MOMENTS OF INERTIA OF BAT WINGS AND BODY

By MIKAEL THOLLESSON and ULLA M. NORBERG

*Department of Zoology, University of Göteborg, Box 250 59, S-400 31
Göteborg, Sweden*

Summary

The moments of inertia of the wings about the shoulder joint and about the roll axis were estimated in eight species of bats, using strip analysis. The moment of inertia of the bat's trunk about the roll axis was estimated by assuming the body and head to be ellipsoids. The slopes of the regressions of moment of inertia of one wing about the shoulder joint (J_w) *versus* body mass (m_{tot}), wing span (b) and wing area (S) were as expected for geometrically similar animals of different size. The exponent for J_w *versus* body mass in bats deviates from that found for birds, while the exponent for J_w *versus* wing span does not. A multiple regression was used to show that J_w may be estimated by:

$$J_w = 4.49 \times 10^{-3} m_{tot}^{0.53} b^{2.15} S^{0.65} .$$

The mean value of the moment of inertia originating from the trunk is 7 % of the bat's total moment of inertia (of wings and body combined) about the roll axis. The mass of one wing (m_w) was plotted against body mass for the eight bat species, which gives:

$$m_w = 0.112 m_{tot}^{1.11} .$$

The slope for our bats, 1.11, is similar to that obtained for birds, 1.10. Adaptations to reduce the moments of inertia may be more important for increasing a bat's flight agility (roll acceleration) than for decreasing the total mechanical power required to fly. The influences of wing moment of inertia and wing shape on manoeuvrability and agility are discussed.

Introduction

In powered flight, a flying bat must do work with its flight muscles to move the wings in order to generate lift and thrust. The rate at which this work is done is the mechanical power required to fly. The mechanical power is the sum of the *aerodynamic power*, which is the power needed to elicit sufficient aerodynamic force, and the *inertial power*, which is the power needed to oscillate the wings. The aerodynamic power consists of three components: the *induced power* is the rate of work required to generate lift and thrust, whereas the *wing profile power* and *parasite power* are the powers needed to overcome form and friction drag of the wings and body, respectively.

The connection between wing and body shape and the elicited aerodynamic forces is given by, for example, Pennycuick (1975, 1989) and Norberg (1990). The induced power is the main power drain in hovering and slow flight, and to minimize this component the weight should be low and wing span long. Form and friction drag are high in fast flight and, to minimize wing profile power, the wing area should be small. To minimize parasite power, the body should be slim and streamlined.

Inertial power may be of importance in hovering and slow flight, and moment of inertia is important for a bat's manoeuvrability and agility. An estimate of the inertial power, P_{iner}, is given by:

$$P_{iner} = 16J_w\pi^2f^3\Phi^2 \,, \tag{1}$$

where J_w is the moment of inertia of one wing about the shoulder joint, f is wingbeat frequency and Φ is wingbeat amplitude (see Norberg, 1990). The inertial power is lower in medium and fast flight than in hovering and slow flight, since both f and Φ decrease with increased flight speed (Pennycuick, 1975, 1990). Norberg (1976a) estimated the inertial power to be less than 5 % of the total power in *Plecotus auritus* flying close to its minimum power speed. The inertial power is considered to be more important at lower speeds and in hovering (Norberg, 1987).

The upper limit of wingbeat frequency is considered to be set by the strength of bones, muscles and tendons accelerating the oscillating limb (Hill, 1950; Pennycuick, 1975, 1990). Variables affecting wingbeat frequency are body mass, wing span, wing area, wing moment of inertia and air density (Pennycuick, 1990). Using a combination of multiple regression and dimensional analysis, and assuming that wing moment of inertia scales with body mass (m) and wing span (b) as $J_w \propto mb^2$, Pennycuick (1990) showed that wingbeat frequency would scale with the wing's moment of inertia as $f \propto J_w^{-1/6}$. An increase in the moment of inertia by, for example, 10 % would then cause a slight decrease in wingbeat frequency by 1.8 %, and the inertial power would scale with J_w as $P_{iner} \propto J_w^{1/2}$.

The ability to make tight manoeuvres can be separated into two different components, the radius of the turn, which is a measure of manoeuvrability, and the roll acceleration, which is a measure of agility (Norberg and Rayner, 1987). The roll acceleration is inversely proportional to the moment of inertia about the roll axis (Andersson and Norberg, 1981; Norberg and Rayner, 1987).

The moment of inertia about the roll axis originating from the body has been assumed to equal in magnitude that originating from the wings; Aldridge (1985) estimated the body moment of inertia to be 0.84×10^{-6} kg m^2 in *Plecotus auritus*, which is about eight times as large as our result, and a little less than our value for the wing moment of inertia. There are very few data available on moments of inertia in flying animals. A recent paper (Kirkpatrick, 1990) describes the scaling of moment of inertia of bird wings, but there are only a few measurements of moment of inertia of bat wings.

The purpose of this investigation is to find out how moments of inertia of the wings and body scale with various morphological characteristics. We have

addressed the following questions. (1) How does wing moment of inertia in bats scale with body mass, wing span and wing area, and are the regression equations compatible with the rule of geometric similarity? (2) Do the above regressions for bats deviate from those found for birds? (3) What is the relative importance of the moment of inertia about the roll axis originating from the body and from the wings? (4) Are there any differences in wing moment of inertia among bats with different wing shapes and flight behaviour? We have also discussed how moments of inertia affect a bat's flight performance.

Materials and methods
Definitions
The notation, symbols and units used in this paper follow the recommendation of IUPAP (1978), and we use SI units. We use the definitions of morphological flight variables given by Norberg (1981a, 1990). *Total mass (body mass)*, m_{tot}, is the total mass of the bat, *trunk mass*, m_t, is the mass of the trunk, *head mass*, m_h, is the mass of the head, and *wing mass*, m_w, is the mass of one wing which, of course, equals the sum of the masses of all the chordwise wing strips shown in Fig. 1A. *Wing span, b,* is the distance between the wing tips of the bat with extended wings and their leading edges held along a straight line normal to the long axis of the body. *Wing area, S,* is the total area of the two wings (in the extended position), the tail membrane (uropatagium) and the body area in between the wings and tail, that is, the area of the total silhouette with the head excluded.

The overall shape of the wing can be described by the *aspect ratio, AR,* a measure of wing narrowness, defined as the wing span divided by the mean wing chord. It can be estimated as b^2/S. Wing-tip indices were introduced by Norberg and Rayner (1987). The *wing-tip shape index, I,* is determined by the relative sizes of the hand wing (the wing part distal to the fifth digit) and the arm wing (the wing part between the body and the fifth digit) and so is a measure of wing-tip angle and hence of wing-tip shape independent of the extent of the hand wing. It is given by $I=T_s/(T_l-T_s)$, where T_s is the *wing-tip area ratio*, given by the ratio of the hand-wing area to the arm-wing area, and T_l is the *wing-tip length index*, given by the ratio of the length of the hand wing to the length of the arm wing. *Wing loading, WL,* is weight divided by wing area ($m_{tot}g/S$, where g is acceleration due to gravity). Both flight speed and the radius of a banked turn are dependent on wing loading; any characteristic flight speed is proportional to the square root of wing loading, whereas the radius of turn is directly proportional to wing loading. Species with a low wing loading can thus fly slowly and make tight turns. *Relative wing loading, RWL,* is an index of wing loading of geometrically similar animals and with the effect of size removed. It can be expressed as $m_{tot}g/Sm_{tot}^{1/3}$ (Norberg, 1990).

The *moment of inertia* is a mechanical property defined as

$$J = \int r^2 dm,\qquad(2)$$

where r is the distance from the fulcrum (axis) about which mass m is revolving.

Animals used and their flight behaviour

The moments of inertia of one wing about the shoulder joint and about the roll axis were determined for 18 individual bats representing seven different species (listed in Table 1) of which two belong to the Megachiroptera and five to the Microchiroptera. Data for one additional microchiropteran species, *Nyctalus noctula*, are from Rayner (1986). This measurement is the mean of data for several individuals (number not given).

Since most bat species are vulnerable and have been placed under protection, the study had to be carried out with available (dead) material. Most of the animals had been kept in sealed plastic bags in a freezer, but we only used bats that had not decreased significantly in mass. Bats that had lost considerable weight (more than can be explained by ordinary weight fluctuations) were not included in the investigation.

Five of the bat species belong to the same family (Vespertilionidae), all of which are insectivorous. A sixth insectivorous species is *Otomops martiensseni*, belonging to the family Molossidae. Of the insectivorous bats, *O. martiensseni*, *N. noctula*, *Vespertilio murinus* and *Eptesicus nilssoni* are open-area foragers that often fly at high altitudes. *E. nilssoni* also often forages around tree crowns, but avoids dense vegetation. *Pipistrellus pipistrellus* prefers open forest spaces. *Plecotus auritus* forages among vegetation with high manoeuvrability and is able to hover. Frugivorous bats, such as *Rousettus aegyptiacus* and *Epomophorus anurus*, often commute long distances to forage and cling onto branches during foraging.

Procedure

Total body mass and length, and width and height of the body and head were measured before the specimen was pinned to a board covered with millimetre graph paper. The wings were outstretched with their leading edges more or less along a straight line, as they were estimated to be in the middle of the downstroke, and in a position giving a quite tense patagium. Wing span was then measured in this position. The shape of the wing was drawn on the millimetre paper, and this was used to determine wing area by counting the squares enclosed by the bat outline.

The wing was then cut into a number of chordwise strips, varying from 10 strips of 10 mm width for the smaller specimens, to 16 strips of 15 mm width for the largest. Because of the lower mass at the wing tip, the distal strip was usually cut a little wider than the other strips. These strips were placed in plastic bags (to prevent desiccation) and weighed on a Mettler B6 analytical balance with a resolution of 0.1 mg.

Calculations and statistical analysis

When estimating a wing's moment of inertia about the shoulder joint, using strip analysis, the moments of inertia about the long (chordwise) axis of each individual strip should be taken into account. The moment of inertia about an axis parallel to

a principal axis through the centre of gravity of a rectangular plate (wing strip) is obtained by means of a relationship called the *parallel-axis theorem* (or Steiner's proposition), given in any handbook on mechanics. The theorem states that the moment of inertia about the new axis is the moment of inertia about the original axis (through the centre of gravity) plus the mass of the object (strip) times the square of the distance between the two axes. If we assume each strip to be a thin rectangle, the moment of inertia of one wing about the shoulder joint, J_w, is given by:

$$J_w = \sum_{n=1}^{k} \left(m_n r_n^2 + \frac{m_n w_n^2}{12} \right) \tag{3}$$

for the k strips of the wing, where m_n is the mass, w_n is the width of the nth strip and r_n is the distance from the shoulder joint to the centre of gravity of the nth strip, as indicated in Fig. 1A. The moment of inertia about the centre of gravity for each strip (the second term of the equation) will be negligibly small if the rectangle (strip) is sufficiently narrow. Ignoring this term, the wing's moment of inertia about the shoulder joint is expressed as:

$$J_w = \sum_{n=1}^{k} m_n r_n^2 . \tag{4}$$

This equation was used by Norberg (1976a), Rayner (1986) and Kirkpatrick (1990). Equation 4 will give a slight underestimation, which in our case was about 0.1 %, compared with the value obtained from equation 3. Since the difference is so small, we used the simple equation (equation 4) to give values comparable with those obtained for bats and birds by the other authors.

The chordwise position of the centre of gravity of each strip is taken to be located in the strip's centre line. The distance Δr_n from the strip's proximal edge to its centre of gravity (Fig. 1A) is then:

$$\Delta r_n = w_n/2 . \tag{5}$$

The position of the centre of gravity for the most distal strip should be calculated as for triangles as $\Delta r_n = w_n/3$, but this would give only about a 0.1 % lower value of the moment of inertia of the distal strip. Since errors in the investigation in general are much larger, we used the model with the centre of gravity in the strip's centre line throughout.

The wing's moment of inertia about the body length axis, J_{wr}, was calculated using the distance from the roll axis to the centre line of the nth strip, $r_{n(ra)}$ (instead of r_n), as indicated in Fig. 1A.

The following procedure was used to estimate the moment of inertia originating from the body (head included). The head and body were considered to be ellipsoids mounted on one another with major axes coinciding (Fig. 1B). They were also assumed to have equal density and uniform mass distribution, so the
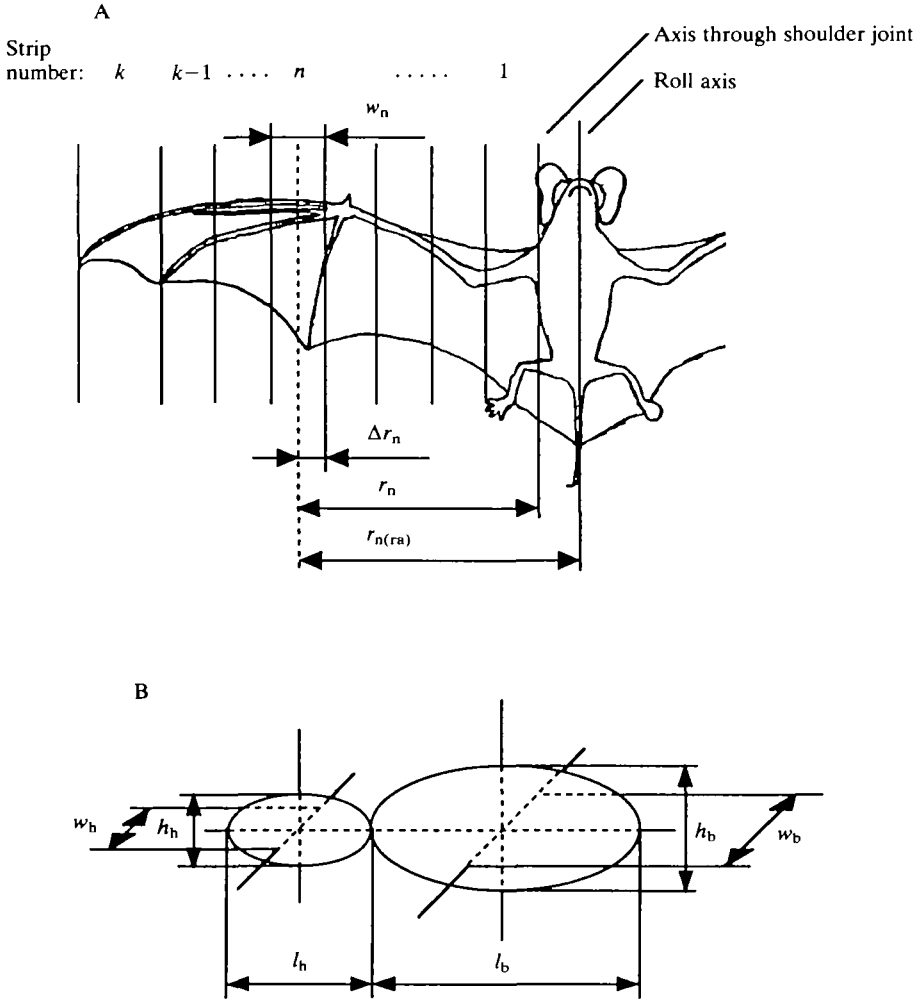
Fig. 1. (A) Method for estimating the moment of inertia of a bat's wing about the shoulder joint and about the roll axis. Each wing was cut into k chord-wise strips, measuring the distance from shoulder joint, r_n, and from the roll axis, $r_{n(ra)}$, to the centre of each strip. The mass of each strip was measured and the moment of inertia was estimated according to equation 4. w_n is the width of strip n, and Δr_n is the distance from the proximal edge of strip n to its centre of gravity. (B) Measurements used to estimate the combined moments of inertia of the body and the head about the roll axis. See text for explanation.

calculations are based on volume distribution between head and trunk rather than on mass distribution.

The volume V_e of an ellipsoid is:

$$V_e = \frac{4\pi}{3} \frac{l}{2} \frac{w}{2} \frac{h}{2} = \frac{\pi l w h}{6}, \tag{6}$$

where l is the length, w is the width and h is the height of the ellipsoid, and the moment of inertia of the ellipsoid is:

$$J_e = \frac{m}{5}\left(\frac{h^2}{4} + \frac{w^2}{4}\right) = \frac{m}{20}(h^2 + w^2) \tag{7}$$

(Alexander and Vernon, 1975). The mass of the head is estimated as the combined mass of the head, m_h, and trunk, m_t, multiplied by the volume proportion that the head makes up of the combined volume of the head and trunk, $V_h/(V_h+V_t)$, as:

$$m_h = \frac{m_{t+h}V_h}{V_h + V_t}. \tag{8}$$

Using equations 6, 7 and 8, the combined moment of inertia of the body and head about the roll axis becomes:

$$J_{br} = \frac{m_{t+h}}{20}\left[\frac{l_h w_h h_h(w_h^2 + h_h^2) + l_t w_t h_t(w_t^2 + h_t^2)}{l_h w_h h_h + l_t w_t h_t}\right], \tag{9}$$

where indices t and h refer to trunk and head, respectively, and m_{t+h} is the mass of the trunk and head together.

Finally, the combined moment of inertia of wings and body plus head about the roll axis can be calculated as:

$$J_{roll} = 2J_{wr} + J_{br}. \tag{10}$$

The mean value of the moment of inertia of one wing, J_w, for each species was plotted against total (=body) mass, wing span and wing area, respectively, in double logarithmic diagrams, and wing mass was plotted against body mass. The relationships are expressed by a fitted power function $y=ax^b$, where a is the y-intercept and b is the regression coefficient. The regression coefficient was calculated according to the reduced major axis method (=model II regression in Sokal and Rohlf, 1981), with 95% confidence limits as described by Rayner (1985).

The Pearson product-moment correlation coefficient was calculated to describe the correlation, and the t-test (Bailey, 1976) was used to test if the slope of a regression line differed from other slopes or from an expected theoretical value. Finally, multiple regression was used to express the moment of inertia of the wing as a function of body mass, wing span and wing area. The relative deviation of the actual, observed value from the regression value was then plotted against wing-tip length and shape indices in order to find any correlations between these variables.

Results

Wing moment of inertia

The morphological measurements of the eight bat species are listed in Table 1, and the moments of inertia of the body and wings are given in Table 2. Using total body mass (m_{tot}), wing span (b) or wing area (S) as the predictor, we arrived at the

Table 1. *Body mass and wing dimensions of eight species of bats*

Species	Code	N	m_{tot} (kg)	m_w (kg)	b (m)	S (m²)	T_l	I	AR	WL	RWL
Pteropodidae											
Rousettus aegyptiacus	Ra	1	0.104	1.03×10^{-2}	0.530	0.0465	1.08	1.45	6.4	22	47
Epomophorus anurus	Ea	2	0.0504 / 0.0548	4.38×10^{-3} / 4.36×10^{-3}	0.400 / 0.402	0.0290 / 0.0293	1.49	1.26	5.8	18	47
Vespertilionidae											
Pipistrellus pipistrellus	Pp	6	0.0053 (0.0005)	3.67×10^{-4} (1.09×10^{-4})	0.209 (0.007)	0.0065 (0.0005)	1.18	1.74	6.7	8.0	46
Nyctalus noctula	Nn	?	0.0265	1.50×10^{-3}	0.344	0.0161	1.43	0.99	7.4	16	54
Eptesicus nilssoni	En	3	0.0099 (0.0015)	8.51×10^{-4} (1.99×10^{-4})	0.277 (0.012)	0.0115 (0.0009)	1.21	1.54	6.7	8.4	39
Vespertilio murinus	Vm	1	0.0141	8.58×10^{-4}	0.298	0.0122	1.50	0.95	7.3	11	47
Plecotus auritus	Pa	1	0.0090	5.85×10^{-4}	0.270	0.0123	1.19	1.43	5.9	7.2	34
Molossidae											
Otomops martiensseni	Om	4	0.0356 (0.0015)	2.74×10^{-3} (2.51×10^{-5})	0.449 (0.014)	0.0217 (0.0009)	1.42	1.33	9.3	16	49

Data for *Nyctalus noctula* are from Rayner (1986) and the values are means, and wing-tip length and shape indices are from Norberg and Rayner (1987) for all species except for *Eptesicus nilssoni*, which was examined in this study. Where $N=2$, both values are given. N is the number of individuals of each species, m_{tot} is total mass, m_w is wing mass, b is wing span, S is wing area, I is wing-tip shape index, AR is aspect ratio, WL is wing loading and RWL is relative wing loading, T_l is wing-tip length index, I is wing-tip length index. For m_{tot}, m_w, b and S the standard deviation is given after the mean when more than one specimen was examined.

Table 2. *Wing moment of inertia, J_w, body moment of inertia, J_{body}, and total moment of inertia about the roll axis, J_{roll}*

Species	J_w (kg m^2)	N	J_{body} (kg m^2)	N	J_{roll} (kg m^2)	N
Rousettus aegyptiacus	5.00×10^{-5}	1	9.44×10^{-6}	1	1.59×10^{-4}	1
Epomophorus anurus	1.31×10^{-5} 1.67×10^{-5}	2	3.91×10^{-6} 2.95×10^{-6}	2	4.29×10^{-5} 5.08×10^{-5}	2
Pipistrellus pipistrellus	4.29×10^{-7} (5.5×10^{-8})	6	8.44×10^{-8} (1.3×10^{-8})	6	1.28×10^{-6} (1.9×10^{-7})	6
Nyctalus noctula	3.91×10^{-6}	?	6.10×10^{-7}	1	1.07×10^{-5}	1
Eptesicus nilssoni	1.58×10^{-6} (1.6×10^{-7})	3	2.09×10^{-7} (6.3×10^{-8})	3	4.64×10^{-6} (5.5×10^{-7})	3
Vespertilio murinus	1.77×10^{-6}	1	2.34×10^{-7} 3.44×10^{-7}	2	5.81×10^{-6} 5.69×10^{-6}	2
Plecotus auritus	1.10×10^{-6}	1	1.20×10^{-7} 0.80×10^{-7}	2	1.88×10^{-6} 2.70×10^{-6}	2
Otomops martiensseni	1.22×10^{-5} (8.5×10^{-7})	4	1.60×10^{-6} (9.5×10^{-8})	4	3.61×10^{-5} (4.3×10^{-6})	4

N is number of individuals examined.

When more than one specimen was examined, the standard deviation is given after the mean value. Where $N=2$, both values are given.

The value of J_w for *Nyctalus noctula* is from Rayner (1986), and is a mean value.

following allometric equations for the moment of inertia (J_w) of one wing about the shoulder joint:

$$J_w = 1.70 \times 10^{-3} m_{tot}^{1.57} \quad (r=0.990), \tag{11}$$

$$J_w = 1.10 \times 10^{-3} b^{5.16} \quad (r=0.989), \tag{12}$$

and
$$J_w = 1.47 \times 10^{-3} S^{2.57} \quad (r=0.985), \tag{13}$$

where r is the correlation coefficient. The plots of the moment of inertia *versus* body mass, wing span and wing area are shown in Fig. 2A,B and C, respectively. Geometric similarity predicts that the moment of inertia *versus* body mass, wing span and wing area should yield a slope of 5/3 (=1.67), 5.0 and 5/2 (=2.5), respectively. The slopes obtained for bats do not deviate significantly from these theoretical values; the 95% confidence limits are 1.36–1.82, 4.43–6.01 and 2.15–3.06, respectively.

The multiple regression of moment of inertia as a function of flight morphology (total mass, wing span and wing area) can be expressed as:

$$J_w = 4.49 \times 10^{-3} m_{tot}^{0.53} b^{2.15} S^{0.65} \quad (r=0.997). \tag{14}$$

The high correlation coefficients (0.985–0.997) of equations 11–14 indicate that any of these equations can be used to estimate wing moment of inertia in bats.
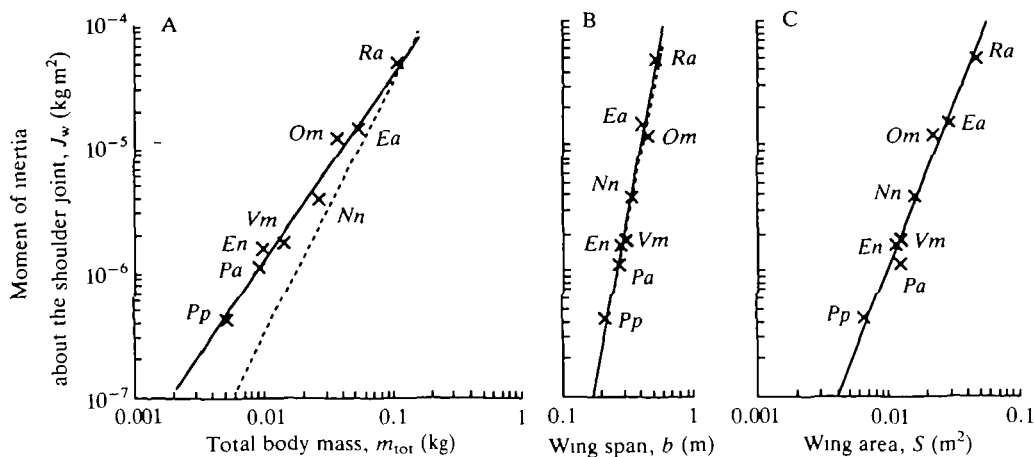
Fig. 2. (A) Double logarithmic plot of moment of inertia of one wing about the shoulder joint *versus* body mass. The slope of the reduced major axis (1.57) does not differ significantly from the value expected under the assumption of geometric similarity (1.67). The regression line (dashed) obtained for birds (slope=2.05) by Kirkpatrick (1990) is inserted for comparison. (B) Double logarithmic plot of moment of inertia of one wing about the shoulder joint *versus* wing span. The slope of the reduced major axis (5.16) does not differ significantly from the value expected under the assumption of geometric similarity (5.0). The regression line (dashed) obtained for birds (slope=5.08) by Kirkpatrick (1990) is inserted for comparison. (C) Double logarithmic plot of moment of inertia of one wing about the shoulder joint *versus* wing area. The slope of the reduced major axis (2.57) does not differ significantly from the value expected under the assumption of geometric similarity (2.5). The specific names of the bats are given in full in Table 1.

Wing-tip shape and wing-tip length indices

Deviations from the estimated moment of inertia about the shoulder joint, using multiple regression (equation 14), *versus* wing-tip shape (I) and wing-tip length (T_1) indices are shown in Fig. 3A,B.

V. murinus and *N. noctula* have the lowest wing-tip shape indices of these species (that is, the most pointed wing tips), and both have lower wing moments of inertia about the shoulder joint than average for the bats as predicted from equation 14. *P. auritus* also has a low moment of inertia but more rounded wing tips. The highest wing-tip shape indices (most rounded tips) occur in *P. pipistrellus* and *E. nilssoni,* which both have higher moments of inertia than the other bats.

E. anurus, V. murinus, O. martiensseni and *N. noctula* have the largest wing-tip length indices and *R. aegyptiacus* the lowest, whereas *P. pipistrellus, P. auritus* and *E. nilssoni* have rather low indices. Of the species with large wing-tip length indices, *E. anurus* and *O. martiensseni* have higher moments of inertia than predicted from equation 14, whereas the other two have lower values than predicted. *P. auritus,* which has a low moment of inertia, has a much smaller wing-tip length index. *P. pipistrellus* and *E. nilssoni,* which have the highest wing
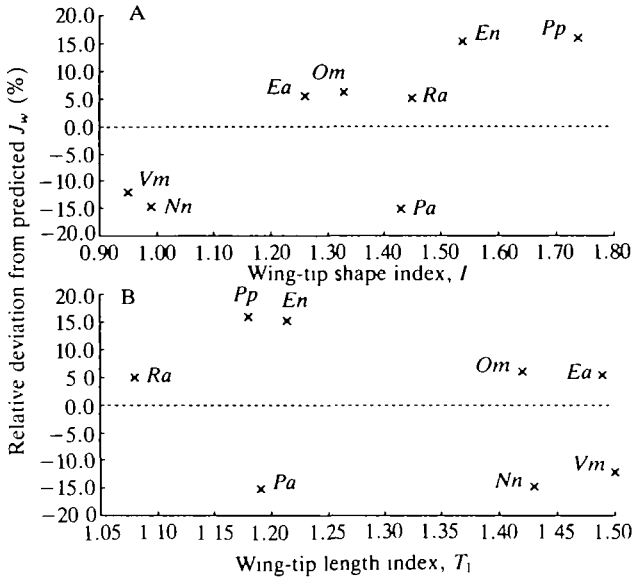
Fig. 3. Relative deviation of J_w for each species from the moment of inertia of one wing about the shoulder joint, as estimated from the multiple regression (equation 13), *versus* wing-tip shape index I (A) and wing-tip length index T_1 (B). Specific names are given in full in Table 1.

moments of inertia, have wing-tip length indices that are as low as that of *P. auritus*.

Body moment of inertia

The moments of inertia calculated for the body alone are shown in Table 2 and Fig. 4. The mean value of the moment of inertia originating from the body is 7 % of the animal's total moment of inertia about the roll axis, and in no single individual was it more than 10 %.

Wing mass versus body mass

Norberg and Rayner (1987) suggested that wing mass in bats may increase at least in proportion to wing area or to wing span squared, that is, at least to mass$^{0.67}$. Our data show that the mass of one wing increases with body mass as:

$$m_w = 0.112 \, m_{tot}^{1.11} \quad (r=0.989), \tag{15}$$

that is, that wing mass increases more than in direct proportion to body mass. The slope is similar to the one obtained for birds by Kirkpatrick (1990). His regression obtained for 17 bird species was $m_w=0.0974 \, m_{tot}^{1.10}$, and the slope of 1.10 was significantly different from the predicted slope of 1.0 for geometrically similar animals. However, the slope of 1.11 for our eight bat species is not significantly
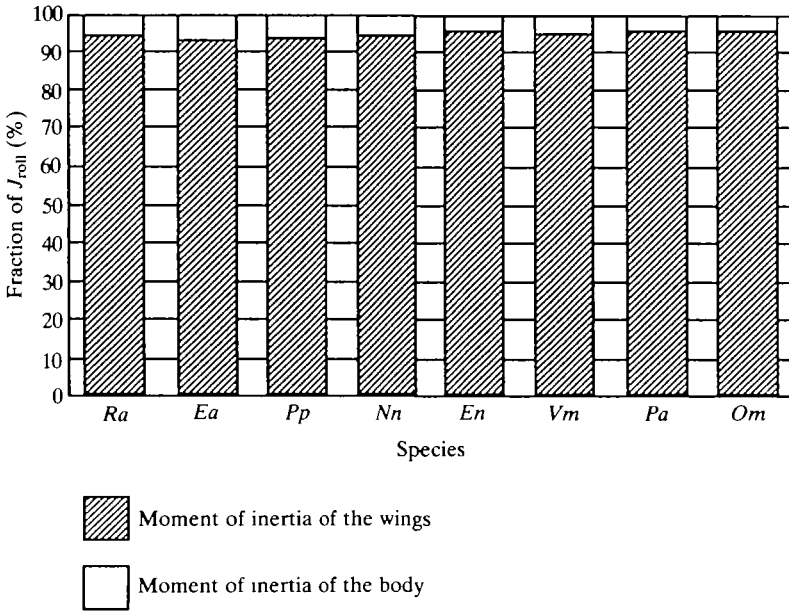
Fig. 4. Estimated relative distribution of moment of inertia of body, J_{br}, and wings, $2J_{wr}$, about the roll axis for eight species of bats. The symbols used to identify species are shown in Table 1.

different from 1.0 (the 95 % confidence limit is 0.95–1.29), which may be due to the small sample size. Fig. 5 is a double logarithmic plot of the mass of one wing *versus* body mass for bats. The regression line for birds is inserted for comparison.

Discussion

Kirkpatrick (1990) examined a number of bird species and arrived at the following equations for wing moments of inertia *versus* body mass and wing span:

$$J_w = 3.76 \times 10^{-3} m_{tot}^{2.05} \tag{16}$$

and
$$J_w = 9.23 \times 10^{-4} b^{5.08}. \tag{17}$$

The exponent for wing moment of inertia about the shoulder joint *versus* body mass obtained for bats (equation 11) is significantly different from that for birds (equation 16; $P<0.05$), whereas the slopes for moment of inertia *versus* wing span in bats and birds (equations 12 and 17) do not differ significantly from each other. Kirkpatrick did not give any equation for wing moment of inertia about the shoulder joint *versus* wing area (our equation 13).

The estimate of inertial power using equation 1 will be an overestimate, since the inertial power is reduced during the upstroke when the arm wing flexes (Norberg, 1976b). In *P. auritus* in slow flight, the wing moment of inertia during the upstroke is reduced by approximately 50 %, and the total inertial power makes up only about 2 % of the total mechanical power required to fly
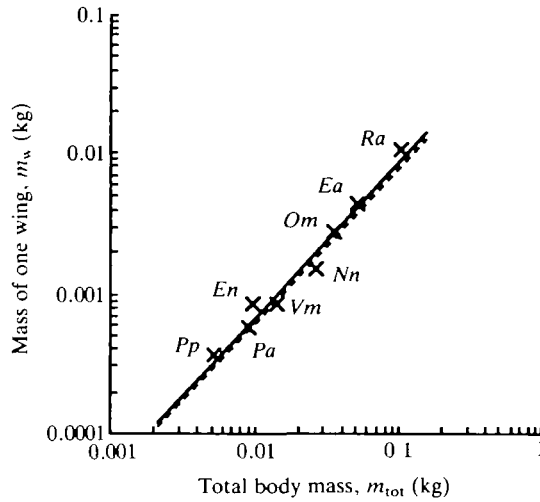
Fig. 5. Double logarithmic plot of the mass of one wing *versus* body mass for eight species of bats.The slope of the reduced major axis (1.11) does not differ significantly from the value expected under the assumption of geometric similarity (1.0). The regression line (dashed) obtained for birds (slope=1.10) by Kirkpatrick (1990) is inserted for comparison. Specific names are given in full in Table 1.

(Norberg, 1976*b*). Minimization of the moment of inertia is probably more important for a flying animal's manoeuvrability and agility than for bringing about an overall decrease in the power required for flight.

Norberg (1981*b*) and Norberg and Rayner (1987) suggested that one way to reduce wing moment of inertia is to have wing muscles and thick bones located as proximally as possible, that is, to have a long hand wing in relation to the arm wing (large T_1) or an overall short wing. The bat species in our sample that have a lower than average J_w, as estimated from the multiple regression in equation 13 (species below the line in Fig. 3B: *P. auritus*, *N. noctula* and *V. murinus*), tend to have a larger mean value of T_1 (1.39) than species with a higher J_w (T_1=1.24; species above the line in Fig. 3B). However, the correlation coefficient is low ($r=-0.363$), which may be due to the small sample size. *P. auritus* differs from the others in having a low wing-tip length index and a low moment of inertia. Its short wings in relation to body mass contribute to the low J_w, and its low T_1 may instead be related to the marked ability to flex the wings (to control wing moment of inertia), as discussed below.

Norberg and Rayner (1987) discussed relationships between wing design and manoeuvrability and agility in bats. *Manoeuvrability* is usually defined as the minimum radius of turn the animal can attain. The radius of a banked turn is proportional to the square root of the wing loading, so high manoeuvrability is obtained in bats with low body mass and large wings. *Agility* is the maximum roll acceleration during the initiation of a turn and measures the ease or rapidity with which the flight path can be altered.

Flying bats may detect insects at ranges of only a few metres so they must make rapid manoeuvres to pursue and catch a prey, that is, have high *agility*. To initiate a turn, a net rolling moment must be produced and this can be done by differential twisting or flexing of the wings, or by unequal flapping of the two wings, giving asymmetrical aerodynamic roll moments (torques) (Norberg, 1976c). The torque M is proportional to speed v squared, wing area and wingspan, $M=(1/2)\rho C_{rm}v^2Sb$, where ρ is air density and C_{rm} is the coefficient of roll moment. C_{rm} is influenced by wing shape and will be greatest on large wings with broad, rounded tips (high T_s, high I and low AR). Thus, at a given speed, *long broad wings with rounded tips* will give large aerodynamic torque M. Large M can also be obtained by high speeds, but high speeds cannot be obtained by large wings (which give a low wing loading). Therefore, *either* a high optimum speed *or* large wings would be needed to maximize M. So, low M is obtained by the large size of the wings in slow-flying species (which have low wing loadings) and by the high speed in fast-flying species (which have high wing loadings).

The fastest entry into a turn is achieved at the maximum angular acceleration, α_{roll}, available to the animal, which is the aerodynamic torque divided by the total roll moment of inertia of body and wings:

$$\alpha_{roll} = M/J_{roll} \qquad (18)$$

(Andersson and Norberg, 1981). To enhance rapid manoeuvres, a bat should thus have a large M and/or a small J_{roll}. In slow-flying species *broad wings* and *wide wing tips* (large wing-tip shape index I) are the important characteristics for maximization of the aerodynamic rolling moment M, whereas in fast-flying species *thin body*, *short wings* and *pointed wing tips* (small I) provide a low J_{roll} for high roll acceleration. Roll movements are often accompanied by flexure of the wings to reduce wing span and moments of inertia. Flexure is most readily achieved with relatively long arm wings (low T_1), since wing flexion occurs mainly at the arm wing while the hand wing is kept straight and extended laterally. Wing flexion may be most important for the slow-flying species, in which the long wings contribute to making J_{roll} large. In fast fliers, the aerodynamic rolling torque M is large because of the large speed component; low I and high AR ensure that wing mass is not concentrated towards the wing tips.

In summary, *manoeuvrability* is increased by low body mass and low wing loading, allowing small turning radii, and high *agility* (high roll acceleration) can be achieved by large aerodynamic torque and/or low wing moment of inertia

---

Fig. 6. Hypothetical selection pressures for high agility (=high roll acceleration, α_{roll}) and high manoeuvrability in fast-flying compared with slow-flying insectivorous bats. $\alpha_{roll}=M/J_{roll}\propto v^2Sb/J_{roll}$, where M is the aerodynamic roll moment (torque), v is flight speed, S is wing area, b is wing span and J_{roll} is the roll moment of inertia of body and wings combined. I is wing-tip shape index, T_1 is wing-tip length index, AR is aspect ratio, WL is wing loading and J_w is the moment of inertia of one wing about the shoulder joint.

Low flight speed   High flight speed
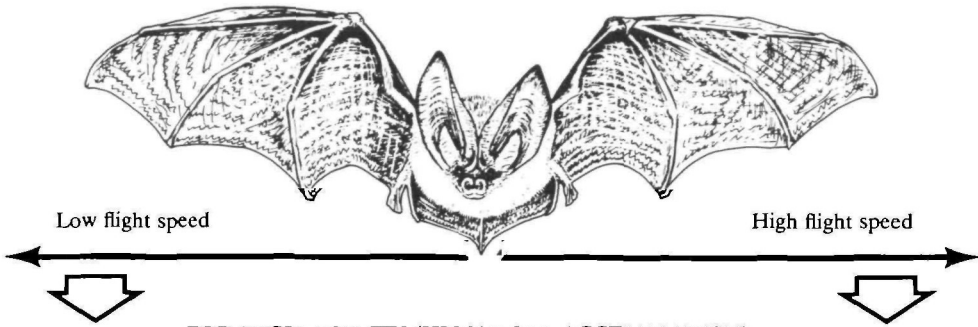
FOR HIGH AGILITY (HIGH ROLL ACCELERATION):

Increased M:
large I (broad, rounded wing tips)
low AR (broad wings)
long wing span, large wing area

Increased influence on J_{roll}:
small T_1 (short hand wings for high
wing flexibility)

Increased M:
high v:
   high WL (small wing area)

Decreased J_{roll}:
large T_1 (long hand wings)
small I (pointed wing tips)
high AR (narrow wings)
short wing span, thin body

- -

FOR HIGH MANOEUVRABILITY (SMALL RADIUS OF TURN):

Decreased WL:
low body mass
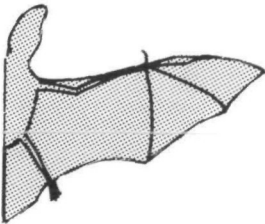large wing area

Decreased WL:
low body mass

- -

EXAMPLES:

Plecotus auritus:

large I, small T_1,
low AR, low WL

Pipistrellus pipistrellus,
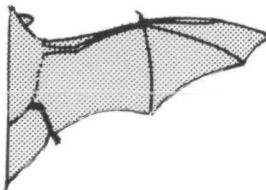*Eptesicus nilssoni*:

very large I, small T_1,
low AR, average WL

Nyctalus noctula,
Vespertilio murinus,
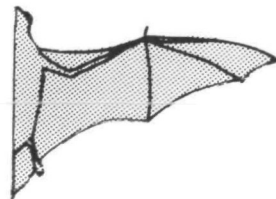*Otomops martiensseni*:

small I, large T_1,
high AR, average–high WL

lower J_w than predicted
from equation 14

higher J_w than predicted
from equation 14

lower J_w (*Nn, Vm*) or
slightly higher J_w (*Om*)
than predicted from equation 14

Fig. 6

(Fig. 6). For low inertia, wing span should be small but wing-tip length index T_1 should be large (long hand wings), wing-tip shape index I should be small (pointed tips) and aspect ratio AR should be high (narrow wings), characteristics that ensure that wing mass is not concentrated towards the wing tips. Large aerodynamic torque can be obtained by high flight speeds or large wings and broad wing tips (large I and low AR), but not both, since high speeds are correlated with high wing loadings (small wings). For maximum wing flexure and the greatest possibility of controlling wing inertia, the arm wing should make up a large proportion of the wing length (low T_1). These possible selection pressures for increased agility conflict with each other, and bats with different flight speeds seem to have solved this problem in different ways, as demonstrated in Fig. 6.

Among the insectivorous species, those flying primarily in open areas at high altitudes (*O. martiensseni, N. noctula, V. murinus*) have higher T_1 (longer hand wings) and smaller I (more pointed wing tips) than the other species (Table 1, Fig. 3), and they also have the highest aspect ratios AR and relative wing loadings RWL (Table 1). These species possess all the characteristics defined above that would decrease wing inertia. *N. noctula* and *V. murinus* have lower AR but higher RWL than *O. martiensseni*, and thus more expensive and relatively faster flights. Because they seem to be committed to flying fast, and therefore have small wings and high wing loadings, they may be precluded from enhancing the aerodynamic torque M (which is already large because of the high flight speeds), so for high agility they must reduce inertia as far as possible (Norberg and Rayner, 1987). The short wings in *N. noctula* and *V. murinus* provide not only high wing loadings and high flying speeds but also contribute to making moment of inertia J_w low (Fig. 3).

P. pipistrellus and *E. nilssoni* , which usually fly close to vegetation but in open spaces during foraging, have shorter hand wings (lower T_1) and more rounded wing tips (higher I) than the open-area foragers (Table 1). They have average values of aspect ratio among the bats investigated here and among bats in general, and they have much higher wing moments of inertia than predicted from the multiple regression (equation 13 and Fig. 3). They have relatively large wings, which tends to increase the aerodynamic torque M, so they may not have the same pressure to reduce wing inertia for high agility. Both species are small, which makes wing loading relatively small and manoeuvrability high.

P. auritus forages among vegetation, sometimes hovering and gleaning. It has the lowest aspect ratio, which makes its flight more expensive, and it perches between foraging bouts. It has the wing characteristics that provide high agility in slow flight, such as large I (rounded wing tips) and low AR (broad wings), and a low T_1 (short hand wing) giving good control of wing inertia (great ability to flex the wings). It has a lower J_w than predicted from the multiple regression (equation 13 and Fig. 3). Long-eared bats have low wing loading and can make tight turns, that is, they have high manoeuvrability. With their larger, more cambered wings and much lower wing loadings they can readily increase lift and hence obtain good agility without having wings specialized for low inertia (Norberg and Rayner, 1987).

References

ALDRIDGE, H. D. J. N. (1985). On the relationships between flight performance, morphology and ecology in British bats. PhD thesis, University of Bristol.

ALEXANDER, R. McN. AND VERNON, A. (1975). The mechanics of hopping by kangaroos (Macropodidae). *J. Zool., Lond.* **177**, 265–303.

ANDERSSON, M. AND NORBERG, R. Å. (1981). Evolution of reversed sex dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* **15**, 105–130.

BAILEY, N. T. J. (1976). *Statistical Methods in Biology.* London: Hodder and Stoughton.

HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Scient. Prog.* **38**, 209–230.

IUPAP (1978). Symbols, units and nomenclature in physics. *Physica* **93A**, 1–60.

KIRKPATRICK, S. J. (1990). The moment of inertia of bird wings. *J. exp. Biol.* **151**, 489–494.

NORBERG, U. M. (1976a). Aerodynamics, kinematics, and energetics of horizontal flapping flight in the long-eared bat *Plecotus auritus. J. exp. Biol.* **65**, 179–212.

NORBERG, U. M. (1976b). Aerodynamics of hovering flight in the long-eared bat *Plecotus auritus. J. exp. Biol.* **65**, 459–470.

NORBERG, U. M. (1976c). Some advanced flight manoeuvres of bats. *J. exp. Biol.* **64**, 489–495.

NORBERG, U. M. (1981a). Allometry of bat wings and legs and comparison with bird wings. *Phil. Trans. R. Soc. Ser. B* **292**, 359–398.

NORBERG, U. M. (1981b). Flight, morphology and the ecological niche in some birds and bats. *Symp. zool. Soc. Lond.* **48**, 173–197.

NORBERG, U. M. (1987). Wing form and flight modes in bats. In *Recent Advances in the Study of Bats* (ed. M. B. Fenton, P. A. Racey and J. M. V. Rayner), pp. 43–56. Cambridge: Cambridge University Press.

NORBERG, U. M. (1990). *Vertebrate Flight. Mechanics, Physiology, Morphology, Ecology and Evolution.* Berlin: Springer Verlag.

NORBERG, U. M. AND RAYNER, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Phil. Trans. R. Soc. Ser. B* **316**, 335–427.

PENNYCUICK, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner and J. R. King), pp. 1–5. London: Academic Press.

PENNYCUICK, C. J. (1989). *Bird Flight Performance. A Practical Calculation Manual.* Oxford: Oxford University Press.

PENNYCUICK, C. J. (1990). Predicting wingbeat frequency and wavelength of birds. *J. exp. Biol.* **150**, 171–185.

RAYNER, J. M. V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool., Lond.* **206**, 415–439.

RAYNER, J. M. V. (1986). Flapping flight aerodynamics and the evolution of flight in bats. *Biona Report* **5**, 27–74.

SOKAL, R. R. AND ROHLF, F. J. (1981). *Biometry.* New York: Freeman, 2nd edn.