

# Assessing Flight Potential of the Invasive Asian Longhorned Beetle (Coleoptera: Cerambycidae) With Computerized Flight Mills

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## Abstract

The Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae: Lamiinae), is an invasive woodborer that poses a serious threat to urban and natural landscapes. In North America, this beetle is a quarantine pest, and populations are subject to eradication efforts that consist of the identification, removal, and destruction of infested host material, and removal or prophylactic treatment of high-risk host plant species. To enhance Asian longhorned beetle eradication protocols in landscapes with extensive host availability, we assessed the dispersal potential of male and female adults of varying age, mating, and nutritional status using computerized flight mills. In total, 162 individuals were tethered to computerized flight mills for a 24-h trial period to collect information on total distance flown, flight times and velocities, and number and duration of flight bouts. Adult Asian longhorned beetles (in all treatments) flew an average of 2,272 m within a 24-h period, but are capable of flying up to 13,667 m (8.5 miles). Nutrition and age had the greatest impacts on flight, with Asian longhorned beetle adults >5 d of age that had fed having greater overall flight performance than any other group. However, mating status, sex, and body size (pre-flight weight and elytron length) had a minimal effect on flight performance. This information will be useful for refining quarantine zones surrounding areas of infestation, and for providing greater specificity as to the risk the Asian longhorned beetle poses within invaded regions.

**Key words:** Cerambycidae, dispersal, flight activity, flight mill, invasive species

The introduction, establishment, and spread of invasive species are a serious, ongoing problem affecting contiguous and fragmented (i.e., urban) forest ecosystems worldwide (Liebhold et al. 1995, Nowak et al. 2001, Perrings et al. 2005, Pimentel et al. 2005, Holmes et al. 2009, Hulme 2009, Kovacs et al. 2010). The effects these non-native organisms have when introduced into novel landscapes are often long-lasting and multifaceted, with negative impacts on ecological processes and economic productivity (Liebhold et al. 1995, Pimentel et al. 2000, Zavaleta et al. 2001, Lodge et al. 2006, Lovett et al. 2006, Kenis et al. 2009). More than 450 non-native forest insects are established in the United States (Aukema et al. 2011). Invasive woodborers have been estimated to cause the largest negative economic and ecological impacts (Nowak et al. 2001, Brockerhoff et al. 2006, Kovacs et al. 2010, Aukema et al. 2011), and their establishment often leads to management strategies focused on rapid detection and eradication using a variety of

mechanical and chemical techniques (Brockerhoff et al. 2006, Haack et al. 2010, Herms and McCullough 2014).

The Asian longhorned beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae: Lamiinae), is a cryptic polyphagous woodborer that kills trees in urban (i.e., fragmented) and contiguous landscapes (Nowak et al. 2001, Hu et al. 2009, Simberloff and Rejmánek 2011). The Asian longhorned beetle is native to China and Korea and was first detected in North America in 1996, likely introduced through infested wood packing material (Haack et al. 1997). Since then, several other Asian longhorned beetle populations have been detected throughout the northeastern United States, Canada, and Europe (Haack et al. 2010, Meng et al. 2015). In North America, the Asian longhorned beetle is a quarantine pest, and populations are subject to eradication efforts that consist of the identification, removal, and destruction (via chipping, grinding, or burning) of infested host material, in addition to the

removal or prophylactic treatment (i.e., preventative pesticide application) of high-risk host species (Smith et al. 2009, Meng et al. 2015). These efforts have led to the successful eradication of the Asian longhorned beetle from Islip, Manhattan, and Staten Island, New York; Carteret and Jersey City, New Jersey; Chicago, Illinois; and Boston, Massachusetts (Meng et al. 2015). However, recently detected infestations in Worcester, Massachusetts (MA), and Bethel, Ohio (OH), present unique challenges to ongoing eradication efforts due to the establishment of these populations within heavily wooded suburban or rural landscapes that are connected to contiguous tracks of eastern deciduous hardwood forests (Trotter and Hull-Sanders 2015). Due to the high availability of susceptible hosts over an expansive range, information on the maximum dispersal potential of this beetle could benefit current eradication efforts in MA and OH by helping to refine quarantine zones and surveying protocols.

Field studies investigating the dispersal behavior of the Asian longhorned beetle have been conducted in the native range using a variety of tracking methods, including mass-mark-recapture, individual mark-release-recapture, and harmonic radar (Wen et al. 1998, Smith et al. 2001, Smith et al. 2004, Williams et al. 2004, Bancroft and Smith 2005). These studies documented movement rates ranging from less than 1 (Wen et al. 1998) to 30 (Smith et al. 2004) m/d with seasonal dispersal distances up to 2,600 m (Smith et al. 2004). The results obtained from these investigations were instrumental to the development of eradication protocols in North America. However, the inherent limitations of performing dispersal studies in the field (e.g., low recapture rates, and limited distances and duration of feasible tracking) make it virtually impossible to determine long-distance dispersal potential using these methods (Yamamura et al. 2003, Franzén and Nilsson 2007).

Laboratory studies utilizing flight mills may provide the best option for gaining insight into the long-distance flight capabilities of an insect due to their easy use within a controlled environment (Schumacher et al. 1997, Lu et al. 2007, Sarvary et al. 2008, Hoddle et al. 2015, Hoddle and Hoddle 2016). Nevertheless, there are recognized limitations with flight mill studies. Laboratory studies may not be truly representative of flight performance in the field because they cannot simulate the environmental stimuli encountered by a flying insect in the wild (Taylor et al. 2010). Although laboratory studies do lack environmental components that potentially influence flight behavior, they can be useful to quantify basic attributes such as frequency of flight bouts, and the maximum distance, velocity, and duration of flight, all of which are almost impossible to collect accurately in the field (Shelton et al. 2006, Dubois et al. 2010, Lopez et al. 2014). In addition, laboratory investigations allow for easier manipulation of test individuals, facilitating study of the interacting effects of biotic conditions (i.e., sex, mating status, age, etc.) on flight performance, thereby providing a greater overall assessment of an insect's dispersal potential (Schumacher et al. 1997, Chen et al. 2006, Dubois et al. 2010, Chen et al. 2011). To determine the dispersal potential of the Asian longhorned beetle, adults of varying age, mating, and nutritional status were flown on flight mills to ascertain their combined effects on flight performance.

## Materials and Methods

### Collection and Rearing of Asian Longhorned Beetle Adults for Flight Mill Studies

Asian longhorned beetle adults were reared from infested *Acer saccharum* Marshall, *Acer rubrum* L., and *Acer negundo* L. logs that were collected between April to June 2014 and January to April

2015 in Bethel, OH, placed inside screened rearing barrels (56 by 74-cm high-density polyethylene drum, New Pig, Tipton, PA) or "pop-up" field cages (1.5 by 1.5 m, BioQuip Products, Rancho Dominguez, CA), and held under ambient laboratory conditions [14:10 (L:D) h,  $24 \pm 4^\circ\text{C}$ ]. During June to August 2014 and 2015, adults were collected daily from rearing barrels or cages, sexed, and randomly assigned to one of 16 experimental treatments (Tables 1 and 2). Following assignment to treatments, adults were placed in either 1.89-liter (12.2 by 12.1 by 18.4 cm) or 2.84-liter (12.2 by 12.1 by 21.3 cm) plastic rearing containers (Rez-Tech Corp. Plastic Jar Division, Kent, OH) for virgin and mated treatment combinations, respectively, until flown. Rearing containers had a 10-cm-diameter ventilation hole that was covered with fine metal mesh screen, and were held under ambient laboratory temperature and humidity conditions with artificial lighting [14:10 (L:D) h,  $24 \pm 4^\circ\text{C}$ ] to simulate natural sunlight (14-W 6500K T5 fluorescent bulbs, Lithonia Lighting, Conyers, GA).

### Assignment of Asian Longhorned Beetle Adults to Experimental Treatments

Each adult beetle was assigned to one of the following categories: starved or fed, virgin or mated, and young or old (Tables 1 and 2). Adults in starved treatments were placed into rearing containers without food and provided with water via a moist cotton wick until flown. Fed adults were placed inside rearing containers provided with *A. rubrum* twigs (with minor foliage attached) and water (via a moist cotton wick), which were replaced every 3–4 d. Virgin beetles were obtained by collecting adults that emerged inside their respective rearing barrels or tents without others of the opposite sex and placing them individually into rearing containers upon collection. Mated individuals were acquired by placing one male and one female together inside a rearing container until copulation was observed. Adult beetles less than 2 d post-emergence were considered "young," and adults more than 5 d post-emergence were considered "old" due to the rapid increase in mortality of individuals in starved treatments following day 5.

### Recording Flight Parameters Using Computerized Flight Mills

Eight flight mills were used during this study, which was conducted at the United States Department of Agriculture (USDA), Center for Plant Health Science and Technology (CPHST) laboratory [14:10 (L:D),  $24 \pm 4^\circ\text{C}$ ] located in Bethel, OH. Artificial lighting was used to simulate natural sunlight. A detailed description of the mechanisms involved in measuring and recording flight data using these computerized flight mills (designed and built at the University of California, Riverside) is provided in Lopez et al. (2014). Briefly, each flight mill was connected to a laptop computer via a USB4 Encoder Data Acquisition Device (US 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 (VBA) macros in Microsoft Excel, which calculated average flight velocity, total flight duration time, number of flight bouts (movement of more than 5 s before coming to a complete stop), and distances flown during each flight bout over a 24-h period by individual adults. Flight periodicity was determined using a binary scale system to calculate the occurrence of flight (i.e., a flight bout) during four 15-min increments within each hour of the 24-h trial period. A score of 0 indicated that no flight bouts were recorded during the specified 15-min interval, whereas a score of 1

**Table 1.** Average (mean  $\pm$  SE) flight parameters measured for starved *A. glabripennis* adults under varying sex, age, and mating status

Flight parameter	Starved						
	Male			Female			
	Young		Old	Young		Old	
	Virgin	Mated	Virgin	Mated	Virgin	Mated	
Total distance flown (m)	969.51 $\pm$ 227.98	940.06 $\pm$ 191.75	248.16 $\pm$ 119.35	616.02 $\pm$ 258.90	418.72 $\pm$ 116.06	614.38 $\pm$ 210.60	884.59 $\pm$ 365.24
Total flight time (min)	15.69 $\pm$ 3.79	18.80 $\pm$ 5.65	11.91 $\pm$ 5.00	11.94 $\pm$ 2.92	4.67 $\pm$ 1.26	14.66 $\pm$ 4.33	11.57 $\pm$ 3.60
Flight velocity (m/s)	1.07 $\pm$ 0.19	1.26 $\pm$ 0.27	0.37 $\pm$ 0.15	0.99 $\pm$ 0.33	1.35 $\pm$ 0.37	0.79 $\pm$ 0.17	0.97 $\pm$ 0.28
No. of flight bouts	15.00 $\pm$ 7.98	23.67 $\pm$ 10.16	29.88 $\pm$ 15.68	19.57 $\pm$ 8.39	2.78 $\pm$ 0.43	22.13 $\pm$ 7.69	13.29 $\pm$ 4.09
Flight bout time (s)	145.86 $\pm$ 45.55	131.19 $\pm$ 41.33	28.29 $\pm$ 7.85	156.27 $\pm$ 72.99	107.81 $\pm$ 25.39	68.11 $\pm$ 23.37	62.36 $\pm$ 20.59
Elytron length (mm)	15.93 $\pm$ 0.89	16.82 $\pm$ 0.85	16.72 $\pm$ 0.76	15.91 $\pm$ 0.74	18.49 $\pm$ 1.09	17.44 $\pm$ 1.04	17.80 $\pm$ 0.88
Pre-flight weight (g)	0.53 $\pm$ 0.08	0.61 $\pm$ 0.09	0.54 $\pm$ 0.07	0.47 $\pm$ 0.05	0.80 $\pm$ 0.13	0.67 $\pm$ 0.09	0.63 $\pm$ 0.11
<i>n</i>	12	9	8	7	9	8	7

indicated that a flight bout had occurred. The scores for each hour were added (with a maximum score of four) to determine the frequency of flight for every individual flown during the 24-h trial period.

### Attachment of Asian Longhorned Beetle Adults to Flight Mills

Immediately prior to attachment to the flight mill, adults ( $n = 162$ ) were weighed with a precision balance (model GF-600, A&D Engineering, San Jose, CA), then tethered by the pronotum to a 0.5-mm carbon steel flight mill arm (FMA) wire (30.5 cm in length) via an FMA attachment (see below), and left for 24 h (Fig. 1). The FMA attachment was made from a small (0.59-mm-diameter by 28-mm-long) L-shaped wire that was flattened at one end (for insect attachment) and connected directly at the other end to the FMA via a standard socket crimp (model 809-043, Glenair, Glendale, CA). Individual Asian longhorned beetle adults were attached to the FMA by fastening them by the pronotum using hot melt adhesive. A piece of modeling clay, approximately the same weight as the tethered beetle, was placed at the opposite end of the FMA to counterbalance the weight of each adult. After gluing and prior to recording flight data, we confirmed that individuals could move their wings freely (Fig. 1). Adults were attached to the flight mills approximately 5–10 min before trials were initiated. Following each 24-h flight trial, individual Asian longhorned beetle adults were detached from flight mills (each adult was only attached to the flight mill for a single 24-h flight trial), and elytron length was measured with an electronic 0–200-mm digital caliper. Following each flight trial, any dead ( $n = 1$ ) or escaped ( $n = 3$ ) individuals were excluded from the analyses, though this was rare (<3% of beetles flown). In addition, approximately 10% of individuals did not fly ( $n = 16$ ) and were excluded from the analyses.

### Statistical Analysis

The flight performance of Asian longhorned beetle adults ( $n = 142$ ) under varying age, mating, and nutritional status was analyzed using analysis of covariance (ANCOVA). 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:  $y^{0.5}$ ; number of flight bouts:  $\log(y)$ ; and average flight bout time:  $\log(y)$ . Tukey–Kramer tests were used to conduct pairwise comparisons for each significant factor in the ANCOVA. 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 (Cary, NC; SAS Institute Inc. 2008).

## Results

### Average Total Flight Distance

The average total distance flown by Asian longhorned beetle adults during the 24-h flight period (Tables 1–3; Fig. 2) was significantly influenced by nutritional status ( $F_{1,138} = 43.27$ ,  $P \leq 0.0001$ ), with fed adults flying greater distances than starved individuals. Age was also significant with respect to total distance flown ( $F_{1,138} = 6.56$ ,  $P = 0.01$ ), with old beetles (i.e., > 5 d post emergence) flying farther.

**Table 2.** Average (mean  $\pm$  SE) flight parameters measured for fed *A. glabripennis* adults under varying sex, age, and mating status

Flight parameter	Fed					
	Male			Female		
	Young	Old	n	Young	Old	n
Total distance flown (m)	1420.74 $\pm$ 392.21	3523.11 $\pm$ 1522.46	8	1101.56 $\pm$ 284.47	1582.34 $\pm$ 879.14	9
Total flight time (min)	26.88 $\pm$ 7.50	35.72 $\pm$ 13.92	8	16.38 $\pm$ 5.22	23.26 $\pm$ 9.40	9
Flight velocity (m/s)	1.35 $\pm$ 0.29	1.62 $\pm$ 0.35	8	1.29 $\pm$ 0.27	0.89 $\pm$ 0.31	9
No. of flight bouts	45.22 $\pm$ 18.25	16.88 $\pm$ 8.78	8	20.75 $\pm$ 9.61	23.29 $\pm$ 11.56	9
Flight bout time (s)	64.27 $\pm$ 16.81	178.21 $\pm$ 49.31	8	81.56 $\pm$ 22.59	168.44 $\pm$ 89.78	9
Elytron length (mm)	16.07 $\pm$ 0.81	16.14 $\pm$ 0.91	8	16.91 $\pm$ 1.09	16.39 $\pm$ 1.51	9
Pre-flight weight (mg)	0.59 $\pm$ 0.09	0.64 $\pm$ 0.10	8	0.67 $\pm$ 0.11	0.73 $\pm$ 0.20	9
n	9	11	13	8	7	11

A significant interaction between nutritional status and age ( $F_{1,138}=16.87$ ,  $P \leq 0.0001$ ) existed; old, fed adults flew further than old, starved adults ( $F_{1,138}=56.66$ ,  $P \leq 0.0001$ ). However, nutritional effects were not significant in the total flight distance of young ( $< 5$  d post emergence) Asian longhorned beetle adults ( $F_{1,138}=3.08$ ,  $P=0.08$ ). Sex, mating status, pre-flight weight, and elytron length did not influence total average distance flown during a trial period ( $P > 0.05$ ).

#### Average Total Flight Duration

The average total flight time of Asian longhorned beetle adults during the 24 h trial period (Tables 1–3) was significantly affected by nutritional status ( $F_{1,130}=37.83$ ,  $P \leq 0.0001$ ) and age ( $F_{1,130}=13.34$ ,  $P=0.0004$ ), resulting in longer flight times for fed and old individuals, respectively. Significant interactions were observed between nutritional status and age ( $F_{1,130}=9.29$ ,  $P=0.003$ ), sex and age ( $F_{1,130}=4.34$ ,  $P=0.04$ ), and nutritional status, sex, and mating status ( $F_{1,130}=5.42$ ,  $P=0.02$ ). Contrasts of these variables revealed that the effects of nutrition were significant for both young ( $F_{1,131}=4.94$ ,  $P=0.02$ ) and old individuals ( $F_{1,131}=24.30$ ,  $P \leq 0.0001$ ), while age was only significant when beetles were fed ( $F_{1,131}=37.83$ ,  $P \leq 0.0001$ ). Sex was marginally significant in young individuals ( $F_{1,131}=4.50$ ,  $P=0.04$ ), while the effects of age were only significant in female Asian longhorned beetles ( $F_{1,131}=15.38$ ,  $P=0.0001$ ); young females flew shorter distances than old females. The interactions between nutritional status, sex, and mating status revealed significant effects of nutrition in virgin females ( $F_{1,131}=22.71$ ,  $P \leq 0.0001$ ), as well as mated ( $F_{1,131}=13.81$ ,  $P=0.0003$ ) and virgin ( $F_{1,131}=9.79$ ,  $P=0.002$ ) males; fed virgin females flew longer than starved virgin females, and mated and virgin males flew longer when fed than when they were starved. The effects of sex were significant in fed, mated individuals ( $F_{1,131}=5.33$ ,  $P=0.02$ ), resulting in shorter flights in fed, mated females than in fed, mated males. In addition, mating status was observed to be marginally significant in starved female Asian longhorned beetles ( $F_{1,131}=4.47$ ,  $P=0.04$ ); starved virgin females flew shorter flights than starved mated females. Finally, body size (i.e., pre-flight weight and elytron length) did not have an effect on average total flight duration ( $P > 0.05$ ).

#### Average Velocity

The average velocity of Asian longhorned beetle adults during flight (Tables 1–3) was significantly affected by pre-flight weight ( $F_{1,136}=7.17$ ,  $P=0.008$ ), and elytron length ( $F_{1,136}=6.38$ ,  $P=0.01$ ), with larger adults flying faster than smaller individuals (coefficient estimation  $\pm$  SE =  $1.10 \pm 0.41$  and  $-0.12 \pm 0.05$ , respectively). A significant interaction was observed between nutritional status and sex ( $F_{1,136}=4.26$ ,  $P=0.04$ ). The effect of sex was significant when beetles were fed ( $F_{1,136}=5.07$ ,  $P=0.03$ ), while nutrition was significant only in males ( $F_{1,136}=6.17$ ,  $P=0.01$ ), resulting in faster flights in fed males than in fed females. Age and mating status did not influence the average velocity of Asian longhorned beetles ( $P > 0.05$ ).

#### Total Number of Flight Bouts

Nutritional status ( $F_{1,139}=8.08$ ,  $P=0.005$ ) and age ( $F_{1,139}=6.28$ ,  $P=0.01$ ) had a significant impact on the total number of bouts flown by Asian longhorned beetle individuals, resulting in an increased number of flight bouts in old, fed individuals. However, the number of flight bouts was not affected by sex, mating status, or body size ( $P > 0.05$ ).

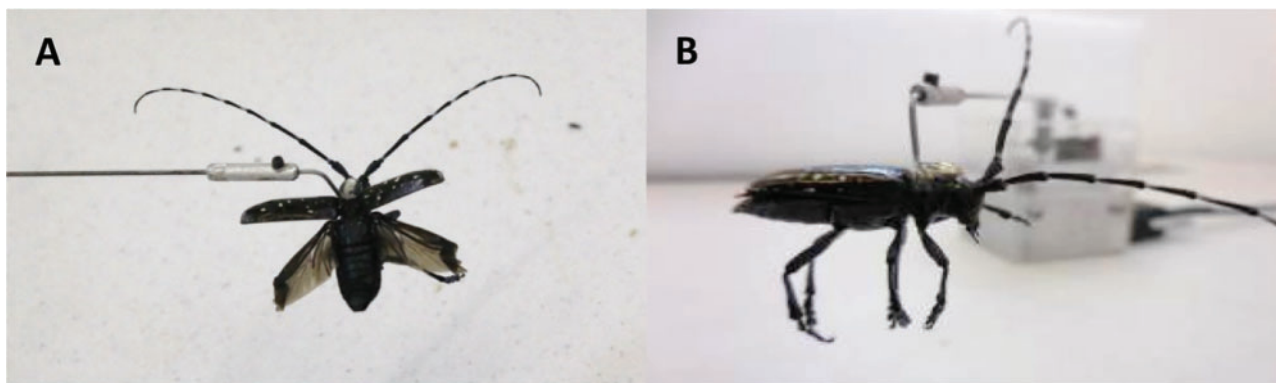


Fig. 1. (A) Above and (B) side view of *A. glabripennis* attachment onto computerized flight mills.

**Table 3.** Average (mean  $\pm$  SE) flight parameters measured for *A. glabripennis* adults flown in all treatment combinations

Flight parameter	Average (mean $\pm$ SE)
Total distance flown (m)	2271.75 $\pm$ 238.74
Total flight time (min)	28.95 $\pm$ 2.44
Flight velocity (m/s)	1.24 $\pm$ 0.07
No. of flight bouts	26.09 $\pm$ 3.06
Flight bout time (s)	133.45 $\pm$ 11.94
Elytron length (mm)	16.87 $\pm$ 0.23
Pre-flight weight (g)	0.66 $\pm$ 0.03
<i>n</i>	142

#### Average Duration of Flight Bouts

The average time individual Asian longhorned beetle adults flew during each flight bout (Tables 1–3) was significantly influenced by nutritional status ( $F_{1,137}=6.70$ ,  $P=0.01$ ) and elytron length ( $F_{1,137}=9.52$ ,  $P=0.003$ ; coefficient estimation  $\pm$  SE =  $-0.10 \pm 0.03$ ). Consequently, flight bouts were longer in fed individuals, but shorter in adults with a longer elytron. However, there was no significant effect on average flight bout time due to sex, mating status, or pre-flight weight ( $P > 0.05$ ). Significant interactions were observed between nutritional status and age ( $F_{1,137}=12.29$ ,  $P=0.0006$ ). The effects of age were significant in fed ( $F_{1,137}=9.32$ ,  $P=0.003$ ) individuals, which resulted in a general increase in average flight bout time compared with starved adults. Effects of nutrition were observed in old Asian longhorned beetle adults ( $F_{1,137}=18.49$ ,  $P \leq 0.0001$ ), which flew shorter flight bouts when starved.

#### Flight Periodicity

The periodicity of Asian longhorned beetle flight was determined by attaching adults to flight mills at various times throughout the day and ranking the frequency of flight for each hour flown (on a 1–4 scale) during the 24-h trial period. The average (mean  $\pm$  SE) frequency of flight (Fig. 3) showed that Asian longhorned beetles had flight bouts occurring regularly throughout the day. However, the majority of flights occurred during late afternoon to late evening (i.e., from 15:00 to 21:00).

#### Discussion

To enhance Asian longhorned beetle eradication protocols in landscapes with extensive host availability, we assessed the dispersal potential of male and female adults of varying age, mating, and

nutritional status using computerized flight mills. On average, these beetles flew approximately 2.3 km (1.4 miles) during the 24-h trial period, with a maximum distance of approximately 13.7 km (8.5 miles). As our experiments were conducted under laboratory conditions and did not take into account the propensity of beetles to take flight, our average and maximum distance results were much higher than those documented in previous field studies (Wen et al. 1998, Smith et al. 2001, Smith et al. 2004, Williams et al. 2004, Bancroft and Smith 2005). In fact, the average distance flown in 24 h from all Asian longhorned beetles in this study was similar to the maximum seasonal dispersal distance (2600 m) recorded by Smith et al. (2004), the highest previously documented distance flown by adult Asian longhorned beetles. While information on the flight propensity and dispersal behavior of the Asian longhorned beetle suggests that the majority of adults do not tend to disperse widely within a host stand, our results indicate that some beetles do have the capability of traveling long distances (approximately 5% of individuals flown during this study traveled  $> 8$  km) within a 24-h period. These results agree with those reported in Trotter and Hull-Sanders (2015), who stated that rare dispersal events may be as long as 8 km based on records of Asian longhorned beetle-infested trees detected in Worcester, MA. In addition, our data show that the Asian longhorned beetle conducted diurnal and nocturnal flights, which could increase the capacity for flight activity. This information is important because it indicates that this beetle may move more frequently than previously thought. It also points to the potential for some individuals to make long-distance dispersal events that may lead to the formation of small, isolated populations outside of known quarantine zones. Incorporating this information into dispersal models such as those developed in Trotter and Hull-Sanders (2015) could help provide greater specificity as to the risk of Asian longhorned beetle establishment, especially in landscapes with high host availability.

The nutritional status and age of Asian longhorned beetle adults had the greatest overall influence on flight performance. The total distance, flight time, and number and duration of flight bouts were greater in old ( $> 5$  d post-emergence), fed individuals. As flight is an energy-intensive activity, the enhanced flight performance of fed adults is not surprising (Thompson and Bennett 1971, Candy et al. 1997). In addition, the general increase in the flight performance of old, fed individuals is likely attributed to a greater amount of energy resources available in adults that had more time to feed before flight trials were conducted. Our results are similar to those of David et al. (2013–2015), who reported that the increased flight capacity of aged, fed *Monochamus galloprovincialis* (Olivier) (Coleoptera:

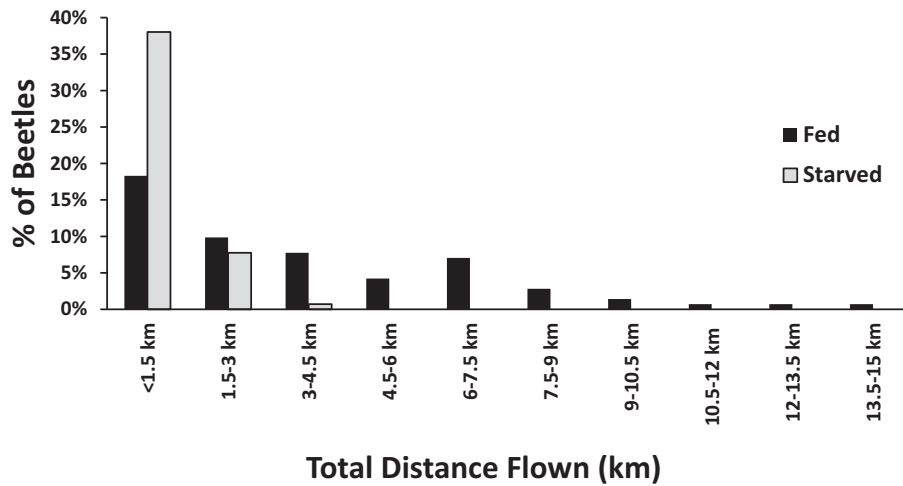


Fig. 2. Percentage of fed and starved *A. glabripennis* sorted by total distance (km) flown over a 24-h period.

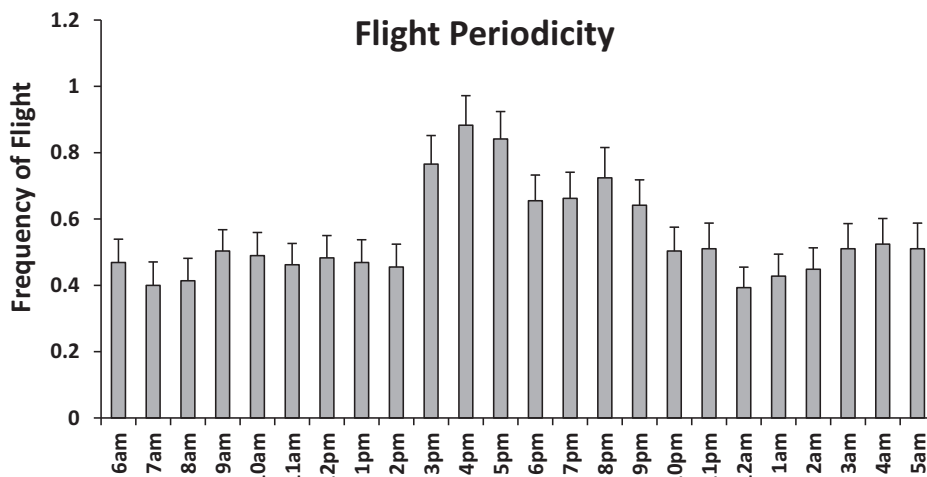


Fig. 3. Average (mean  $\pm$  SE) frequency of *A. glabripennis* flight over a 24-h period. Flight periodicity was determined using a binary scale system to calculate the occurrence of flight (i.e., a flight bout) during four 15-min increments within each hour of the 24-h trial period. A score of 0 indicated that no flight bouts were recorded during the specified 15-min interval, whereas a score of 1 indicated that a flight bout had occurred. The scores for each hour were added (with a maximum score of four) to determine the frequency of flight for every individual flown during the 24-h trial period.

Cerambycidae) was likely influenced by accumulation of energy from feeding over time.

Mating status and sex had no impact on flight parameters such as total flight distance, number of flight bouts, or duration of flight bouts. Similarly, mating status and sex had no impact on the flight capacity of the plum curculio (*Conotrachelus nenuphar* [Herbst] Coleoptera: Curculionidae) (Chen et al. 2006) or goldspotted oak borer (*Agrilus auroguttatus* Schaeffer [Coleoptera: Buprestidae]) (Lopez et al. 2014). However, significant interactions were observed between mating status and nutrition in female Asian longhorned beetles, which resulted in longer flight periods in starved mated females compared with starved virgins. This result could imply that under starved conditions, mated females may be more likely to disperse to find a suitable host tree (maturation feeding is necessary for egg development in female Asian longhorned beetle adults), whereas virgin females may tend to fly less to maximize mate-finding. Although there was no interaction with nutritional status, flight duration of mated females of emerald ash borer (*Agrilus planipennis* Fairmaire [Coleoptera: Buprestidae]) was also found to be

significantly greater when compared with unmated females, suggesting that females of this species may be pre-disposed for dispersal flights following mating (Taylor et al. 2010).

The overall body size (pre-flight weight and elytron length) of Asian longhorned beetles had no influence on the majority of flight parameters, including total flight distance, duration, and the number of flight bouts. However, pre-flight weight and elytron length did have a significant effect on average velocity, resulting in faster flights from larger individuals. In contrast, adults with greater elytron length had shorter flight bouts than smaller individuals. Although the flight performance of insects tends to increase as the percentage of flight muscles (compared with total body mass) increases, the size of these muscles can fluctuate based on a variety of factors (e.g., local population density and food availability), and are therefore not always correlated with overall body size (Marden 2000). This variability can lead to inconsistent relationships between insect body size and flight performance. For example, larger body size was associated with the increased flight performance of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae)

(Evenden et al. 2014), and goldspotted oak borer (Lopez et al. 2014), but had no impact on red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae) (Ávalos et al. 2014), or the six-toothed bark beetle, *Ips sexdentatus* (Boerner) (Coleoptera: Curculionidae) (Jactel 1993).

Understanding the biological characteristics of an invasive species is fundamental to the development of effective, species-specific management strategies (Sakai et al. 2001, Jongejans et al. 2008, Liebhold and Tobin 2008, Trotter and Hull-Sanders 2015). Information on the maximum dispersal potential of the Asian longhorned beetle is needed to understand the physiological limits of this beetle, and to incorporate these data into management protocols, especially in areas with high host availability such as Bethel, OH, and Worcester, MA. Our results reveal much higher dispersal capabilities than had been previously recorded, especially in old, fed individuals. Utilizing these new biological data in risk assessment analyses and dispersal models could improve our understanding of Asian longhorned beetle ecology and better help predict the spread and subsequent occurrence of new populations, thereby improving rapid detection and eradication of this destructive pest.

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