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Flight Performance of *Agrilus planipennis* (Coleoptera: Buprestidae) on a Flight Mill and in Free Flight

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Abstract Computer-monitored flight mills were used to record the flight performance of the emerald ash borer, *Agrilus planipennis* Fairmaire. Flight performance of fed and unfed, and mated and unmated beetles of both sexes were recorded and compared. Mated females flew further per day and longer than unmated females or males. Mated females that were allowed to feed between flight periods flew an average of 1.3 km/day for four days; 10% flew more than 7 km/day. Measurements of free-flight speed using a mirror and a high-speed camera were used to calibrate the flight mill results, permitting absolute estimates of flight performance to be made. Free-flight speeds were approximately three times the speeds recorded by the flight mills. The median corrected distance flown by mated females was >3 km with 20% flying >10 km and 1% flying >20 km. The flight performance of mated females suggests a considerable capacity for range expansion by this invasive species. The implications for quarantine and control are discussed.

Keywords Dispersal · emerald ash borer · flight endurance · flight speed · invasive species · migration · range expansion

Introduction

The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire, is a buprestid native to China, Japan, Korea, and the Russian Far East that has recently become established in

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the Great Lakes region of North America. Adult EAB fly in June and July, the females laying up to 250 eggs in crevices in the bark of its ash tree (*Fraxinus* spp.) host. Development takes 1 or 2 years during which time the larvae feed by tunneling in the cambium layer; the galleries eventually girdle the trees and cause death. EAB appears to have coevolved with Asian ash trees that exhibit some resistance while native North American species are highly susceptible (Liu et al. 2003; Liu et al. 2007; Rebek et al. 2008). Evidence to date suggests that all North American ash species succumb to EAB within 1 to 3 years of establishment (Poland and McCullough 2006). Ash is one of the most common forest trees in the eastern US and Canada as well as being a favored urban shade tree on streets, in parks, and private gardens. It is estimated that almost 8 billion ash trees or 2.6% of trees in timberlands in the United States are threatened by this beetle (USDA-FS 2009), with about 12% of urban street trees being ash species (Federal Register 2003; MacFarlane and Meyer 2005). Thus, the invasion of this beetle is alarming to urban and forest tree managers, as well as nursery growers and homeowners. In view of its devastating impact, the rate of range expansion both through natural and human-aided dispersal is a major concern.

Emerald ash borer was originally found in the Detroit, Michigan and Windsor, Ontario metropolitan areas in 2002, although evidence from dendrochronology research suggests a much earlier date of introduction, probably about 1990 (Siegert et al. 2007). Since its discovery, the known range of EAB has extended from the Detroit-Windsor area through much of Lower Peninsular Michigan, north into the Upper Peninsula and Sault Ste. Marie, Ontario, south into Ohio and Indiana, west into Illinois and Wisconsin, and east into Pennsylvania and across Essex County into Middlesex County, Ontario. Although some expansion in range is due to anthropogenic actions, for example the isolated outbreak in Maryland and Virginia caused by shipment of infested nursery stock (USDA-APHIS 2009), the rapid expansion of the range over a very broad front is likely due to the beetle's own dispersive capabilities.

In Canada, where the infestation was originally confined to an area of land between Lake St. Clair and Lake Erie, a 10 km ash-free corridor or "firebreak" was established in 2004 within which all ash trees were felled and removed to prohibit reproduction. By 2006, this quarantine strip had been breached, and EAB were established east of the firebreak with an outlier population in London, Ontario, 100 km east of the line (Marchant 2006). While the London population is almost certainly the result of human activities, the population immediately east of the firebreak was either due to EAB presence before its establishment or subsequent invasion by flight. The 10 km swath across Essex County would present a barrier to many insects, but preliminary data of EAB flight performance obtained using computer-monitored flight mills suggested EAB were capable of crossing a 10 km wide ash-free zone and establishing populations (Bauer et al. 2004; Taylor et al. 2006, 2007). In this paper we present more data with detailed analyses, including calibration of our earlier relative estimates of flight performance.

Material and Methods

The measurement of insect flight performance requires estimates of a number of variables: periodicity and thresholds for flight, frequency and duration of bouts of flight, total duration and speed of flight, and rate of fuel utilization and size of fuel reserves. The simultaneous estimation of these variables presents a number of problems, and the experimental conditions required to measure the factors quantitatively may not be appropriate for reliable qualitative observations of behavioral factors and vice versa. Insect flight mills have been used extensively to establish potential flight range and rate of fuel utilization starting with Krogh and Weis-Fogh (1951, 1952). For our study of EAB flight performance, we monitored flight activity with a suite of eight flight mills attached to a computer.

Flight Mills

The flight mills we used were originally designed to record the flight of leafhoppers (Hemiptera: Auchenorrhyncha) (Taylor et al. 1992). The mills use steel Number 2 entomological pins suspended in a magnetic field for the bearings, AlNiCo magnets rated at 3,000 oersted peak magnetizing force (Magni Power Co., Wooster, OH) to minimize friction, and silica capillaries for the flight mill arm to minimize weight. In a subsequent study, some minor modifications were made to the electronics to accommodate faster flying sap beetles (Coleoptera: Nitidulidae) (van Dam et al. 2000). For this study, we further modified the flight mills to support the heavier and faster flying EAB by replacing the magnets with more powerful 5,500 oersted ceramic magnets (Magni Power Co., Wooster, OH). While holding the pin in the magnetic field more securely, the stronger magnets also increasing the torsional drag and the effort required to turn the mill. How much extra effort was required by EAB is impossible to estimate as the beetles wrenched the pin from the weaker field in a few revolutions. Up to 16 flight mills can be monitored 10 times per second (10 Hz) by a computer that monitors the tethered insects via an interface that transmits a pulse every time an infra-red light beam is interrupted by an aluminum foil square on one end of the arm. The insect is attached at the pronotum to the other end of the arm using rubber cement. We chose to monitor eight mills at 20 Hz to accommodate the fast flying EAB.

The monitor program saves the time of each light beam occultation (to the nearest 0.01 s) to a log file on the hard drive. The program cycles continuously until it is terminated, at which point the log file is read and sorted and each channel analyzed. From the time of every occultation on each channel, the total number of revolutions and the duration of each revolution are calculated. Following termination of a run the program computes a number of bout statistics from these basic data:

1. The number of laps flown, the distance (= laps * 57 cm circumference), duration, and the average flight speed (= distance/duration) of each individual flight bout;
2. The mean and variance of number of laps/bout, distance flown/bout, duration/bout, and flight speed/bout for each individual insect;
3. The total distance flown, the total time spent flying, and the total time spent resting by each individual insect;
4. The sample means and variances for all variables across all insects in the run.

Insects

Emerald ash borer adults were reared from heavily infested green (*Fraxinus pennsylvanica* Marsh) and white (*F. americana* L.) ash trees in southeastern Michigan. The trees were felled between January and April of 2003 and 2004, and cut into logs ~50-cm long with a chainsaw. The infested ash logs were held in cold storage at 4°C until beetles were needed for experiments. Beetles were reared in the USDA-FS Northern Research Station laboratories in East Lansing, Michigan, at 20–25°C, 40–60% RH, and 24-h lighting by placing the infested logs in individual cardboard emergence tubes (20–30 cm in diameter by 60 cm long) (Saginaw Paper Tube, Saginaw, MI), and allowing beetles to emerge. Each beetle-emergence tube was capped on one end with a plastic lid to exclude light, and the other end was sealed with a plastic lid modified by the addition of a translucent plastic screw-top collection cup from which emerging beetles were collected daily for about a week once emergence began (4–5 weeks after removal from chill). After emergence, the beetles were sexed by presence/absence of an aedeagus. They were maintained in a growth chamber at 24°C, 16:8 L:D, and 70% RH in single-sex groups of about 10 in ventilated, adult-holding cups, which were made by taping together the openings of two, 355-ml clear plastic cups (Maui Cup, Letica Corp., Rochester, MI). The cups were ventilated by cutting the bottom from the top cup and hot-gluing metal window screening over the hole. EAB adults were fed greenhouse-reared shamel or tropical ash (*F. uhdei* Linglesh) foliage, which was maintained by inserting its petiole through Parafilm® sealing a 20-ml glass scintillation vial filled with reverse osmosis water. Every 3 or 4 days the insects were provided with a fresh vial containing foliage and a cotton wick to draw reverse osmosis water.

For attachment to the flight mill, a beetle was first cooled on an ice pack for no more than 5 min. Under a dissecting microscope, a small droplet of rubber cement was placed on the tip of a bent #0 insect pin and attached to the beetle's pronotum. After attachment, the free end of the pin was inserted into one end of the silica capillary flight arm, which was hung from the upper magnet of the mill's magnetic field. Recording commenced as soon as the arm was released. Sometimes beetles began to fly immediately, and at other times, there was a lengthy rest period prior to flight. Runs lasted from 6 to 96 h. The room temperature was 23–29°C, while humidity ranged from 40% to 70%. The flight mills were illuminated by two banks of two 4 ft F40C50 Chroma 50 General Electric fluorescent tubes. These have a chromaticity of 5,000°K which is equivalent to a sunny day at noon. The lamp holders were suspended 30 cm above the Plexiglas flight mill covers, one light bank above four flight mills. All lights were on whenever any flight mills were in use.

Experiments

Because the effect of handling during attachment to the flight arm on the flight behavior of subjects is unknown, and possibly unknowable, interpretation of flight mill results presents a formidable problem. By comparing the performance of two or more experimental groups of comparable size, the problem of behavioral interference may be partially overcome (Rowley et al. 1968). From preliminary trials with randomly chosen individuals (male, female, newly eclosed, mature, virgin, and mated), it was determined that EAB typically flew 1.5–2.0 revolutions/s (1.5–2.0 Hz). To minimize the number of laps resulting from coasting included in the data set, the criterion for a true lap was defined to be a lap of 2.00 s or less so the monitor program ignored revolutions less than 0.5 Hz. This may have resulted in the exclusion of some genuine low speed flights, but visual observation suggested that such flights were very rare. The majority of observations showed the beetles to be flying at 1.5–2.5 Hz with burst up to ~3.5 Hz when actually flying. This observation suggests that the mills imposed an upper limit of 3.5–4.0 Hz on flight and that therefore bout pattern and time-averaged flight speed were more relevant statistics than instantaneous flight speed.

Preliminary Trials—No Food or Rest in Constant Light Preliminary trials were conducted to obtain a rough idea of how long and how fast EAB adults could fly while attached to the flight mill. Runs were conducted for up to 96 h in constant light. Many species automatically open their wings when tarsal contact is lost (Dingle 1965). This does not appear to be the automatic response of EAB, as many individuals failed to fly immediately after being suspended from the flight arm. Beetles that failed to fly immediately were left in place and all but two flew within an hour. No attempt was made to stimulate flight.

It was during this exploratory period that we discovered that the power of some beetles was such that the arm could be wrested from the magnetic mount, requiring the installation of more powerful 5,500 Oersted ceramic magnets. Analysis of these data were restricted to defining frequency distributions for number of bouts, bout duration, flight speed while flying, and total distance flown. These parameters were computed from the data recorded by the monitor without regard for sex and mating or feeding status.

Following these preliminary trials to obtain rough performance estimates, a series of five flight runs was made under a range of conditions which are described below. Using the data obtained in these five treatments, a series of comparisons of flight performance was made: 24:0 vs. 16:8 L:D; males vs. females; mated vs. unmated females; and rested vs. unrested females. Because the number of beetles subjected to the treatments was variable and because some treatments were to be used in more than one comparison, analysis of variance could not be used. Consequently all comparisons were made by Student's *t*-test and are described following the treatment descriptions.

Treatment 1. Males—No Food and Rest in Constant Light Twenty-three 6–8-day-old unmated males that had not had access to females were weighed and then attached individually to the flight mill. They were flown in 6 batches of 2 to 5 for 24 h in constant light. They were permitted no food or water, nor were perches available. Resting could be achieved only by folding the wings while suspended. The frequency distributions for number of bouts, bout duration, instantaneous flight speed, and total distance flown were computed from the data recorded by the monitor and used in the comparisons described below.

Treatment 2: Virgin Females—No Food and Rest in Constant Light Twenty 6 to 8-day-old unmated females were weighed before they were flown in 3 batches of 4–8, for 24 h in constant light. They were permitted no food or water, nor were perches available. Flight performance distributions were computed and used in the comparisons described below.

Treatment 3: Virgin Females—No Food and Rest in 16:8 Light:Dark Fifty-four 6 to 8-day-old unmated females were flown in 7 batches of 6–8 for 24 h under 16:8 L:D conditions starting within 2 h of scotophase. They were permitted no food or water, nor were perches available. Flight performance distributions were computed and used in the comparisons described below.

Treatment 4: Mated Females—No Food and Rest in 16:8 Light:Dark Forty 6 to 8-day-old females were transferred, two to a cup with two males. Although males in the wild have been observed to mount females with alacrity and persistence (Lelito et al. 2007), there was no immediate response of males to females amongst the EAB in the lab. Thus, the beetles were kept in cups with food (*F. uhdei*) and water for two days, after which time the females were assumed to be mated based on earlier observations. More recently, Pureswaran and Poland (2009) found that 90% of EAB female–male pairs held in similar containers successfully mated within 5 h, so we are confident that most, if not all females were mated. They were then weighed and flown on the mill for up to 96 h in 16:8 L:D conditions. While on the flight mill they were permitted no food or drink, nor were perches present for them to alight and rest. Flight performance distributions were computed and used in the comparisons described below.

Treatment 5: Mated Females—With Food and Rest in 16:8 Light:Dark Thirty-two 6 to 8-day-old females were placed in containers with males. Following 2 days with the males, at which time they were presumed to be mated, they were weighed and flown for up to 5 days. After 8 h of flight on the mill with the lights on, they were removed and placed in cups with food (*F. uhdei*) and water for 16 h. The cups were kept at 23–29°C and 8 h light and 8 h dark before being reattached to the same mill for another 8 h of flight with the lights on. The 32 first-day flights were included in Treatment 4 data, and the 64 subsequent flights constitute the data for this treatment. Flight performance statistics (the number of flight bouts, total time spent flying, total distance flown, and average instantaneous flight speed) were computed and used in the comparisons described below.

Comparisons

Comparison 1: Males vs. Virgin Females Flight parameters of 23 males flown in constant light and without rest (Treatment 1) were compared with parameters of 20 virgin females in constant light (Treatment 2) without rest.

Comparison 2: Constant Light vs. 16:8 Light:Dark Flight parameters of 20 virgin females flown in constant light (Treatment 2) were compared with parameters of 54 virgin females flown in 16:8 L:D (Treatment 3).

Comparison 3: Mated vs. Virgin Females Flight parameters of 54 virgin females flown in 16:8 L:D without food or rest (Treatment 3) were compared with parameters of 72 mated females flown in 16:8 L:D without food or rest (40 from the first day of Treatment 4 and 32 from the first day of Treatment 5).

Comparison 4: Males vs Mated Females Flight parameters of 23 males flown without rest in 24 h light (Treatment 1) were compared with parameters of 54 virgin females flown without rest periods in 16 h light (Treatment 3).

Comparison 5: Flight with Rest Periods vs. Continuous Flight Flight parameters of 72 mated females flown without rest in 16:8 L:D (40 from Treatment 4 and 32 from the first day of Treatment 5) were compared with 64 mated females flown with rest periods in 16:8 L:D (32 from each of the second and third days of Treatment 5).

Calibration

Due to the numerous extraneous factors involved with flight mill experiments, it is generally impossible to directly link observed flight behavior with flight behavior in nature. Although a very accurate measurement of distance flown in a fixed time period can be calculated from average speed and time flown, it cannot be correlated with distance flown under natural conditions. However, the approach taken in this study allows for comparisons between groups (sex, mating status, and food and rest), permitting relative differences in performance to be estimated which are reasonable and are probably a good reflection of the natural situation. While the actual flight performance parameters are not representative, the shapes of the distributions are likely to be close to reality (Gatehouse and Hackett 1980). The relative differences between the distributions may be influenced by tethering only if there is an interaction between being tethered and the flight response to the treatment factors, which seems improbable.

It has generally been supposed that the recorded distances flown by insects on a flight mill are underestimates because the insects must first accelerate the arm up to speed (overcome the moment of inertia) when they initiate flight, and then overcome the friction of conventional bearings or the torsional resistance of magnetic mounts, and air resistance of the arm to which they are attached while in flight. The loss caused by these effects is collectively the parasitic drag. Additional sources of error include inconvenience of being attached to the arm and lift provided by the arm. Thus, Flight mill speed = Natural flight speed – Inertial drag – Torsional drag – Inconvenience factor + Lift.

Handling and gluing the subject to the arm are generally thought to inhibit flight (Kennedy and Booth 1963a, b; Rowley et al. 1968; Spiewok and Schmolz 2006), but there is also evidence that tethered insects may be more active than those in free flight (Cockbain 1961). Thus, the fourth term could be either positive or negative, while the last term makes more energy available for forward movement (Riley et al. 1997) and higher flight speed. Thus, it is not certain that the “true flight speed” is greater than the speed recorded on a flight mill. In order to be able to draw conclusions about flight in the wild, flight mills must be calibrated. There are very few instances where this has been possible (Krogh and Weis-Fogh 1951, 1952). Hence the use of relative change by comparing flight by males, females, mated, unmated, etc.

Absolute Estimation

We report here some of the results of an ongoing research study to track EAB flight using harmonic radar and Schottky diode-based transponders (Windell and Kautz 2007). The objective of that study was to determine the maximum weight of transponder a flying beetle could carry by simulating the Schottky diode with small pieces of metal attached to the pronotum. The larger the diode that could be added without seriously affecting its natural flight characteristics, the larger the insect's radar image and therefore the range at which it could be tracked. We will present here the methods used in this study sufficient to explain how we calibrated our flight mill study results to derive absolute estimates of flight performance.

A white sheet was attached to the walls in one corner of a 6 × 10 m room. A mirror 1.5 m high by 1.8 m wide was positioned touching the wall to the left of the corner such that the angle formed by the mirror and the wall from mirror to corner was 135° (Fig. 1). A 30 cm long stick to serve as a launch platform for the beetles was placed 64.7 cm from the intersection of the mirror and wall on a line running through the intersection and making a 45° angle with the wall. A Photron FASTCAM Ultima APX high-speed camera with an array of 1,024 by 1,024 ultra-sensitive 17.5 µm CMOS sensors capable of imaging 2,000 times per second was used to record flights for 3 s into 8 GB of memory. The camera was placed about 646 cm from the wall such that half the image contained the mirror and half the wall from the mirror to the corner. Thus, the camera viewed the beetle on the right side and its mirror image on the left making it possible to determine position regardless of the direction the beetle flew. The three dimensional space comprising the object and its mirror image was about 84 cm high × 168 cm wide × 100 cm deep. The camera's viewing area (the front of the imaginary volume contained by the mirror and the adjacent wall) was set at 1,024 (wide) × 512 (high) pixels, and the frame rate was 250 frames per second which resulted in file sizes of 400–700 MB for a 1.0 to 1.5 s flight. The video images were turned into two sets of 2-D coordinates using the camera's Photron Motion Tools software package. These two sets of 2-D coordinates were turned into 3-D coordinates in an Excel spreadsheet using an algorithm to be described elsewhere.

The basic concept was to obtain a flying beetle's X and Y coordinate position from the front face of the imaginary volume and to calculate the EAB's depth into the volume (the Z coordinate) from the reflected image's X and Y coordinates. The analysis used to map the two pairs of 2-D coordinates (generated by the video analysis software) into 3-D space actually utilizes only the X coordinate of the forward (real) view and uses both X and Y coordinates of the reflected image. A steel ruler was placed so as to appear in the mirror image to serve as a calibration marker so that the pixel-based coordinates could eventually be converted to distances. The steel ruler was placed at different locations to check the accuracy of the analysis.

Due to time constraints, flights were restricted to female EAB, in part because they are the agents of dispersal (Taylor et al 2006) and because, being larger than males, they were more likely to be able to carry the transponder in the field. The

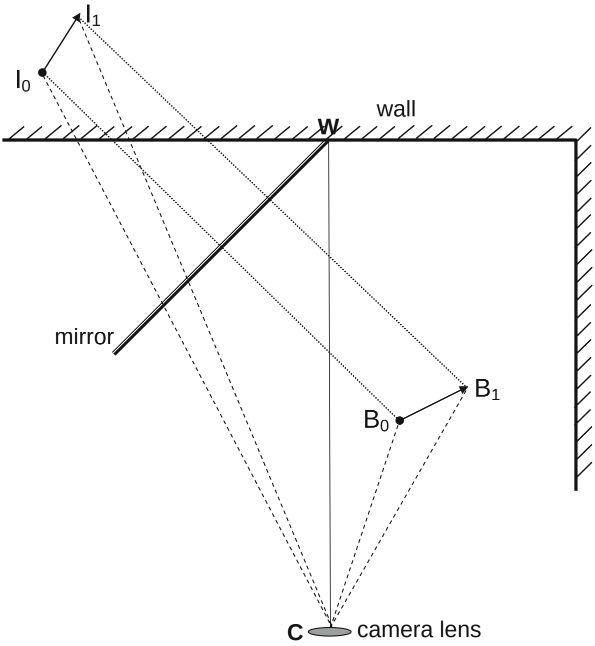

Fig. 1 Diagram showing the setup of the free-flight experiments, shown here in two dimensions. A high-speed video camera perpendicular to the 135° vertex made by the mirror and wall simultaneously films the movement of a beetle from $\mathbf{B_0}$ to $\mathbf{B_1}$ and its image in the mirror $\mathbf{I_0}$ to $\mathbf{I_1}$. The actual distance moved in between frames **0** and **1** are calculated from the angles $\mathbf{B_0CW}$, $\mathbf{B_1CW}$, $\mathbf{I_0CW}$ and $\mathbf{I_1CW}$ which are determined by the positions on the video image knowing the distance **CW** (646 cm). The logic is the same in three dimensions, except that there are two more vectors corresponding to the vertical axis not visible in this plan projection. A complete description is in Windell and Kautz (2007).

EAB used in this portion of the study were reared as described above. Flights were conducted on 1 and 2 June 2005 about a week after eclosion. Beetles were weighed before and after the load was attached. To simulate potential transponders, small pieces of plastic or paper clip were glued to the pronotum of each beetle. The method used to attach the weights, as well as the position, were the same as the flight-mill tether. Weights ranged from ~1.5 mg to ~17 mg including the rubber cement used for attachment. Both weighted and unweighted beetles were flown. These data were used in two comparisons: Comparison 6 compared free flight speed of mated female beetles with and without weights; and Comparison 7 compared flight speed of mated females in free and tethered flight.

Results

General Observations

A total of 177 EAB were flown on flight mills; 23 males, 82 virgin females, and 72 mated females. Figure 2 shows the frequency distribution of distance flown in 24 h by all EAB without regard for the experimental treatment. Eight 1 day old, unfed virgin females flown in the preliminary trial are included in Fig. 2 but not in any analysis. Thirty-two of the mated females were flown on multiple occasions resulting in 64 data sets for flight performance following rest; only the first 24 h are included in Fig. 2. More than half of the beetles flew >750 m, 20% flew >3 km, and 1% flew >6 km in tethered flight. The time spent flying varied from a few minutes out of 24 h to 105 min over a 5-day period. Tethered EAB adults flew up to 2.8 km/day at time-averaged speeds ~0.36±0.10 (± SD) m/s (1.30±0.35 kph). There was much less variation in the instantaneous speed: 1.0±0.05 m/s (3.4±0.17 kph). Clearly the mill imposed a substantial speed penalty on the beetles; they were either flying at 1.5–2.0 Hz or not at all. Transients at the beginning of a flight bout were not discernable, whereas the end of a bout was characterized by one or two revolutions coasting which the monitor mostly ignored.

Mated females flew almost 2.5 times as far as unmated females. Females flown for 8 h/day and allowed to rest, feed, and drink for 16 h, continued to make long flights for up to 5 days: the maximum distance flown being 7.2 km in 4 days and with 12% flying >5 km. Considering the entire data set, the frequency distribution of distance flown was roughly lognormal (Fig. 2) with about half flying >750 m, but the long tail demonstrates that some EAB can fly considerably further. Of those that flew more than a few minutes, flight distances ranged from 71 to 2,426 m for fed, 6-day-old females. Two unfed, newly emerged females flew 716 and 804 m. Flight ranged from 53 to 5,233 m for males. Although few EAB continued to fly after 20 h of tethering, one 3-day-old male flew 1,653 m and 3,580 m in two consecutive 20-h blocks of time, for a total of 5,233 m in 40 h.

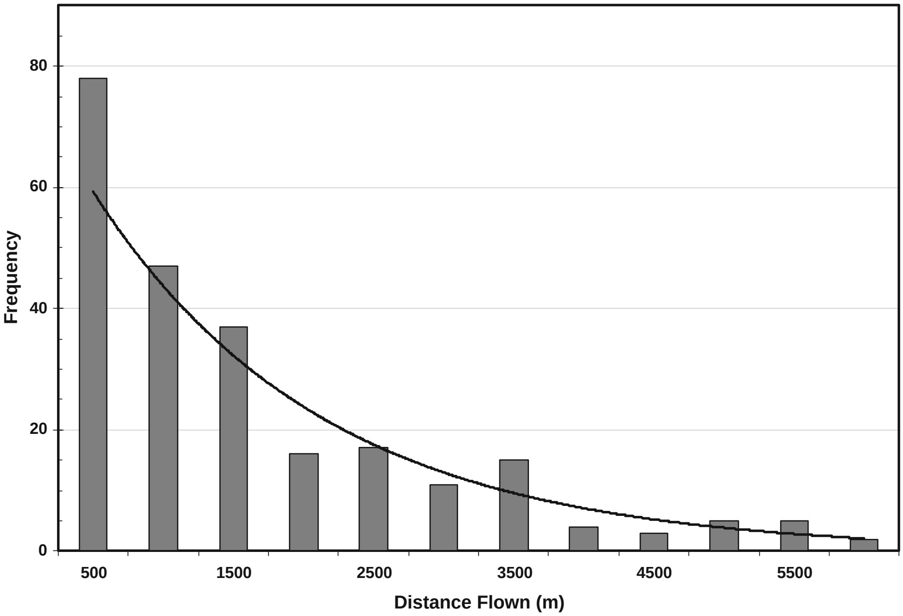

Fig. 2 The distance flown in 24 h by all emerald ash borer adults flown on the flight mill during the course of this study (N=177) is approximately lognormally distributed. More than half of the beetles flew >750 m, 20% flew >3 km, and 1% flew >6 km in tethered flight.

The time-averaged flight speed of 1.30 kph occurred on average in bouts of about 2 min each. The individuals that flew the furthest in 24 h typically started with 2–4 min flight bouts followed by idle periods of about 4–7 min. During the first hour or so, the ratio of flight to rest time increased from 1:2 to 1:1, but after about 2 h, the idle time increased, raising the flight to rest ratio to about 1:25 at 24 h. Figure 3 shows typical examples of bout pattern of a male flown in 24 h light and a mated female flown in 16:8 h light and dark. The distributions of flight and rest times were approximately normally distributed on log scale with the time spent resting approximately 25 times the flight time overall (Fig. 4). This overall pattern was seen repeatedly, especially with the longer distance fliers of both sexes, although the details of the bout patterns differed greatly between individuals (Fig. 3).

Comparison of distance flown and age of one to twelve day-old beetles showed no correlation (r^2=0.028), with members from each day-age cohort flying from near zero to 2 km in 24 h. Examination of the distribution of bouts showed that while most flight was in light, flight also occurred in every hour of darkness (Fig. 3). There was no relationship between size (weight) and distance flown (r^2=0.061) or total time spent flying (r^2=0.034).

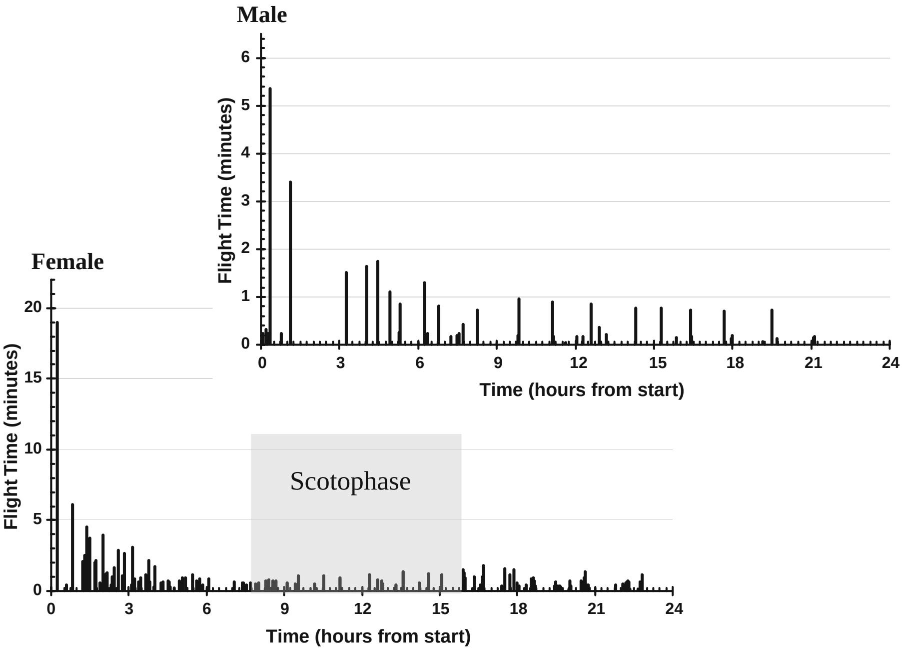

Fig. 3 Typical pattern of flight bouts of emerald ash borers on the flight mill over a 24 h period. Upper figure shows the bout pattern of a male flown in constant light, lower figure is a mated female flown in 16:8 (L:D). Both individuals flew in every hour of the day and the female flew in dark as well as light. The pattern of female flight shows increased activity but not as a consequence of the light pattern: the pattern of flight by unmated females in constant light and in 16:8 (L:D) is more like the male illustration than the female.

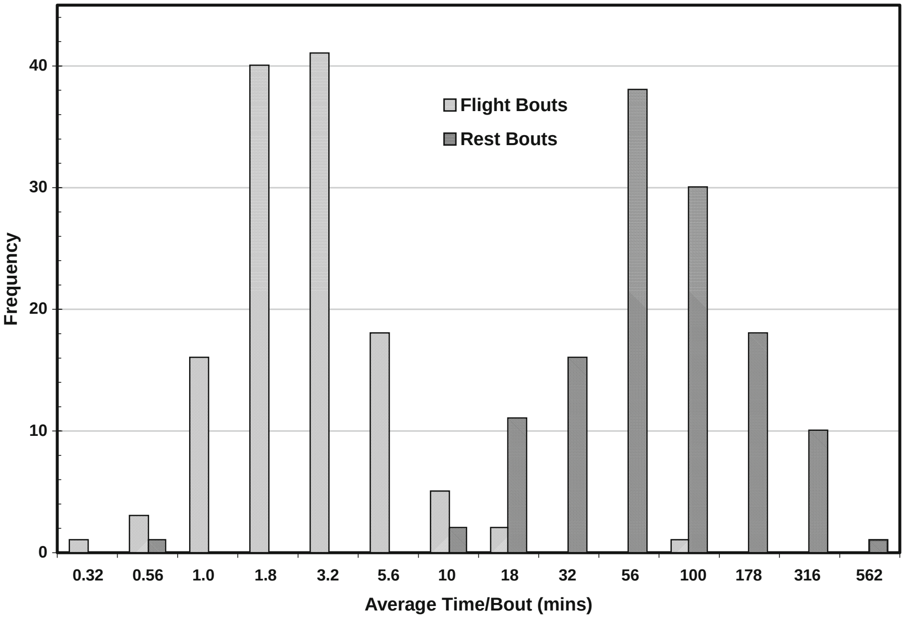

Fig. 4 The average time spent flying per bout (*left*) and time spent resting between bouts (*right*) by emerald ash borers on the flight mill (16:8, L:D). On average, approximately one hour in every 24 was spent flying. ($N=242$, includes flights on multiple days).

Experiments: Relative Estimates

Comparison 1: Males vs. Virgin Females Comparison of the flight performance of eight-day old males and virgin females flown in constant light for 24 h revealed that males spent significantly more time flying and flew further in more bouts than virgin females (Time, $t_{41}=2.18$, $p=0.035$; Distance, $t_{41}=2.14$, $p=0.038$; Number of bouts, $t_{41}=2.97$, $p=0.005$). However, there was no difference in average flight speed ($t_{41}=0.77$, $p=0.45$).

Comparison 2: Constant Light vs. 16:8 Light:Dark Four variables were used to compare the flight performance of eight-day old virgin females flown for 24 h in constant light or 16:8 L:D: number of activity bouts, total time spent flying (min), total distance flown (m), and average flight speed (kph). Average flight speed, distance flown, and time spent flying did not differ between the two sets (Speed, $t_{33}=0.78$, $p=0.44$; Distance, $t_{33}=0.88$, $p=0.39$; Time, $t_{33}=1.81$, $p=0.079$). However, the number of bouts did differ ($t_{33}=2.35$, $p=0.034$). Examination of the primary data files with the event times showed that in many instances a light change (both on and off) was followed by an increase in flight activity (number and duration of bouts). Thus, the slightly different time spent flying (significant at the 0.08 level) by beetles in alternating light and dark is almost certainly a function of the increase in bout frequency induced by the change in light regime.

Comparison 3: Mated vs. Virgin Females In 16 h light and 8 h dark, mated females flew more than twice as long as virgin females (82 vs. 34 min, $t_{117}=5.51$, $p<0.0001$)

and covered nearly 2.5 times the distance (2,029 vs. 821 m, $t_{117}=6.20$, $p<0.0001$) in twice the number of flight bouts (65 vs. 32 bouts, $t_{117}=2.99$, $p=0.003$) over 24 h. The average flight speeds were almost identical (1.31 vs. 1.30 kph, $t_{117}=0.14$, $p=0.89$).

Comparison 4: Males vs. Mated Females Although the number of flight bouts is apparently influenced by changing the light level and males were only flown in constant light, while mated females were flown in 16 h light 8 h dark, the flight parameters for males and mated females were compared. There were no differences in time spent flying and distance flown by females in 16 vs. 24 hour light (Comparison 2), thus the highly significant differences between males and mated females in these parameters are certainly real (Time, $t_{93}=4.29$, $p<0.0001$; Distance, $t_{93}=3.65$, $p=0.0004$). Again, there was no difference in flight speed ($t_{93}=1.52$, $p=0.13$). However, the difference in average number of bouts in 24 h (65 vs. 33 bouts; $t_{93}=2.60$, $p=0.011$) was the same as obtained in the comparison between mated and unmated females (65 vs. 32 bouts).

Comparison 5: Flight with Rest Periods vs. Continuous Flight The flight results of mated females flown for 8 h in light and permitted food and 16 h of rest in 8 h light and 8 h dark were accumulated over 3 days to standardize to 24 h for comparison with mated females not permitted rest and flown continuously for 24 h. The number of bouts per 24 hr of flight was almost identical for flights with rests and continuous flight (64.6 h vs. 65.4 h; $t_{135}=0.06$, $p=0.95$). However, the total time spent flying by rested beetles was twice that spent by beetles in continuous flight (159 min vs. 83 min; $t_{135}=7.11$, $p<0.0001$). As flight speeds were also virtually identical (1.31 kph vs. 1.30 kph; $t_{135}=0.11$, $p=0.91$), the distance flown by rested beetles was also twice that of unrested beetles (4,081 m vs. 2,029 m; $t_{135}=4.61$, $p<0.0001$).

Absolute Estimates of Flight Performance

Comparison 6: Weighted vs. Unweighted Free Flight Speed The free flight tests were conducted with 76 mated female EABs of which 25 flights were discarded because they flew downwards, or not at all, and a few flights were discarded because of purely technical difficulties. Of the remaining 51 beetles, 34 carried weights and 17 flew without weights to establish a baseline.

Flight duration ranged from 0.62 s to 2.06 s, averaging 1.1±0.32 s (± SD) before leaving the observation area. The distances computed ranged from 0.64 to 2.03 m, resulting in computed flight speeds of 0.77 to 1.65 m/s (2.76–5.94 kph), with an average of 1.14±0.19 m/s (4.12±0.68 kph). The fastest female EAB carrying a weight flew 1.65 m/s over a 1.83 m flight path carrying a 9.86 mg load. This individual was one of the oldest tested. She weighed 54.2 mg prior to weight being added and carried a load that was 18% of her body weight. The heaviest weight a female EAB carried during flight was 16 mg or 38% of body weight. The females used for analysis averaged 45.3±6.88 mg and the loads ranged from 2.3% to 38% of body weight.

Free flight speed of female EAB declined significantly with load (Fig. 5). The 16 females with no load were included in this regression as they “fix” the intercept at the average speed for no-load females. The relationship between flight speed and load is highly significant ($F_{1,49}=27.4$, $p<0.0001$, $r^2=0.36$) with the fitted equation given by:

$$SpeedWithLoad = 4.53 - 0.083\,Load \tag{1}$$

Rearranging the fitted regression Eq. 1, the expected free flight speed of female EAB *without* load may be calculated from:

$$SpeedNoLoad = SpeedWithLoad + 0.083\,Load \tag{2}$$

Using Eq. 2 to remove the effect of load on flight speed, it is possible to use the data of weighted free flight speed to define the frequency distribution of free flight speed without load.

Comparison 7: Tethered Flight vs. Free Flight Speed Often there is a positive relationship between size of insect and flight performance (Johnson 1969): this was not the case with EAB. None of the comparisons of average flight speed (see Comparisons 1–5 above) were significantly different even though females are typically >50% larger than males (females weighed 43.5±6.9 mg vs. 25.8±8.3 mg for males). There was considerable variation in distance flown during flight bouts of tethered beetles, but this variation was not related to beetle weight; the fitted equation, $Distance = 0.038 \cdot Weight - 0.098$, is not significant ($p>0.65$) and has $r^2=0.061$.

Mean flight speed in free flight was three times that of the mean flight mill speed (4.53±0.54 kph vs 1.29±0.37 kph) (Fig. 6). Although differences in flight speed were significantly different ($t_{168}=40.2$, $p<0.0001$), the standard deviations were not ($t_{168}=1.47$, $p=0.16$). These parameters define the fitted normal distributions shown in Fig. 6. Neither empirical distribution is significantly different from the fitted normal distribution. Thus, we conclude that the impact of the flight mill is to reduce the measured flight speed by a factor of approximately three. Assuming the duration

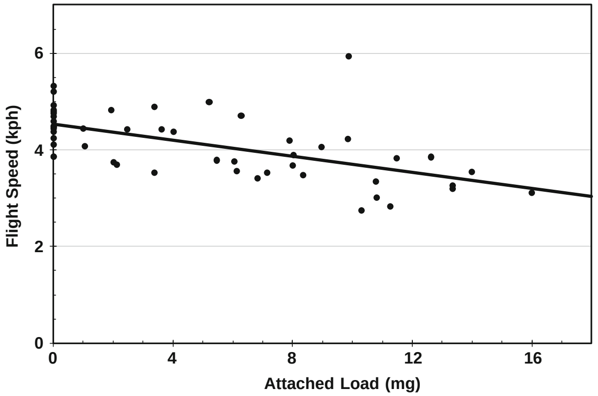

Fig. 5 Flight speed versus attached weight load. ($N=51$) Fitted equation is $Speed=4.53-0.083 \cdot Load$ is significant at $p<0.0001$ and has $r^2=0.36$.

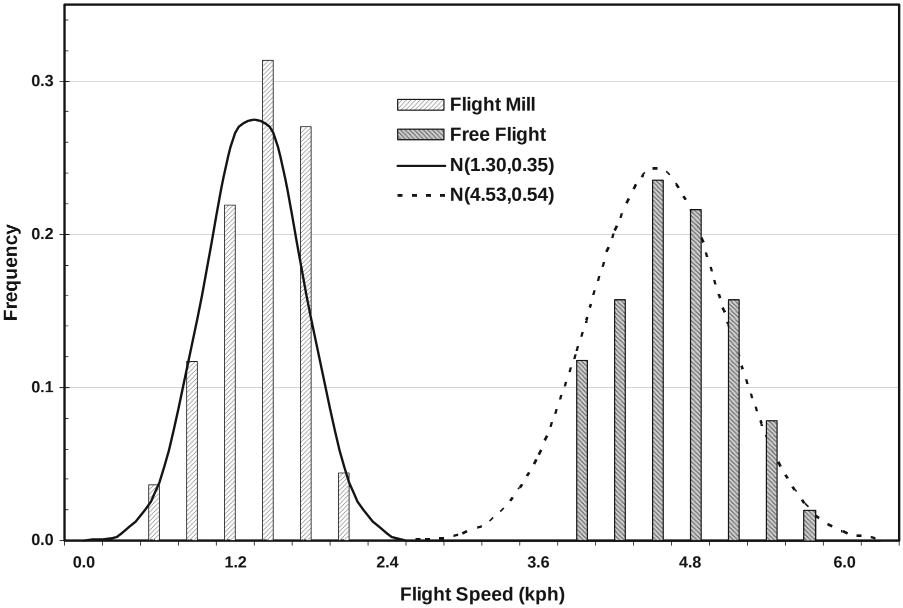

Fig. 6 Flight speed of mated female emerald ash borers on the flight mill (*left*, $N=114$) and in free flight (*right*, $N=51$). The fitted normal distributions are: flight mill, mean=1.30, standard deviation=0.35; free flight, mean=4.53, standard deviation=0.54. The standard deviations are not significantly different ($t_{186}=1.47$, $p=0.15$), but the means are ($t_{186}=40.2$, $p<0.0001$) with free flight 3.25 kph greater than flight on the mill.

of EAB flight on the flight mill is not greater than the same individual could achieve in the wild, we now revise the values in the abscissa of Fig. 2 up by a factor of three.

Discussion

Tethering insects for flight mill studies entails both practical and theoretical problems. It is known that handling can reduce (Kennedy and Booth 1963a, b) or increase (Cockbain 1961) propensity for flight and the smaller the insect, the greater the impact of handling. Emerald ash borer is of medium size and still requires fairly intrusive handling. Thus, we expect handling to have some effect on flight mill performance. Flight chambers offer an alternative to flight mills, provided that flight is continuous for long periods. For species like EAB that take off, fly for a short period, alight, take off again, and repeat this pattern of short flights several times, the flight chamber is unsatisfactory. Thus, despite handling interference, flight mills offer a better alternative for insects, such as EAB, for which flight-bout length and interval are important parameters.

Flight mill design is critical, as we found with EAB; their flight speed and mass were so great that it was necessary to increase the power of the magnets in our mills before we could conduct our experiments. This also served to increase the dynamo effect and the parasitic drag of the arm beyond what a leafhopper would be capable of turning. If parasitic effects are too great, the insect may never succeed in initiating flight, or give up long before any normal threshold for quitting flight is exceeded. If they do fly, insects flying on a mill will consume fuel faster and fly slower than in free flight. Thus, we might expect that measurements of flight speed and endurance from flight mills will be underestimated. This proved to be the case with EAB.

Despite these limitations, however, replicated flight mills remain an important instrument for measuring relative flight performance of even very small insects. Because it has proven to be very difficult, calibration of flight mills to obtain absolute estimates of flight performance has rarely been attempted; Krogh and Weis-Fogh (1952) with desert locust, *Schistocerca gregaria* (Forsk.) and Riley et al. (1997) with *Cicadulina* leafhoppers, using different methods are exceptions. Thus, as Rowley et al. (1968) pointed out, comparisons of performance of two or more experimental groups partially overcomes the problem of interpreting flight mill studies. The assumption that handling and tethering the insects, and the drag imposed by the mill itself, affect behavior and performance of all experimental units equally is probably reasonable. We made that assumption in conducting our flight mill studies. However, it is known that some aspects of the flight behavior are similar on the mill and in the wild. In several moth species (e.g. *Spodoptera exempta* (Walker) (Gatehouse and Hackett 1980), *Anticarsia gemmatalis* (Hübner) (Gatehouse and Woodrow 1987), *Helicoverpa* (= *Heliothis*) *zea* (Hübner) (Cooter and Armes 1993)) the frequency distribution of flight bout lengths on the mill and in the wild are indistinguishable.

Photographic methods of recording insect flight in three dimensions are minimally intrusive, but its ability to measure only the first few seconds of flight is a limitation. El-Sayed et al. (2000) obtained three-dimensional coordinates of flying insects using two cameras, enabling the target insect to be tracked in a stereoscopic field of view as the insect flew through it. This method was developed to assess the attractiveness of various pheromone blends of the grapevine tortrix, *Lobesia botrana* (Den. & Schiff.), following a pheromone plume in a wind tunnel. Adult EAB do not appear to use pheromones although they do respond to volatiles derived from ash trees (de Groot et al. 2008; Crook et al. 2008) and visual stimuli (Francese et al. 2005). Species that respond to pheromones may be tested in wind tunnels where unfettered flight estimates may be obtained. However, there may be differences between flight behavior of plume-tracking insects and insects searching visually, or those engaged in migratory flight. Migratory flight and mate-seeking flight are often not the same; certainly the back and forth tracking across the plume by a suitor is very different from the more linear flight typical during migration. Thus, even in a wind tunnel behavioral uncertainty may be a factor. Obtaining reliable estimates of insect flight performance over long time periods cannot be obtained without interfering with the insect's behavior, and minimally intrusive methods can give only transitory estimates; a sort of behavioral Heisenberg uncertainty principle.

These studies were conducted in a more or less stimulus-free environment; thus, we have no knowledge of what external factors influenced flight thresholds and parameters. It is known from studies of flight in other insects that environmental factors can greatly influence results. For example, Spiewok and Schmolz (2006) found that flight speed of European hornet (*Vespa crabro* L.) workers was independent of temperature, while that of drones was negatively correlated with temperature, and workers reduced their flight speed in low light levels, whereas drones did not. The proportion of individuals initiating flight may also be influenced by mating status as well as the ambient light and temperature conditions. Few tethered green rice leafhoppers (*Nephotettix virescens* (Distant)) could be stimulated to fly more than a few short bouts, but those that did, flew for long periods with one female flying ~7 h non stop, indicating the potential for long distance dispersal (Cooter et al. 2000). Although mating status was unknown, they found that mature females caged with males were more willing to fly than those caged separately. It is not unusual for mated females to be more willing to fly (Johnson 1969) and it is possible that only mated female *N. virescens* are long-distance migrants. It has often been found that reproductive apparatus in migratory insects develop as flight muscles atrophy, the oogenesis-flight syndrome (Johnson 1969). Insects that exhibit the oogenesis-flight syndrome also exhibit a strong correlation between size and flight performance. However, this was not the case with EAB we tested. Like EAB, the beet armyworm (*Spodoptera exigua* (Hubner)) flies and lays eggs repeatedly, but unlike EAB, little difference was found in flight capacity of mated and unmated females on flight mills (Han et al 2008). Our findings that mated EAB females flew longer and further than either males or unmated females suggests that mated females may be programmed to make dispersal flights after mating. As mating normally occurs several days after eclosion and following feeding, this may constitute a migratory flight of the Second Kind (Taylor 1986); the movement undertaken by all members of a population away from their natal site and which may be away from or within the general confines of the natal habitat. This definition of migration contrasts with the more widely known concept of exodus flight that characterizes most of Johnson's (1969) Classes. The practical consequence of these findings is that creating ash-free zones and other quarantine measures may have little chance of success, and if not, such measures are likely counter-productive by possibly stimulating long-distance dispersal flights of gravid EAB females in search of ash trees on which to lay eggs.

Windell and Kautz's (2007) method of estimating free flight speed is similar to that of El-Sayed et al. (2000) but cleverly uses a mirror instead of a second camera. The use of cameras to track flight in real time is a partial solution to the uncertainty principle. Combining the near instantaneous estimation of flight speed using cameras and the long-term performance estimation obtained with flight mills is a new and useful development. However, flight speed in the first few seconds after take-off may not be representative of later flight. Shelton et al. (2006), investigating flight of termites (*Reticulitermes flavipes* (Kollar)) on flight mills, were able to distinguish between acceleration, cruising, and deceleration, and found a diminution of cruising speed with time. Our data show a small but significant ($r^2=0.164$, $p<0.001$) correlation of flight speed and bout number. Examination of the first few seconds of flight showed that EAB accelerated substantially more rapidly than the termites reported by Shelton et al. (2006). Examination of flight bout termination shows deceleration to occur after the beetles had closed their wings. The low-speed cutoff used to delimit flight may obscure the earliest part of the acceleration phase. A detailed analysis of individual flight bouts is currently underway that will permit a comparison of EAB and termite flight patterns. It is not clear to what extent the inertia of the mill arm influences acceleration and deceleration, but it seems likely that the slowing of flight speed with bout number is due to fatigue, which is likely to be more rapid when pulling the mill arm than during free flight.

The use of the photographic method to obtain instantaneous flight speeds represents a new and potentially valuable method for calibrating flight mill studies. As the acceleration periods we observed were very short, the speeds recorded in the initial bouts are very comparable to the speeds recorded immediately following takeoff using the photographic method. The small but significant decline in average speed with bout number amounted to a decline over 24 h of only 7%. Thus, the frequency distributions of flight mill speed is directly comparable to that observed in the photographic study. The similarity in the two distributions (allowing for the shift) is quite remarkable and is unlikely to be coincidence. Therefore we feel quite confident that the upward revision in flight speed by a factor of three is justified and a similar revision to duration and range are realistic.

Obviously, as these data were all obtained in the laboratory, they may not be truly representative of flight performance in the field, especially in non-protected areas between woodlots where flight may be above the boundary layer (Taylor 1974) and strongly influenced by wind. Within the relatively protected areas within wooded areas, these results are probably realistic. As flight in the open, between woodlots, has not been recorded, it remains to be seen how far female EAB might actually fly in search of a host tree. The project for which the photographic study was made will answer that question by permitting individual beetles to be tracked by radar. Confirmation of long distance rapid flight must await completion of the radar study. Our results have shown, however, that EAB has the *capability* of flying considerable distances with and without food and water, certainly further than the quarantine zones initially put in place. Increasing the flight mill estimates by a factor of three suggests that 20% of mated females are capable of flying >10 km in 24 h and 1% able to fly >20 km in 24 h. Even without food and water, the distance these insects are capable of flying is impressive and certainly far enough to cross substantial firebreak zones.

Some of the rapid spread to areas outside Michigan resulted from transport of EAB-infested ash by human activities (e.g. infested ash nursery stock from Michigan sold in Maryland and Virginia). Models of the spread of EAB confirm the importance of both transport modes (Muirhead et al. 2006) and highlight the regulatory difficulties (BenDor et al. 2006). Many of the isolated infestations that continue to be discovered in Ohio, Indiana, Illinois, Missouri, Virginia, West Virginia, Wisconsin, and Quebec, Canada are clearly anthropogenic, but the steady range expansion out from the Detroit-Windsor Metro Area is due to the natural dispersal of EAB (Siegert et al. 2008). Knowledge of flight behavior and physiology are essential to estimate dispersal capabilities for developing strategies to contain or slow the spread of EAB (Taylor et al. 2008). So far, attempts to contain the spread have failed, and failure to understand natural dispersal prior to development and implementation of an eradication plan has clearly impeded attempts to manage EAB in North America.

Using simulation models of the spread of EAB in Prince George's County, Maryland, Sawyer (2007) concluded that assumptions about EAB dispersal capacity that led to the 800 m (one-half mile) ash-free zone is "clearly in need of revision." He examined how an infestation's outermost limit depends on population size, which in turn determines how many individuals are at the extreme of the number-distance curve (Fig. 2), leading to a ragged outmost "edge". His conclusion that random events can place colonizers well beyond the 800 m ash-free zone is well supported by the evidence from Maryland (Sawyer 2007) and Essex County, Ontario (Marchant 2006). This is also consistent with our results. As detection of EAB at low densities is very difficult, this emphasizes the importance of survey and detection at the "edge" of an infestation and prompt action in containing an infestation early.

Using our experimental data to parameterize a simple two dimensional random walk model (Ficke diffusion, Crank 1975) suggests that ~20% of mated females are displaced >250 m while flying ~2 km, and ~1% are displaced ~500 m while flying ~4 km. Pure random walk model is unlikely; few things in nature are truly random. There is generally a systematic component making random walk assumptions improbable (Taylor 1978, 1979, 1980). Neither the models (BenDor et al. 2006; Muirhead et al. 2006; Sawyer 2007) nor our experiments took into account factors such as attraction to host trees, attraction to mates, and the pattern of flights between egg laying, all of which make dispersal more complex than random walk. In order to determine how significant this is for control and containment efforts, we need to know how directional the flights actually are and how receptive mated females are to cues from ash trees for stopping their dispersal flight to settle. These are questions in dire need of answers.

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