THE FLIGHT OF BIRDS

THE FLAPPING CYCLE OF THE PIGEON

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(With Plates 5–8 and 12 Text-figures)

For many years there has been discussion on the details of the wing movements of birds in flight, and many attempts have been made to produce clear cinematograph records of the flapping cycle. Until recently no photographic system has combined a sufficiently short exposure with a rapid repetition rate and a reasonably large field of view.

The development of the Arditron discharge tube has provided a light source which is of very high intensity, and has a flash duration of about 1 μsec. This lamp, though designed for single-flash operation, has been found very suitable for high-speed cinematography.

The purpose of this paper is to describe the cinematographic technique which has been developed, and to give a preliminary account of some of the information which has been obtained on the slow flight of the pigeon.

PHOTOGRAPHIC TECHNIQUE

As stated above, the photographic method is based on the use of an Arditron type tube, the characteristics of which determine the limitations of the method and must, therefore, be considered first.

Lamp. This is a glass tube filled with a gas mixture (chiefly argon) and having electrodes at each end which are photo-emissive.

A third electrode near one end is used to start the discharge; this is known as the trigger electrode. The basic circuit is shown in Text-fig. 1. The condenser A is charged from a source of high voltage (about 8000 V.) which is then disconnected. On applying a pulse of high voltage to the trigger electrode the tube becomes conducting, and the condenser is discharged very rapidly through the tube, giving an intense flash of light. In practice for photography by single flashes, as opposed to repetitive flashing for cinema work,
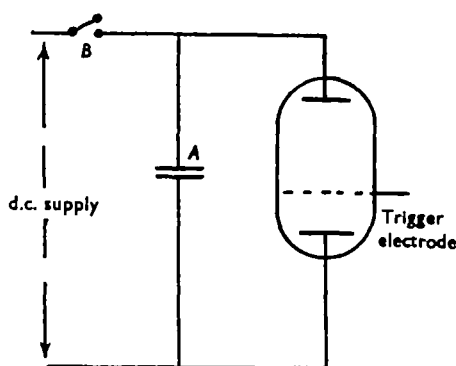
Text-fig. 1. Lamp circuit reduced to its simplest form. The condenser A is charged by the closure of switch B which is then reopened. The lamp is flashed by a voltage pulse applied to the trigger electrode.

the switch *B* is replaced by a resistance of a value which delays the rise of voltage on the condenser, and gives time for the tube to return to a non-conducting state. If this resistance is too small, and the rise of voltage too rapid, the tube flashes spontaneously before the condenser voltage has reached its maximum, thus producing a continuous series of flashes until the power is switched off. For single-flash photography the high resistance and slow recharge is no disadvantage, but for repetition flash work at 50–100 pictures per sec. the necessary conditions are very difficult to satisfy. In the apparatus to be described the resistance-charge method was abandoned and replaced by a rotary switching system linked to the camera; this has given complete satisfaction.

The complete apparatus may conveniently be subdivided into the following sections: switching system, trigger unit, power unit, camera, camera and switch drive, lamp circuits.
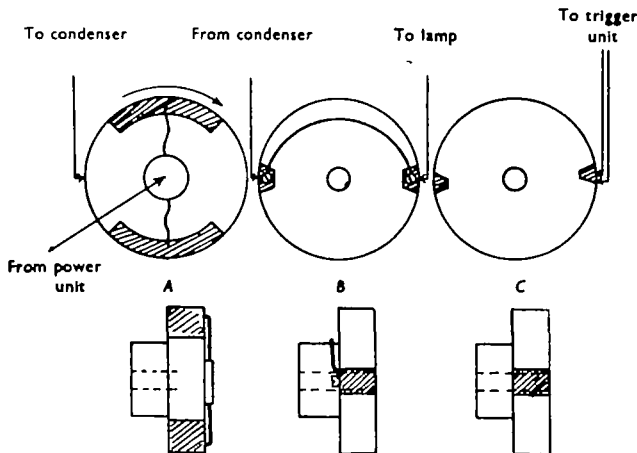

Text-fig. 2. Diagram of the rotary switches. The positions of the various brushes are indicated by arrows, and the switches are drawn in their correct relation for the direction of rotation as shown. (For details see text.)

The switching is carried out by three rotary switches, all mounted on the same shaft; these are shown separated in Text-fig. 2. The charging switch *A* is a Tufnol disk 2½ in. diameter carrying brass inserts on opposite sides, each of these inserts occupying 90° of the circumference and being connected to a brass contact at the centre of the disk. Switch *A* is mounted on the end of the shaft. On the centre contact rests a spring brush which is connected to the power unit, while a second brush connects the flashing condenser with the peripheral segments. The condenser is, therefore, connected to the power unit for half the time cycle. The second switch *B*, which may be called the lamp switch, is mounted on the shaft close to switch *A*. It is a similar 2½ in. Tufnol disk carrying two narrow brass inserts on opposite sides; these inserts are connected together by a copper strip as shown. Pressing against the periphery of the disk and 180° apart are two copper carbon brushes. One is connected to the flashing condenser, and the other leads to the

lamp. The two switches A and B are adjusted relative to each other, so that the contact period of B, which occupies about $\frac{1}{20}$ of the cycle time, occurs in the middle of the off-period of A. The position of these switches in the circuit is shown in Text-figs. 5, 6. The third switch C, which times the flashing of the lamp, is similar to switch B, and carries two narrow contact strips on opposite sides. Two light spring brushes rest side by side on the periphery and the circuit between them is made by the contact strips. Each time this circuit is made a pulse is sent to the lamp from the trigger circuit to be described.

Switch C is adjusted to close when the contacts of switch B are under the brushes. The complete sequence of operations is as follows:

The cycle starts with a contact segment of A just touching the brush leading to the condenser; the power unit is thus connected to the condenser which begins to
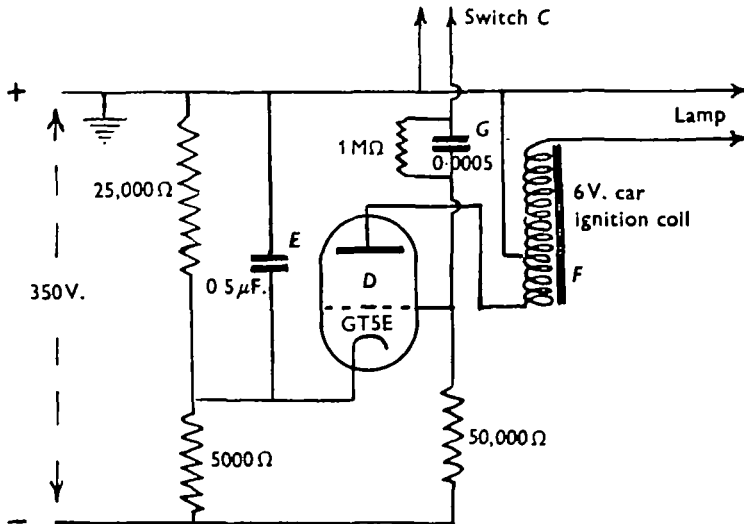
Text-fig. 3. Circuit of the trigger unit. The condenser E is charged from a simple power unit (not shown). When C is closed the grid of the thyratron D is momentarily raised to anode voltage through G. The valve becomes conducting and E is discharged very rapidly through the transformer F, giving a high-voltage pulse which is fed to the lamp.

charge. This connexion is maintained for a further 90° of rotation by which time the charging is complete.

The switches continue to rotate through a further 45° when the circuit is made through switch B connecting the charged condenser to the lamp. While this circuit is made, the triggering pulse is released by the closure of switch C, and the lamp flashes. After a further 45° of rotation switch A is again made and the cycle restarts.

Thus two flashes occur during each revolution of the shaft.

The trigger unit is identical with that described by Edgerton (1932), and is shown in Text-fig. 3. The gas-filled relay D discharges the condenser E when switch C is closed. A pulse of current, therefore, passes through the primary of the transformer F and produces a high-voltage pulse (about 10,000 V.) in the secondary, which is connected to the lamp.

The power unit, Text-fig. 4, is very simple though rather large; it contains a 5 kVA. high-tension transformer fed from the tapped transformer *H* for voltage control. The centre-tapped secondary output can be varied up to about 18,000 V. by adjustment of *H.* This output is rectified by two diode rectifiers (Marconi M.R. 10), and smoothed by condenser *K.* The rectifier filaments are fed from transformer *J.* The resultant d.c. voltage is shown on the meter *L.* The complete unit is built into an angle iron framework, which is enclosed in sheet metal, and fitted with wheels. The latter are essential since the total weight is about 900 lb.

The camera was constructed from an old hand-cranked 35 mm. cine camera. The main modifications are as follows. The claws, all the intermittent mechanism, and the shutter were removed. A new film gate was fitted, and an additional sprocket was fitted in place of the intermittent mechanism, to pull the film smoothly and steadily through the gate. A focusing mounting was made to take a new lens
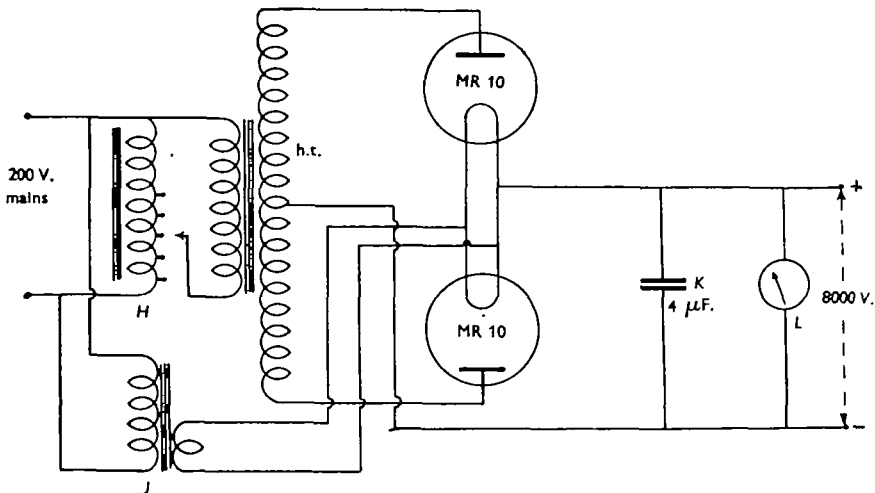
Text-fig. 4. Circuit of main-power unit. For description see text.

(Zeiss Sonnar *f* 2·0). Finally, a coupling was fitted in place of the handle to connect the camera to the shaft carrying the switches. Since the camera was designed to take two pictures per revolution of its shaft, and the rotary switches produce two flashes per revolution, the synchronism between the lamp and camera is perfect.

The camera drive is carried out by a ¼ h.p. electric motor; this is larger than necessary, and therefore gives a very steady speed.

The drive is taken from the motor by a belt to a pulley on the switching shaft. The belt is normally slack, and slips while the shaft is held stationary by a powerful brake. An electromagnet is arranged to release the brake and tighten the belt simultaneously.

The lamp is mounted in a large motor head-lamp reflector on an adjustable stand, and is connected by flexible cables with the lamp switch and trigger unit. All the high-voltage cable is concentric radio-frequency transmission cable with about $\frac{5}{16}$ in. solid polythene insulation and has been tested to 30,000 V.

An alternative circuit using two lamps, to lessen the shadows on the screen behind the bird, was used for the photographs in this paper.

This circuit is shown in Text-fig. 5; the operation is as follows:

On lamp A being triggered, a discharge passes, charging condenser C, it also raises the voltage on the trigger electrode of lamp B via the resistance R. When this voltage is high enough the second lamp becomes ionized and the flashing condenser discharges through the two lamps in series.
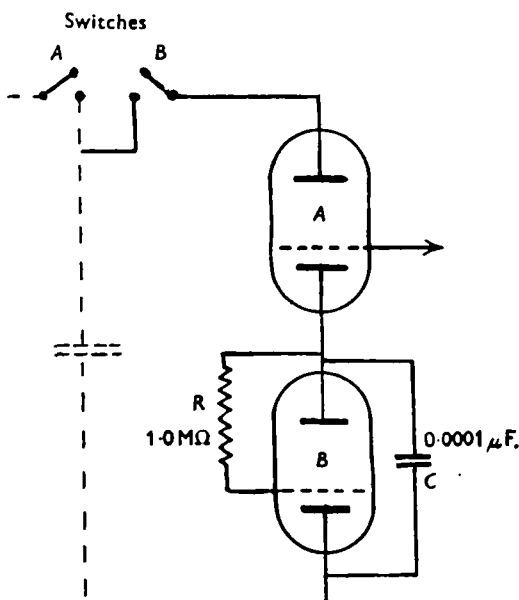
OPERATION

The sequence of operations is as follows. The trigger and power-unit filaments are switched on. The camera is focused and loaded with film. Then the trigger and power-unit high-voltage circuits are made, and the apparatus is ready for use. The motor and electromagnet are both operated by push switches. Actually these are combined mechanically so that the first movement of the push button against light spring pressure completes the motor circuit. The motor starts and reaches full speed, the bird is released, and the button pressed further down against a stronger

Text-fig. 5. Circuit using two lamps. Lamp A is controlled by the trigger unit. Lamp B will flash whenever the voltage across it exceeds about 6000 V. Therefore, when A is triggered it starts to charge C, when the voltage across B is high enough, both lamps become conducting and the flashing condenser is discharged through both in series.

spring. This further movement energizes the electromagnet, and the camera and switches start running.

Within $\frac{1}{10}$ sec. the camera has reached its running speed of 85–95 pictures per sec. On the completion of the shot the button is released; this applies the brake, slackens the belt, and switches off the motor. The camera is stopped by the brake in less than $\frac{1}{15}$ sec. The wastage of film at each end of a shot is not more than 8 in.

The complete layout with two lamps is shown in Text-fig. 6. The flashing condenser is variable in steps of $0\cdot25\,\mu$F. The photographs illustrating this paper were taken using a condenser of $1\cdot0\,\mu$F. charged to 8000 V. and required an output of about 4 kW. from the power unit. The shots varied in length from about 30 to 50 pictures.

Other features of the experimental set-up should be mentioned. First, some photographs were taken against a background ruled in squares (not shown) in order to obtain estimates of the extent and velocity of the wing movements. Secondly, the timing device seen in the corners of the photographs in Pls. 5 and 6 was very

useful to measure the exact interval between pictures. It is a disk carrying an arrow and rotating in front of a larger disk which is subdivided into ten sectors as shown. The small disk is rotated by a synchronous motor at 25 rev./sec., so that it is possible to estimate the time interval to within $\frac{1}{500}$ sec.
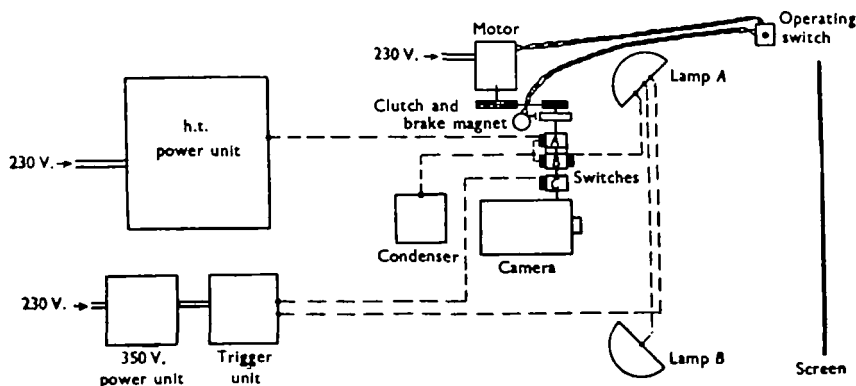
Text-fig. 6. Diagram showing the layout and interconnexions of the separate units. The dotted lines represent concentric polythene cable. The switches are labelled as in Text-fig. 2. (Not to scale.)

FLIGHT ANALYSIS

The wing-beat cycle

It is necessary to consider the wing movements from two points of view. First, relative to the bird, in order to determine the movements of the skeleton and the time relations of the various muscular contractions which are involved in the movement. Secondly, relative to the air, in order to obtain some idea of the nature and magnitude of the aerodynamic forces to which the wing is subjected during the cycle.

Movement relative to the body

The wing-beat cycle may be seen in Pls. 5 and 6. Pl. 5, fig. 1 shows the condition slightly after the beginning of the down beat. The wing is fully extended and the alula is open, thus allowing a high angle of attack around the mid-point of the span (Graham, 1930). The chief muscle active at this phase is m. pectoralis major. The movement which is a simple rotation round the shoulder joint (Pl. 5, figs. 2, 3) continues until it reaches or slightly passes the horizontal (Pl. 5, fig. 4).

Next the tips are seen to swing forward (Pl. 5, fig. 5); during this forward swing the wing starts a complicated series of movements which produce the upstroke. By putting the wing of a pigeon into the positions shown in successive photographs it is possible to trace the skeletal movements which occur, and thus indicate the muscle or muscles which produce such movements. When the articulations of the wing are examined in detail it becomes evident that in the position of Pl. 5, fig. 4 the humerus has almost reached the limit of its downward and forward movement, and therefore that the subsequent forward swing must be associated with flexure within the wing. This flexure involves both the elbow and wrist (Pl. 5, figs. 5, 6). During

this phase, also, the wrist is rotated so that the plane of the primary feather group becomes almost vertical and parallel to the long axis of the body, the muscles involved being m. biceps, flexor carpi ulnaris. By now the activity of m. pectoralis major has ceased, and this point may be taken as the end of the downstroke.

The upstroke is, as stated before, very complex, and so far it is by no means certain which muscles are most important and how flexible is the pattern of their activity. What happens to the wing as a whole is clear. There are at first three movements developing simultaneously: (1) an adduction of the humerus by m. pectoralis tertius, infra spinatus, and later latissmus dorsi; (2) a rotation of the humerus along its long axis so that the radius and ulna become almost vertical (Pl. 6, fig. 1), effected by m. pectoralis minor whose contraction has this result when the humerus is already adducted; (3) a further flexion and supination of the wrist (Pl. 6, fig. 2). When this folding and rotation of the wing is complete a very rapid backward flick ensues (Pl. 6, figs. 2–4). This movement is accomplished by an upward and forward rotation of the humerus around the shoulder joint, coupled with a rapid extension of the wing and pronation of the manus.

The speed of this phase is very high, as can be seen in the spacing of Pl. 6, figs. 2–4. It is clear from the bending of the feathers that the forces at this stage are large, and must be produced chiefly by the extension of the wing under the action of m. triceps and the more distal extensors; also that, since the flick produces a force tending to swing the humerus forward, the movement of the bone must be controlled by a retractor such as m. latissmus dorsi. At the end of the upstroke, where there is no evidence of appreciable aerodynamic forces, and the forward swing continues (Pl. 6, figs. 5, 6), it is probable that m. deltoideus completes the cycle and is followed by the next contraction of m. pectoralis major.

It is convenient for discussion to subdivide the cycle into a number of phases based on the changes of direction of the wing. The simplest scheme is as follows:

(1) *Downstroke*. Begins with the wings vertical, ends with them just below the horizontal and still fully extended (Pl. 5, figs. 1–4).

(2) *Forward swing*. Begins at the end of (1), includes the retraction and rotation of the manus, and ends with the wing tips facing forward and with their surfaces parallel (Pl. 5, figs. 4–6).

(3) *Changeover point*. This is the small time interval where the forward swing has finished and the next stage is about to begin (Pl. 5, fig. 6).

(4) *Backward flick*. This is the phase in which the flexed wing is moved backward and upward and at the same time extended. (Pl. 6, figs. 1–4).

(5) *Extension*. Here the wing, having completed (4), is extended fully prior to the repetition of (1) (Pl. 6, figs. 5, 6).

It is evident that a subdivision as above is quite arbitrary, since the wing in fact passes smoothly from one state to the next. Nevertheless, the output of useful work of the wing is not continuous, and can be related to the different phases described.

If the flight is photographed from in front as in Pls. 7 and 8, it is possible to clarify some of the more complex parts of the cycle.

In Pl. 7, fig. 1, about one-third of the downstroke has taken place. In Pl. 7, fig. 3,

the forward swing is well developed, while in the next figure it is complete. This figure represents the changeover point and corresponds to Pl. 5, fig. 5. Pl. 7, fig. 5, shows the beginning of the backward flick. The flexion and rotation of the wing is clear in this and subsequent figures up to Pl. 8, fig. 1.

In the rest of Pl. 8 the downstroke can be followed through figs. 2–5, while in fig. 6 the forward swing has begun.

Text-figs. 7–12 show the approximate positions of the skeletal elements at various parts of the cycle. The drawings are taken from selected photographs, not necessarily of the same series, the top views being derived geometrically from the other two. The very limited movement of the humerus is evident, also the complicated flexion, rotation and extension during the flick in Text-figs. 10–12.

PATH RELATIVE TO THE AIR

The track and approximate angles of the primary feathers can be seen in Pls. 5–8 during the downstroke, while the separation of the feathers and their rotation during the upstroke is also visible.

There is here a complex sequence of movements which, under the conditions of slow flight, must give a resultant average force which is almost vertical but with a small forward component. In other words, there must be a force equal to the weight of the bird acting in opposition to gravity, and another horizontal force which provides the propulsion.

Since the forward velocity is low and fairly constant it is safe to assume that this component of the air reaction is small. It is clear from the deflexion of the feathers in the photographs, notably Pl. 7, figs. 1 and 6, that both the up- and downstrokes give lift. It is also evident in Pl. 6, fig. 3 and Pl. 7, fig. 6 that a forward component is present during the backward flick. On the other hand, only in Pl. 5, fig. 3 is there any suggestion of a forward force during the rest of the cycle, while in Pl. 7, fig. 3 the forward swing is seen to give a backward component.

It would appear, therefore, that the force cycle is as follows:

During the downstroke there is an upward force with little or no forward inclination. As the wing passes into the forward swing the resultant force is tilted behind the vertical. Then as the upstroke develops the upward force which fell to zero at the changeover point is re-established and is accompanied by a fairly large forward force.

This forward force is maintained throughout the flick, while the lift probably dies away after the middle of this phase. Finally, both lift and propulsive components are absent during the extension.

DISCUSSION

It must be emphasized that the type of flight which has been described is not the normal flight of the pigeon. It is the mode of flight used by the bird either just after take-off or just before landing, where in both cases the forward velocity is very low. It is certainly much more exhausting than fast flight, and cannot be maintained for more than a few seconds. In this type of flight it is probable that the secondary
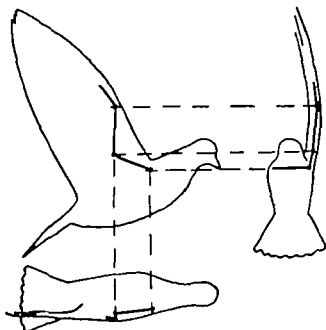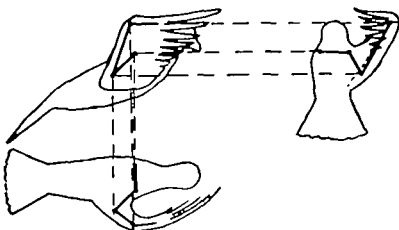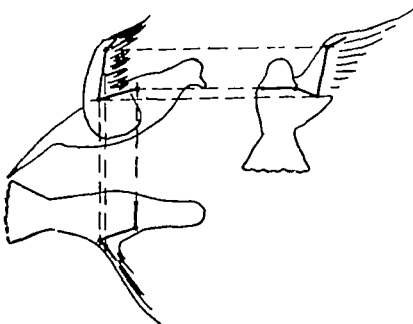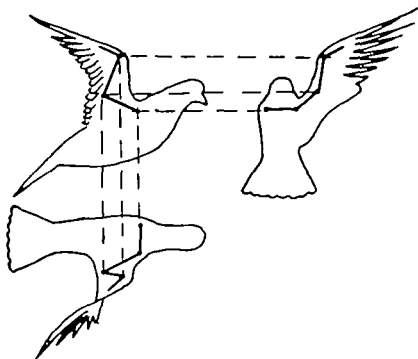
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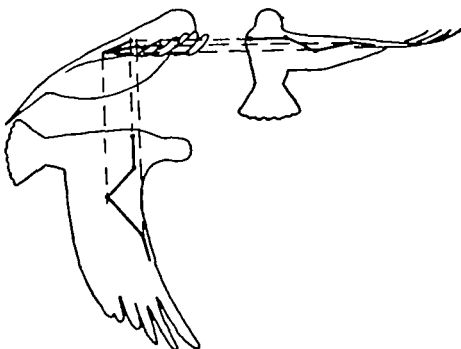
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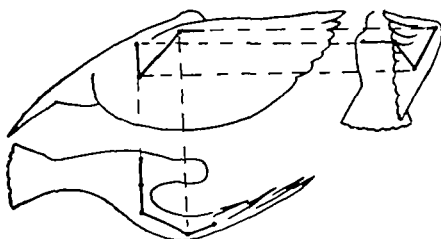
Text-fig. 9.

Text-fig. 10.

Text-fig. 11.

Text-fig. 12.

feathers are of little importance, since their velocity through the air is very low. This is confirmed by the work of Boel (1929), who showed that the slow flight was apparently not impaired when these feathers were removed, while flight was impossible when a part of the distal primaries was cut off. It is suggested, therefore, that the pigeon in slow flight uses only its primary feathers, and that it obtains lift and most or all of the propulsion from the upstroke, but only lift from the down-stroke. Since the bird tires very rapidly the flight must either be very inefficient, or else must throw an undue amount of work on to muscles which are not highly stressed in fast flight.

Until adequate photographs of fast flight are available for study it is only possible to guess at the differences between the two types.

The points of difference which might be expected are (1) the disappearance either wholly or in part of the backward flick, and (2) the transfer of the propulsive function to the downstroke. If this proves to be the case, the work of all the muscles mentioned, except m. pectoralis major and perhaps m. deltoideus, is much reduced, and maintained flight becomes possible.

The path of the wing has been described by many authors and there is general agreement on the course of the down beat, but on the movements and function of the upstroke there are a large number of different opinions. These divergent views arise in two ways: first, the speed is high, making the movement difficult to photograph and impossible to see; and secondly, due to the occurrence of at least two types of upstroke. If consideration is limited to those accounts which describe a movement accompanied by a separation of the primary feathers, the conclusions reached by Headley (1912), Marey (1890), Horton-Smith (1938), and Guidi (1938) appear to be that the primary feathers separate on the upstroke in order to reduce the air resistance. Only Lorenz (1933) seems to postulate any upward force being developed by the wing tip during this part of the cycle. I have some evidence from wind-tunnel tests, which will be dealt with in a separate paper, which suggests that the group of feathers on the hand is behaving as a multi-slotted wing as described by Handley-Page (1921). If this is correct, then the wing under such conditions would have a high value of lift and also a large drag, but this drag would tend to propel the bird forward, since the wing is moving in the opposite direction to the body. This drag may, in fact, be the only source of propulsive component in slow flight.

Finally, there is a point of some functional importance in connexion with the

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Explanation of Text-figs. 7–12

Text-figs. 7–12. Diagrams of the skeletal movements during the flight cycle. Each figure shows the bird viewed from three directions at right angles.

Text-figs. 7–9. Show downstroke with wing fully extended, followed by forward swing. Note that the forward movement is achieved by flexure of elbow and pronation of manus.

Text-fig. 10. Beginning of flick. Shows further flexion of the wing and the backward and upward rotation of the humerus.

Text-fig. 11. Further development of propulsive flick. Continued rotation of the humerus and supination of hand.

Text-fig. 12. Completion of upstroke. Extension of the wing is nearly complete and the manus is returning to the position of Text-fig. 7.

insertion of m. pectoralis major. It has been noted by many workers, for example Headley (1912), that the insertion is on the forward face of the humerus, and that 'Its pull, therefore, tends to lower the front part of the wing relative to the hind part by rotating the bone'.

From the examination of the movement this view appears to be incorrect.

The humerus is never at right angles to the body; it is a fact that during the downstroke, when the wing is fully extended, it makes an angle of not more than 50–60° with the long axis of the body. As a result the pull of the muscle, while clearly tending to rotate the bone, does not necessarily tend to rotate the wing as a whole. In other words, the fact that the humerus has a backward inclination makes its rotation a normal occurrence during the lowering of the wing.

SUMMARY

1. A new high-speed photographic method is described in detail.

2. Illustrations show the results obtained by the application of the technique to the study of bird flight.

3. A detailed account is given of the movements involved in the flapping cycle, with an attempt to indicate the principal muscles active at different parts of the cycle.

4. The basic conditions and limitations of the slow flight of the pigeon are discussed, and the expected differences between it and fast flight are indicated.

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EXPLANATION OF PLATES

PLATES 5 and 6. Pigeon, side view. Ninety-one pictures per sec.

PLATE 5

Fig. 1. Wing in early part of the down beat. The alula is opened, and there is evidence of a forward force on the first two primary feathers.

Fig. 2. Wing horizontal. Forward force not shown.

Fig. 3. Further downward movement. Note the twist of the wing and the beginning of the forward swing. There is probably a slight forward component of force.

Fig. 4. Downward movement complete. Forward movement developing. The bastard wing is still open and the tip is still bent upward, showing that the wing is still active.

Fig. 5. Commencement of the flexure which marks the beginning of the upstroke. Note that the tip feathers are still bent due to pressure on the lower surface.

Fig. 6. Upstroke developing. Flexure of elbow and wrist increasing. Note that the feathers are uncurved, showing that no external work is being done.

PLATE 6

Fig. 1. Upstroke further developed. Flexion has reached its maximum, and the flick is commencing. Note the rotation and bending of the feathers, showing that the air-flow has reversed and an upward force is present.
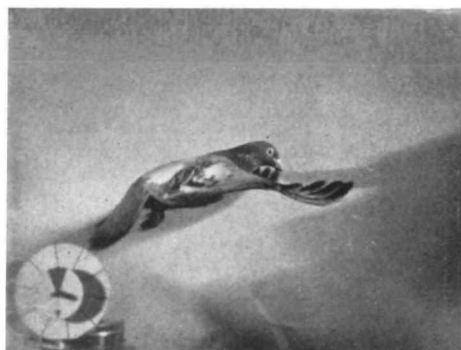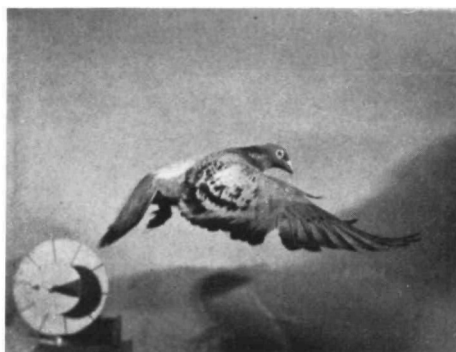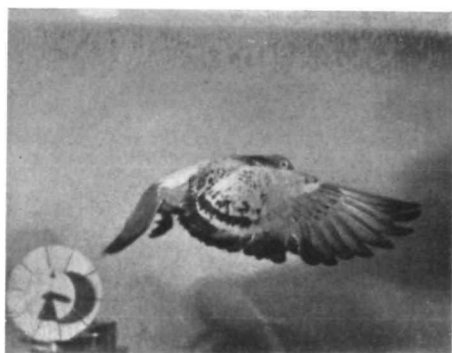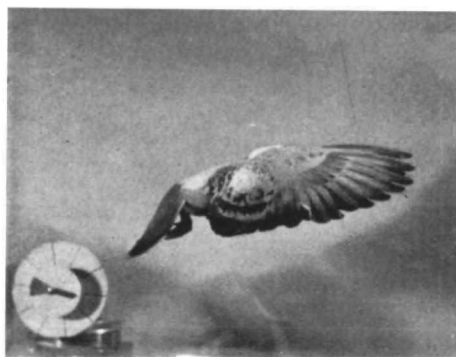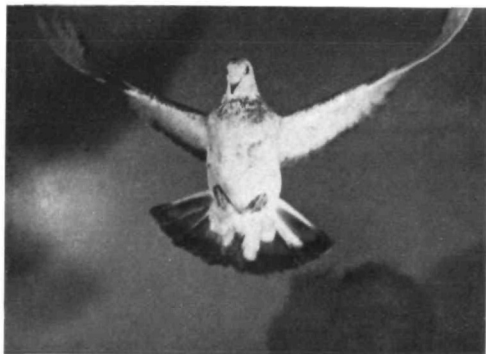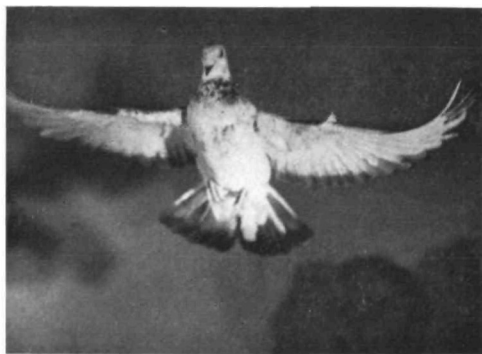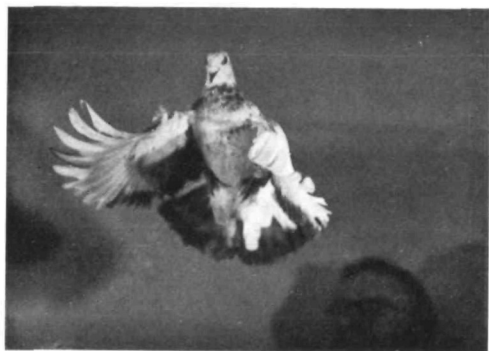
Fig. 1

Fig. 2

Fig. 3

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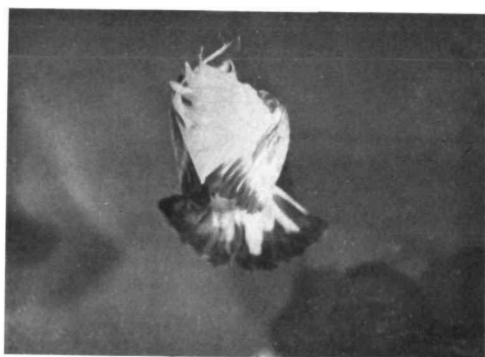

Fig. 5

Fig. 6

BROWN—THE FLIGHT OF BIRDS

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

BROWN—THE FLIGHT OF BIRDS

PLATE 7

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

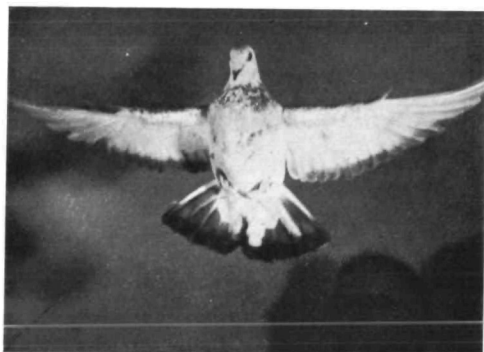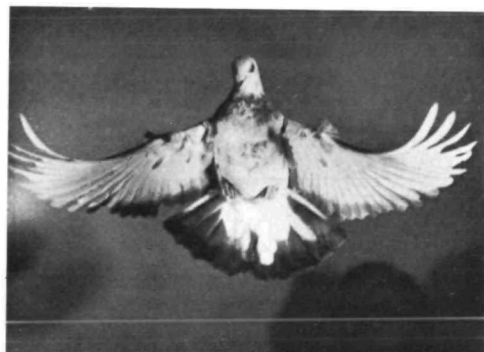BROWN—THE FLIGHT OF BIRDS

Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Fig. 6

BROWN—THE FLIGHT OF BIRDS

Fig. 2. Flick phase of upstroke. Note the rise of the wing as a whole and the upward force on the feathers.

Fig. 3. Upstroke nearly complete. Wing is extending while an upward force is still evident.

Fig. 4. Completion of upstroke. Wing not yet fully extended. Slight bending of tip feathers, therefore movement is still taking place.

Fig. 5. Passive phase with wing extending.

Fig. 6. Beginning of downstroke. Alula is just starting to open.

PLATES 7 and 8. Pigeon, front view. Eighty-five pictures per sec.
Compare with equivalent photographs in side view.

PLATE 7

Fig. 1. Approximately equivalent to Pl. 5, fig. 2.
Fig. 2. Approximately equivalent to Pl. 5, fig. 3.
Fig. 3. Approximately equivalent to Pl. 5, fig. 5.
Fig. 4. Approximately equivalent to Pl. 5, fig. 6.
Fig. 5. Approximately equivalent to Pl. 5, fig. 6 and Pl. 6, fig. 1.
Fig. 6. Approximately equivalent to Pl. 6, fig. 2.

PLATE 8

Fig. 1. Approximately equivalent to Pl. 6, fig. 3.
Fig. 2. Approximately equivalent to Pl. 6, fig. 5.
Fig. 3. Approximately equivalent to Pl. 5, fig. 1.
Fig. 4 as Pl. 7, fig. 1.
Fig. 5 as Pl. 7, fig. 2.
Fig. 6 between Pl. 7, figs. 2 and 3.