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Gallery Productivity, Emergence, and Flight Activity of the Redbay Ambrosia Beetle (Coleoptera: Curculionidae: Scolytinae)

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ABSTRACT Flight and emergence of the redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff, were monitored from March 2011 through August 2012 using Lindgren funnel traps baited with manuka oil and emergence traps attached over individual beetle galleries on infested redbay (*Persea borbonia* (L.) Sprengel) trees. Of the 432 gallery entrances covered with emergence traps, 235 (54.4%) successfully produced at least two adults. Gallery success rates and time until adult emergence were highly variable and strongly depended on time of year galleries were initiated. Successful galleries produced 23.4 ± 2.50 ($\bar{x}$ ± SE) adult *X. glabratus* but one had 316 adults emerge from it. Galleries were active for an average of 231.9 ± 6.13 d but five were active for over 1 yr and one gallery produced beetles for 497 d. In total, 5,345 female and 196 males were collected during the study resulting in a sex ratio of ≈27:1 (female:male) emerging from galleries. Ambrosia beetles other than *X. glabratus* were recovered from 18 galleries or ≈4% of those studied. Beetles that attacked larger diameter trees were more likely to be successful and produce more brood. Lindgren trap captures reflected emergence trap collections but with a delay of about 1 mo between peaks in emergence and capture in traps. Peaks of activity occurred in fall 2011 and spring 2012, but at least some adult beetles were collected using both methods in every month of the year.

KEY WORDS *Xyleborus glabratus*, *Persea borbonia*, exotic, invasive, laurel wilt

The redbay ambrosia beetle, *Xyleborus glabratus* Eichhoff (Coleoptera: Curculionidae: Scolytinae), and its associated fungus *Raffaelea lauricola* (T.C. Harrington, Fraedrich & Aghayeva) are recent introductions to the southeastern United States and are causing extensive mortality to redbay (*Persea borbonia* (L.) Sprengel) trees. Ambrosia beetles, including *X. glabratus,* tunnel and breed within sapwood of dead or dying trees and feed exclusively on cultivated fungi known as ambrosia. *Xyleborus glabratus* is not a known pest in its native range of Southeast Asia and likely attacks only stressed or dying trees, as is common for most ambrosia beetles. However, in the United States, *X. glabratus* bores into living, healthy trees of the family Lauraceae, which includes redbay, and inoculates them with *R. lauricola* resulting in rapid wilting and death (Fraedrich et al. 2008). As the fungus spreads through the tree and it begins to die, greater numbers of *X. glabratus* arrive at the tree (Hanula et al. 2008). Once females successfully bore into the sapwood, they establish galleries in which eggs are laid. Larvae feed on the ambrosia fungus growing on the gallery walls and develop into adults within the galleries. Most of the progeny are females that may stay in the maternal galleries. Their role in their natal galleries is not clear. It has generally been assumed that they stay in the galleries, breed with their brothers and contribute to gallery productivity by producing their own progeny (Biedermann et al. 2009), but this may be the case only after some daughters disperse (Biedermann et al. 2011). Peer and Taborsky (2007), however, found that daughters of *Xyleborinus saxesenii* (Ratzburg) foundresses remained in the galleries where they contributed to fungal garden and brood care, which increased gallery productivity, but they did not produce their own brood. Regardless, at some point the daughters disperse and either locate a new host tree or bore into a new location on the same host. Females are generally mated before leaving a gallery. Brood emerge from the original entrance hole in contrast to most phloem-feeding bark beetle species in which each individual produces its own exit hole upon emergence (McClelland et al. 1978). This behavior of ambrosia beetles simplifies monitoring their emergence and allows for careful observation of a single gallery throughout its active period.

Emergence rates can be inferred from baited trap catches, but there are problems with this approach. For example, Bentz (2006) found that pheromone baited flight-intercept traps caught specimens of *Dendroctonus ponderosae* Hopkins over a period of 130 d, but emergence traps showed an emergence period of

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only 30 d. Emergence of phloem-feeding bark beetles has been examined in some detail (e.g., Coulson et al. 1979, McClellend et al. 1978, Lessard et al. 1990, Bentz 2006), but less is known about the emergence of ambrosia beetles. Norris et al. (1968) looked at the emergence of *Xyleborus ferrugineus* F. and *Xyleborus posticus* Eichhoff and found that both showed diurnal patterns of emergence. Gagne and Kearby (1979) found that black hickory trees (*Carya texana* Buckley) could support *Xyleborus celsus* Eichhoff for up to 2 yr and peak emergence coincided with the beetle's two yearly attack periods.

We developed a simple method of monitoring emergence of ambrosia beetles and used it to examine emergence of *X. glabratus* from individual galleries that were initiated over a 1 yr period from 18 March 2011 through 6 March 2012. Beetle emergence from those galleries was monitored through August 2012. We also examined how emergence was related to timing of gallery initiation, size of the tree attacked, and adult flight activity. Understanding the biology and behavior of *X. glabratus* is an important step in the process of developing effective control strategies.

Materials and Methods

The study area was a riparian forest near Oak Park, GA, composed primarily of redbay and loblolly bay (*Gordonia lasianthus* (L.) Ellis) with scattered remnant loblolly pine (*Pinus taeda* L.). At the time the study was initiated very few redbay trees were dead or exhibiting wilt symptoms, but by the end of the study in August 2012 nearly all large redbay trees in the area were dead.

Between 18 March 2011 and 6 March 2012, a total of 432 emergence traps (Fig. 1) were attached to mature redbay trees infected with laurel wilt. Traps were made by soldering a two-hole pipe strap to a 1.3 cm (0.5 inch) diameter copper street elbow. The tabs of the straps were then cut approximately three quarters through so they could be bent to provide attachment points to the tree. Traps were attached to trees with screws and sealed with silicone caulk to prevent water from entering and beetles from escaping. A 1.3 cm diameter hole was drilled into the lid of a 20 ml scintillation vial so the lid could be slipped over the end of the copper elbow. The lid was sealed to the copper elbow using Goop plumbing adhesive (Eclectic Products, Inc., Eugene, OR). Emerging beetles fell into the scintillation vials that could then be screwed off of the lid for examination of the vial's contents.

In total, 10 trees ranging in size from 10.4 to 26.1 cm DBH (diameter at breast height or 1.4 m above ground) were selected for the study. Some trees selected were recently naturally infected with laurel wilt but were in the very early stages so very few beetle attacks were present. Others were healthy trees on which sections of outer bark were scraped smooth to encourage attacks and make those attacks easy to find. For the first four trees the outer bark was scraped from ground level to ≈2 m high. Scraping resulted in some small areas of phloem and xylem being exposed that were attractive to *X. glabratus* (Hanula et al. 2008) and these areas were usually quickly attacked. On trees selected later in the study, small sections (≈100–200 cm^2) were scraped each week. Once a section of bark was scraped, it was carefully examined for any beetle entry points that were marked with either pencil or a map pin. The following week these sections were again examined for attacks, and emergence traps were placed only over attacks known to have occurred since the last visit. Scraping small sections weekly allowed for emergence traps to be attached to trees every visit for up to 3 mo, whereas scraping the entire lower bole in 1 wk resulted in trees becoming so heavily attacked that new attacks were not easily discerned after a only a few weeks. The standard method of gauging *X. glabratus* entrance holes is to insert a medium size paper clip or similar diameter map pin into the hole to determine if it is the appropriate diameter (Hanula et al. 2008) but, because this could kill the foundress if she was near the entrance, we examined the holes visually to gauge the size likely to be *X. glabratus.* After installation, contents of each trap were checked weekly from 18 March through 14 November 2011 then either weekly or biweekly from 28 November 2011 until 30 August 2012. Vials containing beetles were capped and transported back to the lab for examination under a dissecting microscope. Male and female *X. glabratus* along with any other ambrosia beetles collected were identified using keys from Rabaglia et al. (2006) and a reference collection.

Fig. 1. Emergence trap used to cover individual *X. glabratus* gallery entrances.

In addition to the emergence traps, four 8-funnel Lindgren traps were hung within the study site. Traps were baited with manuka oil lures, Synergy Semiochemical Corp. (Burnaby, BC) that are as attractive as redbay wood to *X. glabratus* (Hanula and Sullivan 2008). Lures were changed every other month from May 2011 until April 2012 then every month until August 2012 because lure longevity changed (Kendra et al. 2011a, Hanula et al. 2013). From May 2011 until July 2011 all four traps were hung at a height of ≈1 m from ground level. In July 2011, two of the four traps were raised to a height of ≈3 m above ground level, and they remained at this height until the end of the experiment. This was done because the study site had extensive underbrush and it was thought that redbay ambrosia beetle may have had difficulty following the odor plume near the ground.

Statistical Analysis. Differences in time until emergence by month of gallery initiation were analyzed by one-way analysis of variance (ANOVA) using the general linear models procedure of the SAS statistical package (PROC GLM, SAS Institute 1985). The Ryan-Einot-Gabriel-Welsch (REGWQ) multiple comparison test (Day and Quinn 1989) was used to separate the mean time until first emergence for each month of trap establishment. Simple linear regression analysis was used to examine the relationships between gallery height from ground level and host tree size (measured as DBH of the tree) to gallery success and productivity (PROC CORR; SAS Institute 1985). Productivity was a measure of the total number of both male and female *X. glabratus* collected from an individual gallery. Length of time a gallery was active was calculated as the number of days between cage installation and the final date on which adult beetles were collected in that cage. A pooled Satterthwaite T-test (PROC TTEST, SAS Institute 1985) was used to analyze the difference in productivity among galleries from which males did and did not emerge, and to compare the number of *X. glabratus* collected in Lindgren funnel traps hung at two different heights. Rates of emergence were calculated by dividing the total number of adults collected on a date by the number of emergence traps containing adult *X. glabratus* on that date.

Results

Of the 432 gallery entrances covered with emergence traps, 235 (54.4%) successfully produced at least two adults. Galleries that produced only one adult were not included in analyses since the recovered beetle was likely the foundress abandoning the gallery for some reason. On average, successful galleries produced 23.4 ± 2.50 ($\bar{x} \pm$ SE) adult *X. glabratus* but one had 316 adults emerge from it. Galleries were active for an average of 231.9 ± 6.13 d but five were active for over 1 yr and one gallery produced beetles for 497 d. In total, 5,345 female and 196 males were collected during the study resulting in a sex ratio of ≈27:1 (female:male). Ambrosia beetles other than *X. glabratus* were recovered from a total of 18 galleries or ≈4% of those covered. These included: *Xylosandrus germanus* Blandford ($N = 2$), *Xyleborinus saxeseni* Ratzeburg ($N = 9$), *Xyleborus affinis* Eichhoff ($N = 4$), and *Xylosandrus crassiusculus* Motschulsky ($N = 3$). Some beetles from other families were also recovered including *Silvanus* sp. (Coleoptera: Silvanidae, $N = 3$ traps), *Tenebroides* sp. (Coleoptera: Trogossitidae, $N = 3$ traps), and *Colydium* sp. (Coleoptera: Zopheridae, $N = 1$ trap). All male broods of *X. glabratus* occurred in six galleries but only one contained multiple (four) males. Galleries from which only females emerged were common ($N = 127$). Successful galleries from which both males and females emerged produced more ($t = -2.33$; $P = 0.0208$; df = 188) adults (29.56 ± 4.23 adults/gallery, $N = 108$) than galleries from which no males emerged (17.80 ± 2.75 adults/gallery, $N = 127$).

Female success (those that produced brood) was generally highest in the summer months of June, July, and August, while only 38% of females that initiated galleries during September were successful and only 28% were successful in October (Fig. 2). Females that initiated galleries in December also had relatively high success as did those that initiated galleries in March 2011, while galleries initiated in February and March 2012 had relatively poor success. Peaks in emergence were similarly timed across cohorts of several months (Fig. 2), for example, emergence from galleries initiated in May occurred at approximately the same time as galleries initiated in June and July. The same was true for galleries initiated from October 2011 through February and March 2012. In addition to having the lowest success rate, galleries initiated in October took the most time for emergence to start. Emergence of the first beetles from those galleries took an average of 207.0 ± 11.0 d, significantly longer than from all other months except September and November (Fig. 3). Galleries initiated in spring through early summer were more successful and produced brood more quickly (Figs. 2 and 3). Galleries initiated from March through August 2011 and February to March 2012 were not significantly different in the length of time to first emergence from them, but they ranged from ≈50 d for May 2011 galleries to nearly 100 d for galleries initiated in March 2012 (Fig. 3).

Adults emerged from galleries in every month and were also caught in attractant baited traps throughout the year, but numbers were lowest in the winter months from December to February (Fig. 4). Both emergence and flight activity peaked sharply in spring 2012. Trap catch of Lindgren traps hung at 1 and 3 m heights was not significantly different ($n = 2$, $P = 0.08$; 1 m, $\bar{x} \pm$ SE = 85.53 ± 27.11 beetles/trap; 3 m, 34.25 ± 8.78 beetles/trap) but trap catches at the higher height had 50% fewer beetles. The rates of emergence relative to adult flight activity were closely related, but with changes in flight activity (indicated by Lindgren trap captures) seen about 1 mo later than those in emergence trap collections (Fig. 4).

Success rates of galleries varied widely between trees and ranged from 90.2% down to 16.7%. Emergence traps were placed over galleries at heights from ground level up to 2.1 m and, among successful galleries within this range, height of a trap was not correlated with either number of beetles produced ($r = -0.114$; $P = 0.108$; $n = 201$), time until initial

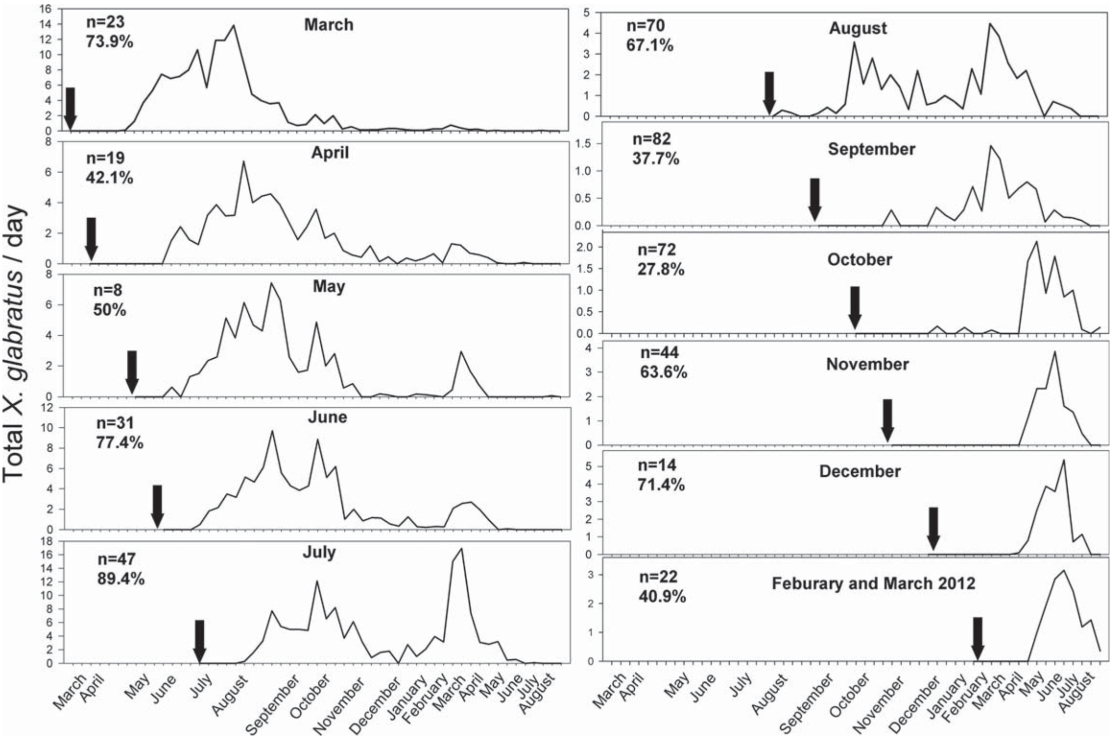

Fig. 2. Total numbers of adult *X. glabratus* emerging per day from galleries initiated during a given month. Numbers of galleries per month (n) and the percent that successfully produced brood are given on each graph. Arrows indicate approximate time of gallery initiation.

emergence ($r = -0.106$; $P = 0.1351$; $n = 201$), or length of time a gallery was productive ($r = -0.006$; $P = 0.9334$; $n = 199$). Size of the host tree (DBH), however, was correlated with success rates of galleries (those that produced brood; Fig. 5a) and the number of beetles produced per gallery (Fig. 5b).

Discussion

Multiple adults were collected from a single gallery in as little as 29 d suggesting some *X. glabratus* completed development in 36 d or less (traps were installed 1–7 d after gallery initiation). Completing the life cycle this quickly was uncommon and only eight galleries produced multiple adults within 40 d. This rate of development is comparable to *Xyleborus celsus*

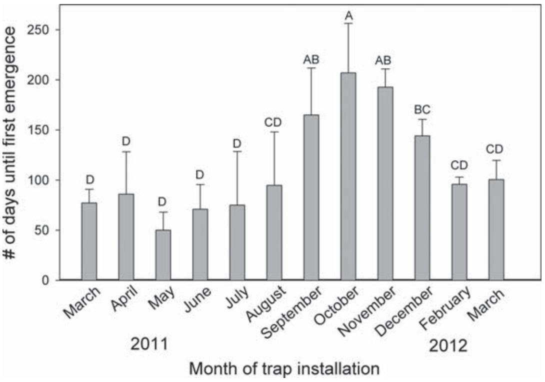

Fig. 3. Number of days ($\bar{x} \pm$ SE) until first adult emergence by month of gallery initiation. Columns with the same letters are not significantly different according the REGWQ multiple comparison test ($\alpha = 0.05$).

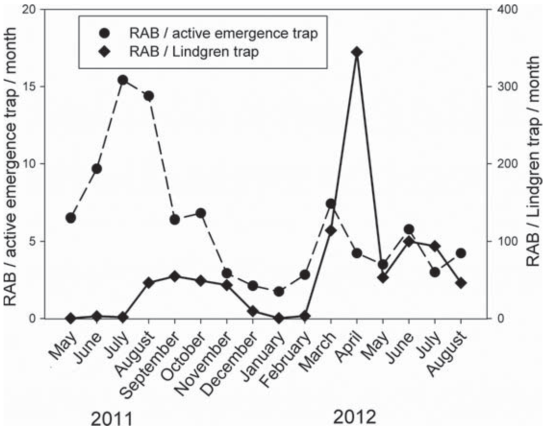

Fig. 4. *X. glabratus* (RAB) flight and emergence activity from May 2011 through August 2012. Lindgren trap captures are the average per trap ($N = 4$). Flight trap data for October 2011 were lost, so an average of September and November was substituted. Rate of emergence was calculated for each month by dividing the total number of adult beetles collected in a month by the number of emergence traps that contained beetles during that month.

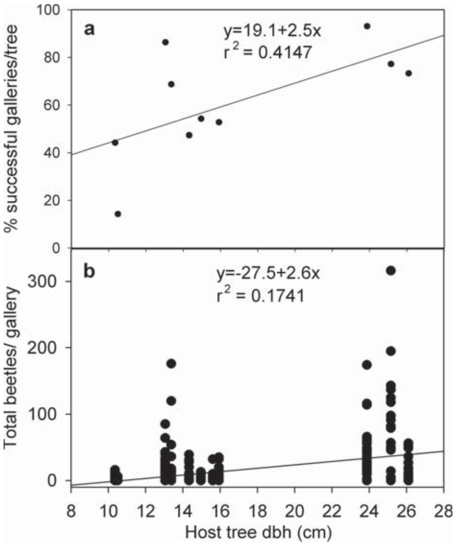

Fig. 5. Effect of host tree size (DBH) on (a) percent of galleries on a tree that successfully produced brood and (b) gallery productivity (total number of adults emerged). Relationships were significant at $P < 0.0001$.

(Gagne and Kearby 1979) that completes development within 40 d. Likewise, Biedermann et al. (2012) reported first mature daughters of *X. saxenesii* occurred in galleries 16–34 d after gallery initiation, first dispersal occurred at 40 d, and multiple dispersing daughters occurred after 60–70 d.

Although development of *X. glabratus* can occur within 40 d, timing of brood emergence was highly dependent on the timing of gallery initiation. Emergence began 50–70 d after gallery initiation in spring and summer months while emergence from galleries initiated during September through December began 150–220 d after initiation. The likelihood that a gallery would be successful was also strongly influenced by the time of year it was initiated.

Beetles were active throughout the year as evidenced by attacks on trees, emergence, and flight activity. This is in contrast to most other ambrosia beetles that are inactive during the winter and begin flight in early spring (Chapman and Kinghorn 1958; Webber and McPherson 1983, 1991; Coyle et al. 2005). Peak of emergence of *X. glabratus* in late summer to early fall of 2011 was consistent with previous reports of peak flight (Hanula et al. 2008, 2011). The spike in emergence activity in spring 2012 was unusual, although Brar et al. (2012) reported a similar early peak in flight activity near Gaineville, FL, in 2011.

The prolonged emergence of *X. glabratus* (232 d on average) suggests some daughters remained in natal galleries in larger, high quality hosts and contributed progeny. Remaining in their natal gallery after maturation may come at a cost to future reproductive output of ambrosia beetles as demonstrated for *X. affinis* Eichoff (Biedermann et al. 2011) but this social behavior benefitted overall maternal productivity of *X. saxesenii* (Peer and Taborsky 2007). Although delaying dispersal can come at a cost for these daughters (Biedermann et al. 2009, 2011), so can dispersal because finding a suitable host and establishing a successful gallery are not guaranteed. For example, Biedermann et al. (2009) reported that only ≈20% of *X. saxesenii* foundresses successfully established productive galleries in the field and only 54% of *X. glabratus* that initiated a gallery were successful. Thus, delaying dispersal and using the existing host resource may ensure daughters produce some offspring.

Almost all of the redbay trees in the study site died during the study period. Previous work showed that larger trees die first (Fraedrich et al. 2008) and that nearly 100% mortality of all redbay over 10 cm DBH occurs within 2 yr of initial laurel wilt detection (Fraedrich et al. 2008, Shields et al. 2011). *X. glabratus* attacks the largest trees first (Fraedrich et al. 2008) and is visually attracted to larger diameter silhouettes (A. E. Mayfield, personal communication) probably because they are more likely to successfully establish a gallery and produce more brood on bigger trees (Fig. 5).

The sex ratio of adults emerging from galleries in the field was ≈27:1 (females: male) that was much higher than *X. glabratus* in vitro where the sex ratio was 8:1 (Maner 2012). This discrepancy could be explained by a failure of some male beetles to emerge from galleries in trees in contrast to culture tubes from which all beetles were extracted. Biedermann (2010) found that male *X. saxesenii* usually only emerge from galleries after all offspring matured and no more eggs were laid, but Peer and Taborsky (2004) reported a male emergence rate of 68% for *X. germanus.* In this study, males emerged from slightly less than half of the successful galleries, but those from which they did were nearly twice as productive on average.

Gallery entrances that received traps were gauged by sight only, so we expected to collect a variety of other ambrosia beetles. For example, Kendra et al. (2011b) captured 17 species in the subfamily Scolytinae arriving at logs of avocado (*Prunus americana* Miller) and lychee (*Litchi chinensis* Sonnerat) in Florida while Carillo et al. (2012) reported 14 species emerging from avocado logs and nine species from swampbay (*Persea palustris* (Rafinesque) Sargent). Conversely, we collected four species. Larger species like *X. crassiusculus* and *X. germanus* were unlikely to be sampled because we excluded them based on gallery entrance size, but others like *X. saxenesii* are similar in size to *X. glabratus.* These results suggest that, although other similar sized ambrosia beetles attack redbay trees they comprise a small proportion of the total.

Redbay ambrosia beetle galleries were very productive over a long period of time and beetles attacked trees throughout the year. Therefore, control strategies targeting this beetle will need to be applied or effective year round to prevent disease transmission.

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