

GLIDING FLIGHT OF THE DOG-FACED BAT *ROUSETTUS AEGYPTIACUS* OBSERVED IN A WIND TUNNEL

By C. J. PENNYCUICK

Department of Zoology, University of Nairobi

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INTRODUCTION

Tilting wind tunnels have been used to study the gliding performance of the pigeon *Columba livia* (PennyCUICK, 1968), and the laggar falcon *Falco jugger* (Tucker & Parrott, 1970). In both cases the bird was trained to fly in the tunnel in such a way as to remain stationary relative to the apparatus, so that its flying speed was equal to the wind speed, which was under the control of the experimenter. The bird's best gliding angle at any particular speed could be found by adjusting the tilt of the tunnel to the flattest angle at which the bird was just able to glide. The present paper describes similar experiments on a bat.

MATERIAL

All the measurements were made on a male *Rousettus aegyptiacus* (Megachiroptera: Pteropodidae), which was the only individual out of an initial group of six which learned to fly in the tunnel. The bats were caught in a cave near Lake Nabugabo in Uganda, where some thousands of them roost, with the help of Dr F. A. Mutere and members of the East African Virus Research Institute at Entebbe, to whom I am most grateful. The bats thrived in captivity on a diet of pawpaw and banana, varied occasionally with other soft, sweet fruits. The bat which eventually learned to fly in the wind tunnel performed best when its diet was adjusted so as to keep its mass at about 118-120 g (on an *ad lib* diet its mass rose to about 140 g).

METHODS

Wind tunnel

The same wind tunnel was used as that described by PennyCUICK (1968), but it was moved from its former site at Bristol to the University of Nairobi prior to the experiments. The working section was octagonal with a diameter of 1 m, and the angle of tilt could be adjusted from -2° to $+30^\circ$ above the horizontal. The tunnel was of open-jet blower layout, the working section being surrounded by a wire mesh cage.

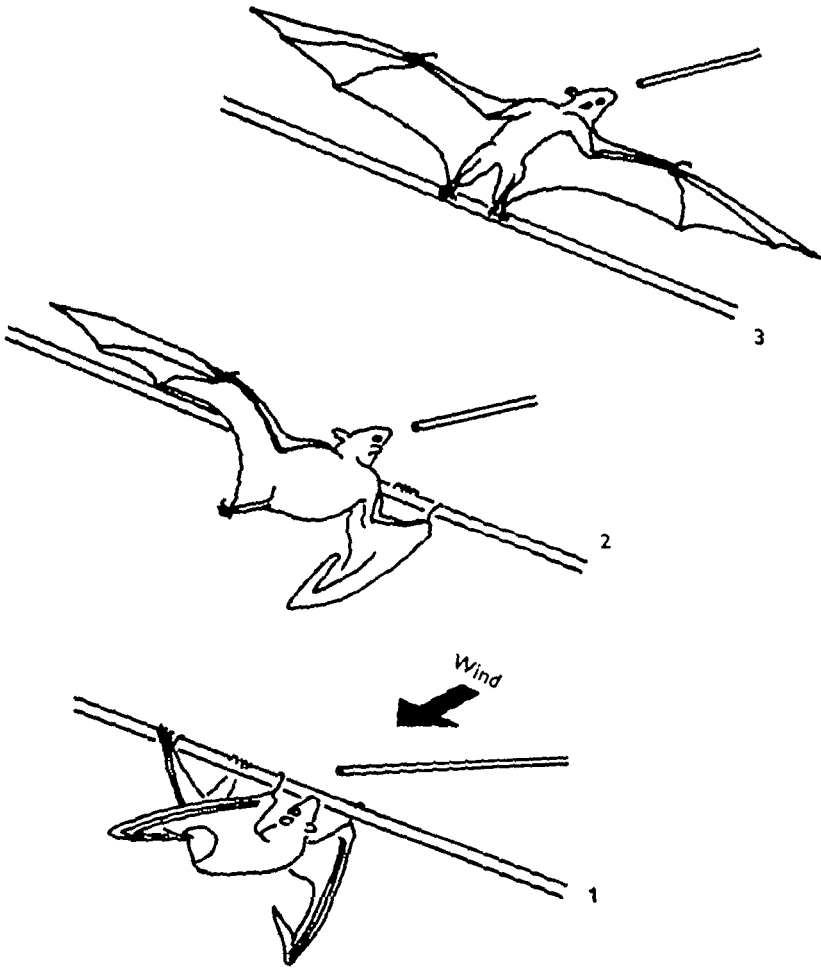
Training

The training method was basically the same as that used for pigeons by PennyCUICK (1968). Training flights and experiments were carried out at dusk or soon after, at which time the bat became active and would go to considerable lengths to obtain a food reward. Banana proved to be by far the most effective inducement.

The first stage of training was to tame the bat until it would fly to the hand for food.

Learning to fly in the wind tunnel was somewhat more difficult than for a pigeon because the bat was unable to stand upright on a perch, and had first to recover from its normal inverted stance before it was in a position to take off.

The bat was first of all suspended from a wooden perch, of 13 mm diameter circular cross-section, which spanned the working section of the tunnel. The reward was offered by means of a Perspex tube of 4 mm inside diameter, filled with banana



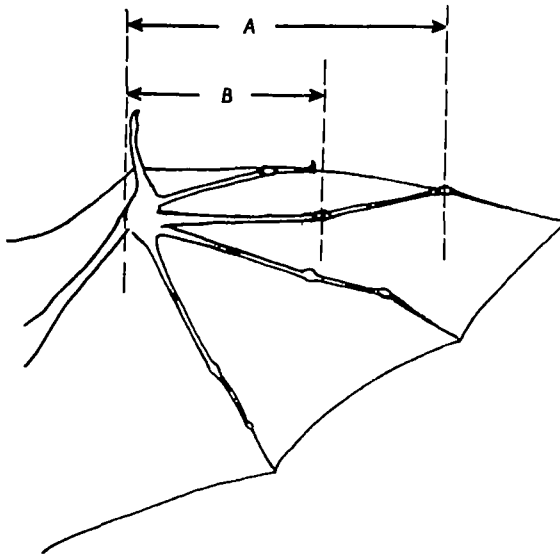
Text-fig. 1. Stages in training the bat to take off from the perch. After reaching stage 3 the bat eventually learned to release its hold on the perch and fly free. The feeding tube was hand-held during training.

pulp, which could be extruded from the end as required by pushing it out with a piston. The bat was first rewarded whenever it raised its head above the *downwind* side of the perch, and it soon learned to spread one wing above the perch in order to raise itself a little higher (Text-fig. 1). Eventually it could lift its body right above the perch, suspending its weight from its wings, but still clinging to the perch with its feet. Two bats were trained up to this stage, of which one learned to release its hold on the perch

After about 10 weeks of almost daily training, and after a further 3 months could fly well enough in the tunnel for measurements to be made. The other one never learned to let go of the perch, and died after about 4 months of training.

Measurement of best gliding angle

When the bat was proficient at flying in the tunnel, the food dispenser was fixed so that the bat had to hover just above the centre of the tunnel in order to feed from it. The bat would climb along the perch to the centre of the tunnel, then take off and fly to the feeder, where it would hover until its mouth was full of banana. It would then fly to the side and land on the wire mesh surrounding the working section, where it would chew and swallow the food, before returning to the perch for another flight. As the individual flights were brief, varying in duration from about 5 s to 1 min, it was not feasible to adjust the wind speed or tunnel tilt during a flight. Instead, the speed was kept constant throughout each session, and the tilt angle was adjusted between flights. Each flight was then scored as either 'definitely able to glide', or 'definitely unable to glide' or 'doubtful'. Because the bat's flight was never as steady as that of a pigeon, it was often difficult to be sure whether it was or was not able to glide, and the true best gliding angle is considered to fall on the borderline between the 'definitely able' and 'doubtful' categories.



Text-fig. 2. The scale of each photograph was determined by measuring two reference lengths on digit 3. Length *A* was measured from the proximal side of the carpal joint to the distal end of the first phalanx, and length *B* from the proximal side of the carpal joint to the distal end of the metacarpal.

Photography

An overhead camera was mounted on a boom above the working section, looking perpendicularly to the airflow, as described by Pennycuick (1968). Initially a Canon Dial half-frame 35 mm camera was mounted in this position, and used for determining wing span and area. Owing to the unsteadiness of the bat's flight, however, it

was difficult to be sure from a single photograph that the wings were in a symmetric gliding attitude, which made the determination of span and area somewhat doubtful. To overcome this difficulty a White 'Stereo Realist' camera was substituted for the Canon Dial. This instrument consists of two separate cameras mounted in a single casting, with their axes parallel and 7.0 cm apart, and with all their controls coupled together, so that two 24 × 23 mm negatives are taken simultaneously on 35 mm film. These were enlarged to make stereo pairs of half-plate (12 × 16.5 cm) prints, which were viewed with a Wild mirror stereoscope. Only those which showed an approximately level and symmetrical attitude of the wings were used to determine wing area.

All the photographs were taken by electronic flash, with the flashgun mounted either beside the camera, or else below the bat, so that the wings were illuminated by transmitted light. Examples of both types of photographs are shown in Pl. 1.

To determine the scale of each photograph two measurements were made on digit 3 of each wing, as shown in Text-fig. 2. This part of the wing was approximately horizontal in all the photographs used. The four estimates of scale so obtained from each photograph were averaged to give the factor used for converting measurements made on the photograph up to life size.

MECHANICS OF THE WING COMPARED WITH THAT OF THE PIGEON

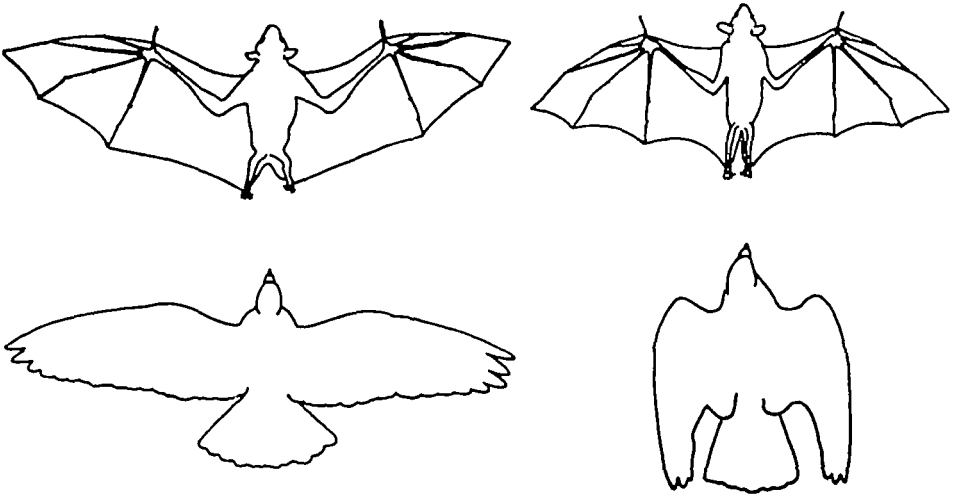
Changes of planform

The stereo photographs provided 24 measurements of wing span and wing area at speeds from 5.5 to 10.0 m/s. The correlation coefficient between wing area and speed was -0.1713 , which is not significantly different from zero. That between wing span and speed was -0.3974 , which is just significant at the 5% level, using a one-tailed test. The corresponding correlation coefficients for the 29 measurements on the pigeon *Columba livia* given by Pennycuick (1968) are -0.8444 and -0.9492 respectively, which are both highly significant ($P \ll 0.001$). The drastic decrease of wing span and area with speed, which is so conspicuous in gliding birds (Pennycuick, 1968; Tucker & Parrott, 1970), was thus not evident in the bat.

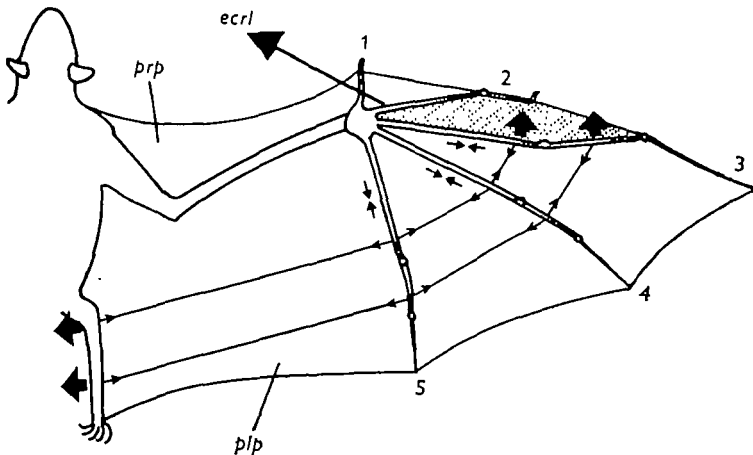
The range of variation of wing area available to the bat was actually somewhat greater than this observation would suggest. The greatest wing area seen in any of the photographs was 566 cm², and the least 399 cm². That is, the bat could reduce its wing area to 70% of the maximum, whereas the pigeon's minimum wing area was 62% of its maximum. Tracings of the two photographs in question are compared in Text-fig. 3, from which it can be seen that the reduction of area is achieved by reducing the angles between the bones supporting the wing, except that between metacarpals 2 and 3. Thus in the attitude of smaller area the humeri are more swept back while the radius is more swept forward, so allowing the propatagium to contract in the spanwise direction, and the fifth metacarpal is more nearly parallel to the body axis, so that the plagiopatagium does the same. The angles between metacarpals 3, 4 and 5 are reduced, allowing the outer wing panels to contract perpendicularly to the bones.

The mechanics of the wing of *Plecotus auritus* have been analysed by Norberg (1970), and the anatomy is similar in *Rousettus* (Dr. U. M. Norberg, pers. comm.). Digits 2 and 3 are interconnected in a special way (Norberg, 1969), and together with the

Small piece of membrane enclosed between them (dactylopatagium minus), constitute a relatively rigid unit, which is resistant to bending in its own plane. The second metacarpal, and hence the whole of this unit, is pulled forward by the extensor carpi radialis longus muscle, and this pull is transmitted through the wing membrane across digits 4 and 5, and thence through the plagiopatagium to the hind leg. The entire



Text-fig. 3. Maximum and minimum wing area in bat and pigeon (see text).



Text-fig. 4. Mechanics of the bat's wing. The stippled area is the dactylopatagium minus, which, together with those parts of digits 2 and 3 which enclose it, forms a rigid unit, resistant to bending in the plane of the membrane (Norberg, 1969). This complete unit is pulled forwards by the extensor carpi radialis longus muscle, of which the direction of pull is indicated by the large arrow marked *ecrl*. This forward pull is transmitted to the membrane attached to the posterior side of digit 3 (broad arrows), and thence through the outer wing panels and the plagiopatagium (*plp*), to be balanced by an opposing inward pull exerted by the hind leg (broad arrows). The lines with open arrowheads represent tension paths through the patagium, which change direction at digits 4 and 5; the bones of these digits are therefore loaded in compression (small solid arrows), as is digit 3 also. The leading edge of the propatagium (*prp*) is held down by the tendon of the occipitopollicalis muscle, which originates on the back of the skull (Norberg, 1970).

wing is thus to be thought of as a single unit under tension, with the membrane stretched between digit 3 and the hind leg, digits 4 and 5 acting as compression members altering the direction of the tension forces (Text-fig. 4). The tension in each of the outer wing panels, and the plagiopatagium, must be approximately equal, and is maintained by elastin fibres within the wing membrane, running parallel to the direction of stretch. When digits 2 and 3 rotate posteriorly, the fibres in all three panels shorten and the skin crinkles as the area of the membrane is reduced. Because of this arrangement the areas of the outer wing panels and of the plagiopatagium are interdependent and have to be adjusted together.

In the bird wing, on the other hand, each flight feather is an independent structure capable of resisting bending moments both in the plane of the wing and normal to it. By overlapping the feathers, the area and planform of the distal part of the wing can be drastically altered without affecting the structural strength of the proximal part. The wing shape characteristic of fast-gliding birds, where the manus is rotated sharply backwards, whilst keeping the inner part of the wing partially extended, would be mechanically impossible for a bat, because it would lead to collapse of the outer wing panels, and this in turn would lead to collapse of the plagiopatagium as well. Thus, while the pigeon in a very fast glide can rotate the morphological 'leading edge' of its wing parallel to the direction of flight, and reduce its wing span to 37% of its maximum value, the bat could not do this, and was only able to reduce its span to 83% of the maximum (Text-fig. 3).

Table 1. *Technical data for the bat at its average weight of 1.16 N, and at different wing areas*

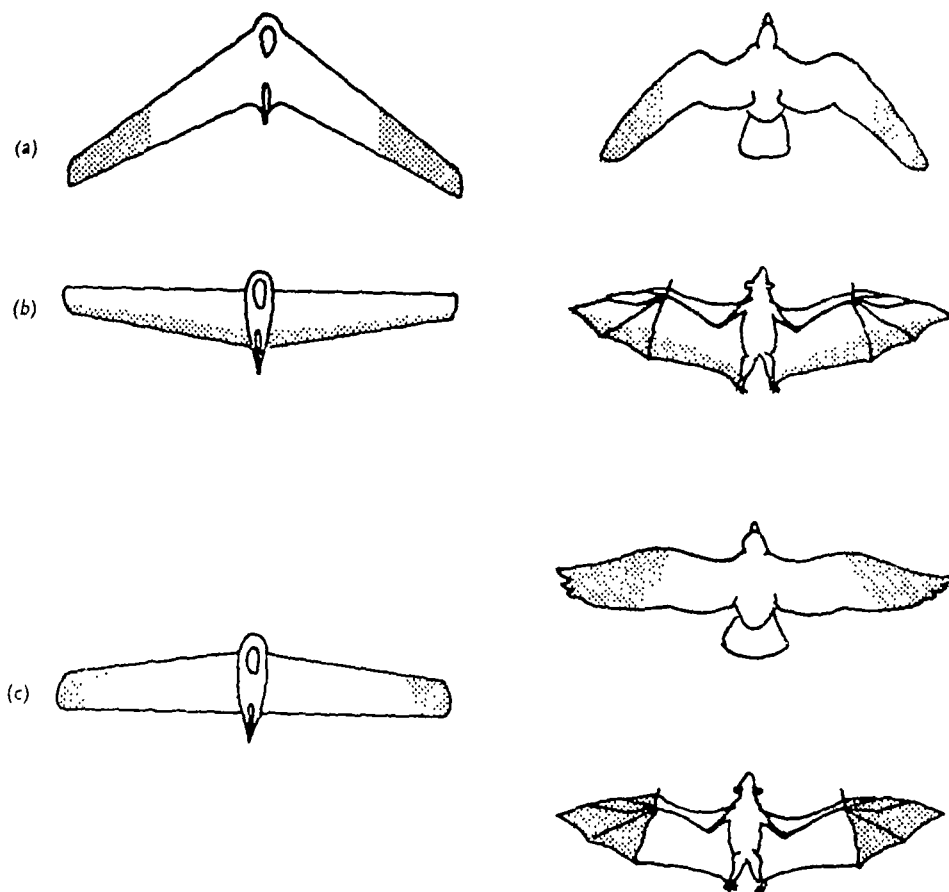
	Minimum area	Average area	Maximum area
Wing area (m ²)	0.0399	0.0462	0.0566
Wing span (m)	0.461	0.494	0.554
Aspect ratio	5.32	5.28	5.42
Wing loading (N m ⁻²)	29.1	25.1	20.5

Although the structure of the bat's wing limits its versatility in one way, it extends it in another, since the arrangement of the fingers allows much more control over the profile shape of the manus than can be achieved with the unjointed feathers of a bird, and this feature is no doubt responsible for the extreme agility of bats when manoeuvring at low speeds.

Wing profile shape

The stereo photographs show that the propatagium is always sharply cambered in flight (Pls. 1, 2). The arrangement is the same as that described in the microchiropteran *Plecotus auritus* by Norberg (1969), the leading edge of the propatagium being held down by the occipito-pollicalis muscle, which originates on the posterior surface of the skull, and whose tendon runs along the anterior edge of the propatagium via the metacarpal of the thumb to the second metacarpal, or thereabouts. (Dr. U. M. Norberg, pers. comm.). This is a muscle unique to bats, which is analogous in action to the tensor patagii muscles of birds.

The upper surface of the proximal part of the wing is not as smooth as in birds. The humerus and radius both project above the wing surface (Pl. 1 *a*), and most probably serve to generate turbulence in the boundary layer. Such an adaptation is readily understandable in relation to the results of Schmitz (1960), who found that in the Reynolds number range in question, a lift coefficient as high as 1.5 could only be obtained if turbulence were artificially introduced into the boundary layers of model wings. The wing surface is also rendered rather wavy by the fact that both the propatagium and the plagiopatagium must bulge upwards to transmit lift to the humerus and radius, so that troughs tend to appear along the anterior and posterior margins of these bones.



Text-fig. 5. Methods of achieving longitudinal stability in tail-less aeroplanes, with suggested equivalents in birds and bats. (a) Sweepback-with-washout (stippled areas twisted in the nose-down sense); e.g. Horten flying wings. (b) Reflex camber (stippled areas deflected upwards), e.g. Fauvel flying wings. (c) Diffuser wing tips (stippled areas deflected downwards), e.g. Northrop flying wings. The mechanisms of these different systems are explained by Weyl (1945a).

A most interesting feature is that the posterior edge of the outer wing panels is normally deflected upwards in steady gliding flight, owing to an upward deflexion of the joints at the distal ends of the fourth and fifth metacarpals, and also of those

between the first and second phalanges of the same digits. Sometimes the posterior edge of the plagiopatagium is deflected upwards as well. This latter effect appears to be under the control of the plagiopatagialis proprii muscles, a group of about 10–12 muscle bundles (visible in Pls. 1*b*, 2), which run antero-posteriorly in the plagiopatagium, posterior to the radius, but without attaching to any part of the skeleton. It appears that when these muscles contract the plagiopatagium becomes S-shaped in section, riding up at the posterior edge, whilst when they are relaxed the plagiopatagium bulges convex upwards over its whole extent (Pl. 2).

The upturned trailing edge is most probably concerned with longitudinal stability and control. Since neither birds nor bats depend on tails for stability, they are to be classified with tail-less aeroplanes in this respect. The principles of stability in such aircraft are well known, and have been explained at length by Weyl (1945*a, b*), who lists four basic ways in which stability can be obtained without using a tail: (1) a combination of sweepback with washout (i.e. twist of the outer part of the wing in the nose-down sense); (2) upward deflexion of the trailing edge of the wing; (3) 'diffuser wing tips', in which the wing tips are bent downwards about an oblique axis: this arrangement confers directional as well as longitudinal stability; (4) sweepforward-with-washin, the opposite combination to (1).

The first three types of stabilizing systems and their suggested use in birds and bats are summarized in Text-fig. 5. It would appear that both birds and bats have diffuser wing tips when gliding slowly with their wings fully spread. In fast gliding flight birds rotate the manus posteriorly whilst keeping the proximal part of the wing extended, and then most probably depend on sweepback-with-washout for stability. Bats cannot rotate their wings in this way, and appear instead to supplement their diffuser tips by upward deflexion of the trailing edge.

The fourth stable arrangement listed above, sweepforward-with-washin, has been tried in aircraft but has certain disadvantages. Neither birds nor bats seem to use it, although it would be mechanically possible for both to do so.

Longitudinal control, as opposed to stability, is apparently achieved in gliding birds by variations of sweepback, so shifting the centre of lift forward or back with respect to the centre of gravity (PennyCUICK & Webbe, 1959). The amount of such movement available to a gliding bat is much more limited, however, and *Rousettus* appears to supplement this action by using its plagiopatagialis proprii muscles as an elevator control. Increasing the upward deflexion of the trailing edge, as in Pl. 2*b*, would give rise to a nose-up pitching moment, and vice versa.

Speed range

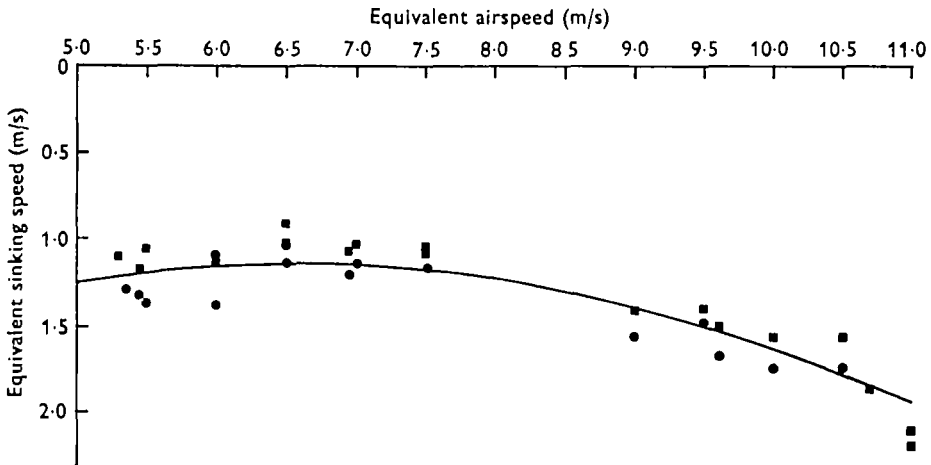
GLIDING PERFORMANCE

Text-fig. 6 shows the results of 33 determinations of best gliding angle at equivalent airspeeds between 5.5 and 11.0 m/s. For any particular occasion the flattest angle at which the bat could definitely glide is plotted, and also the steepest 'doubtful' observation (see p. 835); on a few occasions observations in only one category were obtained. The results are expressed in the form of a conventional glide polar, that is, a plot of equivalent sinking speed against equivalent airspeed.

The bat's minimum gliding speed when at its normal weight was 5.3 m/s, and its maximum lift coefficient was about 1.5. The highest speed at which measurements

ere made was 11.0 m/s ($C_l = 0.33$). At this speed the bat had difficulty in controlling its position in flight, and also in controlling its wings when clambering on the perch or the sides of the cage, and so flight at higher speeds was not attempted because of danger to the bat. The speed range between 7.5 and 9.0 m/s was also avoided because of vibration caused by a mechanical resonance in the tunnel support system.

The Reynolds number range, based on mean chord, was from 3.26×10^4 to 6.79×10^4 .



Text-fig. 6. Glide polar, from wind-tunnel observations of best gliding angle. Circles: flattest angle at which bat was definitely able to glide. Squares: steepest angle at which bat doubtfully able to glide (see text).

The maximum lift coefficient given for the pigeon by Pennycuick (1968) was 1.3, but this figure was based on the sum of wing area and tail area, on the grounds that the tail appeared to contribute some lift. The maximum lift coefficient based on wing area alone would be 1.5, and it is perhaps more consistent to compare maximum lift coefficients on this basis. Tucker & Parrott's (1970) figure of 1.6 for the laggar falcon *Falco jugger* is also based on wing area alone, and in the case of the bat there is of course no choice, since it has no tail, aerodynamically speaking. Thus there seems to be little difference between bat and bird wings in this particular.

Regression analysis

Owing to the absence of any marked changes of wing shape at different speeds the results shown in Text-fig. 6 (to some of which no reliable measurements of wing area or span can be attached) can reasonably be analysed on the assumption that wing planform is independent of speed. A curve of the form

$$V_e = \frac{\beta}{V} + \gamma V^3, \tag{1}$$

can then be fitted through the data, where V_e is the equivalent sinking speed, V is the equivalent airspeed and β and γ are constants. The estimates of the constants calculated by the least-squares method were

$$\beta = 5.51, \\ \gamma = 1.07 \times 10^{-3},$$

and the curve obtained by substituting these values in equation (1) is plotted along with the data in Text-fig. 6.

As explained by Pennycuick (1971) the regression constant β can be used to estimate the span efficiency factor k , defined by the relationship

$$k = \frac{C_{di}\pi A}{C_l^2}, \quad (2)$$

where C_{di} is the induced drag coefficient, C_l is the lift coefficient and A is the aspect ratio. γ gives an estimate of C_{do} , the drag coefficient (referred to wing area) at zero lift. Using average values for the weight, aspect ratio and wing area (Table 1), the estimates of these quantities were

$$k = 2.23,$$

$$C_{do} = 0.0440.$$

In the ideal case of elliptical lift distribution k would be 1. In aeroplane wings k is commonly about 1.1 or 1.2, but a value of 2.23 for k would imply a degree of inefficiency unknown in aeronautical engineering.

The very high estimate of k results from the assumption, implicit in the regression analysis, that the drag rise observed at high lift coefficients (low speeds) is entirely due to induced drag, and that the wing profile drag coefficient is independent of the lift coefficient. An estimate of this (supposedly constant) wing profile drag coefficient is obtained below by subtracting other sources of drag from the total drag. This can be regarded as an extreme assumption, the other extreme being to assume that $k = 1$, and that most of the low-speed drag increase is due to an increase of wing profile drag coefficient at high lift coefficients. These two extreme interpretations will now be more explicitly examined.

Interpretation 1: $k = 2.23$, $C_{do} = 0.0440$

First, if it is assumed that k really is 2.23, then $C_{do} = 0.0440$ represents an estimate of the sum of the body drag coefficient and the wing profile drag coefficient (both referred to wing area). The body drag was separately estimated from measurements on the wingless body of a dead *Rousettus*, which was frozen in the normal flying attitude and mounted on a drag balance, in the same way as was described for the pigeon by Pennycuick (1968). The drag of the body was found to be 0.0460 N at an equivalent airspeed of 7.70 m/s. The mass of this bat when it died was 78.2 g, as compared to an average of 118 g for the individual on which the in-flight measurements were made. The drag measurement was therefore scaled up in proportion to the two-thirds power of the mass, giving an estimate of 0.0608 N for the body drag of the bat which flew in the wind tunnel. Referring this to the average wing area listed in Table 1, the body drag coefficient C_{dob} would be

$$C_{dob} = 0.0364.$$

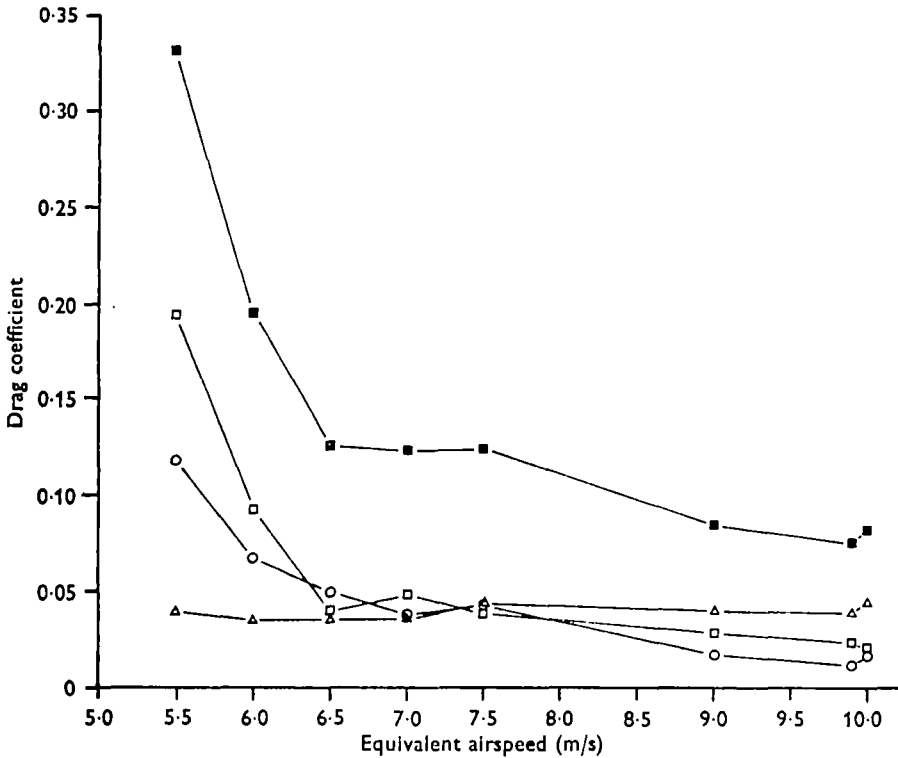
The wing profile drag coefficient C_{dow} can now be estimated as the difference between C_{do} and C_{dob} , so that $C_{dow} = 0.0440 - 0.0364 = 0.0076$.

Interpretation 2: $k = 1$

An alternative method of analysis is to partition the total drag coefficient into three fractions representing induced drag, body drag and the remainder (attributed to wing

profile drag), as was done for the pigeon by Pennycuick (1968). To do this, some assumption has to be made about k , for which an extreme low value is $k = 1$.

The results of analysing the data in this way are shown in Text-fig. 7. The estimated induced drag, assuming $k = 1$, is now not nearly sufficient to account for the high total drag seen at very low speeds, and so it has to be assumed that the wing profile drag coefficient rises sharply at the lowest speeds to the rather high value of 0.19. A similar effect seen in the pigeon was attributed to changes of wing planform, but this explanation would be implausible in the bat.



Text-fig. 7. Drag coefficient analysed on the assumption that the span efficiency factor = 1. Solid squares: total drag coefficient. Open circles: induced drag coefficient. Open triangles: body drag coefficient. Open squares: residual drag coefficient, attributed to wing profile drag. All drag coefficients are referred to wing area, measured from photographs.

Intermediate interpretation

The first interpretation may be doubted, not only on account of the very high value of k , but also because the estimated wing profile drag coefficient C_{dow} is suspiciously low. Schmitz (1960) found that the minimum profile drag coefficient of a cambered plate tested at a Reynolds number of 42 000 was 0.026, and it is perhaps unlikely that the rather irregularly shaped profile of the bat would achieve a C_{dow} less than a third of this, at approximately the same Reynolds number. It is to be expected on the one hand that k would be substantially greater than 1, and on the other hand that C_{dow} would rise appreciably at high lift coefficients, so that the correct interpretation probably lies in between the extremes represented by $k = 2.23$ and $k = 1$. For instance, if one

were to assume that $k = 1.5$, then C_{dow} would be about 0.018 at the higher speed, rising to 0.13 in the neighbourhood of the maximum lift coefficient. The question could probably be resolved by direct measurements of profile drag by the wake traverse method (Pankhurst & Holder, 1952), but unfortunately facilities were not available to try this.

CONCLUSION

The bat's best gliding angle (about 6.8) is slightly better than that of the pigeon, but otherwise its low-speed performance is closely similar. Owing to its inability to reduce the area of the outer part of the wing without collapsing the inner part, the bat is less successful at gliding very fast, and its speed range is not so wide as that of the pigeon. On the other hand, bats are most probably more manoeuvrable than birds in low-speed flight, because of their greater control over the profile shape of the manus. There are thus no grounds for suggesting that the flight of bats is notably 'better' or 'worse' than that of birds. Each has an advantage in certain aspects of performance, but in most respects their abilities and efficiency are much the same.

SUMMARY

1. A bat was trained to fly in a tilting wind tunnel. Stereoscopic photographs were taken, both by reflected and by transmitted light, and measurements of best gliding angle were made.

2. Variation of wing span and area at different speeds was much less than in birds. This is attributed to the construction of the wing, which prevents the bat from folding back the manus in flight, because this would lead to collapse of the plagiopatagium.

3. The trailing edge of the wing is normally deflected upwards in flight, at least in the distal parts. This is interpreted as providing longitudinal stability. The plagiopatagialis proprii muscles appear to act as an elevator, by deflecting the trailing edge of the plagiopatagium upwards.

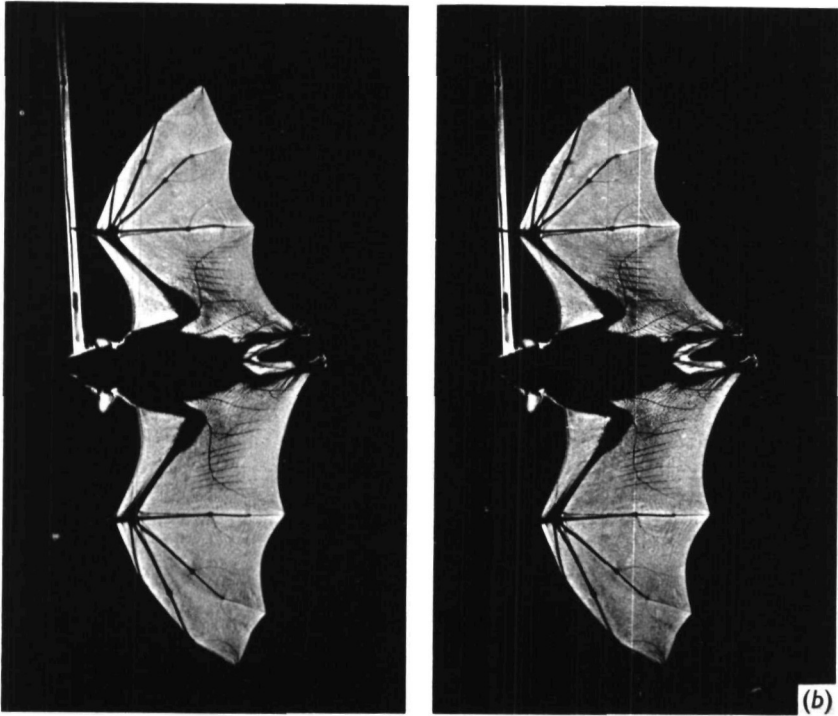
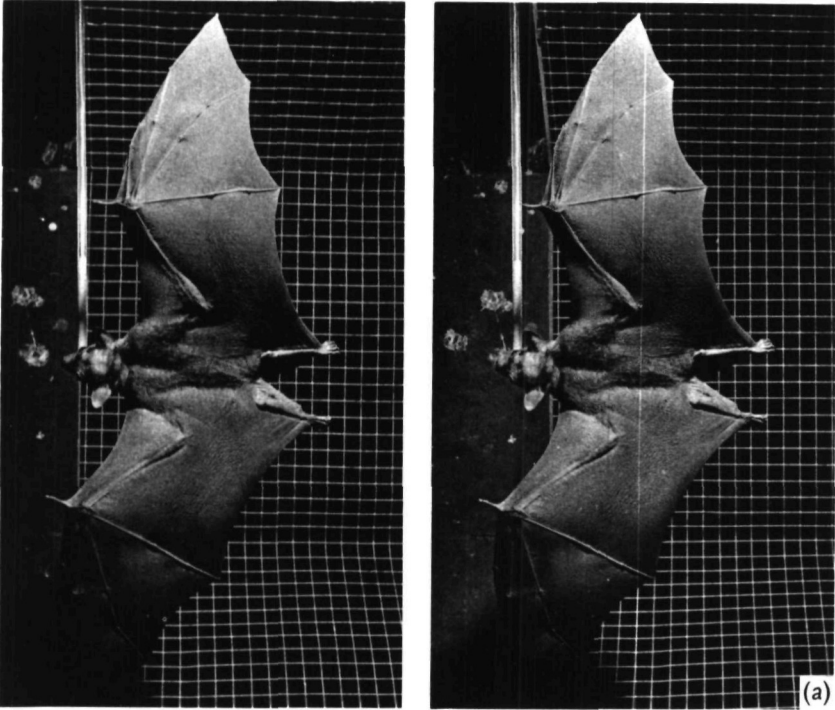
4. The speed range over which the bat could glide was 5.3–11.0 m/s. Its maximum lift coefficient was 1.5, and its best glide ratio 6.8:1. The Reynolds number range, based on mean chord, was 3.26×10^4 to 6.79×10^4 .

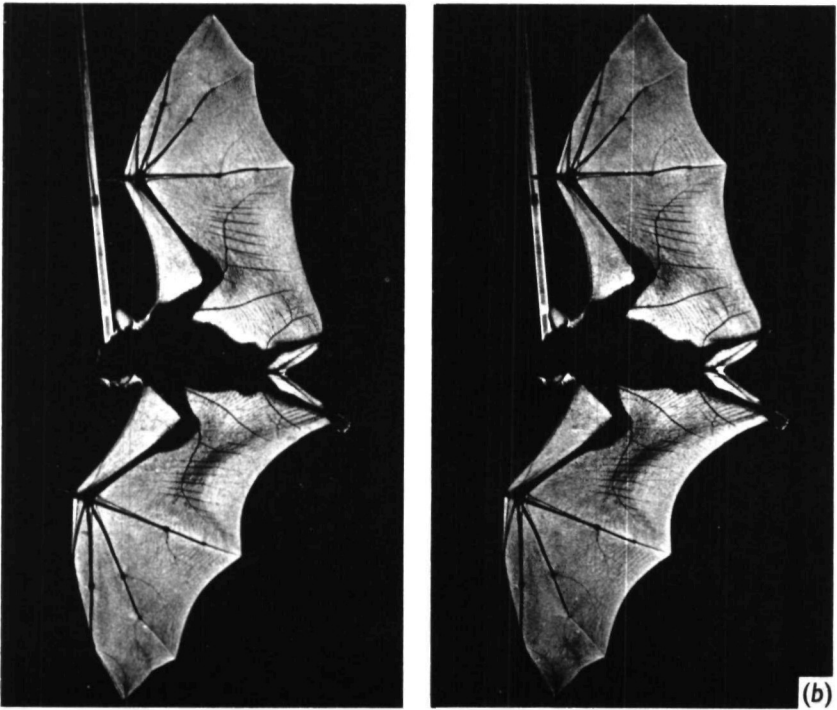
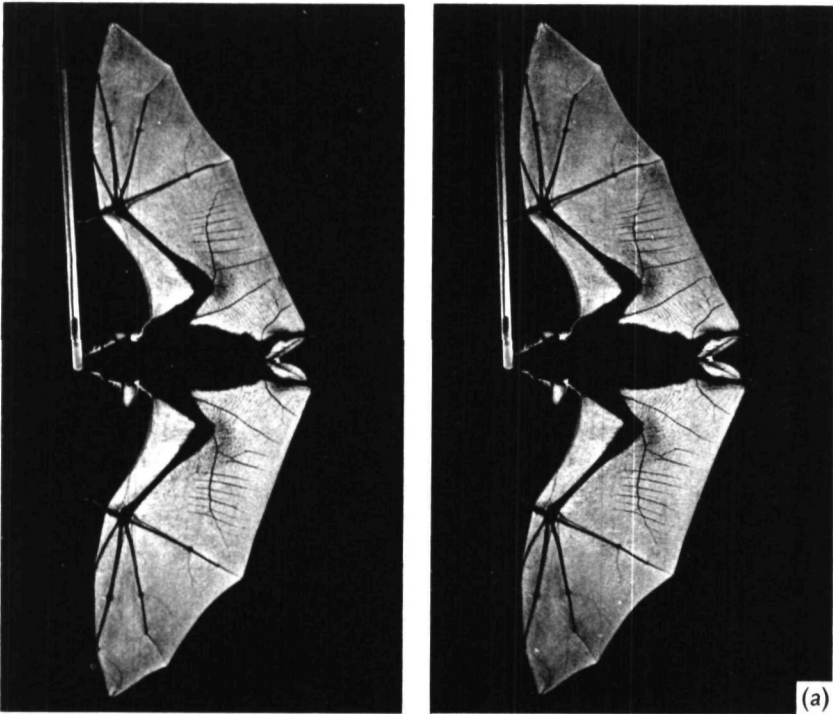
5. A simple regression analysis of the glide polar indicated a very high span efficiency factor (k) and low wing profile drag coefficient (C_{dp}). On the other hand, a drag analysis on the assumption that $k = 1$ leads to an improbably large increase in the estimated C_{dp} at low speeds. It is suggested that the correct interpretation probably lies between these extremes, with $k \approx 1.5$; C_{dp} would then be about 0.02 at high speeds, rising to somewhat over 0.1 at the minimum speed.

6. It would appear that the bat is not so good as a pigeon at fast gliding, but better at low-speed manoeuvring. On most points of performance, however, the two are remarkably similar.

The transport of the wind tunnel from its original site at Bristol to Nairobi was financed by grants from the East African Wild Life Society, the Ministry of Overseas Development and University College Nairobi (now the University of Nairobi) to all of whom I am most grateful.

I have relied heavily on the advice of my colleague Dr F. A. Mutere for general





formation on bat biology, and for the selection of material. I am also indebted to Dr Mutere for organizing the capture of the bats, and also to those members of the staff of the East African Virus Research Institute at Entebbe who helped with this operation. I am indebted to Drs. A. and U. M. Norberg for reading the typescript and making a number of valuable suggestions.

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EXPLANATION OF PLATES

Each pair of photographs should be viewed with a pocket stereoscope, when a three-dimensional image will be seen.

PLATE 1

(a) Symmetrical gliding attitude, with oblique reflected light. The humerus, and more especially the radius, project above the wing surface, as does the third digit; the function of this is thought to be to trigger turbulence in the boundary layer. The trailing edge of the outer wing panels is deflected upwards, mainly as a result of upward deflexion of the metacarpo-phalangeal joint of digit 5, and of the interphalangeal joint of digit 4. There is also slight upward deflexion of the trailing edge of the plagiopatagium, especially of the left wing, and the crinkling of the membrane caused by the antero-posterior contraction of the plagiopatagialis proprii muscles can be seen on both wings.

(b) The area of the outer wing panels (chiropatagium) can be reduced by reducing the angles between metacarpals 3, 4 and 5. The angle between metacarpals 2 and 3 does not change because these two digits are interconnected in such a way as to form a rigid unit which holds the leading edge of the wing forward (Norberg, 1969). Reduced tension in the outer membranes allows them to bulge upwards, and this is even more marked in the plagiopatagium. The radii are always raised when wing area is reduced, so making the area of the proximal parts of the wing appear in the photograph to be less than it really is.

PLATE 2

(a) Symmetrical glide at almost the minimum speed (5.5 m/s). The plagiopatagialis proprii muscles (running antero-posteriorly behind the radius) are fully relaxed, and the plagiopatagium bulges upwards over its full extent. Its inner end, and also the uropatagium, is controlled by the hind legs.

(b) An asymmetrical attitude in which the bat has moved a little too far to the right of the feeder, and is correcting this. The plagiopatagialis proprii muscles of the left wing are strongly contracted, causing the trailing edge of the plagiopatagium to rise sharply; this is augmented by raising the left leg. Although the right leg is depressed, and the right plagiopatagialis proprii muscles are only slightly contracted, there is some upward deflexion of the trailing edge over the whole span of both wings, which would be expected to produce a nose-up pitching moment.