

Flying Faster: Flight Height Affects Orthokinetic Responses During Moth Flight to Sex Pheromone

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Abstract Male Oriental Fruit Moths (*Grapholita molesta*) flew faster toward a pheromone source as they flew higher above striped and dotted floor patterns. The moths significantly ($P < 0.05$) increased their ground speed over floor patterns of transverse stripes or pseudo randomly placed dots. The moths' track angles (flight path angle off the windline) decreased significantly ($P < 0.05$) when they flew 40 cm above the floor patterns vs. flight at 10 cm up, and they tended to steer more upwind flight (smaller course angles) at the upper, 40 cm, height compared to 10 cm up. Turn frequencies and reversal distances across the wind line were also affected by dot density. However, the interaction of small changes in flight speed, course angle, turn widths and turn frequencies are difficult to assess; I have subsumed all their affects into a simple measure of “total distance” flown by the moths by summing the length of all flight vectors analyzed for the other metrics, but no differences were found. By far, the largest change in flight was the positive orthokinetic response to increased flight height above both striped and dotted floor patterns (Fig. 2; $P < 0.05$), and nearly all other changes appear to be entirely due to faster moth flight with little or no changes in steering or turning patterns.

Keywords Oriental fruit moth · *Grapholita molesta* · sex pheromone · flight · vision

Introduction

The odor-mediated upwind flight of male moths toward sex pheromone sources to locate an odor source/mate has long been known to involve an optomotor anemotaxis (Kennedy 1939; Kennedy and Marsh 1974). Upwind movement combined with counter-turning across the wind line leads to fairly stereotypic zigzagging flight paths. Although the cadence of crosswind zigzagging is not as regular as it may

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appear (Willis and Arbas 1998), the nature of the zigzagging, once observed, will not readily be mistaken for anything other than odor-mediated flight, and may be noted as flight “locked on” to the pheromone plume (Kennedy et al. 1980).

The current algorithm for sustained upwind flight toward an odour source (Baker 1989, 1990; Cardé 1984, 1986), requires insects to have an endogenous central nervous system (CNS) counter-turning (cross wind zigzag) generator that is elicited and maintained by intermittent contact with airborne odor (Kennedy et al. 1980, 1981). However, it is clearly a dynamic CNS “program” whose output responds to the wind (e.g., Marsh et al. 1978; Kuenen and Baker 1982a; Willis and Cardé 1990; Willis and Arbas 1991) and altered physical criteria of the pheromone plume (e.g., Cardé and Haganan 1979; Kuenen and Baker 1982b; Charlton et al. 1993; Mafra-Neto and Cardé 1994; Vickers and Baker 1994).

Visual cues are essential for this upwind orientation (Kennedy 1939). Further, Kennedy (1951) observed that locust swarms appeared to move slower when flying close to the ground and faster when flying at greater heights. He hypothesized a servo mechanism of speed control whereby the insect maintains a constant preferred *angular* velocity of image motion over the surface of the eyes. Thus, higher flying insects would need to have a higher ground speed in order for the ground’s pattern to move across their eyes at the preferred angular velocity compared to the ground speed of insects flying closer to the ground. This servo mechanism was supported by studies wherein downwind (down tunnel) movement of the floor pattern slowed free-flying insects’ flight toward a pheromone source (e.g., Cardé and Haganan 1979; Kennedy and Marsh 1974; Kuenen and Baker 1982a) and upwind movement of the pattern increased the insects’ movement upwind toward the odor source (e.g., Kennedy and Marsh 1974; Marsh et al. 1978; Miller and Roelofs 1978).

Kuenen and Baker (1982a) demonstrated that free-flying male Oriental Fruit Moths (OFM; *Grapholita molesta*) and *Heliothis virescens* flying upwind toward pheromone sources positioned at different heights *do* increase their net ground speed with increased flight height; however, the moths did not increase their flight speed enough to maintain a constant angular velocity of image motion across their eyes. It was concluded that the moths were regulating their ground velocities by integrating visual inputs from non-ventral as well as the ventral ommatidia (Kuenen and Baker 1982a). Similarly, Foster and Howard (1999) demonstrated that the light-brown apple moth, *Epiphyas postvittana*, flew upwind faster at greater heights above a wind tunnel floor pattern and Fadamiro et al. (1998) demonstrated that *Prostephanus truncatus* (Coleoptera: Bostrichidae) flew upwind faster at higher flight heights above the flight tunnel’s floor pattern. As with moths (Kuenen and Baker 1982a), Fadamiro’s beetles were less responsive to ventral floor pattern movements when they flew higher up, possibly indicating the insects’ shift to other visual cues present in the tunnel or assay-room for regulating their flight toward the pheromone source.

Alternating colored and white stripes of equal width, necessarily provide a 50 % floor coverage of the selected stripe color, whereas dotted floor patterns can easily be covered at various color/dot densities. However, transverse stripes alternated with wider transverse white stripes will also yield lower floor stripe densities; here we altered dot numbers and stripe spacings to obtain 50 %, 25 % and 12.5 % colored floor coverages. These three coverage densities alter the number of objects (and object edges) that the moths can see and thus mimic these changes that also occur

with changing flight height. Moths were allowed to fly upwind along pheromone plumes at three heights and three pattern densities to examine the effects of height and object (edge) density on their speed and steering. We report here that three floor covering densities elicited only small changes in the upwind speed and steering of OFM males whereas flight height had a profound effect on flight speed as they flew upwind toward a pheromone source.

Materials and Methods

Insects

Oriental fruit moths, *Grapholita molesta* (Busck) (Tortricidae), were reared on a wheat germ and agar-based diet (Yokoyama et al. 1987). All life stages were maintained at 26 ± 1 °C on a 16:8 light:dark cycle. Males were separated from females in the pupal stage. All pupae and adults were held at ca. 85 % RH and had continuous access to an 8 % sucrose solution. Adult males were isolated from females at all times and were segregated daily by age.

Flight Tunnel

The square cross-section flight tunnel (98×98 cm) has a 240-cm-long working section, open at the downwind end with air pushed through the tunnel by a variable speed fan (Kuenen and Rowe 2006). The tunnel is constructed of Plexiglas panels affixed along their long edges to aluminum rails bent 90° in cross-section, and to welded box-section aluminum exterior frames at each end. Tunnel access is through the downwind end or through one side composed of two 130-cm long door panels that slide parallel on closely apposed rails. Wind is provided by a variable speed DC-motor/fan with a rectified voltage-controller. Air is ducted to the upwind end of the tunnel by a flexible “tube” made of polyethylene-sheeting (0.3 mm in thickness) where air passes through two layers of charcoal-and zeolite-impregnated filter material (Quality Filters, Robertsdale, Alabama), held in individual aluminum frames that match the tunnel’s cross section. These filter layers remove volatile chemicals from the air (Heath and Manukian 1992) and reduce large-scale air turbulence. A third frame was covered with a white muslin sheet to enhance the visibility of the moths for the experimenter and further reduce air turbulence. Pheromone laden air and odor plumes are exhausted to the outside by a 20 cm dia. air duct (air speed 3.6 m s^{-1}) positioned 50 cm from the downwind end of the tunnel and at the center height of the pheromone plume. All remaining air passing through the tunnel is re-circulated through the assay room. Odor plumes from rubber septa (below) flowed horizontally straight down the tunnel with slow spread horizontally and vertically so that the plume was approximately circular in cross section with a 15 cm diameter as it exited the tunnel. Lighting in the assay room was from above by four 40-W fluorescent tubes (120 Hz) placed 20 cm to the side and 85 cm above the top of the tunnel. These lights are supplemented by 20 clear 40-W incandescent bulbs, 10 spaced equally along both sides of the tunnel 15 cm below the fluorescent bulbs. Illumination from both set of lights was reflected from a layer of white expanded polystyrene directly above the tunnel,

whereas direct light from the bulbs was blocked from the tunnel by aluminum foil. Light intensity at flight heights (10-to-40 cm) was 345 lx from above, 155 lx from the floor, 215 lx from a white cloth sheet suspended 10 cm outside the non-opening side wall of the tunnel and 160 lx from the clear, opening side of the tunnel as measured by a FisherBrand™ light meter, model 06-662-64 (Fisher Scientific, Friendswood, Texas).

Pheromones

The female sex pheromone of *G. molesta* consists of (*Z*)-8-dodecenyl acetate (Roelofs et al. 1969) plus 5.9 % (*E*)-8-dodecenyl acetate and 3.8 % (*Z*)-8-dodecyl alcohol (Cardé et al. 1979). These compounds were purchased from Bedoukian Research (Danbury, CT, USA), all nominally ≥ 97 % pure. Stock solutions of each compound were made in hexane (10 mg/ml) and then mixed in the appropriate ratios. Serial dilution of this mixture yielded solutions for loading onto red rubber septa (Aldrich Chemical Co., Milwaukee, WI, USA Z12435-48753-022, sleeve type, 9×18 mm). Ten micrograms of this mixture in 10 μ L hexane was applied to the inside bottom of the large end of a rubber septum. The ratio of the pheromone components (Baker and Cardé 1979b) in our solution were 6.5 % (*E*)-8-dodecenyl acetate with 4.9 % (*Z*)-8-dodecyl alcohol in (*Z*)-8-dodecenyl acetate as measured by gas liquid chromatography on a DB-5 column in an HP 6890 gas chromatograph (Agilent Technologies, Palo Alto, CA, USA; after Baker and Roelofs 1981). Overall purity was >95 %.

Floor Patterns and Test Procedures

Floor patterns composed of stripes or dots were printed on a poster plotter (HP Design Jet 4500, Palo Alto, CA, USA) on rolls of white paper (cat. # Q1406A) that was trimmed to 98 cm width and then laid on the floor inside the tunnel. Patterns were transverse 5cm red stripes alternating with three white stripes widths: 5 cm white stripes (50 % floor coverage), 15 cm (25 % coverage), 35 cm (12.5 % coverage). The dotted patterns were 5 cm dia. red dots placed pseudo-randomly on the white paper to yield red-dotted surface areas of 50 % (599 dots), 25 % (299 dots), and 12.5 % (150 dots). For flight tests, floor pattern (red) density was chosen at random within each pattern category and three flight heights were then selected randomly for each pattern. Three moths' flights were recorded to each pattern density and height combination each test day. The nine combinations of dot density and three flight heights were tested first, then 2 months later the nine combinations of stripe density plus three flight heights were tested.

Four-to 6-day-old males were used during the last hour of photophase and the first hour of scotophase, the time of their optimal responsiveness to pheromone (Baker and Cardé 1979a). The moths were conditioned to tunnel wind and light conditions for at least 60 min prior to their individual release from a small aluminum, window-screen cone hand-held in the center of the pheromone plumes. This position was determined to be straight downwind of the pheromone source during smoke visualizations of the plume from a rubber septum of the same size as used for the pheromone. Moths' flight heights were controlled by suspending the pheromone source by a length-adjustable thread, from a hook attached to the top of the tunnel. The hook was positioned on the longitudinal midline of the tunnel 29 cm from the upwind end of the tunnel. The moths maintained their flight height close to the center

of the horizontal plume axis and their lateral flight movements were typically centered on the plume axis, within the range reported previously for plume tracking *G. molesta* males (Kuenen and Baker 1982b; Baker et al. 1984; Willis and Baker 1984). Wind speed was maintained at 75 cm s^{-1} as measured with a Kurz hot-wire anemometer (model 491; Kurz Instruments, Monterey, California; calibrated by timing smoke puffs through a 1.2-m section of the tunnel). During tests, the flight tunnel room conditions were maintained at 23.5–24.5 °C and 45–60 % RH.

Flight Track Recording and Analysis

Upwind flight tracks of the moths were recorded in plan view from above at 30 frames s^{-1} with a Photron FasCam PCI (San Diego, CA; www.Photron.com) digital video camera. The moths' flight tracks were then digitized on a CRT monitor with Mantis32 software (Synceros Inc., Ithaca, New York). The camera head and lens were oriented vertically above the tunnel ceiling (the lens protruded 5 cm through a hole in the expanded polystyrene-covered room ceiling) providing a 65-cm field of view at the 40 cm height. Only this "same" 65-cm of each flight track was analyzed for all three flight heights even though the field of view was wider at lower heights. The upwind end of this 65 cm section was 42 cm from the pheromone source. A carpenter's square (30.5 cm \times 61.0 cm) was video recorded in the horizontal position, each side aligned with the "x" and "y" axes, at each flight height as a calibration object for flight measurements at those heights

To obtain mean course angles, track angles, drift angles, airspeeds and ground speeds, calculations were based on the triangle of velocities method (Fig. 1; Kennedy 1939; Marsh et al. 1978). Data files [consecutive (0.033 s) *x*, *y* coordinate pairs for each flight track] were analyzed with a computer program developed by Kuenen and Baker (1982b) (see also Charlton et al 1993; Kuenen and Cardé 1993, 1994) for calculation of the moths' movement parameters along each track vector (track segment between consecutive locations). The mean track angle was calculated for an entire track by calculating the mean 'x' and 'y' displacements from all the vectors of a given track (using the absolute values for the crosswind component), yielding a mean resultant track vector. This procedure was followed to avoid the error inherent in calculating arithmetic means directly from angle measurements (Batschelet 1981), especially when vector lengths are not equal, as is typical during the dynamic free flight of these male moths (Willis and Arbas 1998). Subsequent calculations and analyses of movement and steering components of males along their flight tracks were also based on this resultant vector and the wind speed vector (Kuenen and Cardé 1993, 1994). A program subroutine (Kuenen and Calderone 1998) calculated the turn apices and their inter-turn distances and durations (inverse of turns s^{-1}). Turn apices were defined as the points where males changed direction across the wind line (Kuenen and Cardé 1993, 1994) and inter-turn reversal distances were taken as the lateral displacement between the apices of consecutive turns (Kuenen and Baker 1982b).

Statistical Analysis

Tests were conducted in a complete randomized block design with only one pattern type, dots or stripes, tested at a time. On eight successive days, three moth flights were

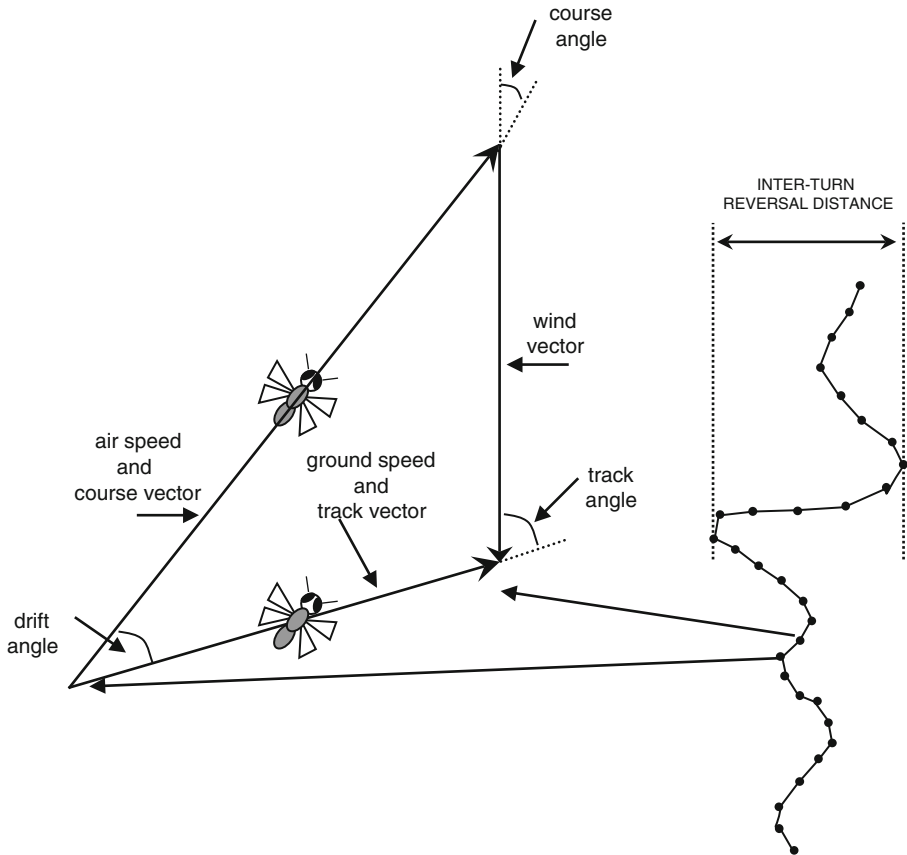


Fig. 1 Schematic representation of a flight track denoting inter-turn reversals and parameters and terminology from the triangle of velocities (after Marsh et al. 1978) used for analysis and description of *G. molesta* tracks. Airspeed: speed of males through the air resulting from the wind and their ground speed. Ground speed: speed of males along their actual track. Track angle: angle of flight vectors (see text) with respect to the upwind direction (0°). Course angle: angle of thrust with respect to the upwind direction (0°). Drift angle: deviation of a moth's course angle to its observed track angle due to displacement by the wind. Wind is from the top of the figure

recorded for each height and floor pattern combination before the next randomly chosen combination was tested. Thus, 24 moths were flown to each of the nine height-pattern combinations, resulting in a total sample size of 216 moths for each floor pattern type. Nine flight parameters of velocity, steering and turning (in Figs. 1, 2 and 3) were analyzed by analyses of variance with PROC GLM in SAS and mean separation tests among treatments were conducted with Tukey's test, also in SAS (SAS 2010); data transformations were not necessary (Bartlett's test for homogeneity of variances).

Results

Moths' net speeds, ground speeds and airspeeds increased significantly ($P < 0.05$) when they flew higher above all floor patterns (Fig. 2a–f). There was a significantly

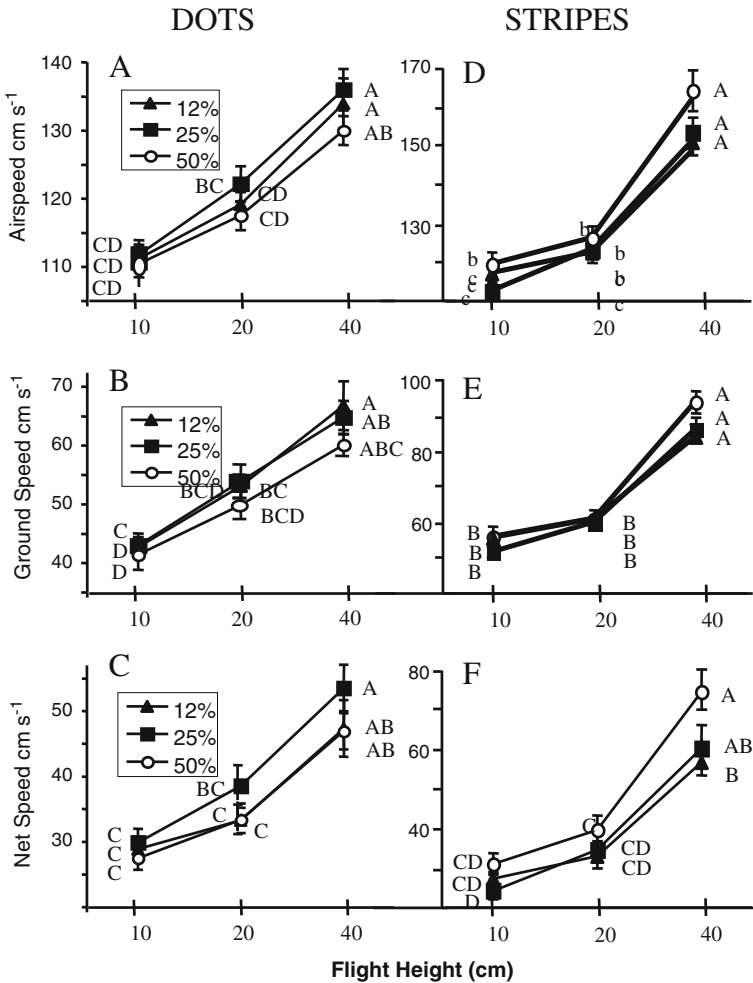


Fig. 2 Mean (+ SEM; $n=24$) airspeeds, ground speeds and net upwind speeds of *G. molesta* flight tracks during upwind flight toward pheromone at three heights over two floor patterns, each at three coverage densities with respect to the entire tunnel floor area. Means having no letters in common are significantly different (Tukey's HSD test; $P<0.05$)

higher ($P<0.05$) net uptunnel speed by moths flying at 40 cm above stripes with 50 % floor coverage (equal red and white stripe widths) compared to moths flying 40 cm up over stripes with only 12.5 % floor coverage (Fig. 2f); however, this was the only pattern related difference among these parameters. The positive orthokinetic response (increased ground speeds) exhibited by the higher flying moths (Fig. 2b and e) is one of the two things the moths can actively control during free flight (Marsh et al. 1978). Since the flights above dotted and striped floor patterns were conducted independently, their measurements cannot be compared directly, but clearly the effects of height on ground speed were nearly identical.

Steering their upwind flight (course angles—the other actively controllable flight response; Marsh et al. 1978) may more likely be expected to be influenced by pattern density since more visual cues over the entire eye could allow for more accurate

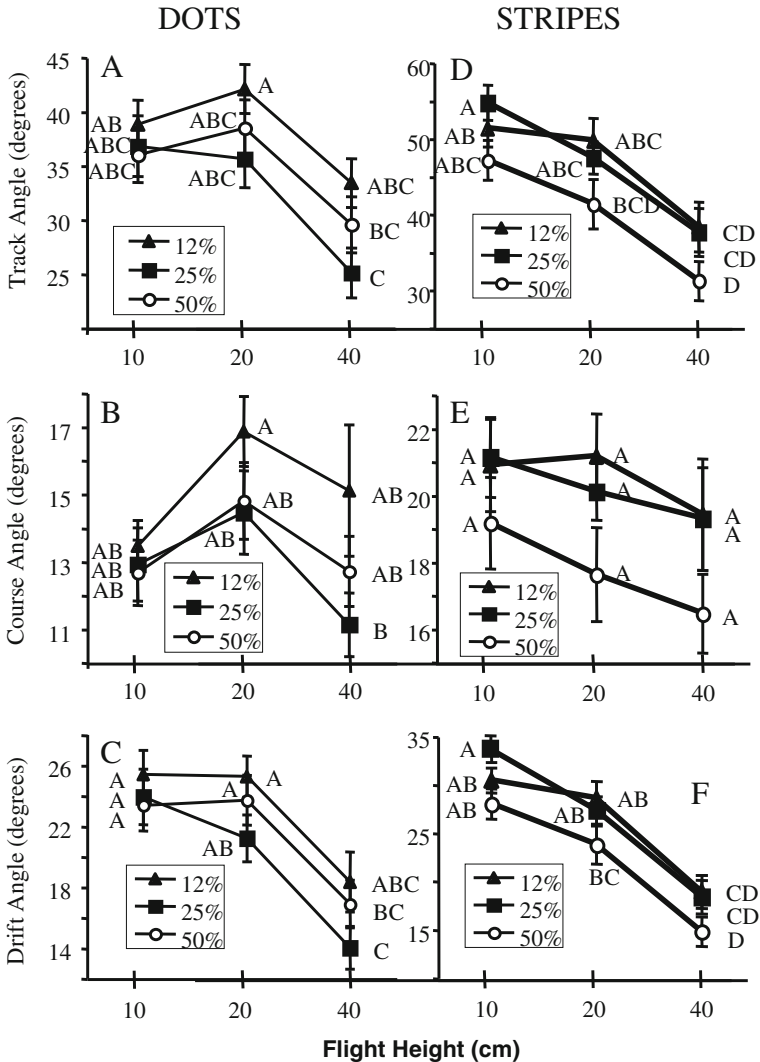


Fig. 3 Mean (+ SEM; $n=24$) track angles, course angles and drift angles of *G. molesta* flight tracks during upwind flight toward pheromone at three heights over two floor patterns, each at three coverage densities with respect to the entire tunnel floor area. Means having no letters in common are significantly different (Tukey’s HSD test; $P<0.05$)

upwind steering. However, there were no differences in course angles among floor pattern densities at each height tested (Fig. 3b and e) and the only significant difference ($P<0.05$) in course angles was between moths flying over 12.5 % dots at 20 cm up compared to moths flying 40 cm up over 25 % floor coverage (dots). In contrast to the lack of trends for course angle changes for moths flying over dots, moths flying over striped floors tended toward more upwind steering (smaller course angles) when red and white stripe widths were equal (Fig. 3e; 50 % floor coverage) and moths trended toward courses steered more directly upwind when the moths flew higher, especially at the two higher stripe densities (25 % & 50 %); however, there

were no significant differences here either (Fig. 3e; $P>0.05$). Differences in track angles above dots were also scarce, though all tended to decrease when moths flew 40 cm up vs. the two lower flight heights (Fig. 3a). Above striped floor patterns, moths' track angles decreased significantly ($P<0.05$; Fig. 3d) when moths flew higher—10 vs. 40 cm up—over all three stripe densities; however, there were no significant differences in track angles among stripe densities. Moths flying over equal stripe widths (50 % floor coverage) had the smallest track angles at each flight height.

For OFM, changes in turn rates and/or inter-turn distances, can be indicative of changes in their flight speed (Kuenen and Baker 1982b); however, we saw few significant differences in the moths' turn rates or inter-turn distances in response to changes in flight height or floor-pattern density (Fig. 4a, b, d and e) although there was a tendency for moths flying over striped patterns to increase their inter-turn distances and reduce their turn frequency as they flew higher above striped floor patterns (Fig. 4d and e). Total distances traveled by the moths only showed one significantly greater distance flown among heights and pattern densities among moths flying over dotted-floor patterns (Fig. 4c; $P<0.05$) and no differences among moths flying over striped patterns. Even trends in the data in relation to flight height and pattern density are scant. The one stand out is moths flying over 12.5 % density dot patterns where moths flying 40 cm up increased their interturn distances (Fig. 4a; $P<0.05$) compared to those flying at 10 cm up. In addition, there was a trend for these wider turning, higher flying moths to turn less frequently, but the differences were not significant (Fig. 4b; $P>0.05$).

Discussion

Although increased net upwind speed has been documented for higher flying insects (*G. molesta* and *H. virescens*—Kuenen and Baker 1982a; *E. postvittana*—Foster & Howard; *P. truncatus*—Fadamiro et al. 1998), these are the first measurements along the insects' actual ground paths over both striped and dotted floor patterns. The analysis of these data should be examined from two perspectives: 1) what changes did the moths make to their steering and orthokinetic output in relation to changes in flight height and 2) how did changes in visual cue density affect the moths steering and orthokinetic output. The moths exhibited significant increases in their motor output (ground speed; Fig. 2a and d) at greater heights, but changes in this and other metrics we measured and calculated were mostly not significantly different regardless of pattern density whether stripes or dots. Only a few trends were found among metrics across all test combinations/treatments that could effect a difference in the overall distances flown by the moths. The paucity of trends in relation to steering or turning parameters above both striped and dotted floor patterns combined with the significant increases in ground speed above both pattern types and all pattern densities, leads me to conclude that previously documented increases in net upwind speed among higher flying insects appears due almost exclusively to increased ground speed among these insects.

Moths flying over dot-pattern floors changed their course angles very little as they flew higher, whereas males flying above transverse stripe patterns, all trended toward smaller course angles (more upwind) as they flew higher (Fig. 3e). In conjunction

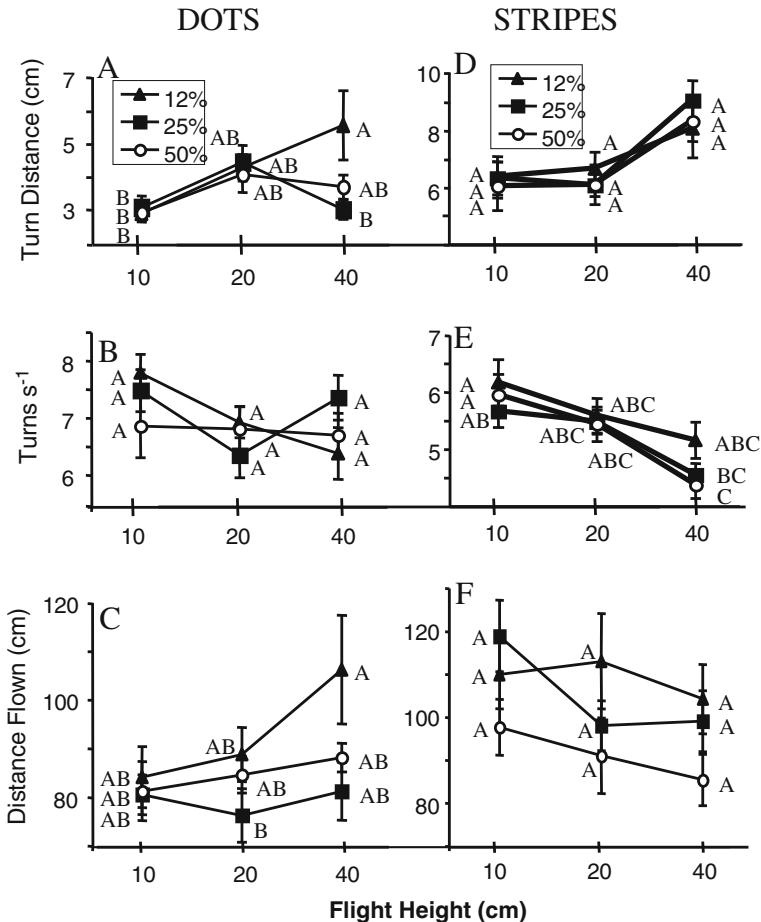


Fig. 4 Mean (+ SEM; $n=24$) inter-turn reversal distances, turn rates and track distance flown of *G. molesta* during upwind flight toward pheromone at three heights over two floor patterns, each at three coverage densities with respect to the entire tunnel floor area. Means having no letters in common are significantly different (Tukey's HSD test; $P<0.05$)

with their higher ground speeds (Fig. 3e), their drift angles were reduced significantly (Fig. 3f) resulting in ground paths (track angles: Fig. 3d) that were “aimed” more directly upwind. Therefore, we might expect that they would have flown shorter distances over the ground as they progressed upwind/up-tunnel, but this was not the case (Fig. 4f). This may have been due in part to their tendency to make longer crosswind traverses (Fig. 4d) at greater heights, but on the other hand they made fewer of them (Fig. 4e) at the upper height which would lead again to track/distance shortening. I must conclude that the few recorded/measured trends and (few) significant changes in some metrics (above), acted in concert to keep the total flight paths essentially equal in length. The same metrics from moths flying over dotted floor patterns were more ambiguous but still/also led to flight paths of nearly equal length (Fig. 4c) at all heights and over all three pattern densities.

Thus, these data lend some support to Kennedy's (1951) original hypothesis of a servo mechanism for increasing flight speed with increasing flight height. However,

angular velocity of image motion was not maintained among the higher, faster moths. As the moths flew higher they should detect more pattern edges (stripes and dots) or whole objects (dots) that should allow them to make more upwind directed movements. Conversely, the lower density floor patterns at low heights would make that more difficult and thus they would fly upwind more slowly. Clearly, my test moths were not affected by pattern/image density except for interturn distances over the lowest dot density (Fig. 4a). Higher flying moths should see a greater number of pattern edges or objects, and in controlled wind tunnel experiments the subtended angle of each object is also smaller; Kuenen et al. (unpublished) have shown that transverse stripes of smaller angular size lead to higher upwind speeds. The transverse stripes and dots provided in this study clearly provided the moths with ample visual feedback to steer and zigzag upwind similarly above all pattern densities; only their ground speed increased.

In addition to the height and pattern density factors tested here, we must remember that these insects are also “tracking” an invisible odor plume. Indeed, protracted loss of contact with a pheromone plume elicits primarily crosswind casting behavior (Kennedy 1983) whose turns typically widen over time without upwind progress (but see also Kuenen and Cardé 1994). This odor-mediated flight likely has different algorithms for flight speed control than insects not engaged in plume following toward an odor source. Future experiments on pattern-object size, orientation and contrast will likely shed light on other factors affecting moths’ flight speed and control as they follow odor plumes. The height control of free-flying insects afforded us by the use of pheromone plumes should also lead us to be cautious in our interpretations of this idiosyncratically constrained flight mode.

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