

Optomotor regulation of ground velocity in moths during flight to sex pheromone at different heights

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ABSTRACT. Males of two species of moths (*Grapholitha molesta* (Busck) and *Heliothis virescens* (F.)) were flown in a sustained-flight tunnel in horizontal pheromone plumes. The up-tunnel velocity of the moths increased with increasing height of flight and for *G. molesta* was independent of tunnel wind velocities. Use of moving ground patterns verified that the height of flight above the ground was the factor related to the changes in up-tunnel velocity. Even though up-tunnel velocity increased with increased flight height, angular velocity of image motion did not. Males appeared to use visual cues from the ground pattern and from other sources to determine their up-tunnel velocities. The relationship of preferred retinal velocities to optomotor anemotaxis is discussed.

Key words. Wind tunnel, optomotor control, flight control, ground velocity, pheromone, flight height, retinal velocity, *Grapholitha molesta*, *Heliothis virescens*.

Introduction

Various aspects of the control of insect flight behaviour have been examined, including the use of vision by the insect to maintain a general upwind orientation (Kennedy, 1940; Kennedy & Marsh, 1974; Marsh *et al.*, 1978). A great deal of work has been performed with tethered insects, and the resultant interpretations have been applied to free-flying insects (e.g. Götz, 1968, 1972; Vogel, 1966, 1967).

It has been hypothesized, based on field observations of free-flying migratory locusts, that flying insects maintain a constant or 'preferred' velocity of image motion across the eye, which leads to a constant average ground velocity that is not affected by limited changes in ambient wind velocity (Kennedy, 1951). As a consequence of maintaining this

constant or 'preferred' retinal velocity the insect should exhibit changes in net ground velocity (Fig. 1) as it changes height above the surface (Kennedy, 1951). The independence of ground velocity from changes in ambient wind velocities has been demonstrated for untethered mosquitoes, aphids, and *Drosophila*, flying in wind tunnels (Kennedy, 1940; Kennedy & Thomas, 1974; David, 1979; respectively).

Attention has recently been directed toward understanding the mechanism(s) employed by male Lepidoptera in locating a pheromone source (Farkas & Shorey, 1972; Kennedy & Marsh, 1974; Marsh *et al.*, 1978; Kennedy *et al.*, 1980, 1981), and although it is now generally understood that optomotor feedback from the ground or other objects is necessary for source location, other interesting aspects of the interaction of vision and flight in a pheromone plume have been largely ignored. Using two moth species, we conducted

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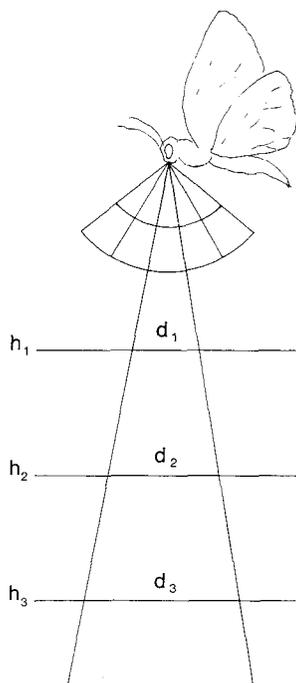


FIG. 1. Diagrammatic representation of a free-flying moth's visual encounters while flying at different heights. At greater heights (h_1 , h_2 , h_3) greater distances (d_1 , d_2 , d_3) will have to be covered in a given time if the angular velocity of image motion (retinal velocity) is to remain the same at each height.

experiments to examine the effects of flight height on ground velocities and airspeeds of males flying to a pheromone source.

The advantage of using a male's response to sex pheromone lies in the ability of the experimenter to dictate the untethered insect's flight height by specifying a horizontal plume height, due to the moths' propensity to remain in the (time-averaged) pheromone plume. We report here that ground velocity varies directly with height of flight, and does not vary with wind velocity. A constant retinal velocity of image motion, however, was not maintained concurrent with the increasing ground velocities.

Materials and Methods

General

Oriental fruit moths, *Grapholitha molesta* (Busck), were reared on small green thinning

apples (Baker *et al.*, 1981). Tobacco budworm moths, *Heliothis virescens* (F) were reared on a modified pinto bean diet (Shorey & Hale, 1965). Males of both species were separated from females in the pupal stage and were aged daily after emergence. Adults and larvae were maintained at $25 \pm 2^\circ\text{C}$ on 16 h light:8 h dark (LD 16:8) and LD 14:10 cycles for *G. molesta* and *H. virescens*, respectively, and from emergence males were always isolated from females. Adults had continuous access to 8% sucrose.

Males were flown in a clear plastic (polycarbonate) wind tunnel (modified after Miller & Roelofs, 1978) with a working section 1 m wide at floor level, 0.90 m high, and 3.65 m long. A moveable belt ('treadmill'), with alternating 10-cm black and 10-cm white transverse stripes, was positioned 1.5 cm below the 6-mm-thick clear plexiglass floor. It could be driven downwind (by a rheostat-controlled 1/15 hp electric motor) at up to at least 350 cm/s, measured by a wheel-driven bicycle speedometer.

Air flow was provided by a 1-hp three-blade fan blowing through two layers of muslin (individually supported by an aluminium window screen) and a final layer of polyester. The cloth layers smoothed the air flow so that a TiCl_4 smoke plume from a rubber septum was level and c. 15 cm wide at the downwind end of the tunnel, and c. 10 cm wide in the tunnel's centre (at a wind velocity of 58 cm/s).

Mean wind velocities were measured by an Anemotherm® (Model 60) hot-wire anemometer and regulated by a voltage-monitored variac powering the fan. Wind velocities were measured cross-sectionally in the working section of the tunnel at both the pheromone release platform (see below) and halfway down the length of the tunnel. Measurements were taken at 7.5 cm intervals from 12.5 to 65 cm above the tunnel floor and laterally (at each height) from the tunnel's centre toward the sides. These measurements were taken with wind velocities of 40, 58, 78 and 88 cm/s, measured at 20 cm above the centre of the tunnel floor. At all measurement points changes in wind velocity were less than $\pm 10\%$ from the expected.

G. molesta males were flown at a light intensity of 80 lux, provided by fluorescent overhead lights diffused by a layer of expanded

polystyrene, while *H. virescens* males were flown at 5 lux provided by four voltage-regulated, 3-W incandescent lights diffused by reflection from the polystyrene ceiling. Pheromone was scavenged from the tunnel by a 30-cm diameter exhaust pipe (air speed in centre = 2.9 m/s) which was aligned with the centre of the plume. The rest of the air from the tunnel re-circulated through the room.

Beginning *c.* 1 h before lights off during the period of maximal response to pheromone (Baker & Cardé, 1979a), 4–6-day-old *G. molesta* males were acclimated to tunnel conditions for at least 5 min before being individually released from aluminium screen cones hand-held in the centre of the pheromone plume (Baker *et al.*, 1981). *H. virescens* males were acclimated to tunnel light conditions for at least 45 min, then transferred to individual release cages (6 cm long × 6 cm diam. (3.15 wires/cm) galvanized mesh). They were then acclimated to test conditions for another 15 min. Males were released by placing individual cages open-side up on a screen platform positioned at the bottom of the pheromone plume. Males of both species generally flew up and out of their release cages and then descended, while station-keeping, until 'locking onto' the pheromone plume and proceeding up-tunnel toward the pheromone source (as in Marsh *et al.*, 1978; Kennedy *et al.*, 1980).

Pheromones

All pheromone components were dispensed from rubber septa (A. H. Thomas Co. No. 8753-D22, sleeve type, 5 × 9 mm) positioned in the centre of a 15 × 15 × 0.05-cm-thick, galvanized steel plate serving as an adjustable platform. The plate was attached to a thin brass rod which was looped around the vertical rod of a ring stand and could be moved up and down in height. The ring stand was positioned so that the platform was in the middle of the tunnel 30 cm from the upwind end of the tunnel's working section.

All septa were impregnated with pheromone by applying the specific blends in 10- μ l aliquots in hexane. Septa for *G. molesta* received 10 μ g of a blend of 5.9% (*E*)-8-dodecenyl acetate and 3.8% (*Z*)-8-dodecenyl alcohol (Cardé *et al.*, 1979) in (*Z*)-8-dodecenyl

acetate (Roelofs *et al.*, 1969). The formulation of this optimal ratio (Baker & Cardé, 1979b) was verified by gas-liquid chromatography (GLC) on a 10% XF-1150 (50% cyanoethyl, methylsilicone on 100–120 mesh Chromosorb W-AW DMCS) 2 m × 2 mm i.d. glass column, with N₂ carrier flow at 25 ml/min at 160°C (Baker & Roelofs, 1981). All the components had < 0.5% volatile impurities as determined by GLC analysis on the XF-1150 column (Baker & Roelofs, 1981). The solution was applied to the inside bottom of the large end of the septum. Septa were stored at -20°C between 2-h uses, and were used for up to 4 weeks.

Septa for *H. virescens* were impregnated in their small end with 10 μ g (*Z*)-11-hexadecenal (Z11-16:Ald), 0.5 μ g n-tetradecanal (14:Ald), and 0.25 μ g (*Z*)-9-tetradecenal (Z9-14:Ald). The Z11-16:Ald and the Z9-14:Ald contained < 2% volatile impurities and the 14:Ald contained < 0.1% volatile impurities as determined by GLC on XF-1150. New septa, loaded 1.5 h before use, were used each day. All steel surfaces contacted by pheromone were rinsed with acetone before each use.

Experimental criteria

Fifty moths were flown (tested) to each experimental condition in a randomized complete block design. Five moths were flown per block per treatment, and the block means, rather than the individual moths' velocities, were analysed by two-way analysis of variance and Duncan's new multiple range test. Square root or log₁₀ transformations were employed where needed as indicated by Bartlett's test of homogeneity of variances.

Up-tunnel velocity (net displacement per unit time up the wind line) of males in all experiments was determined by timing with a stop watch (to the nearest 0.1 s) the duration of in-plume flight up the centre 1.22-m section of tunnel (1.22 m/time). Obvious large excursions from the plume (including halted progress toward the source, and apparent station-keeping outside the plume) were excluded from the time measurements, whereas all within-plume time was measured (including periods of within-plume arrestment, when they occurred). Moths making more than three large excursions from the plume

were not used. Measuring flight in the centre section gave a reading of the true up-tunnel velocity of males in contact with pheromone and moving above the ground at a steady height and rate. Vertical movements during the moths' up-tunnel flights were rarely observed to exceed the boundaries of the time-averaged pheromone plume (i.e. a maximum of c. 10 cm).

Experiments

Up-tunnel velocity versus flight height.

To test the basic hypothesis that moths maintain a 'preferred' retinal velocity (increase their up-tunnel velocity with increasing flight height) males of each species were tested at 20, 30 and 40 cm above the tunnel floor and changes in up-tunnel velocity were examined. Tunnel wind velocity was maintained at 58 cm/s.

Up-tunnel velocity versus flight height and wind speed. In order to determine whether wind velocity affected the moths' up-tunnel velocities, the following experiments were performed. *G. molesta* males' up-tunnel velocities were measured at 20, 40 and 60 cm above the floor with tunnel wind velocities of 24–88 cm/s. *H. virescens* were similarly tested at 20, 30 and 40 cm above the tunnel floor with tunnel wind velocities of 24, 58 and 88 cm/s.

Up-tunnel velocity versus downwind ground pattern velocity. To verify that it was indeed the height above the ground pattern, not some other tunnel features that mediated the observed up-tunnel velocity changes, we performed several experiments employing a moving floor pattern. Moving the striped floor pattern in the downwind direction can slow, stop, or reverse the net progress toward the source of moths orienting to pheromone (Kennedy & Marsh, 1974; Miller & Roelofs, 1978; Cardé & Hagaman, 1979). If the moths' up-tunnel velocity changes were determined or influenced by height, a higher downwind ground pattern velocity would be required to halt the moths' up-tunnel progress when they flew at greater heights.

H. virescens males were flown at 20 and 30 cm above the tunnel floor (tunnel wind velocity was 58 cm/s). The ground pattern was moved in the downwind direction and its

velocity adjusted to hold the moths stationary in the tunnel. 'Stationary' was defined as the moths making less than 30 cm up-tunnel progress (usually < 10 cm) in 3 s with the floor pattern moving at a constant velocity. *H. virescens* males' progress toward the source could not be stopped, only slowed down, while flying at 40 cm above the moving floor. Similarly, *G. molesta* males could not be held stationary at any height above 20 cm, but further experiments on the reduction of up-tunnel velocity by the moving pattern were performed.

G. molesta males were tested at 20, 40 and 60 cm and *H. virescens* at 20, 30 and 40 cm above the tunnel floor with the ground pattern stationary, or moving in the downwind direction at 60 or 100 cm/s. In only these experiments the portion of the pattern prior to the measuring section was covered with green blotting paper because, when the treadmill was moving, most moths would either not leave their flight cages or, upon initiating flight, would be 'swept' quickly out of the tunnel and up the exhaust pipe. With the blotting paper in place, however, upon reaching the measuring section with the ground pattern moving, the moths' progress toward the source was either slowed or stopped, and as before, the duration of the flight through the centre 1.22-m measuring section of the tunnel (above) was recorded for those moths that were capable of moving through it. If a moth could not move through this section in five attempts it was recorded as an 'infinite moth' and for purposes of calculation 30 s of flight time were ascribed to it. From preliminary testing it was observed that < 5% of all moths unable to traverse the measuring section in five attempts could traverse it at all (some moths were observed for more than 10 min).

Flight control outside the wind tunnel. To ascertain whether uncontrolled visual cues in the tunnel were causing the velocity increases with increasing flight height, *G. molesta* males were flown over a larger ground pattern at various heights above the floor of an open room which should have distanced any other visual cues. *H. virescens* males were not tested.

A three-speed window fan with a double layer of cheese-cloth over the output end was placed in the centre of a 15 × 6 × 3 m room. A floor pattern of alternating black and white

10-cm stripes (black stripes painted on newsprint) was placed on the floor downwind of the fan. The adjustable pheromone platform used in the wind tunnel was positioned near the centre of the fan, the fan and platform height being changed together. A narrow horizontal plume was produced that remained level for *c.* 2 m before beginning to dissipate. The end of the plume was exhausted out an open room door with room air being replaced by the building air conditioning system. Moths were released from screen cones held in the plume at the end of a 1-m rod. This added distance eliminated the apparently spontaneous movements toward a vertical object (the experimenter) before the moths locked onto the plume. The nearest objects to the moths at the release point were the experimenter's body and the fan (each *c.* 2 m distant).

The *G. molesta* were flown at 20, 40 and 60 cm above a striped pattern 1.8 m long \times 1.4 m wide, and timed as they flew from 1.15 m to 0.35 m from the front of the fan. The test was then repeated with the striped pattern much larger (3.75 m long \times 2.75 m wide), and the moths were timed as they flew from 1.5 m to 0.7 m from the front of the fan. Finally, this latter setup was retested using the fan from the wind tunnel plus its air-smoothing muslin sheets instead of the window fan. This produced a narrow horizontal plume $>$ 5 m long which was directed out the open door, and the moths' flights were timed as they flew from 1.6 m to 0.6 m in front of the muslin sheets.

In these studies, the use of wider treadmill patterns along with the greater distancing of visual cues was designed to test whether or not size limitations imposed by the tunnel led to any apparent behavioural artefacts.

Results

Up-tunnel velocity versus flight height

It is clear that males of both species increased their up-tunnel velocity as their flight height increased (Fig. 2). For *G. molesta*, the increase was significant only for the difference between 20 and 40 cm up, but for *H. virescens* the difference between 20 and 30 cm was significant. Above 40 cm up, flight speed changes were negligible (Figs. 3 and 4).

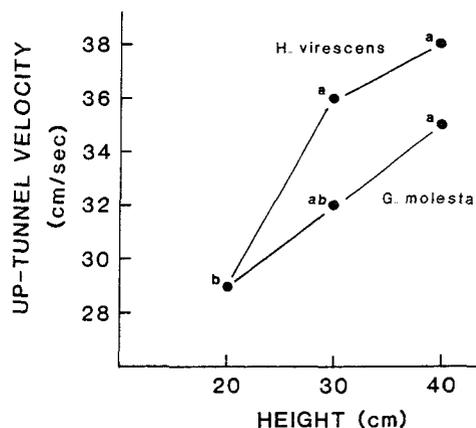


FIG. 2. Up-tunnel velocities of *G. molesta* and *H. virescens* males flying in a horizontal pheromone plume placed at three heights. Points along each line having no letters in common are significantly different ($P < 0.05$, Duncan's new multiple range test). Fifty males were tested at each point; wind speed, 58 cm/s.

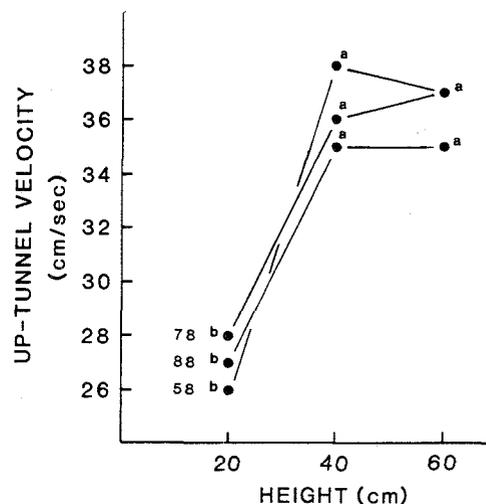


FIG. 3. Up-tunnel velocities of *G. molesta* males flying in a horizontal pheromone plume placed at three heights and with three tunnel wind velocities (small figures; in cm/s). Points having no letters in common are significantly different ($P < 0.05$, Duncan's new multiple range test). Fifty males were tested for each combination of height and wind velocity.

Up-tunnel velocity versus heights and wind speed

G. molesta males exhibited the same significant increase in up-tunnel velocity when their flight height increased from 20 to

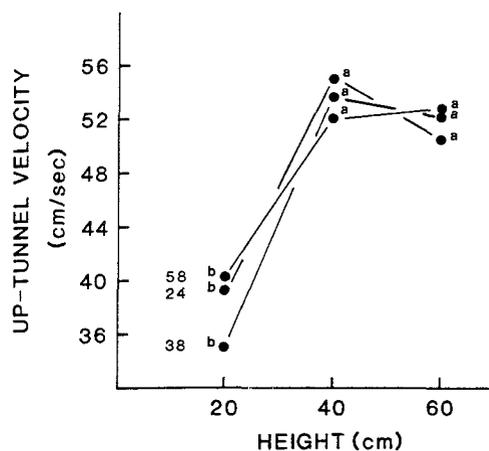


FIG. 4. Up-tunnel velocities of *G. molesta* males flying in a horizontal pheromone plume placed at three heights and with three tunnel wind velocities. Details as in Fig. 3.

40 cm ($P < 0.05$) and lack of change above 40 cm at all the wind speeds tested (from 24 to 88 cm/s (Figs. 3 and 4)). Wind velocity had no significant effect upon the up-tunnel velocities at any height ($P > 0.05$), implying that the moths were modifying their air-speeds as a consequence of maintaining a constant or 'preferred' retinal velocity.

When *H. virescens* males were tested similarly, however, the results were not as clear. Between 20 and 40 cm up, the moths showed no significant increase in their up-tunnel velocity in winds of less than 60 cm/s, though at the 88-cm/s wind the increase was just significant (Fig. 5). Flight was not tested at 60 cm up, so the 'levelling off' seen in *G. molesta* was not detected. Perhaps in part due to its large size relative to the pheromone plume, *H. virescens* may have been more affected by changes in plume structure at higher wind velocities than *G. molesta*, leading to higher up-tunnel velocities at the higher wind velocities, where the time-averaged plume and lateral flight excursions were both narrower.

Up-tunnel progress versus down-tunnel ground pattern velocity

When they were flying upwind at a height of 20 cm, *H. virescens* males could be stopped by moving the ground pattern in the down-tunnel direction at a mean velocity of 44 cm/s.

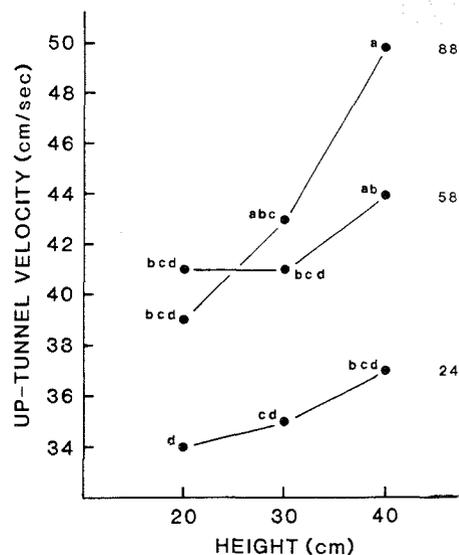


FIG. 5. Up-tunnel velocities of *H. virescens* males flying in a horizontal pheromone plume placed at three heights and with three tunnel wind velocities. Details as in Fig. 3.

To stop them at the 30-cm flight height required a significantly faster mean ground pattern velocity of 60 cm/s ($P < 0.05$). This supports the results of the earlier experiments that the height of flight above the ground influenced up-tunnel velocities. As indicated in Materials and Methods, neither *H. virescens* nor *G. molesta* males could be held in stationary flight at a 40-cm flight height above the moving ground pattern at up to the treadmill's maximum down-tunnel velocity.

When *G. molesta* males were tested at constant ground pattern velocities while flying at 20, 40 or 60 cm above the tunnel floor, the same trend of increases in up-tunnel velocity with height was seen as when the ground pattern was stationary (Fig. 6). However, at 20 cm up, the up-tunnel velocities were much lower when the floor was moving, apparently due to the greater ventral image velocity produced by the moving pattern. At this height many moths could not traverse the measuring section of the tunnel, and at the higher pattern velocity only fourteen of the fifty moths initiating up-tunnel flight traversed the measuring section of the tunnel compared with twenty-nine out of fifty doing so at the lower pattern velocity and fifty out of fifty doing so for the stationary pattern. The

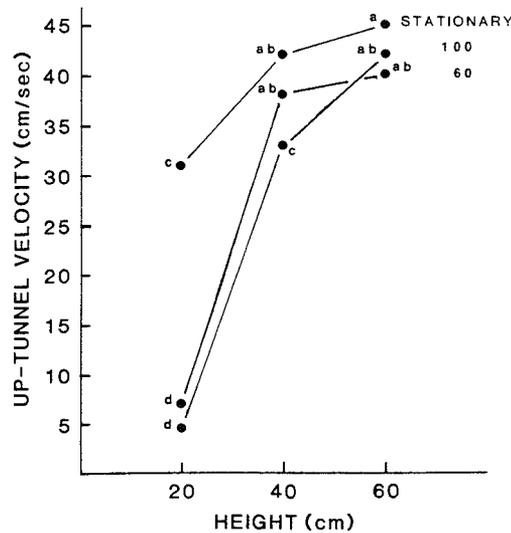


FIG. 6. Up-tunnel velocities of *G. molesta* males flying in a horizontal pheromone plume placed at three heights with a stationary ground pattern or with the ground pattern moving in the downwind direction at two speeds (small figures given as cm/s); wind speed, 58 cm/s. Other details as in Fig. 3.

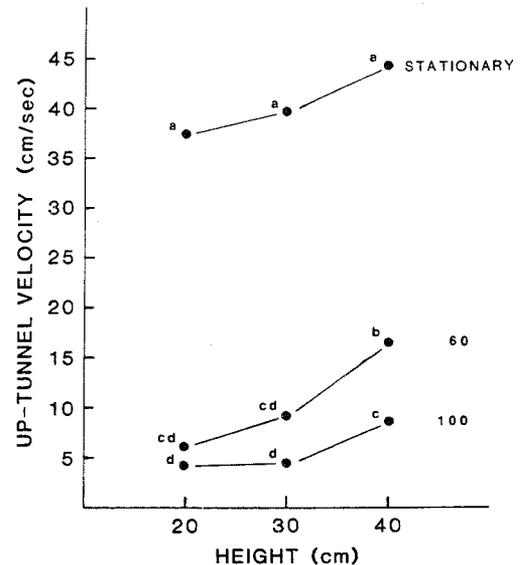


FIG. 7. Up-tunnel velocities of *H. virescens* males flying in a horizontal pheromone plume tested against ground pattern movement as for *G. molesta* in Fig. 6. Details as in Fig. 6.

moving pattern had no significant effect at the 60-cm flight height.

As for *G. molesta*, when *H. virescens* were tested with constant ground pattern velocities, the higher ground pattern velocity decreased the males' up-tunnel velocity more than the lower pattern velocity did (Fig. 7). At the 20 cm height and higher pattern velocity only three out of fifty males traversed the measuring section of the tunnel compared with twenty-one out of fifty doing so for the lower pattern velocity, and fifty out of fifty when the pattern was stationary. The moving ground pattern significantly reduced the up-tunnel velocities relative to flight over the stationary pattern at all three heights. The lack of a significant increase in up-tunnel velocity with height by the control moths is similar to that at low wind speeds shown in Fig. 5.

Flight control outside the wind tunnel

G. molesta males exhibited the same pattern of ground velocity changes with flight height in the large open room as they did while flying in the tunnel (Fig. 8): there was a significant ground velocity increase when flight

height was raised from 20 to 40 cm, but none when it was further raised to 60 cm. These results occurred whether the patterned section of floor beneath the males was about as narrow as the wind tunnel treadmill (140 cm) or much wider (275 cm), and whether the wind was produced by the window fan or by the smoothed airflow from the tunnel's fan system. The levelling off of ground velocity increase above 40 cm therefore appears not to have been caused by a flight tunnel artefact due to visual cues from the ceiling or wall reflections, etc.

Discussion

It is clear from the above experiments that, while orienting toward a pheromone source, males of these two species generally increased their ground velocity as their height of flight increased. This increase in ground velocity was independent of wind velocity and appeared to have an upper limit under our experimental conditions. These results lend support to Kennedy's (1951) optomotor hypothesis of flight speed control in relation to height and

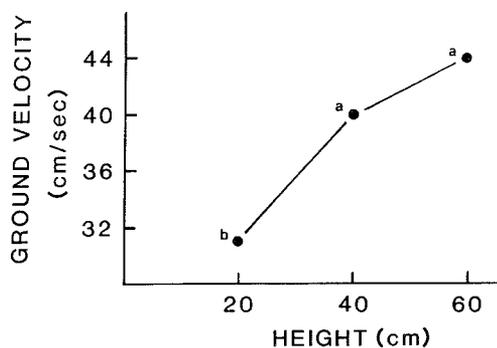


FIG. 8. Ground velocity of *G. molesta* males flying in a horizontal pheromone plume placed at three heights in an open room. Velocities are means from three experiments (see text). A total of 105 males were tested at each height. Other details as in Fig. 3.

wind velocity. The technique of flying moths in a pheromone plume restricted the flight height of the moths to within a few centimetres about the plume axis. This appears to be the first clear experimental demonstration of the effects of flight height on the ground velocity of untethered insects.

For *G. molesta* and for *H. virescens* throughout the heights tested, ground velocity varied in relation to flight height only up to a maximum, where velocity no longer increased significantly (Figs. 2, 3, 4 and 8). It may be that this levelling off of the velocity increase is a manifestation of a true 'maximum compensatory height' which may be due to one of the following conditions (Kennedy, 1951): (1) the ground pattern was no longer resolvable; (2) the moths could not further increase their airspeed to make noticeable changes in the retinal velocity, i.e. they had reached their physiological limits of airspeed. However, preliminary experiments (Kuenen & Baker, unpublished) indicate that *G. molesta* males can maintain (at least briefly) airspeeds of more than 2.5 m/s, well above the airspeeds observed in the present experiments. Moreover, if the ground pattern were no longer resolvable, then up-tunnel progress toward the source could no longer continue (Kennedy, 1940) unless other visual cues were employed. Therefore, although a maximum compensatory height with respect to the ground pattern may have been reached in these experiments, other visual cues may have augmented the levelling off effect.

When *H. virescens* males were flown at 20 and 30 cm above a stationary floor pattern, their up-tunnel velocities were 29 and 36 cm/s, respectively (Fig. 2). When the pattern was moved downwind to reduce their up-tunnel velocities to zero, however, the pattern velocities needed to accomplish this were 44 and 60 cm/s, i.e. greater than the flight speeds. This indicates that the moths must have been receiving information from stationary visual cues in the tunnel or the surrounding room.

G. molesta males flying in an open room also exhibited a levelling off of ground velocity at 60 cm, just as they did in the tunnel, so extraneous visual cues from within the tunnel may not have been involved for them. Room cues, however, may have been, including those from the experimenter and fan, c. 2 m away. A moth's ground velocity would then be the resultant of all the appropriate visual inputs, and in order to induce stationary flight, a higher than predicted ground pattern speed would be required to balance the inputs from the stationary room cues. The relative input in terms of area of the eye exposed or the degree to which each input is used (David, 1979; Jeanrot *et al.*, 1981; Moore *et al.*, 1981) must be determined for these moths by future experiments.

If it is the relative inputs of all visual cues that determine the ground velocity of the moth, we may assume that the ground pattern no longer measurably influenced the moths' flight velocity when the 60 cm height was reached by *G. molesta*. This assumption is supported by the observation that the highest flying *G. molesta* moths' ground velocities could not be slowed significantly by the ground pattern moving in the down-tunnel direction at speeds up to 200 cm/s. Presumably these moths then set their 'ground' velocity by other visual cues. It is interesting that *Choristoneura fumiferana* (Clemens) males' velocities of flight toward a pheromone source are more strongly influenced by an overhead moving pattern than by a ventral one (C. J. Sanders, personal communication).

The diagram in Fig. 1 implies that doubling the height should result in a doubling of the ground velocity, which should happen if the angular velocity of image motion is to remain constant. This did not occur in any of our experiments. In fact, even though significant

increases in up-tunnel velocity occurred with increased flight height, angular velocity actually decreased. In the initial experiment with *G. molesta*, for example, the males' mean ventral image velocity decreased from $83^\circ/\text{s}$ at the 20 cm height to $50^\circ/\text{s}$ at the 40 cm height. Similarly, when the ground pattern was used to stop the upwind progress of *H. virescens* males, the angular velocity of ventral image motion (ground pattern) was slightly less for males at the 30 cm height ($115^\circ/\text{s}$) than for males at the 20 cm height ($126^\circ/\text{s}$).

In the light of the implication that the moths use visual cues other than those from the ground pattern, this lack of maintenance of constant angular velocity of ventral image motion is not inconsistent. It is possible that the balancing of inputs from all visual cues led to a mediating of the effects of height on ground velocity and as a consequence resulted in a lower ventral angular velocity of image motion than would be expected if the moths were watching only the ground below them.

Despite our inability at this time to deduce the cause of the upper limit on ground velocity of the moths orienting in our tunnel, it is clear that an optomotor system allowed *G. molesta* males to maintain a constant ground velocity even under varying tunnel wind velocities. To maintain their constant ground velocities, the moths necessarily changed their airspeeds directly with the changes in tunnel wind velocities (Kennedy, 1940; Marsh *et al.*, 1978).

In our tunnel, significant ground velocity changes occurred with even relatively small changes (10–20 cm) in flight height above the striped floor pattern, whereas Kennedy's (1951) optomotor hypothesis, based on field observations of migratory locusts, expected changes of height in the order of metres to produce changes in ground velocity. This difference may merely reflect the ecological and behavioural constraints placed on mate-finding compared with migration. In nature male Lepidoptera orienting toward a female will be in close proximity to ventral, lateral or dorsal visual cues, since females 'call' while on plant surfaces, usually during low wind velocities (Kaae & Shorey, 1972). This close proximity to visual cues, coupled with the requirement for speed and accuracy of orientation to both maintain plume contact and successfully locate the caller before other

males do, may have led to the evolution of a finely tuned optomotor system sensitive to small changes in the visual field.

Migratory locusts, on the other hand, are evidently selected for traits that allow much greater flight altitudes as well as ground velocities. Their optomotor system may be optimal for the conditions of rapid displacement over open ground, and may not be tuned to small course or track adjustments. Kennedy (1951) measured locust ground speeds in the order of 3–4 m/s and their airspeeds were often considerably higher, whereas the highest mean up-tunnel velocity measured by us for either moth species was 0.5 m/s and the highest mean airspeed was 1.38 m/s.

It is possible that the constraints imposed by preferred retinal velocities and maximum compensatory heights could significantly affect captures of males in pheromone traps. Optimum trap heights have been empirically determined for some moth species (Lewis & Macaulay, 1976; Marks, 1978; Riedl *et al.*, 1979), although no clear explanation has been given as to why particular heights are best for captures.

The preferential capture may reflect the pre-pheromone stratification of flying males in the population, or may be indicative of optimal positioning of plumes over visual patterns for the average wind velocities of an area. Males flying in plumes high above a surface pattern at low wind velocities might tend to fly too fast to maintain plume contact in order to attain a preferred retinal velocity. Conversely, at higher wind velocities high above a surface, the airspeed necessary to attain the preferred retinal velocity may be physiologically expensive or impossible to achieve. In both cases trap catches would be reduced at high heights relative to lower ones where conditions allowing more favourable ground velocities and airspeeds would occur.

It is conceivable that at high trap heights over a visually fine-grained crop canopy, the ground pattern would become unresolvable to the moth's eyes, making optomotor anemotaxis to the pheromone source impossible unless enough lateral visual cues were nearby. Thus, pheromone traps above the maximum compensatory height would have minimal effectiveness. Our knowledge of the mechanisms regulating flight and orientation is far

from complete but further information should enhance our understanding and increase the dependability of pheromone monitoring and control procedures.

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