Entomol. 30:1036–1040. <https://doi.org/10.1603/0046-225x-30.6.1036>
- Smith MT, Tobin PC, Bancroft J, et al. 2004. Dispersal and spatiotemporal dynamics of Asian longhorn beetle (Coleoptera: Cerambycidae) in China. Environ. Entomol. 33:435–442. <https://doi.org/10.1603/0046-225x-33.2.435>
- Straw NA, Tilbury C, Fielding NJ, et al. 2015. Timing and duration of the life cycle of Asian longhorned beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in southern England. Agric. For. Entomol. 17:400–411. <https://doi.org/10.1111/afe.12120>
- Straw NA, Fielding NJ, Tilbury C, et al. 2016. History and development of an isolated outbreak of Asian longhorned beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in southern England. Agric. For. Entomol. 18:280–293. <https://doi.org/10.1111/afe.12160>
- Torson AS, Zhang ML, Smith AJ, et al. 2021. Dormancy in laboratory-reared Asian longhorned beetles, *Anoplophora glabripennis*. J. Insect Physiol. 130:104170. <https://doi.org/10.1016/j.jinsphys.2020.104179>
- Trotter RT III, Hull-Sanders HM. 2015. Quantifying dispersal of the Asian longhorned beetle (*Anoplophora glabripennis*, Coleoptera) with incomplete data and behavioral knowledge. Biol. Invasions 17:3359–3369. <https://doi.org/10.1007/s10530-015-0961-9>
- Trotter RT III, Keena MA. 2016. A variable-instar climate-driven individual beetle-based phenology model for the invasive Asian longhorned beetle (Coleoptera: Cerambycidae). Environ. Entomol. 45:1360–1370. <https://doi.org/10.1093/ee/nvw108>
- Trotter RT III, Pepper E, Davis K, et al. 2018. Anisotropic dispersal by the Asian longhorned beetle (*Anoplophora glabripennis*): quantifying spatial risk and eradication effort with limited biological data. Biol. Invasions 21:1179–1195. <https://doi.org/10.1007/s10530-018-1894-x>
- Turgeon JJ, Orr M, Grant C, et al. 2015. Decade-old satellite infestation of *Anoplophora glabripennis* Motschulsky (Coleoptera: Cerambycidae) found in Ontario, Canada outside regulated area of founder population. Coleop. Bull. 69:674–678. <https://doi.org/10.1649/0010-065X-69.4.674>
- Turgeon JJ, Gasman B, Smith MT, et al. 2022. Canada's response to invasion by Asian longhorned beetle (Coleoptera: Cerambycidae) in Ontario. Can. Entomol. 154:1–87. <https://doi.org/10.4039/tce.2021.60>
- Ugine TA, Gardescu S, Hajek AE. 2011. The effect of exposure to imidacloprid on Asian longhorned beetle (Coleoptera: Cerambycidae) survival and reproduction. J. Econ. Entomol. 104:1942–1949. <https://doi.org/10.1603/ec11139>
- USDA APHIS. 2023. ALB South Carolina quarantine boundary. Animal and Plant Health Inspection Service. [accessed 2023 Oct 9]. https://www.aphis.usda.gov/plant_health/plant_pest_info/asian_lhb/downloads/albmaps/south-carolina-regulatory-boundary.pdf.
- Xu T, Teale SA. 2021. Chemical ecology of the Asian longhorn beetle, *Anoplophora glabripennis*. J. Chem. Ecol. 47:489–503. <https://doi.org/10.1007/s10886-021-01280-z>