# THE FLIGHT OF BIRDS

## II. WING FUNCTION IN RELATION TO FLIGHT SPEED

By R. H. J. BROWN
*Zoological Department, University of Cambridge*

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(With Plates 6 and 7)

In a previous paper (Brown, 1948), the movements of the wing of a pigeon in slow flight were analysed. With the help of a new photographic technique further work on the flight movements at different forward velocities has been carried out. In this paper the analysis is extended with additional information obtained from normal cine-photography. Certain improvements and simplifications in the flash cinematographic methods are also described.

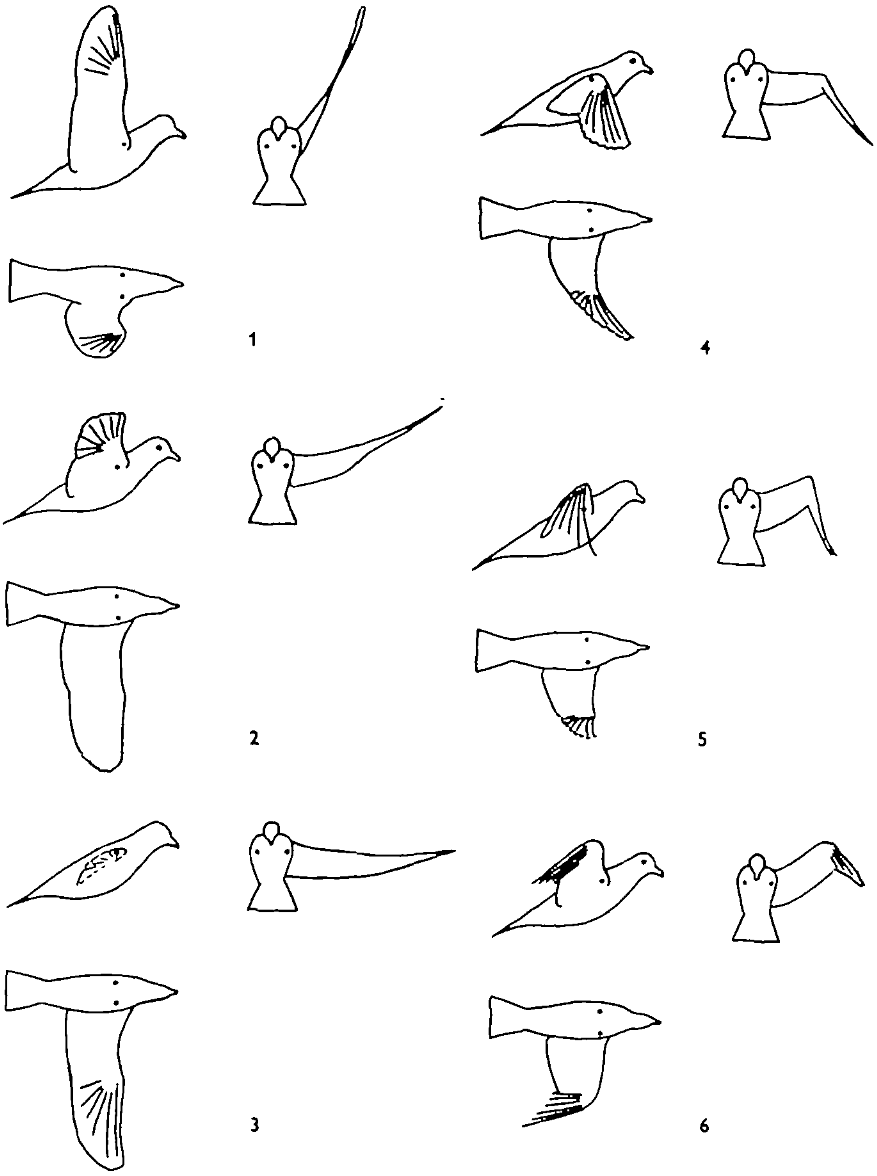
### METHOD

The photographic methods are essentially similar to those previously described. The film is moved steadily past the camera lens, and the lamp or lamps are flashed at intervals such that the pictures are correctly spaced on the film. In the equipment as first used this was achieved by a complex system of rotary switches which had rather a short life. The modifications are described in the appendix.

The photographs of the fast flight were taken as the bird was flying along a 200ft. passage to its cage at one end. It was found that the pigeons could be easily trained to fly straight to the cage, and became accustomed to the lights and camera which were set up in an open doorway about 100 ft. from the beginning of the flight path.

### FLIGHT ANALYSIS

The movements of the wing in slow flight have already been described in detail (Brown, 1948). It will be apparent from Text-fig. 1–6, published in the present paper, that at medium speed (20 m.p.h.) the movements of the wing are very different from those during slow flight throughout a large part of the beat cycle. The first aspect to be considered is the wing movements relative to the bird. The cycle may be taken as starting at the top of the downstroke. The wings are fully extended and are about 50° above the horizontal (Text-fig. 1). They then move downward and slightly forward through an arc of about 90° (Text-figs. 2 and 3, Text-figs. 1–6). The upstroke then starts with a slight flexure of the elbow. As the distal ends of the radius and ulna rise the wrist is flexed and the manus supinated; the primary feathers are depressed and turned backwards (Text-fig. 4). As the rise of the inner part of the wing continues it finally involves the tip feathers (Text-fig. 5), which by now are pointing backwards and are slightly spread. The rise continues until the wrist is approaching its starting point (Text-fig. 6), but before this is reached the




Text-figs. 1–6. The wing-movement cycle of a pigeon at 20 m.p.h.

Text-fig. 1. Beginning of the downstroke, wing fully extended.
Text-fig. 2. Middle of downstroke showing twisting of wing tip to give forward drive.
Text-fig. 3. Near end of downstroke, velocity is falling and angle of attack is falling.
Text-fig. 4. Beginning of upstroke. Flexure and retractions of wrist tip feathers, unstressed wrist rising.
Text-fig. 5. Middle of upstroke. Primaries are being swung violently backwards, giving a forward drive.
Text-fig. 6. End of upstroke. After the flick the primaries remain unstressed until the wing extends for the next downstroke.

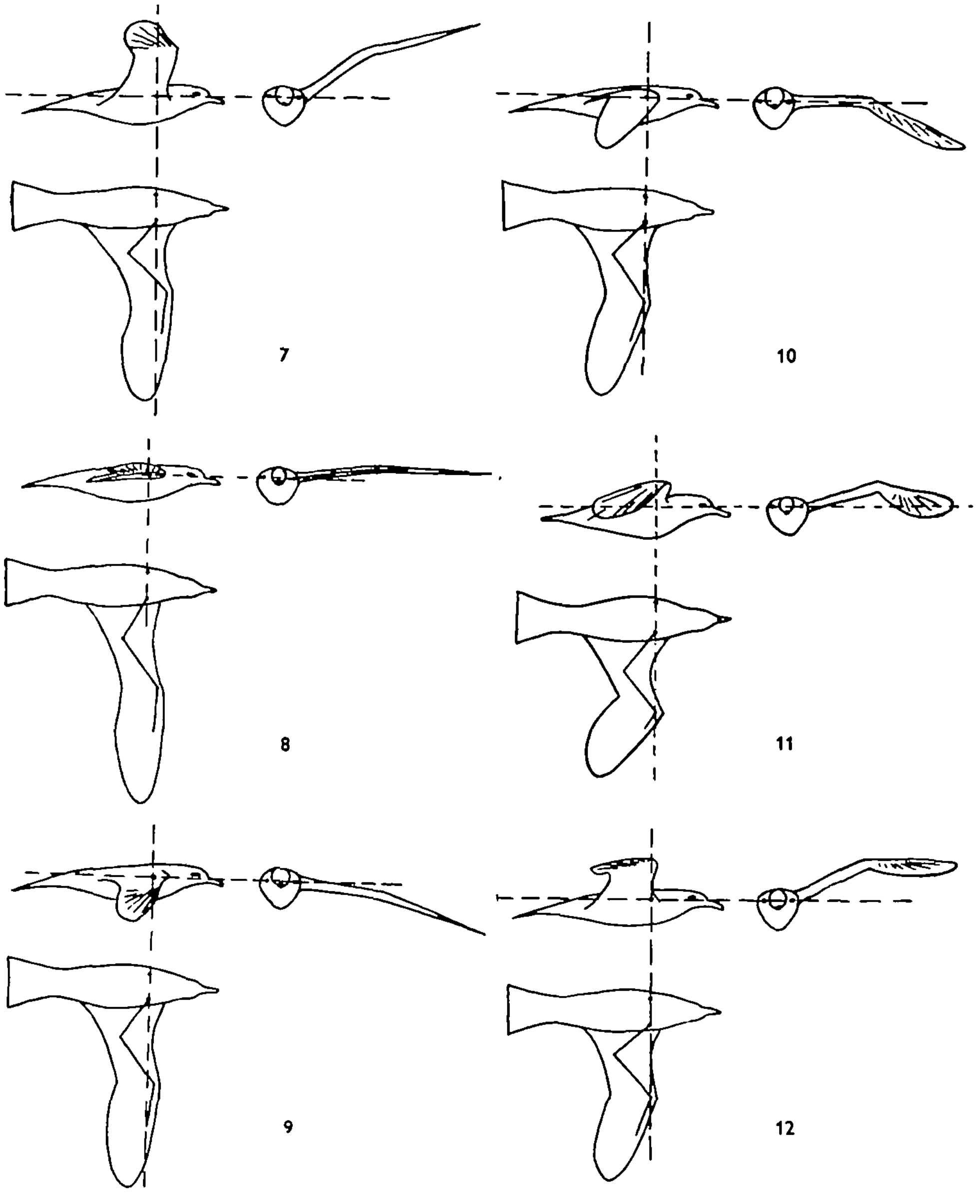
elbow and wrist are extended, the hand is pronated and the primaries spread for the next downstroke.

In this type of flight the body is nearly horizontal. The downstroke is similar to that occurring in slow flight, but the upstroke is much simpler, since there is only a slight backward flick of the primary feathers. The main muscles involved in the movements are fairly obvious. The downstroke is clearly performed by the pectoralis major. The flexure must be produced within the wing by the biceps flexure carpi ulnaris and other intrinsic flexors of the wrist and carpals. When the elbow and wrist are flexed, but not before, the pronation of the manus can take place. This movement is probably aided by air pressure on the backwardly moving tip, but is initiated by muscular action, probably by the pronator brevis.

The first effect produced when the wing moves backwards and upwards under the action of the supracoracoideus, latissimus dorsi and scapulo-humeralis; the initial stage produced is a propulsive flick of the primary feathers, while later the tip feathers are folded over each other and their angle of attack becomes zero. While the tip is undergoing this fairly complex movement the inner part of the wing is slightly flexed and rotates relatively slowly in a vertical plane round the shoulder joint. During this phase all the lift must be produced by the proximal part of the wing, which is being lifted by the air reaction; the muscles limit rather than aid this movement.

The forward movement which completes the cycle must arise from the contraction of the deltoideus, while the extension of the wing is clearly carried out by intrinsic muscles such as the triceps, patagialis group, and the extensor metacarpi radialis. At the same time this extension produces pronation in readiness for the next down-beat.

The wing movements in fast flight are very similar to those occurring at medium speed (Text-figs. 7–12 and Pl. 7) in the wing-beat cycle of a gull at high speed, which only differs from that of a pigeon in its slower rate of beat and smaller amplitude. The downstroke is simple, having only a slight forward movement (Text-figs. 7–9). The upstroke has no propulsive flick and the wing moves relatively slowly. For example, it occupies 0·5–0·6 of the cycle time as compared with about 0·2–0·3 at take-off. As the wing rises (Text-fig. 10) the inner part is only slightly flexed whilst the tip feathers are folded and retracted (there is little or no backward movement at the wrist). As this phase is completed the wing extends and the tip swings forward (Text-fig. 12). The complete cycle is therefore a simple up-and-down movement of the region of the wing lying proximally to the wrist, with a roughly circular movement of the distal region; forward and down, backward and up. The musculature involved is clear. The downstroke is produced by the contraction of the pectoralis major, and it is the only muscle involving any appreciable work. Since the air reaction is tending throughout to lift the wing, the upstroke need only be limited and controlled by muscular action, i.e. relaxation of the pectorialis major. The flexions and extensions of the wing are produced by the intrinsic muscles as described before, and since there is no propulsive flick, it requires only little muscular effort.




Text-figs. 7–12. The wing movements during normal flight of a gull

Text-fig. 7 Beginning of downstroke. The wing is fully extended and is moving with no forward component relative to the bird.

Text-fig. 8. Middle of downstroke. This shows slight twisting of the tip to give a forward force.

Text-fig. 9. End of downstroke. The wing is still fully extended and the whole is still lifting.

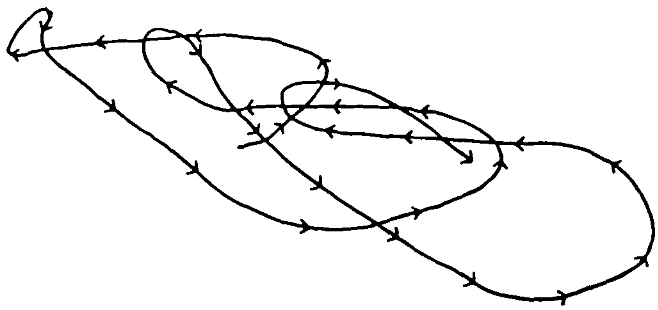
Text-fig. 10. Beginning of upstroke. Flexure at the wrist and slight retraction, increase of angle of attack of the arm to compensate for loss of tip lift.

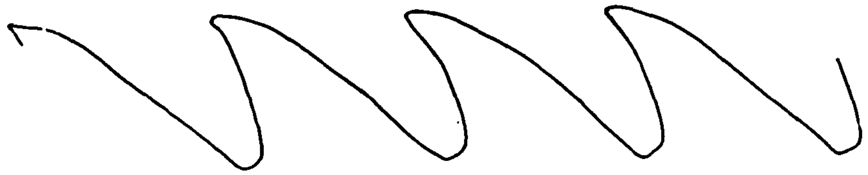
Text-fig. 11. Middle of upstroke. The primaries are folded over each other and are unstressed. Slight further retraction of wrist and increased angle of attack.

Text-fig. 12. End of upstroke. The wing is extending and the primaries are swinging forward again for the next downstroke.

*Track relative to the air*

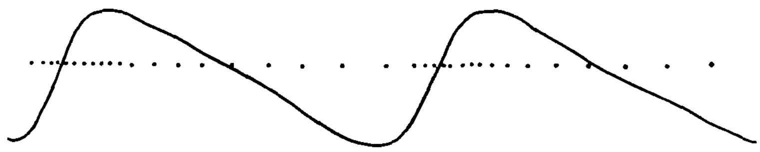
At the take-off the tip of the wing moves along a path which may be described as a series of linked figure eights (Text-fig. 13), with the forward velocity of the body remaining constant or falling as the wing moves forward and down, and then increasing as the tip travels upward and back (Brown, 1948). As the forward speed





Text-fig. 13. The wing-tip track of a pigeon landing. Note the very large backward and forward components of motion.

Text-fig. 14. The wing-tip track of a pigeon at 18 m.p.h. Here backward movements are greatly reduced and there is only momentary reversal of an air-stream direction on the primary feathers.

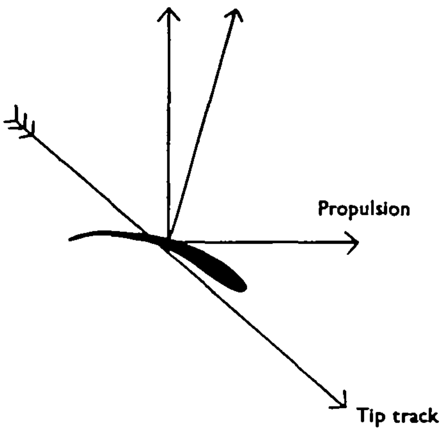


Text-fig. 15. The wing-tip track of a swan shortly after take-off. The dots indicate the position of the head in successive pictures. Note the absence of backward movement of the wing and the loss of speed, as shown by the spacing of the dots on the upstroke.

increases the backward movements decrease, and the tip track becomes opened out as shown in Text-fig. 14, and the body moves with no measurable change in velocity. In normal fast flight there is no backward movement of the tip, which traces out a simple waved track, and in birds with a slow wing beat it is possible to see a drop in body speed during the upstroke (Text-fig. 15).

*Air forces*

The air reaction at take-off has been described (Brown, 1948). As the speed increases the long axis of the body tends to become horizontal and the reaction of the tip feathers during the downstroke has a forward component (Text-fig. 16). This is shown by the forward bending of the feathers in Pl. 6, fig. 6. The upstroke is propulsive during the flick, but this phase is less important than it is at take-off. Nevertheless, the tip feathers develop a propulsive component of force during parts of both the up- and downstrokes, while the inner part of the wing maintains lift throughout the flapping cycle.



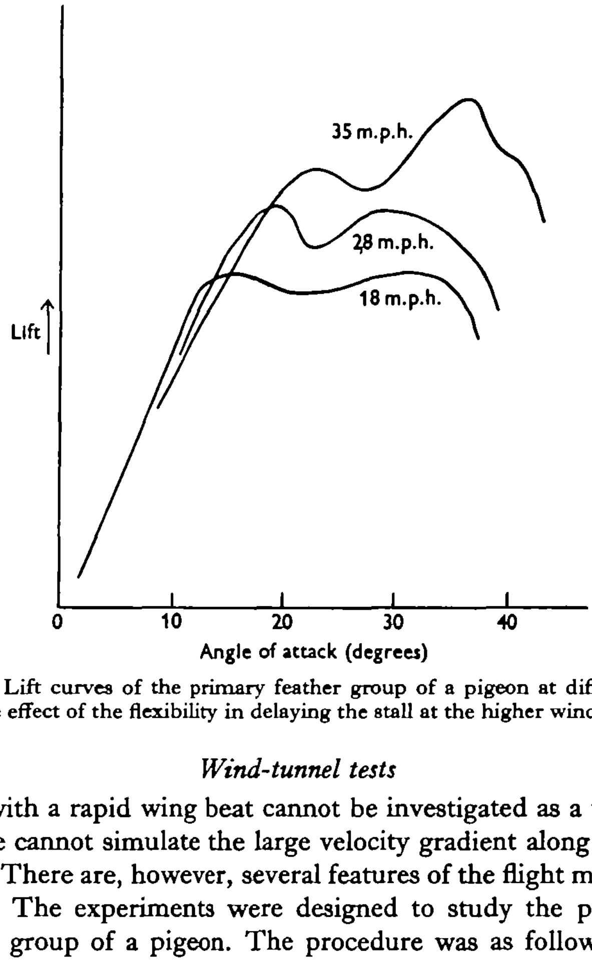

Text-fig. 16. This diagram shows how the downward- and forward-moving wing tip can give the propulsive force.

In normal fast flight it is clear from Text-figs. 7–12 and Pl. 7 that the proximal part of the wing must behave as a fixed aerofoil, while the tip provides propulsion during the downstroke only, and is passive on the upstroke.

The above account may be summarized in tabular form:

| | Take-off | Medium speed | Normal high speed |
|---|---|---|---|
| Downstroke: | | | |
| Wing tip: | | | |
| Angle of attack | Positive | Positive | Positive |
| Angle relative to direction of flight | Positive | Negative | Negative |
| Function | Lift | Propulsion and lift | Propulsion and lift |
| Inner wing: | | | |
| Angle of attack | Positive | Positive | Positive |
| Angle relative to direction of flight | Positive | Positive | Positive |
| Function | Lift | Lift | Lift |
| Upstroke: | | | |
| Wing tip: | | | |
| Angle of attack | Positive (feathers inverted) | Positive (feathers inverted) | Zero or slightly positive |
| Angle relative to direction of flight | — | — | Positive |
| Function | Propulsion and lift | Propulsion and lift | Absent |
| Inner wing: | | | |
| Angle of attack | Positive (high) | Positive | Positive |
| Angle relative to direction of flight | — | Positive | Positive |
| Function | None | Lift | Lift |

At take-off, the air speed over the inner part of the wing is very low, and the air reaction from it can contribute little or nothing to the total lift of the wing. Boel (1929) showed that this was true by cutting off the secondary feathers of a pigeon without impairing the take-off. It can be demonstrated, however, that a bird treated in this way cannot do more than fly under take-off conditions for a short time, and is apparently unable to increase its forward speed. On the other hand, trimming off part of the tip feathers prevents normal take-off; while the bird can still glide, it is unable to maintain height.




Text-fig. 17. Lift curves of the primary feather group of a pigeon at different speeds. Note the effect of the flexibility in delaying the stall at the higher wind speeds.

*Wind-tunnel tests*

Small birds with a rapid wing beat cannot be investigated as a whole in a wind tunnel since one cannot simulate the large velocity gradient along the wing which occurs in flight. There are, however, several features of the flight mechanism which can be studied. The experiments were designed to study the properties of the primary feather group of a pigeon. The procedure was as follows. The feathers were mounted in a wooden holder so that they occupied the positions they would have in a fully spread wing tip, and their bases were fixed into the holder by paper strips simulating the covert feathers. The complete structure was mounted in a wind tunnel and its properties measured under various conditions. Text-fig. 17 shows the lift curves of the primary feather group at different speeds in the attitude of the downstroke. It will be seen that the curve of the lift against nominal incidence varies with speed. The term nominal incidence is used because the figures cannot show the actual angles of incidence of the flexible system; the angles plotted are degrees of rotation of the wing mounting rod from the position at which the lift is zero. It is clear from the curves that the stalling is very gradual. This is not a stall as is found in rigid structure, but rather a tip incidence-limiting effect produced by the onset of stalling on the proximal part of the wing. This results in a backward movement of the centre pressure and an increased torsion, so that over the range of plotted angles above 15–20°, the actual angles of attack of the tip feathers may not increase as the wing mounting is rotated; this effect is important, in that it produces an almost unstallable wing tip.

A flexible structure such as a bird's wing can have no fixed aerodynamic properties, for these clearly change as the forces on the wing change.

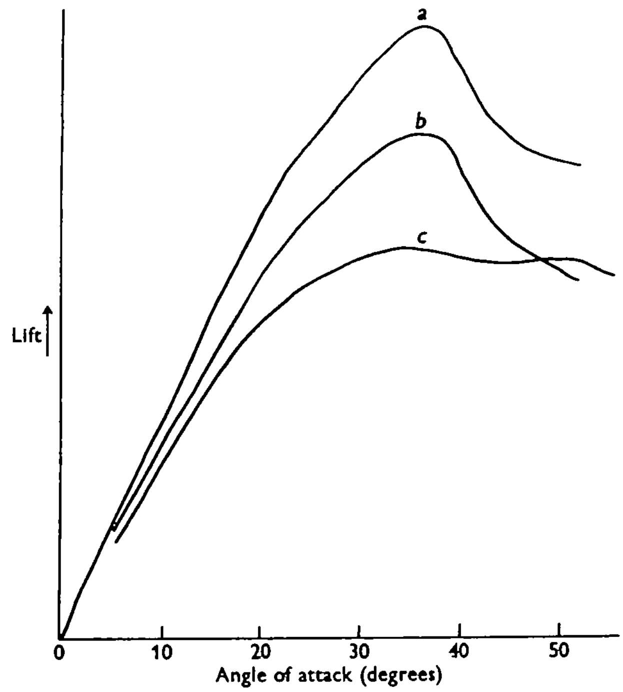
The flexible wing also compensates automatically for changes in muscular effort. If, at take-off, the wing-beat velocity is increased, the component of air speed normal to the plane of the wing is increased. In a rigid wing this would result in a greater angle of attack and might lead to stalling, but the larger forces at the higher speed twist the flexible structure and limit the angle. This is another important feature of the tip structure. In the photographs it is clear that, even though the feathers are not emarginated they separate during the downstroke when subjected to the high stresses of take-off. The properties of the wing tip in such a condition cannot be known exactly but must have the effect of preventing, or delaying, the stalling of the tip.

Measurements were made of the same group in a position simulating the backward flick of the upstroke and gave interesting results. There is no doubt that in this phase the proximal part of the wing can contribute nothing to the lift of the wing as a whole. At this stage of the flight, the tip moves backwards with the line through the feather bases, making an angle of about 90° with the air flow. The feathers separate and rotate, and each acts as a separate aerofoil. It has been suggested by Boel (1929) and others that the rotation is under muscular control. There seems no evidence that (*a*) the feather shafts can rotate and (*b*) that there is any musculature to produce such a movement; the natural elasticity of the feather can account for the observed rotation.

With the tip feathers mounted as described, they were adjusted so that the lamina of each feather rested lightly against the underside of the feather behind. The air stream was directed on to the dorsal surface, and the feathers were seen to separate as the angle of attack was increased. The curve of lift against an angle is shown in Text-fig. 18*a*.

Next, the feathers were rotated so that there was a slight gap between them when they were unstressed. This gap increased when the feathers were flexed by the air stream. The appropriate lift curve is shown in Text-fig. 18*b*; finally, they were rotated so that each lamina was pressing firmly against the next feather. The separation taking place in the air stream was small and the curve was as shown in Text-fig. 18*c*. It will be seen that the conditions of '*b*' and '*c*' both give values of lift coefficient lower than '*a*', which is as close an approximation as possible to the conditions found in the unstressed wing of the live bird.

In these experiments (carried out at an air speed of 50 ft. per sec.) neither Text-figs. 18*b* nor *c* gave lift forces sufficient to balance the weight of the bird. This fact and the observation that the curve (Text-fig. 18*a*) gave the highest L/D ratio, together suggest that the feathers separate by virtue of their own elasticity and not by muscular activity. The low L/D ratio (reaching a maximum in these tests of about 4) may be of little importance, since the wing tip is moving through the air in a direction opposite to the direction of flight, and its drag is therefore in fact a propulsive force.




Text-fig. 18. Lift curves of the primary feathers of the pigeon with the wind directed on to the dorsal surface. (For explanation see text).

## DISCUSSION

In a previous paper (Brown, 1948) it was pointed out that the take-off flight therein described was not to be considered as normal flight since it was not impaired by the removal of the secondary feathers (Boel, 1929).

It was suggested that the differences to be expected between slow and fast flight were: (*a*) disappearance of the backward flick, and (*b*) transfer of the propulsive function to the downstroke. This has now been confirmed and evidence presented which shows that as the speed increases so the flick of the tip feathers gradually decreases and the body tends to approach in a horizontal position. The downstroke becomes nearly vertical and of smaller amplitude and develops a greater forward component of reaction from the tip feathers.

There is general agreement on the function of the wing on the downstroke in fast flight; the inner part gives lift while the tip provides propulsion. Concerning the wing function at take-off there is some divergence of view. Storer (1948) describes what he calls the 'helicopter' and 'variable propeller', used in take-off, and 'reversed propeller' in landing. The author states that the wing-tip feathers can be rotated so as to provide either a backward or forward force, or, in other words, that they can have two stable positions in relation to the air-stream direction. I cannot accept this statement. I am convinced that the feather cannot receive an air stream at an angle of greater than about 15° without becoming unstable. If a single feather is examined in a wind tunnel it will be found that above the angle of maximum lift the feather becomes unstable and flutters violently. At angles below the maximum it has a configuration similar to that illustrated by Storer for the normal state, but the configuration labelled as in reverse flight cannot be seen. I believe, therefore, that under all conditions and speeds of flight, the downstroke is carried out with the tip feathers at a fairly small angle of attack.

During take-off and landing the tip moves along a path whose general direction is against the direction of flight, the reaction from the tip being upward with probably slight forward inclination at the take-off, and a backward one during landing.

The upstroke is much more complex, and the disagreements in the literature are numerous; in part due to the fact that there are a number of different types of wing movements which can be carried out by the same bird, and also that not all birds move their wings in the same way in similar situations.

Several authors (Headley, 1912; Marey, 1890; Horton Smith, 1938; Guidi, 1938) all believe that the primary feathers separate on the upstroke to reduce resistance.

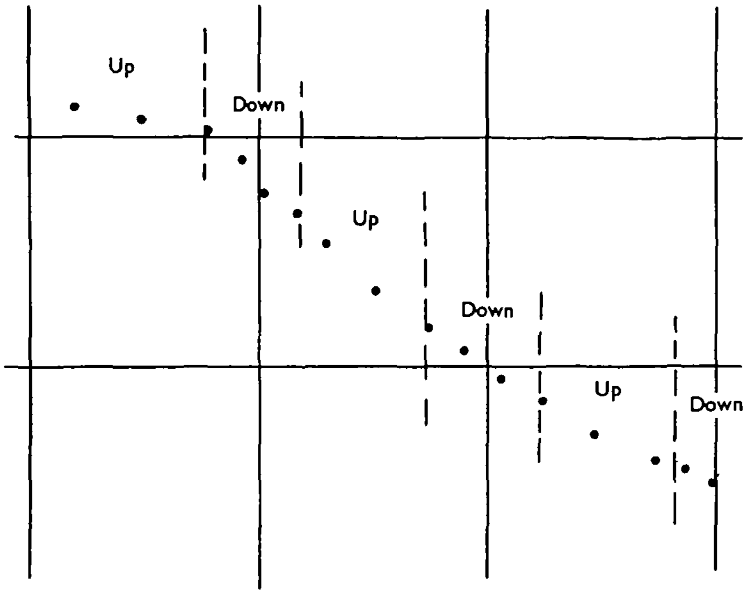
Aymar (1936) suggests that a backward push may be produced, and shows photographs in which the primary feathers are bent forward. Horton Smith (1938) has stated that there is a downward and forward force. This is also the opinion of Storer (1948). Lorenz (1933) on the other hand, believes that the rotation of the feathers produces a series of overlapping aerofoils whose combined reaction is forward and upward.

This is also suggested by the work of Marey (1890) who showed that in the flight of a duck there were two periods of vertical acceleration in the beat cycle.

From inspection and analysis of photographs I am convinced that the view of Lorenz (1933) is correct. During slow flight the upstroke clearly provides propulsion, without loss of height; in fact there is a gain in vertical velocity during climbing flight (Text-fig. 19).

When the flight speed rises after take-off and the body angle approaches the horizontal, the tip flick disappears. At the same time the speed of movement of the wing falls and the tip is carried up passively. There is no evidence in my photographs that the reaction of the air stream on the tip feathers ever has a downward component, as suggested by Horton Smith (1938) and others, and I find it difficult to believe that so inefficient a condition with an upward force on the secondaries and a downward force on the primaries would ever occur except as a momentary transitional phase. It is true that, as Guidi (1938) states, the feathers separate, but I suggest that this action increases lift at take-off rather than reduces air resistance.

Under all conditions where a propulsive upstroke is not used, the tip feathers are folded over each other, rather than separated when the wing is raised; the air stream is never directed against their dorsal surface.




Text-fig. 19. Plot of the movement of a pigeon in climbing flight. The dots represent the position of the shoulder in successive pictures; note the increase in speed during the upstroke.

## APPENDIX

### *Photographic apparatus*

In the course of this work on bird flight it was necessary to develop a flash cinematographic technique which has been of more general use.

An early form of this equipment has been described (Brown, 1945), and the following is an account of a greatly improved version. The basic principle is simple. The object to be photographed is illuminated by a series of flashes of light emitted from special lamps and the reflected light is focused on to a film moving at such a rate that the pictures are correctly spaced along it. The duration of a flash is so short that no appreciable movement of the film takes place within it.

The various units are as follows: camera, drive and flash control switching, low-power pulse generator, power unit and main pulse generator, lamp circuits, monitor and test circuits.

### *Camera*

The camera is a modified hand-cranked 35 mm. cine-camera. The modifications are:

(*a*) Removal of the shutter and intermittent motion.
(*b*) Fitting an additional sprocket to pull the film through the gate.
(*c*) Replacement of the hand-crank by a coupling to engage with the drive unit.

The absence of shutter is not essential, but if present is only of use in limiting the effect of extraneous light at low camera speeds. In the particular camera its inertia would limit the starting acceleration so that the full speed of 90 pictures per second could not be reached in under half a second. Without the shutter the full speed is reached in about $\frac{1}{10}$ sec.

### *Mounting and drive*

The camera is clamped to a board on which is mounted the drive unit. The unit comprises a $\frac{1}{4}$ h.p. electric motor which drives a free pulley on a shaft. This pulley can be locked to the shaft by a clutch. This clutch is operated by a solenoid which at the same time releases a spring-loaded brake. Also on the shaft are: (1) a commutator with two opposite contact bars which perform the flash control switching, and (2) a coupling to engage with the camera shaft.

The drive unit is controlled by a double-circuit push button which is connected by a flex lead to the board. When the button is pressed down against a light spring pressure it makes the motor circuit and the motor starts. Further movement against a heavier pressure completes the solenoid circuit, releases the brake engaging the clutch and starts the camera. The clutch and brake system enables the camera to be run up to full speed in about $\frac{1}{10}$ sec., and stopped in rather less time. This rapid operation is of great value, since it is possible to take shots lasting only $\frac{3}{4}$ sec. or less, with about 65 pictures containing only about 9 pictures at the beginning and 6 at the end, where the time intervals are not uniform.

### *Low-power pulse generator*

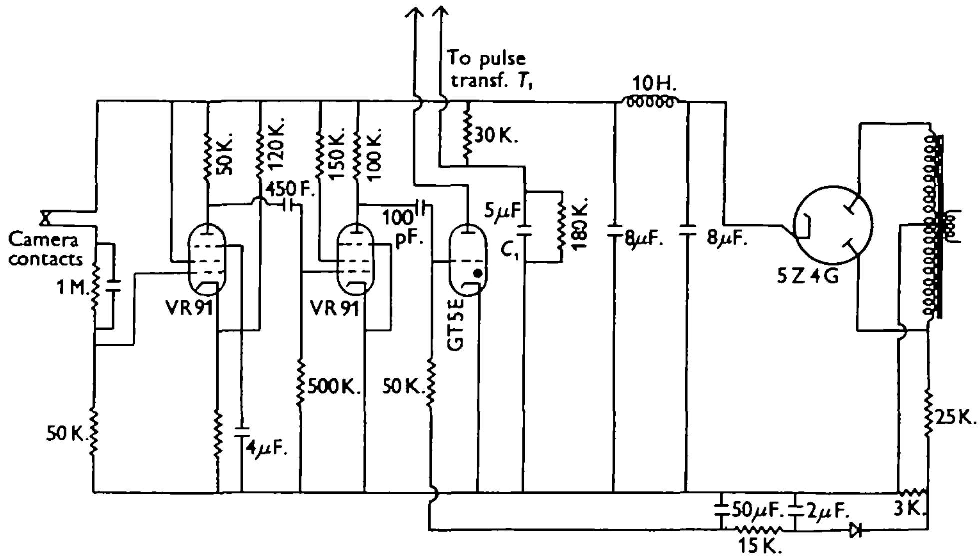
The circuit is shown in Text-fig. 20, and consists of a pulse generating circuit operated by the commutator on the camera drive. The gas-filled relay, GT5E, feeds a pulse from $C$ into the pulse transformer $T_1$, which is a car ignition coil with a new secondary winding. The output is a 15 kV. pulse which operates the lamp circuits.

### *Power unit and main pulse generator*

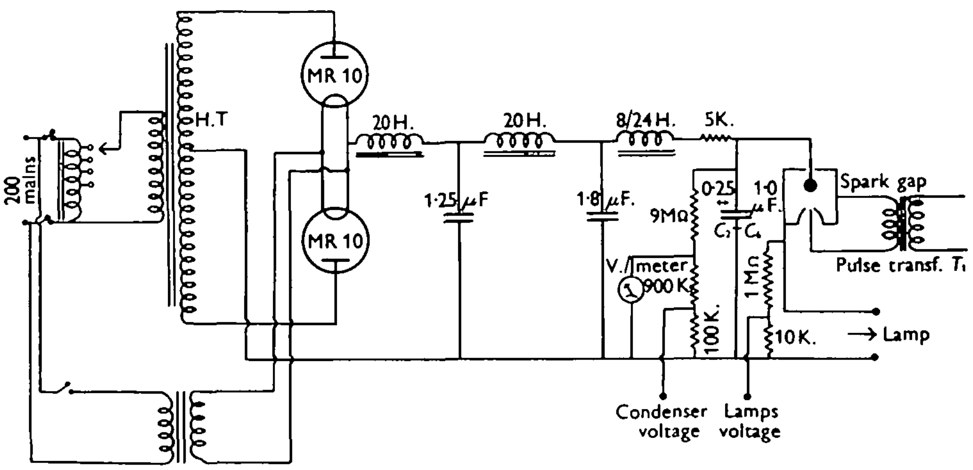
The power has a simple biphase rectification system with choke input smoothing, and can deliver 10,000 V. d.c. at 0·5 A. (Text-fig. 21). This feeds the flash condensers $C_2$–$C_6$ through a choke and resistance to limit the charge rate. These condensers and the triggered spark gap form the high-power pulse generator. When the spark gap (Wilkinson, 1946) receives a pulse from the ignition coil it breaks down and feeds the stored energy of 12–50 joules to the lamp or lamps. The flash is varied by using one or more of the condensers $C_2$–$C_6$ in parallel.

### *Lamp circuits*

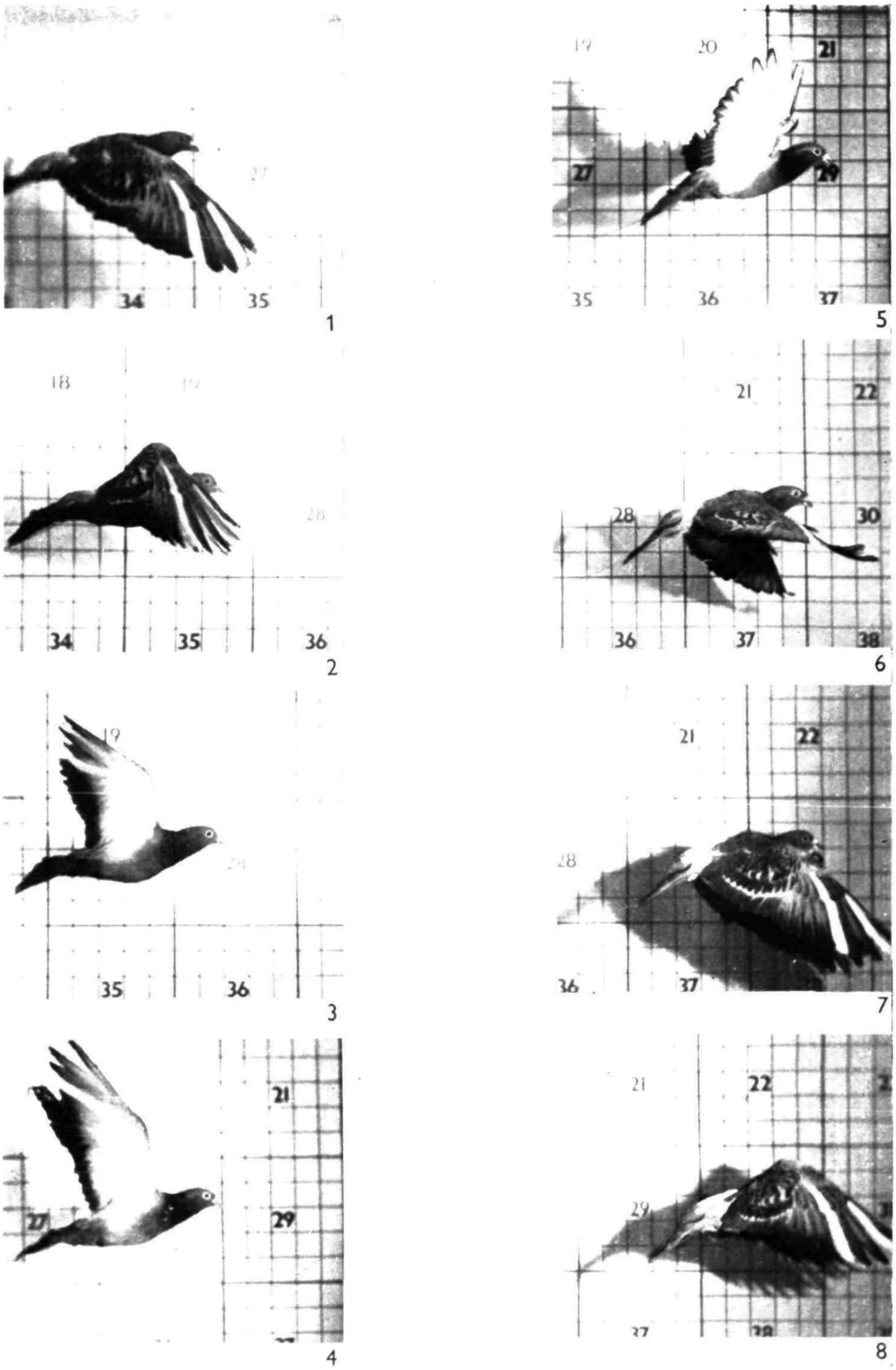
The lamps used are B.T.H. type F.A.I. which were intended to be used at 2000 V. and flashed by a triggering pulse applied to a wire on the outside of the envelope. When fed with a 10 kV. pulse they flash without being triggered. The advantage of using 10 kV. is that for the same power much smaller condensers, which can be charged quickly between flashes, can be used. When using a single lamp it is simply put in series with the spark gap, with a small condenser in parallel with it. Two lamps are normally used, connected in series. The condensers allow the spark gap to maintain ionization by charging the condenser while the voltage builds up on the lamp to the flash level.




Text-fig. 20. The circuit of the low-power pulse generator. For description see text.




Text-fig. 21. Diagram of the main power unit and flashing circuit. The points labelled condenser voltage and lamp voltage are used with an oscilloscope for checking the function of the equipment.



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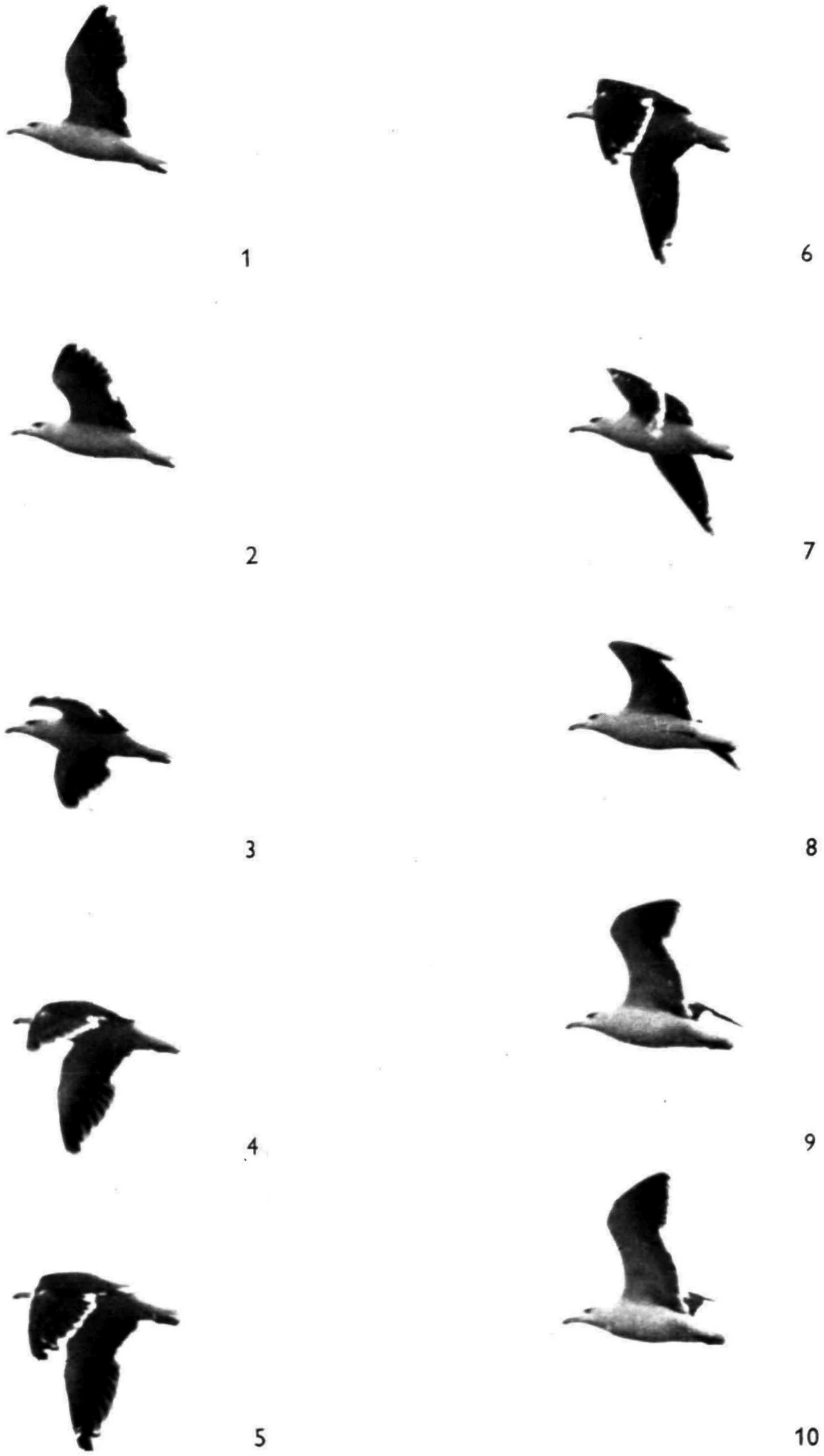


BROWN—THE FLIGHT OF BIRDS

## SUMMARY

1. The changes in the form of the wing movement of different birds with change of air speed are described.
2. The aerodynamic properties of various configurations of the wing are discussed.
3. Reconciliation of various contradictory accounts in the literature is attempted.
4. Improvements in photographic methods are described.


## REFERENCES


AYMAR, G. C. (1936). *Bird Flight*. London.

BOEL, M. (1929). Scientific studies of natural flight. *Trans. Amer. Soc. Mech. Engrs*, **51**, 217–42.

BROWN, R. H. J. (1948). The flight of birds. *J. Exp. Biol.* **25**, 322–33.

GUIDI, G. (1938). A study of the wing-beats of pigeons in flight. *J. R. Aero. Soc.* **42**, 1104–15.

HEADLEY, F. W. (1912). *Flight of Birds*. London.

HORTON SMITH, C. (1938). *The Flight of Birds*. London.

LORENZ, K. (1933). Beobachtetes über das Fliegen der Vögel und über die Beziehungen der Flügel-und Steuerform zur Art des Fluges. *J. Orn., Lpz.*, **81**, 107–236.

MAREY, E. J. (1890). *Vol. des Oiseaux*. Paris.

STORER, J. H. (1948). The flight of birds. *Bull. Carneg. Inst. Sci.* no. 28.

WILKINSON, K. J. R. (1946). Some developments in high-power modulators for radar. *J. Instn Elect. Engrs*, **93**, 1090–1112.


## EXPLANATION OF PLATES

### PLATE 6

Pigeon in flight at medium speed, showing slight forward bending of the feathers during the upstroke (fig. 2) and again in the downstroke (fig. 6).

### PLATE 7

Gull in normal fast flight. No forward bending of the tip feathers in the upstroke (figs. 6–8), and little reduction of area of the inner part of the wing.