CAGE SIZE AND FLIGHT SPEED OF THE TOBACCO HAWKMOTH *MANDUCA SEXTA*

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Summary

Flight speeds and behaviors of the sphinx moth *Manduca sexta* were recorded in chambers of four different sizes (0.57, 8.5, 44 and 447 m^3). Mean horizontal speed increased linearly with the cube root of chamber volume from 0.57 m s^{-1} in the smallest chamber to 3.4 m s^{-1} in the largest. The maximum horizontal speed observed was 5.3 m s^{-1} in the largest chamber. Speeds decreased linearly with the logarithm of hawkmoth proximity to the wall. In a tunnel chamber (the third largest), moths often flew in a scalloped-shaped path. At the top of the scallop, they glided for 1–5 wing beats. In the largest chamber, moths could be recorded flying at angles other than horizontal (0°). At flight angles greater or less than 0°, mean speed decreased linearly with angle until ±40°. At greater angles, speeds remained between 1 and 2 m s^{-1}. Moths also flew closer to the wall at flight angles deviating from the horizontal. An allometric analysis of the flight speeds of insects and birds suggests that *M. sexta* may be able to fly at 7–10 m s^{-1}. We conclude that chamber size limits the flight speed and modifies the flight behavior of the tobacco hawkmoth.

Key words: flight speed, cage size, flight performance, *Manduca sexta*, tobacco hawkmoth.

Introduction

Insects often depend on flight for feeding, mating, dispersal and migration (Pringle, 1957; Johnson, 1969; Nachtigall, 1974). Information on insect flight is critical for some applied areas of biology, such as the study of pollen movement and the spread of diseases. Steady progress has been made on the mechanics of insect flight (Magnan, 1934; Weis-Fogh and Jensen, 1956; Weis-Fogh, 1972, 1973; Ellington, 1984*a–f*; Dudley and Ellington, 1990*a,b*), but there are relatively few published values of flight speeds (Magnan, 1934; Hocking, 1953; Lewis and Taylor, 1967; Johnson, 1969). In part this may be because of the difficulties of following and measuring small objects that move quickly and sometimes along irregular paths. For instance, flight speeds of 0.83 m s^{-1} (Nachtigall, 1974), 3–5 m s^{-1} (Heinrich, 1979) and 0.5–7.6 m s^{-1} (Cooper, 1993) have been reported for bumblebees.

One source of variation in published flight speeds is the behavioral context in which the measurements were made. We expect insects to fly at different speeds when performing different tasks. A male moth seeking a mate often flies up a pheromone plume produced by the calling female. Speeds during this zigzag flight pattern are slow, in the range 0.5–1.5 m s^{-1} (Marsh *et al.* 1978; Kuenen and Baker, 1982; Willis and Arbas, 1991; Willis *et al.* 1994; Mafra-Neto and Cardé, 1994). It is likely that males fly slowly to increase the probability of locating the female (R. T. Cardé, personal communication). May (1991) found that the dragonfly *Anax junius* rarely exceeded 4 m s^{-1} at mating rendezvous sites, but stated that it is probably capable of speeds of 10 m s^{-1}. Observations on the desert locust (Baker *et al.* 1981) and butterflies (Williams, 1930) suggest that insects fly along straighter paths and at more constant speeds while migrating than during other flight activities.

Another reason for variation in published flight speeds may be methodological. In the past, free flight speeds of insects have sometimes been estimated in questionable ways, resulting in very high values. For example, Townsend (1926) suggested that a bot fly could achieve speeds of about 365 m s^{-1} (818 miles h^{-1}). This absurd claim was effectively dismissed by Langmuir (1938). Glick (1939, cited in Johnson, 1969) observed that dragonflies kept up with, and even darted ahead of, an aircraft moving at 40 m s^{-1}. Other examples are more believable, despite the anecdotal nature of the reports and the use of less than ideal techniques. Migrating monarch butterflies have been reported as keeping pace with automobiles traveling at 8.0–11.2 m s^{-1} (Urquhart, 1960). Twinn *et al.* (1948, cited in Johnson, 1969) recorded tabanid flies traveling at 12.5 m s^{-1} while flying beside a train, though Johnson (1969) wonders whether the tabanids were being carried along in the boundary layer of air beside the train.

Other methodologies, using tethered insects or insects flying

in small cages, have resulted in slower flight speeds (Magnan, 1934; Hocking, 1953; Vogel, 1966; Lewis and Taylor, 1967; Nachtigall, 1974; Baker *et al.* 1981; Kutsch and Stevenson, 1981). Vogel (1966) stated that it was doubtful that freely flying *Drosophila melanogaster* could achieve significantly better performances than tethered specimens, because he measured tethered individuals which flew faster ($0.2\,\mathrm{m\,s^{-1}}$) than the speeds they achieved ($0.15\,\mathrm{m\,s^{-1}}$) in a revolving flight mill (Hocking, 1953). However, David (1978) observed top speeds of $0.9\,\mathrm{m\,s^{-1}}$ for freely flying *Drosophila melanogaster*.

Among insects, sphinx moths have a reputation as strong fliers. The *Guinness Book of Records* list sphingids as one of the fastest flying group of insects (Matthews, 1992), achieving speeds of $10–12\,\mathrm{m\,s^{-1}}$. They are renowned for their hovering ability because they drink nectar from flowers on the wing in much the same way as hummingbirds. Sphingids are also known to disperse over long distances and to migrate (Janzen, 1984; Haber and Frankie, 1989). *Manduca sexta* is one of the larger species of sphingids. Its body mass varies from 1 to 3 g with wing lengths of 40–60 mm and wing loadings of $7–15\,\mathrm{N\,m^{-2}}$ (R. D. Stevenson, unpublished observation).

Both the large body size and the relatively high wing loading of *M. sexta* suggest that it would be a fast flier. Our initial goal was to determine the flight speeds that *M. sexta* could achieve. Many hawkmoths, including *M. sexta*, are active at night and thus their behavior is difficult to study in the wild. Therefore, we focused our measurements on recordings in flight chambers. As our measurements proceeded, it became clear that we should systematically investigate the effects of chamber size on flight performance.

Materials and methods
Animals
Experimental insects were raised in the *M. sexta* colony maintained in our department. Several days before pupae were to eclose, they were placed into an incubator (28 °C) and kept on an 8 h:16 h L:D cycle. Each moth was weighed (2.17±0.10 g) and its body and forewing length (51.3±0.70 cm) were measured. Approximately equal numbers of males and females were placed in the experimental chambers (Table 1) 1–2 days after eclosion, where they were kept on the same

8 h:16 h L:D photoperiod. In all cases, dim night lighting was provided either by weak artificial sources (a 30 W bulb, strings of small Christmas tree lights) within the chamber or by natural light which penetrated the plastic covering of the largest chamber. In the three largest chambers, diluted honey in artificial flowers provided nourishment and tobacco plants provided a substratum on which females could lay eggs. The smallest chamber was not large enough to include feeding stations and host plants but still allow us to film the moths.

Chambers and recording techniques
Flight speeds and behaviors were measured in four chambers of different size (Table 1). All these experiments were carried out indoors in 'still' air (air speed no more than $10\,\mathrm{cm\,s^{-1}}$), and therefore flight speed, air speed and ground speed are equal. Initial measurements were made in a tunnel-shaped chamber (Table 1) constructed of black polyethylene over a frame of wood and rope suspended in a corridor. Crepe paper streamers were hung at 3 m intervals along the length of the tunnel. To collect data on flight speed in this chamber, an observer sat about halfway down the tunnel and, with a digital stopwatch, timed the moths as they flew between markers. Measurements were made in the middle of a moth's flight, rather than at the start or the end. We measured over the longest distances possible, but were seldom able to measure flights longer than 9 m (Table 1). To collect data on flight behavior, insects were video-taped parallel to the flight path as they flew directly towards or away from the camera. The recording system consisted of a black and white CCD video camera with high sensitivity to infrared light (Cliftondale Electronics, Inc., Saugus, MA, USA; FT450/12) attached to a Panasonic AG-1960 video recorder. A time code generator (Fast Forward Video, Irvine, CA, USA; model F30) time-stamped the video tape every 1/60 s. Illumination was provided by an infrared light (GTE narrow angle infrared illuminator, diode array). The slow flight speeds observed and the geometry of the chamber and corridor, which made video recordings difficult, encouraged us to record speeds in chambers of other dimensions (Table 1). The 'cage' was simply a wooden frame covered by a fine nylon mesh. The 'room' was a room lined with cheesecloth. And the 'rink' was a flight chamber, constructed of black polyethylene

Table 1. *Characteristics of the flight chambers and velocity recording conditions*

	Chamber dimensions								
Chamber	Length (m)	Width (m)	Height (m)	Grid size (cm×cm)	Field of view horizontal* (m)	Maximum distance wall to moth (m)	Mean track distances (m)	Mean track times (s)	Estimated velocity error ($\mathrm{m\,s^{-1}}$)
Cage	0.58	0.58	0.58	1×1	0.59	0.25	0.18	0.33	0.02
Room	2.02	1.80	2.33	1×1	0.68	0.40	0.34	0.38	0.05
Tunnel	21.0	1.0	2.1	–	–	–	5.49	3.76	0.15
Rink	24.4	6.1	3.0	5×5	2.25	2.00	1.41	0.44	0.15

A video camera system was used to measure flight speed in all chambers except the tunnel, see text for further details.

*The aspect ratio of the camera view ranged from 0.71 to 0.74.

over a frame of water sprinkler pipe, suspended in the University's hockey rink during the off season.

In the cage, room and rink, speeds were measured from video recordings of flights against a background grid (Table 1). The video system described above was augmented with another infrared diode array. The two lights were set on either side of the camera and pointed towards the center of the grid. On the videotape, the moth and one or two of its shadows formed by the lights were seen together. The distance of a moth from the grid was determined from the distance between it and its shadows. To calculate this distance each day, an object was placed at approximately mid-elevation in the grid at four equally spaced distances from the wall (Table 1 lists the maximum distance) and at four evenly spaced distances across the field of view (Table 1). On the basis of the known distance of the object from the wall and the distances between the object and the shadow images in the video recording, linear regressions were derived to predict the distance of the insect from the wall.

Flight paths were measured against the grid. The proportion of this distance corresponding to the moth's distance from the camera, as a fraction of the distance between the grid and the camera, was used as the actual distance traveled (based on similar triangles). The duration of the flight, within 1/60 s, was taken directly from the tape. Only flight paths within 15° of parallel to the grid, and images in which two shadows could be seen, were used to determine flight speeds from the rink. In the two smallest chambers, non-parallel paths and images with only one shadow were used because parallel flights were rare. For each chamber, the mean track distances, mean track times and the uncertainty associated with the velocity measurements are given in Table 1.

Air temperatures ranged from 24 to 28°C in the cage, room and rink and from 16 to 19°C in the tunnel. We were unable to control temperature in the two largest chambers. However, we do not believe that this is a significant problem because *M. sexta* is a highly endothermic insect and, over an air temperature range of 16–28°C, average thoracic temperature during flight will be about 40°C and will vary by less than 2°C (Heinrich, 1970; R. D. Stevenson, unpublished observations).

Results

Flight speed

Horizontal flight speed increased with chamber size from a mean of 0.57 m s^{-1} in the smallest chamber to 3.38 m s^{-1} in the largest chamber (Table 2). When speed was plotted against the cube root of chamber volume, there was a clear linear relationship (Fig. 1A). In the largest chamber, moths flying far from the wall flew faster (Fig. 1B). Maximum speeds in each chamber were about twice as fast as mean speeds (Table 2).

Because the linear regression analyses of the cube root of cage volume and log(distance to the wall) both explained about 75% of the variance in the data (Fig. 1), we used stepwise regression (excluding data from the tunnel, where there were no distances to the wall recorded) to determine which of the

Table 2. *Horizontal flight speeds in chambers of different sizes*

Chamber	Flight speeds (m s^{-1})			2 S.E.M.	N
	Mean	Maximum	Minimum		
Cage	0.57	1.51	0.17	0.1	38
Room	1.02	1.91	0.37	0.15	37
Tunnel	1.58	3.3	0.83	0.13	62
Rink	3.38	5.3	1.61	0.20	93

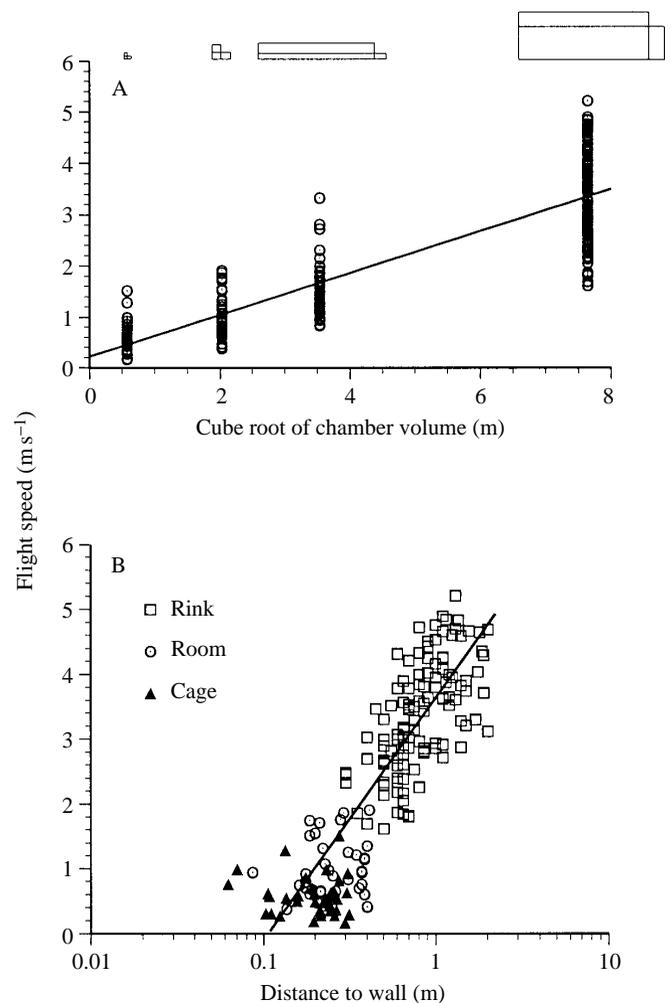See Table 1 for chamber dimensions.

Fig. 1. (A) Flight speed increases linearly with the cube root of chamber size. Speed = 0.41(chamber volume)$^{1/3}$ + 0.22, r^2=0.75, N=230. Samples sizes are given in Table 2. The four outline drawings show chamber length, width and height (Table 1) drawn to scale to illustrate chamber size and shape graphically. (B) Horizontal speeds increase as the distance from the wall increases in the rink: speed = 2.89log(distance to the wall) +3.63, r^2=0.40, N=127. There is no significant relationship between horizontal speed and distance to the wall in the room and cage. The regression relationship for all the data combined is speed = 3.77log(distance to the wall) + 3.55, r^2=0.75, N=185.

A
Scalloping flight

Glide from this point

Depth
0.08±0.01 m

Distance
1.07±0.12 m

Duration
0.57±0.06 s

Glide duration
0.1±0.02 s

B
Wing position during glide phase

1   2   3   4   5   6   7   8   10   11   12
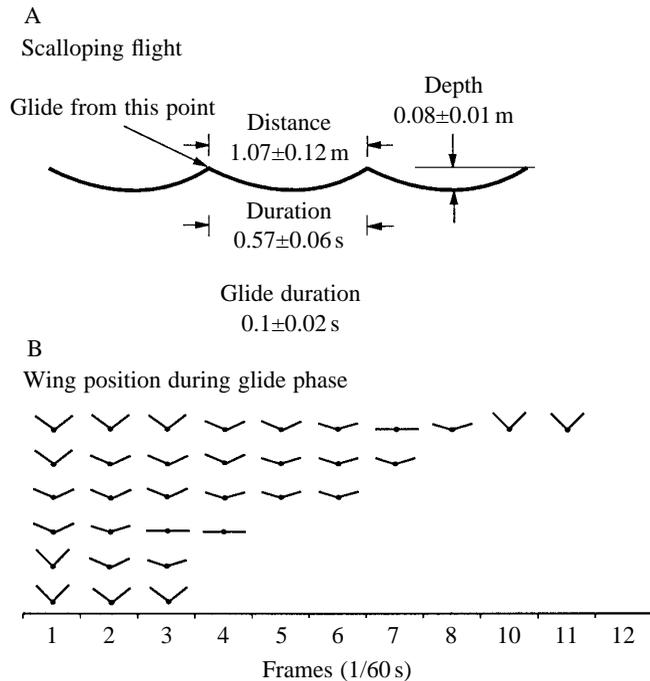Frames (1/60 s)

Fig. 2. (A) Schematic diagram of the scallop-shaped flight tracks of moths. Sample sizes for the distance, depth and duration measurements are 49, 38 and 41, respectively, and values are means ±2 S.E.M. Note that gliding is initiated at the highest point in the scallop track. (B) Examples of wing position during gliding. Wings are held at angles ranging from a V at 45° to perpendicular to the body. The average glide duration was 0.1±0.02 s (N=11).

two variables was a better predictor of flight speed. The cube root of cage volume was the first variable entered into the regression equation and it explained about 73 % of the variance. Log(distance to the wall) was then added as a second significant variable and r^2 increased from 0.73 to 0.81.

Flight behavior

Insects flew slowly or hovered in the smallest chamber. In the room, insects exhibited escape behavior by flying against the ceiling cloth towards the light. They moved between feeding stations where they hovered and drank artificial nectar. Females flew in and around host plants to lay eggs and males investigated resting moths for opportunities to copulate. These same flight behaviors were observed in the two larger chambers.

In the tunnel, moths flew regularly from one end to the other. They often used a slow forward flight with an arcing track in the vertical direction, which we have termed 'scalloping' flight (Fig. 2A). At the highest point in the arc, hawkmoths often held their wings still in a gliding position (Fig. 2B). An effort was made to quantify this pattern. The lengths were estimated visually: mean (±2 S.E.M.) distance and depth of the arc were 1.07±0.12 m (N=49) and 0.08±0.01 m (N=38), respectively. On the basis of the video records, the mean duration of each scallop was 0.57±0.06 s (N=41) and the mean duration of the glide was 0.093±0.022 s (N=11) or about 2.5 wing beats.

In the rink, there were many straight flight tracks that deviated upwards or downwards from the horizontal (0°, Fig. 3A). Flights at angles that deviated by more than 40° were much rarer than flights at more moderate angles (Fig. 3A). Flight speeds varied systematically with flight angle (Fig. 3B). When moths flew at steep downward angles (−90° to −40°), flight speed averaged between 1 and 2 m s^{-1}. As the flight-track angle increased from −40° to 0°, mean speeds increased from about 2 to 3.3 m s^{-1}. As the flight-track angle continued to increase to approximately 40°, flight speeds along the flight path again decreased to about 1.5 m s^{-1}. At angles greater than 40°, flight speeds were similar to those at large downward angles. The maximum speed observed was 5.9 m s^{-1} at a downward angle of 13°. Speeds above 5 m s^{-1} occurred at angles between −10 and +10°. Minimum speed varied between 1 and 1.5 m s^{-1} irrespective of track angle.

The relationship between flight speed and flight angle (Fig. 3B) depended on the proximity of the hawkmoth to the wall. Hawkmoths flying close to the wall flew slower (Fig. 3D). Stepwise multiple regression was used to determine whether log(distance to the wall) or flight angle was a better predictor of flight speed. Two independent assessments were made using flight-track angles equal to or greater than −40° but less than 0° and angles greater than 0° but less than or equal to 40°. For both sets of data, log(distance to the wall) was the first variable entered into the regression equation yielding r^2 values of 0.29 and 0.41 for the downward and upward directions, respectively. In both cases, flight-track angle was also entered into the equation as a significant variable. The addition of angle as a variable increased the overall r^2 values to 0.42 and 0.51, respectively.

Discussion
How fast can Manduca sexta fly?

Willis and Arbas (1991) reported flight speeds of 1.30 m s^{-1} (males) and 1.35 m s^{-1} (females) in *M. sexta* for odor-modulated upwind flight (a pheromone plume for males, tobacco leaf scent for females), against wind speeds up to 2.00 m s^{-1} in a wind tunnel. Faster speeds were observed in the present experiments. Mean horizontal flight speed in the rink was 3.38 m s^{-1} and the maximum horizontal speed observed was 5.3 m s^{-1} (5.9 m s^{-1} at a downward angle of 13°). However, these speeds seem unimpressive when compared with those of other Lepidoptera, including both moths (Riley *et al.* 1990) and butterflies (Dudley and Srygley, 1994), where speeds of between 5 and 10 m s^{-1} have been recorded in the wild. *M. sexta* is larger than these moths and butterflies and has higher wing loadings (>7 N m^{-2}), both of which correlate with greater flight speeds in butterflies (Dudley and Srygley, 1994). To determine how *M. sexta* compared, we plotted flight speed as a function of body mass for insects and birds (Fig. 4); flight speeds of *M. sexta* in the rink are similar to those of butterflies in insectaries (Betts and Wootton, 1988; Dudley, 1990) but slower than those of butterflies (Dudley and Srygley, 1994) and other insects in the field. On the basis of
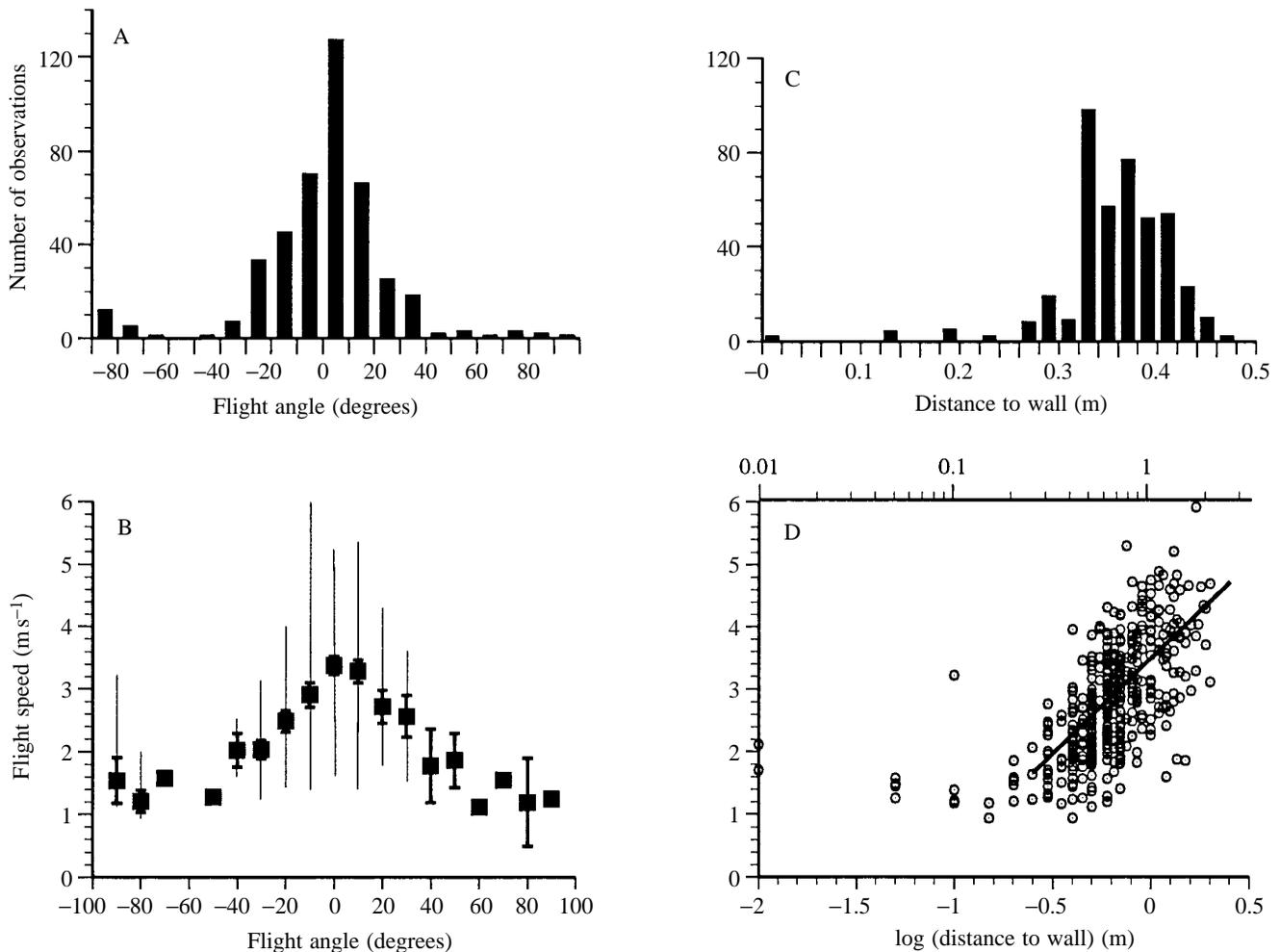
Fig. 3. (A) The number of flight tracks as a function of flight path angle measured in the rink. Most of the 424 flights occurred at angles between +40 ° and −40 °. The largest single group (*N*=127) flew horizontally (between +5 ° and −5 °). (B) Means ± 2 S.E.M. and the range of flight speeds as a function of flight path angle. Flight speeds decreased linearly with flight angle for angles between 0 and ±40 °. Maximum values paralleled the trend for the mean, while minimum values were independent of angle, ranging between 1 and 1.5 m s^{-1}. For angles with absolute values greater than 40 °, flight speeds averaged between 1 and 2 m s^{-1}. (C) The number of flight tracks as a function of the distance from the wall. Most flights occurred at about 0.4 m from the wall. (D) At distances greater than 0.2 m, flight speed increased linearly with log(distance from the wall): speed = 2.86log(distance to the wall) + 3.43, r^2=0.39, *N*=399. This plot includes data used for the horizontal flight analysis of Fig. 1B.

these comparisons, we estimate that *M. sexta* could achieve speeds of 7–10 m s^{-1} in the field.

### Effects of cage size and proximity to the wall on flight

Our results clearly show that chamber size limits flight speed (Fig. 1A). To our knowledge, the impact of chamber size on flight speed has never been critically examined, but there is evidence in support of a chamber effect based on research with Lepidoptera by Srygley and Dudley (1993), who measured flight speeds of freely flying butterflies and reported that flight speeds were several times faster in the wild than in an insectary (measured by Dudley, 1990). When the allometric equations for flight speed as a function of body mass, based on Dudley and Srygley's (1994) work on freely flying tropical butterflies, are plotted on the same graph with Dudley's (1990) allometric equations derived from measurements of many of the same

species in a flight chamber (Fig. 4), it is clear that flight speeds are 2–4 times faster in the wild than in flight chambers. This conclusion is consistent with observations on the neotropical day-flying moth and the migratory locust (Table 3).

A cage size effect may explain some recent results obtained by Cooper (1993). In studies of bumblebees climbing vertically with food in their stomachs, Cooper (1993) reported constant flight speeds of about 0.5 m s^{-1}. Her calculations indicated that the maximum speed to which bees could accelerate in half the tube height (given that they also had to slow down) was 5 m s^{-1}. However, the dimensions of the chamber were only 0.15 m×0.15 m×1.81 m. The cube root of the chamber volume gives a linear dimension of 0.34 m, which, when compared with the bumblebee's wing length, gives a ratio of 34:1. This would be equivalent to *M. sexta* flying in a chamber with a linear dimension of 1.7 m, a cage size which clearly restricts

Fig. 4. A comparison of *Manduca sexta* flight speeds (mean and range of speeds in the largest chamber) with the air speeds of other insects and birds. This comparison suggests that *M. sexta* could achieve flight speeds of $7–10\,\mathrm{m\,s^{-1}}$ in the wild. The insect data recorded in the field are from Rüppell (1989), DeVries and Dudley (1990), Dudley and DeVries (1990) and May (1991). These data are mainly for dragonflies and damselflies. The insect data recorded in the laboratory are from Magnan (1934), Vogel (1966), Dudley and DeVries (1990) and Yager *et al.* (1990). Most of these data are from Magnan (1934) and include species from five orders: Neuroptera, Lepidoptera, Coleoptera, Diptera and Hymenoptera. The regression lines for butterflies during free flight in an enclosure and in the field are taken from papers by Dudley (1990) and Dudley and Srygley (1994) respectively. The flight speeds of birds are taken from Welham (1994).
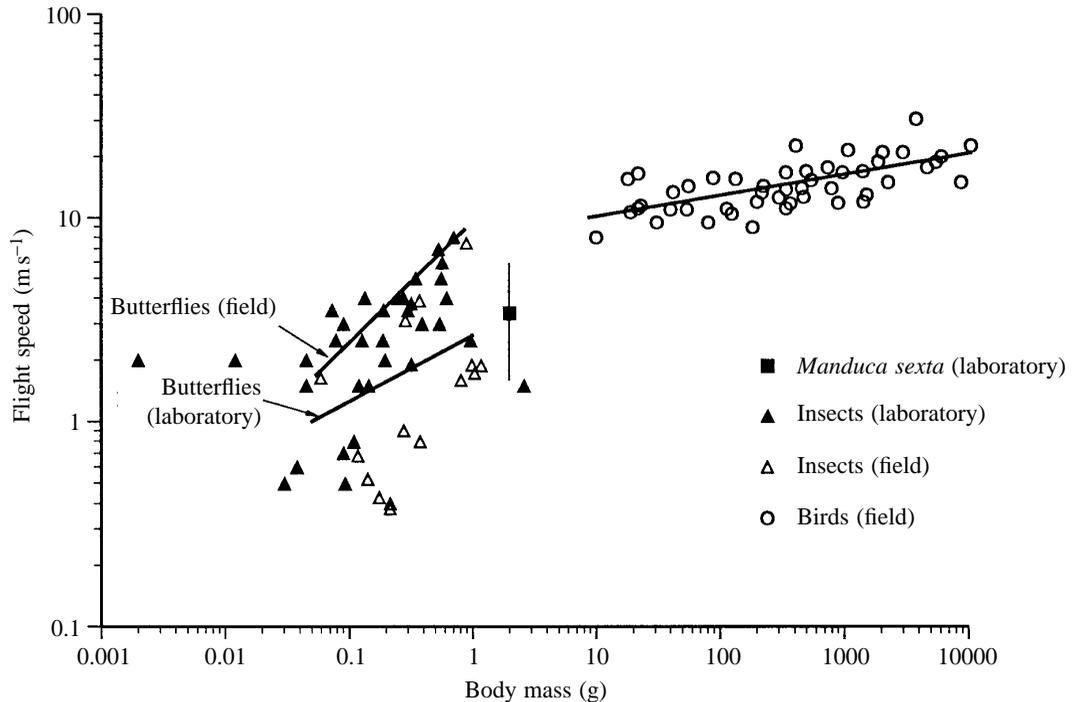
flight speeds (Fig. 1A). If this ratio is a valid way to compare insects of different sizes in cages of different sizes, then the size of the bumblebee chamber may have restricted flight speeds.

The hawkmoths flew more slowly when close to the wall in the large chamber (Figs 1B, 3D). It seems reasonable that animals would reduce their speeds of locomotion within an enclosed space, given the consequences of a collision with the chamber walls. In horizontal flight, the distance to the wall influenced speed (Fig. 1B). In flights made at angles other than the horizontal, both the angle and the distance to the wall were correlated with flight speed (Fig. 3D).

Wind tunnels are also used to study insect flight. This raises the concern that the size of the wind tunnel might influence flight performance. Comparisons are difficult, however, because in wind tunnels animals experience a different set of mechanical and visual inputs from those that they experience in a flight chamber. Furthermore, experimenters using wind tunnels often provide additional visual cues for the insects (David, 1979; Kuenen and Baker, 1982; Cooper, 1993). Therefore, the perceived volume of the tunnel and distance to the tunnel walls may be altered. Systematic investigations of the enclosure size and the distance to the nearest wall for other species and better information about flight performance in the field will help to clarify the relationship between the perception of space and flight speed.

Flight behavior

Flight behavior was strongly influenced by chamber size. In the smallest chambers, flight speeds were slow. In fact, when the advance ratio, equal to the forward velocity of the insect divided by the mean maximum velocity of the wing, is less

Table 3. *Comparisons of mean and maximum flight speeds and speeds of the three insect species under different conditions*

Species	Flight speed		% Greater	Comment	Source
	Mean ($\mathrm{m\,s^{-1}}$)	Maximum ($\mathrm{m\,s^{-1}}$)			
Urania fulgens	3.9	6	54	Migrating	DeVries and Dudley (1990)
Urania fulgens	2.37	3.74	58	Insectary	Dudley and DeVries (1990)
Locusta migratoria	4.6	6.1	33	Migrating	Baker *et al.* (1981)
Locusta migratoria	3.3	4.7	42	Tethered	Baker *et al.* (1981)
Parasphendale agrionina	1.9	2.6	37	Stable flight	Yager *et al.* (1990)
Parasphendale agrionina	3.76	4.92	31	Evasive flight	Yager *et al.* (1990)

than 0.1, the animal is effectively 'hovering' (Ellington, 1984*c*). For *M. sexta*, hovering occurs at flight speeds less than about $0.5\,\mathrm{m\,s^{-1}}$ (wingbeat frequency, 27 Hz; wing length, 50 mm; stroke amplitude, 1.7 rad). Thus, in the smallest chamber, *M. sexta* could be classified as hovering almost all the time. Hawkmoths were not restricted to hovering in the larger chambers.

The scalloping mode of flight described here is characterized by an unpowered gliding phase and a powered flapping phase. An alternation between gliding and flapping is often observed among butterflies (e.g. Gibo and Pallett, 1979) and birds (Rayner, 1977). However, the flight tracks of these animals do not have the same scalloped shape (Fig. 2) and the duration of their glide phase is relatively longer. The gliding phase of the hawkmoth lasted no more than 5 wing beats and covered distances of approximately 0.1 m. Most observers would probably not identify this as gliding flight. Although the characteristic arcing shape of the flight tracks was observed mainly in the tunnel, it also occurred in the largest chamber.

We know of no comparable data to those shown in Fig. 3 on flight speeds as a function of flight-track angle. As angles increased and decreased from the horizontal, flight speeds decreased. One might expect the animals to fly at slower speeds when they are climbing because of the additional power needed to overcome gravity, but the slower speeds observed when they fly downwards are not consistent with this interpretation. An alternative view is that the flight speeds were reduced because the animals were flying towards a barrier, the ceiling or the floor of the chamber. The correlation between flight speed and distance to the wall (Figs 1B, 3D) supports this interpretation.

The range of flight speeds and behaviors we observed in the present study suggests that there is much still to be learned about the flight performance of insects. We are confident that *M. sexta* can fly faster than the maximum value we have recorded, but new experimental approaches using bigger chambers, wind tunnels or measurements in the wild will be required to measure it. Our data should caution others about the influence of cage size on flight speeds and styles. The phenomenon may prove to be important for other forms of locomotion (e.g. swimming), as the recent paper by Tang and Boisclair (1993) suggests. A variety of approaches in the laboratory and field are necessary to document the flight capabilities of insects.

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