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Analysis of Anemotactic Flight Tendencies of the Spotted Lanternfly (*Lycorma delicatula*) during the 2017 Mass Dispersal Flights in Pennsylvania

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Abstract Video-recordings were made of adult spotted lanternflies, *Lycorma delicatula*, taking flight from apple trees in an orchard in northeast Pennsylvania in September, 2017 during a mass dispersal flight event involving thousands of adults. The trajectories of adults flying upwind in straight and level or gradually descending flight allowed them to traverse only up to ca. 40 m in a single flight-bout. Many did not make it to trees or bushes that were at even shorter distances than this and they landed in the grass. Flight tracks of 162 adults launching themselves into the wind from the upper branches of apple trees were video-recorded in plan view from below by a camera placed on the ground aimed straight up at the sky. The tracks were then digitized and analyzed using a triangle of velocities technique to determine the degree to which the adults were progressing in a directly upwind flight track, with the wind vector experienced by each adult calculated from the adults' flight track itself. Average airspeeds of upwind-flying *L. delicatula* had been previously measured in another group of adults and shown to not vary with wind speed. The headings (direction of thrust) of adults in the video frames were determined by matching the image of the adult in each video frame with a template image of a pinned adult of a known distance from the camera and heading. Matching the body axis in this way works for this species because the adults flying in these elongated fairly straight flight paths did so with forewings spread out flat to the ground with little discernable roll. Having determined airspeed and heading plus ground speed and track for each set of images allowed the third side of the triangle of velocities — the wind velocity vector — to be calculated for each flying adult at whatever altitude or lateral location in the camera's field of view it was flying. Adult *L. delicatula* were found to head upwind in flight at 10.7° off the wind line to produce resulting track angles of progression over the ground averaging 30.9° off the wind line due to this discrepancy between their headings and the wind velocities into which they were flying. The wind velocity vectors provided by a ground-based anemometer during the periods each adult was flying through the video frames deviated from the wind velocity vectors calculated using the triangle of velocities technique by nearly 22° and were 50% lower in wind speed than the calculated vectors taken at the higher altitudes and locations each adult was flying. The triangle of velocities technique might provide a new way of using certain species of insects as free-flying anemometers to take wind velocity readings at different heights and spatial locations that are not attainable through the use of ground-based anemometers.

Dedicated to the Memory of Professor J. S. Kennedy, First to Describe Optomotor Anemotaxis and Triangle of Velocities for Studying Insect Flight Behavior

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Introduction

The spotted lanternfly (SLF), *Lycorma delicatula* (Hemiptera: Fulgoridae) is a U.S.- invasive pest species native to China, Vietnam and India that is now threatening vineyards, fruit orchards, and hardwood forests in Pennsylvania and the northeast U.S. It was first detected in one county in Pennsylvania in fall of 2014 (Pennsylvania Dept. of Agriculture 2017) and was limited in its distribution during 2015 to a small portion of one county in eastern Pennsylvania (Barringer et al. 2015; Dara et al. 2015). However, it has since spread to a large area that in 2017 comprised over 15,000 km^2 (Pennsylvania Department of Agriculture 2017) in a quarantine zone spanning 13 Pennsylvania counties. Recent detections during 2017 and 2018 have been reported also in two neighboring states – Virginia and New Jersey.

By the time *L. delicatula* was discovered in Pennsylvania in 2014, it had already established itself as a pest in Korea and Japan (Kim and Kim 2005; Han et al. 2008; Lee et al. 2009; Kim et al. 2011; Tomisawa et al. 2013). In Korea, where it had been previously introduced from China (Han et al. 2008), the copious amounts of honeydew due to the feeding of *L. delicatula* create extensive deposits of sooty mold that negatively affects the quality of harvested cultivated grapes (Kim and Kim 2005; Lee et al. 2009). Infestations of *L. delicatula* now threaten to harm the $28 M grape industry of Pennsylvania, the large grape industry of New York, and the tree fruit industries of these and other surrounding states. In 2017 significant numbers of SLF adults were observed for the first time feeding in large numbers on black walnut trees, and so the threat of *L. delicatula* to hardwood forests in Pennsylvania and the rest of northeastern U.S. is of deep concern, especially to Pennsylvania's $17B/yr. hardwood forest products industry.

Our studies during 2017 documented a seasonal progression of adult activities, including a first- and second-week focus on feeding, a second-week transition to short flights from the foliage of one tree to another, and second- and third-week transition to longer, straight-line flights over open ground of 20–40 m. Beginning in the second week in September 2017, a massive dispersal flight event occurred, involving perhaps tens of thousands of *L. delicatula* in several areas of eastern Pennsylvania such that several shopping centers, gas stations and fruit orchards were inundated with thousands of flying and crawling *L. delicatula* adults. Even before this flight dispersal episode it had become apparent to us in 2017 with the great amount of flying we were suddenly seeing, we needed to learn anything we could about any preferred directionality to these flights related to wind, visual landmarks, or anything else in order to give practitioners an idea of where the infestation might be expected to spread to in the coming years.

Just prior to the beginning of that large flight dispersal event we had begun focusing our efforts on trying to understand whether there was any directionality to the longer straight-line flight tracks related to flight dispersal behavior, with the goal of possibly being able to predict the directions and distances over which current infestations might spread to. Such high incidences of longer-range sustained flight by individuals in *L. delicatula* populations had not been observed before in the U.S., Korea, or Japan. Our studies included measuring the average airspeeds and ground speeds of one set of flying adults by timing them using a stopwatch and landmarks set 10 m apart as they flew directly upwind over mown grass, and then video-recording and analyzing flight tracks that another set of individual flight-dispersing adults attained during their flights in wind. Our analyses allowed us to determine the degree to which *L. delicatula* adults were oriented with respect to the wind during the first several seconds after take-off.

Materials and Methods

Ground Speed/Airspeed Measurements

On September 7 and 8, 2017, we established two locations at which adult *L. delicatula* were flying out of trees on which they were not feeding, but rather seemed to be using as waystations along their longer flight-dispersal paths. At both locations the adults were launching themselves predominantly into the wind from the upwind sides of the foliage they had been resting on. One location (Site 1) consisted of a stand of 10 white pine trees ca. 8 m in height (Fig. 1) where the adults were

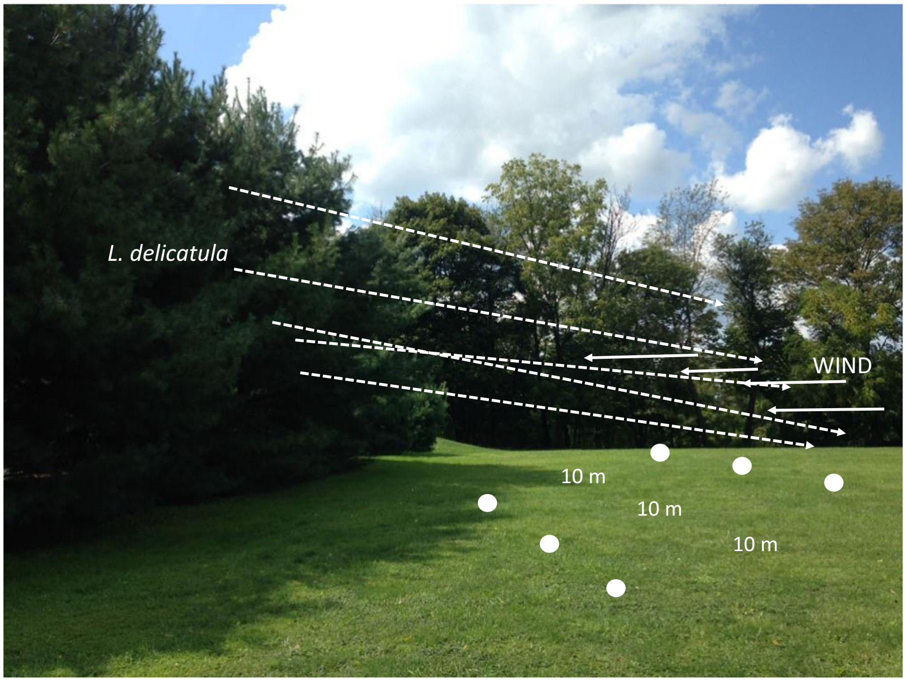

Fig. 1 View of the Site 1 study area at which the ground speeds and airspeeds of flying *L. delicatula* were measured. The distance from the white pine trees at left to the tallest tree in the tree line at far right in the figure is 40 m. *L. delicatula* adults launched themselves only from the windward sides of the white pine trees and flew upwind (solid white arrows are depictions of the general wind direction) across the lawn over our 10 m-spaced pylons in level or gradually descending straight-line flight paths. The dashed lines/arrows are just generalized depictions of flight paths, not actual paths. The observer checked the wind-vane on the hand-held anemometer to ensure that the flight path of the adult was directly into the wind, and then audio-recorded on a smartphone the time it took for each adult to traverse the 10 m distance by announcing "start" and "stop" when the adult flew over the near pylon and then the far pylon, respectively. The observer then within 1 s audio-recorded the wind velocity that had occurred during the flight

taking flight into the wind and toward a line of large hardwood trees 40 m away. The second site was ca. 3 km west of Site 1 and consisted of a single weeping cherry tree ca. 8 m in height out of which the adults were taking flight into the wind toward a line of large hardwood trees 40 m away. At both locations there was mown grass over which the adults flew, with many adults being able to reach the lines of trees 40 m away during their straight-line upwind flights, but with many others falling short of the trees and landing in the grass.

At Site 1 we set up several pairs of 30-cm-high orange traffic cones spaced 10 m apart with the cones closest to the trees being stationed ca. 10 m from the trees (Fig. 1). For one set of readings to obtain ground speeds and airspeeds of *L. delicatula* on the first day of adult flights, we used a hand-held anemometer on top of which was mounted a tissue paper wind vane consisting of a glass micro-test tube mounted on the tip of an insect pin such that the tissue paper plus test tube could swing freely to indicate wind direction (Baker and Haynes (1987). The anemometer was typically held at a height of ca. 1.7 m (eye-level) with the operator ensuring that when an adult's progress was being timed, the tissue-paper wind vane was showing that the wind line was in line with the flight track of the individual being monitored. This ensured that the adult being monitored was progressing along a straight-upwind flight track just as it began traversing the two pylons and its ground speed was being measured.

As each adult flew upwind from the foliage, its passage over the first, and then the second, pylon was verbally recorded onto a smartphone by saying "start" as the adult flew over the first pylon and "stop" when it flew over the second pylon 10 m away (Fig. 1). The observer was stationed half-way between the downwind and upwind pylons for the best timing of the lanternfly's start and finish of the 10 m. Within 1 s after "stop" was declared, the reading shown on the anemometer for wind speed was read by the operator and verbalized onto the smartphone. The entire procedure was practiced for ca. 20 min to ensure a smooth and reproducible recording technique. Most of the flights that were recorded began with an adult launching itself from heights of between 3 and 5 m, with the flight paths either staying level or gradually descending to result in the adults being between 1 and 3 m high after they traversed the pylons. The audio recordings were later played back and transcribed to determine the time elapsed over the 10 m, and hence, the ground speed of each adult. The wind speed occurring during each adult's directly upwind flight was then added to the ground speed to determine the airspeed each adult was achieving during their particular flight into the wind at that wind speed.

Video Recordings of Flight Tracks

Video recordings of adults were made at a third site (Site 3), a commercial apple orchard at which a mass dispersal flight occurred on September 12, 2017. This commercial orchard and vineyard was ca. 3.5 km southeast of Site 1. The *L. delicatula* seemed to be in-transit through the apple trees, with little feeding observed by the adults that seemed to have flown into the orchard from unknown areas such as from woodlots bordering the orchard. Although little feeding was observed on apples, large numbers of adults were found to have settled into, and were extensively feeding on, the commercial grape plantings adjacent to the apple trees (Fig. 2).

Recordings were made of flights occurring from near the tops of the two end-trees in the final row of 6-m-tall apple trees that were adjacent to, and downwind of, 12 rows of 3-m-tall dwarf apple trees that ran parallel to the rows of the larger trees (Fig. 2). A long woodlot containing several 20-m-tall oak trees ran parallel to the rows of apple trees and was ca. 100 m upwind from the last line of tall apple trees where the video recordings were made (Fig. 2). The flights we recorded at that time all were in the generally upwind direction, as was the total mass movement of thousands of adults through the orchard. Approximately 2 m upwind of the large end-tree in that last row of large apple trees, a Samsung Galaxy SIII mini smartphone was placed on a laptop's hand-rest that was placed on the ground, with the smartphone's camera pointing directly upward toward the sky to give a flat upward plane of focus (Fig. 2). A Gill Windsonic two-axis anemometer was placed 1.0 m above the ground 1.5 m to the left of the smartphone. Thus the anemometer was upwind of the large apple trees out of which the *L. delicatula* adults were flying but downwind of the shorter trees that could have contributed some turbulence-related deviations to the anemometer readings. Adult *L. delicatula* were videotaped as they flew from the top of the large apple tree through the smartphone camera's field of view and then over the tops of the 3-m-tall dwarf apple trees farther upwind, with their flight tracks recorded against the sky (Fig. 2). The images of other adults flying upwind, but at higher altitudes, also appeared in the field of view of the camera (Fig. 3), and these lanternflies had apparently taken flight from other large apple trees located still farther downwind of the camera.

Flight Track Analyses

Image Processing/Data Extraction

Video data was acquired on a Samsung Galaxy SIII mini smartphone, which captures color video at a resolution of 1280 × 720 pixels at 30 frames per second. Programs written using Labview (National Instruments) were used to process the video in several stages. For further detailed descriptions of methodologies and formulae used in image processing and analysis please see the Supplemental Materials section. Background subtraction was first performed to isolate moving objects. In this operation, parts of the image that do not change from frame to frame are removed. The locations of objects in each background-subtracted frame were detected and estimated. Following the detection stage, objects moving in relatively straight lines along trajectories were identified to distinguish the spotted lantern flies from other insects and moving tree leaves (Fig. 3). Images within the trajectories that were unusable (image too small and/or blurry (insect too high); wings not flat (distorted left-right symmetry)) were removed manually. These comprised close to 1/3 of the total images. Scale, heading and location measurements (Fig. 4a-c) of the remaining usable detected background-subtracted images were made by comparing each flying *L. delicatula* image with the photo-template image of the *L. delicatula* adult of known scale and heading (Reddy and Chatterji 1996). Any slight left-right asymmetries in images due to a slight but immeasurable amount of roll could increase the amount of error variance around the mean heading direction, but would not change the calculation of the mean heading itself, assuming that there is an equivalent amount of left- and right-error-uncertainty of roll in these images.

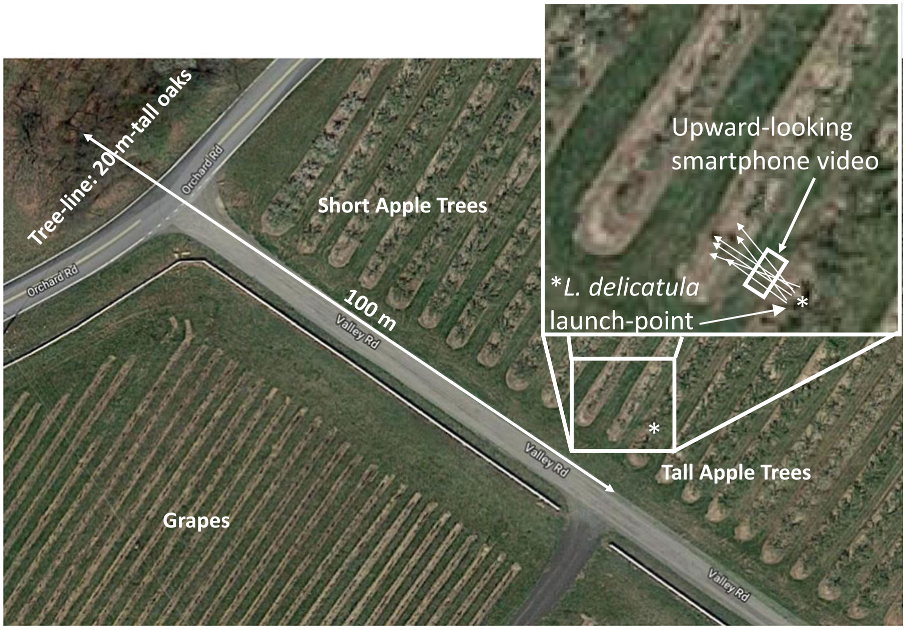

Fig. 2 Aerial view of the Site 3 study area that comprised a commercial apple orchard with many rows of 6-m-tall trees ("Tall Apple Trees") and rows of a shorter, 3-m-tall dwarf variety ("Short Apple Trees"). A large commercial vineyard is located to the left of the road ("Grapes"). Inset shows an enlargement of the small number of trees where a smartphone was laid lengthwise on the ground, as indicated by the white rectangle in the inset. The smartphone obtained a planar, horizontal view of the sky that videotaped the *L. delicatula* generally flying upwind (many white arrows pointing toward the left) in level or gradually descending flight. Many of the adults in the recordings had launched themselves from the large apple tree on the end of the row (asterisk) but many others had originated from trees farther downwind (lower right in photo). The adults flew upwind, both into or across many of the rows of smaller apple trees at left

The height of each *L. delicatula* image was assumed to be inversely proportional to scale estimates, where the constant of proportionality was determined by photographing a dead female *L. delicatula* having a 4.7-cm-diam. wingspan that had been pinned to a wall with wings spread out in normal flight position and photographed from 1, 3, and 9 m away from the camera. We had measured the average wingspan of 10 adults to be 4.71 ± 0.23 S.D. cm, and so the variation in the size of images is less than 5%. In reality only one image is necessary for calibrating height because the width of the insect in the image is inversely proportional to the distance from the image-plane of the camera (excluding optical effects such as blurring) and so the assumptions of a linear magnification equation were met. The height of each flying spotted lanternfly thus was compared to that of the pinned lanternfly photographed on the wall at the 3 m distance.

Height estimates allowed the x and y components of the insects' ground velocities to be computed using two adjacent-in-time location estimates. Assuming the airspeed of the insects is constant, the triangle-of-velocities method (Kennedy 1940) (Fig. 4a-c) combining the heading/airspeed vector and the ground velocity vector was used to calculate the x and y wind velocity components. The difference between the wind direction and an adult's heading was calculated every 1/30 s for all flight tracks to discern the relationship between flight heading and wind direction (Fig. 8a). Likewise, the difference between wind direction and the adult's resultant flight path direction was calculated every 1/30 s to see how far off the wind-line the adults were displacing, on average (Fig. 8b).

Ground Anemometer Measurements

The anemometer's test-based, RS-232 output was captured using Microsoft hyperterminal at a rate of four measurements per second and stored to disk. At the beginning of each video, the text that appeared on the screen of the laptop was recorded with the video camera so that the video recording could be synchronized with the anemometer data. Anemometer data were upsampled in the frequency domain (via zero padding the

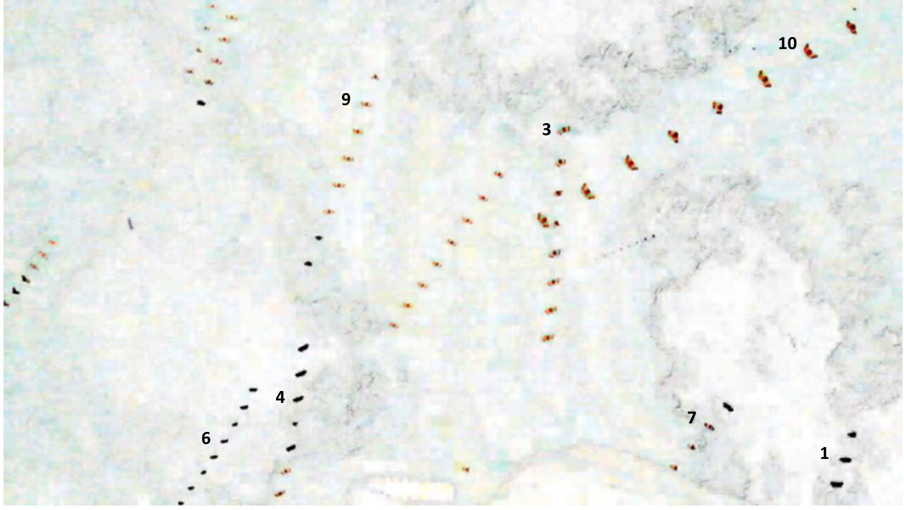

Fig. 3 Digitized/processed images of 11 *L. delicatula* adults flying simultaneously over the video-recording camera's field of view on Sept. 12, 2017. Each track is a succession of freeze-framed 1/30 s images of the progression of an adult over the camera. Clouds and blue sky have been background-subtracted to better discern the images of the flying adults. The numbers 1, 3, 4, 6, 7, 9, 10 refer to the single freeze-frame images of adults shown in the single images in Fig. 5, for which the vectors for ground speed and track angle, airspeed and heading, and wind speed and direction are displayed for that single 1/30 s image of the adult numbered here

DFT) from 4 to 30 Sa/s to match the video frame rate of 30 frames per second before analysis.

Video records of 162 adults were made and analyzed this way, with vectors for the triangle of velocities displayed in color to show the differences between the triangle-of-velocities-calculated wind velocities (black vectors) at any altitude and location in the sky and the vectors measured by the ground-based anemometer (blue vectors) at exactly the same time but at a 1 m height at a fixed location (Figs. 4d,e and 5).

Results

From August 7 to August 15, 2017 during the earliest emergence of *L. delicatula* adults, we observed an early

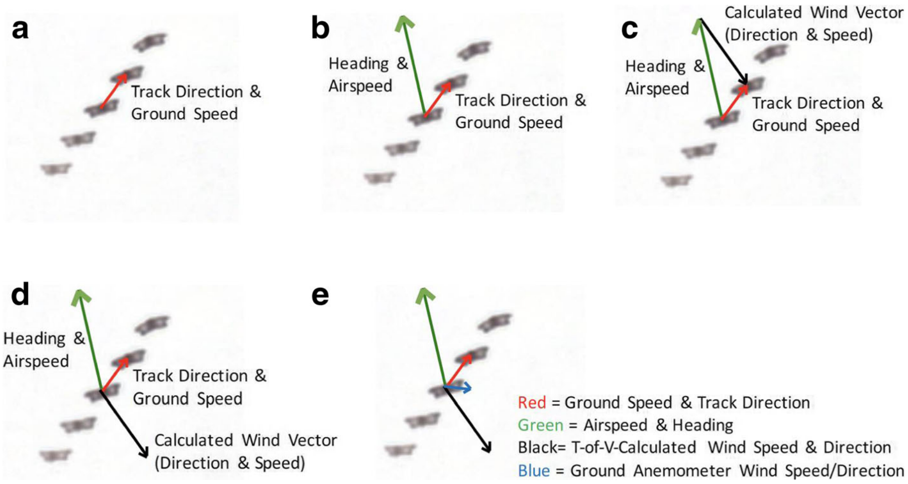

Fig. 4 The triangle of velocities using vectors of ground speed and track angle (**a**) and airspeed and heading angle (**b**) to calculate the third side of the triangle, i.e., the wind velocity vector (**c**) where the adult *L. delicatula* was flying. In **d**, the wind velocity vector from the triangle has been moved to better represent its actual position where it influences the adult's resultant flight track

Fig. 5 The black numbers in bold above each adult's freeze-framed image here correspond to the numbered single images shown in the digitally processed flight tracks in Fig. 3**.** Triangle-of-Velocity-calculated wind speeds experienced by each flying *L. delicatula* adult are shown in black numbers below each image, and ground speeds are shown in red. Ground-anemometer-measured wind speeds measured at this same 1/30-s interval for each adult are shown blue. The invariant airspeed measured for these adults is shown in the green vectors, the lengths of which are scaled for height of flight (size of the adult's image). Vector directions and lengths for ground speed, airspeed, triangle-of-velocity-calculated, and ground-anemometer-measured wind speeds in each image are depicted as red, green, black and blue lines, respectively. Comparison of the black triangle-of-velocity-calculated wind speed numbers with those of the blue anemometer readings demonstrates how much the local wind speeds encountered by flying adult *L. delicatula* at the locations and altitudes at which they were flying can vary from each other as well as from the single reading (here 0.85 m/s) recorded by the ground-based anemometer at this 1/30-s interval

period of local plant-to-plant adult flights after which longer-range straight-line plant-to-plant flights occurred. The peak of these later flights, which we will call "long-range dispersal flights" occurred between Sept. 7 and Sept. 21. We performed our airspeed measurements on Sept. 7 and our flight track video recordings on Sept. 12. We observed that the flight-dispersing adults of both sexes had thin, black abdomens, but during the post-flight-dispersal period — the end of September — there was a prevalence of plump, yellow-abdomen females that were so large they had trouble flying or walking. These plump, relatively sedentary adults — both males and females — were the ones that we observed for the first time *in copula*. We hypothesized that the thinner, flight-dispersing females were in a pre-mated, physiologically immature state, and that they were embarking on these 10–50 m flights from plant to plant in order to try to find new trees on which to feed to repletion so that they could complete their sexual development, form mature eggs, and then mate.

At the three sites we visited there was a distinct upwind bias of both males and females for launching themselves into the wind in flight from any tall structure. At the first two sites, no adults were found on the downwind, leeward sides of either the white pine trees at the first site (Fig. 1) or the weeping cherry tree at the second site. All adults took flight from the upwind, windward sides of these trees, although some adults could be seen arriving to land on the leeward sides, having flown there from unknown downwind starting points. Approximately equal numbers of males and females were involved in these flights. Samplings of SLF landing on the lawns at these two sites revealed 70 males and 61 females that had failed to fly all the way across the 40 m of lawns to reach the tree lines at these sites.

Although the adults did not seem to be able to generate much lift and all of them flew in either level or gradually descending flight paths, they were not slow flyers. Their mean ground speed across our 10 m-spaced pylons was 3.51 m/s (±0.94 S.D.; $N = 44$). The mean airspeed of these upwind-flying adults was 4.64 m/s (±0.92 SD; N = 44). The mean wind speed into which they were flying was 1.17 m/s (±0.62 S.D.; N = 44). These measurements showed that *L. delicatula* did not adjust their airspeeds in-flight to maintain a constant ground speed in different wind velocities, because their ground speed decreased when flying against stronger winds (Fig. 6a). Thus, *L. delicatula* adults seemed to set their flight motor at a certain level and maintain that level at an average airspeed of 4.64 m/s regardless of the strength of the headwind they were flying into (Fig. 6b).

At the commercial apple orchard, we found that *L. delicatula* adults were more likely to take flight upwind from the apple tree foliage when the wind velocity measured by the ground-based anemometer was below ca. 1 m/s and less likely to fly when it gusted to 2 m/s (Figs. 7a, b). Other recordings from down the row of trees showed that in more moderate wind speeds the adults appeared to be more likely to fly when there were lulls in the wind speeds (Figs. 7c, d) and less likely to fly when there was a sudden increase in speed, regardless of how low a speed was occurring at the time (Figs. 7c, d).

Our calculations every 1/30 s of the wind velocity vectors into which each individual adult was flying at their respective altitudes and locations in the video recordings revealed that the average adult headed into the wind on an average of 10.7° (± 28.3 S.D.; *N* = 162 adults) off the wind line to the right (Fig. 8a). The resultant track directions (movement over the ground) of the adults averaged 30.9° (± 42.9 S.D.; N = 162 adults) off the wind line to the right (Fig. 8b) with an average ground speed of 2.65 m/s (± 1.20 S.D.; N = 162). The flight tracks in the video recordings were not long enough to be able to determine whether the adults were making in-flight corrections for off-wind-line flight tracks in order to steer more directly upwind while in flight.

The wind directions calculated using the triangle of velocities at the locations and altitudes where the adults were flying (Fig. 9a) differed by a mean of 21.9° (± 66.2° S.D.) (Fig. 9c) from those registered by the 1 m-high ground-based anemometer at the exact same times as each triangle of velocities wind vector was calculated (Fig. 9b). The ground-based anemometer registered a bimodal distribution of angles over the course of all the recordings that were coupled with each of the vectors calculated from the flights of each adult (Fig. 9b). This differed from the unimodal distribution of triangle-of-velocities-calculated wind vectors (Fig. 9a). These differences are not surprising, given the disparity in altitudes and lateral positions of the *L. delicatula* from that of the one-meter-high anemometer at its fixed location. This illustrates the importance of being able to calculate wind vectors occurring within the local air mass through which an insect is flying.

The wind speeds calculated using the triangle of velocities at the altitudes and locations where the adults were flying (Fig. 10a) averaged 2.75 m/s (±0.93 S.D.; *N* = 1491 vectors) for adults flying at altitudes from 1 to 4 m high, and 2.98 m/s (± 1.32 S.D.; *N* = 1615 vectors) for those flying at heights of 4 to 9 m. The individually calculated wind speeds calculated for all heights that were experienced by each *L. delicatula* adult were ca. twice as high (Mean = 2.83 ± 1.08 S.D.) (Fig. 10a) as the wind speeds that were measured by the ground-based anemometer (Mean = 1.52 m/s ± 0.52 S.D.) at the exact same time each adult was creating its images in the video frames (Fig. 10b).

Discussion

The *L. delicatula* adults recorded in flight in this study launched themselves predominantly into the wind and

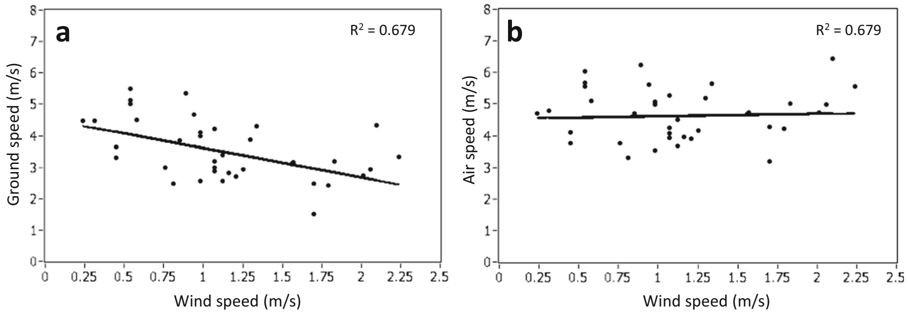

Fig. 6 Ground speeds and airspeeds of 44 *L. delicatula* adults measured at Site 1 on September 7, 2017, using a hand-held anemometer and 10-m-spaced pylons (Fig. 1) over which adults flew upwind from white pine trees over a 40-m-long lawn area in level or slightly descending flight paths. **a** as wind speeds increased, *L. delicatula* ground speeds decreased, indicating that they were not increasing their airspeeds to maintain a preferred ground speed when flying into stronger winds. **b** regardless of the velocity of wind the adults were flying into, they did not change their airspeeds, maintaining a mean airspeed of 4.64 m/s (± 0.92 SD; *N* = 44)

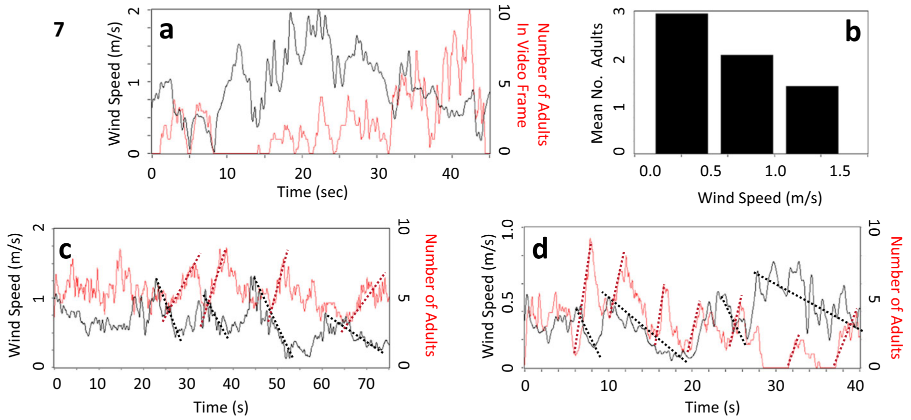

Fig. 7 Ground anemometer readings (black wavy lines in **a**, **c**, **d**) coupled with video recordings of the number of *L. delicatula* seen in the video frames (red wavy lines in **a**, **c**, **d**) at different wind speeds. It should be remembered that according to our results, the wind speeds at the altitudes and locations where adults were seen flying in the video are actually more than double the wind speeds depicted here that were recorded by the ground anemometer. A lag time of 4.0 s was incorporated into the data for adult numbers displayed here relative to the wind speed data in order to account for the observed delay in adults taking off whenever wind-lulls occurred. **a** A 45 s recording during which the wind speed (black) reached 2 m/s at the ground anemometer and then subsided to below 1 m/s, whereupon the number of adults seen flying in the video frames (red) increased to between 5 and 10 adults; **b** Mean numbers of adults in **A** flying in wind speeds of between 0 and 0.5 m/s, 0.5–1.0 m/s, and 1.0–1.5 m/s as measured by the ground anemometer; **c** In a 75 s recording during more moderate wind speeds there appeared to be increases in the numbers adults seen flying in the video frames (highlighted here by upward-going dashed red lines) whenever there was a decrease in wind speed (downward-going dashed black lines), and conversely a decrease in the numbers seen flying whenever the wind speed increased; **d** Even in much lower wind speeds as in this 40 s recording, the numbers of adults seen flying seemed to increase (red dashed-line highlights) whenever there was a decline in wind speed (black dashed lines)

progressed upwind through our video frames at an average of 30.9 ° off the upwind-line by heading an average of 10.7 ° off the wind line. Our calculations from the video recordings showed them advancing upwind at an average ground speed of 2.65 m/s (± 1.20 S.D.; $N = 162$), which, if they flew in bouts of 10 s and performed 10 such bouts, they will have progressed 265 m in a generally upwind direction. It remains to be determined how many flight-bouts are performed by a typical *L. delicatula* adult before they stop flying and settle in a new location to perhaps feed some more, mate, and lay eggs.

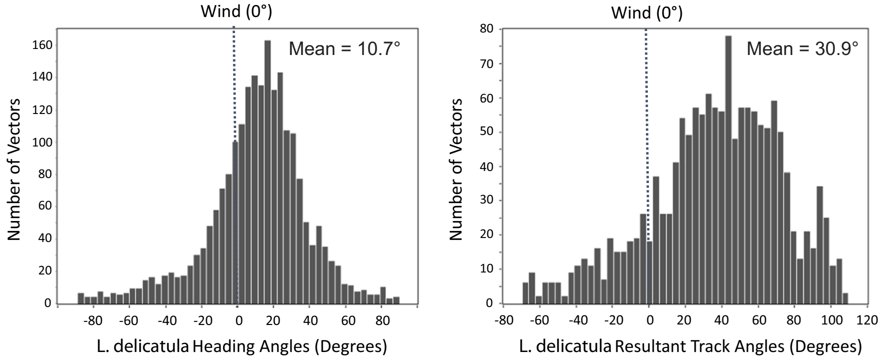

Fig. 8 **a** Heading angles of all the flight vectors for 162 *L. delicatula* adults flying through the video recording field of view relative to the triangle-of-velocities-calculated wind angles in which they were flying. The difference between the wind direction and an adult's heading was calculated for each 1/30-s vector to show the distribution of wind-minus-heading vectors. Mean heading was 10.7° ± 28.3 S.D. ($N = 3106$ vectors) off the wind line; **b** Resultant track angles of these same adults, which are farther off the wind line due to the speed and direction of the wind into which they were flying. The mean track angle of these adults was 30.9° ± 42.9 S.D. off the wind line (N = 3106 vectors). The difference between wind direction and the adult's resultant flight path direction was calculated for each 1/30-s vector to show the distribution of wind-minus-flight-track vectors

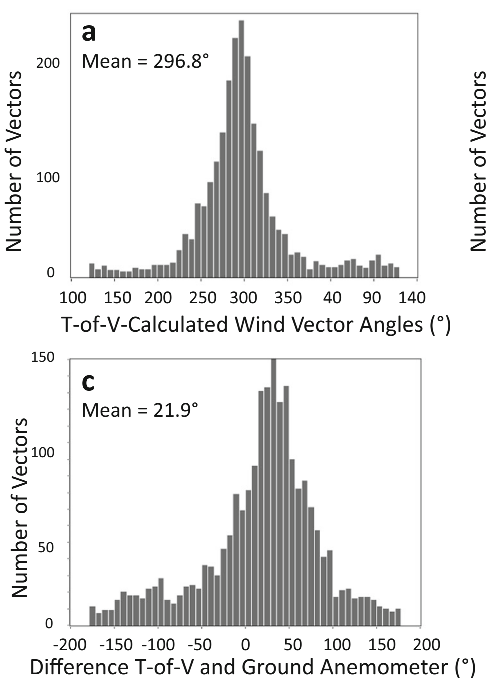

Fig. 9 Wind directions (raw 360° angles from analyses) during each of the 1/30 s vectors of the flights of 162 adults through the video recording field of view that were registered by: **a** the triangle of velocities calculations at the heights and locations where the adults were flying**;** and **b** the ground anemometer at a 1 m height located 1.5 m from the video recorder. In **c** the differences are displayed comparing each wind direction vector calculated every 1/30 s using the triangle of velocities to the wind directions measured by the ground anemometer recorded at the same 1/30 s period. The mean difference between vectors is 21.9° ± 66.2 S.D. (N = 3106 vectors)

We had measured the adults as flying at an average airspeed of 4.64 m/s and used this in our triangle-of-velocities calculations for the flight tracks in the video recordings. The fact that these adults did not alter their airspeeds to try to maintain a preferred ground speed argues for a lack of optomotor anemotaxis while in flight, because they did not appear to have optically sensed—or else they ignored—the apparent speed of the motion of edges past them during flight. Whether due to poor optical resolution of edges or to poor edge-motion discrimination our *L. delicatula* adults gave no indication that they have a preferred velocity of apparent image motion that they try to maintain. The lack of evidence that they adjust their airspeeds to maintain a set ground speed is an indication that the regulation-of-ground speed aspect of in-flight optomotor anemotaxis (Kennedy 1951; Kennedy and Thomas 1974) was not being performed by these *L. delicatula* adults.

The lack of airspeed adjustment to control ground speed in *L. delicatula* has been found in another field-dispersing insect, the moth *Uranea fulgens.* The airspeeds of these moths were found to not vary as they flew low over water during their dispersal flights in various (unmeasured) wind speeds and directions (Sane et al. 2010). Conversely, measurements of the flight tracks and ground speeds of individuals of the migrating desert locusts, *Schistocerca gregaria* showed that they maintained a preferred ground speed while flying upwind into winds of different velocities, and therefore they must have been altering their airspeeds to maintain this set ground speed (Kennedy 1951), using a preferred apparent velocity of image motion to do so. The locusts were also shown to maintain such a preferred velocity by lowering or raising their heights of flight whenever they apparently were not physiologically able to generate the appropriate airspeeds in a particular wind at a particular altitude (Kennedy 1951).

Regardless of our adults' apparent inability to perform optomotor anemotaxis, they did, however, exhibit a pre-flight anemotaxis because they launched themselves predominantly into the wind, as was measured from video flight tracks at Site 3 (Fig. 8) and observed at the two other observation sites. Because the duration of the upwind-launched flight was so brief, i.e., ca. 10–

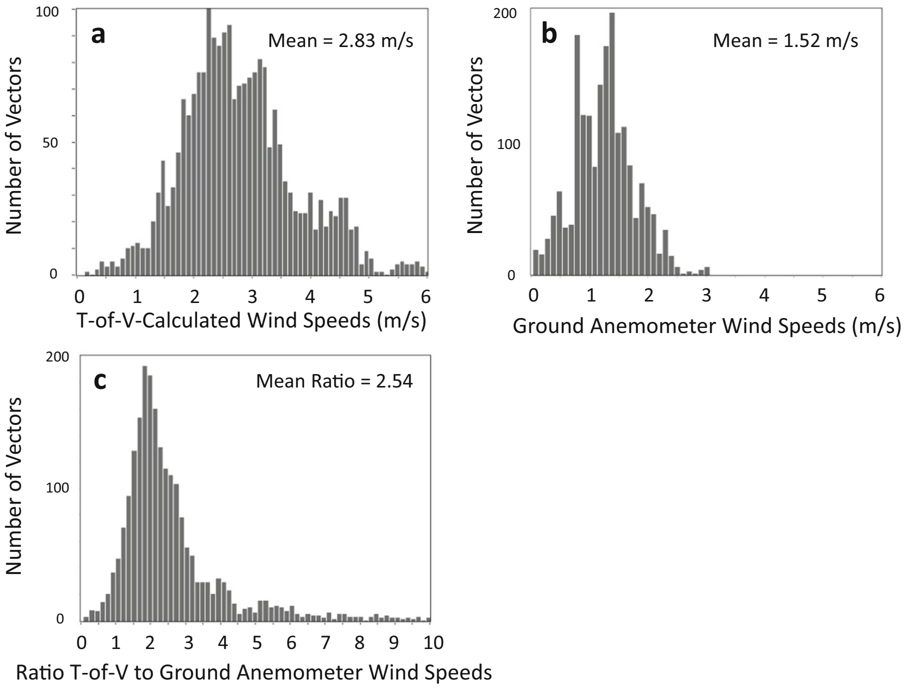

Fig. 10 Wind speeds during all the 1/30 s adult flight vectors through the video recording field of view that were recorded using: **a** the triangle of velocities calculations at the heights and locations where the adults were flying: and **b** the ground-based anemometer at a 1 m height and located 1.5 m from the video recorder. The panel in **c** represents the all the ratios of wind speed vectors recorded each 1/30 by the triangle of velocities calculations compared to those of the ground anemometer. The mean ratio of the triangle of velocities wind speeds each 1/30 s to those of the ground anemometer is 2.54 ± 1.44 S.D.

15 s, the resultant path remained roughly upwind for a distance of up to 40 m before the adult landed either in any trees ahead of them or fell short to land in grass. We observed adults that had landed in the grass after a flight-bout to either flight-hop upwind from the grass or else walk toward the nearest vertical silhouette and climb up toward the top to launch themselves into the wind again. The silhouettes came from either a bush, tree, fencepost, or an observer standing on the lawns.

These results strongly suggest that at the take-off stage of flight, *L. delicatula* adults can sense wind direction mechanoreceptively and perform anemotaxis while on the foliage before take-off. This behavior would represent a “first aim, then shoot” form of anemotaxis (sensu Kennedy 1986). Aim-then-shoot anemotaxis resulting in upwind progress in step-by-step fashion has been shown to be performed by other insect species, including cabbage root flies, *Delia brassicae* (Hawkes et al. 1978) and potato tuberworm moths, *Phthorimaea operculella* (Tejima et al. 2017). Unlike these two types of insects, however, whose aim-then-shoot anemotaxis was shown to have been stimulated by host-plant or pheromone odors, there is thus far no evidence from four years of field observations by our research group that the reiterative bouts of anemotaxis by *L. delicatula* involve olfaction. Rather, these upwind flight-bouts seem to have been stimulated in 2017 by overfeeding in the increasingly high-density populations of *L. delicatula* that had been feeding at the same locations for three years in a row and depleting the resources at these sites. The apparent over-feeding manifested itself in 2017 as visible yellowing and withering of the branches of their preferred host trees, *Ailanthus altissima,* which we observed ourselves and was reported at many locations throughout the region. If this current view is true and plant-to-plant flight-bouts are needed to find a suitable tree to complete an adult’s feeding, the reiterative performance of the observed 20-to-40-m-long bouts could probably generate a general upwind displacement of no more than a few hundred meters over many days. The total distance traveled would depend on how many iterations needed to be performed before a suitable tree was found.

In our studies we were not able to control the visual surround, nor of course were we able to control the wind direction related to the visual surround at the three sites we used. At the first and second sites there were tree-lines in the upwind direction only 40 m away (Fig. 1) that could have also served as visual stimuli to perhaps enhance the apparent focusing of the flights in the upwind direction (i.e., also toward the trees). However, at the third site, the apple orchard, there was no equivalent set of tall visual objects in the lanternflies' upwind sight-line, The adults were taking flight from the tops of 6-m-tall mature apple trees and beginning their flights upwind (Fig. 8), flying over 3-m-tall dwarf apple trees toward a tree-line 100 m away comprised of predominantly 20-m-tall oaks (Fig. 2). Despite having only this 100-m-distant tree-line upwind and very low on the horizon, the adults clearly launched themselves into the wind and maintained a generally upwind resultant flight track for tens of meters. Further work is needed to distinguish more clearly between the influence of wind after take-off vs. the effect of visual stimuli such as nearby trees and tree-lines in creating resultant flight directions.

The technique used here to calculate the wind velocities occurring at the altitudes and locations where adult *L. delicatula* were flying provides a novel way to use flying insects as anemometers. In the Sane et al. (2010) study, the researchers were able to measure the airspeeds of the low-flying flight-dispersing *Uranea fulgens* moths over water by maintaining an anemometer's position directly behind each moth and deftly operating a fast-moving motor boat to keep up with the moth. This technique allowed the moths' airspeeds to be measured, but the wind speeds and wind directions, i.e., the wind vector in the air mass each of them was flying through, remained unmeasured.

Our technique in which we calculated the wind vectors from the insect's heading and airspeed and its resulting displacement-direction and speed could be useful for other species of insects. Currently, the technique would be most easily able to be employed for insects whose headings are readily determined by their body postures, i.e., as in *L. delicatula* that fly flat to the ground with little roll. Thus, the direction their longitudinal body axis is pointing is their heading, which is able to be simply determined from plan-view video records. Also needed for this type of calculation is a measurement of the insects' average airspeed and a demonstration that the insect does not vary its airspeed with changes in wind speed. The adult *L. delicatula* in this study met these criteria and so their flight tracks were able to be used to calculate the wind vectors where each adult was flying. Adult *L. delicatula* were thus able to be used as free-flying anemometers for measuring the local wind vectors that each adult was experiencing in its local air mass.

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