Agrilus auroguttatus exit hole distributions on *Quercus agrifolia* boles and a sampling method to estimate their density on individual trees

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Abstract—In recent decades, invasive phloem and wood borers have become important pests in North America. To aid tree sampling and survey efforts for the newly introduced goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), we examined spatial patterns of exit holes on the boles (trunks) of 58 coast live oak, *Quercus agrifolia* Née (Fagaceae), trees at five sites in San Diego County, southern California, United States of America. *Agrilus auroguttatus* exit hole densities were greater at the root collar than at mid-boles (6.1 m above ground). Dispersion patterns of exit holes on lower boles (≤ 1.52 m) were random for trees with low exit hole densities and aggregated for trees with high exit hole densities. The mean exit hole density measured from three randomly chosen quadrats (0.09 m^2) provided a statistically reliable estimate of the true mean exit hole density on the lower bole, with <25% error from the true mean. For future sampling and survey efforts in southern California oak forests and woodlands, exit hole counts within a 0.09 m^2 quadrat could be made at any three locations on lower *Q. agrifolia* boles to accurately estimate *A. auroguttatus* exit hole densities at the individual tree level.

Résumé—Au cours des dernières décennies en Amérique du Nord, des insectes envahissants perceurs du phloème et du bois sont devenus d'importants ravageurs. Afin de faciliter les travaux d'échantillonnage et d'inventaire des arbres en rapport avec l'agrile du chêne *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) récemment introduit, nous examinons la répartition spatiale des trous d'envol sur les troncs de 58 chênes verts côtiers de Californie, *Quercus agrifolia* Née (Fagaceae), dans cinq sites du comté de San Diego, dans le sud de la Californie, États-Unis d'Amérique. Les densités des trous d'envol d'*Agrilus auroguttatus* sont plus grandes au niveau du collet qu'à la mi-hauteur (6,1 m au-dessus du sol) du tronc. Les patrons de répartition des trous d'envol sur la partie inférieure du tronc ($\leq 1{,}52$ m) sont aléatoires chez les arbres à faible densité de trous d'envol et contagieux chez les arbres à forte densité de trous d'envol. La densité moyenne des trous d'envol mesurée dans trois quadrats (0,09 m^2) choisis au hasard fournit une estimation statistiquement fiable de la véritable densité moyenne des trous d'envol sur le tronc inférieur avec <25% d'erreur par rapport à la moyenne véritable. Dans les travaux futurs d'échantillonnage et d'inventaire dans les forêts et les terrains boisés du sud de la Californie, on pourrait faire le dénombrement des trous d'envol dans un quadrat de 0,09 m^2 à n'importe quels de trois sites sur des troncs inférieurs de *Q. agrifolia* afin d'estimer avec précision les densités des trous d'envols d'*A. auroguttatus* à l'échelle des arbres individuels.

Received 30 January 2012. Accepted 12 March 2012.

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doi:10.4039/tce.2012.68.

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https://doi.org/10.4039/tce.2012.68 Published online by Cambridge University Press

Introduction

Detections of nonindigenous phloem-boring and wood-boring forest insects entering the United States and Canada have increased in recent decades (Mattson *et al*. 1994; Aukema *et al*. 2010). Frequently, little is known about the natural history of invading wood borers because the species are not of economic concern within their native ranges. Cases where indigenous insects were found outside their native range in a new region feeding on novel host species have also become of recent concern (Rabaglia and Williams 2002; LaBonte *et al*. 2005; Dodds *et al*. 2010; Coleman and Seybold 2011). Survey efforts are important components of management programs for these invasive species to detect new infestations, as well as to monitor size and rate of increase of currently infested areas. Development of efficient and reliable survey tools increases the land area than can be effectively monitored for changes in invasive borer populations.

The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is a poorly known borer that was recently detected in southern California, United States of America (Coleman and Seybold 2008a, 2008b, 2011). Genetic evidence suggests that the source for the invasive population is southeastern Arizona, United States of America, where the species has been collected throughout the 20th century (Coleman and Seybold 2011; Coleman *et al*. 2012b). Its native host species appears to be Emory oak, *Quercus emoryi* Torrey, and silverleaf oak, *Q. hypoleucoides* A. Camus (Fagaceae) (Coleman and Seybold 2011). *Agrilus auroguttatus* likely arrived in southern California years before its first collection record there in 2004 (Westcott 2005), perhaps by way of infested firewood from southeastern Arizona (Coleman and Seybold 2008b; Coleman *et al*. 2011). This was not likely a range expansion, but a human-mediated introduction, because 600–700 km of the Sonoran Desert separate this beetle's native range in southeastern Arizona from its current introduced range in southern California (Coleman and Seybold 2011). Annual aerial surveys in San Diego County indicate that *A. auroguttatus* has been associated with mortality of >21 000 coast live oaks, *Q. agrifolia* Née, and California black oaks, *Q. kelloggii* Newberry, since 2008 (Coleman and Seybold 2011).

Determination of borer density within trees is often difficult due to cryptic larval feeding in host phloem, cambium, and/or sapwood tissues (Nielsen 1981). *Agrilus auroguttatus* larvae feed mainly at the phloem/sapwood interface (Coleman and Seybold 2008a), which can be 4–7 cm deep from the outer bark surface in *Q. agrifolia*. Trees containing high densities of larvae and adult emergence holes are often the largest individuals on the landscape (Coleman *et al*. 2012a), ranging from 50 to 150 cm in diameter at breast height (DBH, at 1.37 m from the ground) and may be difficult or too costly to fell for determination of within-tree larval distributions. Eggs are difficult to locate and identify in the field, presumably due to their small size and cryptic placement by females in bark cracks (Coleman and Seybold 2008a). Emerging adults create D-shaped exit holes ~4 mm in width (Hishinuma *et al*. 2011) that are distinct from exit holes of other native Buprestidae and Cerambycidae (Coleoptera) species that develop within *Q. agrifolia* tree boles in southern California, and produce round, oblong or crescent-shaped exit holes 5–13 mm in width (Brown and Eads 1965; Swiecki and Bernhardt 2006). Prior to the introduction of *A. auroguttatus*, we could not find any records of economically or ecologically important *Agrilus* species that produce a D-shaped exit hole and attack the main bole of southern California oaks (Fisher 1928; Brown and Eads 1965; Furniss and Carolin 1977; summarised in Coleman and Seybold 2008b). Exit hole counts are a nondestructive, relatively simple survey method. A single evaluation of exit hole density reflects the cumulative number of adults produced by a tree at the time a survey is conducted. The change in exit hole densities between two evaluations indicates the number of adults that emerged over the time interval between evaluations.

Monitoring and survey efforts for infestations of other wood borers often focus on tree health-rating systems that incorporate external symptoms such as crown dieback and density of borer exit holes on tree boles to evaluate cumulative and current infestation levels (Fierke *et al*. 2005; Smitley *et al*. 2008). These health-rating systems categorise levels of borer-related damage on an individual tree basis and can also be extrapolated to the stand level. Emphasis on borer infestation and population size within individual trees is important because spatial and temporal patterns

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of borer infestations can vary widely within stands, where many trees remain healthy while others become severely infested (Nielsen 1981; Fierke *et al*. 2007). A health-rating system has been developed for *A. auroguttatus* that incorporates crown dieback, occurrence of bark staining (a symptom of dying vascular tissue), exit hole counts on lower boles, and presence/absence of woodpecker foraging (Coleman *et al.* 2011; Hishinuma *et al*. 2011). Specific spatial and height patterns of *A. auroguttatus* exit holes on host tree boles have not been quantified, although emergence appears to occur with highest frequency at breast height and near the root collar and rarely from small diameter branches ($<$12.7 cm; T.W. Coleman, personal observation). Complete counts of all exit holes on lower boles can require a substantial amount of survey time for large trees with high emergence densities. Development of a sampling protocol that provides a reliable estimate of the emerged population of adults from lower boles and requires sampling only a small amount of bark surface area would be helpful to estimate population sizes at the tree level for management efforts as well as for studies of basic natural history, ecology, and population dynamics.

Our objectives were to identify trends in *A. auroguttatus* emergence hole densities with bole height on *Q. agrifolia*, encompassing the root collar to mid-bole and to search for differences in these trends among trees of various apparent infestation levels (*i.e.*, according to crown dieback condition). We also investigated detailed spatial patterns of *A. auroguttatus* exit holes on lower ($\leq$1.52 m) *Q. agrifolia* tree boles where sampling was easier to determine (1) spatial dispersion (*i.e.*, aggregated, uniform, or random) and whether dispersion varied among trees of apparently different infestation levels according to crown dieback condition, as well as (2) variability in exit hole density by bole aspect and height. We predicted that exit hole densities would be greatest on lower boles compared with mid-boles and on the warmer south-facing aspect of boles – trends observed among other *Agrilus* species (Akers and Nielsen 1990; Vansteenkiste *et al*. 2004; Timms *et al*. 2006). We also sought to develop a reliable and efficient sampling method that would reduce labour efforts for surveying exit holes on severely infested trees by selecting samples from several 0.09 m^2 quadrats to estimate true mean lower bole exit hole density.

Materials and methods

Study sites

We sampled *Q. agrifolia* from five oak woodland or forest sites within the current zone of *A. auroguttatus* infestation in San Diego County, California, at ~ 1200 m in elevation. We selected sites that included *Q. agrifolia* of various low, intermediate, and high degrees of crown dieback to search for differences in the relationship between exit hole density among five sampling heights that ranged from root collar to mid-bole on trees at various stages of infestation. Pine Creek Trailhead ($n = 10$ trees; 32.83681°N, 116.54264°W), Noble Canyon Trailhead ($n = 20$ trees; 32.84967°N, 116.52241°W), and Cottonwood ($n = 5$ trees; 32.70715°N, 116.49099°W), all in the Descanso Ranger District, Cleveland National Forest, California were all open-canopy *Q. agrifolia* woodlands that contained trees of various crown dieback categories that we used for counts of exit holes at five different bole heights.

We chose separate sites that contained dead trees and those with severe and intermediate levels of crown dieback for intensive lower bole sampling because we expected that these trees would demand a large amount of survey time. They would likely contain high exit hole densities and would require substantial sampling effort to quantify the cumulative population of emerged adults if we counted all emergence holes on the lower bole. William Heise County Park, Julian, California ($n = 12$ trees; 33.04259°N, 116.58429°W) and Roberts' Ranch, Descanso Ranger District, Cleveland National Forest, California ($n = 11$ trees; 32.82878°N, 116.62296°W) were both severely infested sites that we utilised for intensive sampling of lower boles. William Heise County Park was a closed-canopy mixed oak-pine forest that included *Q. agrifolia*, *Quercus kelloggii*, *Quercus chrysolepis* Leibmann, *Pinus coulteri* Lambert ex D. Don (Pinaceae) and *Pinus jeffreyi* Balfour, whereas Roberts' Ranch was an open-canopy oak woodland of *Q. agrifolia* and *Quercus engelmannii* Greene.

Bole height sampling

We constructed a square sampling window of cardboard cut to the quadrat size of 1 ft_2 and

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sampled exit holes on 35 *Q. agrifolia* trees from Pine Creek Trailhead, Noble Canyon Trailhead and Cottonwood at five different heights along main boles: 0 m (root collar), 1.5 m (5 ft, just above breast height), 3.0 m (10 ft), 4.6 m (15 ft), and 6.1 m (20 ft). We sampled two quadrats at each height on the north-facing and south-facing bole aspects, combining them for a mean value at each height. Tree selection for height sampling was limited by trees that were accessible safely by ladder. We also measured height of trees with a clinometer at 20 m from the base of each bole. Tree size and height were similar among trees used for bole height sampling (see Results: Study sites).

Intensive lower bole sampling

With the same sampling quadrat described above, we quantified *A. auroguttatus* exit hole densities on the entire surface area of each bole beneath 1.52 m for a total of 642 sample quadrats on 23 *Q. agrifolia* from Roberts' Ranch and William Heise County Park. We did not sample sections of bole that included low branches, were covered by rocks, or when the final sampling column was not large enough to fit inside the quadrat window. Tree size was similar among trees used for intensive lower bole sampling (see Results: Study sites).

Data analyses

We conducted all data analyses with the statistical package R (R Development Core Team 2011) except for repeated measures analyses of variance (ANOVA), which we conducted with SigmaPlot® (Systat Software Inc., San Jose, California, United States of America). For all general linear models, model checks included examination of influence points as well as standardised residual and normal probability plots. If model assumptions of normality or homogeneity of variance were violated, we transformed data by square or square root after adding a constant of 0.5 to each response value. We used two-way ANOVA to examine variation in tree size (DBH) and tree height by site and crown dieback category for both portions of the study. We assigned statistical significance at $P < 0.05$ and all error terms are presented as one standard error (SE) from the mean.

Bole height analyses

To determine the relationship between mean exit hole density and bole height at the five heights sampled by crown dieback category, we used analysis of covariance (ANCOVA). We used a two-way ANOVA to test whether exit hole density differed at the root collar compared with mid-bole (6.1 m) as well as by crown dieback condition and the interaction between these two main effects. For this data set, even the transformed data were nonnormal, so we performed the ANOVA on ranks and then used Holm's means separation test on each main effect.

Lower bole analyses

On trees selected for intensive sampling on lower boles, we first compared mean exit hole density per quadrat among crown dieback conditions and site and the interaction between these two factors (two-way ANOVA). We then used ANOVA to examine variability in mean exit hole density per quadrat by bole aspect and simple linear regressions to examine variability in mean exit hole density by height (0–1.52 m) on lower boles.

To determine spatial dispersion patterns of exit holes on lower boles we calculated mean crowding (m^*) per tree according to Lloyd (1967):

$$m^* = m + (\delta^2/m) - 1$$

where we substituted the sample variance for δ^2, the true variance, and the sample mean for m, the true mean. We then applied linear regression to m^* values with m as the independent variable, where each coordinate pair represented an individual tree, modelled separately for each crown dieback category. We tested to see if the estimated slope parameter (b) of each regression equation was significantly different from 1. If $b = 1$, dispersion of exit holes was random; if $b < 1$, dispersion of exit holes was uniform; and if $b > 1$, dispersion of exit holes was aggregated (Iwao 1968; Davis 1994).

We used repeated measures ANOVA to compare the true mean exit hole density of all quadrats from each tree against the mean density within randomly selected quadrat(s) from the same tree. We repeated this random selection of quadrat(s) five times for each tree within each crown dieback category and sample size of quadrats to calculate mean exit hole density per quadrat for sample sizes of: one, two, three, four, and five quadrats. This produced a total

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of 14 models (quadrat sample size of one was not modelled for the 25–50% dieback category because data could not be transformed to meet model assumptions) for comparisons of sampling reliability and optimisation among seven trees for the 25–50% dieback category, and eight trees each for the >50% dieback and dead crown categories. In addition to hypothesis testing of randomly selected samples against the true mean for a measure of reliability, this method allowed for examination of the root mean square error (RMSE) term, which can be compared among models to search for an optimal sample size (Crook *et al*. 2007). Mean square error (MSE) was obtained from the repeated measures ANOVA and reflects the squared deviation of exit hole density on each tree in each repeated sampling from the mean exit hole density estimated from all trees and repeated samplings. The square root of the MSE, the RMSE is expressed in the same units as the estimator (John 1971) and we present the RMSE for each model as a percentage of the true mean exit hole density for each crown dieback category (%RMSE). Smaller RMSE values and thus smaller %RMSEs indicate better estimators.

Results

Study sites

Mean DBH of trees used for bole height sampling did not vary significantly by site or dieback category ($P > 0.05$) with an overall mean of 79.7 ± 4.8 cm. Mean height of these trees did not vary by site or dieback category ($P > 0.10$) with an overall mean of 13.1 ± 0.04 m. Mean DBH of trees used for lower bole sampling did not vary significantly by site or dieback category ($P > 0.10$) with an overall mean of 51.5 ± 2.7 cm.

Exit holes by bole height

The interaction between crown dieback category and bole height was significant (Fig. 1, $F_{4,15} = 4.16$, $P = 0.02$), where *A. auroguttatus* exit hole density decreased with increasing bole height across the five heights sampled in *Q. agrifolia* with dead crowns and those with >50% dieback, yet remained constant with bole height in *Q. agrifolia* with <50% dieback. Exit hole density was significantly different between root collar and mid-bole across all dieback categories (6.1 m, Fig. 2, $F_{1,64} = 8.07$, $P < 0.01$). Exit hole density also varied significantly among crown dieback categories at both heights where trees with dead crowns contained greater densities of exit holes than those with <50% dieback and those with >50% dieback contained greater densities than those with <25% dieback (Fig. 2, $F_{4,64} = 18.31$, $P < 0.01$). The interaction between crown dieback category and bole height was not significant and so we removed it from the model.

Fig. 1. Mean (±SE) *Agrilus auroguttatus* exit hole density by *Quercus agrifolia* crown dieback category (key upper right) and bole height. Sample sizes were: dead = 8, >50% dieback = 6, 25–50% dieback = 7, 10–25% dieback = 8, <10% dieback = 6.

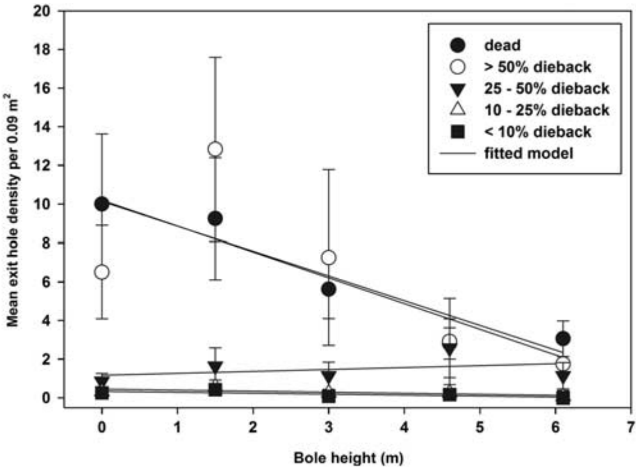

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Fig. 2. Mean (±SE) *Agrilus auroguttatus* exit hole density at the root collar compared to mid-bole (6.1 m) on *Quercus agrifolia* by crown dieback category (key upper right). Upper and lowercase letters represent significant differences due to height and crown dieback category according to Holm's means separations test, respectively. Sample sizes are the same as in Figure 1.

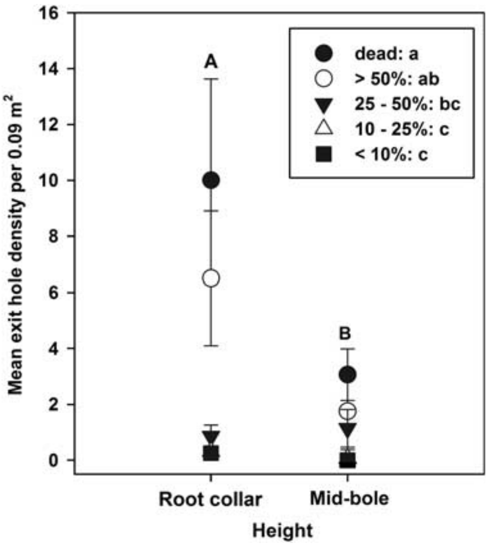
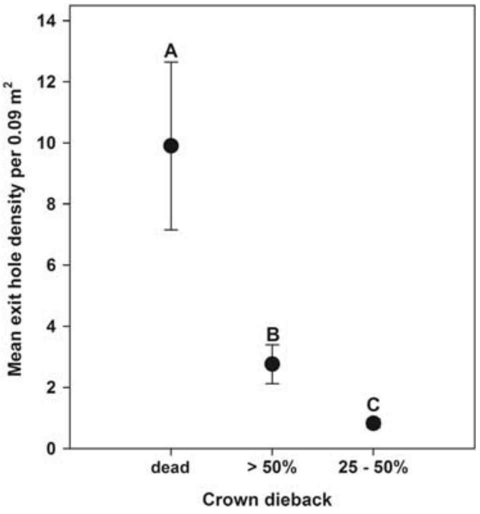


Fig. 3. Mean (±SE) *Agrilus auroguttatus* exit hole density on *Quercus agrifolia* lower boles by crown dieback categories. Sample sizes were: dead = 8, >50% dieback = 8, 25–25% dieback = 7. Different letters above means represent statistical differences according to Holm's means separations test.



Exit holes on lower boles

Cumulative exit hole density of *A. auroguttatus* on lower *Q. agrifolia* boles ranged from 0.25 to 25.79 exit holes per 0.09 m^2, with an overall mean among all trees sampled of 4.49 ± 1.21 exit holes per 0.09 m^2. Variability in exit hole density was greater among and within dead individuals than living trees. Mean density ranged from 1.13 to 25.79 and SEs ranged from 0.21 to 2.28 exit holes per 0.09 m^2 among dead trees. Means ranged from only 0.25 to 6.48 and SEs ranged from 0.25 to 0.70 exit holes per 0.09 m^2 among living trees. Mean exit hole densities per quadrat did not vary by site, although they varied significantly by crown dieback category where densities were greatest on dead trees, intermediate on trees with >50% dieback and least on trees with 25–50% dieback (Fig. 3, $F_{2,17} = 11.33$, $P < 0.01$). Exit holes on lower boles with completely dead crowns and >50% dieback were mildly, but significantly aggregated since $b > 1$ for each regression, respectively (Fig. 4A, $b = 1.50 \pm 0.14$, $t = 3.56$, $P < 0.01$; Fig. 4B, $b = 1.18 \pm 0.05$, $t = 3.42$, $P < 0.05$). Exit holes on lower *Q. agrifolia* boles with 25–50% crown dieback were randomly dispersed since the slope parameter (*b*) of the regression between *m* and *m** was not statistically different from one (Fig. 4C, $b = -0.20 \pm 0.6$, $t = 2.01$, $P > 0.05$). On lower boles, exit hole density did not vary significantly by height (25–50% dieback: $F_{1,32} = 0.65$, $P = 0.43$; >50% dieback: $F_{1,38} = 0.34$, $P = 0.56$; dead: $F_{1,38} = 0.15$, $P = 0.70$) or bole aspect (25–50% dieback: $F_{3,24} = 0.64$, $P = 0.60$; >50% dieback: $F_{7,41} = 0.74$, $P = 0.64$; dead: $F_{6,36} = 0.28$, $P = 0.94$) among all crown dieback categories (not shown).

All 14 repeated measures ANOVA were unable to reject the null hypothesis that the mean of the five randomly selected quadrat(s) tested differed significantly from one another or from the true mean exit hole density (Table 1). RMSE as a percentage of the true mean for each dieback category was least for models that tested the mean of either four or five randomly selected quadrats. %RMSEs were generally greatest for 25–50% dieback category models, intermediate for >50% dieback category models and least for dead crown models. For all crown dieback

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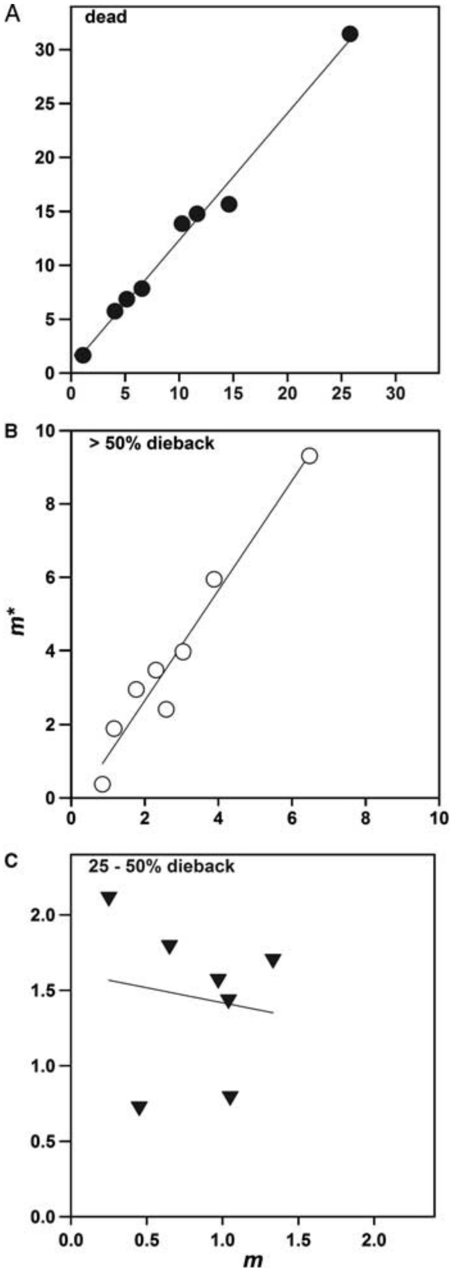
Fig. 4. Regression of sample means (m) versus mean crowding (m^*) to identify spatial dispersion of *Agrilus auroguttatus* exit holes on lower *Quercus agrifolia* boles of varying crown dieback categories. Dispersion of exit holes was aggregated for (A) and (B) since the slope parameter (b) of their respective plotted equations, $m^* = 1.12m + 0.55$ and $m^* = 1.50\,m - 0.34$, was significantly >1 ($P < 0.05$). Dispersion of exit holes was random for (C) since the slope of the plotted equation, $m^* = 1.62 - 0.2\,\mathrm{m}$, was not significantly different from 1 ($P > 0.05$).



categories, when quadrat sample size increased from two to three, %RMSE was reduced by 10–12%, yet when quadrat sample size increased from three to four or five, %RMSE was not reduced by more than 5%.

Discussion

Exit hole densities

The overall mean of *A. auroguttatus* cumulative emergence hole density observed in this study (4.49 ± 1.21 exit holes per $0.09\,\mathrm{m}^2$, range = 0.25–25.79 exit holes per $0.09\,\mathrm{m}^2$) was generally consistent with that reported for both native and exotic *Agrilus* species on their preferred host species in North America. At heavily infested sites, the range of exotic emerald ash borer, *A. planipennis* Fairmaire, densities (17–170 exit holes per m^2 or 1.53–15.30 exit holes per $0.09\,\mathrm{m}^2$) on white ash, *Fraxinus americana* Linnaeus, and green ash, *Fraxinus. pennsylvanica* Marshall (Oleaceae) was smaller than that of *A. auroguttatus*, although the overall mean (89 exit holes per m^2 or 8.01 exit holes per $0.09\,\mathrm{m}^2$) was greater (McCullough and Siegert 2007). On dying northern red oak, *Quercus rubra* Linnaeus, and black oak, *Quercusa velutina* Lamarck, native two-lined chestnut borer, *Agrilus bilineatus* (Weber), density ranged from 17 to 138 exit holes per m^2 (1.53–12.42 exit holes per $0.09\,\mathrm{m}^2$) (Haack and Benjamin 1982). Native bronze birch borer, *Agrilus anxius* Gory, densities ranged from 54 to 251 exit holes per m^2 (4.86–22.59 exit holes per $0.09\,\mathrm{m}^2$) on *Betula pendula* Roth (Betulaceae) (Akers and Nielsen 1990).

Exit hole trends with bole height

Adult emergence densities from the lower bole likely intensified as trees neared mortality and populations of emerging adults were variable with bole height in trees at less advanced stages of infestation (Fig. 1). Studies of other *Agrilus* species often compared density on the lower bole to that in the upper bole or branches of live trees and found that exit holes and/or larval densities were greater on the lower bole (main bole versus branches in Ball and Simmons 1980; 0 m versus 4 m in Loerch and Cameron 1984; below and above 10 m in Vansteenkiste *et al.* 2004). For *A. anxius* this relationship was no longer significant when densities were

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Table 1. Mean *Agrilus auroguttatus* exit hole density (±SE) estimated from one to five quadrats on *Quercus agrifolia* with different degrees of dieback.

	Number of randomly selected sampling quadrats				
	1*	2	3	4	5
25–50% dieback					
True mean		0.82 (0.15)[†]	0.82 (0.15)	0.82 (0.15)	0.82 (0.15)
Draw 1		1.00 (0.39)	1.00 (0.27)	0.57 (0.16)	0.66 (0.16)
Draw 2		0.71 (0.34)	0.90 (0.23)	0.64 (0.19)	0.94 (0.09)
Draw 3		1.00 (0.31)	0.95 (0.33)	0.68 (0.20)	1.17 (0.37)
Draw 4		1.36 (0.28)	0.86 (0.25)	0.82 (0.18)	0.91 (0.27)
Draw 5		0.86 (0.34)	0.48 (0.25)	0.86 (0.27)	1.00 (0.29)
df		6	6	6	6
F		0.564	1.054	0.646	0.682
P		0.727	0.405	0.647	0.641
%RMSE[‡]		34	22	17	19
>50% dieback					
True mean	2.76 (0.64)	2.76 (0.64)	2.76 (0.64)	2.76 (0.64)	2.76 (0.64)
Draw 1	1.50 (0.33)	4.13 (1.75)	2.08 (0.63)	4.56 (1.60)	2.03 (0.43)
Draw 2	4.63 (1.98)	3.81 (0.93)	3.33 (0.88)	2.59 (0.98)	2.78 (0.86)
Draw 3	2.63 (1.24)	2.25 (0.59)	1.83 (0.26)	2.53 (0.76)	3.13 (1.00)
Draw 4	3.75 (1.69)	2.94 (0.92)	2.08 (0.81)	3.59 (1.50)	3.50 (0.91)
Draw 5	2.63 (0.92)	2.25 (0.53)	3.61 (1.40)	3.63 (1.21)	2.75 (0.57)
df	7	7	7	7	7
F	1.117	0.798	2.512	1.565	1.704
P	0.369	0.558	0.082	0.196	0.160
%RMSE	57	31	21	23	16
Dead					
True mean	9.90 (2.75)	9.90 (2.75)	9.90 (2.75)	9.90 (2.75)	9.90 (2.75)
Draw 1	8.88 (2.75)	10.31 (2.62)	9.33 (2.95)	10.25 (2.77)	10.60 (4.05)
Draw 2	13.00 (4.00)	10.94 (4.42)	7.88 (1.75)	11.19 (2.58)	10.65 (3.23)
Draw 3	9.38 (3.24)	6.94 (1.76)	9.00 (2.31)	10.00 (3.77)	9.33 (2.30)
Draw 4	10.00 (3.80)	10.00 (2.60)	9.50 (2.99)	10.47 (2.55)	8.60 (1.77)
Draw 5	6.50 (1.84)	11.69 (3.40)	11.58 (3.87)	10.72 (3.47)	9.68 (3.00)
df	7	7	7	7	7
F	1.079	0.720	0.874	0.708	0.209
P	0.389	0.613	0.508	0.622	0.956
%RMSE	31	25	14	12	18

Results are presented for each of five independent random draws. Statistics are the results of repeated measures ANOVAs testing the consistency of the quadrat sample size over the draws and the true mean.

[*] Data transformation for one quadrat from trees with 25–50% dieback did not meet normality assumptions and so was not tested.

[†] Untransformed means are reported (±SE), although for models all data were square root transformed after adding 0.5 to original values.

[‡] RMSE presented as a percentage of the true mean exit hole density per quadrat among all trees sampled for each crown dieback category tested again excluding true means from the model.

ANOVAs, analyses of variance; RMSE, root mean square error.

adjusted according to available bark surface area (Loerch and Cameron 1984). *Agrilus auroguttatus* exit hole densities were greater at the root collar than at mid-bole (6.1 m, Fig. 2), although we did not adjust densities by available bark surface area. Since clear differences in exit hole densities on lower boles emerged according to crown health (*i.e.*, crown dieback category, Fig. 3), future sampling efforts could be focused on this portion of the bole to detect differences in the size of the

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emerged population of *A. auroguttatus* among crown dieback categories.

Small populations of emerging *A. auroguttatus* from trees with <50% crown dieback were consistent with Ball and Simmons' (1980) observations of low *A. anxius* numbers emerging from trees with only moderate levels of crown dieback. Dying phloem and cambium tissue has been noted in hosts following complete *A. anxius* development (Ball and Simmons 1980), although larvae cannot survive in dead phloem (Balch and Prebble 1940). *Agrilus auroguttatus* exit hole density on *Q. agrifolia* lower boles increased linearly with increasing proportion of dying phloem and cambium tissue (based on the personal observations of L.J.H.), implying that dying vascular tissue may also be a result of development to adulthood in this species. Haack and Benjamin (1982) noticed differences in life history characteristics among *A. bilineatus* larvae developing near the crown compared with those within the lower bole in *Q. rubra* and *Q. velutina*. *Agrilus bilineatus* larvae in upper boles left the cambial region to pupate near the outer bark earlier in the season than those in lower boles, consistent with movement of cambial death beginning at the crown and progressing downwards. Prepupae were also larger and more of them completed development in lower compared with upper boles (Haack and Benjamin 1982). If the same trend in cambial death beginning in the upper bole and moving downwards is true for *Q. agrifolia*, then a similar phenomenon may be influencing greater densities of *A. auroguttatus* in lower compared with mid-boles. This may be the case when trees are nearing mortality (*i.e.*, >50% dieback), such that *A. auroguttatus* densities increase in the lower bole because cambial death prevents development to adulthood above the lower bole.

Exit hole patterns on lower boles

Aggregated dispersion patterns such as those exhibited by exit holes on *Q. agrifolia* with dead crowns and those with >50% dieback, are common among insects at high population levels and may be indicative of oviposition patterns or food preference (Lloyd 1967; Davis 1994). *Agrilus auroguttatus* females oviposit singly or in small clumps under laboratory conditions (based on the personal observations of L.J.H.), larvae create meandering feeding galleries that may wander far from initial oviposition sites (based on the personal observations of T.W.C.) and spatial variability in larval feeding habitat suitability is unknown. Aggregated patterns observed in this study may simply be a result of accumulated adult emergence on the lower bole over several successive *A. auroguttatus* generations. Other *Agrilus* species have been found more frequently on the sunnier southern aspects of tree boles (Akers and Nielsen 1990; Vansteenkiste *et al.* 2004; Timms *et al.* 2006), a trend that we did not observe for *A. auroguttatus*. The open canopies of southern California oak woodlands may provide adequate sun exposure to all aspects of *Q. agrifolia* boles compared with closed-canopy forests with limited light penetration in northeastern North America or northern Europe where some of those studies were conducted. Sunny exposures could be chosen by *A. auroguttatus* females as oviposition sites, although we were unable to identify any neonate attacks in this study. Furthermore, exit hole distributions may not be an indicator of spatial dispersion at other life stages. Shibata (1984) found that dispersion patterns of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) oviposition scars and larvae differed from those of exit holes and larval mines, suggesting that competition for space and/or resources was not consistent among life stages.

Despite aggregation of exit holes among trees with high *A. auroguttatus* cumulative emergence densities, randomly selected quadrat(s) from anywhere on lower boles (≤ 1.52 m) were statistically reliable estimators of true mean exit hole densities on the lower bole (Table 1). Estimator error as a function of the true mean (%RMSE) tended to decrease as the sample size of randomly selected quadrats increased, although a sample size of three produced error terms <25% for all three crown dieback categories. A 25% error in sampling has been reported as acceptable for other phytophagous insect sampling plans (Church and Strickland 1954; Southwood 1978; Crook *et al.* 2007). The %RMSE did not drop appreciably (>5%) if four or five quadrats were selected rather than three. We suggest that an optimal number of three quadrats sampled per tree for any *Q. agrifolia* tree exhibiting >25% crown dieback would provide adequate estimates of exit hole densities

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at the individual tree level and reduce labour effort during future sampling. This estimate may also provide a reasonable value for the density of exit holes up to 6 m above ground for trees with $<50\%$ dieback. For dead trees or trees with $>50\%$ dieback, a correction factor would need to be applied to estimate exit hole density up to 6 m above ground.

Conclusions

We found that *A. auroguttatus* exit hole densities on a preferred host in southern California, *Q. agrifolia*, were generally consistent with those reported for other native and exotic *Agrilus* species in North America. *Agrilus auroguttatus* exit hole density was greater at the root collar than at mid-bole (6.1 m) and the lower bole (≤ 1.52 m) proved to be an adequate portion of the stem for focus of sampling efforts. Even though exit hole spatial dispersion patterns were not consistent among trees with differing levels of crown health, the mean exit hole density from three randomly chosen quadrats (0.09 m^2) on the lower bole provided a statistically reliable estimate of the true mean exit hole density ($<25\%$ error) for all *Q. agrifolia* trees tested. These results imply that for future sampling and surveys of emergence densities, exit hole counts within a 0.09 m^2 quadrat could be made at any three locations on the lower bole of *Q. agrifolia* with $>25\%$ crown dieback in southern California oak forests or woodlands to accurately estimate cumulative emerging populations of *A. auroguttatus* at the individual tree level. Application of a similar sampling method for other borer species may be possible, but should follow a careful examination of exit hole spatial dispersion patterns and trends in exit hole densities with bole height.

Acknowledgements

Authors thank Mike Jones (University of California-Davis, Department of Entomology) and Grayland Walter (United States Department of Agriculture Forest Service) for field assistance as well as T.J. Kring, J.F. Negrón and two anonymous reviewers for helpful comments on an earlier version of the manuscript. This work was supported by a Special Technology Development Program grant (#R5-2010–02) from the United States Department of Agriculture Forest Service, Forest Health Protection, Region 5, by the United States Department of Agriculture Forest Service Northern and Pacific Southwest Research Stations and by the University of California, Davis.

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