Biology of the European oak borer in Michigan, United States of America, with comparisons to the native twolined chestnut borer

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Abstract—In 2010–2011, we studied the European oak borer (EOB), *Agrilus sulcicollis* Lacordaire (Coleoptera: Buprestidae), in Michigan, United States of America, and made comparisons with the native twolined chestnut borer (TLCB), *Agrilus bilineatus* (Weber). EOB adult flight began and peaked before TLCB. More EOB females were captured on purple and white compared with yellow and green sticky traps. More TLCB females were captured on purple, followed by yellow, green, and white, respectively. Male EOB and TLCB did not show a significant colour preference. EOB completed development primarily from areas of artificially girdled trees where the phloem had died soon after trees were girdled, while TLCB usually developed in areas of girdled trees that had some live phloem present. Both EOB and TLCB successfully attacked and emerged from girdled *Quercus alba* Linnaeus, *Quercus robur* Linnaeus, and *Quercus rubra* Linnaeus (Fagaceae) trees. No live EOB or TLCB were found in two ungirdled and apparently healthy *Q. robur* trees that were dissected. EOB attacked and emerged from *Q. alba*, *Q. robur*, *Q. rubra*, and *Quercus velutina* Lamarck trap logs. Differences in the pronotal groove and terminal processes can be used to distinguish EOB from TLCB larvae. Five species of parasitoids were reared from EOB and four from TLCB.

Résumé—Nous avons étudié en 2010–2011 l'agrile européen du chêne (EOB), *Agrilus sulcicollis* Lacordaire (Coleoptera: Buprestidae), au Michigan, États-Unis d'Amérique, et l'avons comparé à l'agrile du châtaignier (TLCB), *Agrilus bilineatus* (Weber), une espèce indigène. La période de vol de EOB débute et atteint son sommet avant celle de TLCB. Plus de femelles EOB ont été capturées sur des pièges collants violets et blancs que sur des pièges jaunes et verts. Le plus grand nombre de femelles TLCB a été capturé sur des pièges violets, puis par ordre sur des jaunes, des verts et des blancs. Les mâles EOB et TLCB ne montrent aucune préférence significative de couleur. Les EOB complètent leur développement principalement dans des zones d'arbres annelés artificiellement chez lesquels le phloème est mort peu après l'annélation des arbres, alors que les TLCB se développement généralement dans des zones d'arbres annelés chez lesquels il reste du phloème vivant. Tant les EOB que les TLCB attaquent avec succès les chênes *Quercus alba* Linnaeus, *Q. robur* Linnaeus et *Q. rubra* Linnaeus (Fagaceae) annelés et en émergent. Aucun EOB ni TLCB vivant n'a été trouvé lors de la dissection de deux chênes *Q. robur* non annelés et à apparence saine. Les EOB attaquent les billes de chênes *Q. alba*, *Q. robur*, *Q. rubra* et *Q. velutina* Lamarck utilisées comme pièges (trap logs) et en émergent. Des différences dans le sillon du pronotum et des processus terminaux peuvent servir à distinguer les larves de EOB et de TLCB. Cinq espèces de parasitoïdes ont été obtenues par élevage de EOB et quatre de TLCB.

Introduction

The European oak borer (EOB), *Agrilus sulcicollis* Lacordaire (Coleoptera: Buprestidae), is native to most of Europe where it attacks primarily *Quercus* Linnaeus (Fagaceae), and occasionally *Castanea* Miller (Fagaceae), *Carpinus* Linnaeus (Betulaceae), and *Fagus* Linnaeus (Fagaceae) (Bílý 2002; Evans *et al.* 2004; Jendek and Grebennikov 2009). Adult EOB lay eggs in the bark crevices of host trees. Eggs hatch and the larvae bore into the subcortical region where

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they feed and eventually pupate (Bílý 2002). In Europe, EOB and two other *Agrilus* Curtis species, *Agrilus biguttatus* (Fabricius) and *Agrilus angustulus* (Illiger), have been associated with oak decline (Moraal and Hilszczanski 2000; Evans *et al.* 2004; Hilszczanski and Sierpinski 2008). However, *A. biguttatus* is considered to be the most destructive of these three oak-infesting *Agrilus* species (Moraal and Hilszczanski 2000).

In 2008, EOB was first discovered in Ontario, Canada (Jendek and Grebennikov 2009), and later the same year in Michigan, United States of America (Haack *et al.* 2009). Previously unidentified and misidentified specimens of this beetle were later found that date back to 1995 in Ontario (Jendek and Grebennikov 2009), and 2003 in Michigan (Haack *et al.* 2009). Many of these specimens were captured on sticky traps used in surveys and studies of the emerald ash borer, *Agrilus planipennis* Fairmaire, an exotic borer introduced into the United States of America and Canada that has become a serious pest of ash, *Fraxinus* Linnaeus (Oleaceae) (Haack *et al.* 2002; Cappaert *et al.* 2005; Poland and McCullough 2006; Kovacs *et al.* 2010). In Michigan, EOB has emerged from *Quercus robur* Linnaeus, a native host of EOB in Europe (Haack *et al.* 2009), and in Ontario it has emerged from *Q. rubra* Linnaeus (Jendek and Grebennikov 2009). The current known geographical range of EOB in North America as of 2013 includes 10 counties in southern Michigan, United States of America, two counties in northwestern New York, United States of America, and six counties in southeastern Ontario, Canada (National Agriculture Pest Information System 2013; B. Gill, Canadian Food Inspection Agency, personal communication). It is likely that the range of EOB in North America is much larger than what has been documented to date, given that there are currently no federal or state/provincial quarantines for EOB in either Canada or the United States of America. Therefore, few delimiting surveys have been conducted for EOB.

EOB adds to the list of at least 42 native *Agrilus* species that are associated with *Quercus* in North America (Nelson *et al.* 2008; Haack *et al.* 2009). Although no direct *Quercus* mortality has been linked to EOB since its discovery in North America, its association with *Quercus* decline in Europe raises concerns regarding potential impacts it could have on *Quercus* in North America when combined with other significant *Quercus* pests such as the native twolined chestnut borer (TLCB), *Agrilus bilineatus* (Weber) (Haack *et al.* 2009). In 2010–2011, we conducted several life history studies on EOB in southern Michigan including: seasonal flight, attraction to different colours of sticky traps and artificially girdled trees, host preference and within tree distribution, larval morphology, and parasitism. In addition, whenever possible, we collected similar data on TLCB so that comparisons could be made between the two species.

Materials and methods

Study sites

Studies took place in *Quercus* provenance plantings at two sites in southern Michigan, United States of America. The first site was at the Michigan State University, Tree Research Center (TRC), Ingham County (42.67°N, 84.47°W), which consisted of primarily *Q. robur* and some *Quercus alba* Linnaeus. The second field site was at the Michigan State University, Kellogg Experimental Forest (KF), Kalamazoo County (42.37°N, 85.36°W), which consisted of a mixture of *Q. robur*, *Q. alba*, and *Q. rubra*. Trees at each site were ~30 years old and averaged 13 m in height.

Trap colour and seasonal flight

Sticky traps were used to determine seasonal flight and the trap colours most effective for capturing *Agrilus* adults in 2010 and 2011. We tested green, purple, white, and yellow sticky traps that were 15-cm-wide × 30-cm-tall. Studies have shown that buprestid adults are often attracted to the colours green, purple, and white (Sakalian *et al.* 1993; Oliver *et al.* 2003; Oliver *et al.* 2004; Francese *et al.* 2005; Crook *et al.* 2009; Petrice *et al.* 2013). Yellow is the standard colour used for sticky traps that are readily available through multiple retailers and are used to capture numerous species of leaf feeding insects. A FieldSpec Pro full range spectrophotometer (Analytical Spectral Devices, Inc., Boulder, Colorado, United States of America) was used to measure spectral reflectance of each colour tested. Reflectance was measured approximately every 3 nm within the visible and near-infrared portion of the spectrum (350–1000 nm). Green (peak reflectance: 530–536 nm, 57.6%), purple (433–436 nm, 26.7%), and white (peak reflectance: 436–438 nm, 96.0%) traps were cut from sheets of corrugated plastic (Coroplast, Inc., Vanceburg, Kentucky, United States of America), and yellow traps (peak reflectance: 561–572 nm, 70.4%) were standard insect sticky traps (Olson Products, Inc., Medina, Ohio, United States of America). One card of each of the four colours was stapled to a single, 1-m-long wooden pole in random order with 15 cm spacing between cards. All traps, including yellow sticky traps, were coated on each side with clear Pestick™ insect glue (Hummert International, Earth City, Missouri, United States of America). Wooden poles with traps were placed on *Q. robur* and *Q. alba* trees situated along the edges of the plantations or on trees that were open grown and exposed to the sun. Wooden poles with traps were suspended horizontally using twine, just below the foliage on the lower limbs of trees with no more than one pole per tree and a minimum of 10 m between trees with traps. Traps were suspended between 1.5–2.0 m above the ground. In 2010, 10 sets of traps (40 traps total) were placed at each site on 12 May. In 2011, 10 sets of traps were placed at KF on 4 May, and 12 sets of traps were placed at TRC on 10 May. All *Agrilus* adults were removed from traps every week through early July, after which all *Agrilus* were removed at two-week intervals through August. Insects were frozen until they were cleaned with hexane to remove Pestick™, and prepared for identification. All *Agrilus* were sexed and identified to species using the keys in Fisher (1928), Wellso *et al.* (1976), and MacRae (2003). Keys of North American *Agrilus* did not include EOB, so specimens that resembled its species description (Jendek and Grebennikov 2009) and voucher specimens in our collection, were sent to James Zablotny (United States Department of Agriculture Animal Plant and Health Inspection Service, Romulus, Michigan, United States of America) for confirmation. Voucher specimens are stored at Michigan State University Insect Collection, East Lansing, Michigan, United States of America.

Girdled trees

Attraction to girdled trees and within-tree distribution was studied for EOB and TLCB on *Q. robur* trees that were girdled in 2010 or 2011. Trees were girdled to cause stress, which is known to enhance attraction of trees to several species of *Agrilus* beetles (Cote and Allen 1980; Haack and Benjamin 1982; Dunn *et al.* 1986; McCullough *et al.* 2009). In 2010, we girdled 12 *Q. robur* trees at TRC by making a single girdle ~1 m above the ground on each tree using a chainsaw. Girdles were deep enough to sever the cambium and the outer few growth rings of xylem on each tree but depth did vary slightly among trees. Girdled trees were located on the edge of each plantation. We girdled six trees on 15 April 2010, just before leaf flush, and six more trees on 21 May 2010, just after leaf expansion was complete. Tree diameter at breast height (DBH, 1.3 m above the ground) ranged from 14 to 27 cm (mean = 19 cm). We recorded if foliage of girdled trees appeared healthy, *i.e.,* green and fully expanded, or showed evidence of stress, *i.e.*, wilting or browning, on 4 June and 12 August 2010. These 12 trees were left standing until they were felled in January–February 2011. When the trees were felled, we cut a 1-m-long tree section below the girdle (~0–1 m above the ground), another directly above the girdle (~1–2 m), and then a section every 2 m along the main stem, stopping ~2 m from the top of each tree. We also cut 1-m-long sections from two branches in the mid-crown to upper crown of each tree. One half of each tree section was dissected and the other half was placed in a rearing container indoors (ambient temperature of ~22 °C) soon after the tree was felled to allow insects to complete development and emerge. In addition, two *Q. robur* trees that were not girdled and appeared healthy were felled in March 2011 at TRC and a 0.5-m-long section was cut and dissected from 1, 4, and 8 m above the ground to determine if these apparently healthy trees had been attacked.

In 2011, we girdled 21 *Q. robur* trees at TRC, including eight trees on 8 March (when the trees were dormant), six on 4 May (just before leaf flush), and seven on 27 May (just after full leaf expansion). Tree DBH ranged from 11.8 to 30.8 cm (mean = 20.3 cm), and each tree was double girdled with a chainsaw ~1 m above the ground, with girdles ~5 cm apart and a minimum depth of 2.5 cm into the xylem tissue. Trees were double girdled in 2011 to increase the level of tree stress because some single-girdled trees from 2010 showed no effect from girdling at the end of the 2010 growing season.

At KF, we girdled 18 trees in 2011, six trees each of *Q. alba*, *Q. robur*, and *Q. rubra*, to determine EOB host preference. We girdled three trees of each species on each of the following dates: 4 May (just before leaf flush) and on 27 May (just after leaves were fully expanded). Trees were double girdled following the same procedure used at TRC in 2011. Tree DBH ranged from 17.2 to 26.0 cm (mean=20.6 cm).

For all trees girdled in 2011, we recorded if foliage appeared healthy or stressed on 6 June and 8 August 2011. The girdled trees were left standing until they were felled during February–March 2012, after which a 0.5-m-long section was removed from each tree just below the girdle (~0.5–1.0 m above the ground), just above the girdle (~1.0–1.5 m), and at mid-stem (~4.5–5.0 m). We also collected several branches and twigs from each tree for rearing to determine if EOB developed in smaller host material. Logs, branches and twigs were placed in rearing containers soon after trees were felled and held indoors at ~22 °C to allow insects to complete development and emerge.

Trap logs

Trap logs of different *Quercus* species were cut from the trunks of *Q. alba*, *Q. robur*, *Q. rubra*, and *Quercus velutina* Lamarck trees that appeared to be healthy, *i.e.,* buds and expanding leaves appeared healthy throughout the crown, and therefore assumed to be uninfested by *Agrilus*. Trap logs were cut on 6 May 2010 and placed at KF and TRC on 12 May 2010 to allow natural colonisation by *Agrilus*. Logs were 1 m long and ranged from 9 to 18 cm diameter (mean = 15 cm). Five replicates were placed at each of the two sites and each replicate consisted of one log of each oak species. Each log within the replicates was stood upright ~15 cm from other logs in the replicate and tied to a metal fence post that was driven into the ground. Replicates were at least 25 m apart and situated along the edge of the oak plantings. Logs were collected in February 2011 and transported to our laboratory where one half of each log was dissected and the remaining half was placed in a rearing tube and held indoors (ambient temperature ~22 °C) to allow insects to complete development and emerge.

Log dissections

Tree and trap log sections were stored at 5 °C until dissections were performed in the laboratory, usually within 1–4 weeks after they were collected from the field. Before dissecting tree and trap log sections, the diameter and length were recorded. Also, mean bark thickness (outer and inner bark combined) of each section was determined by averaging measurements taken at four equidistant points around the log circumference. Then, bark was carefully removed with a drawknife and the location of each larva found was recorded, *i.e.,* feeding in inner bark, or pupal cell in outer bark or wood. The amount of live phloem, *i.e.,* tissue cream coloured and moist as opposed to brown and drying, was visually estimated to the nearest 5% for each tree section dissected from girdled trees.

All *Agrilus* larvae found were examined under a dissecting microscope and it was apparent, based on *Agrilus* larval characters described by Bílý (1982) and Chamorro *et al.* (2012), that there were two species of *Agrilus* in the logs. We reared a subset of the two larval morphotypes to adults to determine the species for each. Parasitoids found on *Agrilus* larvae were placed in petri dishes and held at 24 °C and 75% humidity in growth chambers to allow them to complete development. The *Agrilus* cadaver that the parasitoids were found on was used to determine which *Agrilus* species was parasitised. Adult parasitoids that were reared from *Agrilus* cadavers in petri dishes or emerged from logs were preserved in 95% ethyl alcohol and sent to specialists for identification.

Statistical analyses

Mean number of adults captured per trap, pooled by sample dates within years, on different coloured sticky traps in 2010 and 2011 was compared using PROC Mixed (SAS 2008), with study site and sampling year as random variables. Adult flight was compared by calculating percent of total adults of each *Agrilus* species captured for each collection date at each site within each sample year. Degree-day accumulations, calculated with the numerical integration method with 10 °C as the base temperature and 1 January as the start date, for adult flight were taken from Michigan State University Enviro-Weather (2011). The weather station used for TRC degree-day data was located at the Michigan State University Horticulture Teaching and Research Center, ~1 km west of the TRC study site, and the weather station used for KF degree-day data was located at the Kalamazoo Nature Center, ~20 km west of the KF study site.

Insect emergence (or dissection) density was calculated by dividing the number of beetles recovered by the surface area of the respective log they emerged (or were dissected) from. The density of EOB or TLCB per m^2 for different tree heights, girdle dates, foliage conditions, tree species, and trap logs species was compared using PROC GLM (SAS 2008). Density values were transformed using Log 10 prior to analyses to help normalise the data. Means were separated using Student–Neuman–Keuls multiple range test when they were significantly different at the $P < 0.05$ level.

Results and discussion

Trap colour and seasonal flight

In 2010, EOB flight had already started at both study sites before the first trap collections were made on 21 May at TRC and 24 May at KF (Fig. 1), and thus timing of initial flight could not be determined. Degree-day accumulations (DD; base = 10 °C; start date = 1 January) for the first collection were 208 at TRC and 282 at KF. At TRC in 2010, the peak EOB capture rate was during the weekly collection period ending on 28 May (294 DD). Most EOB collected at KF were from the first trapping period, so we cannot be sure if our traps documented the actual peak flight at KF or if the peak had already occurred prior to us placing traps in the field.

In 2011, the first trap collection at KF was on 12 May (126 DD) and 1 EOB was collected on that day (Fig. 2). No EOB had been captured at TRC when traps were checked for the first time on 13 May (116 DD), while one EOB had been captured at TRC when traps were checked on 16 May (120 DD). In 2011, EOB flight peaked on 9 June (336 DD) at TRC. At KF, only three EOB adults were captured in 2011 (12 May = 126 DD; 20 May = 163 DD; 10 June = 369 DD), and therefore it was not possible to determine when peak flight occurred.

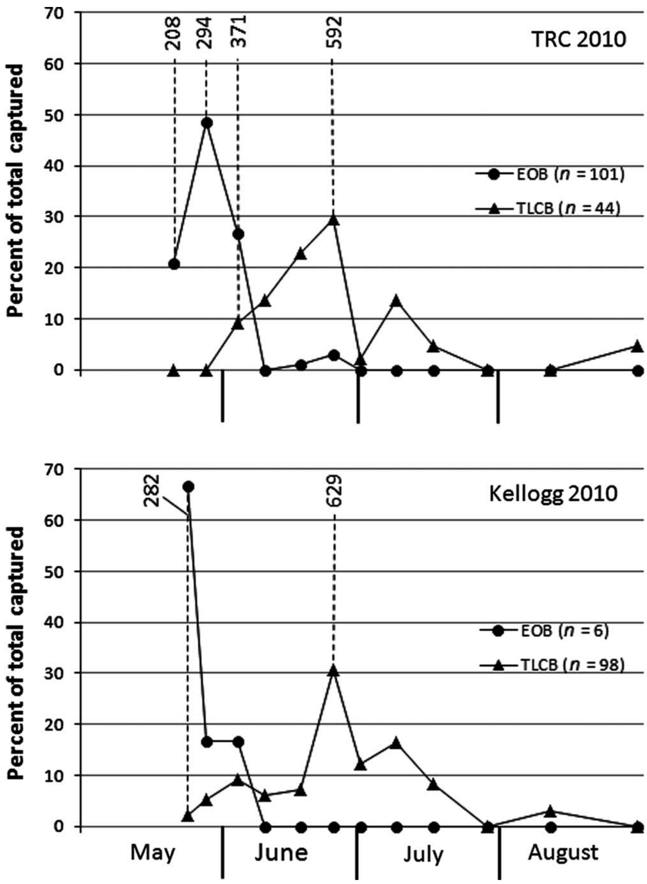
Initial flight for TLCB generally started after EOB initial flight in 2010 and 2011 (Figs. 1–2). At TRC, TLCB peak flight occurred approximately four weeks after EOB peak flight in 2010, and approximately two weeks after EOB peak flight in 2011. The same trend occurred at KF, however, we lacked data for EOB peak flight to make exact comparisons. Degree-day accumulations for TLCB peak flight ranged from 592 at TRC to 629 at KF in 2010, and 458 at TRC and 524 at KF in 2011. Our TLCB adult flight data are consistent with what has been previously documented for TLCB in southern Michigan (Wellso *et al.* 1976), as well as similar latitudes in the states of Wisconsin (Haack and Benjamin 1982), Pennsylvania, and New York, United States of America (Cote and Allen 1980).

Purple and white were the most attractive colours to EOB females based on mean number of adult females captured per trap (Table 1). EOB males did not show a significant preference to any particular trap colour, although it should be noted that many more females were captured than males (sex ratio = 1.00♂:6.60♀). TLCB females were most attracted to purple, followed by yellow traps, while males did not show any significant preference (Table 1). As with EOB, the sex ratio of TLCB was skewed towards females (sex ratio = 1.00♂:2.32♀).

Previous studies have found *Agrilus* adults, including *A. planipennis*, to be highly attracted to purple and green (Oliver *et al.* 2003; Francese *et al.* 2005; Crook *et al.* 2009; Petrice *et al.* 2013). There is some anecdotal evidence that suggests that *Agrilus anxius* is significantly attracted to white, presumably because many of its hosts, *Betula* Linnaeus (Betulaceae) species, have white bark (Petrice *et al.* 2013). It is unclear why EOB is attracted to white given that *Quercus* bark is usually a shade of gray. Species belonging to another buprestid genus, *Chrysobothris* Eschscholtz, have also shown some attraction to white sticky traps (Oliver *et al.* 2003; Petrice *et al.* 2013).

It is possible that the placement of traps in the lower canopy and close to the ground may have influenced attraction and sex ratios of *Agrilus*. Francese *et al.* (2010) found that male

Fig. 1. Mean percent of European oak borer (EOB), *Agrilus sulcicollis* (Coleoptera: Buprestidae) and twolined chestnut borer (TLCB), *A. bilineatus*, captured on sticky cards by date in 2010 at two locations in southern Michigan, United States of America (TRC, MSU Trees Research Center, Ingham Co.; KF, Kellogg Forest, Kalamazoo Co.). Degree days (base 10 °C; start date 1 January 2010) are listed at the top of each figure for the approximate date of initial flight and peak flight of each species.

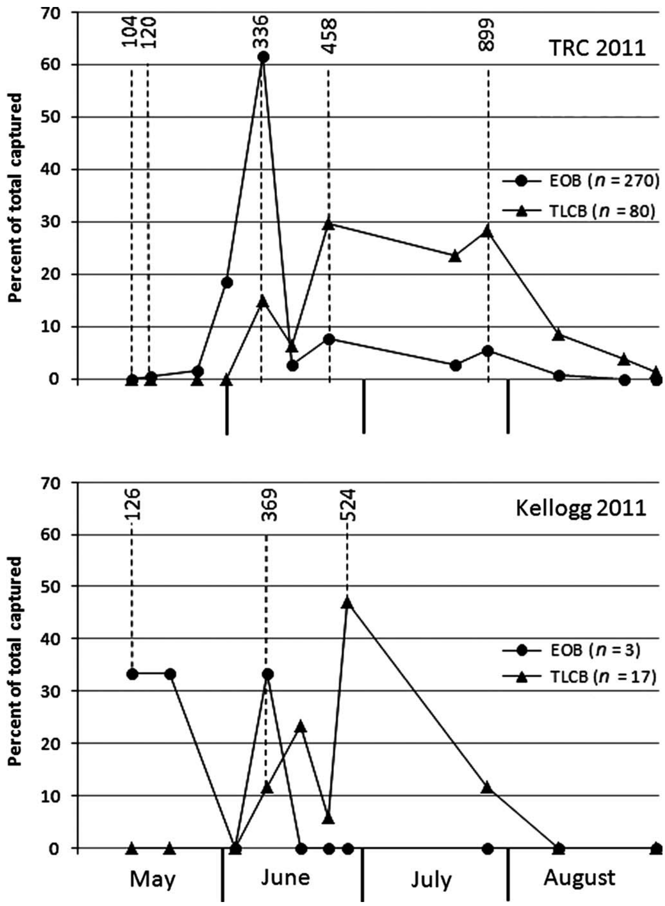


A. planipennis capture rates were highest when traps were suspended mid-canopy in ash trees as opposed to 1.5 m above the ground. Furthermore, *A. planipennis* females tend to be more attracted to purple than males, while *A. planipennis* males tend to be more attracted to green traps compared to females (Crook *et al.* 2009; Francese *et al.* 2010). Perhaps if our traps had been suspended higher in the tree canopies, more *Agrilus* males would have been captured and they would have shown a significant trap colour preference.

Seasonal development

Most (95%; $n = 324$) EOB larvae had completed development, and constructed and entered their pupal cells when tree sections were dissected in January–February 2011 from the *Q. robur* trees that had been girdled and subsequently attacked in the spring and summer of 2010. Similarly, 97% ($n = 691$) of TLCB individuals were mature larvae and had entered their pupal cells when the tree sections were dissected in January–February 2011. Assuming that all trees were attacked the same year that they were girdled, most EOB and TLCB completed development in one year and thus were univoltine at our study sites. Both species have been reported as being primarily univoltine with the exception of populations found in more northern ranges or individuals under less than optimal host conditions (Palm 1959; Cote and Allen 1980; Haack and Benjamin 1982; Bílý 2002).

Fig. 2. Mean percent of European oak borer (EOB), *Agrilus sulcicollis* (Coleoptera: Buprestidae) and twolined chestnut borer (TLCB), *Agrilus bilineatus*, captured on sticky cards by date in 2011 at two locations in southern Michigan, United States of America (TRC, MSU Trees Research Center, Ingham Co.; KF, Kellogg Forest, Kalamazoo Co.). Degree days (base 10 °C; start date 1 January 2011) are listed at the top of each figure for the approximate date of initial flight and peak flight of each species.



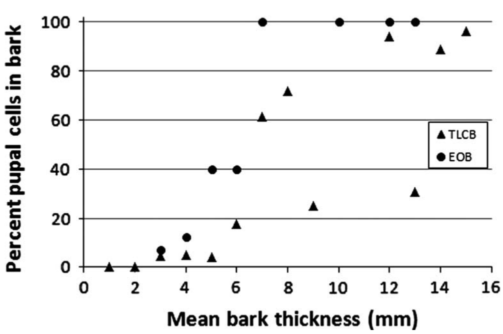
Although the exact number of larvae was not recorded, the majority of mature EOB and TLCB larvae encountered were doubled over in their pupal cells. These doubled-over larvae have been referred to as J-larvae by some authors and as prepupae by others; see Duan *et al.* (2012) for a comparison of J-larvae and prepupae. Almost 89% ($n = 309$) of the EOB pupal cells were created in the bark as opposed to the outer xylem, compared with only 19% ($n = 669$) of TLCB pupal cells being created in the bark. Interestingly, Bílý (2002) reported that EOB preferred to pupate in the xylem, however, bark thickness was not mentioned. In the present study, few EOB pupal cells were constructed in the bark when mean bark thickness (inner + outer bark) was < 4 mm, whereas there was a sharp increase in the percent of pupal cells in the bark when mean bark thickness was 5 mm or greater (Fig. 3). The percent of TLCB pupal cells in the bark sharply increased when mean bark thickness was 6 mm or greater. This slight difference compared with EOB, is likely attributed to the fact that TLCB adults (and thus mature larvae) are slightly larger than EOB (Fisher 1928; Bílý 1982). All EOB pupal cells were constructed in the bark when mean bark thickness was 7 mm or greater, while some TLCB pupal cells were constructed in the outer sapwood even when mean bark thickness exceeded 10 mm. Emergence of

Table 1. Mean number of male and female (EOB), *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, adults captured per trap per trapping season on different coloured sticky traps suspended from live *Quercus robur* and *Quercus alba* branches May–August 2010 and 2011 in Ingham County and Kalamazoo County, Michigan, United States of America (data pooled by site and year).

	Mean number of adults per trap			
Trap colour	EOB males	EOB females	TLCB males	TLCB females
Purple	0.6 ± 0.2a*	7.6 ± 2.0a	0.9 ± 0.4a	3.3 ± 1.3a
White	0.9 ± 0.3a	3.8 ± 0.8a	1.1 ± 0.6a	0.6 ± 0.3c
Yellow	0.5 ± 0.2a	1.4 ± 0.4b	1.1 ± 0.2a	1.6 ± 0.4ab
Green	0.6 ± 0.2a	0.6 ± 0.2b	0.8 ± 0.3a	1.2 ± 0.5bc
P	0.5074	0.0001	0.4336	0.0001
F	0.78	14.66	0.93	8.03
df	3, 70	3, 94	3, 63	3, 85

EOB = European oak borer; TCLB = twolined chestnut borer.
*Means followed by the same letter (within columns) are not significantly different at the $P < 0.05$ level (Student–Neuman–Keuls multiple range test).

Fig. 3. Percent of European oak borer (EOB), *Agrilus sulcicollis* (Coleoptera: Buprestidae) and twolined chestnut borer (TLCB), *Agrilus bilineatus*, pupal cells constructed in bark of *Quercus robur* trees in comparison to mean bark thickness (both inner and outer bark were combined) of logs they were dissected from.



EOB from logs reared in the laboratory averaged 14 days before TLCB. The sex ratio for *Agrilus* adults reared in the laboratory from 2010 girdled trees was 1.0♂:1.5♀ ($n = 110$) for EOB and 1.0♂:1.0♀ ($n = 424$) for TLCB.

Within-tree distribution

We reared or dissected EOB from 80%, TLCB from 83%, and both EOB and TLCB from 67% of the 30 *Q. robur* trees girdled at TRC in 2010 and 2011. In 2010, EOB were recovered only from tree sections above the girdle, while TLCB was recovered both above and below the girdle (Table 2). There was a trend for EOB and TLCB densities to be higher between 3 and 7 m above the ground in 2010; however, these differences were not significant for either *Agrilus* species because of the high variation among trees (Table 2). In 2011, significantly more EOB were found immediately above the girdle and at mid-bole compared with below the girdle, while significantly more TLCB were found below the girdle compared with immediately above the girdle and at mid-bole (Table 3). All 2011 girdled trees died quickly as a result of the double girdle (two rings of cutting), compared with trees that were girdled once (one ring) in 2010. The only live phloem that remained in 2011-girdled trees was below the girdle, while the phloem above the girdle was discoloured and appeared dead when trees were cut in the winter following girdling. In contrast, Tluczek *et al.* (2011) reported that ash trees girdled in mid-spring died below the girdle while the tissue above the girdle appeared healthy when trees were dissected the winter following girdling. In their study, however, trees were only phloem girdled, *i.e.,* only the outer and inner bark was removed and the xylem tissue was not severed and therefore upward conduction in the outer xylem was probably not greatly impacted. In addition, Tluczek *et al.* (2011) found that *A. planipennis* grew larger and faster below the girdle as compared with above the girdle.

Table 2. Mean densities per m^2 of bark surface area of EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, that were dissected from logs or emerged from logs reared indoors soon after felling, and the percent of phloem that was alive at the time of felling at different heights above the ground for *Quercus robur* trees that were girdled in spring 2010 and felled January–March 2011 in Ingham County, Michigan, United States of America.

	EOB per m^2 bark		TLCB per m^2 bark		
Tree height (m)	Dissected	Emerged	Dissected	Emerged	% Phloem alive
0.5 (below girdle)	0	0	18.1 ± 6.9	11.7 ± 3.6	60.0 ± 13.1
1 (above girdle)	22.1 ± 17.7	9.2 ± 3.7	21.9 ± 12.5	21.2 ± 7.9	73.2 ± 13.9
3	44.0 ± 39.5	21.8 ± 15.1	33.0 ± 14.0	25.1 ± 10.0	78.2 ± 10.7
5	48.7 ± 35.3	35.0 ± 14.3	54.1 ± 21.4	30.3 ± 11.3	77.7 ± 10.1
7	39.7 ± 33.4	21.5 ± 12.5	46.9 ± 15.3	39.1 ± 12.2	89.5 ± 7.2
≥8	14.1 ± 10.9	5.8 ± 5.8	37.8 ± 13.0	14.3 ± 6.6	72.7 ± 11.9
Branches	22.8 ± 21.6	16.2 ± 5.9	20.4 ± 7.8	10.2 ± 5.1	20.4 ± 7.8
P	0.4849	0.3066	0.8752	0.6098	
F	0.94	1.28	0.040	0.75	
df	6, 28	6, 21	6, 70	6, 70	

EOB = European oak borer; TCLB = twolined chestnut borer.

Table 3. Mean densities per m^2 of bark surface area of EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, that emerged from logs reared indoors soon after felling collected from different positions within *Quercus robur* trees girdled March–June 2011 and felled January-March 2012 in Ingham County, Michigan, United States of America.

Tree height	EOB emerged per m^2	TLCB emerged per m^2
Below girdle	0.3 ± 0.3b*	8.9 ± 3.1a
Above girdle	57.9 ± 24.9a	0.6 ± 0.3b
Mid bole	68.2 ± 14.4a	0.4 ± 0.4b
Branches and twigs	1.9 ± 0.8b	0 ± 0b
P	0.0007	0.0001
F	6.29	21.10
df	3, 76	3, 72

EOB = European oak borer; TCLB = twolined chestnut borer.

*Means followed by the same letter (within columns and within sites) are not significantly different at the $P < 0.05$ level (Student–Neuman–Keuls multiple range test).

Host material examined in this study ranged from a maximum of 32 cm in diameter for lower-trunk sections and a minimum of 0.6 cm in diameter (measured at midpoint) for twigs. EOB adults emerged from logs that were up to 31 cm in diameter and twigs as small as 2.6 cm in diameter (measured at the exit hole). Some studies in Europe report that EOB prefers the upper crown and branches of trees (Moraal and Hilszczanski 2000; Hilszczanski and Sierpinski 2008). We did not see this preference in our study; however, the trees in our study succumbed to EOB attack because they were artificially girdled, while the European studies mentioned above examined trees that were attacked by EOB under natural conditions. TLCB emerged or was dissected from tree sections up to 32 cm in diameter and twigs as small as 2.3 cm in diameter.

Effect of girdle date

Mean number of EOB per m^2 of bark surface area that emerged from reared material was significantly higher for trees girdled in late spring compared with early spring in 2010, and the mean number of EOB per m^2 found in the dissected tree sections showed the same trend as the reared material but was only marginally significant (Table 4). The mean number of TLCB per m^2 that emerged or were recovered upon dissection did not vary significantly among the girdle dates. Half of the trees girdled in late spring 2010 showed evidence of stress on 4 June, which was two weeks after trees were girdled and during EOB peak flight, whereas none of the trees girdled in early spring appeared stressed at this time (seven weeks after they were girdled; Table 4). In temperate climates, trees are most

Table 4. Mean densities per m^2 of bark surface area of EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, that were dissected from logs or emerged from logs reared indoors soon after felling and percent of trees showing foliage decline (wilting) in June and August for *Quercus robur* trees that were girdled at different dates in 2010 and 2011, and felled January–March 2011 and 2012, respectively, in Ingham County, Michigan, United States of America.

		% Trees declining		EOB per m^2		TLCB per m^2	
Year	Girdle date	June	August	Dissected	Emerged	Dissected	Emerged
2010	Early spring	0	40	0.1 ± 0.1a*	0 ± 0b	38.0 ± 16.4a	24.1 ± 8.6a
2010	Late spring	50	67	21.0 ± 17.5a	9.5 ± 4.6a	29.2 ± 12.6a	21.1 ± 7.2a
	P			0.0894	0.0435	0.4002	0.7506
	F			3.62	5.51	0.78	0.11
	df			1, 9	1, 9	1, 9	1, 9
2011	Winter	100	100		54.7 ± 28.0a		1.8 ± 0.7a
2011	Early spring	100	100		36.6 ± 7.4a		6.2 ± 3.7a
2011	Late spring	100	100		16.8 ± 6.3a		3.7 ± 1.5a
	P				0.1680		0.8929
	F				1.54		0.86
	df				2, 18		2, 18

EOB = European oak borer; TCLB = twolined chestnut borer.
*Means followed by the same letter (within columns and within years) are not significantly different at the $P < 0.05$ level (Student–Neuman–Keuls multiple range test).

effectively killed if they are girdled when root carbohydrates are most depleted (Noel 1970), which would have been the case for late spring girdled trees in our study, which had just completed leaf expansion before they were girdled. However, our single girdle method and inconsistent girdling depths in 2010 may have also influenced effectiveness of girdling given that all trees that were girdled with a double girdle in 2011 died quickly (discussed below) despite the time of the season they were girdled.

No live *Agrilus* were found in the two ungirdled control trees that were dissected in March 2011. However, some galleries were found where the *Agrilus* larvae had tunnelled in 2010 and died. The appearance of these galleries resembled TLCB galleries that we had encountered during previous log dissections where most of the tunnelling was perpendicular to the wood grain, as compared with EOB galleries that were mostly parallel with the wood grain (T.R.P., personal observation). In addition, the remaining ungirdled *Quercus* trees at the study sites that were not used for this study did not show evidence of decline in 2010 or 2011.

The decline and death of the 2010 late-spring girdled trees coincided with EOB peak flight in 2010, while these same trees were most likely dead, except for tissue below the girdle, when TLCB flight peaked around 25 June 2010. TLCB was only found below the girdle on trees that appeared stressed in early June, while EOB was only found above the girdle in these same trees (data not shown). Foliage of the trees girdled in early spring 2010 did not appear to be stressed during EOB peak flight and these trees were not attacked by EOB. We did not evaluate foliage condition of girdled trees during TLCB peak flight, however, two of the early-spring girdled trees showed evidence of stress when they were evaluated on 12 August 2010 and TLCB was found both above and below the girdle on both of these trees. TLCB was only found above the girdle in early-spring girdled trees that did not appear stressed in August (data not shown).

To further illustrate the difference in host condition preference between EOB and TLCB, trees girdled in 2010 were grouped according to evidence of stress in June regardless of girdle date (Table 5). Girdled trees showing stress in June had significantly higher EOB densities and significantly lower TLCB densities compared with girdled trees with foliage that appeared healthy in June. Furthermore, in the trees that

Table 5. Mean densities per m^2 of bark surface area of EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, that were dissected from logs or emerged from logs reared indoors soon after felling, and if foliage appeared stressed, *i.e.,* wilting or browning, on 4 June 2010 for *Quercus robur* trees girdled on 15 April or 21 May 2010 and felled in January–March 2012 in Ingham County, Michigan, United States of America.

	EOB per m^2		TLCB per m^2	
Foliage appeared stressed in June	Dissected	Emerged	Dissected	Emerged
No	0.2 ± 0.2b*	0.2 ± 0.2b	44.9 ± 10.6a	28.5 ± 6.0a
Yes	41.5 ± 33.4a	18.5 ± 5.0a	2.2 ± 1.0b	6.4 ± 2.1b
P	0.0003	0.0001	0.0009	0.0292
F	33.54	44.66	23.23	6.70
df	1, 9	1, 9	1, 9	1, 9

EOB = European oak borer; TCLB = twolined chestnut borer.
*Means followed by the same letter (within columns) are not significantly different at the $P < 0.05$ level (Student–Neuman–Keuls multiple range test).

had both live TLCB present and appeared stressed on 4 June, we only found TLCB below the girdle where some live tissue still remained.

Mean number of EOB or TLCB that emerged per m^2 of bark did not vary significantly among the three 2011 girdle dates (Table 4). All girdled *Q. robur* trees showed evidence of stress in June, likely because of the effectiveness of the double-girdle treatment interrupting translocation regardless of when the trees were girdled. All 2011-girdled trees were dead before EOB and TLCB flight peaked in 2011, with the exception of late-spring girdled trees and EOB peak flight. As discussed in the previous section, TLCB were mostly found below the girdle where some live tissue remained in the trunk, while most EOB were found above the girdle where most tissue was moribund.

Apparently, TLCB prefers at least some live phloem for larval development, while EOB prefers to develop in recently dead phloem. Haack and Benjamin (1982) found similar results for TLCB, where live larvae were only found below the girdle of artificially girdled oak trees, and only dead TLCB larvae were found above the girdle where all phloem had died. Dunn *et al.* (1986) found that TLCB was attracted to girdled oaks within 24 hours after trees were girdled, however, TLCB attraction to these trees decreased as trees died. In contrast, Bílý (1982) noted that EOB developed in live trees, however, we did not find evidence of this in our study.

Table 6. Mean densities per m^2 of bark surface area of EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, that emerged from logs reared indoors soon after felling for different *Quercus* species girdled May–June 2011 and felled January–March 2012 at Kellogg Forest, Kalamazoo County, Michigan, United States of America, in 2011.

Species	EOB emerged per m^2	TLCB emerged per m^2
Quercus robur	3.1 ± 1.3a*	5.9 ± 3.9a
Quercus rubra	0.2 ± 0.2b	1.2 ± 0.6a
Quercus alba	2.6 ± 1.0a	4.8 ± 3.4a
P	0.0475	0.5506
F	3.76	0.62
df	2, 15	2, 15

EOB = European oak borer; TCLB = twolined chestnut borer.
*Means followed by the same letter (within columns) are not significantly different at the $P < 0.05$ level (Student–Neuman–Keuls multiple range test).

Host tree species

Foliage of all 2011-girdled trees for each of the three oak species tested showed evidence of stress in June. EOB emerged from all three oak species that were girdled in 2011 (Table 6). This is not surprising, given the large number of oak species that EOB attacks in Europe (Bílý 2002; Evans *et al.* 2004; Jendek and Grebennikov 2009). Significantly more EOB were reared from *Q. robur* and *Q. alba* trees compared with *Q. rubra* trees (Table 6). *Agrilus biguttatus*, a species frequently associated with EOB in Europe, rarely attacks North American *Q. rubra* trees that have been planted in Europe (Moraal and Hilszczanski 2000). TLCB emergence did not vary significantly among these three oak species, all of which have been documented as hosts of TLCB (Nelson *et al.* 2008; Hansen *et al.* 2011).

Trap logs

EOB attacked and successfully emerged from traps log of all four *Quercus* species tested (Table 7). Although fewer EOB were recovered from *Q. rubra* logs in absolute terms, no significant differences were found among *Quercus* species. Studies in Europe have reported that EOB attacked *Quercus* logs in slash piles from recent logging activity (Hedin *et al.* 2008), so it is not surprising that many of our trap logs were well infested by EOB. TLCB were dissected only from *Q. robur* logs and emerged only from one *Q. alba* log (Table 7). To our knowledge, it has never been documented that TLCB will lay eggs on and successfully develop in cut logs. It is possible that *Q. robur* and *Q. alba* trees were infested with TLCB before they were cut even though the trees appeared healthy and showed no external signs or symptoms of infestation such as dead crowns or limbs, bark damage from woodpeckers foraging for larvae, or D-shaped exit holes. However, we feel that this is highly unlikely given that TLCB usually completes its development in one year throughout its North American range (Cote and Allen 1980; Haack and Benjamin 1982). Furthermore, trees were cut for trap logs well before TLCB adult flight began in 2010, so adult TLCB would not have had an opportunity to oviposit on them before logs were placed at the study sites in 2010. Nevertheless, the low number of reared and dissected TLCB compared with EOB from trap logs illustrates how uncommon it is for TLCB to infest and develop in trap logs. Moreover, Haack and Benjamin (1980) found that most TLCB larvae died if trees were cut in June, soon after oviposition and larval eclosion, and left on the forest floor throughout the summer.

Distinguishing larvae of EOB from TLCB

During examination under a dissecting microscope of mature fourth instar EOB and TLCB larvae that had not yet entered their pupal cells and J-larvae recovered from pupal cells, we noted differences in the shape of the pronotal groove, which allowed for easy separation of the larvae of these two species. The pronotal groove of TLCB, when viewed dorsally, *i.e.,* abdominal spiracles were visible from above, was bifurcate near its posterior end, while the pronotal groove of EOB remained entire along its length (Figs. 4A, 4B). The terminal processes, as defined by Chamorro *et al.* (2012), or urogomphi by others (Cote and Allen 1980; Haack and Benjamin 1982; Loerch and Cameron 1983; Petrice *et al.* 2009), on the 10th abdominal

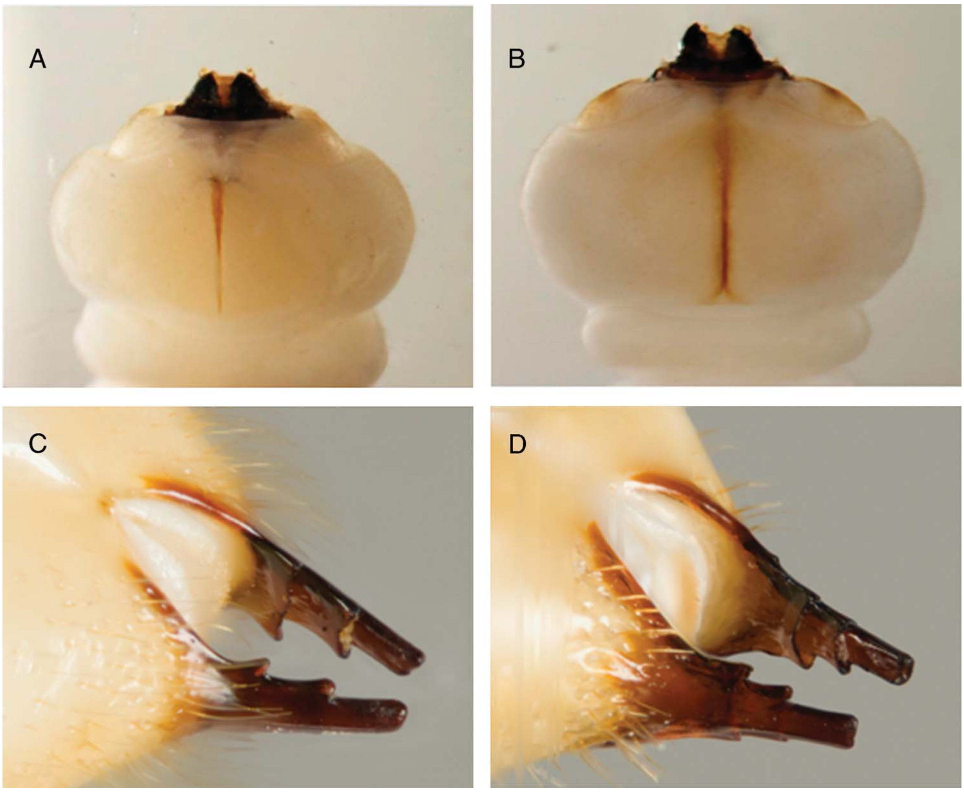
Table 7. Mean densities per m^2 of bark surface area of EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae) and TLCB, *Agrilus bilineatus*, that emerged from logs reared indoors soon after they were removed from the field in February 2011 for 1-m-long logs cut from different *Quercus* species from live, uninfested trees and placed in oak plantings in late spring 2010 at two sites in southern Michigan, United States of America.

	EOB per m^2		TLCB per m^2	
Species	Dissected	Emerged	Dissected	Emerged
Quercus alba	38.6 ± 30.1a*	23.1 ± 16.8a	0b	1.6 ± 1.6a
Quercus robur	48.4 ± 29.7a	39.7 ± 15.4a	2.0 ± 1.1a	0a
Quercus rubra	7.9 ± 3.1a	4.7 ± 3.3a	0b	0a
Quercus velutina	28.9 ± 16.9a	28.7 ± 11.9a	0b	0a
P	0.9303	0.2907	0.0200	0.4040
F	0.15	1.30	3.67	1.00
df	3, 36	3, 36	3, 36	3, 36

EOB = European oak borer; TCLB = twolined chestnut borer.

*Means followed by the same letter (within columns) are not significantly different at the $P < 0.05$ level (Student–Neuman–Keuls multiple range test).

Fig. 4. Pronotal groove and terminal processes of European oak borer (EOB), *Agrilus sulcicollis* (Coleoptera: Buprestidae) on left (A and C) and twolined chestnut borer (TLCB), *Agrilus bilineatus*, on right (B and D).



segment also differed between the two species. The basal excretory duct on the inner, lateral surface of each terminal process was straight or sometimes jagged in EOB, whereas it was slightly concave and smooth in TLCB (Figs. 4C, 4D). Also, the general shape of the EOB terminal processes appeared more laterally flattened compared with TLCB. Drawings and descriptions of EOB larvae can also be found in Palm (1962) and Bílý (1999).

Parasitoids

At least nine species of hymenopteran parasitoids were reared from the girdled trees and trap logs (Table 8). Examination of *Agrilus* cadavers from which parasitoids were individually reared confirmed five of these species attacked and emerged from EOB larvae, while four species were confirmed from TLCB larvae. None of the five species reared from EOB have been previously reported in the literature to attack EOB. *Leluthia astigma* (Ashmead) (Hymenoptera: Braconidae) was the only parasitoid species, of the four reared from TLCB, which had not been previously reported from TLCB in the literature (Krombein *et al.* 1979; Taylor *et al.* 2012). The braconids *Atanycolus cappaerti* Marsh and Strazanac, *L. astigma*, and *Spathius simillimus* Ashmead were reared from both EOB and TLCB in this study. In addition, five of the species reared have been reported from emerald ash borer, *A. planipennis* (Table 8; Bauer *et al.* 2005; Cappaert and McCullough 2009; Duan *et al.* 2009; Kula *et al.* 2010; Taylor *et al.* 2012).

Summary

Our studies in southern Michigan found that EOB adult flight began and peaked before TLCB initial and peak flight. EOB females were most attracted to purple and white sticky traps, while males did not show a significant

Table 8. Hymenoptera parasitoid species that were dissected from or emerged from girdled *Quercus* trees and trap logs that were infested with EOB and TLCB in Ingham Co. and Kalamazoo Co., Michigan, United States of America in 2010 and 2011, confirmed host association by positive identification of cadaver (EOB, *Agrilus sulcicollis* (Coleoptera: Buprestidae); TLCB, *Agrilus bilineatus*) and rearing immature parasitoids to adults, and if host-parasitoid association has been previously reported in the literature for each species.

Species	Family	Host (number confirmed)**	Number reared‡
Atanycolus cappaerti Marsh and Strazanac*,†	Braconidae	EOB (11), TLCB (1)	781
Balcha indica (Mani and Kaul)†	Eupelmidae	EOB (2)	140
Eupelmus Dalman species	Eupelmidae	None confirmed	13
Eurytoma petiolata Förster group	Eurytomidae	None confirmed	20
Leluthia astigma (Ashmead)†	Braconidae	EOB (6), TLCB (1)	167
Metapelma spectabile Westwood	Eupelmidae	EOB (1)	30
Phasgonophora sulcata Westwood*,†	Chalcididae	TLCB (9)	58
Spathius simillimus Ashmead*,†	Braconidae	EOB (3), TLCB (8)	743
Xorides calidus (Provancher)	Ichneumonidae	None confirmed	1

*Species reported in the literature as attacking *Agrilus bilineatus*.
† Species reported in the literature as attacking emerald ash borer, *Agrilus planipennis*.
**Number of parasitoid–host associations that we confirmed by identifying *Agrilus* larvae or cadaver and successfully rearing immature parasitoids to adults.
‡ Total number of parasitoid adults that emerged from girdled trees and traps logs that were reared in the laboratory.

colour preference. Almost all EOB and TLCB larvae completed development within one growing season, and thus are primarily univoltine in southern Michigan, but may require two years to complete development under some circumstances. EOB attacked and completed development in all three species of girdled *Quercus* trees and all four species of *Quercus* trap logs in our study, suggesting it will be able to develop in most North American *Quercus* species. EOB prefers more moribund tissue compared with TLCB, and therefore it will likely not be an aggressive tree killer like TLCB. There are several parasitoids that attack EOB in North America, and most of these are known parasitoids of TLCB.

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