Effects of Body Size, Diet, and Mating on the Fecundity and Longevity of the Goldspotted Oak Borer (Coleoptera: Buprestidae)

VANESSA M. LOPEZ[1] AND MARK S. HODDLE[1,2,3]

Ann. Entomol. Soc. Am. 107(2): 000–000 (2014); DOI: http://dx.doi.org/10.1603/AN13158

ABSTRACT The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is an invasive wood-borer that was recently introduced into southern California from southern Arizona, and has caused the rapid mortality of thousands of native oaks. Biological control of *A. auroguttatus* is a management strategy of high interest, but is in its early stages, which is due, in part, to a lack of information on the basic biology and life history of this beetle. To address this shortcoming, studies were conducted in quarantine on the realized lifetime fecundity of *A. auroguttatus*, which was determined by comparing oviposition and larval emergence rates of females subjected to different dietary and mating treatments. Longevity and body size were also recorded for male and female adults under these treatments. Mean *A. auroguttatus* lifetime oviposition and larval emergence were similar in females that were continuously paired with either one or two males. Virgin females laid significantly fewer eggs and no larval emergence resulted from unfertilized eggs. The number of mates did not affect mean *A. auroguttatus* adult longevity, but a carbohydrate-enriched diet increased both mean longevity and lifetime oviposition by as much as 46 and 250%, respectively. There was no correlation between adult body size and lifetime oviposition, days to initial oviposition, larval emergence, and adult longevity. However, hind tibia length was marginally correlated with total oviposition period. For mass rearing *A. auroguttatus* eggs in the laboratory, pairing females with one male and providing adults with a continuous diet of 10% honey-water and oak foliage is recommended.

KEY WORDS *Agrilus auroguttatus*, classical biological control, invasive pest, fecundity, longevity

The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is a serious invasive pest of native oaks in southern California. Initially detected in San Diego County, CA, in 2004 (Westcott 2005), this wood-boring beetle was likely introduced into the area through the movement of infested oak firewood from its native range in southern Arizona. In Arizona, *A. auroguttatus* preferentially attacks oaks that are in decline (e.g., Emory oak, *Quercus emoryi* Torrey, and silverleaf oak, *Quercus hypoleucoides* A. Camus), and has never been considered a significant forest pest (Coleman et al. 2012). The impact of *A. auroguttatus* in southern California is much more severe than that observed in Arizona, as this insect aggressively attacks and kills healthy coast live oak (*Quercus agrifolia* Nee), California black oak (*Quercus kelloggii* Newberry), and canyon live oak (*Quercus chrysolepis* Liebmann) (Coleman and Seybold 2008a). Mortality of these native species is estimated at >22,000 trees within the 212,460-ha infestation zone in San Diego (Coleman et al. 2011) and, more recently (2012), Riverside County (Jones et al. 2013).

Oak woodlands are unique environments in California that are composed of diverse native flora and fauna, and they contain the highest levels of biological diversity of any broad habitat in the state (Allen-Diaz et al. 2007). As foundation species, oaks greatly influence the functioning of these ecosystems because they impact microclimates, affect energy and nutrient inputs, and provide essential habitat and food resources for a variety of native wildlife (Ellison et al. 2005). Oak habitat is also economically important in California because it enhances property values (Diamond et al. 1987), provides more than two-thirds of range land for domestic livestock (Huntsinger et al. 1997), and is of significant esthetic and recreational value (Standiford and Tinnin 1996).

Management strategies for *A. auroguttatus* control are limited to protecting individual, highly valued trees (i.e., systemic and topical insecticides are used); preventing the spread of this insect through the sanitation of infested oak wood (i.e., wood solarization and grinding infested wood); or outreach efforts on the risks of moving infested firewood to reduce inadvertent spread into new areas. At this time, biological control may be the only feasible long-term method for controlling this pest on a forest scale because, compared with pesticide use, host-specific natural enemies are more likely to provide sustainable long-term cost-effective control with fewer nontarget impacts. How-

[1] Department of Entomology, University of California, Riverside, 900 University Ave., Riverside, CA 92521.
[2] Center for Invasive Species Research, University of California, Riverside, 900 University Ave., Riverside, CA 92521.
[3] Corresponding author, e-mail: mark.hoddle@ucr.edu.

ever, developing a biological control program requires an understanding of the pest's fundamental biological and life-history traits, of which nothing is known for *A. auroguttatus.* Before 2008, the only information available for *A. auroguttatus* was collection records from its native range in Arizona (Coleman and Seybold 2008b, 2011).

Before *A. auroguttatus* was determined to be a significant cause of decline and mortality to native California oak species in 2008, there was no information available on the biology or life history of this insect (Coleman and Seybold 2008b). Since 2008, field studies in southern California suggested that most *A. auroguttatus* larvae complete their development to adulthood in a single year (Haavik et al. 2013). However, some larvae and pupae are present under bark in October, which indicates that some individuals may require >1 yr to complete development (Coleman and Seybold 2008a, Haavik et al. 2013). In the laboratory, *A. auroguttatus* adults feed on oak foliage. However, leaf feeding is minor and has never been observed in the field. After ≈2 wk of feeding under laboratory conditions, females are reproductively mature and begin to lay eggs individually on oak bark or artificial substrates. *A. auroguttatus* eggs have rarely been observed in the field due to their small size (≈1 mm in width) and cryptic coloration. However, based on information from other *Agrilus* species (Loerch and Cameron 1984, Liu et al. 2007), it is likely that individual eggs are placed in bark crevices, which coupled with small size further compounds the difficulty of visual detection in the field. Once eggs hatch, larvae burrow through the bark to reach the vascular cambium, where they create feeding galleries. Repeated feeding damage to the phloem/xylem interface by *A. auroguttatus* larvae eventually results in tree death (Coleman and Seybold 2008b). When larval development is complete, larvae tunnel to the outer phloem to create pupal chambers underneath the outer bark. Following pupation, emerging adults chew D-shaped emergence holes to exit the tree.

The lack of information regarding the basic biology and life history of *A. auroguttatus* poses a significant challenge to our understanding and, ultimately, management of this pest. Knowledge of the biology and life history of a pest can aid in the selection of natural enemies for incipient biological control programs, as it may guide foreign exploration for natural enemies which will have the greatest deleterious impact on the pest by targeting the most vulnerable life stages (Shea and Kelly 1998, Buhle et al. 2005). Information about the occurrence and persistence of specific life stages and the effects of adult size on the abundance and viability of offspring can help with the development of laboratory-based mass-rearing programs for *A. auroguttatus.* In addition, quantification of expected lifetime and reproductive capabilities will increase understanding of factors affecting *A. auroguttatus* population dynamics, which could be useful in risk assessment models that rely on estimates of population growth and dispersal (Venette et al. 2010).

Currently, laboratory rearing of *A. auroguttatus* is restricted to the egg and neonate larval stages, and eggs are produced from field-collected adults or late-instar larvae that emerge as adults in the laboratory. Methods for rearing *A. auroguttatus* from eggs to the adult stage have been investigated using emerald ash borer (*Agrilus planipennis* Fairmaire) rearing techniques such as an artificial diet (Blossey et al. 2000, Gould et al. 2011), as well as egg (L. S. Bauer, USDA Forest Service, personal communication) and larval insertions (Duan et al. 2011, Duan and Oppel 2012) into cut oak branches. None of these methods used for *A. planipennis* were successful in rearing *A. auroguttatus* from the egg to adult stage in quarantine. However, the ability to rear viable eggs in the laboratory from field-collected adults led to a focused search for egg parasitoids in Arizona, that, if found, could be evaluated as potential biological control agents of *A. auroguttatus* in California. Surveys for egg parasitoids were initiated in 2012 using sentinel egg masses, and resulted in the collection of the first known egg parasitoid of this beetle, a currently undescribed *Trichogramma* species (Lopez and Hoddle 2013). Determining factors that affect rearing of *A. auroguttatus* eggs in the laboratory would help maximize the number of eggs that could be used for research programs on this pest. For example, an abundant and a predictable egg supply would enable the deployment of sentinel eggs in both the native and introduced range of this beetle to survey for unknown species of egg parasitoids that could be considered for use in a classical biological control program. In addition, enhanced egg production techniques using field-collected *A. auroguttatus* in the laboratory would also be advantageous for testing the host specificity of potential biological control agents, and for mass rearing egg parasitoids for use in a classical biological control program against *A. auroguttatus* in California. Further, the degree-day requirements and egg hatching rates for *A. auroguttatus* across multiple temperatures could be quantified to provide a better understanding of how varying temperatures affect the development of this life stage.

An insect's reproductive success can be affected by its size, nutrition, and access to mates. Body size has been shown to be correlated to fecundity in many insect species (Honěk 1993, French and Hammack 2010, Lauzière et al. 2000). Nutritional quality (i.e., diet) and mating frequency have been demonstrated to influence insect longevity and reproduction (Tisdale and Sappington 2001, Keena 2002, Millar et al. 2003, French and Hammack 2011). Therefore, it is likely that the size of adult *A. auroguttatus,* nutritional quality, and mating success could influence the reproductive biology of this beetle both in the laboratory and nature. Consequently, the objectives of the studies reported here were: 1) to determine the effects of diet and mating status on the realized lifetime fecundity of *A. auroguttatus* females by comparing oviposition and larval emergence rates of females subjected to different dietary and mating treatments; and 2) to investigate the relationship between longevity and body size in adult male and female *A. auroguttatus*

maintained under different diet and mating treatments. This laboratory investigation under quarantine conditions provides the first detailed life-history data for *A. auroguttatus.*

Materials and Methods

Rearing of *A. auroguttatus* Adults. *A. auroguttatus* adults were reared from infested *Q. agrifolia* and *Q. kelloggii* trees at two locations in southern California. In March–April 2011, infested trees were felled at various locations (exact locality data were not recorded) within the Cleveland National Forest, San Diego County, CA; cut into rounds (≈30 by 60 cm); and placed inside 15–30 emergence tents (1.83- by 1.83- by 1.83-m Lumite screen portable field cages, Bioquip Products, Rancho Dominguez, CA) located at the Camp Ole U.S. Forest Service Fire Station, Mt. Laguna, CA. The following April (2012), infested *Q. agrifolia* and *Q. kelloggii* trees were felled at William Heise County Park, Julian, CA (33° 02′ N/116° 35′ W; 1,280 m), and similarly cut into rounds and tented at William Heise County Park. From June to August each year, adults were collected daily from the emergence tents. Immediately after collection, live adults were transported under permit (CDFA Permit No. = 2664; USDA-APHIS permit No. = P526P-10-00667) to the Insectary and Quarantine Facility at the University of California, Riverside County. In addition, in April 2012, bark containing prepupae and pupae was removed from *A. auroguttatus*-infested *Q. agrifolia* and *Q. kelloggii* trees at William Heise County Park, and transported to the Insectary and Quarantine Facility at the University of California, Riverside, under the same permits. Newly emerged adults were collected daily from infested bark in quarantine from May to June 2012.

Following field cage and quarantine collections, recently emerged *A. auroguttatus* adults (<24-h-old) were randomly selected for placement into treatment combinations that were assembled from a mixture of different mating and diet treatments. For every treatment combination, the emergence date of adults was recorded, and newly emerged adults were introduced into 2.13-liter hand-grip rearing containers (11.7 by 12.1 by 18.1 cm, Candy Concepts Inc., Pewaukee, WI) held under ambient laboratory conditions (photoperiod of 14:10 [L:D] h, 23 ± 2°C, 30 ± 2% relative humidity [RH]) in quarantine, and where they remained until death. Each rearing container had a 6-cm-diameter ventilation hole that was covered with fine metal mesh screen, and standard white coffee filter paper (11.1 cm diameter base, Ambiance, Amerifoods Trading Co., Los Angeles, CA) was provided as an oviposition substrate. The coffee filter paper was cut into ≈10-cm-diameter rounds and placed directly underneath the rearing container lid. A fine metal mesh screen was placed on top of the filter paper, which held the paper in place, secured the ventilation hole, and provided adults with a textured substrate for gripping while ovipositing. This method of acquiring eggs has been used successfully for *A. planipennis* (Juli Gould, USDA-APHIS-PPQ, personal communication).

Experimental Design. A factorial design was used in this study. The two experimental factors were number of mates and diet type, consisting of four and three levels, respectively. Covariates included three measurements of body size (elytron length, elytron width, and tibia length). The four mating treatments (i.e., levels) were as follows: one male only (treatment 1 [T1]), one female only (treatment 2 [T2]), one female paired with one male (treatment 3 [T3]), and one female was paired with two males (treatment 4 [T4]) to maximize mating opportunities and sperm availability. For the duration of the study, adults within each mating treatment were randomly assigned to one of the following three diets (i.e., levels): water only, water and *Q. kelloggii* foliage, and 10% honeywater solution with *Q. kelloggii* foliage. Condiment containers (59 ml, First Street, Amerifoods Trading Co., Los Angeles, CA) with an ≈1-cm-diameter hole in the lid were used to hold each diet type. A cotton dental wick (3.8 by 1 cm, nonsterile Wrapped Rolls, Richmond Dental and Medical, Charlotte, NC) was placed into the lid hole, which allowed adults to safely access diet liquids. *Q. kelloggii* leaves used in specified diets were placed into condiment containers (holding respective diet liquids) through the lid hole along with a cotton wick. Diets (including condiment containers and dental wicks) were replenished every 3–4 d, a time interval shown in preliminary studies to be adequate.

Data Collection. The time (in days) to initial oviposition, realized weekly and lifetime fecundity, and total oviposition period for each female in each treatment were determined by removing the coffee filter paper daily (and replacing with fresh paper) and counting the number of eggs laid. Coffee filter papers were labeled by date and rearing container identification number, and were held in sealed petri dishes (photoperiod of 14:10 [L:D] h, 23 ± 2°C, 30 ± 2% RH) until larval emergence (i.e., eclosion of eggs) was complete. Larval emergence holes from eggs on each paper were counted. Egg counts were used to calculate average weekly and lifetime oviposition for individual *A. auroguttatus* females in each of the four mating treatments. Weekly oviposition of females within each mating treatment was calculated using the average number of eggs oviposited every 7 d following the initial oviposition event of each respective female. Larval emergence counts were used to calculate lifetime and percentage larval emergence for *A. auroguttatus* females in all treatments. Male and female longevities were recorded daily for all treatments.

Body size of males and females from all treatments was estimated by removing the right hind tibia and right elytron of each adult, and slide mounting in a balsam/clove oil mix to measure elytron length and width and tibia length. To slide mount each *A. auroguttatus* adult's tibia and elytron, a balsam mix was made from ≈80% Canada balsam (CAS #8007-47-7, Spectrum Chemical Manufacturing Corporation, New Brunswick, NJ) and 20% clove (bud) oil (CAS

#80000-34-8, Spectrum Chemical Manufacturing Corporation). Two separate drops of the balsam mix (≈2 cm in diameter) were placed individually near the center of a glass microscope slide for placement of the tibia and elytron (each placed in the center of one of the two respective drops). A cover slip was placed over the mounted specimens, and the labeled slide was placed into a slide warmer until the balsam mix solidified. After solidification, the elytron length, elytron width, and hind tibia length were measured. Tibia length was measured using a stereoscope eyepiece micrometer (calibrated with a stage micrometer), and elytron length and width were measured with an electronic 0- to 200-mm digital caliper.

Statistical Analyses. Female oviposition (the number of eggs oviposited per lifetime, time in days to initial oviposition, and total oviposition period in days), larval emergence rates, and adult longevity were analyzed using analysis of covariance (ANCOVA) to determine the effects of body size, diet, and mating treatment on reproductive output. Total oviposition period and larval emergence data were not transformed before analysis. However, the time to initial oviposition was analyzed on an inverse scale, and the number of eggs laid per lifetime and adult longevity were log transformed to satisfy normality assumptions. Females fed a water-only diet had zero oviposition during this study and were therefore excluded from all oviposition data analyses. In addition, larval emergence was analyzed using observations with nonzero oviposition data. Tukey-Kramer tests were used to conduct pairwise comparisons for each significant factor in the ANCOVA. Finally, three measures of body size (elytron width, elytron length, and tibia length) were analyzed with ANCOVA to determine if a correlation between female fecundity and adult longevity existed. A *t*-test was used to compare the mean body sizes of male and female *A. auroguttatus* used in this study. All statistical analyses were conducted at the 0.05 level of significance and were performed using SAS 9.2 (SAS 2008).

Results

Fecundity. There were no significant differences between 2011 and 2012 for the total number of eggs laid per lifetime of experimental female *A. auroguttatus* ($F = 0.68$; df = 1, 50; $P = 0.42$), time to initial oviposition ($F = 0.94$; df = 1, 47; $P = 0.34$), total oviposition period ($F = 0.80$; df = 1, 48; $P = 0.38$), larval emergence ($F = 0.01$; df = 1, 17; $P = 0.94$), or adult longevity ($F = 0.29$; df = 1, 161; $P = 0.59$); therefore, the data from these 2 yr were pooled together. The average (mean ± SE) lifetime oviposition period (days), days to first oviposition, percentage larval emergence, and male (excluding T1) and female longevity (days) are shown in Table 1. The average (mean ± SE) weekly oviposition rates of females in T2, T3, and T4 fed either a water and *Q. kelloggii* leaf diet or a 10% honey-water and *Q. kelloggii* leaf diet are shown in Fig. 1. The mean number of eggs oviposited by *A. auroguttatus* females paired with zero, one, or

Table 1. Comparison of average (mean ± SE) fecundity and longevity characters for *A. auroguttatus* females paired with either zero (one ♀), one (one ♀ × one ♂), or two (one ♀ × two ♂) males, and fed water only (H_2O), water and *Q. kelloggii* foliage (H_2O and leaves), or a 10% honey-water and *Q. kelloggii* foliage (H-H_2O and leaves) diet

Character	One ♀			One ♀ × one ♂			One ♀ × two ♂		
	H_2O	H_2O and leaves	H-H_2O and leaves	H_2O	H_2O and leaves	H-H_2O and leaves	H_2O	H_2O and leaves	H-H_2O and leaves
Days to first oviposition	0.0	17.0 ± 5.1Aa	15.9 ± 3.7Aa	0.0	8.6 ± 0.9Ba	10.1 ± 0.7Ba	0.0	14.6 ± 2.8ABa	10.9 ± 2.3ABa
Total oviposition period (d)	0.0	43.0 ± 10.5Aa	63.5 ± 13.0Ab	0.0	43.6 ± 7.4Aa	85.8 ± 13.6Ab	0.0	53.8 ± 6.0Aa	77.7 ± 19.0Ab
% lifetime larval emergence	0.0	0.0	0.0	0.0	83.4 ± 4.0%Aa	72.6 ± 7.0%Aa	0.0	67.0 ± 10.2%Aa	69.2 ± 8.9%Aa
Female longevity (d)	17.8 ± 2.5Aa	83.8 ± 10.6Ab	106.8 ± 20.8Ac	16.5 ± 2.6Aa	72.1 ± 6.3Ab	122.1 ± 19.5Ac	13.3 ± 2.3Aa	75.6 ± 7.8Ab	109.1 ± 24.3Ac
Male longevity (d)	–	–	–	12.5 ± 2.1Aa	37.1 ± 6.0Ab	77.9 ± 20.1Ac	12.5 ± 1.7Aa	46.7 ± 5.3Ab	73.8 ± 13.8Ac
n	11	12	11	8	8	8	6	8	7

Means within each row followed by the same uppercase letter are not significantly different in mating treatment analyses, and means within each row followed by the same lowercase letter are not significantly different in diet treatment analyses based on Tukey-Kramer means separation with $\alpha = 0.05$ (SAS 2008).

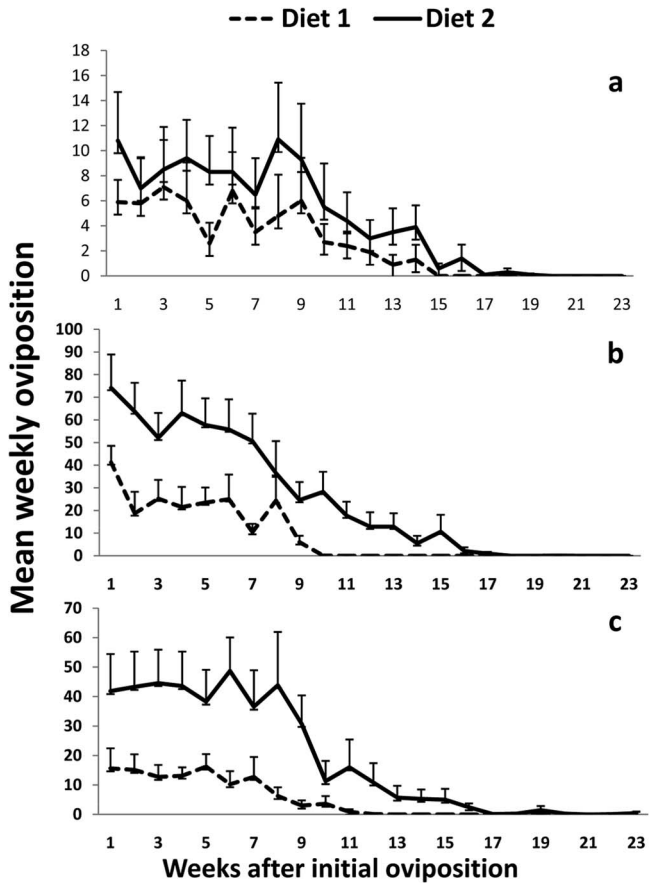

Fig. 1. Mean (±SE) weekly number of oviposited eggs following the initial oviposition of females fed a water and *Q. kelloggii* foliage diet (Diet 1), or a 10% honey-water and *Q. kelloggii* foliage diet (Diet 2), and paired with (a) zero males (one ♀ only), (b) one male (one ♀ × one ♂), or (c) two males (one ♀ × two ♂). Females fed a water-only diet (Diet 3) laid zero eggs throughout this study and were excluded from this figure.

two males, and fed water and *Q. kelloggii* foliage or a 10% honey-water and *Q. kelloggii* foliage, is shown in Fig. 2. The mean number of larvae that emerged from eggs oviposited by *A. auroguttatus* females paired with zero, one, or two males, and fed water and *Q. kelloggii* foliage or a 10% honey-water and *Q. kelloggii* foliage, is shown in Fig. 3. Larval emergence did not differ between mating or diet treatments. All females fed a

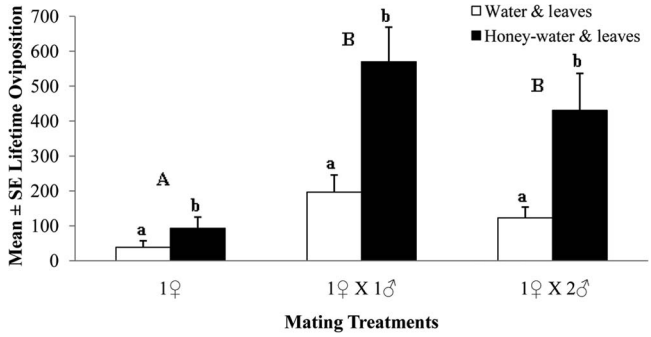

Fig. 2. Mean number of eggs oviposited by *A. auroguttatus* females paired with zero (one ♀), one (one ♀ × one ♂), or two males (one ♀ × two ♂), and fed water and *Q. kelloggii* foliage (water and leaves), or a 10% honey-water and *Q. kelloggii* foliage diet (honey-water and leaves). Females fed a water-only diet laid zero eggs throughout this study and were excluded from this figure. Different uppercase letters indicate a significant difference between mating treatments, and lowercase letters indicate a significant difference between diet types based on Tukey-Kramer means separation test with $\alpha = 0.05$ (SAS 2008).

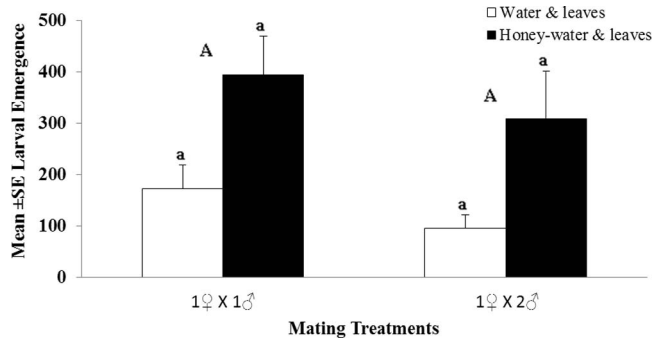

Fig. 3. Mean number of larvae that emerged from eggs oviposited by *A. auroguttatus* females paired with zero (one ♀), one (one ♀ × one ♂), or two males (one ♀ × two ♂), and fed water and *Q. kelloggii* foliage (water and leaves) or a 10% honey-water and *Q. kelloggii* foliage diet (honey-water and leaves). Different uppercase letters indicate a significant difference between mating treatments, and lowercase letters indicate a significant difference between diet types based on Tukey-Kramer means separation test with $\alpha = 0.05$ (SAS 2008).

water-only diet laid zero eggs (Table 1) and were excluded from Figs. 1–3.

Body Size. Adult body size was measured for all males ($n = 87$) and females ($n = 80$) used in this study. The average body size for males was 7.03 ± 0.06 mm (elytron length), 1.20 ± 0.03 mm (elytron width), and 1.56 ± 0.01 mm (tibia length). The average body size of females was 7.73 ± 0.07 mm (elytron length), 1.31 ± 0.01 mm (elytron width), and 1.68 ± 0.02 mm (tibia length). Females were significantly larger than males in elytron length ($t = 8.16$; df = 163; $P \leq 0.0001$), elytron width ($t = 2.69$; df = 163; $P = 0.0079$), and tibia length ($t = 5.82$; df = 163; $P \leq 0.0001$).

Influence of the Number of Mates on Female Fecundity and Adult Longevity. The number of males paired with female *A. auroguttatus* had a significant effect on lifetime oviposition ($F = 16.38$; df = 2, 50; $P \leq 0.0001$) and days to initial oviposition ($F = 9.20$; df = 2, 47; $P \leq 0.0005$). Total oviposition period ($F = 0.07$; df = 2, 48; $P = 0.94$) and larval emergence rates ($F = 0.97$; df = 1, 17; $P = 0.34$) were not influenced by the number of males housed with each female. No larvae emerged from eggs laid by unmated (T2) females. Pairwise comparisons using Tukey-Kramer showed that females with no access to males (T2) laid significantly fewer eggs over their lifetime than females with access to one male (T3) ($t = -6.03$; df = 50; $P \leq 0.0001$) or two males (T4) ($t = -4.42$; df = 50; $P \leq 0.0001$). In addition, females with no access to males (T2) experienced initial oviposition significantly later (≈5–8 d) than females with access to one (T3) male ($t = -3.42$; df = 47; $P = 0.004$).

The number of males paired with females had no significant effect on adult (male and female) longevity ($F = 0.41$; df = 3, 161; $P = 0.75$) across treatments. However, male and female longevities were significantly different ($F = 7.35$; df = 1, 161; $P = 0.008$), with females, on average, living ≈6–94% longer than males (Table 1). The average longevity for T1 males fed a water-only ($n = 7$) diet was 12.4 ± 2.1 d. Males in T1 fed a water and *Q. kelloggii* diet ($n = 8$) lived, on average, 53.9 ± 6.4 d, and males fed a 10% honey-water and *Q. kelloggii* ($n = 8$) diet lived, on average, 91.3 ± 17.2 d.

Influence of Diet on Female Fecundity and Adult Longevity. Diet type had a significant effect on lifetime oviposition (Fig. 2). Females fed 10% honey-water and *Q. kelloggii* leaves laid more eggs over their lifetime ($F = 15.49$; df = 1, 50; $P = 0.0003$) and had a longer oviposition period ($F = 5.74$; df = 1, 48; $P = 0.02$) than females fed a water and *Q. kelloggii* diet (Table 1). However, diet type had no significant effect on average larval emergence rates ($F = 1.51$; df = 1, 17; $P = 0.23$) (Table 1).

Adult longevity was significantly affected by diet type ($F = 81.17$; df = 2, 161; $P \leq 0.0001$). Male and female *A. auroguttatus* adults lived significantly longer when fed a 10% honey-water and *Q. kelloggii* leaf diet than a water and *Q. kelloggii* ($t = 5.10$; df = 161; $P \leq 0.0001$) or water-only diet ($t = 11.80$; df = 161; $P \leq 0.0001$) (Table 1).

Influence of Body Size on Female Fecundity and Adult Longevity. Adult body size was not significantly correlated with the majority of measured fitness parameters listed in Table 1. Lifetime oviposition, the main parameter used to assess fitness of individual female *A. auroguttatus*, was not correlated with elytron length ($F = 0.05$; df = 1, 50; $P = 0.82$), elytron width ($F = 0.34$, df = 1, 50; $P = 0.56$), or tibia length ($F = 0.03$; df = 1, 50; $P = 0.87$). The period until initial oviposition was not correlated with any *A. auroguttatus* body measurement ($P \geq 0.05$). Tibia length, however, was significantly, but marginally, correlated with the total oviposition period ($F = 4.43$; df = 1, 48; $P = 0.04$) of females. In addition, elytron length, elytron width, and tibia length did not have a significant relationship with larval emergence or adult (male and female) longevity ($P \geq 0.05$).

Discussion

Influence of the Number of Mates on Female Fecundity and Adult Longevity. *A. auroguttatus* females mate frequently when paired with males (V.M.L., per-

sonal observation). Several hypotheses to explain the benefits of multiple matings by females include: 1) a need to replenish depleting sperm supplies (Walker 1980, Sakurai 1998), 2) to ensure viable sperm transfer (Ridley 1988), 3) to replace stored sperm that may be senescing or accumulating mutations (Purdom et al. 1968, Tsubaki and Yamagishi 1991), 4) to enhance sperm competition for increased fertilization (Walker 1980), 5) to acquire male-derived nutrients (Boggs 1990), or 6) to promote genetic variability among offspring (Caldwell and Rankin 1974, Williams 1975, Fox 1993, Jennions and Petrie 2000). A meta-analysis conducted by Arnqvist and Nilsson (2000) determined that multiple matings by female insects increased realized lifetime fecundity by 30–70%, but analyses did not specifically determine the possible effects of a female mating multiple times with the same male (monogamy) or multiple times with different males (polyandry) (Bybee et al. 2005).

Although the study conducted by Bybee et al. (2005) determined that polyandry in female *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae) was detrimental to reproductive success in comparison with monogamy, *A. auroguttatus* lifetime oviposition and larval emergence were similar in females that were continuously paired with either one or two males. In this laboratory study, the comparable fecundity of polyandrous and monogamous females suggests that the cost of mating with multiple males (i.e., male harassment or exceeding optimal mating frequency) may potentially cancel out any possible benefit gained from acquiring the additional sperm of a second male. Several benefits of polyandry in insects (e.g., enhanced genetic variability and vigor among offspring) can likely be quantified by examining the quality and reproductive fitness of offspring. However, due to the restraints of rearing this beetle from egg to adult in the laboratory, the fitness (i.e., reproductive success and size) of *A. auroguttatus* monogamous and polyandrous-produced offspring was not investigated. Finally, virgin *A. auroguttatus* females had significantly delayed initial oviposition (≈57–98%) than monogamous females, and laid significantly fewer eggs from which no larvae emerged in comparison with mated (monogamous and polyandrous) females. Even though virgin females were capable of oviposition, all eggs laid by these females were nonviable (nonviable eggs appeared shrunken, shriveled, and lacked melanization) and did not hatch.

The number of males did not have an effect on *A. auroguttatus* adult female longevity. Several studies have shown that the number of mates a female has access to may influence female longevity, either by increasing longevity through the benefits of male-derived nutrients (Fox 1993, Fox et al. 1995) or decreasing longevity due to repeated male sexual harassment (Alcock et al. 1978, Walker 1980, Rice 2000), or through toxic substances in male seminal fluids (Fowler and Partridge 1989, Chapman et al. 1995). The similar longevity of females paired with zero, one, or two males indicates that the potential benefits and/or costs of mating on *A. auroguttatus* female longevity were either absent or too low to be quantified under quarantine conditions.

Influence of Diet on Female Fecundity and Adult Longevity. Lifetime oviposition for *A. auroguttatus* was greatest when females were fed a diet of a 10% honey-water solution and *Q. kelloggii* foliage, was reduced to zero when females were fed a water-only diet, and was intermediate when females were fed a water and *Q. kelloggii* leaf diet. Longevity was significantly greater when adults were fed a 10% honey-water and *Q. kelloggii* leaf diet. Sugar-enriched diets are known to increase the fecundity (Benschoter and Leal 1976, Heimpel et al. 1997, Baggen and Gurr 1998, Marchioro and Foerster 2013) and longevity (Benschoter and Leal 1976, Haynes 1985, Fadamiro and Baker 1999, Lauzière et al. 2000, Tisdale and Sappington 2001, Simmons et al. 2012) of many insects, and are therefore a useful and cost-effective addition to mass-rearing programs. *A. auroguttatus* females had an ~140–250% increase in average lifetime egg production, an approximate 44–97% increase in total oviposition period (i.e., 21–42 d longer), and lived, on average, ≈23–50 d longer (i.e., 27–69% longer) when given an additional carbohydrate resource in the form of 10% honey-water than females that were fed *Q. kelloggii* leaves and water only. The lack of oviposition from females given only water suggests that adult feeding on oak leaves is a necessary requirement for *A. auroguttatus* egg maturation and oviposition. However, the lack of diet-induced effects on *A. auroguttatus* larval emergence indicates that egg viability was not influenced by the consumption of additional carbohydrates in the 10% honey-water solution in combination with oak leaves.

Influence of Body Size on Female Fecundity and Adult Longevity. Lifetime oviposition, time to initial oviposition, larval emergence, and male and female longevity were not influenced by *A. auroguttatus* adult body size (i.e., elytron length or width, or hind tibia length). However, tibia length was marginally correlated with the total oviposition period of *A. auroguttatus* females. According to Honěk (1993), female size is usually a good indicator of potential fecundity, although there are studies where no significant relationships were found (Slansky 1980, Boggs 1986, Johnson 1990, Ohgushi 1996, Klingenberg and Spence 1997).

Large body size can enhance reproductive success in adults through physiological and behavioral advantages such as increased egg load and egg size (O'Neill and Skinner 1990, Ellers et al. 1998), and male competition for mates (Hanks et al. 1996, Forslund 2000). Adult body size and fecundity in female insects are genetically determined and modified by environmental conditions during development, which may influence reproduction and growth (Honěk 1993). Body size can also influence longevity, although factors such as temperature, diet, and the overall health of an individual (e.g., effects of sub-lethal chronic microbial infections) may play a greater role (Carroll and Quiring 1993, Nylin and Gotthard 1998, Sokolovska et al. 2000). As *A. auroguttatus* adults were reared from a

number of different oak hosts growing in the Cleveland National Forest, the environmental conditions during larval development (i.e., host quality) are unknown, but may have influenced the fecundity and longevity recorded in these experiments for both smaller and larger *A. auroguttatus* adults.

We conclude that information on the basic aspects of the reproductive biology of *A. auroguttatus* is a necessary foundation for developing species-specific management strategies targeting this pest, and for understanding and assessing factors affecting invasion risk into new areas. At this time, classical biological control is seen as the best option for managing *A. auroguttatus* in a forest environment, as the spread of this pest has become too great to control, contain, and eradicate with pesticides. Surveying for and identifying suitable egg parasitoids of *A. auroguttatus* from its home range in southern Arizona using sentinel egg masses is currently the major focus in the development of a classical biological control program for this pest (Lopez and Hoddle 2013). Our current inability to rear *A. auroguttatus* from eggs to adults in quarantine has changed the original focus of the biological control program from larval and pupal parasitoids found during surveys in Arizona (e.g., the parasitoid *Calosota elongata* Gibson [Hymenoptera: Eupelmidae]) (Gibson 2010, Coleman and Seybold 2011, Coleman et al. 2011) to prospecting for egg parasitoids. In the northeastern United States, release of *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), a solitary egg parasitoid of *A. planipennis*, has contributed up to 48% parasitism in emerald ash borer study sites (Duan et al. 2012). Although almost nothing is known about the parasitoid fauna associated with *A. auroguttatus* eggs, this life stage is easily obtainable in the laboratory from field-collected adults and can be easily and rapidly deployed at appropriate field sites in Arizona as sentinel egg masses before being returned to quarantine to rear out parasitoids (Lopez and Hoddle 2013). The results of work presented here demonstrate that to maximize the fecundity and longevity of *A. auroguttatus* females for mass rearing eggs in the laboratory, pairing females with one male and providing adults with a continuous diet of 10% honeywater and oak foliage is recommended. Further investigation into *A. auroguttatus* biology, such as the fecundity of singly mated females and the influence of different temperatures on adult longevity, egg production, and developmental rates, will help to determine whether continuous mating is necessary and the optimal temperatures to maximize fecundity and subsequent egg hatch.

Acknowledgments

We thank Mike Lewis, Allison Bistline, and Ruth Amrich (University of California, Riverside), as well as Amanda Mansfield, Scott Mansfield, and William Joseph, for their assistance with field and quarantine work. Thanks to Tom W. Coleman, Michael Jones, Greyland Walter (USDA Forest Service-Forest Health Protection, Region 5), and Laurel Haavik (Great Lakes Forestry Ctr, Sault Ste Marie, Canada) for providing infested oak logs used in this study. We also thank Karen Huaying Xu (University of California, Riverside) for help with statistical analyses. The comments of Paul F. Rugman-Jones, Anna L. Soper, and anonymous reviewers greatly improved earlier versions of this manuscript. We are very grateful to San Diego County Parks and Recreation and the William Heise County Park staff, especially David Moniz and Roger Covalt, for providing infested trees used in this study. We also thank the Camp Ole U.S. Forest Service Fire Station in Mt. Laguna, CA, for providing a secure location for our *A. auroguttatus* rearing tents. Funding for this study was supported, in part, by two agreements between the USDA Forest Service and the UC Riverside Department of Entomology: Cooperative Agreement #09-CA-11420004-357 and Joint Venture Agreement #10-JV-11272172-059.

References Cited

Alcock, J., E. M. Barrows, G. Gordh, L. Hubbard, L. Kirkendall, D. W. Pyle, T. L. Ponder, and F. G. Zalom. 1978. The ecology and evolution of male reproductive behaviour in the bees and wasps. Zool. J. Linnean Soc. 64: 293–326.

Allen-Diaz, B., R. B. Standiford, and R. D. Jackson. 2007. Oak woodlands and forests, pp. 313–338. *In* M. G. Barbour, T. Keeler-Woolf, and A. A. Schoenherr (eds.), Terrestrial Vegetation of California. University of California Press, Berkeley, CA.

Arnqvist, G., and T. Nilsson. 2000. The evolution of polyandry: multiple mating and female fitness in insects. Anim. Behav. 60: 145–164.

Baggen, L. R., and G. M. Gurr. 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Biol. Control 11: 9–17.

Benschoter, C. A., and M. P. Leal. 1976. Food requirements of adult cotton leaf perforators in the absence of cotton: effects of natural sugars on longevity and reproduction. Ann. Entomol. Soc. Am. 69: 432–434.

Blossey, B., D. Eberts, E. Morrison, and T. R. Hunt. 2000. Mass rearing the weevil *Hylobius transversovittatus* (Coleoptera: Curculionidae), biological control agent of *Lythrum salicaria*, on semiartificial diet. J. Econ. Entomol. 93: 1644–1656.

Boggs, C. L. 1986. Reproductive strategies of female butterflies: variation in and constraints on fecundity. Ecol. Entomol. 11: 7–15.

Boggs, C. L. 1990. A general model of the role of male-donated nutrients in female insects' reproduction. Am. Nat. 136: 598–617.

Buhle, E. R., M. Margolis, and J. L. Ruesink. 2005. Bang for buck: cost-effective control of invasive species with different life histories. Ecol. Econ. 52: 355–366.

Bybee, L. F., J. G. Millar, T. D. Paine, and C. C. Hanlon. 2005. Effects of single versus multiple mates: monogamy results in increased fecundity for the beetle *Phoracantha semipunctata.* J. Insect Behav. 18: 513–527.

Caldwell, R. L., and M. A. Rankin. 1974. Separation of migratory from feeding and reproductive behavior in *Oncopeltus fasciatus.* J. Comp. Physiol. 88: 383–394.

Carroll, A. L., and D. T. Quiring. 1993. Interactions between size and temperature influence fecundity and longevity of a tortricid moth, *Zeiraphera canadensis.* Oecologia 93: 233–241.

Chapman, T., L. F. Liddle, J. M. Kalb, M. F. Wolfner, and L. Partridge. 1995. Cost of mating in *Drosophila melano-*

gaster females is mediated by male accessory gland products. Nature 373: 241–244.

Coleman, T. W., and S. J. Seybold. 2008a. Previously unrecorded damage to oak, Quercus spp., in southern California by the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae). Pan-Pac. Entomol. 84: 288–300.

Coleman, T. W., and S. J. Seybold. 2008b. New pest in California: the goldspotted oak borer, *Agrilus coxalis* Waterhouse, p. 4. U.S. Dep. Agric. Forest Service. Pest Alert. R5-RP-022. 28 October 2008.

Coleman, T. W., and S. J. Seybold. 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, U.S.A. Coleopt. Bull. 65: 93–108.

Coleman, T. W., V. Lopez, P. Rugman-Jones, R. Stouthamer, S. J. Seybold, R. Reardon, and M. S. Hoddle. 2011. 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, T. W., A. D. Graves, M. Hoddle, Z. Heath, Y. Chen, M. L. Flint, and S. J. Seybold. 2012. Forest stand impacts associated with *Agrilus auroguttatus* Schaffer (Coleoptera: Buprestidae) and *Agrilus coxalis* Waterhouse in oak woodlands. For. Ecol. Manage. 276: 104–117.

Diamond, N. K., R. B. Standiford, P. C. Passof, and J. LeBlanc. 1987. Oak trees have varied effect on land values. Calif. Agric. 41: 4–6.

Duan, J. J., and C. Oppel. 2012. Critical rearing parameters of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae) as Affected by host plant substrate and host-parasitoid group structure. J. Econ. Entomol. 105: 792–801.

Duan, J. J., C. B. Oppel, M. D. Ulyshen, L. S. Bauer, and J. LeLito. 2011. Biology and life history of *Tetrastichus planipennisi* (Hymenoptera: Eulophidae), a larval endoparasitoid of the emerald ash borer (Coleoptera: Buprestidae). Fla. Entomol. 94: 933–940.

Duan, J. J., L. S. Bauer, J. A. Hansen, K. J. Abell, and R. Van Driesche. 2012. An improved method for monitoring parasitism and establishment of *Oobius agrili* (Hymenoptera: Encyrtidae), an egg parasitoid introduced for biological control of the emerald ash borer (Coleoptera: Buprestidae) in North America. Biol. Control 60: 255–261.

Ellers, J., J. J. Van Alphen, and J. G. Sevenster. 1998. A field study of size–fitness relationships in the parasitoid *Asobara tabida.* J. Anim. Ecol. 67: 318–324.

Ellison, A. M., M. S. Banks, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, G. M. Lovett, et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3: 479–486.

Fadamiro, H. Y., and T. C. Baker. 1999. Reproductive performance and longevity of female European corn borer, *Ostrinia nubilalis:* effects of multiple mating, delay in mating, and adult feeding. J. Insect Physiol. 45: 385–392.

Forslund, P.Å.R. 2000. Male–male competition and large size mating advantage in European earwigs, *Forficula auricularia.* Anim. Behav. 59: 753–762.

French, B. W., and L. Hammack. 2010. Reproductive traits of northern corn rootworm (Coleoptera: Chrysomelidae) in relation to female and male body size. Ann. Entomol. Soc. Am. 103: 688–694.

French, B. W., and L. Hammack. 2011. Multiple mating, fecundity, and longevity in female northern corn rootworm (Coleoptera: Chrysomelidae) in relation to body size. Ann. Entomol. Soc. Am. 104: 834–840.

Fowler, K., and L. Partridge. 1989. A cost of mating in female fruit flies. Nature 338: 760–761.

Fox, C. W. 1993. Multiple mating, lifetime fecundity and female mortality of the bruchid beetle, *Callosobruchus maculatus* (Coleoptera: Bruchidae). Funct. Ecol. 7: 203–208.

Fox, C. W., D. L. Hickman, E. L. Raleigh, and T. A. Mousseau. 1995. Paternal investment in a seed beetle (Coleoptera: Bruchidae): influence of male size, age, and mating history. Ann. Entomol. Soc. Am. 88: 100–103.

Gibson, G.A.P. 2010. Calosota Curtis (Hymenoptera, Chalcidoidea, Eupelmidae): review of the New World and European fauna including revision of species from the West Indies and Central and North America. ZooKeys 55: 1–75.

Gould, J. R., T. Ayer, and I. Fraser. 2011. Effects of rearing conditions on reproduction of *Spathius agrili* (Hymenoptera: Braconidae), a parasitoid of the emerald ash borer (Coleoptera: Buprestidae). J. Econ. Entomol. 104: 379–387.

Haavik, L. J., T. W. Coleman, M. L. Flint, R. C. Venette, and S. J. Seybold. 2013. *Agrilus auroguttatus* (Coleoptera: Buprestidae) seasonal development within *Quercus agrifolia* (Fagales: Fagaceae) in Southern California. Ann. Entomol. Soc. Am. 106: 189–197.

Hanks, L. M., J. G. Millar, and T. D. Paine. 1996. Body size influences mating success of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). J. Insect Behav. 9: 369–382.

Haynes, J. 1985. Sterile boll weevils (Coleoptera: Curculionidae) fed 10% sugar diets: effect on longevity, mating, and flight. J. Econ. Entomol. 78: 783–786.

Heimpel, G. E., J. A. Rosenheim, and D. Kattari. 1997. Adult feeding and lifetime reproductive success in the parasitoid *Aphytis melinus.* Entomol. Exp. Appl. 83: 305–315.

Honeǩ, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. Oikos 66: 483–492.

Huntsinger, L., L. Buttoloph, and P. Hopkinson. 1997. Ownership and management changes on California hardwood rangelands: 1985 to 1992. J. Range Manage. 50: 423–430.

Jennions, M. D., and M. Petrie. 2000. Why do female mates multiply? A review of genetic benefits. Biol. Rev. 75: 21–64.

Johnson, M. D. 1990. Female size and fecundity in the small carpenter bee, *Ceratina calcarata* (Robertson) (Hymenoptera: Anthophoridae). J. Kans. Entomol. Soc. 63: 414–419.

Jones, M. I., T. W. Coleman, A. D. Graves, A. D., Flint, M. L., and S. J. Seybold. 2013. Sanitation options for managing oak wood infested with the invasive goldspotted oak borer (Coleoptera: Buprestidae) in Southern California. J. Econ. Entomol. 106: 235–246.

Keena, M. A. 2002. *Anoplophora glabripennis* (Coleoptera: Cerambycidae) fecundity and longevity under laboratory conditions: comparison of populations from New York and Illinois on *Acer saccharum.* Environ. Entomol. 31: 490–498.

Klingenberg, C. P., and J. Spence. 1997. On the role of body size for life-history evolution. Ecol. Entomol. 22: 55–68.

Lauzière, I., G, Pèrez-Lachaud, and J. Brodeur. 2000. Effect of female body size and adult feeding on the fecundity and longevity of the parasitoid *Cephalonomia stephanoderis* Betrem (Hymenoptera: Bethylidae). Ann. Entomol. Soc. Am. 93: 103–109.

Liu, H., L. S. Bauer, D. L. Miller, T. Zhao, R. Gao, L. Song, Q. Luan, R. Jin, and C. Gao. 2007. Seasonal abundance

of *Agrilus planipennis* (Coleoptera: Buprestidae) and its natural enemies *Oobius agrili* (Hymenoptera: Encyrtidae) and *Tetrastichus planipennis* (Hymenoptera: Eulophidae) in China. Biol. Control 42: 61–71.

Lopez, V. M., and M. S. Hoddle. 2013. Mortality factors affecting *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) eggs in the native and invaded ranges. Biol. Control 67: 143–148.

Loerch, C. R., and E. A. Cameron. 1984. Within tree distributions and seasonality of immature stages of the bronze birch borer, *Agrilus anxius* (Coleoptera: Buprestidae). Can. Entomol. 116: 147–152.

Marchioro, C. A., and L. A. Foerster. 2013. Effects of adult-derived carbohydrates and amino acids on the reproduction of *Plutella xylostella.* Physiol. Entomol. 38: 13–19.

Millar, J. G., T. D. Paine, A. L. Joyce, and L. M. Hanks. 2003. The effects of Eucalyptus pollen on longevity and fecundity of Eucalyptus longhorned borers (Coleoptera: Cerambycidae). J. Econ. Entomol. 96: 370–376.

Nylin, S., and K. Gotthard. 1998. Plasticity in life-history traits. Annu. Rev. Entomol. 43: 63–83.

Ohgushi, T. 1996. Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle. Ecol. Entomol. 21: 47–55.

O'Neill, K. M., and S. W. Skinner. 1990. Ovarian egg size and number in relation to female size in five species of parasitoid wasps. J. Zool. 220: 115–122.

Purdom, C. E., K. F. Dyer, and D. G. Papworth. 1968. Spontaneous mutation in Drosophila: studies on the rate of mutation in mature and immature male germ cells. Mutat. Res. 5: 133–146.

Rice, W. R. 2000. Dangerous liaisons. Proc. Natl. Acad. Sci. 97: 12953–12955.

Ridley, M. 1988. Mating frequency and fecundity in insects. Bio. Rev. 63: 509–549.

Sakurai, T. 1998. Receptivity of female remating and sperm number in the sperm storage organ in the bean bug, *Riptortus clavatus* (Heteroptera: Alydidae). Res. Pop. Ecol. 40: 167–172.

SAS Institute Inc. 2008. SAS 9.2 Enhanced Logging Facilities. SAS Institute Inc., Cary, NC.

Shea, K., and D. Kelly. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. Ecol. Appl. 8: 824–832.

Simmons, A. M., J. C. Legaspi, and B. C. Legaspi, Jr. 2012. Adult survival of *Delphastus catalinae* (Coleoptera: Coccinellidae), a predator of whiteflies (Hemiptera: Aleyrodidae), on diets of whiteflies, honeydew, and honey. Environ. Entomol. 41: 669–675.

Slansky, F. 1980. Quantitative food utilization and reproductive allocation by adult milkweed bugs, *Oncopeltus fasciatus.* Physiol. Entomol. 5: 73–86.

Sokolovska, N., L. Rowe, and F. Johansson. 2000. Fitness and body size in mature odonates. Ecol. Entomol. 25: 239–248.

Standiford, R. B., and P. Tinnin. 1996. Guidelines for managing California's hardwood rangelands. University of California Division of Agriculture and Natural Resources. Leaflet no. 3368.

Tisdale, R. A., and T. W. Sappington. 2001. Realized and potential fecundity, egg fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. Ann. Entomol. Soc. Am. 94: 415–419.

Tsubaki, Y., and M. Yamagishi. 1991. 'Longevity' of sperm within the female of the melon fly, *Dacus cucurbitae* (Diptera: Tephritidae), and its relevance to sperm competition. J. Insect Behav. 4: 243–250.

Venette, R. C., D. J. Kriticos, R. D. Magarey, F. H. Koch, R. H. Baker, S. P. Worner, N. N. Gómez-Raboteaux, D. W. McKenney, E. J. Dobesberger, D. Yemshanov, et al. 2010. Pest risk maps for invasive alien species: a roadmap for improvement. BioScience. 60: 349–362.

Walker, W. F. 1980. Sperm utilization strategies in insects. Am. Nat. 115: 780–799.

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

Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, NJ.

Received 7 October 2013; accepted 27 November 2013.