

A WIND-TUNNEL STUDY OF GLIDING FLIGHT IN THE PIGEON *COLUMBA LIVIA*

By C. J. PENNYCUICK

*Department of Zoology, University of Bristol**

(Received 16 April 1968)

INTRODUCTION

A free-flying pigeon is capable of a variety of steady and unsteady states of flight, such as climbing, descending, turning, gliding, flying horizontally, landing, taking off and so on. This paper is concerned with the mechanics of one type of steady flight, that is, straight gliding flight at constant speed. By 'gliding' is meant a state in which no propulsive power is supplied by the bird's muscles, and in this case the flight path has to be inclined downwards if a constant speed is to be maintained.

The forces developed on a bird in flight depend on its speed relative to the air through which it flies, that is, its 'airspeed'. A bird flying along through still air can have the same airspeed as one which is stationary (relative to the ground), but is suspended in a stream of air moving in the opposite direction. In wind-tunnel experiments the bird or test object is kept stationary while air is blown past it at some speed V , and this is mechanically equivalent to the bird flying through still air at the same speed in the opposite direction. For horizontal flight the air is blown horizontally, but to obtain gliding flight the stream of air has to be inclined upwards.

When testing inanimate objects it is usual to suspend the object in the wind tunnel on some form of support, and blow the air past it: the forces acting upon it are transmitted through the support and measured by balances outside the tunnel. This method cannot be used with a living bird since its geometry is highly variable, and it will not normally take up the same body shape, if restrained, that it would use in free flight. Corpses can, of course, be tested in the conventional way, but in this case some arbitrary body shape has to be selected, and it is difficult to obtain a shape which is used in some known condition of flight—in any case, any one shape will generally correspond to only one (at most) state of free flight.

An alternative approach is to train the bird to remain stationary in the airstream by its own efforts, without any mechanical restraint. In this case, if flight is straight and unaccelerated, the net aerodynamic force acting on the bird must be equal and opposite to its weight, regardless of whether the bird is effectively climbing, descending or flying horizontally. In flapping flight the 'net aerodynamic force' in this sense means the average force over a whole number of wingbeat cycles, but in gliding it is a steady force which can be analysed into various components.

Following the usual convention, the net aerodynamic force (R in Fig. 1) is resolved into a component perpendicular to the airflow, called the 'lift', and a component

* Present address: Department of Zoology, University College Nairobi, P.O. Box 30197, Nairobi, Kenya.

parallel to the airflow called the 'drag' (L and D respectively in Fig. 1). If the airflow is inclined upwards at an angle α to the horizontal, then evidently

$$L = W \cdot \cos \alpha,$$

$$D = W \cdot \sin \alpha,$$

where W is the bird's weight. Thus if W and α are measured, the lift and drag are easily calculated.

The method used here appears to have been first proposed by Raspet (1950), who would doubtless have developed it but for his untimely death in 1960. Greenewalt

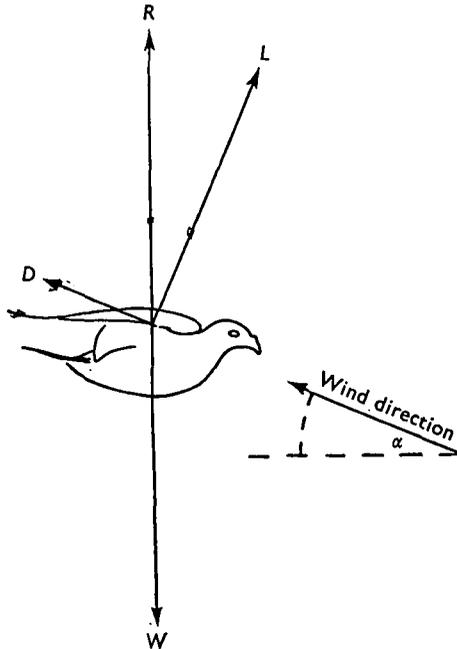


Fig. 1. In straight flight at a constant speed the bird's weight must be exactly balanced by the net aerodynamic force R acting on it. In gliding flight the bird must descend at some angle α below the horizontal—alternatively it can remain stationary in a stream of air inclined upwards at this angle to the horizontal. R is resolved into two components—the drag D , in line with the relative airflow, and the lift L at right angles to it.

(1961) used a horizontal blower to determine the maximum level-flight speeds of hummingbirds (*Trochilidae*), and recently Tucker (1968) has carried out respirometric and other measurements on budgerigars (*Melopsittacus undulatus*) flying in a wind tunnel.

MATERIAL

The pigeons (*Columbia livia*) used were tame birds kept for the purpose, and were allowed to fly free from time to time. Six birds were successfully trained to fly in the wind tunnel (see p. 513), but only one was sufficiently co-operative over a long period to yield good gliding measurements over the entire speed range. The data plotted in the graphs all refer to this one individual, although measurements in parts of the speed range, which in no way conflicted with those presented, were obtained from two other pigeons.

METHODS

The wind tunnel was an open-jet, open-circuit blower, this layout being selected because the whole tunnel had to be mounted on trunnions for tilting, and therefore needed to be short and compact. The main dimensions are shown in Fig. 2.

An octagonal jet 1 m. across was chosen, this being judged the smallest which would satisfactorily accommodate a large pigeon with its wings fully spread (70 cm.). The diameter of the upstream end was limited by the need to fit the tunnel into a stair well 4.3 m. across (the only available site), leaving sufficient room for circulation of

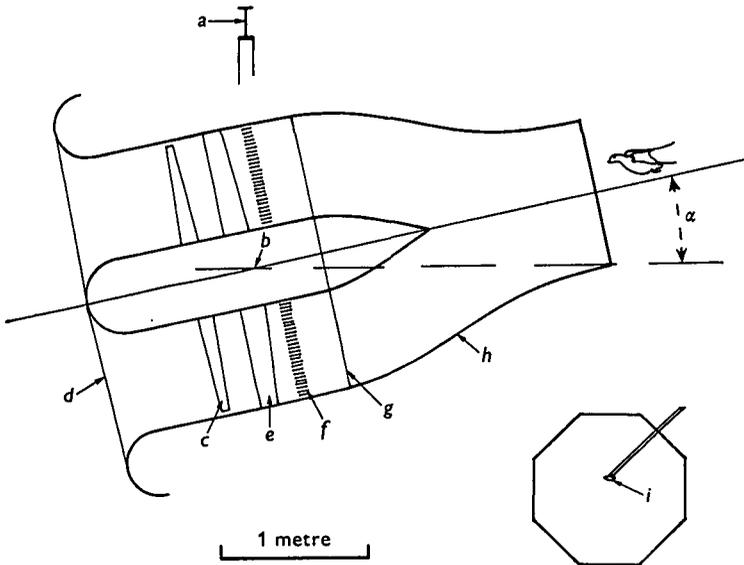


Fig. 2. The wind tunnel is suspended from a support beam *a* and pivoted about a horizontal axis passing through *b*. The fan *c* sucks air in through the intake filter *d* (composed of $\frac{1}{8}$ in. wire mesh). Swirl is removed by a ring of stator vanes *e*, and a 3 in. thickness of $\frac{1}{4}$ in. metal honeycomb *f*. The screen *g* is placed at the upstream end of the contraction *h*. The whole tunnel can be tilted to an angle α above the horizontal. The pigeon flies just outside the end of the contraction, which is octagonal in cross-section (bottom right): the pigeon retrieves food reward from a tea-spoon *i* soldered to the end of a length of $\frac{1}{2}$ in. brass tube passing diagonally across the working section.

air and pedestrians round the outside. A Woods ventilating fan of 1.9 m. diameter was chosen, followed by a ring of stator vanes, a honeycomb and a screen, the latter being placed at the upstream end of the contraction. The contraction ratio was 3.5:1.

The fan was driven by a Dowty 250 hydraulic motor, which was itself driven by a Von Roll HT 25 variable displacement hydraulic pump outside the tunnel, the primary power source being a Newman 60 h.p. 3-phase motor. The hydraulic circuit was designed by Keelavite Hydraulics Ltd., who also supplied the components.

The fan speed could be varied continuously between zero and 650 rev./min. by adjusting the displacement of the HT 25 hydraulic pump, this being done by an electric motor operated remotely from the working position. A second remote control allowed the whole tunnel to be tilted by a pair of hydraulic jacks between -2° and $+55^\circ$ above horizontal. The angle of tilt was read on a large scale beside the operator's

position. The main steel casing of the tunnel with the motor and fan mountings, together with the supporting structure and tilting gear, was built by W. H. Bird and Sons of Bristol, who also carried out the detail design. The contraction and inlet fairing were made of plywood, and added after the main structure was assembled.

The working section, where the pigeon flew, was just outside the end of the contraction. It was enclosed in an octagonal cage of 1 in. \times $\frac{1}{2}$ in. 'Weldmesh', lying 4 cm. outside the edges of the stream, and extending 50 cm. downstream from the end of the contraction. A screen of 1 $\frac{1}{2}$ in. chicken wire prevented the pigeon from escaping downstream: initially another wire screen was placed over the end of the contraction to stop the pigeon from going in, but this was found to be unnecessary, and was removed.

At all stages of design and construction of the wind tunnel, Pankhurst & Holder's (1965) invaluable textbook was found to be indispensable.

Measurement of wind speed

The wind speed was measured by a Pitot-static probe in the upper part of the working section, connected to a manometer calibrated directly in m./sec. Both instruments were made and supplied by Airflow Developments Ltd. The manometer was calibrated on the assumption that the air density was 1.22×10^{-3} g. cm.⁻³, the sea-level value in the I.C.A.O. standard atmosphere, and this value was used in all calculations involving air density. The wind tunnel site was actually 60 m. above mean sea level.

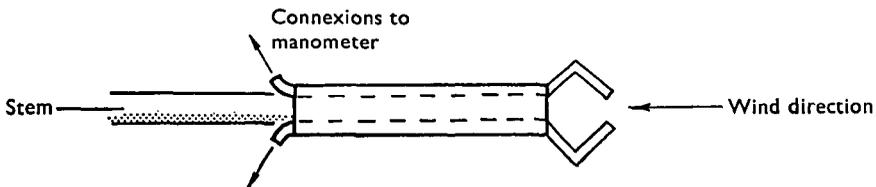


Fig. 3. Yawmeter used to locate horizontal setting of the wind tunnel.

Determination of horizontal

Since α , the angle at which the airstream is inclined to the horizontal, is one of the primary measurements, an essential preliminary was to determine the tunnel position in which the airflow was truly horizontal. This was done with a yawmeter mounted on a cylindrical stem (Fig. 3). The two claws of the yawmeter were connected to opposite sides of the manometer, and in general a pressure difference appeared between them when the wind was turned on. The yawmeter was now rotated through 180° about the axis of its stem, and if the pressure difference between the two tubes remained unchanged, it follows that the flow was then parallel to the stem.

To find the tunnel position for which $\alpha = 0$, the yawmeter stem was first levelled with a spirit level. The tunnel position was then adjusted until rotation of the yawmeter through 180° about the axis of its stem produced no effect on the pressure difference observed between the two claws. The air was then flowing horizontally. This measurement was carried out at two points slightly above the tunnel axis (at the level where the pigeons flew), and 20 cm. either side of the axis. The airflow directions agreed within 0.1° at these two points.

Photography

For each gliding measurement, photographs were required (*a*) from above the bird, at right angles to the airflow, and (*b*) from the side. Cameras for both purposes were mounted on a 'Dexion' framework which tilted with the tunnel.

The overhead camera was a Canon Dial 35 mm. half-frame camera, selected because its clockwork drive allows up to fifteen photographs to be taken by remote control, without rewinding. The lateral camera was a Nikon F. Both were fitted with small electronic flashguns, run off the mains, and in addition a pair of 375 W. photofloods was mounted above the working section, on the same boom as carried the overhead camera; these lamps were normally run in series when the flashguns were in use.

Training method

Pigeons were trained to fly in the tunnel by food reward, consisting of maple peas. These were dropped down a brass tube (streamlined by a sheet metal fairing), which passed diagonally downwards to a point slightly above the centre of the working section. The maple peas appeared in a teaspoon soldered to the end of this tube, whence they were retrieved by the pigeon.

The first stage of training was to tame the pigeon until it would come freely to the hand to be fed, and would submit to being handled. It was then placed on a perch, passing across the working section, from which it could reach the spoon. It was fed from the spoon, and this was repeated until it clearly associated the spoon with food; during this stage the wind speed was initially zero, and was increased in one or two stages to the range in which pigeons fly most easily (13–14 m./sec.).

The perch, which was held in the experimenter's hand, was now held somewhat further from the spoon, so that the pigeon had to crane forward to reach it. Soon the pigeon would take little hops from the perch to reach the spoon, and from this progressed to the point where it would feed with its weight supported on its wings, but with its feet or thighs touching the perch behind. Eventually, as the pigeon gained confidence in relying on its wings alone, the perch could be removed altogether.

Pigeons seemed to find feeding on the wing somewhat unnatural, and at first 'pedalled' vigorously with their feet whenever they took food from the spoon. They could be trained not to do this, however, especially if trained for a while at higher speeds, in the region of 18 m./sec.

Training up to the stage where the perch could be removed took between 1 and 2 weeks, with one or two training sessions per day, each of up to 20 min. The birds had some difficulty at first in controlling their position relative to the spoon, and tended to flap their wings and lower their feet unnecessarily. Measured gliding performance improved progressively over the first few weeks of training.

GLIDING BEHAVIOUR AND PERFORMANCE

Position control

A gliding pigeon which is remaining stationary opposite the spoon must continuously control three types of errors of position: it can drift to left or right, get too high or too low, or can either overtake the spoon or drift away from it downstream. Taking the

last type of error first, if the pigeon starts drifting downstream away from the spoon, it gives a flap or two with its wings, which increases its airspeed and enables it to catch up. If it is approaching the spoon and likely to collide with it, it must increase its drag in order to decelerate, and it does this by lowering its feet into the airstream. The same methods are used for correction of errors above or below the spoon. Extra drag causes steepening of the gliding angle (Fig. 1), and the feet are lowered to bring the pigeon down if it gets too high: if it gets low it flaps its wings to climb back into position. Lateral errors are the easiest to correct, this being done by banking slightly.

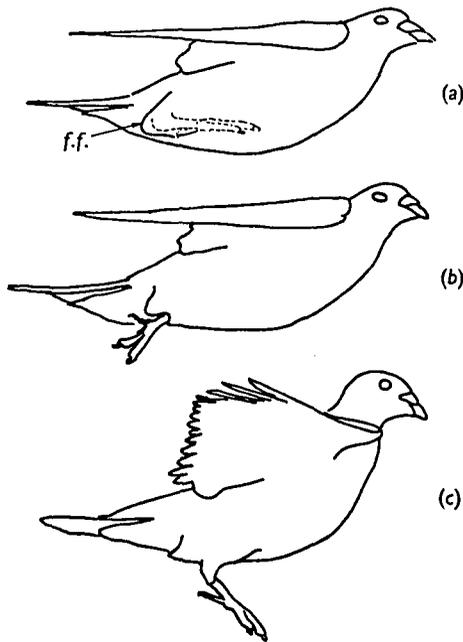


Fig. 4. (a) In free flight pigeons retract the feet in the position shown dotted: the feet are then completely concealed by the flap of flank feathers whose posterior margin is marked *f.f.* (b) When flying in the tunnel pigeons carry their feet trailing below the tail at medium and high speeds. (c) At very low speeds the feet are lowered far below the body and the toes are fully spread.

Longitudinal errors (tendency to catch up the spoon) appear to be the most difficult to control, and rather quick and precise movements of the feet are needed to keep the bird in position. Inexperienced pigeons tended to 'pedal' with their feet, flapping at the same time, but even practised ones carried the feet trailing below the tail when flying in the tunnel, never retracted forwards under the flank feathers in the normal free-flight position (Fig. 4). Attempts were made to fly two pigeons with their feet held in the fully retracted position, by means of rubber bands round the tarsal joints. The birds were, however, unable to maintain position without the use of their feet, and refused to fly after a few seconds.

In slow flight, below about 12 m./sec., the feet were extended far below the body, whereas at higher speeds the more confident and experienced pigeons held them furled below the tail (Fig. 4).

Method of finding best gliding angle

With the windspeed constant the tunnel was slowly tilted up and down, obliging the bird to adjust its lift and drag so as to maintain equilibrium (Fig. 1). If α were made zero (wind blowing horizontally), the pigeon had to resort to normal flapping flight, but as α was increased less and less flapping was required, until at some value of α the bird was just able to glide without flapping its wings. This angle is the *best gliding angle* for that particular speed, and varies at different speeds.

Although pigeons will glide steadily at speeds above about 14 m./sec., at lower speeds they usually flap their wings intermittently, and only glide for a few seconds at a time. This may be because α is below the best gliding angle, or it may be to overcome extra drag caused by inept foot movements, used in position control. Some judgement is needed in watching short glides to see if they are indeed unaccelerated—if α is too small, the pigeon starts drifting downstream as soon as it stops flapping its wings, and this is generally readily apparent.

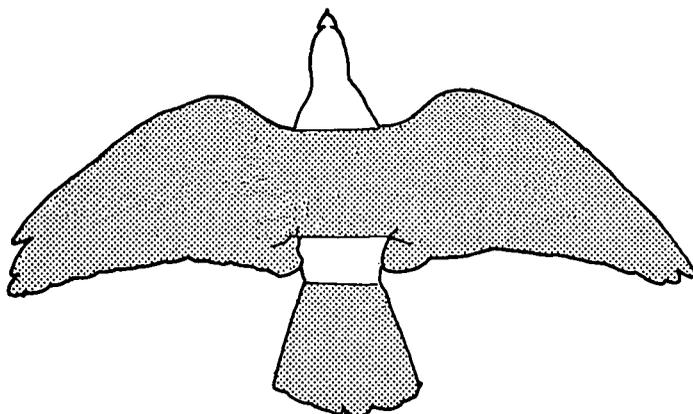


Fig. 5. The stippled areas show the convention used in determining wing and tail areas from overhead photographs.

Gliding measurements

Observations of gliding flight consisted of recording the following quantities when the bird was judged to be at its best gliding angle.

(1) *Weight* (W). Since the bird was necessarily fed during experiments, it was weighed before and after each experiment, and the weight corresponding to any particular observation was estimated by interpolation. Weight increments during an experiment ranged up to a maximum of about 20 g. wt., that is about 5% of the body weight.

(2) *Wind speed* (V). See p. 512.

(3) *Gliding angle* (α)—read off the tilting scale.

(4) *Wing area* (S_w). This is defined as the projected area shown stippled in Fig. 5. It includes a piece of body between the two wings, in accordance with aeronautical engineering convention. Wing area was measured with a planimeter from a photograph taken by the overhead camera, when the bird was gliding steadily. The camera was nominally 1 m. from the bird, but as the bird's vertical position was liable to vary

somewhat, the scale had to be checked for each photograph. This was done by measuring the distance between the tip of the longest primary covert and the tip of the longest primary (Fig. 6): this measurement was easy to make on the photograph, was independent of flexure of the carpal joint, and was not subject to distortion since this part of the manus is always nearly parallel to the airstream in gliding flight.

(5) *Tail area (S_t)*. This was defined as shown in Fig. 5, and was measured in the same way as wing area. Since it seems that the tail contributes some lift at all times in the gliding pigeon, the sum of wing area and tail area was used when calculating lift coefficients and aspect ratios.

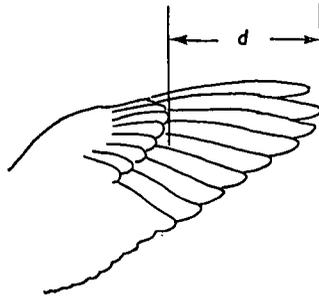


Fig. 6. The distance d between the tip of the longest primary covert and the tip of the longest primary was measured on overhead photographs in order to determine the scale.

(6) *Span (B)*. The greatest horizontal width, measured perpendicular to the airflow on an overhead photograph. This is normally measured from wing tip to wing tip, but at the highest speeds the manus is swept back so far that the greatest width comes half way along the first primary, not at the morphological wing tips.

(7) *Foot position*. This was assessed from a lateral photograph, and was used for estimating the drag contributed by the feet (p. 521). The lateral photograph was not simultaneous with the overhead one, but was taken during steady glide while speed and gliding angle remained unchanged.

Planform changes

Fig. 7 is a set of tracings of overhead photographs of a pigeon in steady gliding flight at various speeds. At the minimum speed, about 8.6 m./sec., the elbow and carpal joints are fully extended, and the flight feathers are spread to the maximum area. The leading edge of the wing, up to the carpal joint, is swept slightly forward. The tail is fully spread.

As speed is increased, there is first of all some flexing of the carpal joint, which results in increased overlapping of the primary flight feathers, with consequent reduction of wing area. At 13 m./sec. the trailing edge of the wing is approximately straight, and the leading edge of the manus is swept back about 30° . With further increase of speed, the manus is further swept back, and the elbow joint is also progressively flexed, bringing the carpal joint closer to the body. At speeds over 20 m./sec. the manus is swept back so far that its 'leading edge' is parallel to the airflow.

These changes of planform result in a range of wing span from 67 cm. at the lowest speeds, to 25 cm. at the highest speed investigated (22 m./sec.). Wing area varies

between 630 and 385 cm.², and aspect ratio between about 6.0 and 1.3 (Fig. 8). The reduction of wing span and area with increasing speed is accompanied by an increase of mean chord from about 10.2 cm. at low speeds to about 20.5 cm. at 22 m./sec. The Reynolds number, based on mean chord, ranges from 60,000 to 300,000.

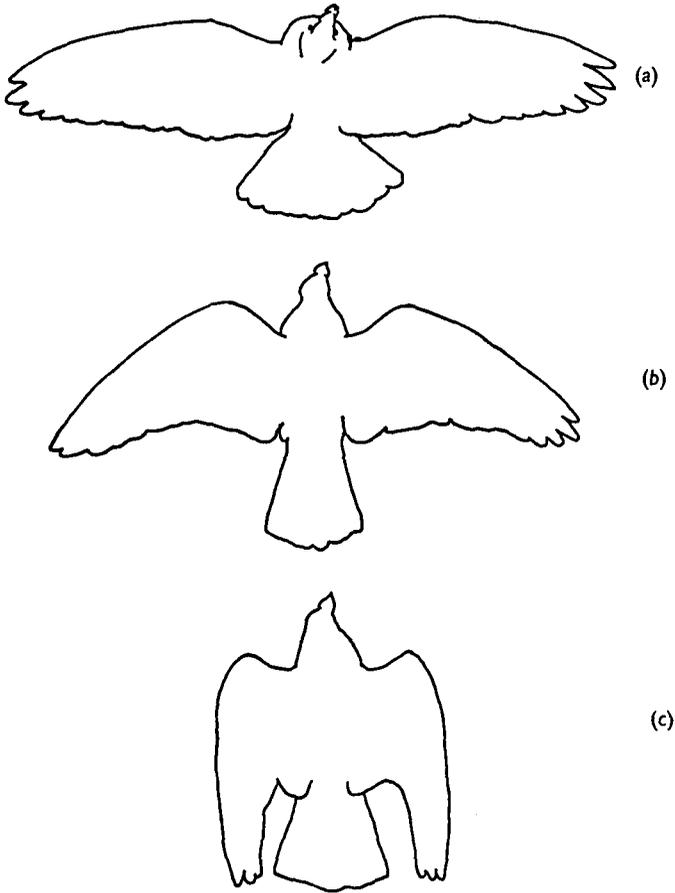


Fig. 7. Outlines traced from overhead photographs of a pigeon gliding steadily at various speeds: (a) 8.6 m./sec., span 65 cm.; (b) 12.4 m./sec., span 57 cm.; (c) 22.1 m./sec., span 25 cm.

Lift coefficient

The lift coefficient C_l is defined as the ratio

$$C_l = \frac{L}{\frac{1}{2}\rho V^2(S_w + S_t)} \tag{1}$$

It is based on the sum of wing and tail areas, since the tail always supplies an upward force during gliding and must be considered part of the lifting surface. A discussion of the function of the tail in longitudinal trim and stability is deferred to a later paper.

The maximum lift coefficient in gliding is about 1.3. Since wing area decreases with speed, the lift coefficient does not decline as rapidly as it otherwise would as speed is increased, and reaches about 0.25 at the highest speeds tested (Fig. 9). If a rubber band

was put round the tail to prevent its being spread, the maximum lift coefficient (still based on the sum of wing and tail areas) was reduced to 1.2. Thus the tail, besides providing some lift, appears to augment the maximum lift coefficient of the wing when fully spread.

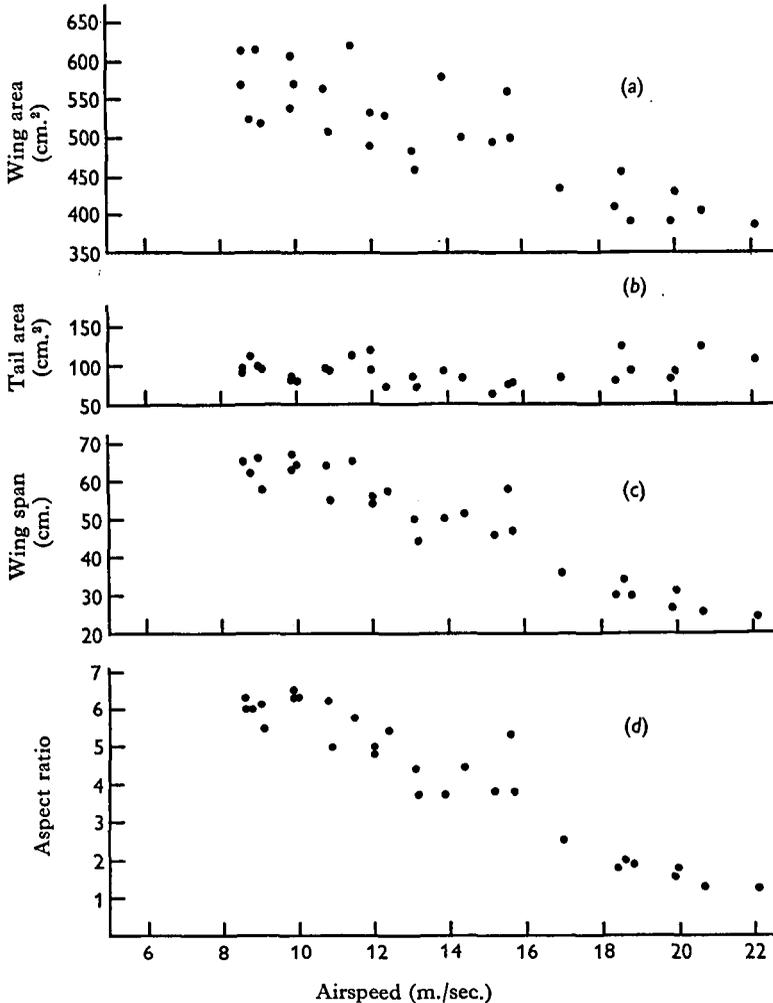


Fig. 8. Measurements of (a) wing area, (b) tail area, (c) wing span and (d) aspect ratio plotted against speed.

Pennycuick (1967), noting that pigeons can hover, calculated that a lift coefficient of at least 3.4 would be required to account for this—an unduly high estimate, since no account was taken of downward induced velocity. When this is rectified, the estimated lift coefficient in hovering is revised to 2.8, but this is still over twice the maximum observed in gliding. There is no inconsistency in this, however, since pigeons do not stall at the minimum gliding speed obtainable in the wind tunnel, but merely refuse to glide, and start flapping their wings. Apart from full spreading of the tail, there is no obvious deployment of high-lift devices at the minimum gliding speed; in one pigeon the alula was raised about 1 mm at this speed, while in the others it

remained flush with the leading edge of the wing. Photographs of the same pigeons in the downstroke of slow flapping flight show the alula prominently raised, and the primaries splayed, bent upwards, and twisted in the nose-down sense, so that there is no difficulty in believing that the lift coefficient is much higher in this condition than in minimum-speed gliding. High-speed film of free-flying pigeons in slow flapping flight shows that the tail is depressed somewhat during the downstroke and elevated during the upstroke, and this too could possibly augment the lift coefficient of the wing.

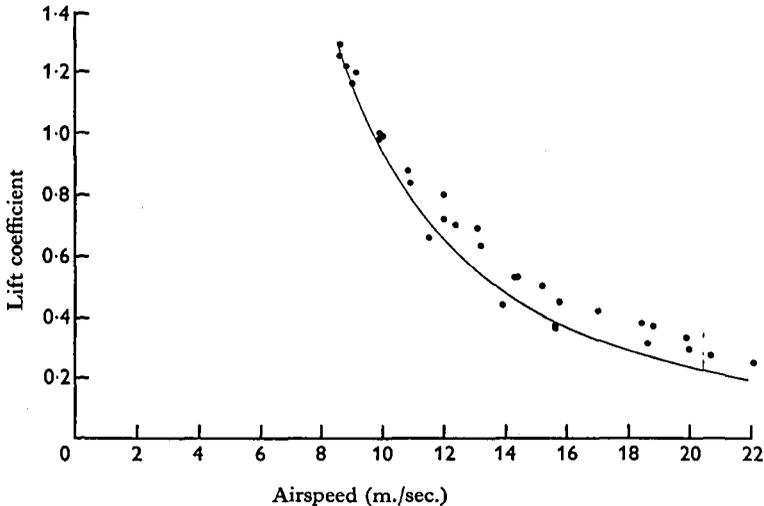


Fig. 9. Lift coefficient plotted against speed. The line shows the values which would be obtained if the wing area were kept at its full (low speed) value at all speeds. The highest value recorded (about 1.3) marks the speed below which pigeons refuse to glide and flap their wings, rather than a true stalling speed.

Variation of drag with speed

Fig. 10 shows the total measured drag minus the estimated drag of the feet (see p. 521), plotted against speed, and represents an estimate of the drag which the pigeon would experience in the normal free-flight configuration, with the feet tucked up under the flank feathers.

The drag drops from a high value at the lowest speeds to about 100 g. wt. at 10 m./sec., giving a lift: drag ratio of about 4 at this speed. This seems to represent the lower end of the pigeon's comfortable speed range in gliding. As speed is increased the drag continues to drop gradually, and reaches a minimum of about 70-75 g. wt. around 18 m./sec., after which it gradually increases again. The lift: drag ratio reaches a maximum of about 6 at speeds in the region of 18-19 m./sec.

The very wide speed range, over which the drag continues to decrease with increasing speed, is highly uncharacteristic of rigid-winged gliders. If the pigeon were to maintain its full wing span at high speeds the drag curve would certainly show a much steeper rise, beginning at a much lower speed, than it actually does, caused by the profile drag of the wing.

The reduction of span as speed is increased means that the pigeon generates *more* induced drag at high speeds than it would if it retained its full span. The long falling

portion of the drag curve between 12 and 18 m./sec. must therefore imply that shortening the wings at high speeds produces a reduction of wing profile drag, which more than offsets the increase in induced drag. This can be demonstrated by analysing the total drag into various components.

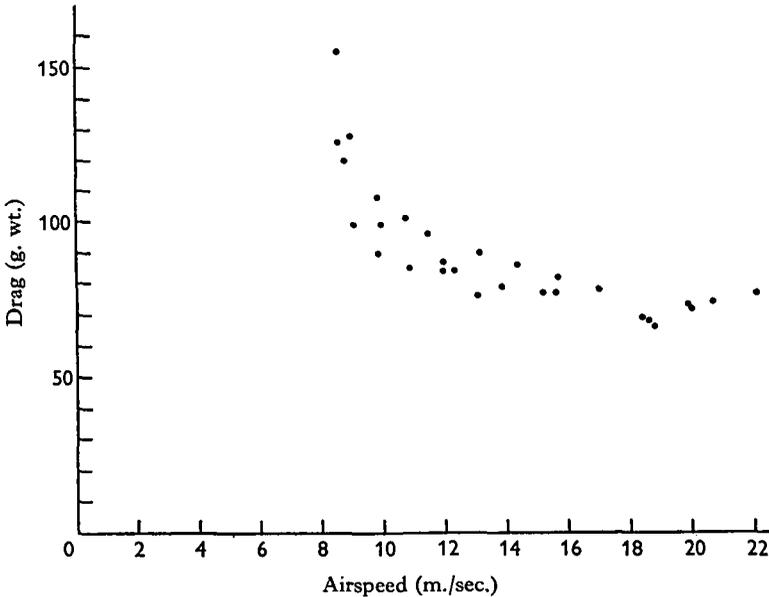


Fig. 10. Total gliding drag, after subtracting the estimated drag of the feet, plotted against speed.

Drag analysis

The total drag was measured directly (p. 510) and was assumed to be due to the following four additive components:

- (1) Body drag.
- (2) Foot drag.
- (3) Induced drag.
- (4) Wing profile drag.

The drag of the body and feet were estimated from the results of supplementary experiments, and the induced drag was calculated. Wing profile drag was assumed to account for the remainder of the total drag, and was estimated by subtracting the other three components from the total drag.

The estimation of the various drag components proceeded as follows.

Body drag

A feral pigeon was captured and killed by chloroforming, after which its wings were removed at the shoulder joint with as little disturbance as possible to the surrounding feathers. The wingless body was frozen in the attitude shown in Fig. 11, with the feet retracted forward under the flank feathers in the normal free-flight position. The body was mounted on the end of a flat brass strip 4 cm. long and 0.15 cm. thick, which continued as twin spikes inserted through the abdominal region. The whole was then

mounted on the end of a length of $\frac{1}{2}$ in. brass tube as shown in Fig. 12, and supported in the working section of the tunnel, which was set horizontal. The brass rod was pivoted, and the drag moment acting on it was measured by a horizontal spring balance, after preliminary experiments to determine the exact position of the pivot and the zero error of the balance. The measured drag moment was corrected by subtracting the drag moment of the pivoted bar, carrying a dummy mounting strip but no body. The corrected drag moment, divided by the distance from the pivot to the axis of the body, gave the drag of the body.

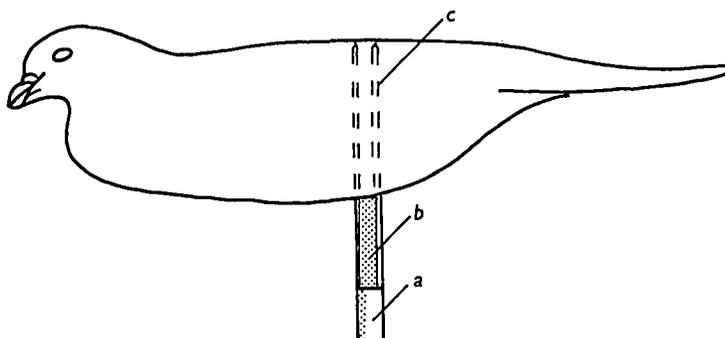


Fig. 11. To estimate the drag of the body, a frozen, wingless body was mounted on the end of a length of $\frac{1}{2}$ in. brass tube (a), via a short length of flat brass strip (b), with chamfered edges. The latter continued as two sharpened prongs (c) on which the body was impaled.

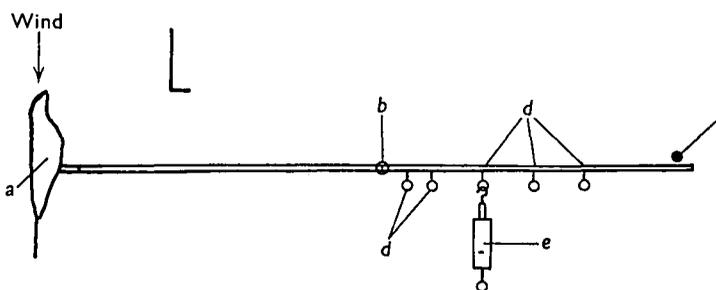


Fig. 12. Diagram of the balance used for measuring the drag of parts of dead pigeons. The specimen (a) was mounted as shown in Fig. 11 on one end of a length of $\frac{1}{2}$ in. brass tubing pivoted in a ballrace at b, and restrained by the stop c. Several attachment points d were provided at different distances from the pivot, and a spring balance e was attached to one of these to measure the drag moment.

Fig. 13 shows the measured drag at a series of speeds from 8 to 20 m./sec. The maximum frontal area of the body was 36 cm.², and the drag coefficient, based on this area, averaged 0.43. The drag coefficient showed no tendency to change progressively with speed, the extreme values being 0.42 at 12 m./sec. and 0.46 at 8 m./sec.

Foot drag

Unlike the body drag, the drag of the feet is under the control of the bird. The feet are used to adjust the gliding angle in rather the same way as the airbrakes of a glider, and are in constant use for fine control of position when a pigeon flies in the tunnel. (p. 514).

In free flight the ankle joints are normally flexed, so that the tarsi and feet come forward, and are completely covered by the flank feathers (Fig. 4). In this position the feet would presumably contribute little or no drag. When a small amount of additional drag is required, the tarsal joints are extended, and the feet are carried, with the toes furred, beneath the tail (Fig. 4). From this position, airbrake action is quickly obtained by lowering the feet and spreading the toes (Fig. 4).

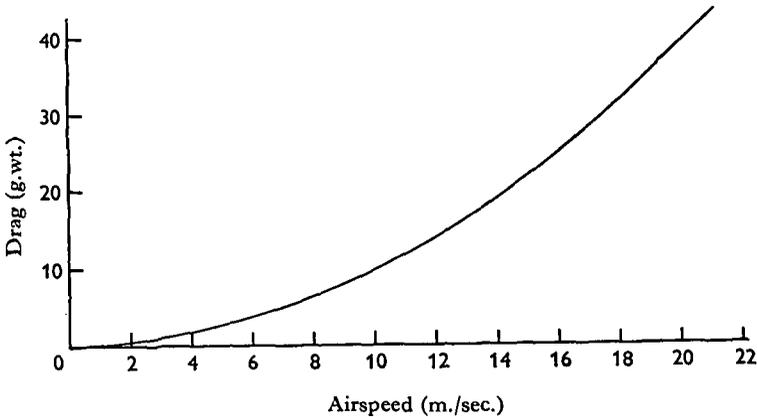


Fig. 13. Measured drag of a wingless body, plotted against speed.

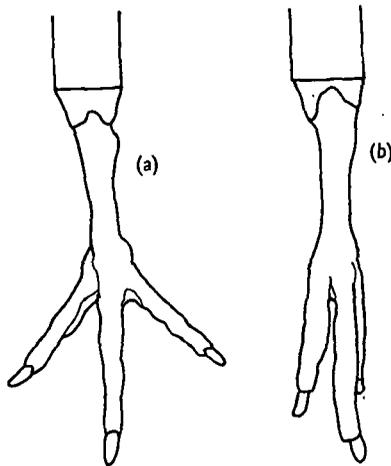


Fig. 14. Pigeons' feet fixed in formalin and mounted as shown in Fig. 12 for drag measurements, (a) with toes fully spread, and (b) with toes furred. Drag coefficients were calculated from frontal areas as seen in this view.

To estimate foot drag, the feet of a freshly killed pigeon were cut off just above the ankle joint and fixed in 10% formalin for a fortnight. During fixing, one foot was pinned in the fully spread position (Fig. 14a) and the other as shown in Fig. 14b. When sufficiently rigid, the feet were mounted in the end of the pivoted brass tube (Fig. 12), and their drag was measured by the same method as was used for body drag. The results are plotted in Fig. 15.

The fully spread foot makes a highly effective airbrake, having a drag coefficient based on frontal area of 1.10-1.25. At the pigeon's minimum gliding speed of about 8.6 m./sec., however, the maximum drag that can be obtained from both feet only amounts to about 6 g. wt., and at this speed pigeons usually keep both feet fully spread all the time. As speed is increased, the toes are first furled, then progressively raised posteriorly. At medium and high speeds, pigeons use only a part of their potential airbrake capacity to maintain position in the tunnel, generally amounting to between 6 and 14 g. wt.

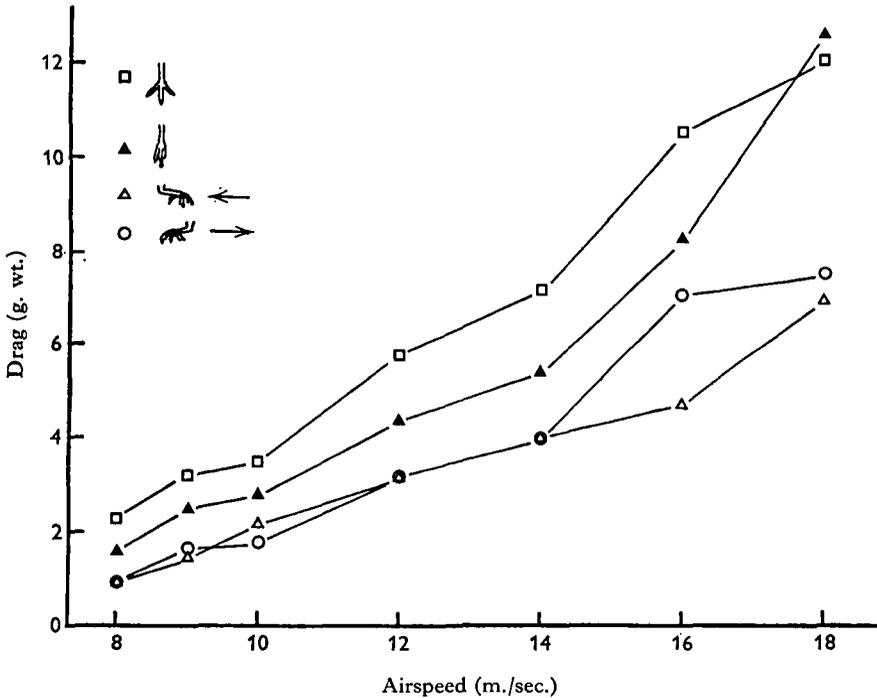


Fig. 15. Measured drag of pigeons' feet in various positions—key at top left.

Induced drag

The induced drag D_i was calculated on the assumption of elliptical spanwise lift distribution, from the formula

$$D_i = \frac{L^2}{\frac{1}{2}\rho V^2 \pi B^2} \tag{2}$$

where L is the lift, ρ the air density, V the speed and B the wing span. This would normally be considered a somewhat optimistic estimate of induced drag, but the shape of the pigeon's wing departs so far from those of conventional aeroplanes that caution is needed in drawing analogies. It may be noted, for instance, that in the high-speed configuration the wing-tip vortex will presumably circulate around the backward-pointing wing tip, a situation whose consequences are not readily deduced from conventional wing theory. In the absence of a comprehensive theory, it seems best to begin with the simple assumption of elliptical lift distribution, represented by equation (2).

It is unlikely that the true induced drag would be less than the calculated value, but it could be higher if the lift distribution were other than elliptical.

Fig. 16*a* shows the calculated induced drag plotted against speed. The line shows the curve which would be obtained if the wing span were kept constant at 65 cm. It can be seen that the pigeon will not glide at very low speeds, where the induced drag would increase sharply, but starts flapping its wings below about 8.6 m./sec. At speeds above about 11 m./sec., wing span starts to be reduced, causing an increase in induced drag above the dotted line. At high speeds the induced drag rises to about 20–25 g. wt. as wing span is progressively reduced.

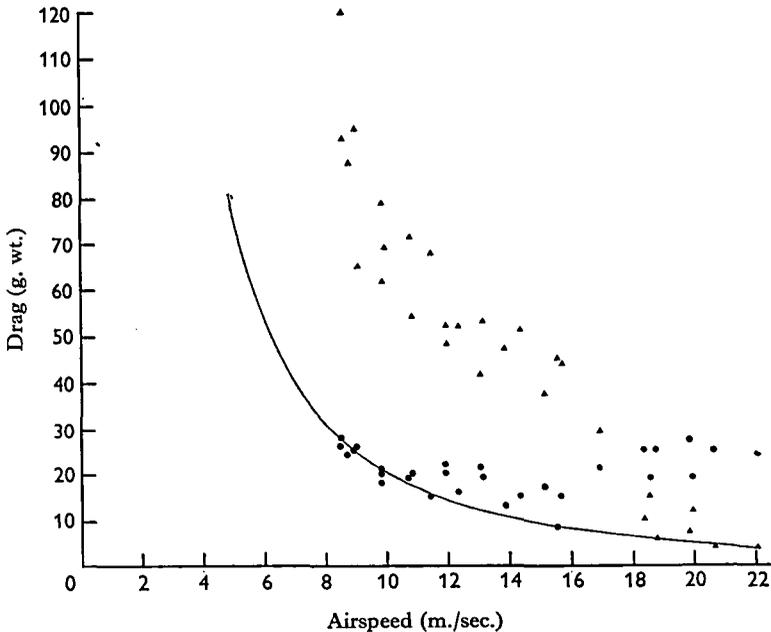


Fig. 16. (a) Circles—estimated induced drag. The line shows the values which would be obtained if the span remained constant at its maximum (low speed) value. (b) Triangles. Wing profile drag, estimated by subtracting other components from the measured total drag.

Wing profile drag

The wing profile drag, obtained by subtraction as explained on p. 510, shows a very marked decrease with speed. The present assumptions imply that the high drag observed at low gliding speeds (Fig. 10) consists mainly of wing profile drag, not of induced drag as would at first sight appear. This conclusion might, of course, have to be revised if subsequent investigation were to show that the induced drag is much higher than has been assumed; the error would, however, have to be improbably large to invalidate the main conclusions, since the wing profile drag, as calculated here, is about three times the induced drag at low speeds. Wing profile drag and induced drag meet in the region of 20–30 g. wt at speeds of about 17–18 m./sec.

The very low values of wing profile drag calculated for speeds above 18 m./sec. should be regarded with reserve because of doubts inherent in the subtractive method of

calculation. In particular, foot drag becomes more and more sensitive to small changes of foot position as speed is increased, and any errors made in estimating this component are reflected in the estimated wing profile drag.

DISCUSSION

The general nature of the planform changes associated with speed (pp. 516–517) has been known since the observations of Hankin (1913) on vultures (Aegyptiinae) and other gliding birds. Pennycuick & Webbe (1959) observed these changes in gliding fulmars (*Fulmarus glacialis*) and interpreted them as being simultaneously (a) control movements, bringing about changes of longitudinal trim needed in speed control, and (b) an adaptation to good ‘penetration’, that is the ability to glide over a wide range of speeds without serious deterioration of the gliding angle, which is an important consideration in soaring. The latter aspect is put into quantitative form for the pigeon in Fig. 16, and depends on the bird’s ability to reduce its wing area by increasing the amount of overlap of the feathers.

Bats would presumably not be able to control their wing area to the same extent. They have muscle fibres in the patagium which can reduce its area at the expense of crinkling the skin, but it seems hardly likely that a planform approaching that shown in Fig. 7c would be possible in a bat. This may be one reason why bats have apparently never been recorded soaring (Felten, 1960).

SUMMARY

1. A technique for training pigeons to fly in a tilting wind tunnel is described, and a method of determining lift and drag in gliding flight is explained.

2. Drag measurements were made on wingless bodies and preserved feet in supplementary experiments. The results were used to analyse the measured total drag of live pigeons into (a) body drag, (b) foot drag, (c) induced drag, and (d) wing profile drag.

3. As speed is increased, gliding pigeons drastically reduce their wing span, wing area and aspect ratio. The increased induced drag resulting from this is more than offset by a very large reduction in wing profile drag.

4. Although the lift:drag ratio is at best 5.5–6.0, changes of wing area and shape keep it near its maximum, up to speeds at least twice the minimum gliding speed.

The construction of the wind tunnel was financed by a grant from the Science Research Council, and I am extremely grateful to that body, and to the late Prof. J. E. Harris, F.R.S. for backing the project before it could be proved that the technique would work. I am deeply indebted to members of the Department of Aeronautical Engineering of the University of Bristol for continual help and advice throughout the design construction and testing of the wind tunnel, especially to Mr T. V. Lawson, Dr J. Tinkler and Mr J. Flower. I am also most grateful for substantial amounts of manual labour contributed during construction, principally by Dr D. R. Jones, Mr D. Curry and my wife.

REFERENCES

- FELTEN, H. (1960). Fliegende Säugetiere. In H. Schmidt (Ed.) *Der Flug der Tiere*, pp. 113-34. Frankfurt: Kramer.
- GREENEWALT, C. H. (1961). *Hummingbirds*. New York: Doubleday.
- HANKIN, E. H. (1913). *Animal Flight: A Record of Observation*. London.
- PANKHURST, R. C. & HOLDER, D. W. (1965). *Wind Tunnel Technique*. London: Pitman.
- PENNYCUICK, C. J. (1967). The strength of the pigeon's wing bones in relation to their function. *J. exp. Biol.* **46**, 219-33.
- PENNYCUICK, C. J. & WEBBE, D. (1959). Observations on the fulmar in Spitsbergen. *Brit. Birds* **52**, 321-32.
- RASPET, A. (1950). Performance measurements of a soaring bird. *Aeronaut engng Rev.* **9**, no. 12, 14-17.
- TUCKER, V. A. (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. exp. Biol.* **48**, 67-87.