Assessing the Flight Capabilities of the Goldspotted Oak Borer (Coleoptera: Buprestidae) With Computerized Flight Mills

Author(s): Vanessa M. Lopez, Michael N. Mcclanahan, Laurie Graham, and Mark S. Hoddle
Source: Journal of Economic Entomology, 107(3):1127-1135. 2014.
Published By: Entomological Society of America
URL: http://www.bioone.org/doi/full/10.1603/EC13525

FOREST ENTOMOLOGY

Assessing the Flight Capabilities of the Goldspotted Oak Borer (Coleoptera: Buprestidae) With Computerized Flight Mills

VANESSA M. LOPEZ,[1] MICHAEL N. MCCLANAHAN,[2] LAURIE GRAHAM,[3]
AND MARK S. HODDLE[1,4,5]

J. Econ. Entomol. 107(3): 1127–1135 (2014); DOI: http://dx.doi.org/10.1603/EC13525

ABSTRACT The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is native to southern Arizona and is an invasive wood-boring beetle that has caused considerable mortality to native oak species in southern California. Assessing the dispersal capabilities of this woodborer may help to determine its potential environmental and economic risk within the invaded region, and possibly assist with the development of species-specific management strategies. The flight performance of *A. auroguttatus* adults under different age, mating, and nutritional status was assessed by tethering individuals to computerized flight mills for a 24-h trial period to collect information on total distance flown, flight times and velocities, number and duration of flight bouts, and postflight weight. The nutritional status and body size (i.e., elytron length) of *A. auroguttatus* adults had a significant influence on overall flight performance. Mating status and gender had no significant influence on total flight distance, duration, velocity, and flight bout time. Significant interactions between nutritional status and age were observed in the overall flight performance of *A. auroguttatus*, with decreased flight activity in old (≈6 d of age) starved individuals during a 24-h trial period. Overall, results of these flight mill assays indicate that *A. auroguttatus* is unable to disperse long distances across habitats that lack suitable oak hosts. This work supports the hypothesis that human-aided transportation via infested oak firewood from southern Arizona across the Sonoran desert likely caused the initial introduction, and subsequent satellite infestations of *A. auroguttatus* within southern California's native oak woodlands.

KEY WORDS dispersal, flight activity, flight mill, invasive species

When introduced insects become pestiferous in adventive areas, studies examining their dispersal capabilities can aid in determining the biological and abiotic factors that may influence rates of spread and establishment into new areas. Invasive species, such as insect pests, can be particularly damaging to forest ecosystems, causing severe economic and environmental impacts (Pimentel et al. 2000, Lovett et al. 2006, Holmes et al. 2009, Kenis et al. 2009). Millions of dollars are spent annually managing insect forest pests because their negative effects on invaded ecosystems are often widespread and long-lasting (Pimentel et al. 2005, Kovacs et al. 2010, Van Driesche et al. 2010). Therefore, identifying and understanding traits that promote the proliferation and expansion of invasive species in natural forest ecosystems can help to determine the potential environmental and economic risk these species pose, and possibly allow the development of species-specific management strategies that mitigate their negative effects.

The goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), is a small (adults are ≈10 mm in length) invasive wood-boring pest of native oaks within urban and natural environments in southern California (CA). Indigenous to southern Arizona (AZ), *A. auroguttatus* was likely introduced into southern CA through the transportation of infested oak firewood, and was initially detected in the Cleveland National Forest, San Diego County, CA, in 2004 (Westcott 2005). In this area, >212,460 ha of native forest are infested with this pest and it has been estimated that ≈25,000 coast live oak (*Quercus agrifolia* Née), California black oak (*Quercus kelloggii* Newb.), and canyon live oak (*Quercus chrysolepis* Liebm.) have been killed because of larval feeding damage to the phloem/xylem interface (Coleman et al. 2012a, USDA-FS-FHM 2013).

Owing to the proximity (≈550 km) of the native AZ range of *A. auroguttatus* to southern CA, Westcott (2005) hypothesized that this species naturally expanded its distribution into CA. However, this seems unlikely due to significant geographical barriers such

---

[1] Department of Entomology, University of California, Riverside, CA 92521.

[2] Bourns College of Engineering (Retired), University of California, Riverside, CA 92521.

[3] Department of Biology, University of California, Riverside, CA 92521.

[4] Center for Invasive Species Research, University of California, Riverside CA 92521.

[5] Corresponding author, e-mail: mark.hoddle@ucr.edu.

as the Mojave and Sonoran deserts, which lack suitable oak hosts required for adult feeding (i.e., oak leaves) and larval development (i.e., live oak trees in the red oak group, section *Lobatae,* with trunk diameters >12 cm).

In 2009, a satellite infestation was found at Marion Bear Memorial Park in urban San Diego, CA, ≈32 km west of major infestation zones (Coleman et al. 2012b). Another satellite infestation was discovered in fall 2012, in Idyllwild, Riverside County, CA, ≈70 km north of the closest known infestation (Jones et al. 2013). It is unknown how *A. auroguttatus* spreads to these new areas, but the movement of infested oak firewood is the most likely explanation for the appearance of these isolated populations. The proximity of initial CA populations to recreation areas such as the Laguna Mountain Recreation Area in the Cleveland National Forest, Rancho Cuyamaca State Park, and William Heise County Park (all in San Diego County with recreational camping facilities) anecdotally supports the hypothesis that *A. auroguttatus* was introduced from AZ into southern CA through firewood associated with outdoor recreational activities (e.g., camping). Although firewood movement is suspected to be a major dispersal mechanism for *A. auroguttatus,* the alternative hypothesis, natural dispersal by flight, cannot be discounted because information on the flight potential of this beetle is lacking.

Flight mills are a practical tool for gaining insight into the flight capabilities of an insect owing to their easy use within a controlled environment. However, because the behavioral effects of handling during attachment to the flight mill are largely unknown and difficult to define and quantify, flight mill studies may need to be interpreted with caution (Taylor et al. 2010). An approach for overcoming this challenge may be to simply compare the performance of two or more experimental groups of comparable size (Rowley et al. 1968). Through comparison, insight into the effects of biotic conditions (i.e., sex, mating status, age, etc.) on flight performance is obtained and can help in the overall assessment of an insect's dispersal potential. Another criticism of flight mill studies is that they may not be truly representative of flight performance in the field because they are conducted in the laboratory, and therefore lack environmental stimuli normally encountered by a flying insect in the wild (Taylor et al. 2010). Although laboratory studies lack environmental components that potentially influence flight behavior, they can be useful for research attempting to quantify basic attributes such as the frequency of flight bouts, and distance, velocity, and duration of flight. These types of data are almost impossible to collect accurately in the field. At a minimum, flight mill studies provide estimates (with measures of variation) of certain flight-related characteristics that can later be used for designing field dispersal studies and interpreting data from these experiments.

Dispersal characteristics of invasive insects may be influenced by variable traits such as age, sex, and mating status. Understanding these effects on flight activity may help enhance risk assessment analyses that are aimed at developing effective management strategies, such as the implementation of quarantine zones around newly infested areas (Landis 2004, Neubert and Parker 2004, Lodge et al. 2006, Jongejans et al. 2008, Sarvary et al. 2008, Koch et al. 2009). Because the flight capabilities of *A. auroguttatus* were unknown before this study was conducted, adults of varying age, mating, and nutritional status were flown on flight mills to determine their combined effects on flight performance. This work is the first to evaluate the dispersal potential of *A. auroguttatus.*

Materials and Methods

Collection and Rearing of *A. auroguttatus* Adults for Flight Mill Studies. Field-collected *A. auroguttatus* adults were reared from infested *Q. agrifolia and Q. kelloggii* trees that were felled in April 2012 at William Heise County Park, Julian, CA, cut into rounds (≈30 by 60 cm), and placed inside 15 emergence tents (1.83 by 1.83 by 1.83-m Lumite screen portable field cages, Bioquip Products, Rancho Dominguez, CA). During June to August 2012, adults were collected daily from emergence tents (located at William Heise County Park), each of which contained ≈15 *A. auroguttatus*-infested oak rounds. From these daily collections, adults were immediately sexed (Coleman and Seybold 2010), and randomly assigned to 1 of 16 experimental treatments shown in Tables 1 and 2. Following treatment designation, adults were placed in 1-l hand-grip rearing containers (9.2 by 9.5 by 14.6 cm, Candy Concepts Inc., Pewaukee, WI) until flown. Rearing containers had a 4-cm-diameter ventilation hole that was covered with fine metal mesh screen, and were held under ambient laboratory conditions (14:10 (L:D) h, 24 ± 4°C, 35 ± 5% RH).

Designation of *A. auroguttatus* Adults to Experimental Treatments. The treatment combinations shown in Tables 1 and 2 were created by immediately designating field-collected male and female *A. auroguttatus* adults to one of each of the following categories: starved or fed, virgin or mated, and young or old. Adults in starved treatments were placed into rearing containers without food or water until flown. Fed adults were placed inside rearing containers provided with host plant leaves (*Q. kelloggii*) and water (via a moist cotton wick), which were replaced every 3–4 d, a time interval shown in preliminary studies to be adequate. To obtain virgin beetles, adults that emerged inside their respective rearing tents without others of the opposite sex were placed individually into rearing containers on collection. Mated individuals were acquired by placing one male and one female together inside a rearing container until copulation was observed and documented. Typically, copulation occurred shortly after adults were paired, although occasionally (≈25% of matings), several days of observation were needed to confirm mating had occurred. Adult beetles that were <2-d-old were considered "young," and adults that were >5 d of age were considered "old."

Table 1. Average (mean ± SE) flight parameters measured for starved *A. auroguttatus* adults under varying gender, age, and mating status

Flight parameter	Starved							
	Male				Female			
	Young		Old		Young		Old	
	Virgin	Mated	Virgin	Mated	Virgin	Mated	Virgin	Mated
Total distance flown (m)	379.85 ± 89.54	270.23 ± 69.87	253.26 ± 122.59	145.81 ± 99.76	926.15 ± 177.85	900.12 ± 198.50	422.14 ± 103.70	197.68 ± 79.20
Total flight time (min)	46.74 ± 10.81	40.36 ± 9.17	46.74 ± 25.34	13.30 ± 7.31	80.55 ± 18.49	82.29 ± 15.78	52.29 ± 10.21	33.12 ± 8.22
Flight velocity (m/s)	0.14 ± 0.02	0.13 ± 0.04	0.09 ± 0.03	0.15 ± 0.07	0.27 ± 0.07	0.18 ± 0.03	0.14 ± 0.03	0.08 ± 0.02
No. of flight bouts	126.9 ± 24.7	116.2 ± 23.9	108.9 ± 41.8	35.5 ± 15.6	178.6 ± 36.7	160.3 ± 21.18	178.8 ± 34.9	95.5 ± 22.1
Flight bout time (s)	19.49 ± 2.60	24.72 ± 4.05	18.12 ± 2.69	17.49 ± 3.14	25.72 ± 3.22	30.03 ± 4.74	19.02 ± 2.66	19.6 ± 2.8
Elytron length (mm)	6.99 ± 0.18	7.16 ± 0.12	7.16 ± 0.19	7.11 ± 0.18	8.25 ± 0.07	7.74 ± 0.18	8.16 ± 0.14	8.32 ± 0.14
Total wt loss (mg)	2.90 ± 0.81	1.91 ± 0.28	1.90 ± 0.35	2.18 ± 0.40	2.36 ± 0.43	1.83 ± 0.30	2.23 ± 0.26	2.23 ± 0.23
n	10	11	10	11	11	12	13	13

Table 2. Average (mean ± SE) flight parameters measured for fed *A. auroguttatus* adults under varying gender, age, and mating status

Flight parameter	Fed							
	Male				Female			
	Young		Old		Young		Old	
	Virgin	Mated	Virgin	Mated	Virgin	Mated	Virgin	Mated
Total distance flown (m)	592.15 ± 188.28	654.08 ± 158.61	1078.22 ± 240.04	1011.62 ± 185.37	1077.22 ± 475.43	842.23 ± 195.61	1889.46 ± 494.39	1761.26 ± 253.28
Total flight time (min)	59.59 ± 15.60	71.79 ± 16.32	83.55 ± 15.01	81.90 ± 17.50	73.26 ± 30.46	63.96 ± 18.28	84.76 ± 19.72	108.35 ± 18.60
Flight velocity (m/s)	0.23 ± 0.06	0.27 ± 0.08	0.18 ± 0.03	0.30 ± 0.06	0.22 ± 0.04	0.28 ± 0.08	0.41 ± 0.05	0.28 ± 0.03
No. of flight bouts	152.5 ± 30.3	172.0 ± 40.0	169.2 ± 29.7	160.8 ± 30.6	106.9 ± 26.1	109.6 ± 25.1	108.3 ± 17.0	226.2 ± 33.7
Flight bout time (s)	23.97 ± 3.47	29.53 ± 4.11	27.99 ± 4.26	34.35 ± 5.47	33.62 ± 9.56	33.34 ± 6.84	45.77 ± 8.38	75.13 ± 43.52
Elytron length (mm)	7.13 ± 0.23	7.04 ± 0.17	6.98 ± 0.17	6.98 ± 0.22	7.65 ± 0.29	7.65 ± 0.32	7.79 ± 0.14	8.01 ± 0.08
Total wt loss (mg)	2.40 ± 0.34	2.20 ± 0.39	2.64 ± 0.43	2.85 ± 0.30	2.50 ± 0.40	4.02 ± 0.90	3.25 ± 0.39	3.77 ± 0.26
n	10	10	11	13	10	12	12	13

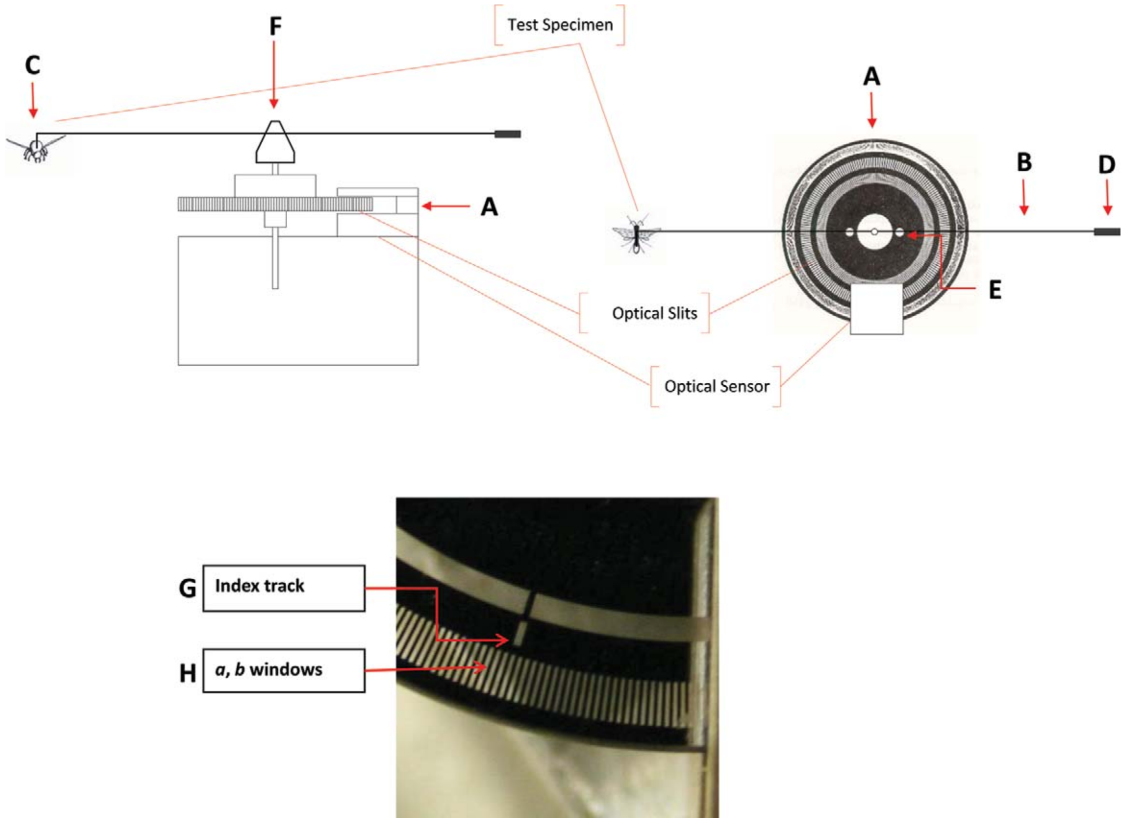

Fig. 1. Diagram of flight mill used to investigate the flight capabilities of *Agrilus auroguttatus*. The encoder (including the encoder disc's optical slits and sensor) (A), flight mill arm (FMA) (B), L-shaped flight mill arm attachment (C), counterbalance (D), encoder shaft (E), encoder coupling (F), encoder inner index track (G), and encoder disc showing outer ring (H) are illustrated. (Online figure in color.)

Computerized Flight Mills. Seven flight mills were set-up inside a mobile laboratory (14:10 (L:D) h, 24 ± 4°C, 35 ± 5% RH) located at the William Heise County Park in San Diego County, CA. Each flight mill was connected to a laptop computer via a USB4 Encoder Data Acquisition Device (U.S. Digital, Vancouver, WA), which was operated with customized LabVIEW software (National Instruments Corporation, Austin, TX) that recorded flight activity. Raw flight data were summarized using customized Visual Basic for Applications macros in Microsoft Excel, which calculated average flight velocity, total flight duration time, number of flight bouts (movement of >5 s before coming to a complete stop), and distances flown during each flight bout over a 24-h period by individual *A. auroguttatus* adults.

Recording of Flight Measurements. To measure and record insect flight, a quadrature encoder (model 7700, Gurley Precision Instruments, Troy, NY) inside each flight mill (Fig. 1) provided both timing and arc travel direction information from flight activity (described later), which was used to calculate flight parameters including velocity, distance, and duration. The encoder (Fig. 1) is composed of a 33-mm-diameter transparent disc with an opaque pattern of slits extending 2 mm radially near the edge (Fig. 1). The slit pattern allows an IR source to pass through the disc to optical sensors. Two sensors (*a* and *b*) (Fig. 1) are positioned such that if the disc travels clockwise, the rising edge of the *a* pulse is measured first, followed by the rising edge of the *b* pulse. When the disc is traveling counterclockwise, the rising edge of the *b* pulse is detected first. A third detector (*z*) sees a single index slit placed on an inner concentric track to mark the 0 position of the disc, which gives a reference, or home position.

As the encoder disc rotates, the slits pass over the sensors and a square-wave pulse train is generated. The resulting signal pulse train is read by the USB4 Encoder Data Acquisition Device. The acquisition device counts the pulse number since the last index was sensed, and clocks the time delta between rising edges with an internal high-frequency clock. Flight data were generated by attaching the insect to the encoder shaft (Fig. 1) by means of a 0.5-mm carbon steel flight mill arm (FMA) wire (30.5 cm in length) (see explanation). The FMA was supported by the encoder shaft with a coupling (Fig. 1), and an equal length of the FMA wire passed through the coupling.

Fig. 2. Adult *A. auroguttatus* tethered by the pronotum to a flight mill. (Online figure in color.)

For every complete revolution, the end of the FMA travels a distance approximately equal to the circumference of a circle whose radius equals the length of the FMA from the encoder shaft (center of the circle) to the insect specimen. The encoder returns values between 0 and 500 depending on the position of the arm. Because the pulse value 0 (at the encoder index) is equal to 0 radians and the pulse value 500 is equal to 2 radians, these values are converted to radians. To determine the distance traveled between each pulse, the difference between the latest pulse value and the previous pulse value is found. Direction of the FMA's movement (i.e., clockwise or counterclockwise) is taken into account when calculating this difference (note that individual insects are only able to fly in one direction once they are connected to the FMA). The resulting value is converted into radians and the arc length for the angle is calculated. The rate at which the end of the FMA travels for the period between the latest pulse and the previous pulse is calculated from this distance value and the time difference between the latest pulse and the previous pulse.

Calibration of Flight Mills. To estimate the accuracy of the pulse counter, its output was compared with a second calibration pulse counter with five times the resolution of the flight unit being used. The test unit pulse counter and the calibration pulse counter were linked and driven at the same speed by a motor. Pulse frequencies for both pulse counters were measured over a specified period with a TLS 216 Logic Scope (Tektronix, Beaverton, OR). The TLS 216 was calibrated with an HP pulse generator (model 3324A, Hewlett–Packard, Boeblingen, Germany). For each flight calibration sample, the ratio of the calibration frequency to test unit frequency was calculated and compared with the expected ratio of 5.00. Ninety samples were obtained from three randomly selected flight mills and assessed at three different motor speeds. The mean ratio (±SE) from calibration studies was 5.0039 ± 0.0021, confirming the accuracy of pulse information generated by flight mills.

Attachment of *A. auroguttatus* Adults to Flight Mills. Following treatment designation, adults were weighed with a precision balance (model GF-600, A&D Company Ltd., Milpitas, CA), then tethered by the pronotum to the arm of a flight mill (Fig. 2) via the FMA attachment (Fig. 1) and left for 24 h. A piece of modeling clay was weighed and placed at the opposite end of the FMA to counterbalance the weight of each tethered adult (Fig. 1). To attach the study insect to the FMA, *A. auroguttatus* adults were fastened by the pronotum, using high-strength glue (Gorilla Glue Company, Cincinnati, OH), to a small (0.59-mm-diameter by 28-mm-long) L-shaped wire that was flattened at one end. The L-shaped wire with the attached beetle was connected to a standard socket crimp (model 809-043, Glenair, Glendale, CA), which was directly connected to the FMA. After gluing and before flight data being recorded, free wing movement was visually confirmed (Fig. 2). Following each 24-h flight trial, individual *A. auroguttatus* adults were detached from flight mills, immediately weighed, and elytron length was measured with an electronic 0–200-mm digital caliper. After the 24-h flight trial, any dead individuals detached from flight mills were discarded and excluded from the analyses, although this was rare (<5% of beetles flown).

Statistical Analysis. The flight performance of *A. auroguttatus* adults under varying age, mating, and nutritional status was analyzed using analysis of covariance. Covariates included a measurement of adult body size (elytron length) and weight. Measurements of flight performance included total distance flown (m), total flight time (min), average flight velocity (m/s), number of flight bouts, and average flight bout time (s). For analyses of research variables, model assumptions were satisfied by conducting the following mathematical transformations (where y = research variable): total distance flown: $y^{0.3}$; total flight time: $y^{0.35}$; average velocity: $y^{0.4}$; number of flight bouts: $y^{0.5}$; and average flight bout time: $y^{-0.5}$. Tukey–Kramer tests were used to conduct pairwise comparisons for each significant factor in the analysis of covariance. When significant interactions occurred, contrasts to determine the effects of interacting variables were conducted. All statistical analyses were conducted at the 0.05 level of significance and were performed using SAS 9.2 (SAS Institute Inc. 2008).

Results

Average Total Flight Distance. The average total distance flown by *A. auroguttatus* adults during the 24-h flight period (Tables 1 and 2) was significantly influenced by nutritional status ($F_{1,\ 177} = 62.53$, $P \leq 0.0001$), with fed adults flying greater distances than starved individuals. Elytron length had a significant effect on average flight distance ($F_{1,\ 177} = 48.82$, $P \leq 0.0001$), with larger adults flying greater distances than smaller individuals (coefficient estimation for covariate ± SE = 1.49 ± 0.21). Preflight weight, mating status, and gender did not have an effect on the total average distance flown during a trial period ($P \geq 0.05$). A significant interaction between nutritional status and age ($F_{1,\ 177} = 37.74$, $P \leq 0.0001$) existed; old fed adults flew further than old starved adults ($F_{1,\ 177} = 103.83$, $P \leq 0.0001$). However, nutritional effects were not significant in the total flight distance of young *A. auroguttatus* adults ($F_{1,\ 177} = 1.61$, $P = 0.21$).

Average Total Flight Duration. The average total flight time of *A. auroguttatus* adults during the 24-h trial period (Tables 1 and 2) was significantly affected by nutritional status ($F_{1,\ 177} = 17.88$, $P \leq 0.0001$), with fed adults flying longer than starved individuals. Elytron length had a significant effect on average flight duration ($F_{1,\ 177} = 20.77$, $P \leq 0.0001$), with larger adults flying longer than smaller individuals (coefficient estimation ± SE = 2.58 ± 0.57). Preflight weight, mating status, and gender had no significant effect on total flight duration ($P \geq 0.05$). There was a significant interaction between nutrition and age ($F_{1,\ 177} = 14.9$, $P = 0.0002$). Age had an effect on total average flight duration when adults were starved ($F_{1,\ 177} = 12.88$, $P = 0.0004$), but not when adults were fed ($F_{1,\ 177} = 3.52$, $P = 0.06$). However, the effects of nutrition (for both starved and fed adults) on total flight time were significant only in old individuals ($F_{1,\ 177} = 34.47$, $P \leq 0.0001$), which flew less during the 24-h trial period when starved.

Average Velocity. The average velocity of *A. auroguttatus* adults during flight (Tables 1 and 2) was significantly affected by nutritional status ($F_{1,\ 177} = 37.90$, $P \leq 0.0001$), with fed adults flying faster than starved individuals. Elytron length had a significant effect on average velocity ($F_{1,\ 177} = 23.75$, $P \leq 0.0001$), with larger adults flying faster than smaller individuals (coefficient estimation ± SE = 0.08 ± 0.02). There was no significant effect on average velocity due to preflight weight, mating status, or gender ($P \geq 0.05$). However, there was a significant interaction between nutritional status and age ($F_{1,\ 177} = 14.02$, $P = 0.0002$). Age had an effect on average velocity when adults were starved ($F_{1,\ 177} = 13.65$, $P = 0.0003$), but not when adults were fed ($F_{1,\ 177} = 2.53$, $P = 0.11$). However, the effects of nutrition (for both starved and fed adults) on average flight velocity were significant only for old individuals ($F_{1,\ 177} = 51.62$, $P \leq 0.0001$), which had lower average flight velocities when starved. The effects of nutrition were not significant in young *A. auroguttatus* adults ($F_{1,\ 177} = 2.90$, $P = 0.09$).

Total Number of Flight Bouts. The total number of flight bouts in a 24-h flight trial (Tables 1 and 2) was significantly affected by nutritional status ($F_{1,\ 173} = 6.15$, $P = 0.01$) and body size ($F_{1,\ 173} = 10.81$, $P = 0.0012$). Preflight weight had no significant effect on the total number of flight bouts ($P > 0.05$). Significant interactions were observed between nutritional status and gender ($F_{1,\ 173} = 6.13$, $P = 0.01$), age ($F_{1,\ 173} = 9.48$, $P = 0.002$), and mating status ($F_{1,\ 173} = 5.16$, $P = 0.02$). The effects of gender on the number of flight bouts were only observed in fed adults ($F_{1,\ 173} = 4.66$, $P = 0.03$), and in fed adults, these nutrition effects were significant for male *A. auroguttatus* ($F_{1,\ 173} = 11.84$, $P = 0.0007$), but not for females. Alternatively, the significant effects between nutrition and age on the number of flight bouts were observed in starved ($F_{1,\ 173} = 8.36$, $P = 0.004$), old ($F_{1,\ 173} = 16.18$, $P \leq 0.0001$) individuals irrespective of gender. Finally, the interaction between nutritional and mating status showed significant effects in mated individuals ($F_{1,\ 173} = 11.89$, $P = 0.0007$), which had a lower number of flight bouts than virgin adults when deprived of food.

Average Flight Bout Time. The average time individual *A. auroguttatus* adults flew during each flight bout (Tables 1 and 2) was significantly influenced by nutritional status ($F_{1,\ 177} = 31.10$, $P \leq 0.0001$) and body size ($F_{1,\ 177} = 12.84$, $P = 0.0004$). However, there was no significant effect on average flight bout time due to preflight weight, mating status, or gender ($P \geq 0.05$). Significant interactions were observed between nutritional status and age ($F_{1,\ 177} = 14.41$, $P = 0.0002$). The effects of age were significant in starved ($F_{1,\ 177} = 11.95$, $P = 0.0007$) individuals, which resulted in a general decrease in average flight bout time compared with fed adults. Effects of nutrition were observed in old *A. auroguttatus* adults ($F_{1,\ 177} = 46.23$, $P \leq 0.0001$), which flew shorter flight bouts when starved.

Average Total Weight Loss. Nutritional status, preflight weight, and elytron length had a significant effect on total average weight loss following the 24-h flight trial (Tables 1 and 2). Fed adults lost significantly more weight after being tethered to flight mills for 24 h than starved individuals ($F_{1,\ 178} = 19.05$, $P \leq 0.0001$). In addition, *A. auroguttatus* adults with a heavier preflight weight and larger body size (elytron length) lost significantly more weight after being tethered to flight mills for 24 h ($F_{1,\ 178} = 17.35$, $P \leq 0.0001$, and $F_{1,\ 178} = 7.35$, $P = 0.0074$, respectively). Coefficient estimations (±SE) for preflight weight and elytron length were 0.28 ± 0.07, and 0.004 ± 0.001, respectively. Gender, age, and mating status had no significant effect on postflight weight loss ($P \geq 0.05$).

Discussion

Assessing the flight potential of *A. auroguttatus* adults of varying age, mating, and nutritional status using computerized flight mills provided the first information on the dispersal potential of this invasive beetle. The nutritional status and body size (elytron length) of *A. auroguttatus* adults had a significant influence on overall flight performance. The total distance, flight time, velocity, number and duration of flight bouts, and postflight weight loss were greater in larger, fed individuals when tethered to flight mills and flown for a 24-h trial period. Because flight is a very energy-intensive activity, the enhanced flight performance of fed adults is not surprising (Thompson and Bennett 1971, Candy et al. 1997). Although elytron length was correlated with overall flight performance (e.g., flight distance and duration), preflight weight was not. While greater body mass could represent more flight muscle mass, body weight also includes lipid and water content, and nonflight musculature (Shelton et al. 2006), which may explain its lack of influence on *A. auroguttatus* flight. However, the correlation of preflight weight with the total amount of weight lost following 24-h flight trials suggests that heavier adults used more energy-producing resources during flight than lighter individuals.

The influence of mating status and gender did not impact total flight distance, duration, velocity, and flight bout time of *A. auroguttatus.* In contrast, the flight distance and duration of mated emerald ash borer (*Agrilus planipennis* Fairmaire) females was significantly greater than unmated females and males when tethered to flight mills, which suggested that females of this species may be programmed for dispersal flights following mating (Taylor et al. 2010). However, the lack of mating and gender effects on the overall flight performance of *A. auroguttatus* adults is similar to that reported for the plum curculio *Conotrachelus nenuphar* (Herbst) (Chen et al. 2006) and the Chinese white pine beetle (*Dendroctonus armandi*) (Chen et al. 2011), respectively.

Significant interactions between nutrition and age were observed in the total flight distance, flight time, velocity, number of flight bouts, and flight bout time for *A. auroguttatus.* Age had a significant effect on flight performance when adults were starved, but not when adults were fed, which resulted in overall decreased flight activity in old, starved individuals during the 24-h trial period. These results suggest a more pronounced effect of nutrition rather than an age by nutrition interaction because old, starved beetles were essentially starved for a longer period. The reduced flight performance of old *A. auroguttatus* individuals under starvation conditions points to the difficulty for long-distance dispersal by this species across habitats that lack suitable oak hosts, especially considering the age of "old" individuals in this study (typically 6-d-old). Old, starved *A. auroguttatus* flew an average of 255 m in 24 h. Considering the average dispersal capabilities of these individuals, it would take ≈6 yr to travel from oak woodlands in southern AZ to San Diego County (a distance of ≈550 km). When the average distance flown by all individuals (i.e., all treatments pooled) in this study (≈790 m in 24 h) is taken into account, a dispersal of 550 km would require ≈2 yr of continuous flight. Therefore, it appears unlikely that *A. auroguttatus* is capable of range expansion by natural dispersal across geographic barriers such as the Sonoran and Mojave deserts, which was hypothesized by Westcott (2005). Similarly, dispersal between mountain range populations of *A. auroguttatus* in southern AZ, which are also separated by ≈60–150 km of the Sonoran desert, does not seem probable and these populations likely remain isolated from each other.

Comparison of the mitochondrial cytochrome oxidase (COI) gene region across five mountain ranges in southern AZ indicated that populations of *A. auroguttatus* from these "sky islands" are genetically isolated from one another (Lopez et al. 2014), which supports the lack of long-distance dispersal within the native range of this wood borer. When taken together, results from flight mill studies reported here and genetic isolation between relatively close populations of *A. auroguttatus* in southern AZ support the hypothesis that *A. auroguttatus* was accidently transported into southern CA through infested wood and did not invade CA via natural flight. The inadvertent movement of forest pests through firewood is becoming an increasingly important transport vector of woodborers and bark beetles in the United States (Liebhold et al. 1995, Perrings et al. 2005, Brockerhoff et al. 2006, Hulme et al. 2008, Tobin et al. 2010).

In summary, our results suggest that nutrition, body size, and the interaction between nutrition and age are important factors for *A. auroguttatus* dispersal, and this beetle is only capable of flying relatively short distances in a 24-h period. These findings are essential for understanding the overall dispersal risk of *A. auroguttatus* in CA, which is low via natural flight, but high when infested oak firewood is moved long distances. These flight data may be useful for implementing specific management strategies for *A. auroguttatus* and could include the use of "trap" or sentinel trees to detect and provide a semiquantitative measure of migrating *A. auroguttatus.* A similar system is being used for emerald ash borer where natural dispersal from infestation foci is anticipated (Muirhead et al. 2006). These flight data may also help to define quarantine zones surrounding infestation sites, which could help to retard the spread of *A. auroguttatus* within infested regions, thereby preventing further rapid spread of this invasive and highly destructive beetle.

Acknowledgments

We thank Mike Lewis, Allison Bistline, and Ruth Amrich (University of California, Riverside), as well as Gabriel Lopez, Melissa Lopez, and William Joseph, for their assistance with field work. 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 allowing us to set-up and maintain our mobile laboratory at William Heise County Park, and for providing the infested trees used in this study. 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. The comments of anonymous reviewers greatly improved earlier versions of this manuscript.

References Cited

Brockerhoff, E. G., A. M. Liebhold, and H. Jactel. 2006. The ecology of forest insect invasions and advances in their management. Can. J. For. Res. 36: 263–268.

Candy, D. J., A. Becker, and G. Wegener. 1997. Coordination and integration of metabolism in insect flight. Comp. Biochem. Physiol. B Biochem. Mol. Biol. 117: 497–512.

Chen, H., C. Kaufmann, and H. Scherm. 2006. Laboratory evaluation of flight performance of the plum curculio (Coleoptera: Curculionidae). J. Econ. Entomol. 99: 2065–2071.

Chen, H., Z. Li, S. H. Bu, and Z. Q. Tian. 2011. Flight of the Chinese white pine beetle (Coleoptera: Scolytidae) in relation to sex, body weight and energy reserve. Bull. Entomol. Res. 101: 53.

Coleman, T. W., and S. J. Seybold. 2010. Verification of a useful character for separating the sexes of the goldspotted oak borer, Agrilus coxalis auroguttatus (Coleoptera: Buprestidae). Pan-Pac. Entomol. 86: 57–61.

Coleman, T. W., A. D. Graves, M. Hoddle, Z. Heath, Y. Chen, Y., Flint, M. L., and S. J. Seybold. 2012a. Forest stand impacts associated with *Agrilus auroguttatus* Schaffer (Coleoptera: Buprestidae) and *Agrilus coxalis* Waterhouse in oak woodlands. For. Ecol. Manag 276: 104–117.

Coleman, T. W., V. Lopez, P. Rugman-Jones, R. Stouthamer, S. J. Seybold, R. Reardon, and M. S. Hoddle. 2012b. 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.

Holmes, T. P., J. E. Aukema, B. Von Holle, A. Liebhold, and E. Sills. 2009. Economic impacts of invasive species in forests. Ann. N. Y. Acad. Sci. 1162: 18–38.

Hulme, P. E., S. Bacher, M. Kenis, S. Klotz, I. Kühn, D. Minchin, W. Nentwig, S. Olenin, V. Panov, J. Pergl, et al. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J. Appl. Ecol. 45: 403–414.

Jones, M. I., T. W. Coleman, A. D. Graves, M. L. Flint, 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.

Jongejans, E., O. Skarpaas, and K. Shea. 2008. Dispersal, demography and spatial population models for conservation and control management. Perspect. Plant Ecol. Evol. Syst. 9: 153–170.

Kenis, M., M. A. Auger-Rozenberg, A. Roques, L. Timms, C. Péré, M. J. Cock, J. Settele, S. Augustin, and C. Lopez-Vaamonde. 2009. Ecological effects of invasive alien insects. Biol. Invasions 11: 21–45.

Koch, F. H., D. Yemshanov, D. W. McKenney, and W. D. Smith. 2009. Evaluating critical uncertainty thresholds in a spatial model of forest pest invasion risk. Risk Anal. 29: 1227–1241.

Kovacs, K. F., R. G. Haight, D. G. McCullough, R. J. Mercader, N. W. Siegert, and A. M. Liebhold 2010. Cost of potential emerald ash borer damage in US communities, 2009–2019. Ecol. Econ. 69: 569–578.

Landis, W. G. 2004. Ecological risk assessment conceptual model formulation for nonindigenous species. Risk Anal. 24: 847–858.

Liebhold, A. M., W. L. MacDonald, D. Bergdahl, and V. C. Mastro. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. For. Sci. Monogr. 30: 1–49.

Lodge, D. M., S. Williams, H. J. MacIsaac, K. R. Hayes, B. Leung, S. Reichard, R. N. Mack, P. B. Moyle, M. Smith, D. A. Andow, et al. 2006. Biological invasions: recommendations for US policy and management. Ecol. Appl. 16: 2035–2054.

Lopez, V. M., P. F. Rugman-Jones, T. W. Coleman, M. S. Hoddle, and R. Stouthamer. 2014. Population genetics of goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae): investigating the origin of an invasive pest of native oaks in California. Biol. Invasions (DOI: 10.1007/s10530-014-0672-7).

Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. BioScience 56: 395–405.

Muirhead, J. R., B. Leung, C. Overdijk, D. W. Kelly, K. Nandakumar, K. R. Marchant, and H. J. MacIsaac. 2006. Modelling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America. Divers. Distrib. 12: 71–79.

Neubert, M. G., and I. M. Parker. 2004. Projecting rates of spread for invasive species. Risk Anal. 24: 817–831.

Perrings, C., K. Dehnen-Schmutz, J. Touza, and M. Williamson. 2005. How to manage biological invasions under globalization. Trends Ecol. Evol. 20: 212–215.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50: 53–65.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol. Econ. 52: 273–288.

Rowley, W. A., C. L. Graham, and R. E. Williams. 1968. A flight mill system for laboratory study of mosquito flight. Ann. Entomol. Soc. Am. 61: 1507–1514.

Sarvary, M. A., K. A. Bloem, S. Bloem, J. E. Carpenter, S. D. Hight, and S. Dorn. 2008. Diel flight pattern and flight performance of *Cactoblastis cactorum* (Lepidoptera: Pyralidae) measured on a flight mill: influence of age, gender, mating status, and body size. J. Econ. Entomol. 101: 314–324.

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

Shelton, T. G., X. P. Hu, A. G. Appel, and T. L. Wagner. 2006. Flight speed of tethered *Reticulitermes flavipes* (Kollar) (Isoptera: Rhinotermitidae) alates. J. Insect Behav. 19: 115–128.

Taylor, R.A.J., L. S. Bauer, T. M. Poland, and K. N. Windell. 2010. Flight Performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a flight mill and in free flight. J. Insect Behav. 23: 128–148.

Thompson, S. N., and R. B. Bennett. 1971. Oxidation of fat during flight of male Douglas-fir beetles, *Dendroctonus pseudotsugae.* J. Insect Physiol. 17: 1555–1563.

Tobin, P. C., A. Diss-Torrance, L. M. Blackburn, and B. D. Brown. 2010. What does "local" firewood buy you? Managing the risk of invasive species introduction. J. Econ. Entomol. 103: 1569–1576.

(USDA-FS-FHM) U.S. Department of Agriculture Forest Service, Forest Health Monitoring. 2013. Aerial Survey Region 5 database. (http://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046696). (25 January 2014).

Van Driesche, R. G., R. I. Carruthers, T. Center, M. S. Hoddle, J. Hough-Goldstein, L. Morin, L. Smith, D. L. Wagner, B. Blossey, V. Brancatini, et al. 2010. Classical biological control for the protection of natural ecosystems. Biol. Control 1: S2–S33.

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.

Received 29 November 2013; accepted 24 February 2014.