Entomologia Experimentalis et Applicata

DOI: 10.1111/eea.12141

Suitability of native and ornamental oak species in California for *Agrilus auroguttatus*

L.J. Haavik[1]*, A.D. Graves[1,2], T.W. Coleman[3], M.L. Flint[1], R.C. Venette[4] & S.J. Seybold[5]

[1]*Department of Entomology, University of California, Davis, CA, USA,* [2]*USDA Forest Service, Forest Health Protection, Albuquerque, NM, USA,* [3]*USDA Forest Service, Forest Health Protection, San Bernardino, CA, USA,* [4]*USDA Forest Service, Northern Research Station, St. Paul, MN, USA, and* [5]*USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA*

Accepted: 12 October 2013

Key words: host range, invasive species, phloem and wood borer, Section *Lobatae*, Section *Quercus*, Coleoptera, Buprestidae, Fagaceae

Abstract

Goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is a new invasive species in southern California, USA. The extent of the host range of this insect is not known, but this knowledge will have a major impact on assessment of the risks that this pest poses to oaks [*Quercus* spp. (Fagaceae)]. We conducted laboratory tests to determine the potential suitability of native and ornamental oak species for larvae and adults of *A. auroguttatus*. We infested 179 cut logs (from 163 different trees) with eggs or larvae, measured neonate survival and, after 5 months, counted feeding galleries, and noted the proportion of galleries with late instars. Initial larval survival was generally high when larvae penetrated the phloem (range: 62–98% among oak species), and low by the time larvae began to feed at the phloem/xylem interface (range: 0–25% among oak species). The majority of larvae that established a visible feeding gallery survived to the fourth instar (total of 73% for all oak species). Larval galleries were established with greater frequency in red oaks (Section *Lobatae*) compared with other oaks (19 vs. 7 or 4%). All red oaks tested (*Q. agrifolia* Née, *Q. kelloggii* Newberry, and *Q. wislizeni* A. DC.) were likely suitable hosts for larvae. Larvae were apparently able to feed on some of the other oaks (*Q. chrysolepis* Leibmann, *Q. suber* L., *Q. lobata* Née, and *Q. douglasii* Hook & Arn), although it remains unclear whether these species would be preferred hosts under natural conditions. Adult longevity and fecundity varied little by species of oak foliage fed to adults. The host range of *A. auroguttatus* is likely limited by suitability of oak species for the larval rather than the adult life stage. Results support published field observations that red oaks are more suitable hosts than white oaks.

Introduction

Herbivorous insect invasions can occur inter- and intracontinentally, when a species is introduced to a new ecosystem and attacks novel plant species (e.g., Haack et al., 2002; Rabaglia & Williams, 2002; Coleman & Seybold, 2008) or attacks its co-evolved hosts growing in a non-native ecosystem (e.g., Paine et al., 1995; Carnegie & Bashford, 2012). As a result of global change, herbivorous insects may also expand their ranges, and they may encounter new host species (e.g., Ayres & Lombardero, 2000; Logan & Powell, 2001; Bentz et al., 2010). For any of the above situations, the pest's relationship with one or several host species may be known or not. Knowledge of such relationships is critical for predicting the economic and ecological impacts of these pests in new habitats. Pest risk assessments are important tools that rely on basic biological information, including an invasive insect's host range, to forecast its establishment and spread (Yemshanov et al., 2009; Venette et al., 2010).

The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is a new invasive species in southern California, USA (Coleman & Seybold, 2008). *Agrilus auroguttatus* most likely arrived in southern California years before it was first detected in 2004 (Westcott, 2005), and may have been transported there from its native range in southeastern Arizona by way of infested

---

*Correspondence and current address: L.J. Haavik, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste. Marie, Ontario, Canada, P6A 2E5. E-mail: ljhaavik@gmail.com firewood (Coleman & Seybold, 2011; Coleman et al., 2012a). As of early 2013, *A. auroguttatus* has been collected from only two counties in California [San Diego (Coleman & Seybold, 2011) and Riverside (calfire.ca.gov, 2013)]. A risk assessment is needed to evaluate the probability and impact of *A. auroguttatus* spreading beyond its current range.

In southeastern Arizona, *A. auroguttatus* feeds on two red oaks (Section *Lobatae*): Emory oak, *Q. emoryi* Torrey, and silverleaf oak, *Q. hypoleucoides* A. Camus (Coleman & Seybold, 2011; Coleman et al., 2012b). Co-occurring white oaks (Section *Quercus*), Arizona white oak (*Q. arizonica* L.), and gray oak (*Q. grisea* Liebmann) do not appear to be hosts for the beetle (Coleman & Seybold, 2011; Coleman et al., 2012b).

In southern California, *A. auroguttatus* feeds on and kills two red oaks, coast live oak (*Q. agrifolia* Née) and California black oak (*Q. kelloggii* Newberry), and a species that is taxonomically intermediate between red and white oaks, canyon live oak (*Q. chrysolepis* Leibmann; Section *Protobalanus*) (Coleman & Seybold, 2008, 2011). A co-occurring white oak, Engelmann oak (*Q. engelmannii* Greene) is also colonized by *A. auroguttatus*, but at a low frequency in areas with very high beetle population densities (Coleman et al., 2012b).

The ranges of *Q. agrifolia* and *Q. kelloggii* extend from Oregon and northern California south to Baja California (Mexico) contiguously along coastal mountain ranges and throughout the lower elevations of the Sierra Nevada Mountain range (Stuart & Sawyer, 2001). There are other ecologically and economically important oak species native to and planted in California and Oregon that *A. auroguttatus* has not yet contacted within its current range.

Both *A. auroguttatus* larvae and adults feed on oaks. Larvae feed mostly at the phloem/xylem interface, creating meandering galleries that effectively girdle trees when populations are high (Coleman & Seybold, 2008). Adults must feed on oak leaves to complete maturation, but this feeding is not likely to have an adverse effect on tree health (Flint et al., 2013). In the laboratory, adults feed on *Q. agrifolia* or *Q. kelloggii* foliage. Adults are in flight from May to October (Coleman & Seybold, 2008; Haavik et al., 2013). Eggs are rarely observed in the field; females probably oviposit singly or in small clumps in cryptic locations such as bark cracks or under lichens. Upon eclosion, larvae chew directly into the phloem tissue, migrate to the cambial region (i.e., phloem/xylem interface), where they feed on vascular tissue and complete four instars (Haavik et al., 2013). Fourth instars create a pupal cell in the phloem, just underneath the outer bark, where they fold in half upon themselves and overwinter in the typical *Agrilus* spp. hairpin formation (i.e., J-larva) (Coleman & Seybold, 2008; Haavik et al., 2013). In southern California, most of the *A. auroguttatus* population completes one generation per year (Haavik et al., 2013). *Agrilus auroguttatus* colonizes the lower bole ($\leq$2 m) at a higher density than the mid-bole (ca. 6 m), and branches are rarely colonized (Haavik et al., 2012). In southern California, larger trees (>50 cm diameter at breast height, dbh) are infested more often with *A. auroguttatus* than smaller diameter trees (Coleman et al., 2012b).

Our objective was to determine the suitability of several native or ornamental oak species that occur in California and Oregon for both larvae and adults of *A. auroguttatus*. Most of these species occur outside the beetle's adventive range in southern California. For this study, we define a suitable larval host as an oak species in which larvae apparently feed and exhibit evidence of development. We define a suitable adult host as one on which foliar feeding results in adult maturation, mating, and egg production. To determine the suitability of nine different oak species for *A. auroguttatus* larvae, we artificially inserted eggs and neonates into cut logs. We also conducted a no-choice feeding test with adults to determine the effect of the foliage from nine oak species and a co-occurring non-oak species, white alder (*Alnus rhombifolia* Nuttall, Betulaceae), on adult longevity and fecundity.

Materials and methods

Collection and preparation of logs for larval host tests

To test oak suitability for *A. auroguttatus* larvae, we used cut logs in the laboratory. We were not able to use live trees in a wildland or nursery setting because four of the eight oak species of interest do not grow within the current range of *A. auroguttatus* in California, and because this beetle has shown a propensity in the field to naturally infest only large diameter trees (Coleman et al., 2012b). Likewise, field containment procedures are not adequate to allow us to introduce the beetle to standing trees without worsening the current geographic extent of infestation. We conducted tests in 2010 and 2011, and applied different methods in 2011 based on limited success in 2010.

From February to July of 2010 and 2011, we removed one log from each of 163 (74 in 2010, 89 in 2011) un-infested trees at sites in southern and central California (see Table S1 for oak species sample sizes and site information). Logs (range: 0.25–0.5 m long, 11–27 cm in diameter, standardized to 2 000 cm^2 of bark surface area) were cut from the stems of small trees or from the branches of large trees. In the laboratory, we sealed cut ends of each log with a water-based sealant (Anchorseal; UC Coatings, Buffalo, NY, USA) within 2 days of cutting and stored logs in the laboratory at 24 ± 3 °C for 7–10 days (or in cold storage at 4 °C, if stored for longer than 10 days) until eggs or larvae could be inserted.

Collection of infested material to rear adults

In March and April of 2010 and 2011, we removed logs or bark from 10 to 15 naturally infested *Q. agrifolia* cut on the Descanso Ranger District, Cleveland National Forest, San Diego, CA, USA (see geographical coordinates in Table S1). We transported rearing logs and bark to the laboratory and placed them in screen observation cages (1.8 m^3; BioQuip Products, Rancho Dominguez, CA, USA) inside a heated greenhouse (26 ± 7 °C). Once adult emergence began, cages were checked daily and newly emerged beetles were immediately transferred to smaller rearing containers. Beetles were used directly for host tests with foliage and as parents to produce eggs for the larval host test.

Rearing adults and larvae

We adapted procedures used to rear emerald ash borer, *Agrilus planipennis* Fairmaire (Yang et al., 2012). We placed one or two females in a ventilated plastic container (2010: 16 × 8 × 6 cm; Tupperware®, Orlando, FL, USA; 2011: 10 × 10.5 × 16.5 cm; Candy Concepts, Pewaukee, WI, USA) with one or two males, fresh *Q. agrifolia* foliage (replaced every 3–4 days), and a water source. We kept the plastic containers on the laboratory bench underneath a window with a natural photoperiod of ca. L14:D10 at 24 ± 3 °C. We used different oviposition substrates in each year. In 2010, we placed accordion-folded card stock in the plastic containers, and in 2011, we used coffee filters underneath a 2-mm-mesh window screen placed over a ca. 5-cm-diameter circular hole cut through the container's lid. In each year, ca. 75 beetles produced eggs and first instars for the larval host test. In 2011, an additional 104 beetles were used for the adult host test.

Larval host tests

Egg and larval insertions 2010. In June and July of 2010, 2–4 eggs or neonates were placed at least 5 cm apart on each log. First, a circular plug (same size as a gelatin capsule, ca. 4 mm in diameter) of outer bark was removed with an arch punch; a single egg or larva was placed directly on the phloem surface with a fine-tipped paintbrush; and one-half of the capsules were secured over the hole with an insect pin. In total, 109 eggs and 246 larvae were placed on logs.

Larval insertions 2011. In April and May of 2011, we used a different larval insertion technique, modified from procedures developed for *Phoracantha semipunctata* (Fabricius) (Hanks et al., 1993) and *Agrilus anxius* Gory (Ball & Simmons, 1986). With a razor blade, we cut a 5- to 10-mm long v-shaped groove or slit in the outer bark just penetrating the phloem. This v-shape created a tight, crevice-like space that helped larvae attain a purchase to tunnel into the phloem. We lifted a neonate with surface tension on a wetted fine-tipped paintbrush, and carefully placed it inside the groove, making four larval insertions per log. Insertion locations were approximately evenly distributed along the exposed bark surface of logs resting horizontally on the laboratory bench. We placed a dry paper towel over each insertion and taped it in place onto the outer bark.

Evaluation of larval host suitability. To determine whether larvae successfully entered logs, we inspected each entrance site 24 h after insertion with a binocular microscope or hand lens to confirm whether larvae were present. If they were not visible, we assumed that they had successfully entered the log. If they were present and had died, we noted this, and made a second insertion attempt with a new egg or larva. We completed one replicate log of each oak species before infesting the next replicate.

Once all insertions were complete, logs were transferred to 1.8-m^3 screen cages and held with a natural photoperiod at 24 ± 3 °C until December. At this time, we expected that larvae would be fourth instars. Because we were unsure whether larvae required a cold period to complete development, and rather than waiting until the following spring to collect emerged adults, we destructively sampled all logs to assess the presence and extent of feeding galleries and larvae.

We first inspected logs for characteristic D-shaped emergence holes (Hishinuma et al., 2011), then carefully peeled bark from sapwood with a drawknife or a hatchet and hammer. To search for larvae, we cut the bark into pieces with a scissors. Presence or absence of a feeding gallery at the phloem/xylem interface was noted, and width of galleries was measured to the nearest mm. We compared gallery width with approximate head capsule size of each instar to estimate the final instar attained by each larva that survived long enough to establish a visible gallery.

Adult host test: no-choice feeding on foliage

In 2011, to determine if diet during the maturation feeding period affected adult longevity and female fecundity, we implemented a laboratory feeding test of nine oak species and a co-occurring non-oak, *A. rhombifolia* (Table S2), whereby newly emerged mating pairs (five replicates per host species, total n = 50 mating pairs) were held in containers, fed fresh field-collected foliage (replaced every 3–4 days), and provided with an oviposition substrate. Containers were kept on a laboratory bench underneath a window with a natural photoperiod of ca. L14:D10 at 24 ± 3 °C until beetles died. Each replicate contained foliage from a different individual oak tree. Not all replicates were initiated at the same time; in general, one or two replicates of each oak species began before the third and so on. Oviposition substrate (i.e., coffee filters) was replaced twice per week once females became fecund. We recorded observations daily to evaluate adult longevity and fecundity. We used a binocular microscope to inspect coffee filters from containers that contained eggs 1 month after the final female died to assess egg melanization and hatch.

Data analysis

Larval host tests. We assessed suitability of cut logs initially, at the time of artificial insertion (neonate survival and larval entry), and finally, when larvae were allowed to feed within cut logs for at least 4 months (gallery establishment and survival to the fourth instar). Neonate survival was the number of first instars that apparently survived to feed beyond the insertion site per number of neonates introduced to all logs of each oak species or section. Larval entry measured the relative rate at which neonates entered logs to begin feeding, and was the proportion of surviving neonates that required less than 1 day to enter cut logs beyond the visible insertion site (measured in 2011 only). We expected that time required for larvae to enter logs was related to suitability of host material; oak species requiring more time for larvae to enter were likely to be less suitable hosts. Gallery establishment was the proportion of larvae that successfully entered the host and survived long enough to create a visible gallery. Survival to the fourth instar was measured to determine if some larvae, once they had established galleries, were able to grow larger than others; it was the proportion of established galleries of each oak species or section that were wide enough to have been created by a fourth instar.

Within the R statistical environment, version 2.15.0 (R Development Core Team, 2012), we used generalized linear models assuming a binomial distribution of residuals (i.e., logistic regression) to test the four measurements described above by oak species or section [*Lobatae*, *Quercus*, and other (*Protobalanus* combined with *Cerris*)]. We applied Bonferroni correction factors to account for inflation of possible Type I errors from multiple pairwise comparisons. To achieve an overall α-level of 0.05, P-values were adjusted by a factor of eight, four, or two, whereby the null hypothesis was rejected if $P<0.006$, 0.013, or 0.025 for tests by oak species, oak species with established larval galleries, or sections, respectively.

Results of 2010 and 2011 larval host tests were analyzed separately because of the different artificial insertion methods used in each year. We did not analyze egg and larval insertions separately in 2010 because egg and larval insertions were often applied to the same logs and few larvae survived long enough to leave evidence of feeding.

Adult host test. With R (R Development Core Team, 2012), we used analyses of variance (ANOVA) to test the effect of oak species foliage fed to adults on longevity, time until females were fecund, length of time that females remained fecund, total fecundity, egg hatch, and melanization. Females that did not produce any eggs were not included in tests of fecundity because approximately one third of *A. auroguttatus* females do not oviposit in rearing containers when held in the laboratory (LJ Haavik, unpubl.). If ANOVA were significant, Tukey's honestly significant difference (HSD) mean separation tests were applied. When data did not meet model assumptions of normality or homogeneity of variance, we applied the Box-Cox method to determine appropriate transformations of the data to satisfy those assumptions (Box & Cox, 1964). ANOVA were applied to transformations of male longevity ($\lambda = 0.35$), total fecundity ($\lambda = 0.4$), proportion of eggs melanized, and proportion of eggs hatched ($\lambda = 2$ for both). Model checks were as follows: studentized residual plots, normal probability plots, and the Shapiro–Wilk test (Shapiro & Wilk, 1965). We also applied Pearson's correlations to response data to evaluate relationships among longevity and fecundity-related measures. Statistical significance was set at $P<0.05$, error terms are presented as one standard error from the mean (SEM), and means presented in Table 2 are untransformed values.

Results

Larval host tests

In 2010, 79% of eggs and first instars survived to enter logs. Of these 252 successful insertions, 16 larvae (6%) survived long enough to establish a detectable gallery. Of those that created visible galleries, 13 survived to the final instar (81%). No galleries were found within *Q. lobata*, *Q. engelmannii*, or *Q. garryana*. Two fourth instars were recovered: both were from *Q. agrifolia* logs.

In 2011, 90% of first instars survived to enter logs. Of these 405 successful insertions, 35 larvae (9%) survived long enough to establish a gallery. Of those that created galleries, 24 survived to the final instar (69%). No galleries were found within *Q. douglasii*, *Q. engelmannii*, or *Q. garryana*. Four larvae were recovered: two fourth instars from the same *Q. agrifolia* log, one second instar from a *Q. wislizeni* log, and one first instar from a *Q. lobata* log.

Table 1 Results of generalized linear models (binomial distribution of errors) for measures of suitability by oak species (upper portion) and oak section (lower portion) for *Agrilus auroguttatus* larvae

	2010				2011			
	n	χ^2	d.f.	P	n	χ^2	d.f.	P
Oak species								
Neonate survival	333	28.49	8	<0.001[1]	413	27.01	8	<0.001[1]
Larval entry	–	–	–	–	405	29.77	8	<0.001[1,2]
Gallery establishment	252	13.39	8	0.099	405	44.25	8	<0.001[1,3]
Survival to fourth instar	15	3.60	4	0.46	34	2.61	4	0.63
Oak section								
Neonate survival	333	0.09	2	0.96	413	11.72	2	0.003[1]
Larval entry	–	–	–	–	405	6.64	2	0.036
Gallery establishment	252	4.95	2	0.084	405	20.91	2	<0.001[1]
Survival to fourth instar	16	1.00	2	0.61	35	1.10	2	0.58

[1] Significant after Bonferroni corrections.
[2] Model only significant for intercept (i.e., majority of larvae required less than 24 h to enter logs of all host species).
[3] Model only significant for intercept (i.e., majority of larvae did not establish galleries in logs regardless of host species).

In 2010, neonate survival varied significantly by oak species (Table 1, Figure 1A), but not by section (Table 1, Figure 2A), wherein survival was greater in *Q. wislizeni* than in *Q. kelloggii* and did not vary significantly among those and the remaining oaks. In 2011, neonate survival varied significantly by oak species (Table 1, Figure 1B) and section (Table 1, Figure 2B), wherein survival was lowest in *Q. chrysolepis* and greatest in *Q. wislizeni*, *Q. engelmannii*, and *Q. garryana*; it did not vary significantly among those and the remaining oaks. Neonate survival was greater in white oaks (Section *Quercus*) than for species in sections *Protobalanus* and *Cerris*, combined (Figure 2B). Neonate survival in red oaks (Section *Lobatae*) was not significantly different from that in white or other oaks. In 2011, the proportion of first instars that required less than 24 h to enter logs beyond the insertion location (i.e., larval entry) did not vary significantly by oak species or section (Table 1). Most neonates required less than 24 h to enter logs (mean and range among all oak species were 89 ± 3% and 73–100%, respectively).

Although no larvae survived long enough to establish galleries in some oaks, the proportion of larvae that established galleries and the proportion of those larvae that reached the fourth instar did not vary significantly by oak species in 2010 (Table 1; Figure 3A and B) or 2011 (Table 1; Figure 3C and D). The proportion of larvae that established galleries did not vary significantly by section in 2010 (Table 1; Figure 2C), yet it did in 2011 (Table 1; Figure 2D), wherein it was significantly greater in red oaks than in white or other oaks. Of larvae that established galleries, the proportion that reached the fourth instar did not vary significantly among sections in 2010 or 2011 (Table 1; Figure 2E and F).

Adult host test

Beetles readily ate the foliage of, and produced frass from all nine oak species. Some individuals that were offered *A. rhombifolia* leaves ate them and produced frass, but in much smaller quantities than beetles that were fed oak foliage. Ten of the 45 females (22%) did not produce any eggs (see Table 2 for oak species). Female longevity did not vary significantly by oak species, although male longevity did (Table 2). Males lived longest when fed *Q. kelloggii* and shortest when fed either *Q. douglasii* or *A. rhombifolia*; male longevity did not vary significantly among those and the remaining oaks (Table 2). Measures of fecundity did not vary significantly by species of oak foliage that adults were fed (Table 2). Although not included in ANOVA, one female that was fed *A. rhombifolia* produced nine eggs, three of which melanized and later hatched. Some measures of fecundity were significantly correlated, and were thus not likely independent of one another (Table 3). For instance, female longevity was significantly positively correlated with total fecundity, length of time that eggs were produced (i.e., time fecund), and mean number of eggs produced per day (Table 3). Once fecund, females continued to produce eggs until death, resulting in higher measures of fecundity for females that lived longer.

Discussion

Suitability of larval hosts

Survival was generally high when *A. auroguttatus* larvae or eggs were introduced to cut logs but was reduced by the time larvae began to feed at the phloem/xylem interface. However, the majority of larvae that established a feeding gallery reached the fourth instar (81 and 69% in 2010 and

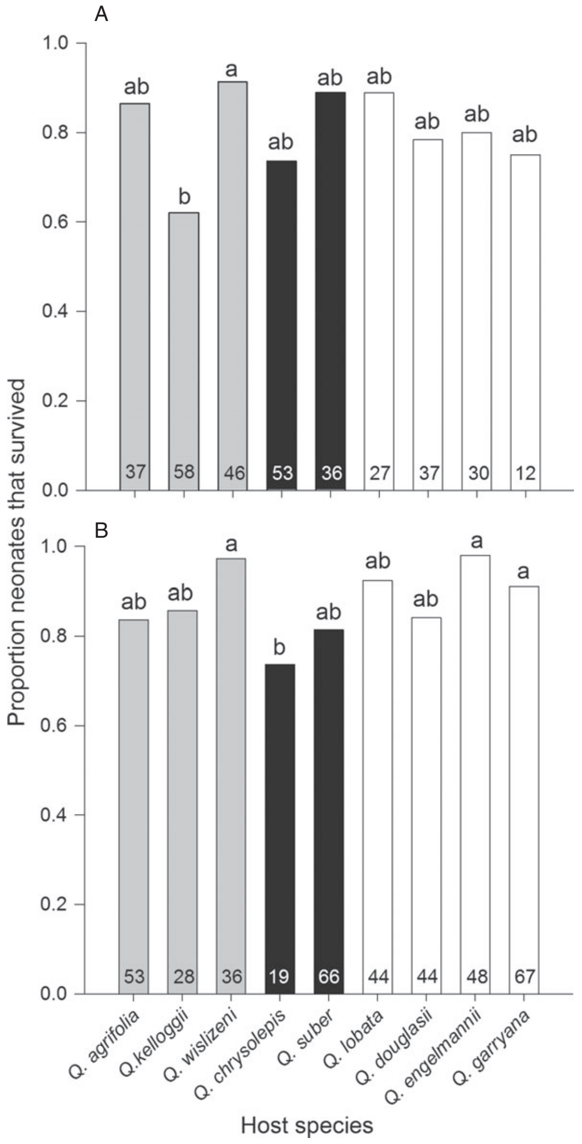

Figure 1 *Agrilus auroguttatus* neonate survival from (A) 2010 and (B) 2011 artificial insertions. Gray bars represent oaks in Section *Lobatae*, black bars represent oaks in other Sections (*Quercus chrysolepis* Section *Protobalanus*, *Q. suber* Section *Cerris*) and white bars represent oaks in Section *Quercus*. (A) and (B) were analyzed separately, and different letters above bars indicate significant differences (χ^2: P<0.006). Sample sizes are indicated at the base of the bars.

2011, respectively). Once larvae had apparently entered the host successfully but had not yet established a visible gallery was a crucial point during development at which most larvae died. In a previous study, we (Haavik et al., 2013) noted the difficulty of sampling early instars of *A. auroguttatus* in standing oak trees in the field, particularly in thick-barked species. Larvae that were no longer visible at the point of insertion had likely started to form a gallery, but the gallery was so small (i.e., narrow and short) that we were unable to locate it.

For subcortical insects, mortality is often greater in early life stages (e.g., egg and early instars) compared with later life stages (e.g., later instars and pupa). High mortality among young larvae was noted in several studies on subcortical beetles (Grimble & Knight, 1970; Linit, 1985; Shibata, 1987; Banno & Yamagami, 1991). On naturally infested paper birch (*Betula papyrifera* Marshall), *A. anxius* mortality was extremely variable, but generally greater in the first instar (range: 0–100%) than in later instars (range: 0–36%) (Barter, 1957). High mortality among young larvae may occur, at least in part, because the effects of food quality are generally greatest for voraciously feeding early instars (Scriber & Slansky, 1981; Cornell & Hawkins, 1995).

Quantitative estimates of buprestid larval survival are rare, but suggest that survivorship during the larval stage is low. For example, only 10–20% of the oak leaf-mining buprestid *Brachys ovatus* (Weber) survived to late instars (Connor, 1988). From 4 to 52% of the oak branch-girdling buprestid, *Coraebus florentinus* Herbst survived to the adult stage, with much of this variation explained by temperature (Cárdenas & Gallardo, 2012). *Agrilus anxius* survival to the adult stage was extremely variable among girdled paper birch trees, and ranged from 0 to 83% (Barter, 1957). Duan et al. (2010) found that only 14–27% of *A. planipennis* eggs artificially placed on green ash (*Fraxinus pennsylvanica* Marshall) trees yielded larvae, while at least 70% of eggs laid by females established. These published results are comparable to the 9–25% of larvae that formed a detectable gallery from artificial infestations on known hosts (*Q. agrifolia* and *Q. kelloggii*) in this study.

We observed significant variation in neonate survival among some oak species – these differences were not generally consistent between years (Figure 1), except that neonate survival was generally high in *Q. wislizeni* (>90%) and all neonates entered logs of this species within 24 h (2011). White oaks may have been more suitable hosts initially than other non-red oaks (Sections *Protobalanus* combined with *Cerris*) (Figure 2B) and red oaks may ultimately be slightly more suitable hosts than white oaks and other non-red oaks (Figure 2D), yet these trends only emerged in 2011 and when individual oak species were pooled by section.

Our results are consistent with field observations that red oaks were infested more often and experienced greater mortality than white oaks (Coleman & Seybold, 2011; Coleman et al., 2012b). Gallery establishment was extremely low in *Q. chrysolepis* logs (≤5%) and no larvae

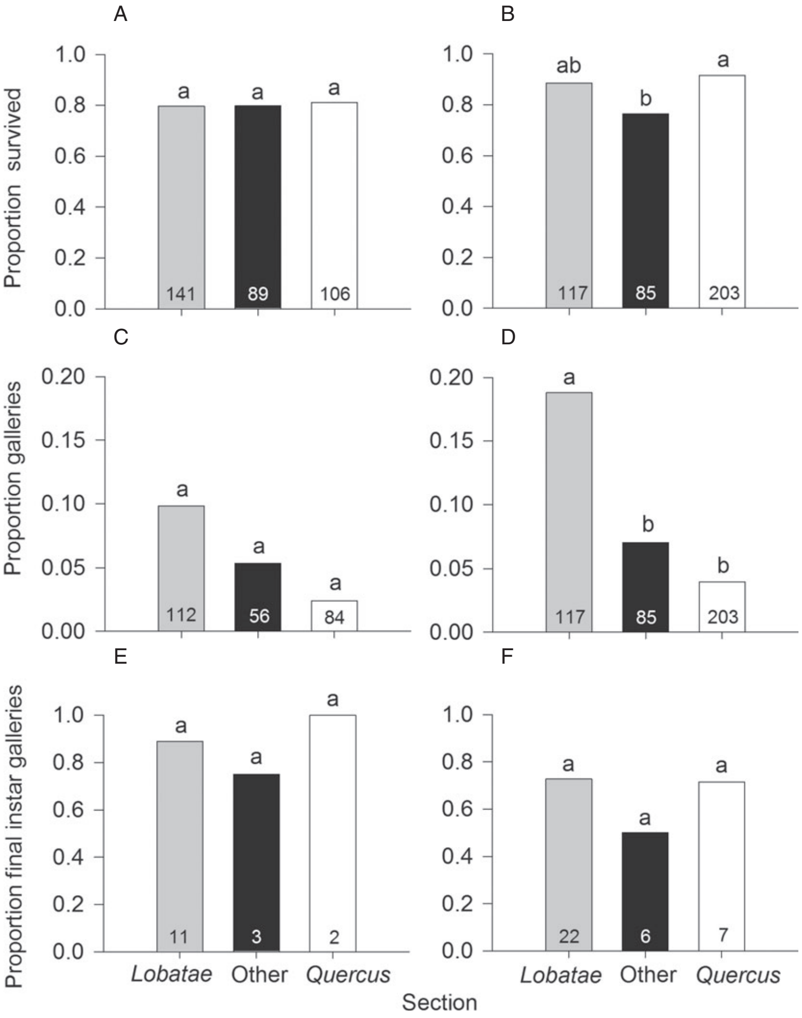

Figure 2 (A and B) Initial and (C–F) final measurements of host suitability for *Agrilus auroguttatus* grouped by oak section and year (A,C,E = 2010; B,D, F = 2011). Gray bars represent oaks in Section *Lobatae*; black bars represent oaks in other sections (*Protobalanus* combined with *Cerris*); and white bars represent oaks in Section *Quercus*. A–F were analyzed separately and different letters above bars indicate significant differences (χ^2: $P<0.025$). Sample sizes are indicated at the base of the bars.

survived to establish galleries in *Q. engelmannii* logs (Figure 3A and C). In contrast, field studies suggest that some *A. auroguttatus* can complete development on *Q. engelmannii*, and *Q. chrysolepis* is frequently colonized by the beetle (Coleman et al., 2012b).

Moisture may be an important, often overlooked, component of host suitability for immature insects (Scriber & Slansky, 1981), and moisture loss from cut logs may have affected success with our artificial insertion methods. *Agrilus* spp. are sensitive to moisture during larval development; if logs or trees become too dry, then larvae will develop more slowly or not complete development at all (Chapman, 1915; Barter, 1957; Haack & Acciavatti, 1992; Moraal & Hilszczański, 2000). However, a lack of moisture might not completely explain our results.

Although not described in the methods, we attempted a rearing method with *A. auroguttatus* that has been successful with *A. planipennis* (Duan et al., 2011). We artificially inserted eggs and larvae into freshly cut *Q. agrifolia* branches (2–5 cm in diameter) sealed at one end with the other end in a tub filled with moistened foam cubes. This method was only 8% successful, which was similar to our results from cut logs (6 and 9% in 2010 and 2011, respectively). However, from the branches, we were able to recover a majority of those larvae that survived to establish a visible gallery in comparison with the recovery of very few larvae from the cut logs. In other words, more larvae remained intact when the thin bark of a small branch was carefully peeled back than when the thicker, drier bark from a larger log was removed more coarsely with a hatchet. If the lack of moisture in the phloem/xylem was the primary cause of larval mortality in our cut log assays, then the branch technique should have had better survivorship, but this was not the case.

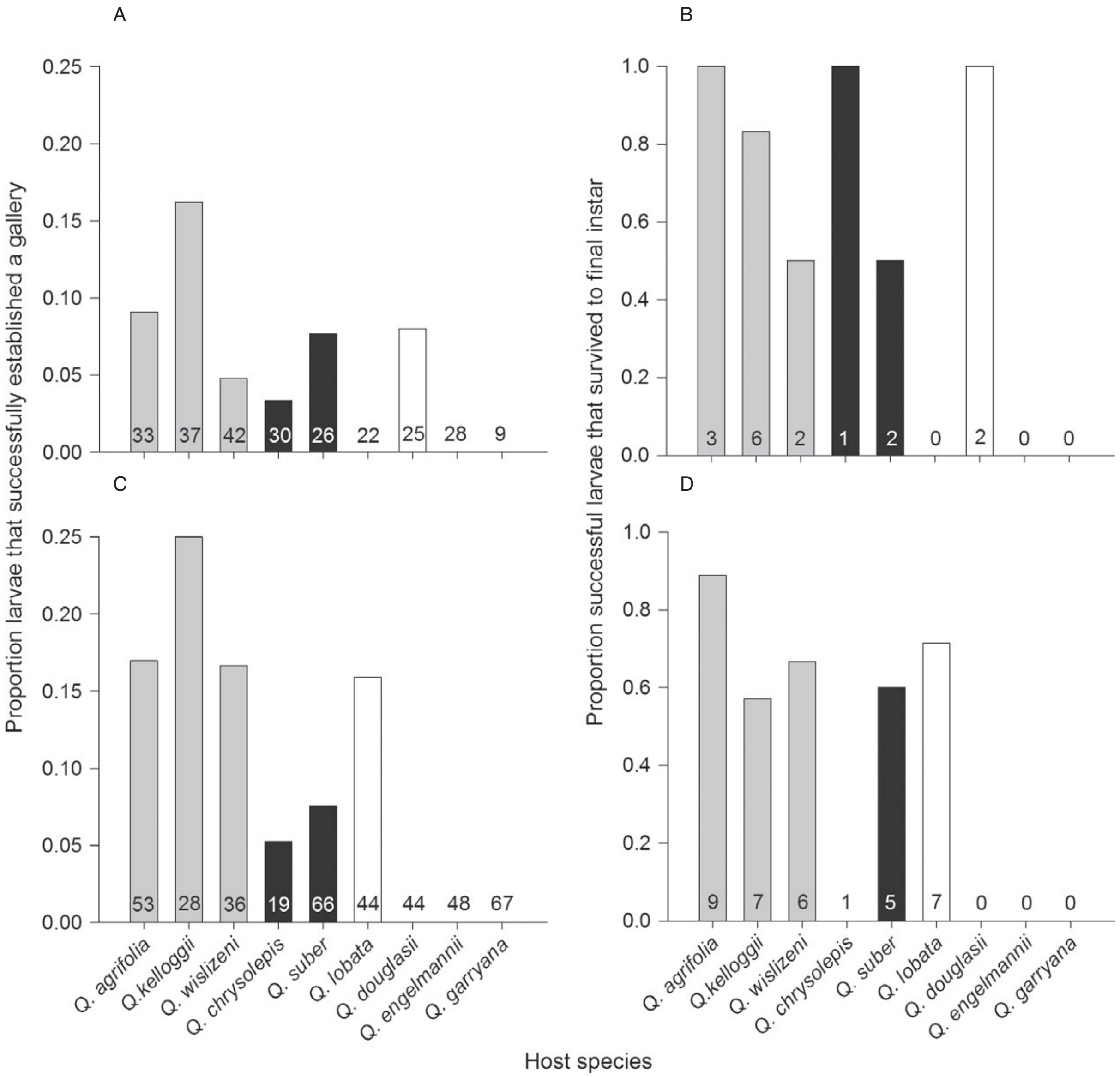

Figure 3 Final measurements of host suitability for *Agrilus auroguttatus* grouped by oak species for (A and B) 2010 and (C and D) 2011. Gray bars represent oaks in Section *Lobatae*; black bars represent oaks in other sections (*Quercus chrysolepis* Section *Protobalanus*, *Q. suber* Section *Cerris*); and white bars represent oaks in Section *Quercus*. A–D were analyzed separately; no difference was significant. Sample sizes are indicated at the base of the bars.

Suitability of adult hosts

Foliage from any oak species that we tested was probably suitable as host material for adults (Table 2). Variation in fecundity among individual females was likely to be more important than species of oak foliage that beetles were fed. For instance, females that lived longer were most fecund, but not most fertile (Table 3). Apparently, all nine oak species contained sufficient nutrition for adults to mature and for females to produce eggs that melanized and hatched. Choice tests, however, can reveal whether *A. auroguttatus* adults prefer some species of oak foliage over others. Studies that evaluated preference and amount of foliage eaten by adult *Agrilus* spp. often found a preference for some host species over others, or that weight gain was greater when fed one host species rather than another (Barter, 1957; Haack & Benjamin, 1982). Akers & Nielsen (1990) reported that although adult *A. anxius* longevity and fecundity varied significantly depending on what

Table 2 Results of no-choice adult *Agrilus auroguttatus* feeding tests on oak (*Quercus* species) and alder (*Alnus rhombifolia*) foliage and ANOVA on longevity and fecundity-related measures [mean (SEM)]

Section	Species	Female longevity (days)	Male longevity (days)	Days until fecund	Time fecund (days)	Total fecundity (no. eggs)	Daily oviposition (eggs per day)	Proportion eggs melanized	Proportion eggs hatched
Lobatae	*Q. agrifolia*[1]	41 (6)	32 (5)ab	13 (1)	20 (5)	77 (28)	3 (1)	0.82 (0.05)	0.52 (0.08)
	Q. kelloggii[1]	57 (10)	60 (12)a	16 (4)	39 (8)	85 (28)	3 (1)	0.62 (0.11)	0.45 (0.12)
	Q. wislizeni[2]	31 (9)	37 (4)ab	15 (1)	23 (3)	120 (15)	5 (1)	0.86 (0.06)	0.77 (0.05)
Quercus	*Q. douglasii*	38 (3)	22 (5)b	11 (1)	21 (5)	52 (27)	2 (1)	0.76 (0.06)	0.59 (0.10)
	Q. engelmannii[1]	37 (8)	36 (2)ab	12 (3)	16 (5)	59 (16)	4 (1)	0.81 (0.05)	0.55 (0.02)
	Q. lobata	39 (4)	41 (4)ab	11 (1)	20 (2)	102 (25)	5 (1)	0.73 (0.05)	0.56 (0.06)
	Q. ilex	41 (5)	32 (6)ab	11 (3)	24 (8)	100 (25)	5 (1)	0.80 (0.03)	0.65 (0.04)
Protobalanus	*Q. chrysolepis*	40 (6)	38 (3)ab	11 (1)	24 (5)	116 (23)	5 (1)	0.74 (0.03)	0.59 (0.04)
Cerris	*Q. suber*[1]	37 (5)	30 (2)ab	15 (1)	15 (3)	75 (36)	5 (1)	0.81 (0.06)	0.62 (0.06)
–	*A. rhombifolia*	28 (5)	26 (6)b	NA	NA	9[4]	NA	0.33[4]	0.33[4]
	F	1.47	3.32	1.09	1.58	0.95	1.45	1.14	1.09
	d.f.	9,40	9,40	8,29	8,31	8,31	8,31	8,31	8,31
	P	0.19	0.004	0.40	0.17	0.49	0.22	0.22	0.40
	Mean of all spp.[3]	41 (2)	36 (2)	12 (1)	23 (2)	86 (9)	4 (0)	0.77 (0.02)	0.58 (0.03)

If ANOVA were significant, different letters after means indicate significant differences (Tukey's HSD: $P<0.05$); n = 5 beetles for each foliage species unless otherwise indicated.

[1] n = 4 for fecundity measures.

[2] n = 3 for fecundity measures.

[3] All species included except *A. rhombifolia*.

[4] n = 1, not included in ANOVA.

Table 3 Pearson's correlation coefficients (r) for adult longevity and female fecundity variables for no-choice adult *Agrilus auroguttatus* feeding tests on all oak species (n = 40). Male and female pairs that were not fecund were not tested. Units for all variables are listed in Table 2.

Variable	Male longevity	Days until fecund	Time fecund	Total fecundity	Daily oviposition	Proportion eggs melanized	Proportion eggs hatched
Female longevity	0.70**	0.20	0.79**	0.38*	−0.20	−0.41**	−0.16
Male longevity		0.36*	0.59**	0.24	−0.08	−0.56**	−0.41**
Time until fecund			−0.22	−0.37*	−0.02	−0.23	−0.14
Time fecund				0.58**	0.58**	−0.41**	−0.15
Total fecundity					0.60**	0.08	0.27
Daily oviposition						0.27	0.38*
Proportion eggs melanized							0.79**

*$P<0.05$; **$P<0.01$.

species of foliage adults fed upon, they could survive and oviposit on several non-larval host species. Similarly for *A. auroguttatus*, suitability of oak species for adults may not necessarily be an indicator of suitability for larvae. Chen et al. (2013) report a tendency for *A. auroguttatus* to prefer the foliage of *Q. kelloggii* over three other oak species.

Risk of *Agrilus auroguttatus* to California oaks

The host range of *A. auroguttatus* is likely limited by suitability of hosts for the larval rather than the adult life stage. Our data support field observations that red oaks are more suitable hosts for larvae than white oaks. Despite low survival after larvae were initially introduced to cut logs, some larvae survived to establish feeding galleries, and often reached the fourth instar, in some logs of all red oaks tested. Two species, *Q. agrifolia* and *Q. kelloggii*, are clearly suitable hosts for the beetle under natural conditions (Coleman et al., 2012b). *Q. wislizeni* is also a suitable host, but is only present at low density and at small diameters in the current range of *A. auroguttatus*, and so far has not been colonized.

It remains unclear from our results whether, in natural conditions, the remaining oaks would be preferred hosts for *A. auroguttatus* larvae. We observed that *A. auroguttatus* larvae may be able to feed upon *Q. suber*, *Q. lobata*, and *Q. douglasii* in the laboratory. However, field observations suggest that where white oaks co-occur with red oaks, the beetle colonizes the latter with much greater frequency and at higher densities than the former (Coleman & Seybold, 2011; Coleman et al., 2012b). Our tests were limited to cut logs because few oak species grow within the currently restricted range of *A. auroguttatus* in southern California. Further studies should examine factors that influence colonization and suitability of naturally infested live oaks, as well as the importance of site and climate conditions on the survival of *A. auroguttatus*.

Acknowledgments

We thank Lauren Walker, Mike Jones, Stacy Hishinuma (all UC-Davis, Department of Entomology), Grayland Walter, Shakeeb Hamud, Susan Schilling (all USDA Forest Service), the Cleveland National Forest for field and laboratory assistance, and Vanessa Lopez, Bud Mayfield, and two anonymous reviewers for helpful comments on an earlier version of the manuscript. We also thank Y. Chen (UC-Davis Department of Entomology) for sharing unpublished data on adult feeding. This study was supported by a Special Technology Development Program grant (#R5-2010-02) from the USDA Forest Service, Forest Health Protection and Research and Development; by the USDA Forest Service Northern and Pacific Southwest Research Stations; USDA Forest Service, Forest Health Protection-Pacific Southwest Region; and by the University of California-Davis.

References

Akers RC & Nielsen DG (1990) Reproductive biology of the bronze birch borer (Coleoptera: Buprestidae) on selected trees. Journal of Entomological Science 25: 196–203.

Ayres MP & Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262: 263–286.

Ball J & Simmons G (1986) The influence of host condition on post first instar development of the bronze birch borer, *Agrilus anxius* (Coleoptera: Buprestidae). Great Lakes Entomologist 19: 73–76.

Banno H & Yamagami A (1991) Life cycle and larval survival rate of the redspotted longicorn beetle, *Eupromus ruber* (Dalman) (Coleoptera: Cerambycidae). Applied Entomology and Zoology 26: 195–204.

Barter GW (1957) Studies of the bronze birch borer, *Agrilus anxius* Gory, in New Brunswick. Canadian Entomologist 89: 12–34.

Bentz BJ, Régnière J, Fettig CJ, Hansen EM, Hayes JL et al. (2010) Climate change and bark beetles of the western US and Canada: direct and indirect effects. BioScience 60: 602–613.

Box GE & Cox DR (1964) An analysis of transformations (with discussion). Journal of the Royal Statistical Society Series B 26: 211–246.

calfire.ca.gov (2013) Invasive forest pest found in Riverside County – fire and forest officials ask public's help to stop spread. Available at: http://calfire.ca.gov/communications/communications_newsreleases_GSOB_Riverside.php (accessed December 17, 2012).

Cárdenas AM & Gallardo P (2012) The effects of temperature on the preimaginal development of the Jewel beetle, *Coraebus florentinus* (Coleoptera: Buprestidae). European Journal of Entomology 109: 21–28.

Carnegie AJ & Bashford R (2012) Sirex woodwasp in Australia: current management strategies, research, and emerging issues. The Sirex Woodwasp and its Fungal Symbiont: Research and Management of a Worldwide Invasive Pest (ed. by B Slippers, P de Groot & MJ Wingfield), pp. 175–202. Springer, New York, NY, USA.

Chapman RN (1915) Observations on the life history of *Agrilus bilineatus*. Journal of Agricultural Research 3: 283–294.

Chen Y, Coleman TW, Jones MI, Flint ML & Seybold SJ (2013) Foliar nutrients explain goldspotted oak borer, *Agrilus auroguttatus*, adult feeding preference among four California oak species. Entomologia Experimentalis et Applicata 149: 57–66.

Coleman TW & Seybold SJ (2008) Previously unrecorded damage to oak, *Quercus* spp., in southern California by the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae). Pan-Pacific Entomologist 84: 288–300.

Coleman TW & Seybold SJ (2011) Collection history and comparison of the interactions of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with host oaks in southern California and southeastern Arizona. USA. Coleopterists' Bulletin 65: 93–108. doi:10.1649/072.065.0224.

Coleman TW, Lopez V, Rugman-Jones P, Stouthamer R, Seybold SJ et al. (2012a) Can the destruction of California's oak woodlands be prevented? Potential for biological control of the goldspotted oak borer, *Agrilus auroguttatus*. BioControl 57: 211–225.

Coleman TW, Graves AD, Hoddle M, Heath Z, Chen Y et al. (2012b) Forest stand composition and impacts associated with

Agrilus auroguttatus Schaeffer (Coleoptera: Buprestidae) and *Agrilus coxalis* Waterhouse in oak woodlands. Forest Ecology and Management 276: 104–117.

Connor EF (1988) Cohort and death assemblage estimates of survival rates and causes of mortality in *Brachys ovatus* (Weber) (Coleoptera: Buprestidae). American Midland Naturalist 120: 150–155.

Cornell HV & Hawkins BA (1995) Survival patterns and mortality sources of herbivorous insects: some demographic trends. American Naturalist 145: 563–593.

Duan JJ, Ulyshen MD, Bauer LS, Gould J & Van Driesche R (2010) Measuring the impact of biotic factors on populations of immature emerald ash borers (Coleoptera: Buprestidae). Environmental Entomology 39: 1513–1522.

Duan JJ, Oppel CB, Ulyshen MD, Bauer LS & Lelito JP (2011) Biology and life history of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae), a larval endoparasitoid of the emerald ash borer (Coleoptera: Buprestidae). Florida Entomologist 94: 933–940.

Flint ML, Jones MI, Coleman TW & Seybold SJ (2013) Goldspotted Oak Borer. University of California Statewide Integrated Pest Management Program, Oakland, California, Agriculture and Natural Resources Pest Notes, Publication 74163, Oakland, CA, USA. Available at: http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn74163.html (accessed September 30, 2012).

Grimble DG & Knight FB (1970) Life tables and mortality factors for *Saperda inornata* (Coleoptera: Cerambycidae). Annals of the Entomological Society of America 63: 1309–1319.

Haack RA & Acciavatti RE (1992) Twolined Chestnut Borer. USDA Forest Service, State and Private Forestry, Northeastern Area, Forest Insect and Disease Leaflet 168, Newtown Square, PA, USA.

Haack RA & Benjamin DM (1982) The biology and ecology of the twolined chestnut borer, *Agrilus bilineatus* (Coleoptera: Buprestidae), on oaks, *Quercus* spp., in Wisconsin. Canadian Entomologist 114: 385–396.

Haack RA, Jendek E, Liu H, Marchant KR, Petrice TR et al. (2002) The emerald ash borer: a new exotic pest in North America. Newsletter of the Michigan Entomological Society 47: 1–5.

Haavik LJ, Coleman TW, Flint ML, Venette RC & Seybold SJ (2012) *Agrilus auroguttatus* exit hole distribution on *Quercus agrifolia* boles and a sampling method to estimate their density on individual trees. Canadian Entomologist 144: 1–12.

Haavik LJ, Coleman TW, Flint ML, Venette RC & Seybold SJ (2013) *Agrilus auroguttatus* seasonal development within *Quercus agrifolia* in southern California. Annals of the Entomological Society of America 106: 189–197.

Hanks LM, Paine TD & Millar JG (1993) Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* (F.). Oecologia 95: 22–29.

Hishinuma S, Coleman TW, Flint ML & Seybold SJ (2011) Goldspotted Oak Borer Field Identification Guide. University of California Agriculture and Natural Resources Statewide Integrated Pest Management Program, Oakland, CA, USA.

Linit MJ (1985) Continuous laboratory culture of *Monochamus carolinensis* (Coleoptera: Cerambycidae) with notes on larval development. Annals of the Entomological Society of America 78: 212–213.

Logan JA & Powell JA (2001) Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). American Entomologist 47: 161–172.

Moraal LG & Hilszczanski J (2000) The oak buprestid beetle, *Agrilus biguttatus* (F.) (Col., Buprestidae), a recent factor in oak decline in Europe. Journal of Pest Science 73: 134–138.

Paine TD, Millar JG & Hanks LM (1995) Integrated program protects trees from eucalyptus longhorned borer. California Agriculture 49: 34–37.

R Development Core Team (2012) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabaglia RJ & Williams GL (2002) Two species of western North American *Hylesinus* Fabricius (Coleoptera: Scolytidae) new to the eastern United States. Proceedings of the Entomological Society of Washington 104: 1058–1060.

Scriber JM & Slansky FJ (1981) The nutritional ecology of immature insects. Annual Review of Entomology 26: 183–211.

Shapiro SS & Wilk MB (1965) An analysis of variance test for normality (complete samples). Biometrika 52: 591–611.

Shibata E (1987) Oviposition schedules, survivorship curves, and mortality factors within trees of two cerambycid beetles (Coleoptera: Cerambycidae), the Japanese pine sawyer, *Monochamus alternatus* Hope, and sugi bark borer, *Semanotus japonicus* Lacordaire. Researches on Population Ecology 29: 347–367.

Stuart JD & Sawyer JO (2001) Trees and Shrubs of California. University of California Press, Berkeley, CA, USA.

Venette RC, Kriticos DJ, Magarey RD, Koch FG, Baker RHA et al. (2010) Pest risk maps for invasive alien species: a roadmap for improvement. BioScience 60: 349–362.

Westcott RL (2005) A new species of *Chrysobothris* Eschscholtz from Oregon and Washington, with notes on other Buprestidae (Coleoptera) occuring in the United States and Canada. Zootaxa 1044: 1–15.

Yang S, Duan JJ, Watt T, Abell KJ & Van Driesche RG (2012) Responses of an idiobiont ectoparasitoid, *Spathius galinae* (Hymenoptera: Braconidae), to host larvae parasitized by the koinobiont endoparasitoid *Tetrastichus planipennisi* (Hymenoptera: Eulophidae): implications for biological control of emerald ash borer (Coleoptera: Buprestidae). Environmental Entomology 41: 925–932.

Yemshanov DD, McKenney W, Pedlar JH, Koch FH & Cook D (2009) Towards and integrated approach to modelling the risks and impacts of invasive forest species. Environmental Reviews 17: 163–178.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Site information and sample sizes of oak species (n) collected for *Agrilus auroguttatus* egg and larval insertions in 2010 and 2011 (NF = National Forest).

Table S2 Site information and sample sizes (n) of oak and alder foliage collected for the adult *Agrilus auroguttatus* no-choice feeding test in 2011 (NF = National Forest).