

THE MOMENT OF INERTIA OF BIRD WINGS AND THE INERTIAL POWER REQUIREMENT FOR FLAPPING FLIGHT

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Accepted 4 May 1995

Summary

The agility and manoeuvrability of a flying animal and the inertial power required to flap the wings are related to the moment of inertia of the wings. The moments of inertia of the wings of 29 bird species and three bat species were determined using wing strip analysis. We also measured wing length, wing span, wing area, wing mass and body mass. A strong correlation ($r^2=0.997$) was found between the moment of inertia and the product of wing mass and the square of wing length. Using this relationship, it was found that all birds that use their wings for underwater flight had a higher than average moment of inertia. Assuming sinusoidal wing movement, the inertial power

requirement was found to be proportional to (body mass)^{0.799}, an exponent close to literature values for both metabolic power output and minimum power required for flight. Ignoring wing retraction, a fairly approximate estimate showed that the inertial power required is 11–15 % of the minimum flight power. If the kinetic energy of the wings is partly converted into aerodynamic (useful) work at stroke reversal, the power loss due to inertial effects may be smaller.

Key words: moment of inertia, bird, bat, inertial power, flapping flight.

Introduction

During flapping flight, flying animals invest power to move the air (aerodynamic power) and to move the wings (inertial power). The inertial power required to accelerate and decelerate the wings during each wing stroke increases with the moment of inertia of the wings. The moment of inertia is small when the wing mass is low and concentrated near the axis of rotation. A lower limit to the moment of inertia of the wing will be set by structural demands. The wings should be able to withstand the loads applied to them (Pennycuik, 1967). The resistance to bending and the breaking moment of the wing bones are determined by their structure, mass and material properties (the same applies to the feather shafts). Kirkpatrick (1994) found that the breaking stress of the bone material of the humerus in a range of bird and bat species was comparatively low. The safety factors of the humeri ranged between 1.41 and 3.99 for bats and between 2.22 and 6.63 for birds. Wing design reflects a compromise between reducing the moment of inertia and maintaining a reasonable resistance to bending and a reasonable safety factor against failure (see Kirkpatrick, 1994).

During hovering in the hummingbird *Amazilia fimbriata fluviatilis*, Weis-Fogh (1972) calculated that the total mechanical work consisted of 53% inertial and 47% aerodynamic work. He estimated that 43% of the total mechanical work is wasted and, therefore, $(53 - 43)/53 \approx$

19% of the inertial work is converted into useful aerodynamic work. Norberg (1976, 1990) estimated that the inertial power requirement of the long-eared bat *Plecotus auritus* was negligible during fast forward flight and was a small fraction of the mechanical power expenditure during slow flight and hovering (2–2.6%). However, a later recalculation gave a value of 16% for slow flight. Norberg *et al.* (1993) estimated the inertial power requirement in a nectar-feeding bat, *Glossophaga soricina*, to be 60% of the total mechanical power required during hovering and 30% during slow forward flight; power losses were estimated to be 45% and 18%, respectively. The inertial power requirement seems to be a significant factor in the total mechanical power demand of vertebrate flyers. Norberg and Rayner (1987) and Norberg (1990) suggested that a low moment of inertia of the wings may also be important for increasing manoeuvrability and agility (the ability to make tight and fast turns).

Some data are available in the literature on the moment of inertia of bird and bat wings (Norberg, 1976; Aravind Babu *et al.* 1978, 1979, 1983; Madan Mohan *et al.* 1981, 1982; Partridge, 1982; Chari *et al.* 1982, 1983; Janaki Rama Rao *et al.* 1983; Aldridge, 1985; Kirkpatrick, 1990, 1994; Tholleson and Norberg, 1991), as well as on insect wings (Sotavalta, 1952, 1954; Ellington, 1984). However, there is a need for more data. In this paper, new measurements of the moment of

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inertia of bird and bat wings are presented, together with morphological data. Using these data, the inertial power requirement was estimated and compared with literature values of the minimum power requirement for flight.

Materials and methods

General morphological parameters

The experimental birds were taken from a collection of birds which had been found dead in the field. They had been enclosed in plastic bags and stored in a freezer. Some specimens had died as a result of road accident or from starvation. Care was taken to use fairly intact specimens with perfectly intact wings, but the measured body mass may occasionally be an underestimate of the original body mass. Species were selected from as many different taxonomic and functional groups as possible. One to three specimens were used for each species and mean values were calculated per species. Twenty-nine bird species (from 22 families) and three bat species (from two families) were used (Table 1).

Body mass (m_b ; in kg) was measured with a sensitive electronic balance (accuracy 0.5 mg) or, when the mass exceeded 200 g, with a less sensitive one (accuracy 0.5 g). The wing span (b) was measured (in m; to ± 1 cm) between the tips of the extended wings. One wing was cut from the body at the shoulder joint; the flight muscles and skin distal to this joint were included in the wing. Wing mass (m_w) was determined (in kg; to ± 0.01 g) and its length (l_w) was measured (in m; to ± 1 mm) as the distance between the humeral head and the tip of the extended wing. The outline of the extended wing was traced onto paper, digitised using a data tablet and the area of one wing (S ; in m^2) was calculated using a BBC computer. Wingbeat frequencies (at normal cruising speed) were taken from Rayner (1988) and J. M. V. Rayner (unpublished results).

Moment of inertia of the wing

The extended wing was fixed, using adhesive tape, to a sheet of Perspex with engraved 1 cm markings. The wing was cut into 9–33 strips of equal width perpendicular to the wing axis (the line between the humeral head and the wing tip). To cut a wing into strips, a flexible ruler was placed along the appropriate marking and each strip was carefully cut with a scalpel and/or a microtome knife. The work area was surrounded by wooden shields, to prevent any loss of feather segments. The material constituting each strip was immediately collected and weighed (to ± 0.5 mg).

The moment of inertia and the centre of gravity of the wing were calculated using a BBC computer. Each wing strip was considered to be a bar, with a homogeneous mass distribution along its width rather than a point mass at the centre of the strip (the method commonly used in the literature). Hence, the moment of inertia I (in $kg\ m^2$) was calculated as:

$$I = \sum_{i=1}^n (m_i d_i^2 + m_i w^2 / 12), \quad (1)$$

where m_i is the mass of strip i (in kg), d_i is the distance between

Table 1. *The family, scientific and common names of the experimental bird and bat species and the identification numbers used in this paper*

Family	Scientific name	Identification number	Common name
Birds			
Podicipedidae	<i>Podiceps ruficollis</i>	1	Little grebe
Ardeidae	<i>Ardea cinerea</i>	2	Grey heron
Anatidae	<i>Melanitta nigra</i>	3	Common scoter
Accipitridae	<i>Accipiter nisus</i>	4	Sparrowhawk
Accipitridae	<i>Buteo buteo</i>	5	Buzzard
Falconidae	<i>Falco tinnunculus</i>	6	Kestrel
Phasianidae	<i>Alectoris rufa</i>	7	Red-legged partridge
Phasianidae	<i>Coturnix coturnix</i>	8	Quail
Rallidae	<i>Gallinula chloropus</i>	9	Grey moorhen
Scolopacidae	<i>Scolopax rusticola</i>	10	Woodcock
Laridae	<i>Larus ridibundus</i>	11	Black-headed gull
Alcidae	<i>Alle alle</i>	12	Dovekie (little auk)
Alcidae	<i>Uria aalge</i>	13	Common murre (guillemot)
Columbidae	<i>Columba livia</i>	14	Rock dove (pigeon)
Strigidae	<i>Strix aluco</i>	15	Tawny owl
Alcedinidae	<i>Alcedo atthis</i>	16	Common kingfisher
Picidae	<i>Picus viridus</i>	17	Green woodpecker
Picidae	<i>Picoides major</i>	18	Great spotted woodpecker
Hirundinidae	<i>Delichon urbica</i>	19	House martin
Muscicapidae	<i>Erithacus rubecula</i>	20	Robin
Muscicapidae	<i>Turdus merula</i>	21	Blackbird
Muscicapidae	<i>Turdus philomelos</i>	22	Song thrush
Paridae	<i>Parus ater</i>	23	Coal tit
Paridae	<i>Parus caeruleus</i>	24	Blue tit
Fringillidae	<i>Fringilla coelebs</i>	25	Chaffinch
Estreldidae	<i>Poephila guttata</i>	26	Zebra finch
Ploceidae	<i>Quelea quelea</i>	27	Red-billed quelea
Sturnidae	<i>Sturnus vulgaris</i>	28	Starling
Corvidae	<i>Corvus frugilegus</i>	29	Rook
Bats			
Vespertilionidae	<i>Myotis mystacinus</i>	30	Whiskered bat
Vespertilionidae	<i>Pipistrellus pipistrellus</i>	31	Pipistrelle
Rhinolophidae	<i>Rhinolophus ferrumequinum</i>	32	Greater horseshoe bat

the centre of strip i and the shoulder joint (in m), w is the width of each strip (in m) and n is the number of strips. This method is slightly more accurate than the 'point mass method', but the difference between the two methods is less than 1% when more than ten strips are cut. For that reason, Tholleson and Norberg (1991) ignored the second term in equation 1.

We ignored the effect of the air being accelerated by the wing (added mass), which, according to Alexander (1977), is justified for birds, but not for insects.

Note that I is the moment of inertia of the fully extended wing. The wings are usually retracted to some degree during

the upstroke and during manoeuvres, resulting in a reduced moment of inertia. I is, therefore, the maximum value of the moment of inertia of the wing. The radius of gyration r_i (in m) is defined as:

$$r_i = \sqrt{I/m_w}, \quad (2)$$

where m_w is the wing mass (in kg).

The distance between the centre of gravity of the wing and the shoulder joint (r_{cg} ; in m) was determined from the strip masses, using a custom-made BASIC computer program, which minimised the net moment of force acting on increasingly accurate estimates of the centre of gravity.

Kinetic energy and inertial power

The kinetic energy (E_{kin} ; in J) of a wing rotating with angular velocity ω (in rad s^{-1}) is given by:

$$E_{kin} = 0.5I\omega^2. \quad (3)$$

The angular velocity ω is a function of time t (in s), wingbeat frequency f (in s^{-1}) and total excursion angle Φ (in rad). Assuming that the wing movement is sinusoidal (compare Weis-Fogh, 1972), the angular wing position as a function of time [$\gamma(t)$; in rad] is given by:

$$\gamma(t) = 0.5\Phi\sin(2\pi ft) + \bar{\gamma}, \quad (4)$$

where $\bar{\gamma}$ is the mean angular position of the wing (in rad).

The angular velocity as a function of time [$\omega(t)$, in rad s^{-1}] is the derivative of equation 4:

$$\omega(t) = d\gamma/dt = \pi\Phi f \cos(2\pi ft) \quad (5a)$$

and the maximal angular velocity of the wing is:

$$\omega_{max} = \pi\Phi f. \quad (5b)$$

During the first half of the downstroke and the first half of the upstroke, the wing is accelerated, gaining kinetic energy. During the latter half of the down- and upstrokes this kinetic energy is dissipated as the wing decelerates back to rest. The kinetic energy (E_{kin}) of one wing reaches a maximum at the maximal angular velocity; combining equations 3 and 5b gives:

$$E_{kin} = 0.5\pi^2\Phi^2 f^2 I. \quad (6)$$

The inertial power required to accelerate or decelerate a wing is equal to the rate of change of its kinetic energy. The kinetic energy of the wing increases from zero to a maximum (equation 6) during the first half of the down- and upstrokes, i.e. in a period of $0.25/f$. Hence, the inertial power required is equation 6 divided by $0.25/f$. During the second half of the down- and upstrokes, the kinetic energy of the wing decreases from the maximum to zero over the same time span, $0.25/f$. Hence, the same inertial power is required, albeit for deceleration of the wing rather than for acceleration. Although the wings are accelerated and decelerated twice during each flap cycle, the inertial power requirement P_{in} (in J s^{-1}) is constant; for two wings:

$$P_{in} = 4\pi^2\Phi^2 f^3 I. \quad (7)$$

Note that many birds and bats retract their wings during the upstroke, reducing I and, hence, E_{kin} and P_{in} . However,

equation 7 should be correct for the downstroke. P_{in} calculated with equation 7 is the maximum inertial power requirement.

The value of P_{in} in Alexander's (1977) equation 10.9 is half of the value calculated using equation 7 in this study (considering that γ_0 in Alexander's equation corresponds to 0.5Φ). Alexander considered only the positive work for the two acceleration phases of a wing beat and calculated the average inertial power by dividing this work by the total duration of a wing beat. In equation 7, the absolute value of the work done for the two deceleration phases is also included, resulting in a doubling of the inertial power requirement.

Error analysis and statistics

Two systematic errors in the calculation of the moment of inertia of the wing (I) have to be considered: mass loss during sectioning of the wing and the effect of the number of strips used. The mass loss was determined for all wings as the difference between the total mass of the wing strips and the original wing mass m_w . The mass loss was approximately 4% and was independent of the number of strips. To obtain more detailed information about mass loss, a pigeon wing was cut at the elbow and wrist, perpendicular to the wing axis. These three sections were weighed every hour for 6 h and once more after 24 h. The mass of each section decreased in an exponential fashion, the proximal section having the largest relative mass loss per unit time and the distal section the lowest (presumably an effect of the proximal position of most soft, wet tissue). On the basis of this experiment, we assumed that I will be underestimated by approximately 2% due to mass loss during sectioning of the wing.

The effect of the number of strips used on the calculated value of I was estimated by recalculating I with pairs of strip masses added together, simulating a measurement with doubled strip width. The difference between this and the original values gives an indication of the effect of the number of strips used (Fig. 1). This analysis indicates that when the number of strips was at least 15, the 'doubled strip width error' was always less than 3%, whereas with ten strips the error was in the range 3–15%. When the above procedure was repeated with tripled and quadrupled strip widths, the calculated value of I increased approximately exponentially. Hence, the difference between the present measurements and the real moment of inertia is probably less than the 'doubled strip width error', and a minimum of ten strips is acceptable.

The measurement error was estimated by assuming that all the measurements of the strip masses were 0.5 mg too low, corresponding to the accuracy of the balance (obviously, this is an extreme case). In the blackbird, the measurement error in the moment of inertia was estimated to be 1.0%; it was 6.4% in the pipistrelle, which had the second lowest wing mass in our sample of flying vertebrates.

Reduced major axis regressions (r.m.a.) were used for the statistical analyses. This method is more appropriate than least squares linear regression, because the errors in the x - and y -coordinates are likely to be of the same order of magnitude (Rayner, 1985). Regressions were performed on the logarithm

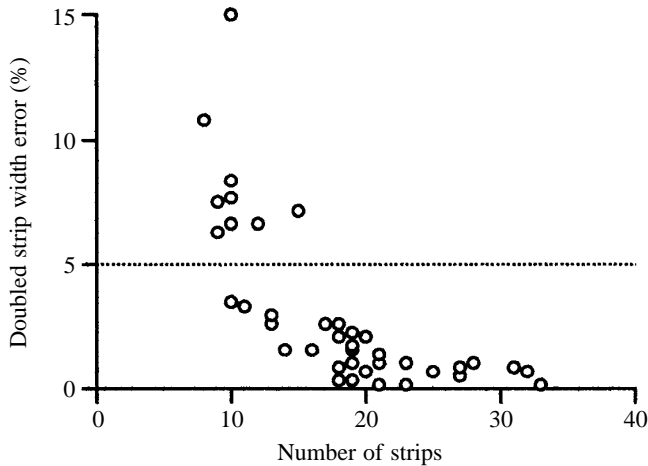


Fig. 1. The 'doubled strip width' error *versus* the number of strips used for the bird and bat wings. The doubled strip width error is the original calculated value of the moment of inertia divided by the moment of inertia recalculated with pairs of strip masses added together, multiplied by 100%. This error gives an indication of the systematic error caused by using a finite number of discrete strips. Note that the doubled strip width error may exceed 5% when the number of strips is 15 or fewer.

of the measurements. Hence, the relationships are of the form $Y=AX^B$. 95% fiducity intervals for the values calculated for B were obtained from the formula in Rayner (1985), which employs the Student's t -test.

The relative moment of inertia (I^*) is the ratio of I to the predicted value of I obtained from r.m.a. regression of I *versus* $m_w l_w^2$ (see Results section),

$$I^* = \frac{I}{A(m_w l_w^2)^B}, \quad (8)$$

where A is the intercept of the r.m.a. regression line with the y -axis and B is the slope of this line. I^* is a measure of the deviation of the value for each bird species from the average values. The I^* value of the bat wings was also determined, although the bat data were not included in the r.m.a. analysis.

Results

The morphometric data for each species are listed in Table 2. The distribution of the strip masses and the results of the r.m.a. regression analysis are discussed below.

Mass distribution of the wing

The distributions of strip mass and strip moment of inertia illustrate structural wing adaptations to reduce the moment of inertia. In birds (e.g. the blackbird *Turdus merula*, Fig. 2A), the proximal part of the wing is characterised by high strip masses and a rather irregular mass distribution. The peaks usually correspond to the elbow and wrist joint. From the wrist to the wing tip, the mass distribution typically declines in a regular fashion. The distribution of the moment of inertia is typically bell-shaped, with the peak slightly distal to the wrist.

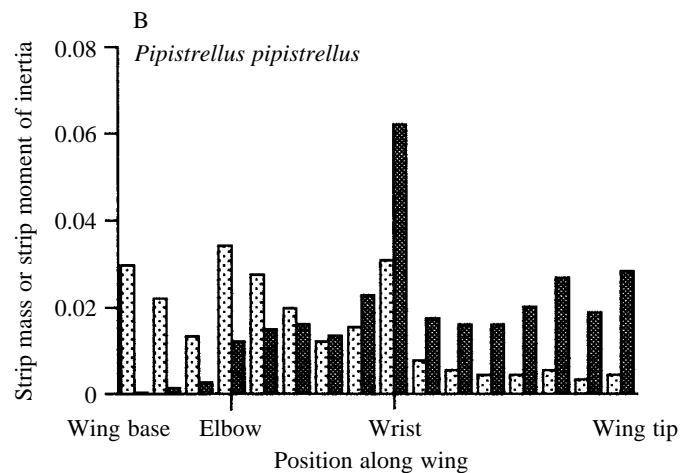
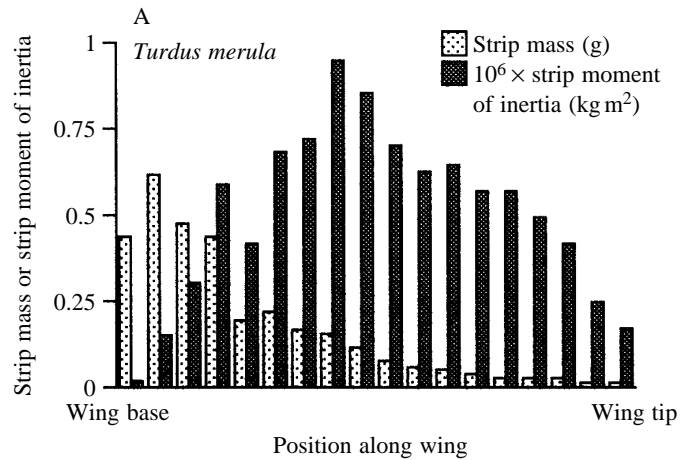


Fig. 2. Wing strip mass and moment of inertia as a function of wing length of (A) a blackbird and (B) a pipistrelle.

The decrease in strip moment of inertia towards the wing tip, despite the rapidly increasing square of the distance from the shoulder joint (see equation 1), is a result of the marked reduction in strip mass towards the wing tip. Feathers play a key role in this pattern. The moment of inertia of one wing of a pigeon *Columba livia*, stripped of its feathers, was measured and compared with values for the intact wing. Although the wing mass had decreased by 25% and the wing length by 47%, the moment of inertia of the featherless wing was still 65% of that of the intact wing (whereas, isometrically, it should have decreased to 21%). Furthermore, the strip moments of inertia of the second primary feather of a grey heron *Ardea cinerea* and a blackbird were determined and also showed a bell-shaped pattern. The low mass and favourable mass distribution of feathers should strongly reduce the overall moment of inertia of bird wings.

In bats (e.g. the pipistrelle *Pipistrellus pipistrellus*, Fig. 2B), the mass is concentrated in the shoulder, elbow and wrist joints (see also Norberg, 1976). Typically, the moment of inertia peaks at the strip containing the wrist joint. The moment of inertia of the bat wings was more than twice that of the bird wings of similar mass and length (Fig. 3, see also Fig. 6).

Table 2. Morphometric data for the birds and bats used in this study

Species (number)	m_b (kg)	$10^3 \times m_w$ (kg)	$10^4 \times S$ (m ²)	l_w (m)	b (m)	r_{cg} (m)	r_i (m)	$10^6 \times I$ (kg m ²)	I^*	f (s ⁻¹)	n
Birds											
<i>P. ruficollis</i>	0.146	4.56	110.1	0.194	0.40	0.053	0.066	20.03	1.44	–	19
<i>A. cinerea</i>	2.140	167.1	1997	0.830	1.72	0.216	0.272	12334	0.99	2.64	21
<i>M. nigra</i> (2)	0.569	38.85	422.6	0.390	0.81	0.108	0.130	656.6	1.17	4.90	19, 20
<i>A. nisus</i> (2)	0.279	22.61	377.0	0.355	–	0.093	0.108	263.0	1.01	4.48	18, 18
<i>B. buteo</i>	0.771	72.51	1142	0.590	1.22	0.155	0.187	2536	1.00	3.19	20
<i>F. tinunculus</i> (2)	–	13.74	356.2	0.355	–	0.086	0.108	159.5	1.03	6.80	18, 18
<i>A. rufa</i>	0.393	19.15	241.1	0.254	0.52	0.060	0.073	100.7	0.93	–	25
<i>C. coturnix</i>	0.132	4.00	91.8	0.164	0.33	0.037	0.046	8.482	0.99	17.8	16
<i>G. chloropus</i> (2)	0.364	14.20	254.9	0.271	0.56	0.065	0.082	95.58	1.04	–	14, 27
<i>S. rusticola</i> (2)	0.163	12.45	254.2	0.279	0.59	0.068	0.083	84.98	1.00	–	27, 28
<i>L. ridibundus</i> (2)	0.256	18.98	442.2	0.461	0.93	0.118	0.146	402.5	1.07	3.50	23, 23
<i>A. alle</i>	0.100	5.04	65.0	0.183	0.38	0.046	0.057	16.18	1.18	9.43	18
<i>U. aalge</i>	0.691	31.07	241.6	0.335	0.68	0.100	0.117	424.8	1.32	9.40	17
<i>C. livia</i> (3)	0.293	22.47	314	0.323	–	0.071	0.088	172.7	0.81	6.71	31, 32, 33
<i>S. aluco</i>	0.398	31.41	617.7	0.421	–	0.111	0.136	578.5	1.10	–	21
<i>A. atthis</i>	0.0343	1.55	62.0	0.130	0.29	0.030	0.039	2.344	1.20	–	13
<i>P. viridus</i>	0.179	11.75	231.0	0.235	0.49	0.051	0.064	47.54	0.85	–	23
<i>P. major</i>	0.0629	4.17	121.8	0.190	0.41	0.042	0.052	11.15	0.92	–	19
<i>D. urbica</i>	0.0152	0.85	51.5	0.140	0.29	0.030	0.040	1.348	1.10	9.35	14
<i>E. rubecula</i>	0.0150	0.69	46.5	0.108	0.22	0.022	0.029	0.581	1.02	16.1	21
<i>T. merula</i> (2)	0.0562	3.14	127.8	0.184	–	0.042	0.054	9.115	1.08	8.55	18, 19
<i>T. philomelos</i> (2)	0.0676	3.39	103.5	0.171	0.37	0.033	0.042	6.098	0.78	10.0	17, 17
<i>P. ater</i>	0.0146	0.84	51.9	0.112	0.23	0.021	0.028	0.673	0.89	–	11
<i>P. caeruleus</i>	0.0095	0.48	42.4	0.095	0.20	0.018	0.024	0.286	0.96	–	10
<i>F. coelebs</i> (2)	0.0199	1.10	55.8	0.116	0.25	0.023	0.030	1.007	0.93	17.3	11, 11
<i>P. guttata</i> (2)	0.0145	0.63	33.0	0.090	0.20	0.019	0.024	0.356	1.00	27.4	9, 9
<i>Q. quelea</i> (2)	0.0151	0.64	46.5	0.100	–	0.026	0.032	0.663	1.47	–	10, 20
<i>S. vulgaris</i>	0.0581	3.70	120.8	0.185	0.39	0.041	0.052	10.16	1.00	11.3	18
<i>C. frugilegus</i> (2)	0.328	28.78	419.8	0.389	0.80	0.080	0.107	326.9	0.80	3.97	19, 20
Bats											
<i>M. mystacinus</i>	0.0039	0.238	25.0	0.096	0.20	0.027	0.035	0.287	1.97	–	10
<i>P. pipistrellus</i> (3)	0.0043	0.241	18.5	0.087	0.21	0.028	0.035	0.291	2.42	13.9	16, 16, 20
<i>R. ferrumequinum</i>	0.0098	0.551	50.2	0.128	–	0.042	0.050	1.377	2.16	10	13

When more than one specimen was measured for a species, the data were averaged; the number of specimens used is given in parentheses after the species name.

The species are listed in the same order as in Table 1.

b , wing span; f , wingbeat frequency; I , moment of inertia of one wing; I^* , relative moment of inertia; l_w , wing length (humeral head to tip); m_b , body mass; m_w , mass of one wing; n , number of wing strips used; r_{cg} , distance between the centre of gravity of the wing and the humeral head; r_i , radius of gyration of the wing; S , area of one wing.

Wing loading, moment of inertia and inertial power

The relationship between wing area and body mass does not differ significantly from isometry (Table 3) and wing loading (m_b/S) increases as $m_b^{0.28}$. Both wing mass and wing length scale with body mass with an exponent slightly (but significantly) greater than predicted for isometry.

The moment of inertia is the product of a mass and the square of a length; hence, isometrically, the moment of inertia is proportional to l^5 and $m^{5/3}$ (Table 3). The exponents of the regressions between moment of inertia and body mass (Fig. 3A) and wing mass (Table 3) are significantly higher than the isometric value of 5/3 (1.95 and 1.79, respectively). The relationship between moment of inertia and wing length does

not differ significantly from isometry. Kirkpatrick (1990) obtained an exponent of 2.05 for the relationship between moment of inertia and body mass for 17 bird species (16 of which are different from the species used in the present paper), which is not significantly different from our value of 1.95 (Table 3). Thollesson and Norberg (1991) calculated an exponent of 1.57 in eight bat species; by adding seven more bat species to these data, Kirkpatrick (1994) arrived at an exponent of 1.61. Both values are significantly lower than our value for birds (Table 3).

Using multiple regression analysis on their bat data, Thollesson and Norberg (1991) found the relationship: $I = m_b^{0.53} b^{2.15} S^{0.65}$ ($r^2 = 0.994$) (note that in this case S is the area

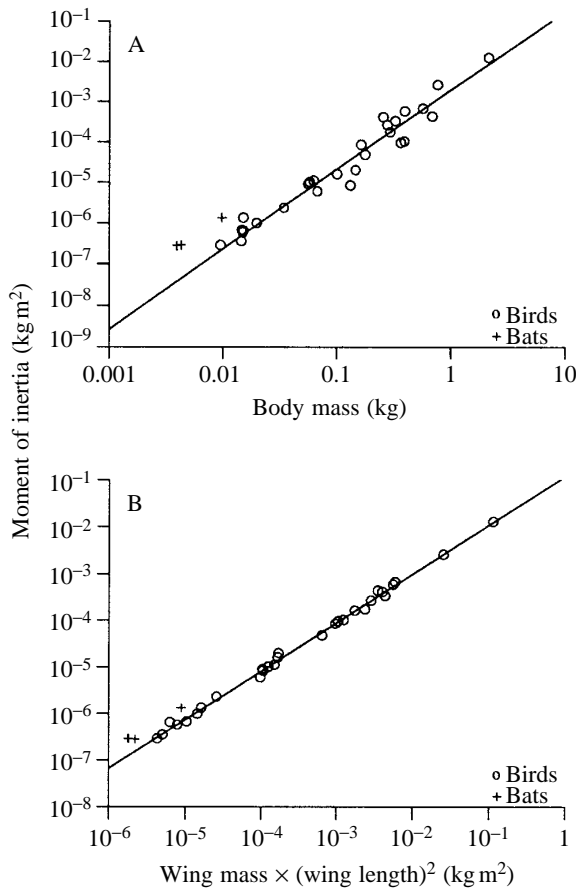


Fig. 3. Moment of inertia of the bird and bat wings *versus* (A) body mass and (B) the product of wing mass and the square of wing length. The r.m.a. regression line for the bird data is indicated in both graphs. Note the double logarithmic scale.

of both wings joined over the thorax). We found an even higher correlation ($r^2=0.997$) for the relationship between the moment of inertia and $m_w l_w^2$ (Fig. 3B; Table 3) (the units of $m_w l_w^2$ are the same as those of I : kg m^2).

The radius of gyration and the centre of gravity both shift outwards (significantly) relative to the wing length with increasing bird size (Table 3; for example, in a bird where $l_w=0.10$, r_{cg} is 21% and r_i is 27% of l_w ; whereas with $l_w=1.0$, r_{cg} is 29% and r_i is 34% of l_w). In other words, the mass distribution of the wings becomes less favourable with increasing bird size.

Predicting the isometric scaling exponent for wingbeat frequency is not simple. Hill (1950) argued that, given an isometric increase of flight muscle volume, frequency should be proportional to $m^{-1/3}$ or l^{-1} . This analysis gives the maximum available frequency. The minimum frequency required to support the body mass in flight can be shown to be proportional to $m^{-1/6}$ or $l^{-1/2}$ (Pennycuik, 1975). In a thorough study of wingbeat frequencies, Pennycuik (1990) performed dimensional analysis on data for wingbeat frequency *versus* body mass, wing span, wing area, wing moment of inertia and air density. This analysis showed that frequency should be proportional to $b^{-2/3}$, where b is wing

Table 3. Statistical parameters for regressions between X and Y

Y	X	r^2	B_{isom}	B	95% fiducity range of B	A
m_w	m_b	0.972	1	1.098*	1.025–1.176	0.0706
S	m_b	0.863	2/3	0.718	0.611–0.844	0.0782
l_w	m_b	0.895	1/3	0.396*	0.345–0.455	0.528
r_{cg}	l_w	0.979	1	1.140*	1.076–1.208	0.287
r_i	l_w	0.986	1	1.099*	1.048–1.152	0.339
I	m_b	0.954	5/3	1.953*	1.787–2.134	0.00194
I	m_w	0.988	5/3	1.785*	1.709–1.864	0.225
I	l_w	0.982	5	4.912	4.656–5.182	0.0428
I	$m_w l_w^2$	0.997	1	1.040*	1.018–1.063	0.118
f	m_b	0.653	$-1/3^a$	-0.440	-0.673 to -0.288	3.228
			$-1/6^b$	-0.440*		
f	l_w	0.877	-1^a	-1.055	-1.290 to -0.863	1.807
			$-1/2^b$	-1.055*		
E_{kin}	m_b	0.959	1^a	1.051	0.938–1.178	0.204
			$4/3^b$	1.051*		
P_{in}	m_b	0.711	$2/3^a$	0.799	0.554–1.153	7.746
			$7/6^b$	0.799*		

Reduced major axis (r.m.a.) regressions were applied to the logarithmic values of the X and Y values. Hence, $Y=AX^B$.

The correlation coefficient (r^2), the predicted value of the exponent B given isometric scaling (B_{isom}) and the regression parameters A and B are shown. These values were calculated using the bird data alone.

A , the intercept of the r.m.a. regression line with the y -axis; B , the slope of the r.m.a. regression line, i.e. the exponent in the relationship between the Y and X ; E_{kin} , maximum kinetic energy of the flapping wing; f , wingbeat frequency; I , moment of inertia of one wing; l_w , wing length (humeral head to tip); m_b , body mass; m_w , mass of one wing; P_{in} , inertial power required to beat the wing; r_{cg} , distance between the centre of gravity of the wing and the humeral head; r_i , radius of gyration of the wing; S , area of one wing.

*Significant difference between B_{isom} and B (5% confidence level).

^aPrediction based on maximum available wingbeat frequency, assuming isometric muscle volume scaling (see Hill, 1950).

^bPrediction based on minimum wingbeat frequency required to support the body mass during sustained flight (see Pennycuik, 1975).

span. Pennycuik's (1990) multidimensional regression has a comparatively high correlation ($r^2=0.897$).

In this study, we used literature data for the wingbeat frequencies (Rayner, 1988; J. M. V. Rayner, unpublished results). Wingbeat frequency decreases with wing length with an exponent of -1.055 (Fig. 4), which is not significantly different from Hill's (1950) predicted exponent of -1 , but is significantly different from $-1/2$ (Pennycuik, 1975). Scholey (1983) also found values close to -1 . However, Rayner (1988), for a wide range of bird species, found that frequency scaled as $m_b^{-0.269}$, if hummingbirds were excluded (the exponent was -0.333 including hummingbirds). This value lies outside the 95% fiducity range of the exponent in our study. Greenewalt (1962) found different exponents for different bird types: -0.36 for *Passeriformes*, -0.19 for shorebirds and -0.24 for ducks. The relationship is, therefore, somewhat sensitive to the particular selection of bird species.

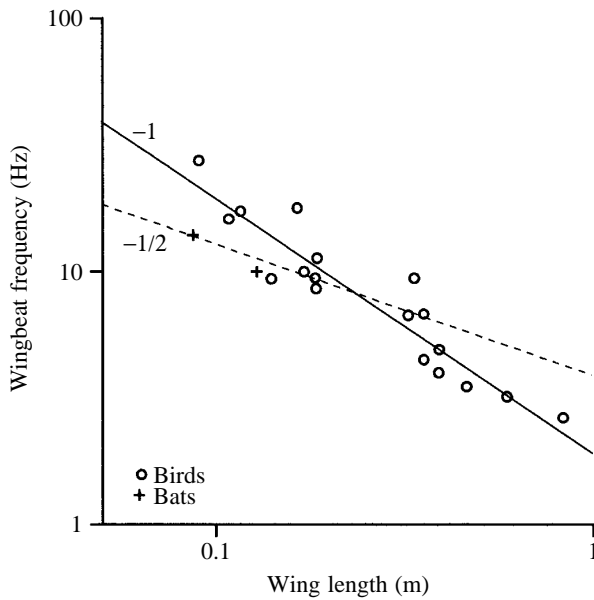


Fig. 4. Wingbeat frequency *versus* wing length. For comparison, the slopes of two predicted relationships (Hill, 1950; Pennycuick, 1975) between frequency and wing length (-1 and $-1/2$) are indicated. Note the double logarithmic scale. Frequency data from Rayner (1988) and J. M. V. Rayner (unpublished results).

Further, note that the correlation of wingbeat frequency with wing length is much higher than that with body mass (Table 3).

Assuming frequency to be proportional to $m^{-1/3}$, kinetic energy should be proportional to m^1 in isometric animals (see equation 6; Φ is constant in isometric animals) and inertial power (equation 7) should be proportional to $m^{2/3}$. If, however, frequency is proportional to $m^{-1/6}$, then kinetic energy would be proportional to $m^{4/3}$ and inertial power to $m^{7/6}$.

Kinetic energy and inertial power were calculated using our data on moment of inertia and literature data on wingbeat frequency (Rayner, 1988; J. M. V. Rayner, unpublished results). Wingbeat amplitude was calculated using the regression equation in Scholey (1983): $\Phi = 1.1048m_b^{-0.119}$. Note that the frequency data are literature observations for each species and the wingbeat amplitudes are estimates based on Scholey's (1983) regression for a range of bird species. The exponent of the regression between inertial power and body mass does not significantly exceed the predicted isometric value of $2/3$, based on the maximum available frequency, but it is significantly different from $7/6$, as predicted with the minimum required frequency (Table 3).

The relationship between inertial power and body mass (Fig. 5) has a rather low correlation ($r^2 = 0.711$), possibly due to errors in the estimations of Φ and f . Inertial power could not be calculated for our bat species, as no data on Φ are available.

Discussion

Relative moment of inertia

The correlation coefficients for the regressions between the moment of inertia and the wing parameters are higher than with

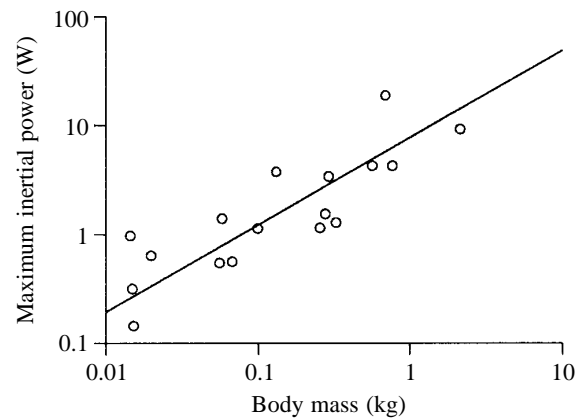


Fig. 5. Maximum inertial power required to flap the wings *versus* body mass. The r.m.a. regression line is indicated. Note the double logarithmic scale.

the body parameters. The best predictor for the moment of inertia is the product of wing mass and the square of wing length: $I = 0.118(m_w l_w^2)^{1.04}$ ($r^2 = 0.997$) (Fig. 3B; Table 3). This suggests that the mass distribution of the wings of each bird species reflects a similar compromise between reduction in the cost of beating the wings and maintaining a reasonable stiffness and strength (see Introduction; see also wing shape factors of insects in Ellington, 1984). In the bats used in the present study, this compromise results in a twofold greater moment of inertia than for birds (Fig. 6). This difference between birds and bats may well be related to the presence of feathers (see above).

The values of I^* (equation 8) ranges between 0.78 and 1.47 (Table 2), with a standard deviation of 0.17. The deviations of I^* from 1.0 (which is the value predicted with the r.m.a. regression analysis of I) may reflect aspects of the ecology of each species (Table 2; Fig. 6). For all birds associated with water, I^* ranges between 1.05 and 1.45. I^* is particularly high for species that use their wings for underwater 'flight' (Fig. 6). The guillemot *Uria aalge* dives up to 180 m deep, using its half-opened wings for propulsion (Pennycuick, 1988), the closely related little auk *Alle alle* is an excellent diver and swimmer (Lippens, 1954), the common scoter *Melanitta nigra* dives well, at depths of up to 9 m, opening its wings while doing so (Johnsgard, 1965) and the little grebe *Podiceps ruficollis* is also a specialist diver and swimmer. It is possible that wings used for underwater flight have to be comparatively strong, resulting in high I^* values. In his multivariate analysis of body mass, wing span and wing area, Rayner (1988) also found that 'diving birds' group together. The high value of I^* for the red-billed quelea *Quelea quelea* (a tropical pest, that devastates food crops and flies in immense, very dense flocks; Bruggers and Elliott, 1989; no. 27 in Fig. 6) and the low I^* values ($I^* < 0.85$) for the pigeon, green woodpecker *Picus viridus*, song thrush *Turdus philomelos* and rook *Corvus frugilegus* are harder to explain. Weis-Fogh (1972) calculated the wing moment of inertia for the hummingbird *Amazilia fimbriata fluviatilis*. Using his data, the value of I^* can be

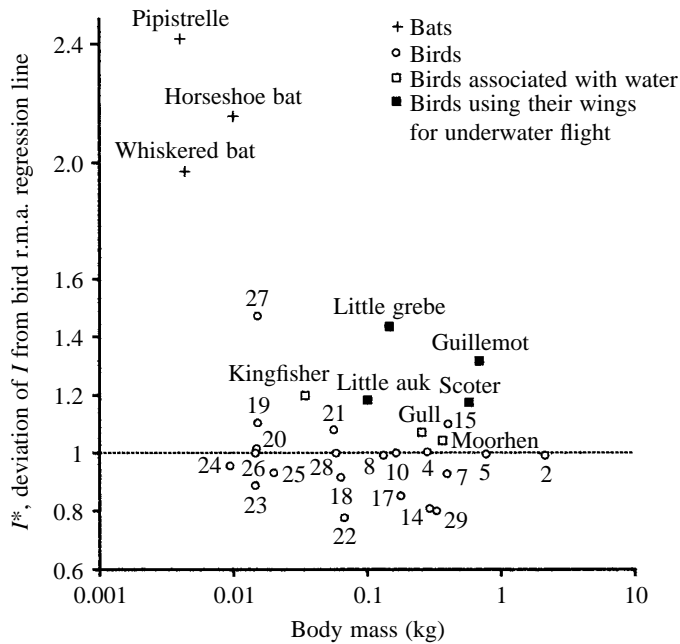


Fig. 6. The deviation I^* of individual values of the moment of inertia (I) from the predicted value of I , based on r.m.a. regression between I and $m_w l_w^2$. The common names of bird species associated with water are indicated. All other birds are indicated using the identification numbers given in Table 1. The water-associated birds all have values of I^* higher than 1.0. In other words, they show positive deviations from the expected value of I . In particular, birds using their wings for underwater 'flight' (filled squares) have high values of I^* . For comparison, bats are also included, although they were not included in the r.m.a. regression analysis. The moment of inertia of these bats is 2–2.4 times the value expected for birds of similar wing dimensions. Note the logarithmic x-axis.

calculated to be 0.56. Considering the extremely high flapping frequency of this species (35 Hz), this very low value of I^* may well be an adaptation for reducing its comparatively high inertial power requirement.

It would be very interesting to compare the present data with those for flightless birds and for species adapted exclusively to underwater flight (e.g. penguins). Unfortunately, at present, such data are not available.

Allometric increase of the centre of gravity and the radius of gyration

The radius of gyration and the centre of gravity both shift outwards relative to the wing length with increasing m_b . This allometric increase may be due to structural demands. Consider the wing as a beam under bending, loaded by the body mass. It is reasonable to assume that a structural demand for wings is an isometric relationship between the radius of wing bending R (in m) and the wing length: R must be proportional to l . The bending moment M (in N m) is:

$$M = EI_{2nd}/R, \quad (9)$$

where E is Young's modulus (in N m^{-2}) and I_{2nd} is the second moment of area (in m^4) (Alexander, 1983). For a geometrically

similar beam, M scales as $l^0 l^4 / l^1 = l^3$ (see equation 9). The actual bending moment applied to the beam is proportional to the product of body mass and wing length; hence, it scales as $l^3 l = l^4$. So, with R proportional to l and with E a constant, I_{2nd} must scale as l^5 rather than isometric scaling as l^4 .

Assuming that, at all wing sizes, a similar structural compromise is reached between minimising mass and preventing failure due to buckling, the cross-sectional area of the beam will be of constant shape and will be proportional to the square root of I_{2nd} . Hence, the cross-sectional area of the beam will scale as $l^{2.5}$ rather than isometric scaling as l^2 . The mass of the beam will scale as $l^{3.5}$ rather than isometric scaling as l^3 .

The outermost parts of the wing are designed to carry load, whereas the more proximal parts also contain tissues with other functions (muscles, blood vessels), which are expected to scale close to the isometric value of l^3 . Hence, the wing mass distribution may well shift distally in larger birds (see also Kirkpatrick, 1994).

Inertial power

The relationship between inertial power and body mass (Fig. 5) allows a comparison with other literature estimates of power requirements of birds and bats. Note that in our calculations wing retraction was ignored, so our P_{in} is the maximum value, which will usually only be required during the downstroke (wings fully stretched). Note also that, owing to the exponents in equation 7, the calculation of P_{in} is sensitive to errors in wingbeat frequency (f) and amplitude (Φ). Since the values we use for both of these parameters are estimates, the inertial power calculation is no more than an approximation. Clearly, more accurate data of flight kinematics are required to make an accurate estimation of the inertial power requirement.

The inertial power requirement (in W) for two wings was found to be $P_{in} = 7.75 m_b^{0.799}$ (Table 3). The scaling of the standard metabolic rate (in W) for a large group of birds has been estimated to be $4.19 m_b^{0.668}$ (Norberg, 1990). Hence, at m_b values of 0.01 and 1 kg, P_{in} is 1.0 times and 1.8 times the standard metabolic rate, respectively. The minimum power required for flight (in W) of birds has been given as $50.2 m_b^{0.73}$ (Norberg, 1990). Hence, at m_b values of 0.01 and 1 kg, P_{in} is 11% and 15% of the minimum power required for flight, respectively.

Comparison with literature data is difficult because the available data on inertial power do not include the power needed for wing deceleration and often do include the effect of wing flexion during the upstroke. To allow comparisons, the literature values should be doubled, to account for deceleration, and our values should be decreased to allow for wing flexion.

Norberg (1976) calculated that inertial power constituted 16% of the total mechanical power requirement for the long-eared bat *Plecotus auritus* (using a corrected estimate of inertial power). Norberg *et al.* (1993) calculated a value of 60% for hovering in the nectar-feeding bat *Glossophaga soricina* and Weis-Fogh (1972) calculated a value of 53% for hovering in the hummingbird *Amazilia fimbriata fluvialis*.

When the inertial power requirement is doubled, the above percentages were recalculated to give 28%, 75% and 69%, respectively.

Assuming an overall inertial power reduction of 25% due to wing retraction, the values for our birds were recalculated to 8.5–12%. These values are much lower than the recalculated literature values mentioned above. The proportion of the total mechanical power requirement comprised by the inertial power for *P. auritus* (Norberg, 1976) is more than twice that of our birds. This may be related to the finding that the moment of inertia of bat wings, on average, was more than twice that of birds of similar dimensions (Fig. 6). The proportions of the total mechanical power requirement comprised by the inertial power for hovering in *A. fimbriata fluviatilis* (Weis-Fogh, 1972) and *G. soricina* (Norberg *et al.* 1993) are even larger. During hovering, the inertial power seems to be a larger fraction of the total mechanical power requirement than during flight at the minimum power speed.

The exponent of the regression of inertial power *versus* body mass is quite similar to exponents found previously for standard metabolic rate and the minimum power requirement for flight (see above); hence, inertial power constitutes a similar proportion of the total power requirement across the range of bird sizes. This is partly due to the rapid decrease of wingbeat frequency with body mass (f is proportional to $m_b^{-1/3}$ rather than to $m_b^{-1/6}$). Furthermore, the positive allometry of the moment of inertia (Table 3) will be largely cancelled by the negative allometry of wingbeat amplitude (Scholey, 1983).

Elastic storage of kinetic energy may strongly decrease the inertial power loss during flapping flight. If the kinetic energy gained during acceleration of the wing were converted into elastic energy during deceleration of the wing, then this elastic energy, in turn, could be used to accelerate the wing during the next wingbeat. Weis-Fogh (1972) argued that the presence of efficient elastic storage mechanisms is essential for hovering insects. The apparent lack of such mechanisms in vertebrate fliers may set an upper limit to their wingbeat frequencies and their ability to hover. Hummingbirds may well operate close to this limit (Weis-Fogh, 1972).

In conclusion, the inertial power requirement should, perhaps, not be ignored in the study of the flapping flight of birds and bats. However, if a large fraction of the kinetic energy of the wing is converted into useful work during stroke reversal, the *power loss* due to wing inertia may be much smaller. Accurate data on wingbeat frequency and amplitude are required to make a reliable estimate of inertial power expenditure.

List of symbols

b	wing span (m)
d_i	distance between centre of wing strip i and shoulder joint [$=(i-0.5)w$] (m)
E	Young's modulus (N m^{-2})
E_{kin}	maximum kinetic energy of the wing during a wing beat (J)

f	wingbeat frequency (s^{-1})
i	wing strip number
I	moment of inertia of the wing (kg m^2)
I^*	I divided by the prediction of I , based on the r.m.a. of I versus $m_w l_w^2$
$I_{2\text{nd}}$	second moment of area (m^4)
l	length (m)
l_w	wing length (m)
m	mass (kg)
m_b	body mass (kg)
m_i	mass of wing strip i (kg)
m_w	wing mass (kg)
M	bending moment (N m)
n	number of wing strips
P_{in}	inertial power required to beat the wing (J s^{-1})
r_{cg}	distance between the centre of gravity of the wing and the shoulder joint (m)
r_i	radius of gyration of the wing (m)
r.m.a.	reduced major axis (method II regression)
R	radius of wing bending (m)
t	time (s)
S	area of one wing (m^2)
w	width of each wing strip (m)
Φ	total excursion angle of the wing (rad)
γ	angular position of the wing (rad)
γ_0	wingbeat amplitude ($\gamma_0=0.5\Phi$)
$\bar{\gamma}$	mean angular position of the wing (rad)
ω	angular velocity of the wing (rad s^{-1})
ω_{max}	maximal angular velocity of the wing during a wing stroke (rad s^{-1})

Ulla M. Norberg, an anonymous referee and Ali Cooper are thanked for their detailed comments, which allowed considerable improvement of the manuscript. Jan W. M. Osse is thanked for his encouragement and his comments on an earlier version of the manuscript. Gareth Jones provided the bats. Sandy Willmott provided a program to calculate the reduced major axis statistics. This paper is the result of an undergraduate research project, forming part of the biology studies of the first author at the Agricultural University of Wageningen, the Netherlands.

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