SHORT COMMUNICATION

THE MOMENT OF INERTIA OF BIRD WINGS

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The moment of inertia of a wing about its proximal end must be known in order to calculate the inertial torque and power required during flapping flight (Ellington, 1984) and it is also one of the morphological features that affects flapping frequency (Pennycuick, 1975, 1990). At present, however, there are very few data on wing moments of inertia of flying animals and thus there is no way of predicting the wing moment of inertia of a flying animal from easily obtainable morphological measurements. Arguments predicting bird wingbeat frequencies (Pennycuick, 1975), following Hill's (1950) argument that the maximum frequency of a vibrating limb is set by the mechanical properties of the muscles and tendons that accelerate and decelerate the limb at each end of the oscillation, have assumed geometric scaling of wing moment of inertia about the shoulder joint. The objective of this study was to determine if the wing moment of inertia of birds does indeed scale geometrically or, if not, how it actually does vary with body size.

The moment of inertia I of any object about a given axis can be estimated by dividing the object into strips parallel to the axis and using the equation:

$$I = \Sigma m r^2 , \qquad (1)$$

where m is the mass of the strip and r is the distance from the axis to the center of the strip. For geometrically similar animals, it follows from equation 1 that the moment of inertia of the wing about the shoulder joint should be proportional to any mass variable to the five-thirds power and similarly it should scale as any length variable to the fifth power.

The moment of inertia of one wing about the shoulder joint was determined for 18 birds of 17 species (Table 1). The birds were intentionally selected to be as morphologically heterogeneous as availability of specimens would allow. The body mass m_b and wing span b of each bird were taken following the procedures outlined by Pennycuick (1989). One datum point (pigeon) was taken from Pennycuick and Lock (1976). The datum point for the noctule bat was taken from Rayner (1986) as a mean of several individuals and the point for the long-eared bat was taken from Norberg (1976; and personal communication). Wing moments of inertia were found by stretching the wings out to their fully extended position,

Table 1. *Morphological measurements of the 18 birds used in the analysis plus those of the two bats*

Species	m_b (kg)	m_w (kg)	b (m)	I_w (kgm^2)
Louisiana water thrush *Seurus motacilla*	0.023	1.13×10^{-3}	0.265	1.35×10^{-6}
Great white heron *Ardea occidentalis*	2.0	0.163	1.86	1.58×10^{-2}
Red-shouldered hawk *Buteo lineatus*	0.390	0.0459	0.975	7.89×10^{-4}
	0.575	0.0540	1.03	9.87×10^{-4}
Green-backed heron *Butorides striatus*	0.170	0.0130	0.700	1.62×10^{-4}
Osprey *Pandion haliaetus*	2.00	0.196	1.70	1.32×10^{-2}
Limpkin *Aramus guarauna*	0.615	0.0474	1.02	1.25×10^{-3}
Mourning dove *Zenaida macroura*	0.092	8.07×10^{-3}	0.435	2.25×10^{-5}
Sora *Porzana carolina*	0.054	2.80×10^{-3}	0.360	6.66×10^{-6}
American redstart *Setophaga ruticilla*	0.007	4.32×10^{-4}	0.195	2.57×10^{-7}
Short-billed dowitcher *Limnodromus griseus*	0.061	4.83×10^{-3}	0.480	2.45×10^{-5}
Belted kingfisher *Ceryle alcyon*	0.104	0.0100	0.550	5.96×10^{-6}
American kestrel *Falco sparverius*	0.080	9.50×10^{-3}	0.585	5.87×10^{-5}
White ibis *Eudocimus albus*	0.540	5.81×10^{-3}	0.980	1.01×10^{-3}
Cattle egret *Bubulcus ibis*	0.270	0.0230	0.900	4.65×10^{-4}
Tricolored heron *Egretta tricolor*	0.340	2.66×10^{-2}	0.890	6.07×10^{-4}
Double-crested cormoront *Phalocrocorax auritus*	0.790	7.49×10^{-2}	1.21	3.03×10^{-3}
Pigeon* *Columba livia*	0.400		0.650	1.83×10^{-4}
Noctule bat† *Nyctalus noctula*	0.027		0.344	3.91×10^{-6}
Long-eared bat‡ *Plecotus auritus*	0.009	5.85×10^{-4}	0.270	1.10×10^{-6}

m_b, body mass; m_w, wing mass; b, wing span; I_w, wing moment of inertia about the shoulder joint.
   * From Pennycuick and Lock (1976).
   † From Rayner (1986).
   ‡ From Norberg (1976; and personal communication).

tacking them in this position to a piece of stiff cardboard or styrofoam and freezing them just long enough for the wings to become stiff. Once frozen, the wings were cut into 10 chord-wise strips of equal width, noting the distances from the proximal ends of the wings to the center of each strip (Fig. 1). Care was taken not to displace
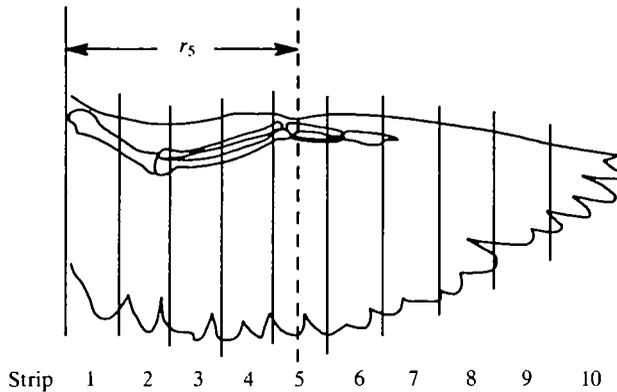
Fig. 1. Method for estimating the moment of inertia of a bird's wing about the shoulder joint. Each wing was cut into 10 equal-width chord-wise strips, measuring the distance r from the proximal end of the wing to the center of each strip. The mass m of each strip was measured and the moment of inertia was estimated using the equation $I_w = \Sigma m r^2$.

the flight feathers out of a natural-looking position during the cutting procedure. Each strip was placed in a plastic bag, making sure to collect all of the pieces of the strips, and allowed to thaw, at which time they were weighed to the nearest 0.1 mg using an Ainsworth type 10N analytical balance. The moment of inertia I_w of each wing about its proximal end was then calculated using equation 1. Values of I_w were plotted against body mass and wing span as double logarithmic plots and a line of best fit was drawn through the data points using the reduced major axis method (Rayner, 1985; standard major axis of Hofman, 1988). The slopes of these lines indicate how wing moment of inertia scales with body mass and wing span, respectively.

The allometric equations determined from the reduced major axis analysis of the data indicate that $I_w \propto m_b^{2.045}$ and $I_w \propto b^{5.082}$ for a group of birds encompassing a 286-fold increase in mass and a 9.5-fold increase in wing span. Fig. 2 shows wing moment of inertia plotted against body mass and wing span on logarithmic coordinates. It is interesting to note that, although not necessarily indicative of how bat wing moment of inertia scales, the points given for bat wing moments of inertia (crosses) lie very close to both reduced major axis lines (the bat data points were not included while doing the reduced major axis analysis for either plot).

Both reduced major axis lines have very high correlation coefficients (0.976 and 0.984) which are highly significant ($P<0.01$), indicating that either equation can serve as a good predictor of wing moment of inertia. By using body mass as a predictor, we can write the allometric equation:

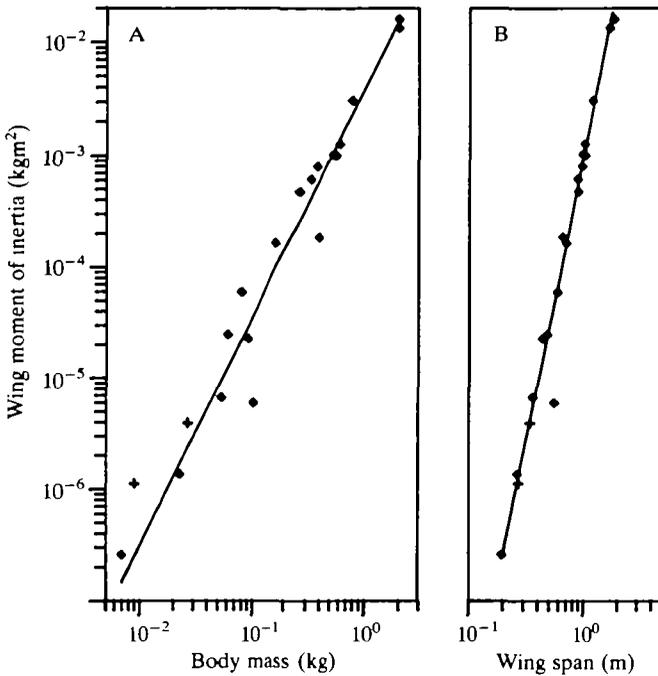$$I_w = 3.76 \times 10^{-3} \, m_b^{2.05} \, . \tag{2}$$

Fig. 2. (A) Double logarithmic plot of wing moment of inertia *versus* body mass. The slope of the reduced major axis line is 2.05, which is significantly different from the predicted slope of 1.67. (B) Double logarithmic plot of wing moment of inertia *versus* wing span. The slope of the reduced major axis line is 5.08, which is not significantly different from the predicted slope of 5.0. The crosses indicate values obtained from bats.

Similarly for wing span:

$$I_w = 9.23 \times 10^{-4} b^{5.08} \tag{3}$$

Geometric similarity predicts that a double logarithmic plot of wing moment of inertia *versus* body mass should yield a slope of 1.67. The estimated slope from the data is 2.05 with 99 % fiducial limits of 2.22 and 1.89. The predicted slope lies outside the fiducial limits and therefore there is a significant difference between the predicted slope and the one estimated from the data. The estimated slope of the reduced major axis line through the plot of wing moment of inertia *versus* wing span is 5.08 with 95 % fiducial limits of 5.38 and 4.80, indicating that there is no significant difference between the estimated slope and the slope of 5.0 predicted by geometric similarity.

For the purpose of predicting bird wingbeat frequencies, Pennycuick (1990) assumed that wing moment of inertia is directly proportional to body mass multiplied by the square of the wing span. That is, a double logarithmic plot of I_w *versus* $m_b b^2$ should yield a slope of 1.0. A reduced major axis analysis of wing moment of inertia *versus* $m_b b^2$ actually yields an estimated slope of 1.14 ($r=0.985$)
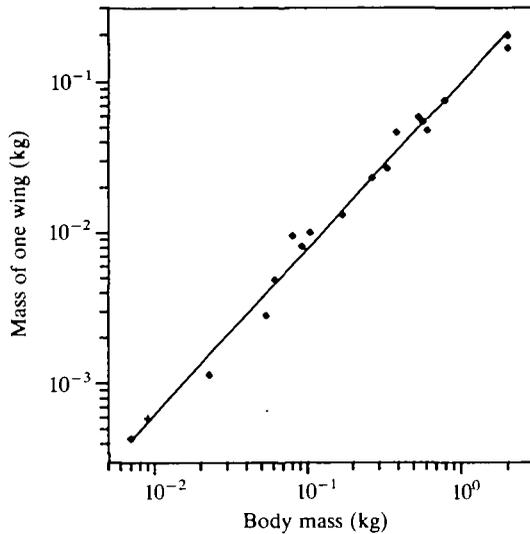
Fig. 3. Double logarithmic plot of the mass of one wing *versus* body mass. The slope of the reduced major axis line is 1.10, which is significantly different from the predicted slope of 1.0. The cross indicates values obtained from the long-eared bat.

with 99 % fiducial limits of 1.19 and 1.09. Pennycuick's assumed slope of 1.0 lies, then, just beyond the lower fiducial limit.

Fig. 3 is a double logarithmic plot of the mass of one wing *vs* body mass for 17 of the birds and the long-eared bat (which was not used in the reduced major axis analysis). The reduced major axis analysis yields the equation:

$$m_w = 9.74 \times 10^{-2} m_b^{1.10} \tag{4}$$

and thus, $m_w \propto m_b^{1.10}$. The correlation coefficient is 0.992 for 17 points, which is significant at $P < 0.01$. The slope, which is 1.10 with 99 % fiducial limits of 1.15 and 1.05, is significantly different from 1.0, which would indicate geometric similarity. The difference is small but, owing to the small amount of scatter about the line, it is significant.

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