



## Population Ecology

# Local dispersal and growth in an island population of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in South Carolina

Meredith S. Bean<sup>1</sup>, R. Talbot Trotter III<sup>2</sup>, Jennifer Chandler<sup>2</sup>, Robert Ritger<sup>1</sup>, Cooper Schroeder<sup>1</sup>, Jess A. Hartshorn<sup>1,4</sup>, Brandon K. Peoples<sup>1</sup>, Kyle Barrett<sup>1</sup>, Scott E. Pfister<sup>3</sup>, and David R. Coyle<sup>\*, 1</sup>

<sup>1</sup>Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, USA

<sup>2</sup>US Department of Agriculture Forest Service, Northern Research Station, Hamden, CT, USA

<sup>3</sup>US Department of Agriculture Animal and Plant Health Inspection Service, PPQ, S&T, Forest Pest Methods Laboratory, Buzzards Bay, MA, USA

<sup>4</sup>Present address: Agriculture Research Development Program, Central State University, Wilberforce, OH, USA.

\*Corresponding author. Department of Forestry and Environmental Conservation, 121 Lehotsky Hall, Clemson University, Clemson, SC 29634, USA  
(Email: [dcoble@clemson.edu](mailto:dcoble@clemson.edu)).

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Invasive populations of *Anoplophora glabripennis* (Motschulsky) threaten forested systems across the globe. Eradication programs in North America can span hundreds of square kilometers, yet eradication efforts are carried out at the individual tree or stand scale. An *A. glabripennis* infestation was discovered in South Carolina in 2020; within this landscape, a small island was found on which 85% of *A. glabripennis* host trees were infested. The removal of all infested trees from the island in 2021 provided an opportunity to use this discrete population as a natural microcosm in which the spatial locations for the 14,615 oviposition sites and 1,611 exit holes in the population were documented. Data show *A. glabripennis* population growth rates varied substantially among individual trees. At the scale of the island, beetle density increased exponentially over time, while the number of infested trees on the island increased at a more moderate rate. The spatial and temporal patterns suggest several causal mechanisms and highlight the need for additional studies including the potential that female preference drives variation among host tree preference and beetle performance. The severity of the *A. glabripennis* infestation within trees was an inconsistent predictor of the age of an infestation, which is a key assumption used in landscape scale models of *A. glabripennis* dispersal. However, overall differences between predicted *A. glabripennis* movement and behavior were similar to that predicted from current risk models, supporting the utility of the landscape scale reconstructions currently used to model *A. glabripennis* spread and risk.

**Keywords:** Asian longhorned beetle, forest pest, invasive species, modeling, prediction

## Introduction

*Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), colloquially called the Asian longhorned beetle, is a polyphagous woodborer native to China and the Korean Peninsula which has become a significant global invader (Keena et al. 2026). The ability of *A. glabripennis* larvae to survive transport as a hidden stowaway in commonly used solid wood packing materials (Keena et al. 2026), combined with a high level of phenological plasticity that allows the beetles to tolerate a broad range of climatic conditions (Trotter and Keena 2016), have made this species a high risk for both North American and European forests. Breeding populations have been found in Austria, Belgium, Canada, Finland, France, Germany, Italy, Turkey, the Netherlands, the United Kingdom,

and the United States. Left unchecked, *A. glabripennis* poses ecological and economic risks to invaded landscapes. Nowak et al. (2001) estimated a cost of more than \$600 billion (United States) to urban centers in the eastern United States, which is likely an underestimate because the additional financial and ecological risk to rural landscapes, forested ecosystems, and communities would greatly increase these costs. Due to the high risk posed by this species, the United States, Canada, and members of the European and Mediterranean Plant Protection Organization have adopted policies of eradication when *A. glabripennis* is detected.

While *A. glabripennis* is considered one of the world's worst biological invaders (Lowe et al. 2000), eradication has been successfully declared in multiple European and North

American landscapes. Eradication programs have found success using intensive visual surveys to find individual infested trees followed by rapid felling and destruction of host tree material to ensure no survival of any life stage of the pest. While this strategy has been effective (Eyre and Barbrook 2021, Marchioro and Faccoli 2021, Turgeon et al. 2022a), the rapid removal of infested material has significantly limited opportunities to collect empirical data regarding *A. glabripennis* behavior, population dynamics, and dispersal in invaded landscapes.

The visual surveys required to carry out these eradication programs are labor-intensive, thus information on behavior and dispersal could be used to focus survey efforts and increase survey (and therefore eradication) efficiency (Aubry et al. 2017, Büyüktaktakın and Haight 2018). Some limited studies have been carried out within eradication programs (eg Trotter and Hull-Sanders 2015, Faccoli and Gatto 2016, Eyre and Barbrook 2021, Turgeon et al. 2022a), though dispersal analyses have depended heavily on studies conducted in the beetle's native range. Smith et al. (2001, 2004) used mark-and-recapture methods in China to estimate dispersal kernels (functions describing the distance and probability of dispersal) and found that 98% of adult beetles dispersed <560 m, with a mean dispersal distance of 266 m; Wen et al. (1998, translated by Hu et al. 2009) found similar dispersal distances of 240 m. Although these studies have supported eradication efforts, they reflect dispersal behaviors and patterns in native habitats and their application in invaded landscapes remains untested.

While generalized models of invasive species spread have been developed (Hudgins et al. 2017), high-resolution, location-specific models of *A. glabripennis* spread are needed to effectively and efficiently monitor and eradicate this pest (Trotter et al. 2023, Bean et al. 2025). The composite Asian Longhorned Beetle Eradication and Risk Tracking tool (hereafter referred to as ALBERT; USDA Forest Service 2025) which includes the ALBRisk model (Trotter and Hull-Sanders 2015, Hull-Sanders et al. 2017, Trotter et al. 2019, 2021, 2023, 2024) was developed to address this need. ALBERT uses models that incorporate tens of thousands of tree location and infestation intensity records collected by eradication programs in the United States to reconstruct patterns of *A. glabripennis* dispersal and estimate the distribution of risk on the landscape. This tool has generated dispersal kernels in US infestations similar to those observed in China. For example, application of ALBERT to infestation data in Bethel, Ohio and Worcester, Massachusetts, United States. infestations indicated that 98% of *A. glabripennis* disperse within 450 and 933 m, respectively. ALBERT and its component tools have also described substantial differences in dispersal pattern and risk among the different infestations in the United States (Trotter et al. 2021, 2023, 2024) highlighting the opportunity to use locally calibrated data to explore the drivers of dispersal and support eradication efforts. The models used by ALBERT are repeatable across multiple landscapes; however, they depend on 2 key assumptions: (i) that the source of the beetle infesting a tree is the nearest tree with an infestation that is older than the receiving tree and (ii) that the quantity of beetle damage within a tree is a proxy for how long the tree has been infested. The high-resolution reconstruction of a complete *A. glabripennis* population could

provide a way to assess these assumptions and the applicability of the models.

*A. glabripennis* biology and resulting damage to host trees provides a physical record that can be used to reconstruct populations. When adult beetles emerge from trees, they leave distinctive exit holes that document both the location and year of emergence. However, reconstructing population growth and movement would require a beetle population that is geographically discrete and small enough to quantify all the exit hole damage. Until 2020, the size of *A. glabripennis* infestations in the United States combined with the need to rapidly remove infested trees has prevented this type of study. In 2020, a new breeding population of *A. glabripennis* was found in Charleston County, South Carolina, United States (Fig. 1A; Coyle et al. 2021), and a small island hosting a beetle population was discovered within this larger landscape. This island included an active and growing *A. glabripennis* population in an isolated stand of host trees (red maple, *Acer rubrum* L. [Sapindales: Sapindaceae]). We used this unique island system to address 3 primary objectives: (i) quantify and describe the growth of the *A. glabripennis* population within canopies and across the stand (island) through time, (ii) determine the *A. glabripennis* adult emergence date on the complete set of exit holes on the island to test the assumption that the level of infestation in individual trees is a predictor of the age of an infestation, a key assumption made by ALBERT, and (iii) use the dated exit holes to reconstruct both the timing and likely sequence of *A. glabripennis* movements within the stand to produce a high-resolution reconstruction of beetle dispersal, and compare this reconstruction with the pattern generated by the suite of analysis tools within ALBERT.

## Methods

### Site Description

The *A. glabripennis* infestation in Charleston County is located within a 198 km<sup>2</sup> regulated area (Fig. 1B) and included >13,000 infested trees as of April 2026 (<https://blogs.clemson.edu/regulatory/april-2026-asian-longhorned-beetle-alb-cooperative-eradication-program-community-update/>). Near the center of the regulated area is Stono River County Park (32°47'08"N, 80°6'44"W), a municipal recreational park that includes an artificial island formed in the late 19th century as a spoils pile of material dredged from the Stono River and surrounding marshes (Fig. 1C). In 2020, the 3.3 ha (8.1 ac) island supported a subtropical maritime forest surrounded by a tidal salt marsh in the brackish waters of the Intracoastal Waterway. Vegetation on the island was dominated by a few large individual native trees, primarily *A. rubrum*, *Pinus taeda* (L.) and *Liquidambar styraciflua* (L.), with a single *Ulmus americana* L.; the mid- and understory was composed primarily of native *Ilex vomitoria* (Ait.) and *Juniperus virginiana* (L.) and the invasive *Triadica sebifera* (L.) Small (Bean 2022). In late 2020, personnel with the Cooperative Asian Longhorned Beetle Eradication Program, a program operated by the US Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS), the Clemson College of Agriculture, Forestry, and Life Sciences, the South Carolina Forestry Commission, and local municipal governments (hereafter referred to simply as the Cooperative Program) carried out a survey of the island as part of the eradication program. This survey identified trees infested with



**Fig. 1.** Location of the *Anoplophora glabripennis* quarantine zone in the southeastern United States (A) and location of the island study site within the quarantine zone (B). The island on which the study took place (C) was connected to the mainland by a bridge. Reprinted from [Bean et al. 2025](#).

*A. glabripennis* and the Cooperative Program initiated the process to carry out a full host tree removal on the island.

### Dating Beetle Damage and Estimating Population Growth

To quantify the distribution of damage within and among trees, tree locations were mapped using a Trimble GPS receiver

(GeoExploreer 3000 Series). A detailed description of the process used to document and remove host trees from the island is provided in [Bean et al. \(2025\)](#). Briefly summarized, in January of 2021, contract sawyers felled all 33 *A. rubrum* host trees on the island (median height of the trees was ~9 m, with the tallest trees growing to nearly 25 m; [Bean et al. 2025](#)) by chainsaw at ground level, and all material >3.8 cm in diameter was cut

into sections that could be removed from the island by hand cart or on a small utility-terrain vehicle. The ends of each tree section were labeled to allow for the reconstruction of the trunks and canopies. All sections with a diameter of <3.8 cm and verified as uninfested were chipped on-site in compliance with USDA APHIS-PPQ Asian Longhorned Beetle Eradication Program requirements (Rose 2014). All material >3.8 cm in diameter and all infested *A. rubrum* sections were moved to the mainland by way of a 330-m long elevated wooden causeway, then transported to the field station at the College of Charleston Stono Preserve (32°44'39"N, 80°10'54"W). The field station was selected for sample processing based on its proximity to the island, the availability of secured space, and the station's location near the center of the regulated area, thus mitigating the risk of moving live *A. glabripennis* on the landscape.

Tree sections were arranged on the ground at the field station, and the ends were matched to reconstruct the approximate vertical architecture of the trees (Bean et al. 2025). The length of each section was documented, and within each section the location of each oviposition pit and exit hole (Fig. 2) was recorded as the distance along the stem from the lower cut on that section. The locations of damage within the canopies were then recorded as the sum of the within-section distance and the total length of the sections from the base of the tree (ground level) to the cut at the bottom of the working section. The total number and type of damage on each section and tree was tabulated and trees were categorized by infestation mirroring the system used by Eradication Program survey personnel: A-level trees, which include only oviposition sites, and B-, C-, and D-level trees, which include <10 exit holes, 10 to 100 exit holes, and >100 exit holes, respectively (Rose 2014), and uninfested trees.

Exit holes were dated using annual growth rings. To accomplish this, subsections of wood containing exit holes were cut (to reduce bulk), labeled, and dried in an ESPEC Platinous Sterling temperature and humidity chamber (ESPEC North America Inc., Hudsonville, Michigan) at 80 °C for ≥24 h to

kill any *A. glabripennis* larvae or eggs within the wood, following the guidance of Dodds et al. (2013). Heat-treated wood samples were allowed to rest for a minimum of 24 h to complete the treatment and deregulation of material. After deregulation, the wood samples were moved to the Clemson University Department of Forestry and Environmental Conservation's wood shop in Clemson, South Carolina (34°40'24"N, 82°50'6"W) where exit holes were sectioned to determine the emergence year. All remaining untreated wood was destroyed on-site at Stono Preserve in compliance with Cooperative Program standard operating procedures.

*A. glabripennis* exit holes are created when the adult beetle chews its way out of the tree. After emergence and during the growing season, the tree cambium continues to grow around the edges of the exit hole forming callus tissue (Copini et al. 2014). With enough time, exit holes are closed off by the callus tissue, leaving a distinctive scar on the surface of the tree. Exit holes that passed through live cambium and had evidence of (or were suspected to have) cambial growth/callus tissue were sectioned by cutting through the center of the hole orthogonal to the stem axis. The face of the wood and cross section of the exit hole was sanded with progressively finer sandpaper grits (starting with 60 and continuing up to 4,000 as needed) to reveal growth ring structure. Coarser grits (up to 600) were applied using a powered belt sander, while finer grits were sanded by hand. Annual rings in the callus wood (if present) around the exit holes were counted under a stereo microscope (Nikon SMZ660, Tokyo, Japan) and tracked radially on cross-sections to identify the year in which the beetle emerged (Fig. 3; Peverieri et al. 2012, Faccoli et al. 2015). Exit holes which passed through live cambium with no evidence of cambial growth were documented as having occurred during the current year, which was 2021. Exit holes which passed through dead portions of cambium (Fig. 3) were noted as such and were not assigned a specific year of emergence. To include undated *A. glabripennis* exit holes in the estimations of population growth, the undated holes for each tree were assigned to years in proportions mimicking the distribution of dated exit holes

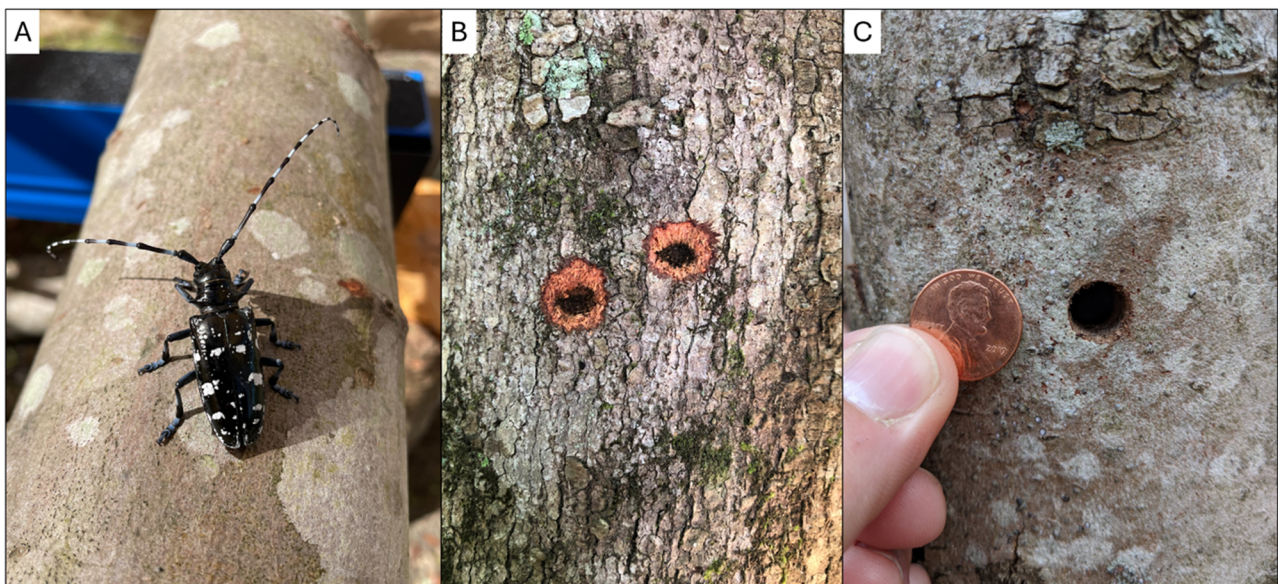


**Fig. 2.** Adult *Anoplophora glabripennis* (A), oviposition pits (B), and exit hole made by adult beetle (C). Photos A and B by D. Coyle, Clemson University; photo C by S. Long, Clemson University.



**Fig. 3.** Cross-sectioned wood sample with *Anoplophora glabripennis* exit hole from 2019. Annotations indicate how the edge of the exit hole is aged corresponding to the tree ring, following the ring to the left (top image) ensures that false rings are not counted. Sample with dead cambium (bottom image), fungal staining, and bark separation. Photos by M. Bean, Clemson University.

within the same tree, recognizing this assumes exit holes that passed through dead cambium were uniformly distributed through time. Tree-specific population growth curves were indexed by assigning the first year of infestation (oviposition) to year 0, with the first year of beetle emergence occurring in year 1.

To estimate the calendar years of oviposition leading to adult emergence, we assumed a univoltine life cycle based on a laboratory-validated *A. glabripennis* phenology model (Trotter and Keena 2016). Recent work (Schmitt et al. 2025a, 2025b) validated the utility of this model under the semitropical conditions found in South Carolina and has shown >90% of the *A. glabripennis* population in this landscape follows a univoltine life cycle. We used these findings to make 2 simplifying assumptions for our analyses: (i) exit holes lag oviposition by 1 year (emergence events dated to year  $T$  are the result of oviposition events at time  $T-1$ ) and (ii) the ratio of emerged adults to eggs (exit holes to oviposition pits) is constant across years.

Between cutting and processing, sampled wood was held outdoors under field conditions allowing *A. glabripennis* larvae to complete development and emerge as adults; adults were collected daily for use in other studies. The emergence of adults combined with the prevention of oviposition allowed the

completion of the last full generation of beetles within the sampled trees. Using the above-described assumptions, the egg-to-adult survival rate was estimated as the slope of a simple linear regression of the number of *A. glabripennis* exit holes as a function of the total number of oviposition pits pooled across trees using R (version 4.5.0; R Core Team 2025). The distribution of exit holes was then plotted for each tree to describe the vertical distribution of infestations through time.

While it would be ideal to reconstruct the timing and growth of *A. glabripennis* infestations within trees using both the oviposition pits and exit holes (sensu Dodds et al. 2013), this approach was unfeasible due to the sheer number of oviposition pits present. The reconstruction of the population was therefore based on the emerged adults from each tree (ie adult exit holes), recognizing that this omits the proportion of the population represented by eggs and larvae that did not survive to adulthood.

Changes in infestation rates through time and among trees could be influenced by the depletion of available resources within trees by infesting beetles. For example, smaller trees might become saturated, leading to reduced infestation levels. To assess this within the context of the limited sample size (infested trees), we evaluated the density of infestation with the total surface area available for infestation (a proxy for tree size) using a linear function ( $\ln$  in R version 4.5.0; R Core Team 2025). While a sigmoid function would be able to identify the plateau or threshold of saturation, the limited sample size made this approach unsuitable, and a linear function was selected to identify the trend that would be expected.

### Link Between Damage Intensity and Infestation Age: Assessing ALBERT

The locations and dates of documented *A. glabripennis* emergence were used to determine the relationship between infestation age and intensity and to reconstruct the movement of adult *A. glabripennis* among trees. The movement of *A. glabripennis* among trees was reconstructed using 2 methods. First, the method used by ALBERT (version 1.0; USDA Forest Service 2025) was used. Briefly summarized, the model assumes that the source of an infesting beetle in a newly infested tree is the nearest already-infested tree, and the relative age of infestations among trees is inferred based on the level of infestation (ie larger infestations are older infestations as denoted by A-, B-, C-, and D-level trees). In this study, the method used by ALBERT is referred to as the inferred reconstruction. The second method takes advantage of the dated exit holes to reconstruct the sequence of infestation events among trees. Using this approach, the individual tree with the oldest emergence date was used as the starting point for the infestation, and subsequently infested trees were identified based on specific years (rather than levels of infestation). We refer to this as the observed reconstruction. In both, the inferred and observed reconstructions, *A. glabripennis* movement among trees is represented by a series of spatial vectors that connect the infested trees. The collections of vectors were tabulated to generate a dispersal kernel using both the inferred and observed datasets.

To compare the direct reconstruction of *A. glabripennis* movement with the results generated by ALBERT, the tool was run using both the locations and infestation levels (A, B, C, and D) identified for each tree to reconstruct an inferred pattern of dispersal. This mimics the approach used in

large-scale reconstructions where the dates of infestation for surveyed trees are not known. The dispersal vectors based on the observed and inferred reconstructions were tabulated to generate dispersal kernels, and differences between the kernels were evaluated using a Kolmogorov–Smirnov test for distribution differences using [www.wessa.net](http://www.wessa.net) (described by Holliday 2017 and detailed in Wessa 2026) in R (version 4.5.0 “How About a Twenty-Six”).

## Results

The survey yielded a total of 14,615 *A. glabripennis* oviposition pits and 1,611 exit holes distributed among 28 of the 33 host trees on the island, with the oldest exit hole on the island dated to 2016 (tree T14, Fig. 4). Assuming a univoltine life cycle (Schmitt et al. 2025a), this tree was the first on the island to be successfully infested in 2015.

### *A. glabripennis* Population Growth Within Trees and Across the Island

The number of oviposition pits provides a statistically significant predictor of the number of exit holes ( $R^2_{\text{adj}}=0.692$ ,  $df=17$ ,  $P<0.0001$ ,  $F=61.55$ , Supplementary Fig. S1), and the slope estimate of 0.128 suggests that <13% of oviposition pits result in an emerged adult. Reconstructions of adult *A. glabripennis* population growth demonstrate substantial variation among the infested trees (Fig. 4). For example, tree T03 had both the highest population growth rate and the largest population of *A. glabripennis*, with nearly 400 beetles emerging in 2021 and 442 beetles over the 5 years the tree was infested (2017 to 2021). Tree T14 had the oldest documented exit hole

(ie infested in 2015) and had 5 adults emerge in 2016 (Fig. 4). Although T14 was infested for 6 generations (years), the emergence rate for the last 3 years plateaued at about 45 adult *A. glabripennis* per year (Fig. 4). While tree T03 was infested 1 year after T14, the infestation in T03 increased at a much higher rate. Other trees (eg T01, T10, T27) exhibited slower *A. glabripennis* population growth, and in some trees (eg T02, T06, T18, T29) *A. glabripennis* populations showed periods of decline. Infestations generally started near the center of mass within a tree, spreading vertically up and down over time (Supplementary Fig. S2).

Placing the *A. glabripennis* population growth curves for each tree on shared axes highlights the substantial variation in population growth rates among this relatively small group of trees, as some trees supported rapid *A. glabripennis* population growth, growth on others was more moderate, and population growth on some trees declined (Fig. 5). Tree T14, which hosted the oldest infestation (and therefore the longest growth curve) had a relatively moderate population growth rate including a year in which the population declined.

The *A. glabripennis* population on the island increased rapidly following establishment, suggesting an exponential increase in the number of beetles through time (Fig. 6). However, the rate of increase in the number of infested trees differed from the rate of increase of the *A. glabripennis* population on the island, with the first 3 years of *A. glabripennis* infestation demonstrating an accelerating rate in the number of infested trees, followed by 3 years in which the number of infested trees increased at a modest linear rate (Fig. 6).

The study trees did not demonstrate statistically significant relationship between tree size and infestation density, and so

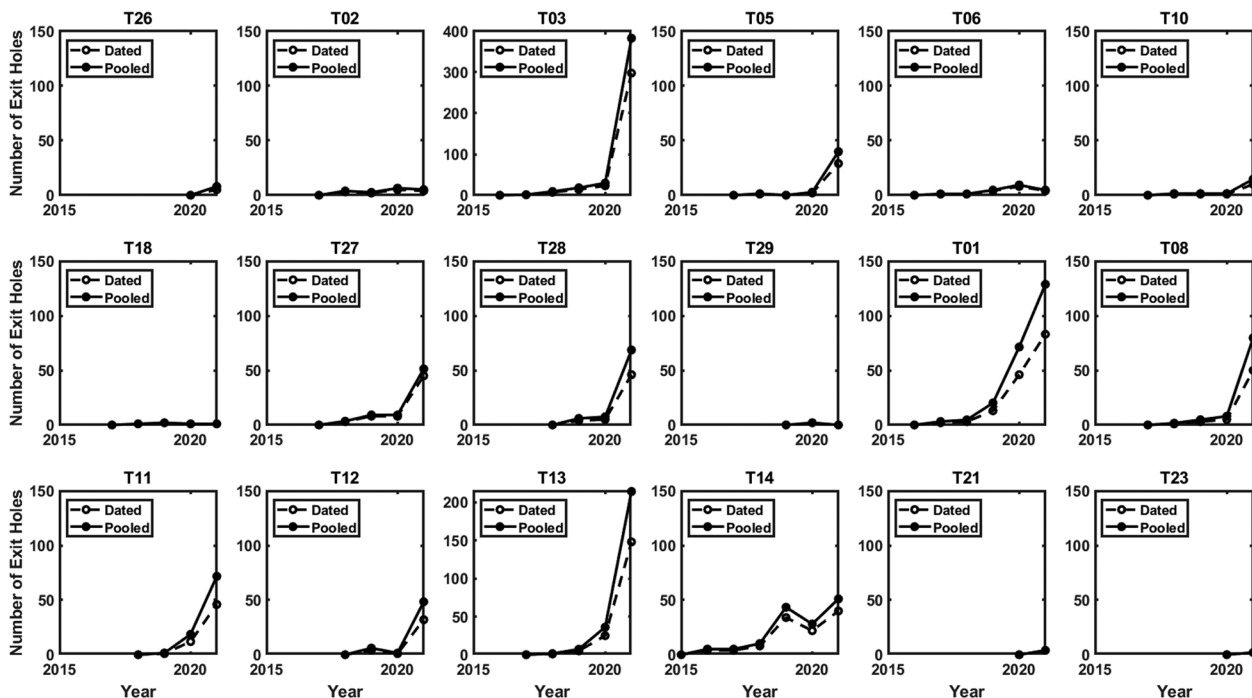


**Fig. 4.** Within individual trees, *Anoplophora glabripennis* populations generally increased over time. Dashed lines represent *A. glabripennis* populations based only on dated exit holes, solid lines represent populations that include undated exit holes. Note the extended y axes for trees T03 and T13. T14 was the first tree on the island to be successfully infested with *A. glabripennis* oviposition in 2015.

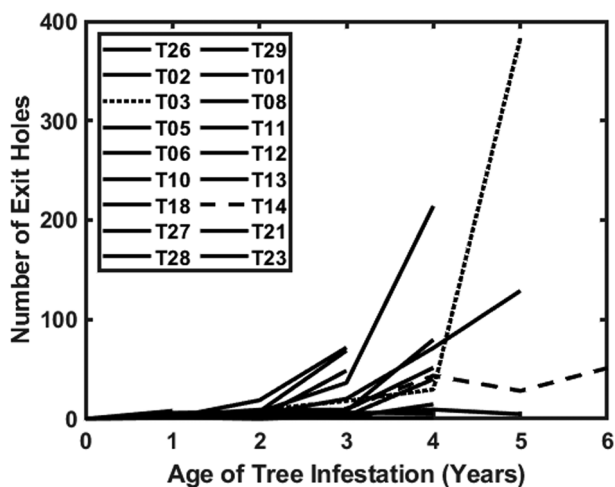


**Fig. 5.** Rates of *Anoplophora glabripennis* population growth varied among trees. The longest-infested tree (T14) is represented by a dashed line the most heavily infested tree (T03) is represented by a dotted line. Note that the population on T14 shows a period of relatively flat population growth.

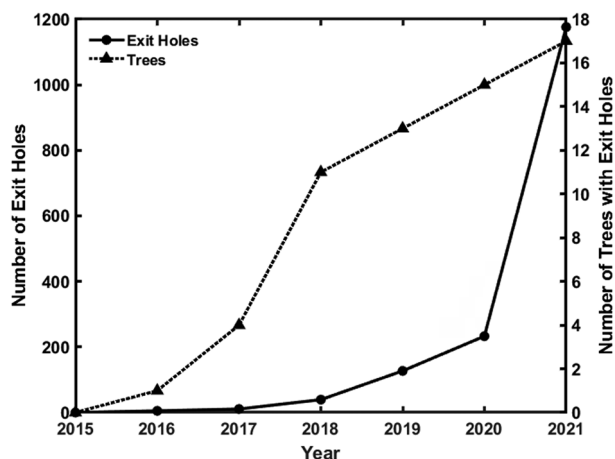


**Fig. 6.** While the number of adult *Anoplophora glabripennis* on the island increased exponentially through time, the total number of infested trees which had produced adults increased at a more modest rate.

no quantitative support is provided for smaller trees having higher infestation densities indicative of resource saturation (Supplementary Fig. S3). However, the data do suggest such a pattern could occur, and do not preclude the potential for this pattern.

### Infestation Age and Intensity

Overall, the 20 trees with *A. glabripennis* exit holes demonstrated a significant, but weak, positive relationship between the duration and intensity of infestations within trees (Fig. 7,  $R^2=0.268$ ,  $P<0.03$ ,  $F=5.844$ ). Trees which were infested longer generally had more exit holes, though the low  $R^2$  value suggests there is significant variation in infestation level through time (a pattern also demonstrated in Figs 4 and 5). Converting *A. glabripennis* infestation levels to a categorical variable reflecting the B, C, and D levels of infestation yields an improvement (Table 1;  $R^2=0.644$ ,  $P<0.0001$ ,  $F=28.944$ ), though it is worth noting that tree T03 would have been treated as the origin tree

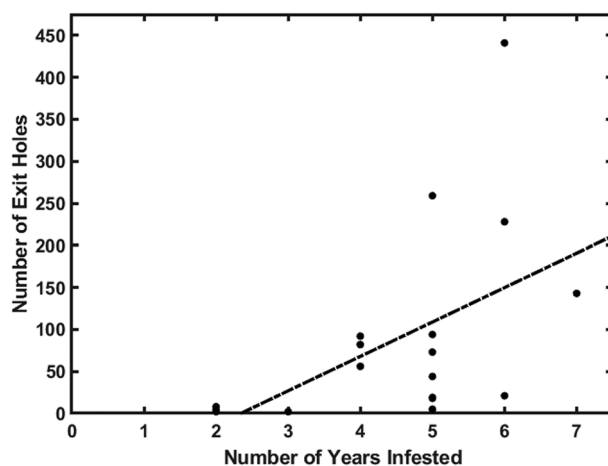


**Fig. 7.** Trees with older *Anoplophora glabripennis* infestations generally showed higher levels of infestation, though variation in the level of infestation is high among long-infested trees, resulting in a heteroscedastic pattern.

for the infestation, while dated exit holes show T14 as the first tree to be infested on the island.

### A. *glabripennis* Spread Across the Island

The 2 methods used to reconstruct the dispersal of beetles across the island (ALBERT and dated exit holes) yielded 2 different spatial patterns (Fig. 8); however, the composite dispersal distances described by the dispersal kernel were effectively the same. Using the infestation category as a surrogate for the age of the infestation (Fig. 8A), the method used by ALBERT, generates a dispersal kernel (Supplementary Fig. S4) in which the median dispersal distance was  $\sim 18.0$  m (Mean  $\pm$  SE:  $29.8 \pm 6.1$  m). The dispersal kernel based on the reconstruction of beetle movements based on dated infestations (Fig. 8B) yielded a similar median dispersal distance (18.9 m; Mean  $\pm$  SE:  $27.7 \pm 5.1$  m). The curves representing the dispersal kernels were not different ( $\chi^2=0$ ,  $P=0.9$ ). Although these values are informative for this population, it is important to note that dispersal distances within the study population are inherently limited by the size of the island and the maximum distance between trees. Distances on larger landscapes in which dispersal is not constrained (or dispersal which includes emigration from the island) would be expected to yield higher values. It is also useful to note that in both examples, the same origin tree was used to standardize the comparisons. When applied to large landscapes in which the true origin tree is not known, ALBERT is initiated using one of the highly infested trees typically found in a group of highly infested trees assumed to have acted as the starting point for the infestation. The selection of the specific origin tree can therefore be somewhat arbitrary due to the proximity of candidate origin trees, and varying this tree has been found to have no functional impact on the estimated dispersal kernels for large landscapes.

### Discussion

*A. glabripennis* movement, particularly dispersal and host selection by gravid females, remains poorly documented under field conditions in invaded landscapes. However, this reconstruction of an isolated *A. glabripennis* population shed light

**Table 1.** Detailed account of each study tree's *Anoplophora glabripennis* infestation history and quantification of damage

| Tree ID | Number of oviposition pits | Number of exit holes | Infestation category |
|---------|----------------------------|----------------------|----------------------|
| T1      | 2,344                      | 232                  | D                    |
| T2      | 966                        | 18                   | C                    |
| T3      | 1,918                      | 442                  | D                    |
| T4      | 127                        | 0                    | A                    |
| T5      | 343                        | 44                   | C                    |
| T6      | 932                        | 21                   | C                    |
| T7      | 3                          | 0                    | A                    |
| T8      | 417                        | 96                   | C                    |
| T10     | 326                        | 19                   | C                    |
| T11     | 1,591                      | 92                   | C                    |
| T12     | 556                        | 56                   | C                    |
| T13     | 1,619                      | 263                  | D                    |
| T14     | 1,374                      | 144                  | D                    |
| T15     | 4                          | 0                    | A                    |
| T16     | 0                          | 0                    | U                    |
| T17     | 0                          | 0                    | U                    |
| T18     | 383                        | 5                    | B                    |
| T19     | 5                          | 0                    | A                    |
| T20     | 22                         | 0                    | A                    |
| T21     | 24                         | 4                    | B                    |
| T23     | 6                          | 2                    | B                    |
| T24     | 63                         | 3                    | B                    |
| T25     | 0                          | 0                    | U                    |
| T26     | 79                         | 8                    | B                    |
| T27     | 710                        | 74                   | C                    |
| T28     | 497                        | 85                   | C                    |
| T29     | 88                         | 2                    | B                    |
| T30     | 0                          | 0                    | U                    |
| T31     | 53                         | 1                    | B                    |
| T32     | 0                          | 0                    | U                    |
| T33     | 83                         | 0                    | A                    |
| T34     | 33                         | 0                    | A                    |
| T35     | 49                         | 0                    | A                    |

on several key biological patterns of this invasive forest pest in an invaded landscape. First, over the course of 6 years (2015 to 2021), the *A. glabripennis* population grew rapidly on the island, with 5 adults emerging in 2016, increasing to nearly 1,200 adults emerging in 2021. This population growth occurred in an environment in which fewer than 13% of the >14,000 *A. glabripennis* oviposition sites led to the emergence of an adult beetle, suggesting that even with limited survival, *A. glabripennis* populations would be expected to increase rapidly in this semitropical environment. Assuming the 5 adults to emerge in the first year represent 13% of the initial oviposition pits, the population was founded with about 38 oviposition pits, a number that is well within the documented capacity of a single female *A. glabripennis* (Keena 2002, Smith et al. 2002, Stone 2025). Although this is conjecture based on fecundity estimates, the *A. glabripennis* population on the study island could have potentially been initiated by a single female, suggesting that a single fecund beetle may contribute to a pattern of stratified dispersal at substantial distances that initiate new local populations. It is also possible that additional adult *A. glabripennis* arrived on the island from the mainland between 2015 and 2021, though this is unlikely in our opinion due to this beetle's relatively low propensity for long distance dispersal.

*A. glabripennis* populations have shown a substantial difference in individual host tree use over time (eg in England, one particular tree yielded nearly an order of magnitude more beetles than other trees; Straw et al. 2016), and we also observed substantial variation in *A. glabripennis* population growth rates among individual trees. While the drivers for this variation are not well understood for this species or within Cerambycidae, multiple mechanisms likely play a role. For example, adult feeding (used as a proxy for host choice) by *Phoracantha solida* (Blackburn) (Coleoptera: Cerambycidae) on *Corymbia* K.D. Hill & L.A.S. Johnson hybrids (Myrtales: Myrtaceae) was influenced by phloem thickness and moisture content (Nahrung et al. 2014). The different *A. glabripennis* population growth rates observed in our study (Figs. 4 and 5) suggest that *A. rubrum* trees likely vary in quality as hosts, which affects larval survival and acceptance by gravid females, leading to the emigration of females from their natal tree (see Hanks 1999). If the low *A. glabripennis* population growth rates on some trees are the result of emigrating females, it is possible that some beetles dispersed to trees with high population growth rates (contributing to their growth), may have left the island entirely, creating a local population sink, or succumbed to mortality prior to reproducing. Direct observations of adult *A. glabripennis* behavior would be necessary to adequately answer these questions. While this work might be possible in *A. glabripennis*' native range, this would not come without challenges; to that end, a novel sterilization technique for gravid *A. glabripennis* (Chandler and Trotter 2025) may offer an opportunity to conduct relevant field experiments in invaded landscapes.

The variation in *A. glabripennis* population growth rates also suggest variation in the rates at which resources in the host trees are depleted by the beetle population. Past work has suggested that *A. glabripennis* is a poor flyer and commonly chose to reinfest their natal host for multiple generations before spreading to a new host (Lingafelter and Hoebeke 2002). This behavior is seen in other cerambycids, such as *Xystrocera festiva* Thomson, which is known to have poor dispersal capabilities and often reinfests the same host trees (Darmawan et al. 2026). However, data from an *A. glabripennis* infestation in Massachusetts suggested that beetles spread from their natal host before the natal host was fully utilized (Hull-Sanders et al. 2017), a pattern supported by the data from this island population.

The general damage pattern within trees was relatively consistent, with the first generation of beetles emerging near the center of the available within-tree habitat, and subsequent generations then spreading vertically in both directions. A related study on this island found the vertical distribution of exit holes to be very similar to oviposition pits (Bean et al. 2025), suggesting the vertical distribution of exit holes may primarily be determined by the distribution of oviposition pits (rather than the result of variation in survival to adulthood at specific heights). However, recent work indicates that not every *A. glabripennis* oviposition pit receives an egg (Stone 2025), suggesting females may be sampling host quality when chewing oviposition pits, and then expressing ovipositional preference by placing eggs in some pits while rejecting others. Other cerambycids in this subfamily (Lamiinae), such as *Monochamus carolinensis* (Olivier) (Walsh and Linit 1985), *Monochamus titillator* (F.) (Rastok 2015), *Anoplophora malasiaca* Thomson (Adachi 1988) and *Anoplophora chinensis* (Forster) (Peverieri and Roversi 2010), also create oviposition pits that do not

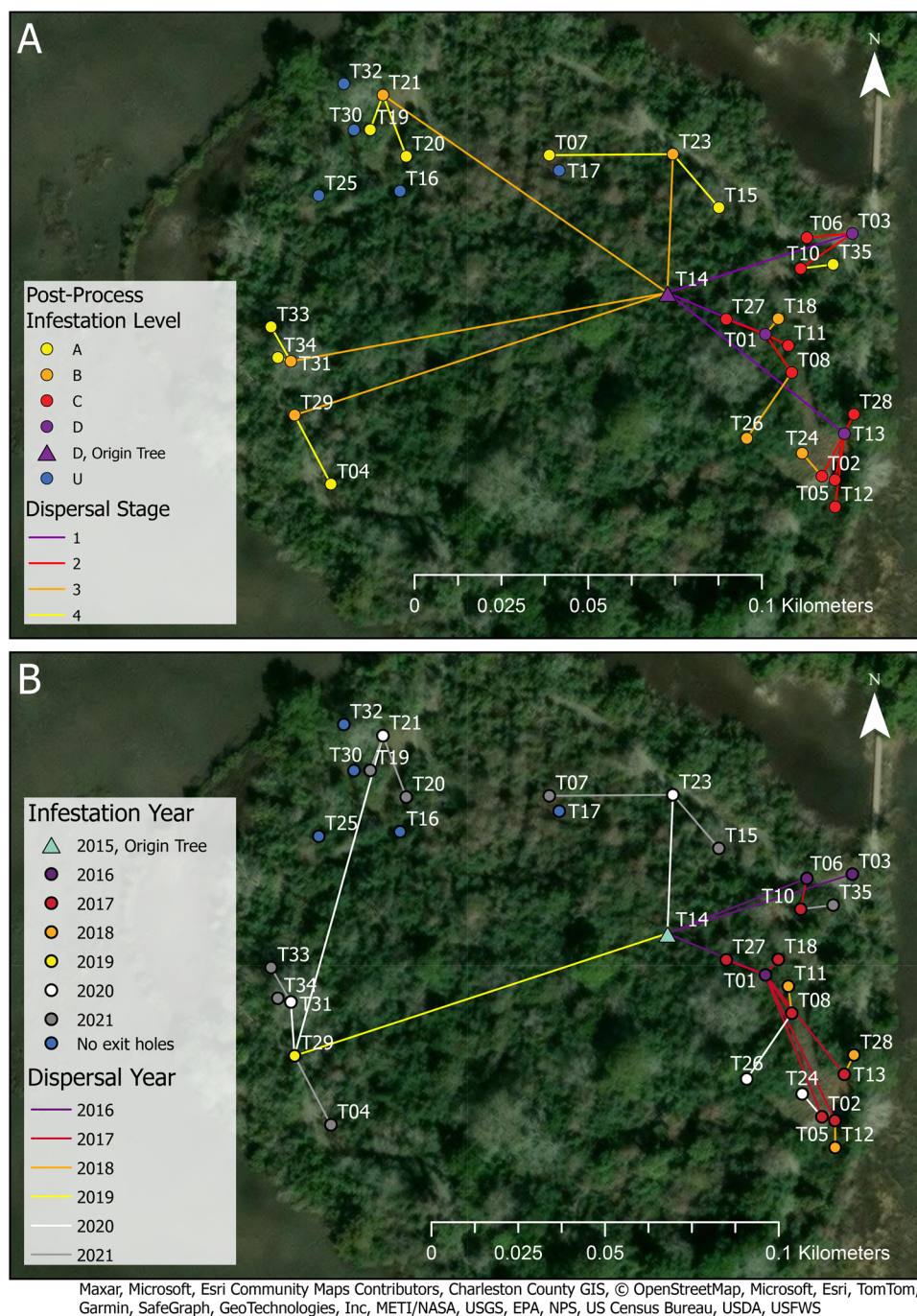


**Fig. 8.** Pattern of *Anoplophora glabripennis* dispersal reconstructed using the assumption that the level of infestation within a tree represents the timing of infestation, as used in ALBRisk (A) and the pattern of dispersal based on reconstructions based on the calendar years in which trees became infested (B). Colors correspond to movement in a given year.

receive eggs. While the vertical distribution of exit holes reflects the distribution of oviposition pits, it is not known if exit holes reflect the distribution of occupied oviposition pits (ie those containing eggs). Data on the distribution of occupied oviposition pits in combination with the distribution of emergence holes would provide an opportunity to evaluate the potential for a preference–performance link in *A. glabripennis* (Jaenike 1978, Vallardes and Lawton 1991).

Despite the exponential increase in this *A. glabripennis* population at the stand scale, the number of infested trees increased

at a more consistent rate (Fig. 6). Given the limited number of trees on the island available to be infested, we might expect the annual number of newly infested trees to approach an asymptote under conditions in which the probability of infestation for a given tree remain constant through time. However, with the exponential increase in the number of adult beetles on the island the propagule pressure on each tree (including those which are uninfested) would be expected to increase resulting in increasing rates of tree infestation up to the point at which all trees are infested and the number of newly infested trees

would drop to zero. In addition, >15% of the *A. rubrum* trees on the island remained uninfested even though the first 5 *A. glabripennis* generations included 415 adult beetles. Similar patterns were observed in Canada (Turgeon et al. 2022b), England (Straw et al. 2016), and Italy (Marchioro and Faccoli 2021), where not all available host trees were colonized prior to management activities taking place. Although the data from this island are limited, the movement of beetles to new host trees was not strictly driven by distance, as uninfested trees were mixed among infested trees (though uninfested trees were mostly located in the northeastern portion of the island). Whether these trees remained uninfested due to female preference, host quality, or host apparency (ie the trees were simply not detected) remains unknown.

Lightly infested host trees (ie those with oviposition pits but few or no exit holes) may represent very new infestations or infestations that failed due to (i) host quality (eg fecundity varied greatly among *Agrilus anxius* Gory [Coleoptera: Buprestidae] adults, even within a host tree species; Akers and Nielsen 1990), (ii) female preference (eg female *Saperda calcarata* Say [Coleoptera: Cerambycidae] tend to oviposit on trees on which they prefer to feed; Broberg and Borden 2005), (iii) population stochasticity (Haack et al. 2017), (iv) predators (eg ants, which are known to predate on cerambycid eggs in the bark; Solomon 1972, Stone 2025), or other factors. More heavily infested trees (ie those with >250 oviposition pits) suggest the relationship between the number of exit holes and the number of oviposition pits may be curvilinear. If so, the ratio of adult emergence to oviposition pits may increase as the number of oviposition pits increases, implying that host suitability increases as population density increases—a pattern observed in other wood-boring beetles (Birch 1948).

Our data showed that overall, trees with older infestations had higher numbers of exit holes, reflecting the general pattern used in ALBERT where the hierarchical infestation (represented by A, B, C, and D categories) are used as a proxy for the relative age of the infestation. However, it is worth noting that the use of the dated exit holes in combination with the trees with oviposition pits only (assumed to be recently infested) produced 6 time periods in which dispersal vectors can occur (ie trees with exit holes were infested by dispersal vectors occurring in years 2, 3, 4, 5, 6, or 7), while the use of the A, B, C, and D categories yields only 4 categories, and therefore 4 time periods in which dispersal vectors can occur.

We also found a weak but consistent link between the age of the *A. glabripennis* infestation and the level of infestation. Although the use of the inferred and observed patterns of dispersal yielded different local patterns (Fig. 8), these patterns yielded very similar overall patterns of *A. glabripennis* dispersal as described by the dispersal kernels. Prediction models are valuable tools that can help determine management strategies for many invasive forest pests, and the integration of empirical field data is necessary to make these models useful and accurate (eg Robinet et al. 2019). For *A. glabripennis*, effective management requires managers to prioritize surveys based on the distribution of risk on the landscape. While the data described here are limited to the reconstruction of a small population, the similarity of the dispersal kernels suggests the differences in reconstruction method at this scale may not alter the predicted spatial risk.

A potential explanation for variation in the levels of infestation among trees could be the availability of tree habitat for

ovipositing females. Under this scenario, small trees might be expected to become saturated resulting in lower levels of infestation. If small trees were saturated, we would expect to see a sigmoid relationship between damage density and available habitat (surface area). An analysis of the trees used in this study does not statistically demonstrate this pattern (Supplementary Fig. S3), though it is worth noting that while the data does not support this pattern, it also does not preclude it as the absence of saturation could be the result of the small number of trees used in this study, or the relatively young state of the overall infestation suggesting small trees had not become resource depleted.

The most effective *A. glabripennis* eradication method currently involves visual ground surveys for infested or damaged host trees followed by their physical removal and destruction (eg Turgeon et al. 2022a), a process that is both labor-intensive and time-consuming. Surveys may be required for millions of trees, and because survey efficacy has limits, multiple surveys may be required. These data suggest that the current tool ALBERT provides a reasonable method to both track survey progress and evaluate the expected impact of proposed management strategies (Trotter et al. 2024). However, these data also suggest the methods used include unaccounted variation. Further studies using larger datasets would benefit the continued development of tools to support efforts to detect and eradicate invasive *A. glabripennis* populations and continue to allow for program improvements that minimize risk and maximize the efficacy of limited eradication resources.

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## Author Contributions

Meredith S. Bean (Investigation [equal], Methodology [equal], Writing—original draft [equal]), R. Talbot Trotter III (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Methodology [equal], Resources [equal], Software [equal], Validation [equal], Writing—review & editing [equal]), Jennifer L. Chandler (Data curation [equal], Formal analysis [equal], Investigation [equal], Writing—review & editing [equal]), Robert Ritger (Data curation [equal], Investigation [equal]), Cooper Schroeder (Data curation [equal], Investigation [equal]), Jess Hartshorn (Formal analysis [equal], Supervision [equal], Writing—review & editing [equal]), Brandon Peoples (Data curation [equal], Formal analysis [equal], Supervision [equal], Writing—review & editing [equal]), Kyle Barrett (Formal analysis [equal], Supervision [equal], Writing—review & editing [equal]), Scott E. Pfister (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Resources [equal]), and David R. Coyle

(Conceptualization [equal], Investigation [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [equal], Writing—original draft [equal], Writing—review & editing [equal])

## Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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## Conflicts of Interest

None declared.

## Disclaimer

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