

FLIGHT IN *DROSOPHILA*

I. FLIGHT PERFORMANCE OF TETHERED FLIES

By STEVEN VOGEL

Biological Laboratories, Harvard University, Cambridge, Mass.

(Received 20 December 1965)

INTRODUCTION

The primary objectives of the present study are the identification of the special aerodynamic difficulties posed by the flight of a small insect and the description of the adaptations with which the fruit-fly resolves these problems. That small size entails special physical problems is an immediate consequence of the behaviour of fluids. For *Drosophila*, the Reynolds number, based on wing chord and wing velocity or on body length and flying speed, is around 100 to 200. Under these conditions, flow is too viscous for true turbulence but sufficiently inertial to sustain local vortices. Skin friction is a major component of the drag of a body, so streamlining is of questionable value and the total drag of any object is high. Moreover, velocity gradients are gentle, giving rise to thick boundary layers which, in turn, reduce the influence of the shape, orientation, and surface details of an object on its aerodynamic characteristics.

Our present understanding of the flight of insects derives mainly from the studies of Weis-Fogh and his collaborators on the desert locust, *Schistocerca gregaria*, a large, migratory, four-winged, synchronous species. Pringle (1957, 1965) has called attention to the dearth of comparable information on insects of dissimilar characteristics. Fruit-flies are small, non-migratory, two-winged, and asynchronous; thus investigation of their flight should clarify the extent to which results obtained on locusts indicate general features of the flapping flight of insects.

The basic approach will be an empirical and experimental investigation rather than a theoretical analysis. Weis-Fogh and Jensen (Weis-Fogh, 1956*a, b*; Weis-Fogh & Jensen, 1956; Jensen, 1956) have documented the utility of this approach, providing a logical point of departure for the present study. Thus their recommendations will be followed and, where possible, the same symbols and conventions and analogous techniques will be used. As a first step, flight performance will be evaluated under conditions approaching, as nearly as is practical, those obtaining in nature.

MATERIAL

Drosophila virilis Sturtevant (Texmelucan strain) were obtained from the Genetics Foundation, University of Texas, and had been reared in the Biological Laboratories on standard cornmeal-molasses-yeast medium at 20° C. for about three years at the time of the experiments described here.

METHODS

1. Performance measurements

Flight performance was measured with flies tethered to a flight balance in the working section of a wind tunnel (see Appendix). Air velocity was monitored with an anemometer consisting of a pair of bead thermistors electrically heated in a Wheatstone bridge, with one bead exposed to the wind, the other shielded from it. The arrangement of the flight balance and associated components is diagrammed in Fig. 1. The lift-measuring element of the flight balance consisted of a force-transducing galvanometer (Vogel & Chapman, 1966). Pendulum *b*, of stainless-steel tubing, could be lifted

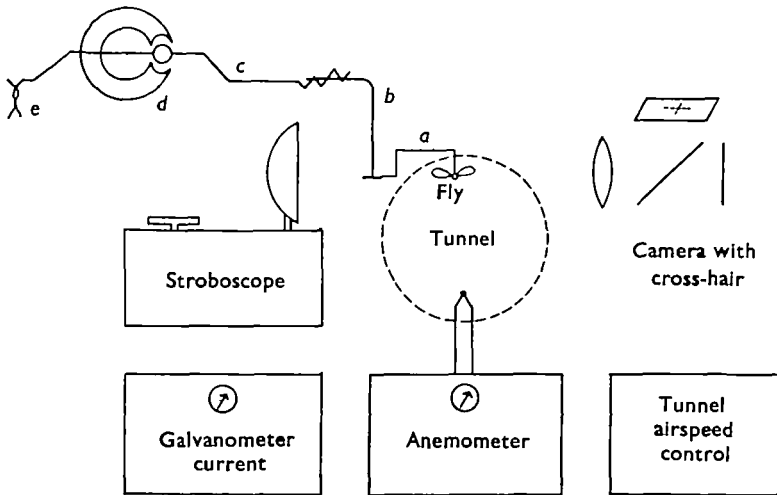


Fig. 1. Arrangement of components for performance measurements. *a*, mount-wire; *b*, pendulum; *c*, front beam of galvanometer; *d*, *e*, counterweights.

off beam *c* of the galvanometer (*d*) for insertion of mount-wire *a*. Counterweights *e* on the rear beam of the galvanometer balanced the weight of the pendulum and mount-wire; the weight of the specimen was tared electrically. Both lift and flying speed were determined with this null-balancing arrangement. Thrust deflected the pendulum forward, while lift elevated the galvanometer beam. The former was balanced by adjusting the airspeed with the tunnel motor control until thrust just balanced drag and the insect attained 'preferred flying speed'. Lift was balanced by increasing the current passing through the galvanometer until the fly returned to the position it occupied before flight was initiated.

The drag of the mount-wire was minimized by reducing the throat diameter of the tunnel to $1\frac{1}{2}$ in. to produce a sharp velocity gradient at the end of the contraction and by positioning the specimen near the edge of the airstream and close to the end of the contraction. Even so, it was significant. In practice, therefore, the tunnel velocity was adjusted, not merely to return the fly to its original position, but rather to push the fly slightly behind this position by a predetermined distance which varied with flying speed. This minor adjustment, changing body angle by at most $2\frac{1}{2}^\circ$, absorbed the drag of the mount-wire.

A 35 mm. single-lens reflex camera with appropriate markings on the ground-glass viewfinder served both for visual adjustments of airspeed and lift-balancing current and for photographic recording of stroke parameters. The lens, of 58 mm. nominal focal length, was reversed and attached to a bellows to provide an image of the fly approximately twice life size. Photographs taken at an exposure of 1/50th of a second recorded wing movements over about four full strokes. Room illumination sufficed for visual adjustments; for photography, two microscope lamps were turned on with a foot-switch less than 0.5 sec. before the exposure and turned off immediately thereafter. In general, the fly's response to illumination did not take place within this brief interval.

Flies, under continuous CO₂ or light ether anaesthesia, were attached to the mount-wire by a technique similar to that of Hollick (1940), with 'Tackiwax' (Central Scientific Co.) as the adhesive. The point of attachment was as far anterior as possible on the mesothoracic scutum, and the mount-wire was oriented dorso-ventrally. After tethering the fly, the mount-wire was bent and twisted to orient the specimen properly. The mount-wire was inserted into the pendulum, the latter was hung on the galvanometer beam, and the weight of the fly was tared. Then a puff of air initiated 'flight'; indeed, moving air not only initiated but also helped to sustain prolonged flights. If flight continued steadily for several minutes and flight posture was 'complete' (pro- and mesothoracic legs tight against the thorax and metathoracic legs extended on opposite sides of the abdomen), measurements were begun. In as rapid succession as possible (less than 10 sec. in all) the following operations were performed. *Airspeed* and *lift* were balanced, thus centring the fly in the field of view of the camera; a photograph was taken; and *frequency of wingbeat* was determined with the aid of an electronic stroboscope (General Radio Co. type 1571-A).

A flight performance was considered 'successful' if it met these criteria: (1) the animal achieved enough lift to support its weight at at least one body angle; and (2) measurements were taken over at least five different body angles before speed, lift, or frequency began to change erratically. This arbitrary elimination of performances below a certain level precluded meaningful averaging of the successful performances of different flies.

2. Parasite drag

At preferred flying speed thrust is the horizontal force necessary to balance parasite drag (the drag of non-lift-producing components of an aircraft). Consequently, the values for thrust in the performance measurements were obtained from data relating drag to speed and body angle, obtained as follows.

Flies were anaesthetized with CO₂ and then killed by exposure to chloroform vapour, a procedure which minimized distortion of body shape. Specimens were selected in which the body was oriented in a posture as similar as possible to that observed in the photographs of tethered flight. Wings and legs were routinely removed; the wings do not contribute to parasite drag except through their interaction with the body, a difficult factor to evaluate. Animals with legs fixed in flight posture have about the same drag as legless animals. The attachment technique was similar to that described for performance measurements except that the mount-wire was waxed to the fly near a wing articulation point and extended laterally. Thus axial rotation of the mount-wire adjusted body angle. The mount-wire was inserted into a short piece of

fine tubing, the latter being cemented to the needle of a force-transducing galvanometer. The drag of the mount-wire without fly was subtracted from each measurement of parasite drag. All measurements were corrected to the dimensions of a standard animal (see below) using the assumption that drag is proportional to the second power of linear dimensions. No animals were used more than one hour after killing.

3. Definitions and conventions

Body angle was the angle between the horizontal tunnel axis and the 'arbitrary long axis' of the fly, a line connecting the top of the neck and the tip of the abdomen. Positive angles indicate that the head was upward; exact values were obtained from the photographs. In the performance measurements body angle was adjusted by the investigator as an independent variable.

To assign co-ordinates to the *extreme wing positions* it was assumed that the wing tip described a closed line on the surface of a sphere whose centre was the wing articulation point, and that this sphere was inscribed with the same co-ordinate system as used in terrestrial navigation. The poles of the sphere were connected by a line parallel to the 'long axis' of the fly and passing through the wing articulation point on the side of the animal facing the camera. For latitudinal or horizontal co-ordinates the pole in front of the fly was designated -90° , that behind, $+90^\circ$. For longitudinal or vertical co-ordinates, straight up was $+90^\circ$, down, -90° . Measurements were obtained from the photographs; they presumed that the camera recorded a true rectilinear projection of the spherical surface.

The *stroke angle*, a term introduced by Weis-Fogh and Jensen (1956), is the great circle distance between the upper and lower wing positions, analogous to 'amplitude' as used by Hollick (1940), Chadwick (1951) and others. This was obtained from the co-ordinates of the extreme wing positions with the aid of a haversine nomograph—a manoeuvre identical to the determination of the distance between two points on the earth from their respective latitude and longitude.

For convenience, the *stroke-plane angle* was defined as the acute vertical angle between the plane of wingbeat (the plane including the four extreme wing-tip positions of the two wings) and the long axis of the fly, rather than referring the stroke-plane to a horizontal plane as done by Weis-Fogh (1956*a*).

To reduce the scatter of experimental data it was necessary to take into account the variation in size among specimens. A large number of measurements revealed that dimensional similarity is preserved among animals encompassing the full range of size variation of this species. To define a 'standard *Drosophila virilis*', the distance between the wing tip and the proximal cross-vein (*lcv*), an easily measurable dimension, was set as 2.00 mm., a value typical of the specimens used. This fixed the other dimensions, as noted in Table 1, and permitted calculation of a single correction factor based on measurement of *lcv* for all experimental animals.

RESULTS

A total of sixteen *Drosophila* gave 'successful' performances on the flight balance. For each animal, four complete sets of observations were averaged at each of five to ten body angles; in all, 484 sets of observations were made. In every case where one

Table 1. Selected dimensions of a standard *Drosophila virilis* and the relationships between these dimensions and the distance between the wing tip and the proximal cross-vein (lxv)

Wing length	3.01 mm.	$1.50 \times lxv$
Wing area	2.88 mm. ² (one surface)	$0.720 \times lxv^2$
Wing mass	4.78 μ g.	$0.597 \times lxv^2$
Wing moment of inertia	10.0 μ g...mm. ²	$0.344 \times lxv^3$
Body mass (non-gravid)	2.00 mg.	$0.250 \times lxv^3$

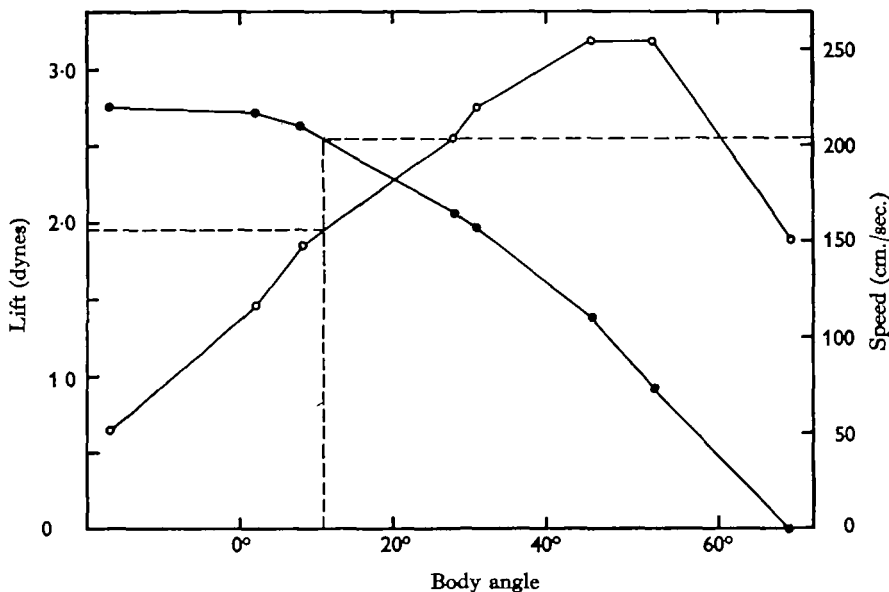


Fig. 2. Flight performance of one specimen. O, lift; ●, 'preferred flying speed'. Dashed lines mark values of body angle and flying speed at 100% lift.

or two of the four determinations measured unusually low lift, the abnormality could be traced to a particularly low stroke angle on the corresponding photograph. Such abnormal determinations, amounting to about 4% of the total number, were omitted from the averages.

Fig. 2 shows the basic performance of one of the sixteen specimens; this individual was typical in magnitude of lift and speed, but better than average in steadiness of performance. The fly achieved a lift equal to body weight (100% lift) at a body angle of 11° and a corresponding forward speed of 205 cm./sec. It again attained 100% lift near zero airspeed, but this latter point is of questionable significance; after exposure to moving air all flies performed erratically in simulated hovering. The plot shows several noteworthy features. Lift is roughly proportional to body angle over a wide range of angles. 100% lift occurs at a body angle differing only slightly from the orientation giving minimum parasite drag (0°). Flying speed at 100% lift is very near the maximum speed of which the animal is capable, even when its weight need not be supported. In addition, at zero airspeed the stroke plane on the corresponding photographs appears horizontal, while at zero lift (by extrapolation) the stroke plane is vertical.

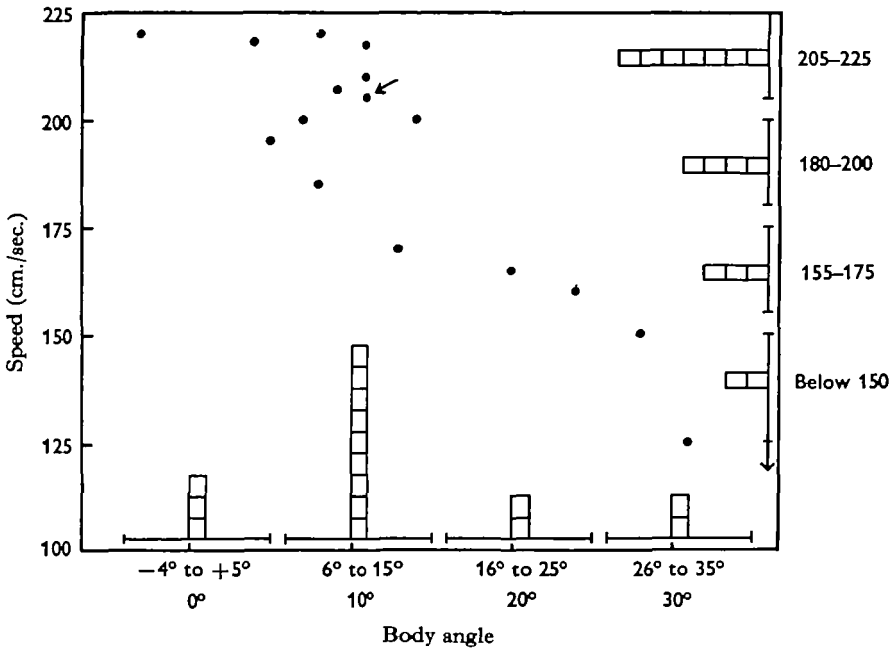


Fig. 3. Scatter plot and histograms summarizing speeds and body angles at which 100% lift was achieved for all sixteen specimens. Arrow marks the fly considered in Figs. 2 and 4.

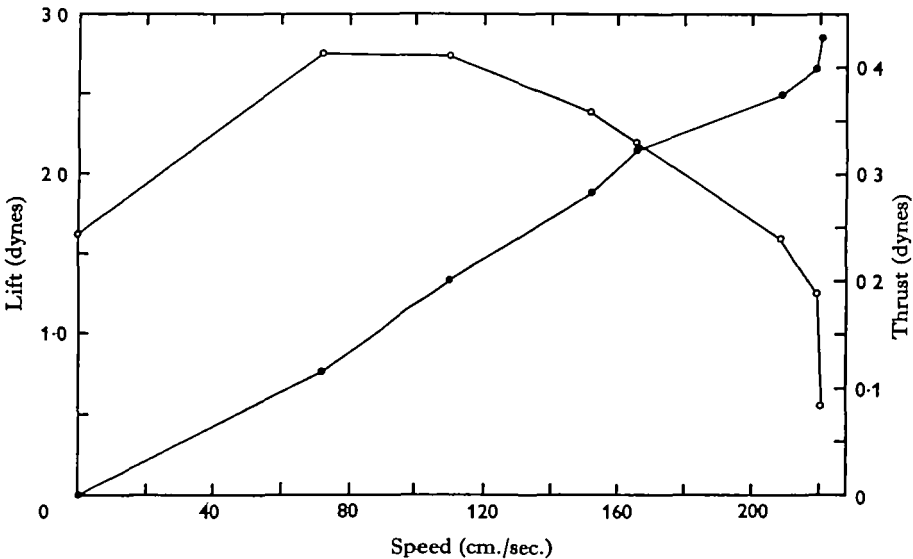


Fig. 4. Lift (O) and thrust (●) corrected to the dimensions of a standard animal.

Fig. 3 groups the flying speeds and body angles at which 100% lift was attained for each of the successful performances. The high degree of individual differences cannot be attributed to any single quantity which was measured. Several corrections were applied to the data, but none greatly reduced the scatter of points. The histograms

provide a means of estimating 'typical' values, but the possibility cannot be dismissed that the 'best' performances are in fact more nearly typical of flight under natural circumstances.

Table 2. Numerical values of parameters in a 'standard performance'

Wingbeat frequency	195 beats/sec.	Top of stroke, latitude	+14°
Lift	2.0 dynes (100%)	Top of stroke, longitude	+80°
Preferred flying speed	200 cm./sec.	Bottom of stroke, latitude	-25°
Body angle	+10°	Bottom of stroke, longitude	-66°
Thrust	0.36 dynes	Stroke angle	146°
		Stroke-plane angle	+68°

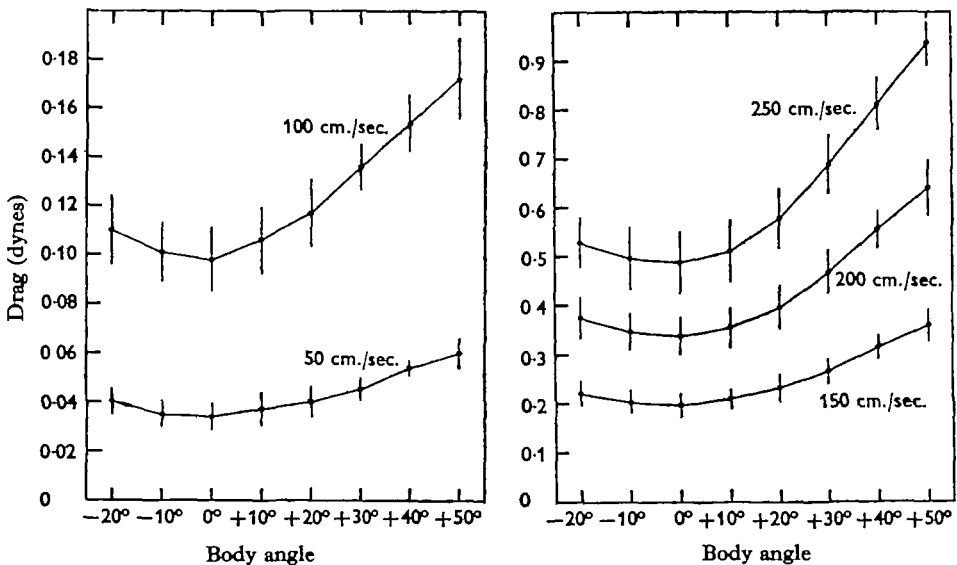


Fig. 5. Parasite drag versus body angle and airspeed for *D. virilis*. Standard deviations are indicated by vertical lines.

Standard lift and thrust for the same fruit-fly considered above are plotted against flying speed in Fig. 4, with body angle treated parametrically. Thrust appears directly proportional to speed rather than to the square of speed; this is due not to any peculiarity of low-speed flow, but to our method of adjusting speed by altering body angles: higher speeds result from lower angles which, in turn, incur relatively less drag. However, if, as seems probable, the fly normally controls the direction of output through adjustment of body angle, the direct proportionality may obtain in level, free flight.

In no single successful performance did any of the stroke parameters show significant and regular variation with body angle. Hence the latter is a most satisfactory independent variable: such changes as we impose upon it are not compensated by shifts in the stroke parameters. While this situation is most convenient for studies of tethered flight, it obviously represents a simplification (by omission) of an effective control system operative in free flight. Conversely, there are apparently no rigid, reflex

connexions between body angle and flying speed and the stroke parameters in *Drosophila*.

From the performance measurements we can assign numerical values to the measured parameters to define the 'standard performance' of a 'standard animal' in level flight at full speed with a full wingstroke (Table 2). These values will be used in subsequent studies of the flight mechanism.

The variation of drag with body angle is plotted for five different airspeeds in Fig. 5. The curves represent averages of complete sets of measurements on six specimens, each of which showed considerable regularity; the comparatively large standard deviations are attributable to differences between the flies. It may be noted that drag is not nearly as dependent on body angle as would be the case for conventional aircraft; in fact the drag at the 10° body angle of a standard performance is only about 5% greater than the drag at 0° .

DISCUSSION

1. *The relationship between tethered and free flight*

In view of the severe restraints imposed by tethered flight it is necessary to examine its relation to flight under more natural circumstances. The primary question is whether freely flying *Drosophila* can give significantly better performances than tethered specimens.

There are several reasons to doubt this possibility. First, the typical maximum airspeed at which body weight was supported, 200 cm./sec., was higher than the maximum speed, 178 cm./sec., which Hocking (1953) recorded in experiments using a revolving flight mill for *D. melanogaster*. Secondly, we have seen (Fig. 2) that when the requirement of 100% lift was removed, the tethered flies attained speeds not much higher than their flying speeds while supporting body weight. This suggests that these speeds are near the maximum velocity as this might be limited by an increasing advance ratio (defined as forward distance travelled per 360° movement of one wing divided by twice the length of one wing). The advance ratio at 200 cm./sec., about 2.1, is, indeed, a reasonable maximum by conventional standards of propeller performance. Thirdly, at the maximum speed at which 100% lift was realized the body was nearly horizontal, the orientation giving least drag. It is reasonable to expect that level, forward flight at maximum velocity will be achieved with a body orientation which minimizes drag. Fourthly, measurements of free-flight velocities of fruit-flies, flying toward a stroboscope just after release, gave lower values (around 120 cm./sec.) than did the present measurements; however, the freely flying animals were climbing along paths 15° to 20° above horizontal.

Flight at zero airspeed (simulated hovering) appears to be a somewhat special case. Flies without prior exposure to moving air performed far more steadily in still air than did those on whom performance measurements had previously been made with the tunnel in operation. In the latter cases, turning off the wind tunnel usually caused immediate loss of flight posture and conspicuous grasping movements by the legs. In all flights in still air, even when flight was steady, the tarsi of the pro- and mesothoracic legs hung down instead of being firmly pressed against the body.

2. *The effects on output of experimental adjustments of body angle*

Output force is composed of two components, one parallel to the horizontal tunnel axis (thrust), the other normal to it (lift). In still air the two are directly comparable, reflecting the rates of creation of air momentum in the backward and downward directions. The resultant, the total force, acts along the same line as the net momentum flux or the propeller wake. In moving air, lift and thrust are no longer comparable since the latter now reflects an increase in momentum flux of an already moving airstream. Consequently, the direction of the output force no longer coincides with the direction of the propeller wake. In short, the ratio of lift to thrust depends, in part, on flying speed, even in the absence of variation of the stroke parameters.

Despite this complication it is clear from the performance measurements that the direction of the output force is primarily established by the body angle. The variations observed in lift and flying speed when the body angle was changed appear explicable in terms of a simple actuator disk with a variable inclination with respect to the wind direction. None of the stroke parameters showed regular alterations with changes in body angle, nor do the results require us to invoke compensatory shifts in the principal unmeasured parameter, the angle of attack.

This simple scheme stands in sharp contrast to the system employed by locusts. In these animals, according to Weis-Fogh (1956*a, b*), 'body angle and lift are independent parameters' and it is 'impossible to influence the lift significantly by changing the body angle between 0° and 15° to 20°'. He describes a parameter, the 'aerodynamic pull', or dorsal force on the insect (Λ), which is nearly constant over a range of body angles from 0° to 110°. The constancy of the aerodynamic pull and the detailed analysis of this 'lift-control reaction' by Gettrup & Wilson (1964) point to receptors sensitive to lift. Weis-Fogh (1956*b*, 1964) has suggested that insects in general may have a receptor system sensitive to and regulating lift, citing Chadwick's (1953) conclusions on *Drosophila* as evidence. However, the aerodynamic pull in *Drosophila* (calculated from the present data for lift, thrust, and body angle) proves to be far from constant, and no other evidence of a 'lift-control reaction' has emerged.

The apparent absence of any 'lift-control reaction' in fruit-flies may be viewed in several contexts. First, a simplification of the flight mechanism is thereby undoubtedly effected. This could be crucial in a small species. Secondly, migratory locusts make long level flights so a reflex normalizing lift to a value near 100% could be quite useful; in the absence of prolonged level flights, *Drosophila* might find little use for such a reflex adjustment. Thirdly, the locust is an elongate object operating at a Reynolds number of several thousand, while the fly is relatively stubby and functions at Reynolds numbers an order of magnitude lower. These factors make the parasite drag of the fruit-fly much less dependent on body angle than is the case in locusts. Indeed, increasing the body angle of a locust from 0° to 15° nearly doubles its drag (Weis-Fogh, 1956*a*), while the same change of orientation in a fruit-fly produces a drag increase of only about 11% (Fig. 5, 200 cm./sec.). Consequently, adjustment of body angle is energetically a less costly means of controlling the direction of output for fruit-flies than would be the case for locusts.

SUMMARY

1. Apparatus has been devised to record the principal parameters of the flight performance of tethered fruit-flies in a wind tunnel.
2. Typically these flies achieve level flight (lift = weight) at 200 cm./sec. and a body angle of $+10^\circ$. Lift varies directly with body angle except at very high angles; the stroke parameters are invariant with body angle.
3. Evidence is presented suggesting that these measurements are applicable to free flight.
4. The adaptive significance of the absence of a 'lift-control' reaction' in fruit-flies is discussed.

This study is part of a thesis submitted to Harvard University for the degree of Ph.D. I gratefully acknowledge the advice and encouragement of Prof. Carroll M. Williams and Prof. Torkel Weis-Fogh. I am also grateful to Prof. W. S. Stone for the culture of *Drosophila*, to Mr R. D. Chapman for assistance with the instrumentation, and to the Society of Fellows for support, both moral and financial.

REFERENCES

- CHADWICK, L. E. (1951). Stroke amplitude as a function of air density in the flight of *Drosophila*. *Biol. Bull., Woods Hole*, **100**, 15-27.
- CHADWICK, L. E. (1953). In *Insect Physiology*. Ed. K. D. Roeder. New York: John Wiley and Sons, Inc.; London: Chapman and Hall, Ltd.
- GETTRUP, E. & WILSON, D. M. (1964). The lift-control reaction of flying locusts. *J. Exp. Biol.* **41**, 183-90.
- HOCKING, B. (1953). The intrinsic range and speed of insect flight. *Trans. R. Ent. Soc. Lond.* **104**, 223-345.
- HOLLICK, F. S. J. (1940). The flight of the dipterous fly *Muscina stabulans* Fallen. *Phil. Trans. B*, **230**, 357-90.
- JENSEN, M. (1956). Biology and physics of locust flight. III. The aerodynamics of locust flight. *Phil. Trans. B*, **239**, 511-52.
- PRINGLE, J. W. S. (1957). *Insect Flight*. Cambridge: Cambridge University Press.
- PRINGLE, J. W. S. (1965). Locomotion Flight. In *The Physiology of Insecta*. Ed. M. Rockstein. New York: Academic Press.
- VOGEL, S. & CHAPMAN, R. D. (1966). Force measurements using d'Arsonval galvanometers. *Rev. Sci. Instrum.* (in the Press).
- WEIS-FOGH, T. (1956a). Biology and physics of locust flight. II. Flight performance of the desert locust (*Schistocerca gregaria*). *Phil. Trans. B*, **239**, 459-510.
- WEIS-FOGH, T. (1956b). Biology and physics of locust flight. IV. Notes on sensory mechanisms in locust flight. *Phil. Trans. B*, **239**, 553-84.
- WEIS-FOGH, T. (1964). Biology and physics of locust flight. VIII. Lift and metabolic rate of flying locusts. *J. Exp. Biol.* **41**, 257-71.
- WEIS-FOGH, T. & JENSEN, M. (1956). Biology and physics of locust flight. I. Basic principles in insect flight. A critical review. *Phil. Trans. B*, **239**, 415-58.

APPENDIX

Low-speed wind tunnel

Several tunnels were constructed and used; only the final design (Fig. 6), which proved superior in most respects, will be described. This rectangular tunnel was constructed of 3 and 4 in. cylindrical stove pipe and was open only at the working section. Joints were sealed with plastic electrical tape, and the complete assembly was mounted

on wooden supports 5 in. above a plywood base. Despite the open working section, the airstream of the tunnel was functionally separate from the air outside. Thus minor air currents due to the motions and breathing of the investigator did not disturb the flow around the specimen.

Immediately behind the working section, a collector, *c*, directed the air into the main tube. Just beyond the second corner, two twelve-bladed titanium axial fans, *f*, were mounted on a common shaft. Between the fans, supporting and centring their bearings, three longitudinally oriented brass stator blades, *s*, extended radially to the tunnel walls. This stator section acted to decrease the interaction of the fans and increased the velocity of flow for a given shaft rotation rate. Rates of up to 10,000 rev./min. were commonly used. The fans were connected to the motor by pulleys and a rubber belt, *b*, mounted on the fan shaft just outside the second corner. The arrangement of pulleys permitted a step up in rotation rate as well as a choice of motor-to-fan speed ratios. A 1/40 h.p. d.c. motor in conjunction with a thyatron speed control provided adequate power and regulation.

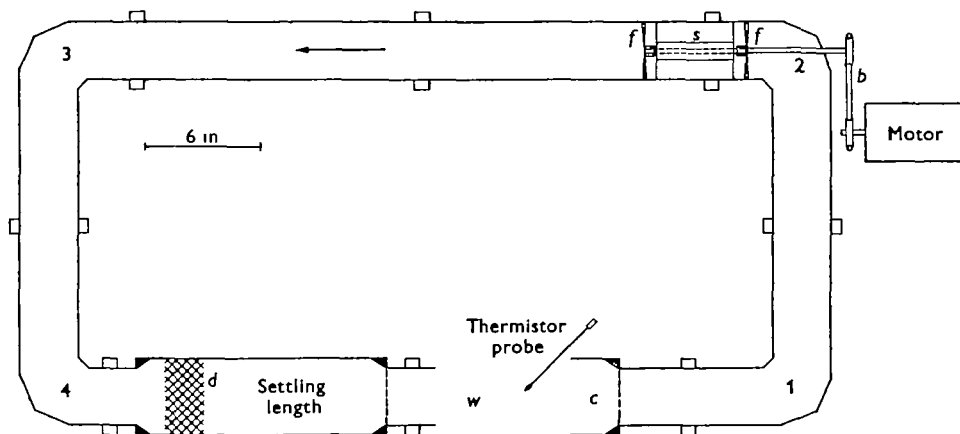


Fig. 6. Plan of the low-speed wind tunnel. *w*, working section; *c*, collector, *b*, belt and pulleys; *f*, fans; *s*, stator section; *d*, diffuser. Corners are numbered; arrow indicates direction of airflow.

Between the fourth corner and the working section, *w*, a section of 4 in. pipe provided a 'setting length' and 'contraction'. The abrupt changes in the diameter of the adaptor pipes were eliminated by packing the corners with 'Plasticene'. A pad of 'rubberized hair' near the upstream end of the settling length served as a 'diffuser', *d*; the location, surprisingly, was important in assuring smooth flow in the working section. While some contraction is necessary as the air enters the working section, in this small tunnel the specific contraction ratio exerted only a minor influence on the velocity distribution across the working section. The 16:9 ratio provided by the adaptor pipes themselves was used except in situations where a higher ratio was needed to produce a particularly sharp gradient at the edge of the airstream.

Flow in the working section of the wind tunnel was free of temporal or spacial irregularities when traversed with the thermistor anemometer. Moreover, a puff of

smoke remained visually discrete for about three circuits of the tunnel. Speed changes imposed by sudden shifts of the motor control were essentially complete within three seconds. Though the long-term speed stability was measured only with the micro-anemometer, the combination of tunnel and anemometer showed no appreciable drift.

Curiously enough, a 'honey comb' of drinking straws inserted downwind from the final contraction led to irregularities in the cross-sectional distribution of velocity: therefore no 'straightener' at all was used. The absence of swirl was demonstrated in the following manner. A flat plate was mounted on a force transducer (Vogel & Chapman, 1966) near the edge of the working section. The relationship between lift and angle of attack was surveyed, the latter being measured with respect to the axis of the tunnel. The resulting graph of lift versus angle of attack passed within two degrees of the origin.