Agrilus auroguttatus (Coleoptera: Buprestidae) Seasonal Development Within *Quercus agrifolia* (Fagales: Fagaceae) in Southern California

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ABSTRACT We investigated seasonal development of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), and physical conditions of the phloem within a preferred host species, coast live oak, *Quercus agrifolia* Née. We sampled infested trees on a monthly basis at two sites in southern California throughout 2011. Measurements of an exposed portion of the head capsule, the peristoma, indicated that there were four larval instars. Pupae and teneral or mature adults were found within trees from April through August. Adults were captured in flight between May and mid-October, with peak flight from July through August. Within-tree *A. auroguttatus* prepupal mortality did not differ between sites and increased significantly from 3 ± 3% in January to 36 ± 9% in March (mean ± SE). Prepupae were present in trees throughout most of the year, which made it difficult to determine generation time; it was likely 1 yr for the majority of individuals, and possibly longer or shorter than 1 yr for others. Seasonal *A. auroguttatus* development, according to within-tree development and adult trap catch, was apparently 2 mo ahead at one site, which had a greater past and current level of *A. auroguttatus* infestation compared with the other. There was also evidence at the more severely infested site that within-tree *A. auroguttatus* population densities were positively related to proportion of dying phloem tissue. This suggested that the level of current infestation affected host tree condition, or that dying tissue was more suitable for larval development.

KEY WORDS invasive species, phloem and wood borer, larval mortality, phloem habitat

In 2008, the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), was linked to oak mortality in San Diego County, CA (Coleman and Seybold 2008). By 2010, over 21,500 oaks died, ≈500,000 ha of oak woodlands and oak-pine forests were affected (USDA–Forest Service, Forest Health Monitoring [USDA–FHM] 2011), and between 2002 and 2010 this affected area had expanded considerably (Coleman and Seybold 2011). Mortality has occurred primarily among two red oak species (both Section *Lobatae*): coast live oak, *Quercus agrifolia* Née, and California black oak, *Q. kelloggii* Newberry. (Coleman and Seybold 2008). *A. auroguttatus* was first collected from southern California in 2004 (Westcott 2005) and genetic evidence suggests that the source population is located in southeastern Arizona (Coleman et al. 2012a). *A. auroguttatus* is indigenous to southeastern Arizona and apparently not an aggressive tree-killer there where its known hosts are Emory oak, *Q. emoryi* Torrey, and silverleaf oak, *Q. hypoleuocoides* A. Camus (both Section *Lobatae*) (Coleman and Seybold 2011). The biology and ecology of *A. auroguttatus* had not been studied before 2008 because it had not been considered an ecological or economic concern in its native region.

After *A. auroguttatus* was discovered in California, a number of researchers have reported on its basic biology. Adult emergence from cut logs begins earlier for logs held at lower elevations (late May at 1,100 m and late June at 1,700 m; Jones et al. 2013). Coleman and Seybold (2008) and Seybold et al. (2010) caught adults from May through November on sticky purple prism traps. In the laboratory, adults feed on oak leaves, mature and mate, and females lay eggs singly or in small clumps inside rearing containers (V.M. Lopez, personal communication). The average female was fecund 13 d after emergence (SE = 0.7; $n = 47$), and eggs hatched in 15–20 d at 20 ± 2°C with a natural photoperiod of ≈14:10 (L:D) h (L.J. Haavik, unpublished data). In the field, females likely oviposit in bark cracks, under lichens, or in other cryptic locations on oaks. Eggs have only been observed in the field once (T.W. Coleman, unpublished data). Larvae feed mostly near the vascular cambium, in both phloem and xylem tissues, creating meandering galleries that are filled with dark black frass and are ≈4 mm wide (Hishinuma et al. 2011). Prepupae, distinguishable in many *Agrilus* spp. when final instars fold in half on

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themselves in a typical hairpin formation, overwinter in a self-constructed cell in the phloem near the outer bark (Coleman and Seybold 2008). The larvae are typical of *Agrilus* spp. and distinct from most other wood borer larvae found within oaks in California by the presence of C-shaped spiracles and pincer-like urogomphi at the tip of the abdomen (Hishinuma et al. 2011). Larvae and pupae have been observed within trees in summer and fall, and the species is thought to be univoltine (Coleman and Seybold 2008).

Our objective was to contribute to a better understanding of *A. auroguttatus* biology. We sampled infested *Q. agrifolia* at two sites on a monthly basis throughout 1 yr (2011) to investigate seasonal development within trees; determine the number of larval instars; estimate prepupal mortality during winter months; and describe the physical condition of the phloem habitat in relation to larval density. We also installed data loggers on *Q. agrifolia* to monitor temperature and traps at both sites to determine the adult flight period. This preliminary information may help direct future studies of *A. auroguttatus* population dynamics and identify vulnerable periods during larval development to be targeted by management programs.

Materials and Methods

Study Sites. We sampled living *A. auroguttatus*-infested *Q. agrifolia* once per month throughout 2011 at two study sites in San Diego Co., CA: Pine Creek (32.83640° N, 116.54304° W at 1,100 m elevation) and Long Valley (32.81453° N, 116.53244° W at 1,200 m elevation). We selected these sites based on two criteria: 1) beetle infestation levels were high, which ensured that enough immature specimens could be collected on a monthly basis to study seasonal development, and 2) these sites were not high-use recreation areas, which had to be avoided when we used semidestructive sampling. Both sites were *Q. agrifolia*-dominant woodlands in the Descanso Ranger District, Cleveland National Forest (Coleman et al. 2012b). Before 1 January 2011, we installed three, two-channel temperature data loggers at both sites (Onset HOBO data loggers, Bourne, MA) to monitor phloem and ambient temperatures. We attached each of these to a live *Q. agrifolia*, drilled a hole, perpendicular to the bark surface that penetrated the phloem, but ended just at the interface of phloem and xylem. We then inserted the probe and smeared caulk around the hole to hold it in place. Data loggers were set to monitor inner bark and ambient temperatures every 2.5 h. In September 2011, we sampled live *Q. agrifolia* at William Heise County Park, Julian, CA (33.04259° N, 116.58429° W at 1,300 m elevation) to obtain 31 additional *A. auroguttatus* larvae to help us to more accurately determine the number of larval instars.

Tree Selection and Semidestructive Sampling. We selected *Q. agrifolia* that were likely to be severely infested; trees had severe crown dieback (≥50%), evidence of woodpecker foraging, or characteristic D-shaped emergence holes (≈4 mm wide) on the lower bole (Coleman et al. 2011, Hishinuma et al. 2011). We did not find evidence of any other *Agrilus* species that produces a similar emergence hole on the main bole of these oaks (Furniss and Carolin 1977, Swiecki and Bernhardt 2006, Coleman et al. 2011).

We conducted semidestructive sampling at arbitrary locations on the lower bole (≤1.52 m above ground), of two to six living *Q. agrifolia* at each site once per month for a total of 35 and 44 trees sampled at Pine Creek and Long Valley, respectively, for the entire study (Table 1). A previous study confirmed that, in severely infested trees, *A. auroguttatus* emergence was randomly distributed with respect to bole aspect and greater on the lower bole compared with the mid-bole (Haavik et al. 2012a). Some trees were sampled more than once throughout 2011 because the number of severely infested trees was limited. We measured diameter at breast height (DBH) (at 1.4 m from the ground) and counted exit holes on the outer bark surface before carefully chipping away pieces of bark with a hatchet to reveal immature or adult *A. auroguttatus.* We identified the life stages as larvae, prepupae, constricted prepupae (i.e., no longer in hairpin formation, now shortened and enlarged just before the pupal stage), pupae, or adults (some were teneral). We also cut excised phloem and bark pieces into small pieces (≈1–6 cm^3) with a scissors to ensure recovery of all larvae, pupae, and teneral adults from the sample. In the field, before extracting specimens from phloem or xylem tissue, we assessed each specimen as alive or dead and counted only live individuals for density and within-tree population estimates. We also counted recently dead larvae that died during the winter months (January–March and November–December). Old cadavers were present within phloem and xylem tissue, but these were dry, shriveled, often moldy, and likely died some time ago. Live larvae and prepupae were transported to the laboratory in 24-well cell culture microplates. Head capsules were measured on the day of field collection (see below: Head Capsule Measurements).

After we sampled the portion of phloem near the bark that contained larvae and prepupal larvae, we measured the surface area of phloem sampled (cm^2), as well as the surface areas of dead, dying, and scar tissues (cm^2). Dying phloem tissue was often associated with a strong bacterial odor and intermediate in color and moistness between reddish, wet, healthy tissue and black, dry, dead tissue. We converted surface area measurements of these phloem conditions to proportions for statistical analyses. Because of the effort involved in sampling into the xylem through 5–10 cm of phloem, often separated by layers of scar tissue, and the likelihood of causing tree death after this kind of mechanical injury, we did not sample the xylem from January through July. One month after peak adult trap catch, we expected larvae to be feeding, so we sampled both phloem and xylem tissues throughout the remainder of the season (August–December).

Trap Placement. We installed four purple prism traps (35.6 × 59.7 cm, Coroplast Inc., Dallas, TX) coated with Tangle-Trap Adhesive (BioQuip, Rancho

Table 1. General information for semidestructive sampling of *Q. agrifolia* phloem and bark for *A. auroguttatus* throughout 2011 at Pine Creek and Long Valley, CA

Site	Sampling date	No. trees	> 50% crown dieback (no. trees)	Woodpecker presence (no. trees)	Mean ± SE DBH (cm)	Total bark surface area removed (m^2)	No., density (per m^2 bark) live within-tree *A. auroguttatus*
Pine Creek	Jan. 11	4	4	3	44.2 ± 5.5	0.72	15, 20.8
	Feb. 21	5	5	5	78.7 ± 17.0	1.46	27, 18.5
	Mar. 20	7	5	6	69.8 ± 8.5	2.05	27, 13.2
	Apr. 20	4[a]	4	4	91.6 ± 7.9	1.90	44, 23.2
	May 21	4[a]	4	2	113.9 ± 21.4	1.31	36, 27.5
	June 20	4	4	3	57.1 ± 4.6	1.40	19, 13.6
	July 18	3	2	2	61.7 ± 7.8	1.41	27, 19.1
	Aug. 15	3[a]	2	3	100.9 ± 29.1	1.36	22, 16.2
	Sept. 14	3[a]	3	3	82.7 ± 28.3	0.98	46, 46.9
	Oct. 11	3	3	2	64.0 ± 12.5	0.70	17, 24.3
	Nov. 1	2[a]	2	1	65.4 ± 1.9	0.38	6, 15.8
	Dec. 19	3[a]	3	3	90.2 ± 27.5	1.35	45, 33.3
Long Valley	Jan. 12	6	5	6	60.2 ± 3.7	1.38	20, 14.5
	Feb. 17	7[a]	7	4	62.3 ± 6.5	4.04	8, 2.0
	Mar. 15	8[a]	8	2	55.4 ± 4.4	2.60	18, 6.9
	Apr. 21	5	4	5	70.5 ± 6.1	1.69	31, 18.3
	May 19	4	3	4	78.9 ± 12.2	1.31	17, 13.0
	June 22	3	3	3	59.8 ± 7.0	1.19	16, 13.4
	July 19	4	4	3	60.6 ± 7.0	1.54	26, 16.9
	Aug. 16	4[a]	2	4	53.4 ± 3.9	1.18	7, 5.9
	Sept. 15	2[a]	2	2	52.1 ± 7.0	0.54	9, 16.7
	Oct. 12	3[a]	4	3	70.2 ± 2.5	1.20	21, 17.5
	Nov. 2	4[a]	3	3	76.6 ± 7.6	1.07	3, 2.8
	Dec. 16	3[a]	3	2	68.3 ± 3.7	1.09	8, 7.3

[a] Some of these trees had been sampled on a previous date.

Dominguez, CA) at each field site on 12 April 2011. We placed traps in sunny areas, approximately an even distance from one another (≈100–200 m apart), and near infested *Q. agrifolia* that we sampled. We mounted traps 2.3 m high with zip ties on 3 m of galvanized steel conduit (1.3 cm diameter), which were placed over 1.2 m of rebar (1.3 cm diameter). We checked traps for adult *A. auroguttatus*, and removed beetles if found, every 2 wk from 20 April until 1 November and once more on 19 December 2011.

Head Capsule Measurements. To determine the number of *A. auroguttatus* instars, we measured an exposed portion of the epicranium, the posteriormost width of the peristoma, a character which differentiated instars for *Agrilus anxius* Gory (Loerch and Cameron 1983). We used a binocular microscope and oc-

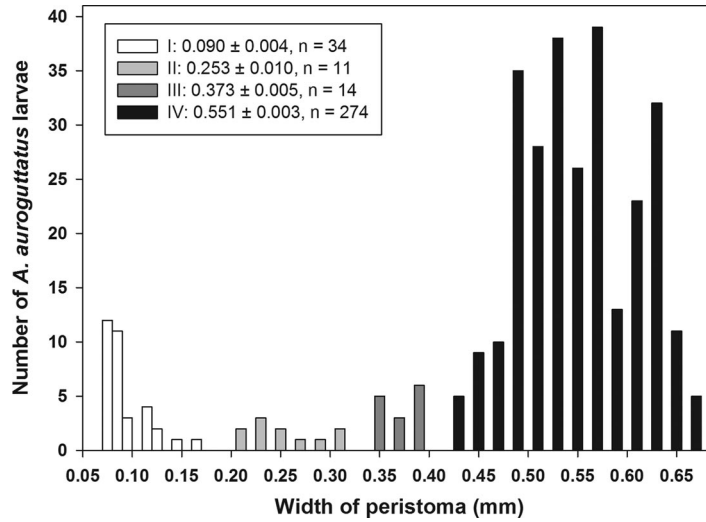

Fig. 1. Frequency distribution of *A. auroguttatus* peristomal widths used to determine number of larval instars. Mean peristomal width (±SE) and sample sizes for each instar are listed in the key (upper left). Larvae were collected in 2011 from Pine Creek and Long Valley (January–December) and William Heise Co. Park (September), CA. There were 313 field-collected larvae and 20 lab-reared first-instar larvae.

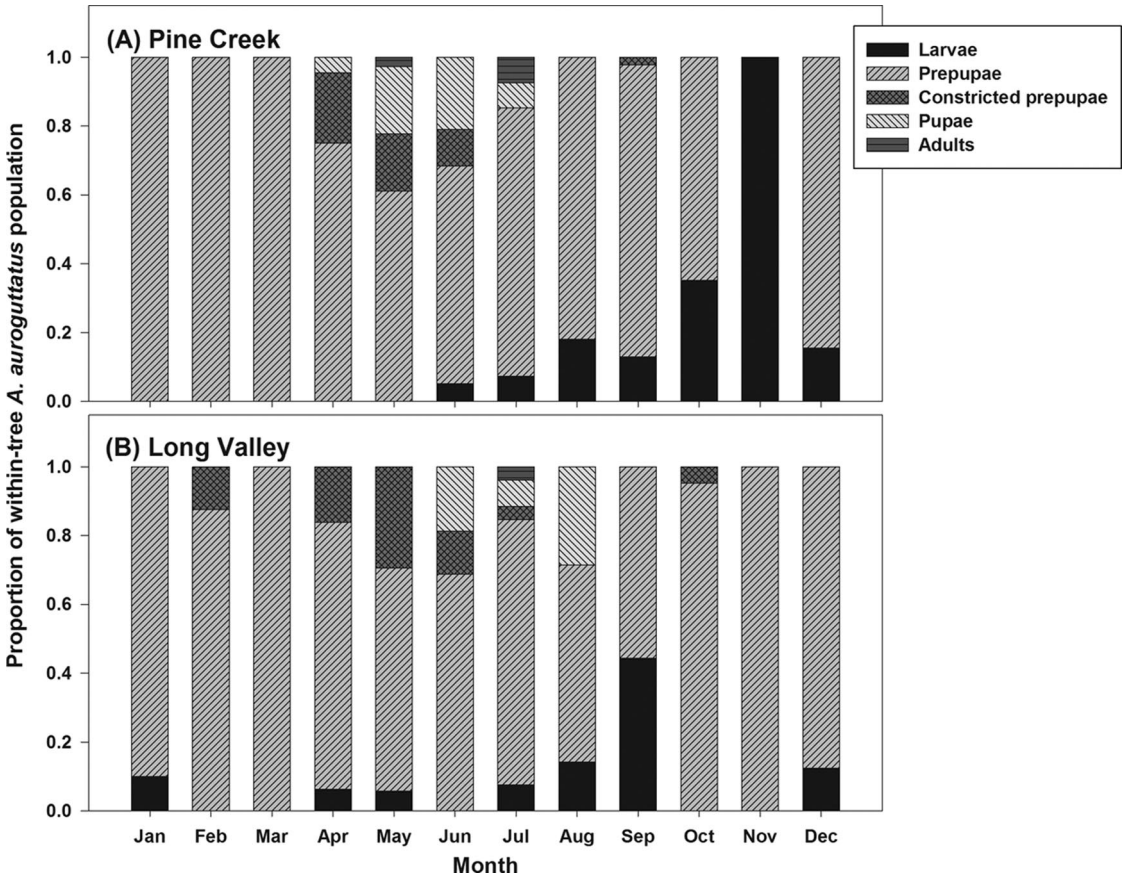

Fig. 2. Proportion of total within-tree *A. auroguttatus* population sampled in each life stage by month throughout 2011 at (A) Pine Creek and (B) Long Valley. Key for life stages is to the upper right of (A). Phloem and xylem were sampled August–December, and phloem only was sampled January–July. See Table 1 for tree sample sizes.

ular reticle to measure the width of the peristoma to the nearest 0.01 mm for all larvae collected from Pine Creek and Long Valley throughout the year and at William Heise County Park in September. To ensure first instars were represented in our analysis, we measured peristomal widths on an additional 20 newly hatched neonates from our laboratory colony.

Data Analyses. We conducted all data analyses within the R statistical environment, version 2.15.0 (R Development Core Team 2012). To determine number of larval instars, we visually inspected the frequency distribution of peristomal width measurements for peaks to indicate different instars. We then assigned each measurement to an instar according to size class limits defined by troughs associated with those peaks. Finally, we applied Brooks' (Dyar's) rule that states that growth of sclerotized structures progresses geometrically between successive instars (Crosby 1973, Loerch and Cameron 1983). Fit of the simple linear regression, of the log of mean peristomal widths for each instar against assigned instar number was used as a check to determine if we might have overlooked instars (Loerch and Cameron 1983).

We used pooled variance *t*-tests to examine differences in exit hole density, immature density (live individuals only), and adult catch per trap (totals for May–October) between sites. We used paired *t*-tests to evaluate differences in mean maximum and minimum daily bark and ambient temperatures between sites from 1 January–15 August (time period that included emergence of ≈90% of adults and when continuous data were available from more than one data logger at each site without malfunction).

Mortality of prepupae (expressed as a percentage of all prepupae recovered) were not normally distributed, so we used the Box–Cox method (Box and Cox 1964) to determine an appropriate transformation ($\lambda = -0.15$) after adding 0.5 to original values. We then used a two-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) to test the effect of month and site on percent mortality separately for late winter of the first generation (January–March) and early winter of the following generation (November–December). We used multiple linear regression to determine whether the independent variables: proportion of dead; dying; or scar tissue; or the month each tree was sampled in were related to the dependent variables: exit hole or immature (live individuals only) density. These densities were nonnormal, so we transformed them as

described above ($\lambda = 0.25$). We tested all possible models for each combination of independent variables separately for the two dependent variables and by site. Nonsignificant regressors ($P \geq 0.05$) were not included in final models, regardless of whether or not their inclusion reduced the MSE or improved the R^2. Model checks included studentized residual plots, normal probability plots and the Shapiro–Wilk normality test (Shapiro and Wilk 1965). Statistical significance was determined as $P < 0.05$ and all errors are presented as 1 SE from the mean.

Results and Discussion

Within-Tree Development. There were four peaks in the frequency distribution of *A. auroguttatus* peristomal widths, indicative of four larval instars (Fig. 1). The linear relationship between the log of mean peristomal width against instar number was significant ($R^2 = 0.93$; $F = 27.18$; df = 1, 2; $P = 0.04$); it was unlikely that any instars were overlooked. Other *Agrilus* spp. in North America also have four instars (Cote and Allen 1980, Haack and Benjamin 1982, Loerch and Cameron 1983, Chamorro et al. 2012), although there is some evidence for five instars in *A. anxius* (Barter 1957). The greatest within-instar variation in peristomal width was during the final instar (Fig. 1). This may reflect differences between the sexes; females are slightly larger than males (Coleman and Seybold 2010).

From spring through fall, different life stages were often collected from the same tree, and relative abundance of recovered life stages generally varied among trees (data not shown). Early instars were difficult to locate within trees (small n; Fig. 1), and were found only from July through November. We were unable to determine relative proportion of early instars or total larval density with confidence because early instars may have been missed or destroyed by sampling. Prepupae were found within *Q. agrifolia* throughout the year at Long Valley and in all months except November at Pine Creek. In general, prepupae comprised the largest proportion of the within-tree *A. auroguttatus* population that we were able to recover (Fig. 2). Pupae and teneral or mature (i.e., fully sclerotized) adults were found within trees from April through August (Fig. 2). Pupae have been collected from cut logs in the field as early as February (L.J. Haavik, unpublished data), which suggests that development time may be reduced by changes in temperature and/or moisture conditions in the phloem. Larvae were found within trees in all months except February and March and constricted prepupae were found within trees from February through October, except not in August (Fig. 2), during which larvae presumably transitioned to the pupal and adult stages.

We observed larvae feeding in the cambial region from August through November, but we are unsure whether they were also feeding from January through July because we did not sample in the xylem then. From August through December, we collected 83% of larvae in the phloem just beneath the outer bark (prepupae not feeding), 4% feeding exclusively in the phloem, and 14% feeding near the cambium (either in the phloem or xylem tissue).

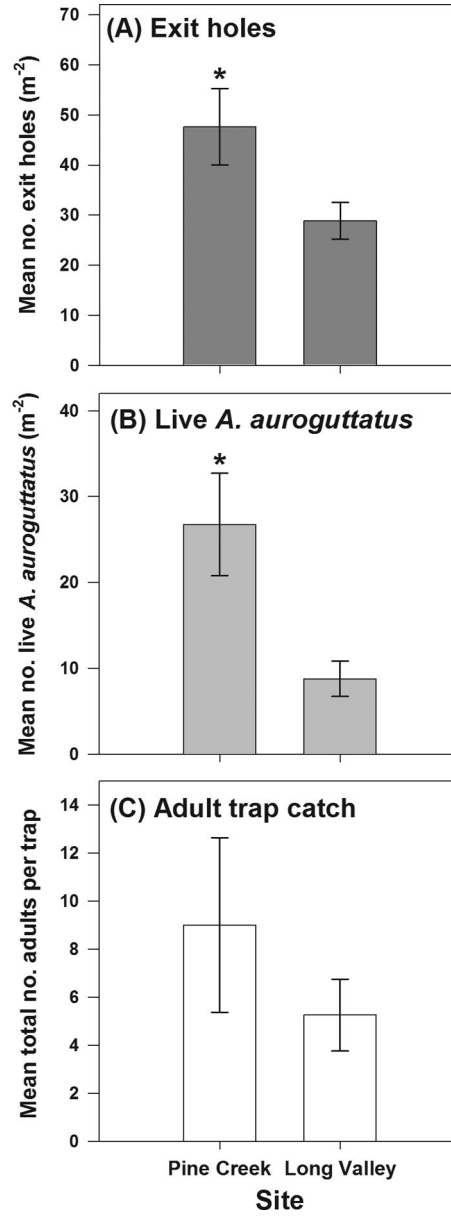

Fig. 3. Mean density of *A. auroguttatus* (A) exit holes on *Q. agrifolia* for all months, (B) within-tree immatures during months when adults were not flying (i.e., all months except May–October), and (C) mean total number of adult *A. auroguttatus* caught per trap from four traps at each site May–October, 2011. *Indicates statistical significance according to Welch's *t*-tests. Sample sizes are: Pine Creek = (A) 45 and (B) 25 trees; Long Valley = (A) 52 and (B) 33 trees.

Generation time was unclear from our results (Fig. 2); it was likely 1 yr for the majority of individuals, and possibly longer or shorter than 1 yr for others. Other

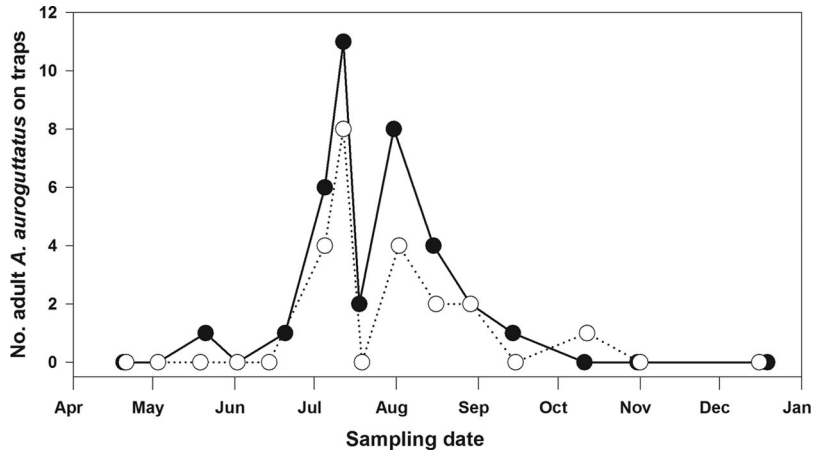

Fig. 4. Seasonal adult *A. auroguttatus* trap catch in 2011 at Pine Creek (black dots, total $n = 36$) and Long Valley (open dots, total $n = 21$). Dots represent total trap catches from four purple prism traps for each site on each sampling date.

Agrilus spp. in North America generally require 1 yr to complete development, although a portion of some populations may require 2 yr (Anderson 1944, Cote and Allen 1980, Haack and Benjamin 1982, Cappaert et al. 2005) and *A. anxius* may require two or more years in northern parts of its range (Balch and Prebble 1940, Barter 1957).

A. auroguttatus has likely been present longer, and populations are currently larger, at Pine Creek than at Long Valley (Fig. 3). Exit hole density, an indicator of cumulative population size among previous generations, was significantly greater at Pine Creek than at Long Valley ($t = 2.22$; pooled df = 63.8; $P = 0.03$; Fig. 3A). *Q. agrifolia* mortality levels were greater at Pine Creek than at Long Valley, and Pine Creek is closer to the believed epicenter of the infestation (Coleman et al. 2012b). The collective density of immatures within trees was also significantly greater at Pine Creek than at Long Valley ($t = 2.85$; pooled df = 29.8; $P = 0.01$; Fig. 3B). However, number of adults caught per trap did not differ significantly between the two sites ($t = 1.02$; pooled df = 18.0; $P = 0.32$; Fig. 3C). The relative proportions of *A. auroguttatus* pupae and adults within trees (Fig. 2) and adult trap catch (Fig. 4) suggested that seasonal development at Pine Creek was ~2 mo ahead of Long Valley.

Although our results are preliminary, the greater size of past and current within-tree *A. auroguttatus* populations at Pine Creek could have weakened trees and created proportionally more suitable host material for faster larval development than was available at Long Valley. A similar phenomenon has been reported for another invasive *Agrilus* species in North America, the emerald ash borer, *A. planipennis* Fairmaire, where development time was longer at newly colonized sites or within newly colonized trees than at sites or trees that had been infested for several years with high beetle populations (Cappaert et al. 2005, Poland and McCullough 2006, Siegert et al. 2010). Cote and Allen (1980) also report that host tree condition can affect generation time of a native *Agrilus* species in North America, wherein development time of the two-lined chestnut borer, *A. bilineatus* (Weber), was longer within more vigorously growing hosts.

We originally conjectured that Long Valley might be cooler than Pine Creek because it is at a slightly higher elevation (1,200 vs. 1,100 m). Cooler temperatures would slow insect development. However, inner bark temperatures recorded from two living *Q. agrifolia* at each site from 1 January through 15 August, indicate that mean daily maximum inner bark temperature was greater at Long Valley than at Pine Creek (Table 2; Fig. 5A) Mean daily maximum ambient temperatures were also significantly greater at Long Valley than at Pine Creek (Table 2; Fig. 5B). Long Valley is a drier site with more sun exposure than Pine Creek, which may explain differences in daily maximum temperatures. Mean daily minimum phloem temperatures during this time period were not significantly different between sites (Table 2; Fig. 5A), although mean daily minimum ambient temperatures were slightly, but significantly greater at Pine Creek than at Long Valley (Table 2; Fig. 5B). Future studies should examine development at sites of varying elevations because *A. auroguttatus* host species in southern California occupy a range of elevations (900–1,800 m).

Adult Flight Period. The first trapped adult *A. auroguttatus* at Pine Creek in 2011 was discovered on 21 May, 1 mo after we placed traps at field sites. No adults were found in traps at Long Valley until 5 July (Fig. 4). At both sites, peak trap catch occurred in July/August

Table 2. Mean ± SE daily max and min. temperatures (°C) recorded from two data loggers on live *Q. agrifolia* each at Long Valley and Pine Creek, CA (1 Jan.–15 Aug. 2011)

	Long Valley	Pine Creek	t^a	P
Max. inner bark	20.12 ± 0.48	16.07 ± 0.42	36.81	<0.0001
Max. ambient	29.65 ± 0.77	20.20 ± 0.53	27.66	<0.0001
Min. inner bark	7.23 ± 0.36	7.29 ± 0.33	0.96	0.34
Min. ambient	3.43 ± 0.35	4.34 ± 0.34	12.95	<0.0001

[a] Paired *t*-tests, df = 226 for all tests.

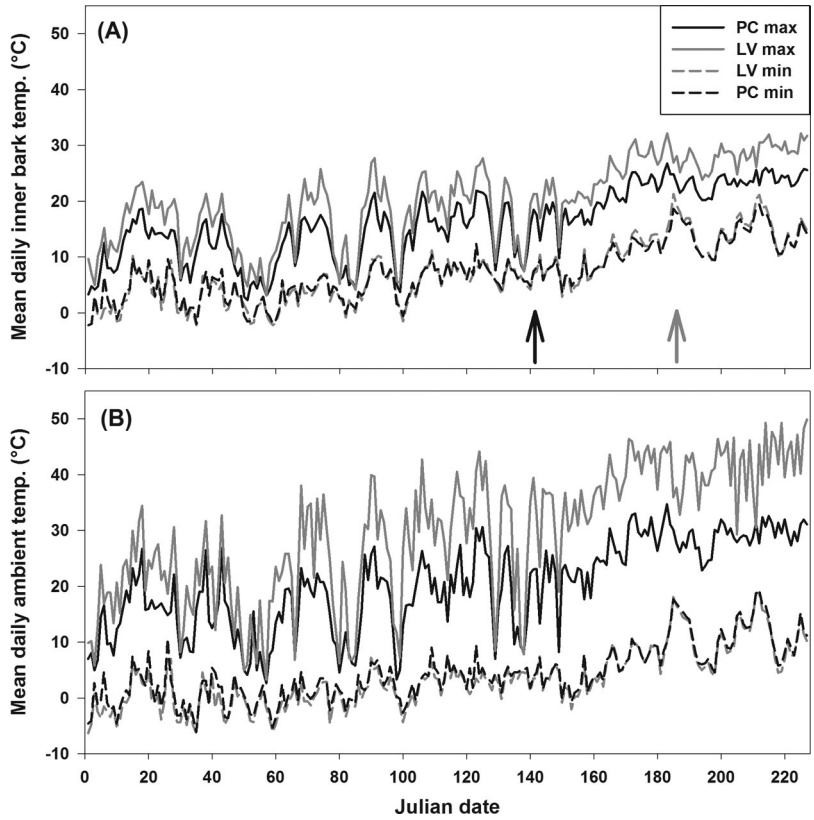

Fig. 5. Mean daily maximum (solid lines) and minimum (dashed lines) inner bark (A) and ambient (B) temperatures at Pine Creek (PC, black lines) and Long Valley (LV, gray lines), recorded from two data loggers at each site attached to live *Q. agrifolia* (1 January–15 August 2011). (A) Arrows correspond to date that the first adult *A. auroguttatus* was found in traps at Pine Creek (black) and Long Valley (gray).

(Fig. 4). We found the last trapped adult at Long Valley on 11 October. This was generally consistent with the flight period (May/June through October/November) and peak (mid-June to mid-July) reported from previous studies (Coleman and Seybold 2008, Seybold et al. 2010). At sites in close proximity to ours, Coleman and Seybold (2008) used the same traps and caught a mean of 25 adults per trap during 1 wk of peak flight activity, which was much greater than our peak trap catch over 2 wk at either site in 2011 (mean of <4 adults per trap; Figs. 4 and 3C). The inconsistency between that study and ours could reflect a decline in the adult *A. auroguttatus* population from 2008 to 2011, site level differences, poor trap efficacy, or trap placement at field sites.

Prepupal Mortality. During late winter, prepupal mortality was greater in March than in January, and mortality in February was no different than in January or March ($F = 4.86$; df = 2, 24; $P = 0.02$). Mean prepupal mortality pooled across both sites was 3 ± 3% in January, 18 ± 9% in February, and 36 ± 9% in March. Prepupal mortality did not differ between sites during late winter ($F = 0.77$; df = 2, 24; $P = 0.47$) or between sites or months during early winter (November–December, overall mean = 36.6 ± 9.7%; $F = 2.81$; df = 1, 8; $P = 0.13$ and $F = 0.61$; df = 1, 8; $P = 0.46$ for month and site, respectively). We observed some dead larvae coated in a gray and white fungus, some covered by parasitic mites (*Pyemotes* spp.; T.W. Coleman, unpublished data) and others were extremely moist and limp sometimes with an orange or deep-yellow pigmentation. While sampling for this study, we encountered the first record in California of the larval parasitoid *Calosota elongata* Gibson (Hymenoptera: Eupelmidae) in the pupal stage enclosed within empty *A. auroguttatus* pupal cells at Pine Creek (Haavik et al. 2012b).

The Phloem Habitat. There was a significant, albeit weak, positive relationship between immature density and proportion of dying phloem tissue at Pine Creek whereby 13% of the variation in *A. auroguttatus* density could be explained by proportion of dying phloem tissue (equation: *density* = 3.34 [±1.37] *proportion dying tissue* +1.98; $R^2 = 0.13$; $F = 5.95$; df = 1, 39; $P = 0.02$). This relationship was not significant at Long Valley (mean proportion of dying phloem tissue = 0.03 ± 0.01; $F = 2.13$; df = 1, 44; $P = 0.15$). Although this provides some evidence that dying phloem tissue was associated with increasing *A. auroguttatus* density, it is unclear whether dying phloem tissue defined a more suitable habitat for *A. auroguttatus* development

within trees or whether it was simply a result of severe current infestation.

Proportion of dead phloem tissue (mean = 0.08 ± 0.03 and 0.08 ± 0.02 at Pine Creek and Long Valley, respectively) was not significantly related to immature density at either site, consistent with studies of other *Agrilus* spp., which suggest that dead phloem tissue is not a suitable habitat for development (Chapman 1915, Balch and Prebble 1940, Barter 1957). There was also no evidence for a relationship between immature density and proportion of scar tissue (mean = 0.10 ± 0.04 and 0.17 ± 0.05 at Pine Creek and Long Valley, respectively) at either site. Production of scar tissue may be an important mechanism of host physical resistance during early larval establishment, as has been observed for other *Agrilus* spp. (Ball and Simmons 1986, Dunn et al. 1990).

There were no significant relationships between exit hole density and proportion of dying, dead or scar tissues (data not shown). Previous generation *A. auroguttatus* density was thus not likely related to conditions in the current phloem habitat. However, our sampling was biased toward trees that likely contained densities of the current generation, so the effect of past infestation on phloem habitat was not measured directly.

Management Implications. This research sheds light on the ecology of *A. auroguttatus* outside of its native range and will be helpful to manage this insect, especially to establish a biological control program. Larvae of *A. auroguttatus* are present all year, which might be ideal for larval parasitoids. However, larvae might need to be in a particular stage to be suitable for parasitism. For example, larval parasitoids seem to prefer third and fourth instars of *A. planipennis* (Ulyshen et al. 2010), partially because larval parasitoids rely on vibrations produced by feeding larvae to locate their hosts. Active larvae of *A. auroguttatus* are present from July–January, so this might be the temporal window for larval parasitoid releases. The thick bark and phloem of *Q. agrifolia* may provide a refuge against parasitism of some *A. auroguttatus* larvae. Although we were unable to find eggs on trees, we expect that egg densities should lag behind adult emergence. Therefore, egg parasitoids might be released from July–September. These background data improve the chances for a successful biological control effort.

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