

FLIGHT IN *DROSOPHILA*

II. VARIATIONS IN STROKE PARAMETERS AND WING CONTOUR

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INTRODUCTION

In the preceding paper (Vogel, 1966), the capabilities of fruit-flies as flying machines were determined in so far as tethered animals could be induced to demonstrate them. The angle between the long axis of the body and the oncoming wind (body angle) appeared to be the major variable establishing the direction of the resultant of lift and thrust under conditions where variations in most stroke parameters were excluded. Yet the parameters considered were not all invariable; indeed, enforcing a constant wing stroke was possible only by setting aside the large number of performances in which these stroke parameters varied. Moreover, one potentially crucial factor, the angles of attack of the wings, was not measured.

In the study reported here, the body angle was fixed and variations in other parameters were recorded as the flies, so to speak, manipulated their own controls. Thus information was obtained showing, within the constraints of the experimental situation, which stroke parameters were fixed, which variable, and the interrelationships among the latter. In addition, details of the configuration of the wings during the stroke were recorded to assess the magnitude and importance of variations in angle of attack and in the topography of the wing surfaces.

MATERIAL

Drosophila virilis, reared and tethered as previously described (Vogel, 1966), were used throughout.

METHODS

1. *Performance and measurements of stroke parameters*

Body angle, speed, lift, thrust, and the stroke parameters stroke angle, stroke-plane angle, frequency, and the extreme wing positions were defined and determined as previously described (Vogel, 1966; Vogel & Chapman, 1966). Body angle was fixed at a single value for all measurements on each individual fly, and performances were selected in which lift and air speed varied erratically. Thus the flight performances were not 'successful' by the criteria formerly applied. As many sets of observations as possible were made of each performance before the animal became completely un-dependable. The use of manual null-balancing techniques for gauging lift and air speed and the slight delay between these adjustments and photographic recording of the wing-stroke imposed serious limitations on accuracy in these erratic performances.

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2. *Wing pitch and surface contour*

Flies were mounted in the working section of the wind tunnel at body angles of about 10° . The camera, equipped as for the performance measurements, was positioned in front of and about 40° above each specimen; it was focused approximately parallel to the plane of vibration of the wings. Exposures were taken by opening the shutter, triggering a single flash of about $1\ \mu\text{sec.}$ in duration from a General Radio Co. 'Strobotac', and then closing the shutter. Consequently, these exposures photographed the wings at random points during the stroke. Because the downstroke occupies more time than the upstroke, about two-thirds of the exposures occurred during downstroke, making this phase more satisfactory for analysis.

Since most flies performed poorly in still air after fixed flight in moving air, photographs were first taken in still air and then with the tunnel in operation. In animals where the stroke angle appeared to be maximal in still air eighteen exposures were made in as rapid succession as possible (about one per 5 sec.). The tunnel was then adjusted to an air speed of 200 cm./sec.—approximately the preferred flying speed—and another eighteen photographs were taken.

These photographs permitted direct observation of the presence or absence of wing twisting and camber. Wing pitch was measured in the following manner. On each photograph the apparent width of the wing was measured at the point of maximum width, conveniently marked by the distal cross-vein. The sine of the inclination of this part of the wing to the camera axis is then given by the apparent width (corrected to scale) divided by the actual width. The camera axis thus set an arbitrary zero above which wing pitch was expressed. The position of the wing was determined as the angle between the long axis of the wing and the long axis of the body as these projected onto the photographs, with the top of the stroke scored as 0° . From these data wing pitch was plotted as a function of the position of the wing with respect to the body during upstroke and downstroke and for air speeds of 0 and 200 cm./sec.

To observe changes in wing configuration at specific points of the stroke cycle the arrangement just described was modified to enable the flies themselves to trigger the flash. Connecting a fly by its tether to the needle of a gramophone cartridge gave an electrical signal whose fundamental frequency was identical to the wingbeat frequency (Roeder, 1951). With appropriate circuitry (including a time delay) this signal could trigger either single flashes of the 'Strobotac' for photography of single points in the stroke or repetitive flashes at the wing-beat frequency for visual observations. This system was usable to air speeds of about 150 cm./sec.; at higher speeds wind on the fly and tethering wire generated spurious signals, and the synchronization of stroboscope and wing-beat was undependable.

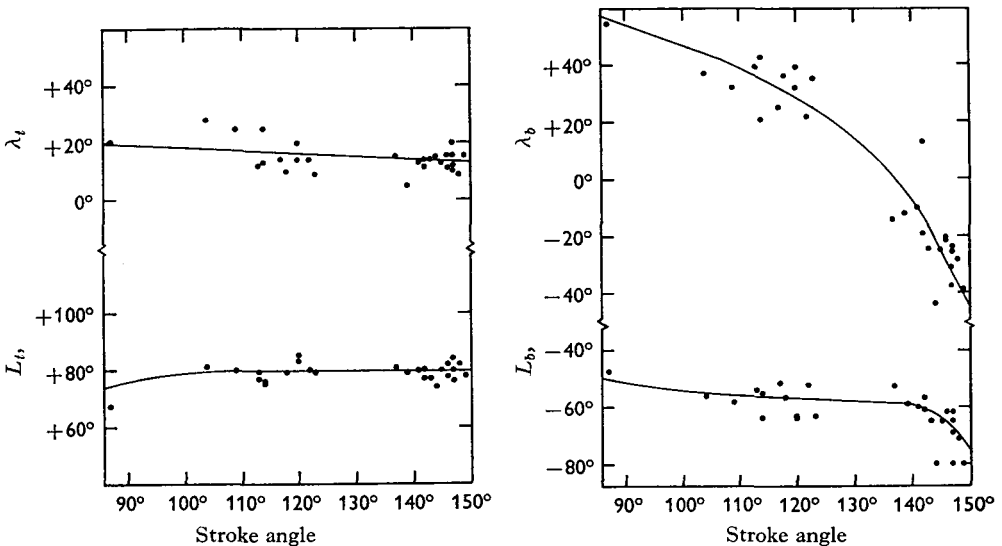
RESULTS

1. *Variations of the stroke parameters in erratic performances*

Five *Drosophila* showed enough variability of output to permit correlation of the magnitude and direction of total force with stroke parameters other than angle of attack. For each of these performances an average of 23 sets of observations were made. Despite considerable scatter in the measurements all flies were qualitatively similar in

performance, and the overall picture is consistent with the results previously obtained from steady fliers (Vogel, 1966).

Text-fig. 1 shows the variation in the coordinates of the upper and lower extreme wing positions with stroke angle for a typical performance. The lower position varies far more than the upper; moreover, this shift in lower position comes principally from displacement of the latitudinal (horizontal) component. The immediate result is that a



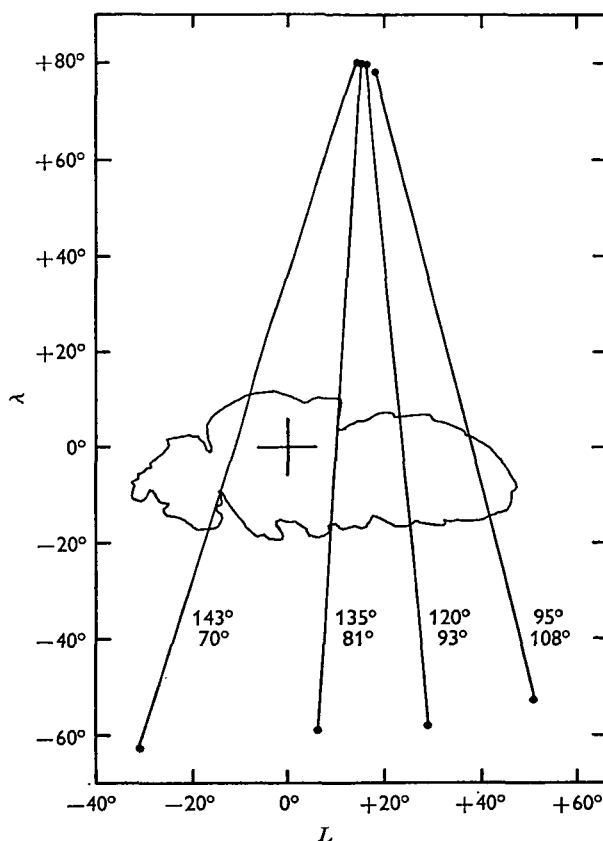
Text-fig. 1. 'Spontaneous' variation in the co-ordinates of the extreme wing positions and in stroke angle. L_t , latitudinal (horizontal); and λ_t , longitudinal (vertical) co-ordinates of upper position. L_b and λ_b , corresponding co-ordinates of lower position. Curves fitted by eye.

change in stroke angle is concomitant with a shift in the plane of the stroke, as illustrated in Text-fig. 2. Reduction in the stroke angle from its maximum value shifts the stroke plane to a more nearly vertical position and, as one would anticipate in the absence of other important factors, reduces lift more than thrust. This severe dependence of lift on stroke angle, particularly at near-maximal stroke angles (Text-fig. 3) explains the greater variability of lift than flying speed in the unaveraged performance data. The stroke plane was never observed to vary independently of the stroke angle; in these fruit-flies the stroke angle, stroke plane, and extreme positions of the wings appear functionally locked together. Changes in this set of mutually dependent parameters affect both the magnitude and direction of the force output.

In no case did wing-beat frequency vary by more than $\pm 10\%$ of the average value despite drastic changes of body angle, flying speed and stroke angle. The only noticeable trends were (1) a tendency for frequency to decline with time during an experiment, and (2) a drop in frequency at very low flying speeds. Only one fly exhibited frequency changes at a single body angle without large alterations of other stroke parameters. Fourteen sets of observations on this animal, held at a body angle of 19° , indicated that lift and thrust were roughly proportional to the square of frequency.

Occasionally differences were noted in the stroke angles of the two wings. Such side-to-side variance could be deliberately evoked by shining a light on one side of the

fly, whereupon the positively phototactic animal increased the stroke angle (and decreased the stroke-plane angle) on the side opposite the light. In an unrestrained specimen the increase in contralateral thrust would have turned the insect toward the light. The accompanying, larger increase in lift would then 'automatically' provide a banked turn.



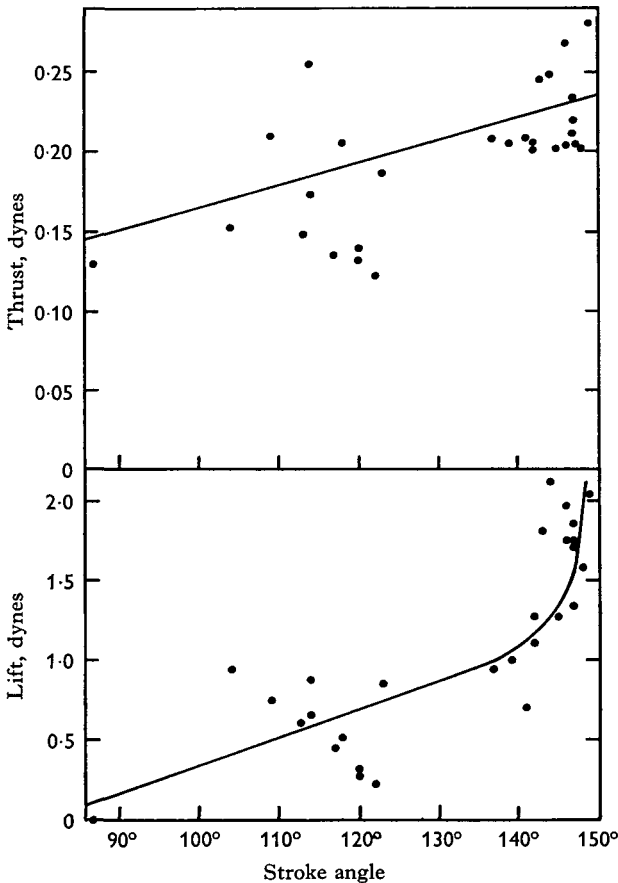
Text-fig. 2. Mercator projection of the co-ordinates of the extreme wing positions for four different stroke angles. Corresponding upper and lower positions are joined by straight lines; next to each are the values of the stroke angles and stroke-plane angles. Data from fitted curves of Text-fig. 1.

2. Wing surface contour

From the stroke photographs of Pl. 1, several points may be noted. The fly wing does not twist along its length to any appreciable extent: changes in wing pitch during the stroke are based on lengthwise rotation of the wing as a whole rather than on twisting. For either a reciprocating insect wing or a rotating propeller on a moving aircraft, the local wind direction varies along the length of the blade. Thus a constant angle of attack can be maintained only by a lengthwise twist of the wing or propeller. Consequently, except at the extreme positions of the stroke and at zero air speed, the angle of attack of the fly wing must vary along its length.

During most of the stroke the wing is held flat, with a cambered profile appearing only in the lower two-thirds of the downstroke. Lengthwise bending (as opposed to

twisting) is observed near the wing base. Both the camber and lengthwise bending are in the opposite direction from that expected for passive deformations caused by the relative wind. Altering the air speed (Pl. 2) causes no change in the surface contour of the wing; however, a slight posterior shift of the stroke plane was regularly observed as the air speed was increased.

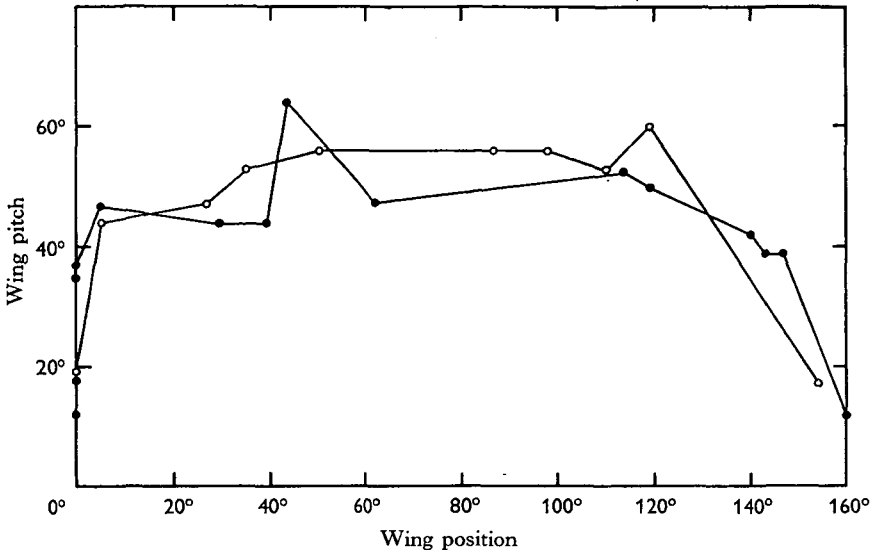


Text-fig. 3. The variation of thrust and lift with changes in stroke angle for the same fly considered in Text-figs. 1 and 2, held at a body angle of 12°.

3. Wing pitch and flying speed

At the distal cross-vein and mid-downstroke the wings move, relative to the body, at about 200 cm./sec. If the animal is stationary, the characteristics of its wing-beat establish both magnitude and direction of the wind on the wings. Addition of a 200 cm./sec. forward velocity alters both magnitude and direction of this relative wind; if the angle of attack is to be maintained at a fixed value for a particular point on the wing and a particular position during the stroke, wing pitch must vary with flying speed. Text-fig. 4 is a typical plot of wing position versus pitch, showing that the pitch of the wings is not significantly different at the two air speeds representing the extremes of normal flight. Similarly, in Pl. 2, pitch appears constant as air speed is

varied. Thus the angle of attack must vary inversely with flying speed and advance ratio; the fruit-fly does not employ a variable-pitch propeller in any conventional sense.



Text-fig. 4. Wing pitch versus angular wing position for downstroke of a tethered fly in (○) still air, and (●) a 200 cm/sec wind. Data from photographs similar to those of Pl. 1.

DISCUSSION

1. *Wing-beat frequency*

The frequency of wing-beat is the most widely investigated feature of insect flight, and the genus *Drosophila* has been accorded particular attention in studies concerned primarily with frequency (Chadwick, 1953). However, wing-beat frequency did not prove to be of especial interest in the present study. In successful performances frequency varies only slightly. Such variations as occur seem random and independent of shifts in other stroke parameters. Lift and thrust appear proportional to the second power of frequency, just as thrust is proportional to the square of revolution rate in aircraft propellers. Most likely the slight variation of frequency and its consequent elimination as an important parameter of control reflect a limitation imposed by the free-running nature of the asynchronous flight musculature (Roeder, 1951).

The relationship between frequency and such parameters as air density may be explained by considering the wings as mechanical oscillators, their effective mass including a fraction of 'boundary layer mass' (Vogel, 1962). This same argument predicts that frequency should rise with increases in either stroke angle or flying speed, since either increase should reduce the moment of inertia of the boundary layer. But the magnitude of the expected changes is too small to have an appreciable effect on force output or to be significant above the random frequency variations present in all the performance measurements.

2. Stroke angle and stroke plane

Of the four co-ordinates which describe the extreme upper and lower positions of the wing only the latitudinal co-ordinate of the lower position varies greatly with changes in stroke angle. This is consistent with the observations of Hollick (1940) on *Muscina* as well as those of Chadwick (1951) on *Drosophila*. Thus the immediate consequence—the functional interdependence of stroke angle and stroke plane—may be widespread in functionally two-winged insects. Conversely, the wing stroke in *Drosophila* shows little variation with changes in body angle or flying speed, by contrast with other diptera (*Muscina*, Hollick, 1940; *Phormia*, Nachtigall, 1966).

The interaction of stroke angle and stroke plane, even if widespread, is clearly not a general feature of the flight of insects. Weis-Fogh (1956) found in locusts only a slight variation of stroke angle in performances encompassing a wide range of average lift as well as changes in the stroke plane which were not simple mechanical consequences of changes in other stroke parameters. Such adjustment of the plane of vibration of the wings with respect to the body appears to be an important control mechanism in bees (Stellwaag, 1916), in wasps (Chadwick and Edgerton, cited by Chadwick, 1953), and in locusts (Gettrup & Wilson, 1964).

3. Angle of attack

Fruit-flies exhibit a remarkable indifference to the precise adjustment of angle of attack in the face of changes in other flight parameters. For any given position during the stroke, wing pitch remains fixed, presumably set by the characteristics of the wing articulation. Since pitch does not vary with flying speed, angle of attack must; since pitch does not vary along the length of the wing, again angle of attack must.

This situation contrasts sharply with that encountered in all previously studied animals, both insect and vertebrate, as well as with man-made aircraft. Larger flies, (Nachtigall, 1966) and locusts (Weis-Fogh, 1956) adjust wing pitch during each stroke by lengthwise twisting rather than rotation; similarly, aircraft propellers are shaped like strongly twisted wings. Both locusts (Gettrup & Wilson, 1964) and hummingbirds (Greenewalt, 1960) use pitch adjustments in the control of flight in a manner analogous to the use of variable-pitch propellers in aircraft, although the animals, with flexible wings, can change the lengthwise twist of the wings rather than being forced to rotate the wing as a whole.

The absence of active control of angle of attack undoubtedly effects significant simplifications in the flight machinery. The pitch changes during the course of each wing stroke may be due entirely to fixed structural characteristics of the articulation since their magnitude and phase are fixed. Furthermore, wing rotation need involve adjustments only at the articulation. By contrast, lengthwise twisting of the wings must be effected by forces applied at the articulation and transmitted by the veins over the entire surface. Although fruit-flies do make use of active alterations of the surface topography of the wings (such as camber during downstroke), they do so to a much less dramatic degree than do larger insects or birds. Perhaps the reduced venation seen in the wings of small insects partly reflects the absence of major adjustments in wing contour during flight.

4. *The control of flight*

The qualitative description of the use of the various stroke parameters for control appears straightforward. Wingbeat frequency varies but little. Wing pitch is fixed and thus angle of attack varies only through changes in the local wind direction. The surface topography of the wings does not change with flying speed, either actively or through passive deformations. The stroke-plane and extreme positions of the wings are locked to the stroke angle, while lengthwise wing twisting is negligible. Consequently the possible avenues of control are rather limited. Body angle seems to be the primary regulator of the direction of the output force and thus the ratio of lift to thrust (Vogel, 1966). Stroke angle is the main regulator of the magnitude of the output force; in addition, through its relationship with the stroke plane, the stroke angle influences the ratio between lift and thrust.

The suggestion that body angle is a major controlling parameter raises a crucial question—how does the fly adjust the body angle? Control of stroke angle, stroke plane, or wing rotation is easily envisaged, for one body part is merely moved with respect to another. But changing body angle requires an aerodynamic mechanism to produce a turning moment about the centre of gravity. Four-winged insects could conceivably generate the necessary pitching torque through control of the relative output of the two pairs of wings. The halteres of the Diptera are ruled out by Pringle's (1957) reminder that their mass is much too low for them to have any direct gyroscopic effect.

Body angle might be controlled through changes in the line of action of the resultant force which the wings exert on the body. Hollick (1940) noted that in moving air an increase in stroke angle is associated with a forward displacement of the line of action of lift and thrust. This probably occurs through the stroke angle–stroke plane inter-relationship described here. But, regardless of its detailed mechanism, moving the resultant anteriorly will elevate the head and increase body angle. One attraction of this scheme is that a fly, beating its wings at maximum stroke angle, would climb steeply. Indeed, this is what one commonly observes, either visually or in stroboscopic pictures of free flight of frightened flies. However, variation of stroke angle is unlikely to be the *sole* means of control of body angle. If this were so, stroke angle would determine *both* magnitude and direction of output. Another degree of freedom seems essential.

A second method for controlling body angle might entail use of the hind legs as 'elevators'. The extended position of the hind legs in flight posture has already been noted (Vogel, 1966; also see Pl. 2). Not only are they directed posteriorly, but, unlike the pro- and mesothoracic legs, they are not held tightly against the body. The hind tarsi may point in any direction from straight back to fully dorsad; velocity maps indicate that they are well exposed to the induced wind from the wings. Hence the metathoracic legs could be effective even during hovering through an arrangement suggestively similar to mounting a ship's rudder behind its propeller to improve low-speed control. Hollick (1940) mentions that, when the stroke angle differs on the two sides, the hind leg on the side of lower stroke angle extends further laterally. This clearly suggests an aerodynamic function for the hind legs. Moreover, many small insects are endowed with bristles, bulges, or pubescence on the hind legs with no such

accoutrements on the first two pair. But, as with the stroke angle, the use of the hind legs as elevators is not likely to be the sole mechanism for the control of body angle; after removal of these legs, fruit flies are able to take off and fly in seemingly normal fashion.

Chadwick's (1953) suggestion of a homeostatic control of aerodynamic power output in *Drosophila* finds little support in the present study. Chadwick's own evidence is mostly negative and involves rather small changes in flight parameters, at least some of which can be more easily explained in simple physical terms (Vogel, 1962). The present measurements show neither constancy of lift nor of power output, not do they present any compelling argument why flies should have constant 'efficiency' or a homeostatic system to distribute imposed stresses among the various flight parameters. Instead they suggest (by comparison with the extensive literature on locust flight) that the evolution of small insects such as *Drosophila* has involved a reduction in the number of parameters which vary at all, either actively or passively, as the flight pattern changes.

SUMMARY

1. In tethered flight in a wind tunnel fruit-flies adjust lift and thrust by shifting the horizontal component of the lower extreme wing position. The upper extreme wing position is nearly constant.
2. Stroke angle and stroke plane are fully interdependent parameters.
3. Angle of attack varies along the length of the wing; no length-wise twisting occurs.
4. Angle of attack varies with flying speed; pitch is unchanged as speed is increased.
5. These characteristics suggest that the flight machinery of fruit-flies is considerably simpler than that of larger flying animals.

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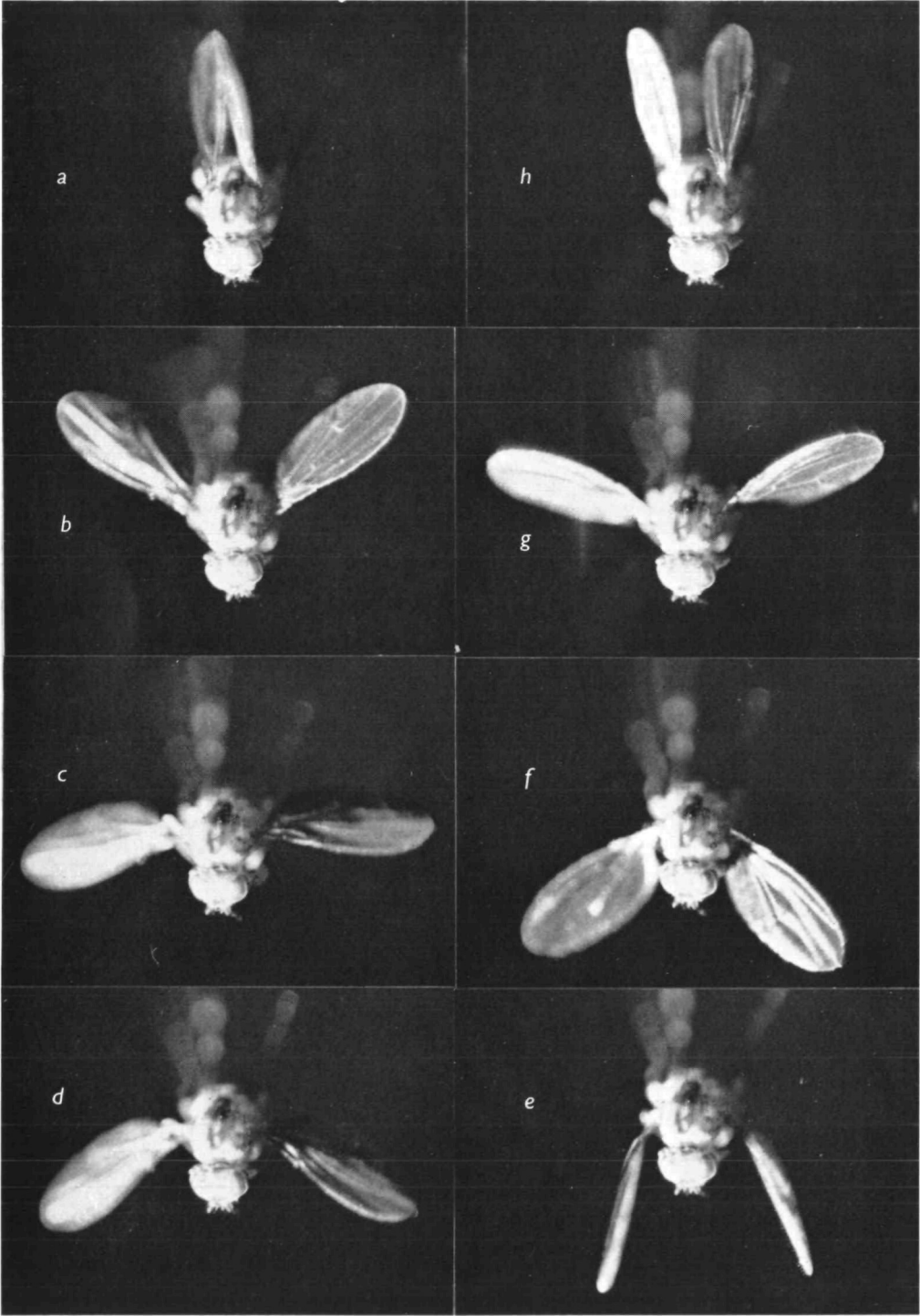
EXPLANATION OF PLATES

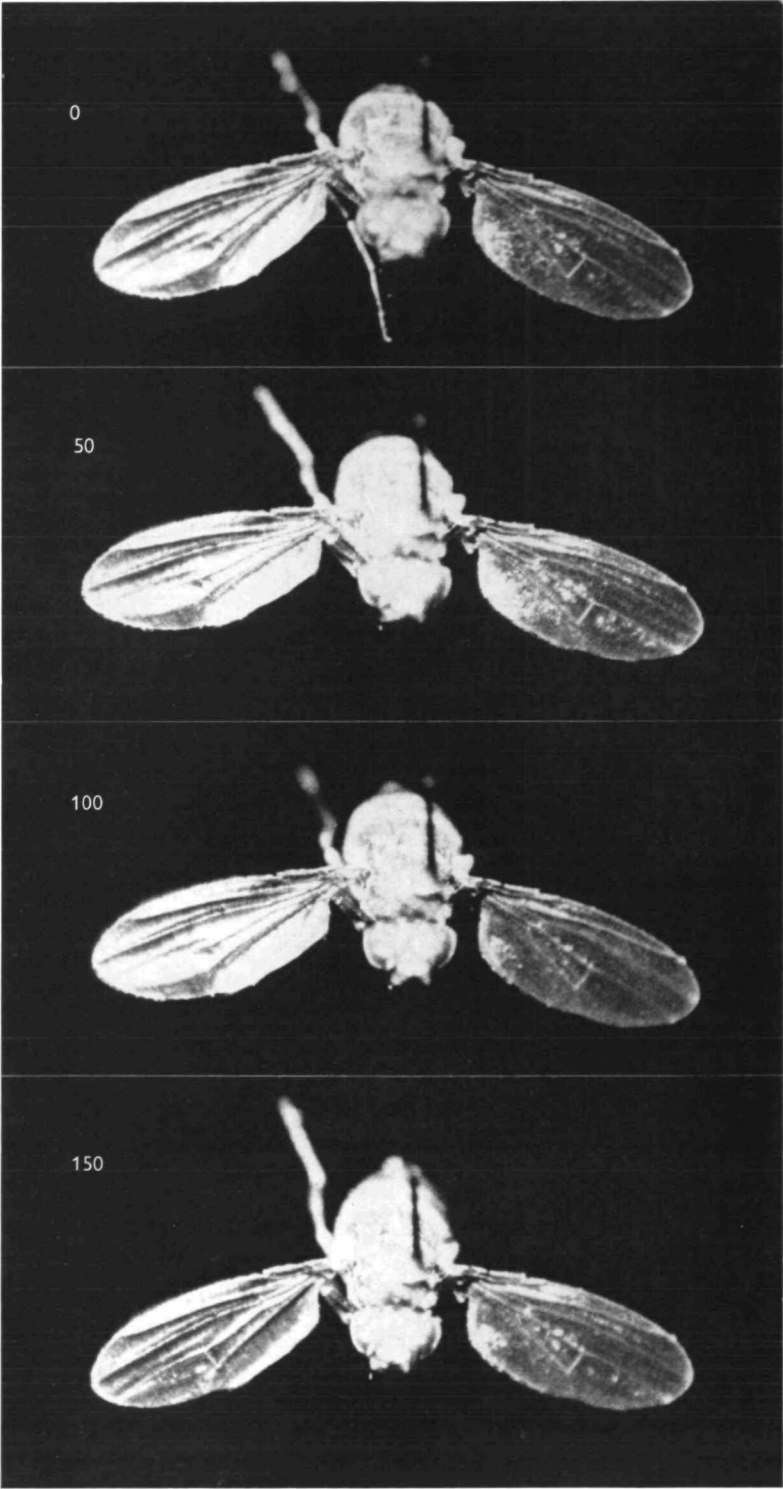
PLATE 1

The wing stroke of *Drosophila*. Time intervals between individual frames are not uniform since the series was assembled from random single exposures. Note the camber of the wings in *b*, *c*, and *d*, and the extended posture of the hind legs (blurs above and lateral to the thorax.)

PLATE 2

A single wing position (early in upstroke) photographed at four different airspeeds (in cm./sec.). Note the similarity in the projected outline of the wings and in the patterns of reflexion of the flash, the latter particularly dependent on wing pitch.





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