HOVERING FLIGHT OF *PLECOTUS AURITUS* LINNAEUS

by

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The long-eared bat, *Plecotus auritus*, often flies about in the crowns of trees hunting insects among the branches. It is very clever in manoeuvering in narrow spaces and hovers easily. It can lift off vertically from the ground, and can move vertically up and down. The purpose of this investigation is to show the principles of the hovering flight; to give a description of the wing-beat cycle and a brief account of the flight mechanics. Hovering in *Plecotus auritus* is earlier described by Eisentraut (1936).

METHODS

High-speed films were taken with a Kodak high-speed camera (time-marking each 1/100 sec) on a flying *Plecotus auritus* for a detailed investigation of the horizontal flight. Film sequences (200-1100 frames per sec) on hovering flight were obtained as a secondary matter, but only side views, thus permitting only a simplified analysis of this flight. Measurements were made on up to 15 wing-beats from three hoverings. The bat (one specimen) flew in a net-tunnel and was lit with 4500 W. Film used was Ilford FP3.

WING-STROKE

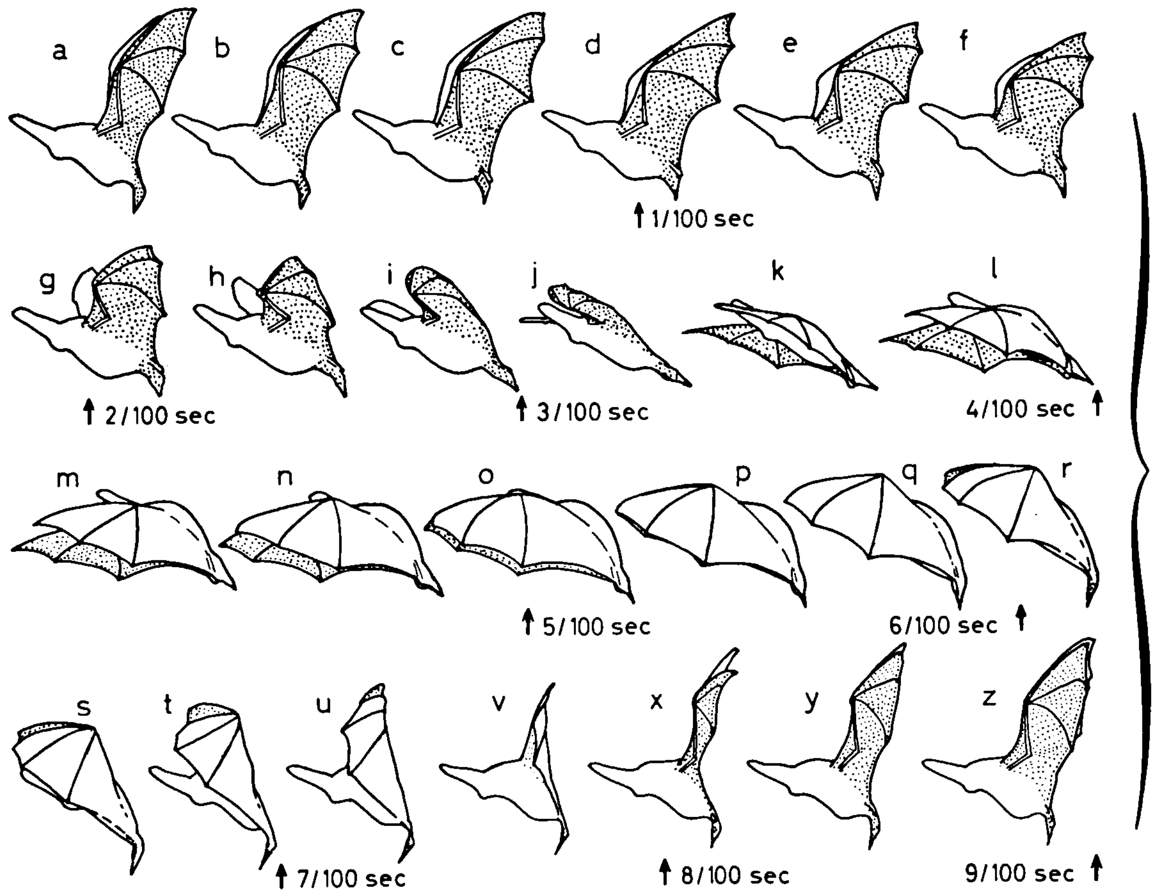
In hovering the long axis of the body is inclined ca. 30° to the horizontal (min. 20°, max. 50°). The inclination of the stroke path is ca. 150° to the horizontal (min. 140°, max. 160°) and ca. 120° to the body. The wing-beat frequency is 10.2-12.5 per sec, the mean speed of the wing tip is ca. 5.2 m/sec (min. 4.5, max. 5.6 m/sec) averaged over the entire cycle, ca. 5.3 m/sec (min. 4.7, max. 5.8 m/sec) averaged over the downstroke, and ca. 5.0 m/sec (min. 4.2, max. 5.7 m/sec) over the upstroke. The greatest speeds of the wing tip are reached in the upper half of the upstroke (10-11 m/sec) and in the middle of the downstroke (8-9 m/sec). The downstroke lasts ca. 46 msec (min. 41, max. 51 msec) and the upstroke ca. 42 msec (min. 37, max. 50 msec).

Additional conditions:

Wing span	26 cm
Wing length	11½ cm
Wing breadth (at level of fifth digit)	5½ cm
Wing area (both wings)	90 cm^2
Membrane area (uropatagium included)	99 cm^2
Weight	9 g
Wing loading	0.1 g/cm^2
Membrane loading	0.09 g/cm^2
Stroke amplitude	120°

The movements of the wings and tail membrane (uropatagium) are shown in figs. 1-3. The downstroke (fig. 1 a-m) starts with the wings extended dorsolaterally. They sweep downwards and forwards fully extended and with high camber, and make sweeping turns upwards and slightly towards each other at the bottom of the stroke. Then the speed of the wings is not definitely broken which would result in a need of powerful acceleration at the start of the upstroke.

The upstroke starts with a slight flexion of the elbow and wrist. A rotation of the humerus causes a rising of the distal part of the radius, thereby making a more favourable angle of attack. Lowering of the uropatagium (and thus the trailing edge of the proximal part of the wing) during the first part of the upstroke also contributes to making a favourable angle of attack. The arm rises upwards and backwards with the hand wing lagging behind (fig. 1 n-s). The ventral sides of the wings then are facing each other. When the radius is inclined 60-70° to the horizontal, extension of the wing starts. A simultaneous reversing rotation of the humerus makes the hand wing produce a rapid backward and upward flick (figs. 1 t-x and 2). The dorsal sides of the wings are then facing each



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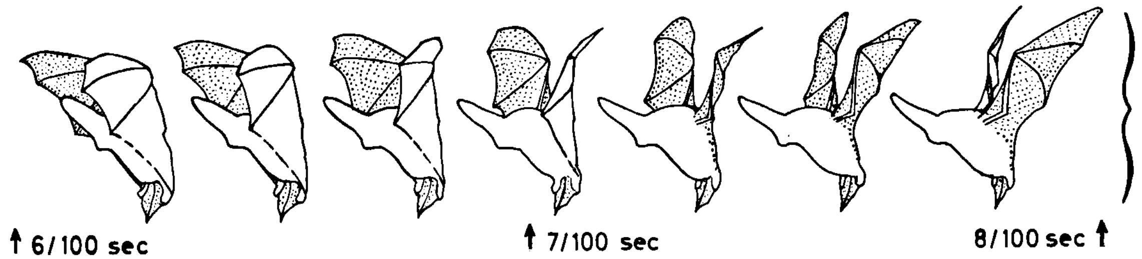

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Fig. 1. The wing-movement cycle of *Plecotus auritus* in hovering flight, viewed from the side. a—m, downstroke; n—z, upstroke. Figs. 1—3 are based on three different representative wing-strokes.

Fig. 2. The flick phase of the upstroke; anterolateral view.

other, the wings being prepared for the downstroke.

During the wing-beat cycle the uropatagium moves up and down as a result of leg movements and by pull exerted by the wing membranes. As pointed out by Vaughan (1959) these movements have two functions: (1) keeping a fairly constant angle of attack of the proximal part of the wing, and (2) maintaining equilibrium of the body during the cycle. He stated that in level flight the uropatagium moves up and down in synchrony with the wing-strokes, which is also the result of my investigation of the level flight. In hovering, however, there is a phase displacement of the tail tip of almost a quarter of a cycle, the uropatagium being

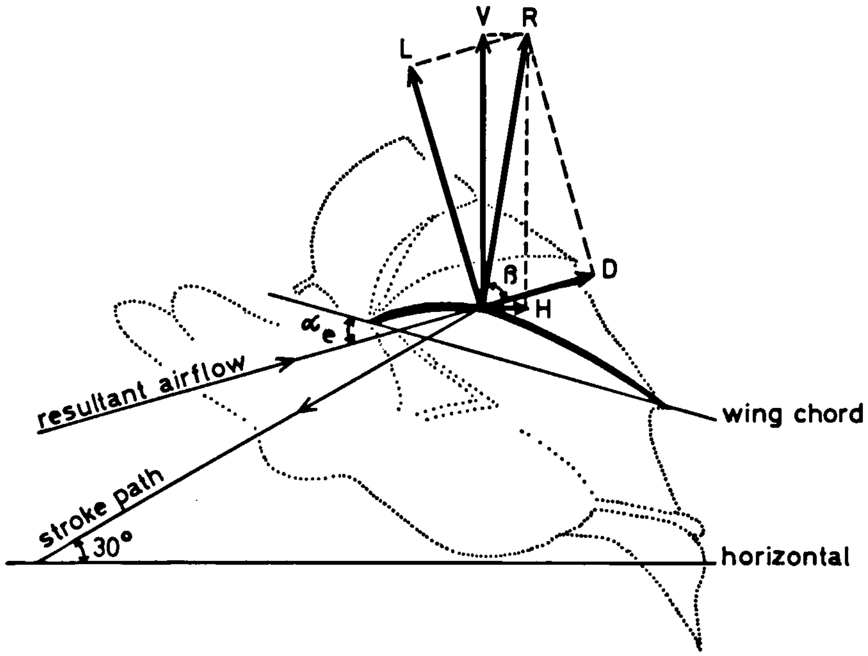

Fig. 4. Schematic diagram indicating the forces acting on the middle of the wing in the middle of the downstroke.

veloped which is upwards and probably with a backward component. Fig. 4 is a schematic diagram showing the forces on the wing in the middle of the downstroke. The wing section along the fifth digit is chosen. This lies about half way from the wing base. In this phase the fifth digit is held almost parallel to the body. The downward flow generated by the wings contributes to making the resultant airflow meet the wings more horizontal than the inclination of the stroke path. The direction of the resultant airstream is arbitrarily chosen in the figure. R is the resultant reaction force exerted by the air against the wing. Its direction is arbitrarily chosen in the figure, too, but depends on the shape of the wing, and the effective angle of attack. In the downstroke it probably is inclined somewhat backwards relative to the vertical. It is usual to resolve this force into two components, one lift component, L, perpendicular to the resultant airflow, and one drag component, D, parallel to the resultant airflow. $L = R \sin \beta$ and $D = R \cos \beta$, where β is the angle between R and the resultant airflow. The resultant aerodynamic force can also be resolved into one vertical upward component, V, and one horizontal backward component, H.

During the first half of the upstroke the wings are partly folded, thereby reducing the area and thus the resistance against the air. During this phase the air reaction on the wing has a forward propulsive component and probably no or a slight vertical downward component.

During the rapid backward flick of the upstroke the dorsal side of the distal part of the hand wing faces posteroventrally (figs. 1 u-x and 2). Thereby a slight vertical upward force may be obtained. This phase is propulsive.

The forces produced may be summarized as follows:

Downstroke: vertical upward force and horizontal backward force.

Upstroke: first half: no or slight vertical downward force and horizontal forward force;

flick phase: slight vertical upward force and horizontal forward force.

The effect of the vertical upward forces is to balance the weight. The backward forces produced during the downstroke cancel the propulsive forces during the upstroke.

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