

## PREDICTING WINGBEAT FREQUENCY AND WAVELENGTH OF BIRDS

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### Summary

Wingbeat frequencies were observed in the field for 32 morphologically diverse bird species, representing 18 families, and ranging in mass from 20 g to nearly 5 kg. A combination of multiple regression and dimensional analysis was used to show that wingbeat frequency ( $f$ ) may be estimated by:

$$f = 1.08(m^{1/3}g^{1/2}b^{-1}S^{-1/4}\rho^{-1/3}),$$

where  $m$  is the bird's body mass,  $g$  is the acceleration due to gravity,  $b$  is the wing span,  $S$  is the wing area and  $\rho$  is the air density. The predicted wingbeat frequency can be used to estimate the power available from a bird's flight muscles, and an estimate of the power required to fly can be obtained for comparison from the computer programs of Pennycuick (1989a). Field observations of airspeed are given for 30 of the 32 species. These are combined with the observations of wingbeat frequency to estimate wingbeat wavelength, and the ratio of wavelength to wing span, which is closely related to the 'advance ratio' as used by Ellington (1984).

### Introduction

Hill (1950) was the first to explore the consequences of the trend (plainly apparent to the naked eye) whereby larger animals oscillate their limbs at lower frequencies than smaller ones of similar type. From his earlier studies of muscle mechanics, Hill deduced that the mechanical power produced by a particular muscle is directly proportional to the contraction frequency, as is the mass-specific power (power output per unit mass of muscle). Each gram of muscle produces less power in a large animal than in a small one. The trend is roughly similar to that of basal metabolic rate *versus* body mass, and Hill followed the implications in some detail for running and swimming animals. His arguments were extended to flying animals by Pennycuick (1972, 1975), and adapted for the case of aerobic muscles, used for prolonged cruising locomotion, by Pennycuick and Rezende (1984), with some modifications of Hill's conclusions. For theoretical calculations that involve matching the power required for locomotion with the power available from the muscles, it is essential to have some way to estimate the contraction frequency in

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different animals, or at least the way in which the frequency changes, as the mass or other characteristics of the animal are varied. There is at present no means of doing this for flying animals.

Underlying Hill's (1950) argument is the principle that the frequency at which muscles contract in steady locomotion is not under the animal's control, or only to a very limited extent. There is a 'natural' frequency, imposed on the animal by the physical characteristics of its limbs, and the forces which they have to overcome. This in turn confines the strain rate, at which the muscles are permitted to shorten, within a narrow range. To be efficient, locomotor muscles have to be adapted to work at a particular frequency, which is done by adjusting the maximum strain rate, that is the 'intrinsic speed' in Hill's terminology (Pennycuick, 1990). In the case of walking animals, Alexander (1976, 1980) has shown that the natural frequency is proportional to  $\sqrt{(g/l)}$ , where  $g$  is the acceleration due to gravity and  $l$  is the leg length. The natural frequency for cruising flight in birds, assuming that one exists, is not so easily determined. Attempts at a dynamical analysis of simplified versions of the problem (Pennycuick, 1975; Rayner, 1986, 1987) have drawn attention to several physical variables which affect the result. The main morphological variables that affect wingbeat frequency are body mass, wing span, wing area and the moment of inertia of the wing. Allometric relationships can be constructed to show how wing span and area depend on body mass, but such plots (and the data in this paper) also show that both variables vary widely, independently of each other, in different species of similar mass. Not much is known about wing moment of inertia, but it has to be assumed provisionally that each of the morphological variables is liable to vary independently of the others. In addition, two 'environmental' variables, the acceleration due to gravity and the air density, also contribute to determining the wingbeat frequency.

The main objective of this paper is to find a relationship, involving the variables mentioned, which can be used to predict a bird's wingbeat frequency in steady cruising flight. As this is essentially a physical problem, a first approach can be made by applying dimensional analysis, a method widely used in classical physics. This does not solve the present problem uniquely, but it severely limits the range of possible solutions. The possibilities are then further narrowed down by regression analysis of field data, consisting of frequency observations on 32 morphologically heterogeneous bird species, for which data on body mass, wing span and wing area were also obtained. As a result of this combination of methods, the solution finally chosen is not restricted to the variables represented in the regression. Field observations of airspeeds were also obtained for all but two of the study species, and these were used to extend the prediction to cover wingbeat wavelength, that is the distance the bird moves forward in one wingbeat cycle.

## **Materials and methods**

### *Study sites and species*

The field data presented in this paper were collected between 1985 and 1989, at

Table 1. *List of study species*

13	<i>Fratercula arctica</i>	Linnaeus	Puffin
30	<i>Uria aalge</i>	Pontoppidan	Common guillemot
32	<i>Alca torda</i>	Linnaeus	Razorbill
35	<i>Catharacta skua</i>	Brünnich	Great skua
37	<i>Stercorarius parasiticus</i>	Linnaeus	Arctic skua
40	<i>Rissa tridactyla</i>	Linnaeus	Kittiwake
47	<i>Larus marinus</i>	Linnaeus	Great black-backed gull
51	<i>Larus argentatus</i>	Pontoppidan	Herring gull
58	<i>Larus atricilla</i>	Linnaeus	Laughing gull
65	<i>Sterna maxima</i>	Boddaert	Royal tern
80	<i>Rynchops niger</i>	Linnaeus	Black skimmer
86	<i>Fulmarus glacialis</i>	Linnaeus	Fulmar
112	<i>Phaethon lepturus</i>	Daudin	White-tailed tropicbird
117	<i>Sula bassanus</i>	Linnaeus	Northern gannet
118	<i>Anhinga anhinga</i>	Linnaeus	Anhinga
120	<i>Phalacrocorax auritus</i>	Lesson	Double-crested cormorant
122	<i>Phalacrocorax aristotelis</i>	Linnaeus	Shag
126	<i>Pelecanus occidentalis</i>	Linnaeus	Brown pelican
128	<i>Fregata magnificens</i>	Mathews	Magnificent frigatebird
183	<i>Ajaia ajaja</i>	Linnaeus	Roseate spoonbill
184	<i>Eudocimus albus</i>	Linnaeus	White ibis
192	<i>Ardea occidentalis</i>	Audubon	Great white heron
194	<i>Ardea herodias</i>	Linnaeus	Great blue heron
196	<i>Casmerodius albus</i>	Linnaeus	Great egret
200	<i>Egretta caerulea</i>	Linnaeus	Little blue heron
325	<i>Cathartes aura</i>	Linnaeus	Turkey vulture
326	<i>Coragyps atratus</i>	Bechstein	Black vulture
352	<i>Haliaeetus leucocephalus</i>	Linnaeus	Bald eagle
360	<i>Falco sparverius</i>	Linnaeus	American kestrel
364	<i>Pandion haliaetus</i>	Linnaeus	Osprey
412	<i>Colaptes auratus</i>	Linnaeus	Northern flicker
614	<i>Tachycineta bicolor</i>	Vieillot	Tree swallow

Names and species numbers from Eisenmann *et al.* (1983).

various sites in South Florida, at Assateague Island, Virginia, and on Fair Isle and Foula in Shetland. Observations are also included on the magnificent frigatebird from Panama (Pennycuik, 1983), and on the white-tailed tropicbird from Puerto Rico. Table 1 is a list of the species included in subsequent tables and graphs. The scientific names follow the North American checklist of Eisenmann *et al.* (1983). This is also the source of the species numbers, except for the shag, for which a deviation was needed as it does not occur in North America. All species have been included for which flapping frequencies in level flight were observed, and for which wing measurements were available.

#### *Body and wing measurements*

Measurements of wing span and area were made by me or by associates who

were familiar with the standard methods for making these measurements (Pennycuick, 1989a). Sample means were used where available, but no species was excluded on the grounds that only one specimen had been measured. Whereas wing span and area can be measured equally well on living birds, or on dead ones that may be emaciated or partially dismembered, means from healthy birds are needed for body mass. The values used for the body masses of American birds were the sample means listed by Dunning (1984). Those for the Shetland birds were species means supplied by Dr R. W. Furness (personal communication). In the case of sexually dimorphic species, the mean of reported male and female masses was used.

#### *Airspeeds*

Airspeed observations were obtained by ornithodolite, on land or on a boat, as described by Pennycuick (1983, 1987a, 1989b). In a variant of these methods, used in open, level habitat, the anemometer pole was mounted on a vehicle, which also supplied electrical power for the ornithodolite. Only observations classified as level cruising flight, flapping or flap-gliding, were included in the samples.

#### *Wingbeat frequencies*

These also refer only to birds in level, cruising flight. In a bird that flaps its wings continuously, wingbeat frequency is determined by counting a whole number ( $N$ ) of wingbeat cycles, and measuring the time ( $t$ ) taken. The wingbeat frequency ( $f$ ) is then defined as  $f=N/t$ . In birds that flap intermittently,  $N$  and  $t$  are measured on a series of uninterrupted wingbeats.  $t$  includes only the time spent actually flapping, not that of periods of gliding or ballistic flight. In species with low wingbeat frequencies, wingbeats can be counted directly, and timed with a stopwatch. However, all the observations presented here were obtained from video recordings. In the early part of the study a Panasonic PK-452S video camera and PV-8000 portable VHS video recorder were used. From autumn 1987, improved image quality was obtained from a Panasonic PV-320 VHS camcorder, with an electronic 'high-speed shutter', capable of yielding sharp images of flapping wings. The original field tapes were played back through a genlock device connected to a Commodore Amiga computer, running a BASIC program which printed a six-digit number on the screen, and incremented this number at the beginning of each new video frame. The composite image was re-recorded on the PV-8000 recorder. The loss of image quality caused by copying was more than offset by the convenience of having each frame of the tape individually numbered. The frame-numbered tape was played back on the PV-8000 recorder in frame advance mode, and frequencies were determined by counting the number of frames for a whole number of wingbeats. The frame rate of the original field recording (nominally 30 Hz under the American NTSC standard) was found by recording a watch to be 29.98 Hz for both the PV-8000 and the PV-320 recorders.

An identifiable point in the wingbeat cycle was needed to define the beginning

and end of a series of wingbeats. The most satisfactory reference point proved to be the moment at which the wing develops its full lift at the beginning of the downstroke. Three events occur more or less simultaneously at this point in the cycle, and one or more of them can be seen from any angle of view. When viewed from ahead, the wing suddenly appears much thinner, as it rotates at the shoulder joint to present an edge-on view. This is the first indication that can be used on a distant bird coming towards the camera. When the image is better defined, the upward bend caused by the lift force can be seen as the wing comes under load. This can also be seen from behind. When viewed from the side, or from below, the wing appears flexed at the wrist throughout the upstroke, then abruptly straightens to its full extent as the load is applied for the downstroke. At a frame frequency of 30 Hz, the wings of most species appeared to 'snap' to the fully extended position, between one frame and the next. The tape was single-stepped until this was seen, and the frame number was noted for the start of an observation. Then, the tape was run at slow speed, counting wingbeats, and finally single-stepped to locate the wing-extension snap defining the end of the observation. The number of wingbeats, starting and finishing frame numbers, species number and some other details were then entered as a record in a database under Microfiche Filer Plus (Software Visions Inc.), a database management program for the Amiga. Filer Plus automatically calculated the wingbeat frequency and included it in the record. Subsequently, all the records for a particular species and type of flight could be selected, and Filer Plus carried out the summations needed for the statistics in Table 3.

Long sequences of continuous flapping flight were broken into consecutive observations, usually of 20 wingbeats each. Flap-gliding birds would often flap for fewer than 20 wingbeats, and the observation then had to terminate when the bird stopped flapping. Five wingbeats was generally taken as the minimum for an observation, but this had to be lowered to three for black vultures, as they seldom flap for more than four wingbeats at a time. In the case of the northern flicker, the only species in the sample to show fully developed bounding flight, it was necessary to accept samples of only two wingbeats, with a consequent increased risk of bias in the frequency estimates. The mean wingbeat frequency for a species, as listed in Table 3, was found by dividing the total number of wingbeats observed by the total number of frames counted, and multiplying by 30. Because the number of wingbeats in an observation was variable, it was felt inappropriate to work out the standard deviation of wingbeat frequency simply by comparing the frequency estimates for different observations. Short observations would then have been given the same weight as long ones. Instead, an observation lasting  $N$  wingbeats was deemed to contribute  $N$  measurements of wingbeat *period*, each equal to the mean period ( $p$ ). The standard deviation ( $s_p$ ) for the wingbeat period was calculated for the set of observations. The estimate for the standard deviation of the frequency ( $s_f$ ) was found from the mean and standard deviation of the period as follows:

$$s_f = s_p / (p^2 - s_p^2) . \quad (1)$$

Table 2. *Air densities for different data subsets*

Data subset	Mean density ( $\text{kg m}^{-3}$ )	S.D. ( $\text{kg m}^{-3}$ )
Florida until January 1987	1.20	0.03
Florida after January 1987	1.22	0.03
Shetland 1986	1.21	0.01
Assateague Island 1989	1.22	0.02

This amounts to halving the interval between the frequency corresponding to a period  $p-s_p$  and that corresponding to  $p+s_p$ . This method of working out the standard deviation reflects frequency variations between observations, but neglects the variation from wingbeat to wingbeat within an observation. In several species, successive observations in the same sequence of continuous flapping flight often gave identical or almost identical frequency estimates. In these species, the standard deviation reflects mainly differences between individuals.

#### *Air density*

All observations were made within 100 m, and most within 20 m of sea level. Air density was estimated from measurements of barometric pressure and air temperature, recorded in the field. These density estimates were recorded in the data files when measuring airspeeds. Means and standard deviations for four phases of the project are shown in Table 2, and are sufficiently close together to justify using a fixed value of  $1.21 \text{ kg m}^{-3}$  for the air density in the subsequent calculations.

### **Results and Discussion**

Table 3 shows estimates of body mass, wing span, wing area and wingbeat frequency for 32 species, together with airspeed estimates for all but two of them, all restricted to steady, level, flapping or flap-gliding flight. Observations were excluded if the bird was judged to be patrolling in search of prey, or doing anything other than flying steadily along. The letters *A-F* following the species identification numbers indicate the proportion of observations (both frequency and airspeed) in which the bird was scored as flap-gliding (or bounding) rather than flapping. Some species normally flap, others normally flap-glide, while still others proceed in either fashion. The concept of the 'natural frequency', introduced above, applies within periods of continuous flapping. A flap-gliding bird supplies less power from its muscles (on average) than it would if it flapped continuously. Presumably power could also be reduced by flapping at a lower frequency and/or amplitude, but this would reduce the strain rate at which the muscles shorten, with an adverse effect on muscle efficiency (Pennycuick, 1990). By flap-gliding, a bird can reduce its average power output without having to change its wingbeat frequency, or the strain rate of its muscles. The incidence of flap-gliding could be used as an index of relative power output, when comparing different types of flight

Table 3. Observed airspeeds, wingbeat frequencies and wavelengths

Species	Mass (kg)	Span (m)	Area (m <sup>2</sup> )	Wingbeat frequency (Hz)				Airspeed (m s <sup>-1</sup> )			Wave-length (m)	<i>H</i>	
				Mean	s.D.	<i>N</i> (obs)	<i>N</i> (wbeats)	Mean	s.D.	<i>N</i> (speed)			
13	A	0.398	0.549	0.0369	9.18	0.749	61	1467	17.6	3.2	200	1.92	3.50
30	A	0.950	0.707	0.0544	8.69	0.479	14	356	19.1	2.5	178	2.20	3.11
32	A	0.620	0.661	0.0462	9.08	0.580	22	444	16.0	2.5	50	1.76	2.66
35	A	1.35	1.37	0.214	3.93	0.285	15	332	14.9	3.8	72	3.79	2.77
37	B	0.390	1.05	0.117	3.61	0.207	5	136	13.3	2.1	20	3.68	3.51
40	A	0.387	0.965	0.101	3.18	0.227	16	249	13.1	2.4	18	4.12	4.27
47	B	1.55	1.65	0.285	2.90	0.196	20	340	13.0	1.9	6	4.48	2.72
51	B	0.950	1.36	0.203	3.05	0.129	11	178	9.9	2.2	9	3.25	2.39
58	C	0.325	1.03	0.106	2.74	0.221	26	461	9.5	1.9	99	3.47	3.37
65	B	0.470	1.15	0.108	3.12	0.284	26	450	10.0	3.1	56	3.21	2.79
80	A	0.300	0.990	0.0888	3.36	0.117	25	424	9.9	1.9	95	2.95	2.98
86	D	0.815	1.13	0.124	4.58	0.183	29	478	13.0	2.8	104	2.84	2.51
112	A	0.370	0.923	0.0847	4.22	0.749	5	86	—	—	0	—	—
117	E	3.01	1.85	0.262	3.53	0.161	26	390	14.9	2.6	32	4.22	2.28
118	D	1.24	1.17	0.173	5.07	0.260	33	412	—	—	0	—	—
120	A	1.41	1.16	0.179	5.03	0.138	172	3116	14.5	1.8	189	2.88	2.48
122	A	1.81	1.04	0.158	5.35	0.208	50	1122	15.4	2.2	103	2.88	2.77
126	F	3.39	2.26	0.450	3.01	0.109	123	1352	10.1	2.8	70	3.36	1.49
128	E	1.47	2.29	0.408	2.24	0.050	7	74	9.3	2.0	95	4.15	1.81
183	C	1.30	1.25	0.226	3.90	0.166	149	2566	11.9	1.8	6	3.05	2.44
184	E	0.900	0.951	0.160	4.65	0.201	70	979	12.9	2.0	120	2.77	2.92
192	A	2.50	1.91	0.493	2.68	0.135	44	794	11.0	1.8	8	4.10	2.15
194	A	1.92	1.76	0.419	2.55	0.114	12	225	9.4	1.6	7	3.69	2.10
196	A	0.874	1.34	0.222	2.79	0.154	49	894	10.6	2.1	59	3.80	2.84
200	A	0.340	0.980	0.134	3.63	0.219	49	902	8.8	1.2	15	2.42	2.47
325	F	1.55	1.75	0.442	2.99	0.078	25	199	10.6	2.4	25	3.55	2.03
326	F	2.08	1.38	0.327	4.53	0.179	33	160	10.8	2.5	16	2.38	1.73
352	F	4.68	2.24	0.756	2.72	0.035	4	65	11.2	0.8	4	4.12	1.84
360	E	0.090	0.502	0.0344	5.70	0.428	32	264	9.1	2.4	49	1.60	3.19
364	C	1.49	1.59	0.300	3.31	0.149	20	360	10.6	2.1	90	3.20	2.01
412	F	0.132	0.510	0.0478	9.19	0.843	29	76	12.7	1.9	16	1.38	2.71
614	C	0.0201	0.320	0.0133	8.72	1.40	15	102	11.3	2.8	129	1.30	4.06

Species numbers are identified in Table 1, and are followed by a code letter indicating the percentage of observations in which the bird was flap-gliding (or bounding) rather than continuously flapping (*A*=0–5%; *B*=5–25%; *C*=25–50%; *D*=50–75%; *E*=75–95%; *F*=95–100%).

*N*(obs), number of frequency observations; *N*(wbeats), number of wingbeats counted; *N*(speed), number of airspeed observations; *H*, ratio of wavelength to wing span.

within the same species, but is not directly related to the determination of wingbeat frequency as such.

#### Dimensional analysis

The first step in the analysis is to draw up a minimum list of variables which

Table 4. *Variables used in dimensional analysis*

Variable	Symbol	Dimensions
Body weight	$mg$	$\text{MLT}^{-2}$
Wing span	$b$	$\text{L}$
Wing area	$S$	$\text{L}^2$
Wing moment of inertia	$I$	$\text{ML}^2$
Air density	$\rho$	$\text{ML}^{-3}$

would have to be taken into account if a dynamical solution were to be attempted, and to list them with their dimensions (Table 4). The six variables mentioned in the Introduction have been reduced to five by combining body mass and the acceleration due to gravity into a single variable (weight). The dimensional method postulates that wingbeat frequency ( $f$ ) is proportional to the product of these variables, each raised to some unknown power, that is:

$$f \propto (mg)^\alpha b^\beta S^\gamma I^\delta \rho^\epsilon. \quad (2)$$

Restrictions on the possible values for the unknown exponents  $\alpha$ ,  $\beta$ ,  $\gamma$ ,  $\delta$  and  $\epsilon$  can be established by considering the physical dimensions. The dimensions of each variable are represented as powers of mass (**M**), length (**L**) and time (**T**), as summarized in Pennycuick (1988). Both sides of proportionality 2 must have the same dimensions ( $\text{T}^{-1}$ ) so we can write an equation for the dimensions:

$$\text{T}^{-1} = (\text{MLT}^{-2})^\alpha \text{L}^\beta (\text{L}^2)^\gamma (\text{ML}^2)^\delta (\text{ML}^{-3})^\epsilon. \quad (3)$$

This can be decomposed into separate equations for the unknown powers of **M**, **L** and **T**:

$$\text{powers of M:} \quad 0 = \alpha + \delta + \epsilon; \quad (4a)$$

$$\text{powers of L:} \quad 0 = \alpha + \beta + 2\gamma + 2\delta - 3\epsilon; \quad (4b)$$

$$\text{powers of T:} \quad -1 = -2\alpha. \quad (4c)$$

The method supplies three equations, but in this application there are five unknowns, so evidently there is no unique solution. However, equation 4c supplies a unique value for one of the variables ( $\alpha=1/2$ ) which can then be substituted in equations 4a and 4b:

$$\delta + \epsilon = -1/2; \quad (5a)$$

$$\beta + 2\gamma + 2\delta - 3\epsilon = -1/2. \quad (5b)$$

Regression analysis of the field data will serve as a guide to the correct values of the exponents, with the restriction that the values eventually chosen must satisfy equations 5.

#### *Multiple regression*

For the regression analysis, wingbeat frequency ( $f$ ) was taken to be the



Table 5. *Partial regression coefficients and their standard deviations*

Variables	Coefficient	S.D.	Estimating exponents	Assumed value
Frequency vs mass	$b_{fm}=0.355$	0.0454	$\alpha+\delta$	1/3
Frequency vs span	$b_{fb}=-1.32$	0.210	$\beta+2\delta$	-1
Frequency vs area	$b_{fs}=-0.0886$	0.113	$\gamma$	-1/4

See text for definitions of exponents.

dependent variable, and the three independent variables were body mass ( $m$ ), wing span ( $b$ ) and wing area ( $S$ ). Each value was transformed into its logarithm, and the three partial regression coefficients, together with their standard deviations, were calculated by the method given in Snedecor (1946), using a BASIC program written for the purpose. The results are presented in Table 5.  $b_{fm}$  is the regression coefficient of wingbeat frequency on body mass, with the other variables held constant at their means, and likewise for the other coefficients. Ideally, measurements of wing moment of inertia would have been obtained for inclusion in the regression, but these measurements are difficult to get, and it was unfortunately not practicable to attempt this. As a practical expedient, we may make the assumption that the moment of inertia is not independent of the other variables, and can be predicted from the body mass and wing span, thus:

$$I \propto mb^2 . \tag{6}$$

It is not known to what extent this is a good assumption, and the errors likely to arise from it will be considered below. Meanwhile, the effect is to modify proportionality 2 by substituting  $mb^2$  instead of  $I$ , raising this to the power  $\delta$ , then collecting the exponents of  $m$  and  $b$  thus:

$$f \propto m^{\alpha+\delta} g^{\alpha} b^{\beta+2\delta} S^{\gamma} \rho^{\epsilon} . \tag{7}$$

*Reconciliation of regression with dimensional analysis*

Inspection of proportionality 7 shows that the regression coefficients represent estimates of the original exponents in various combinations, as indicated in Table 5. They are only estimates, and cannot be accepted as they stand, because the exponents have to be related to each other in such a way as to satisfy equations 5. The reconciliation consists in choosing values that satisfy equations 5, and also do not stray outside the fiducial limits obtained from the regression. There is only a small amount of scope for arbitrary choice, and this will no doubt be narrowed further by the addition of new data in the future. There is some merit (at least aesthetically) in presenting the chosen values in exact fractional form, rather than as decimals, which we do as follows:  $\alpha=1/2$ ,  $\beta=-2/3$ ,  $\gamma=-1/4$ ,  $\delta=-1/6$ ,  $\epsilon=-1/3$ .

If values of wing moment of inertia were known, these values could be used directly in proportionality 2 to give the relationship:

$$f \propto (mg)^{1/2} b^{-2/3} S^{-1/4} l^{-1/6} \rho^{-1/3} . \quad (8)$$

If, as at present, wing moment of inertia has not been measured, and has to be estimated from body mass and wing span, then the exponents have to be combined as in proportionality 7 to give:

$$f \propto m^{1/3} g^{1/2} b^{-1} S^{-1/4} \rho^{-1/3} . \quad (9)$$

The exponents for  $m$ ,  $b$  and  $S$  are amended values of the regression coefficients in Table 5, chosen to make proportionality 9 dimensionally correct. The chosen values of  $\alpha$  and  $\delta$  add up to  $1/3$ , which is within the 95 % fiducial limits for the regression estimate of  $b_{fm}$ . Similarly, the chosen values of  $\beta$  and  $\delta$  make  $\beta + 2\delta = -1$ , which is within the 95 % fiducial limits for the regression estimate of  $b_{fb}$ , while  $\gamma$  is directly estimated by  $b_{fS}$ , and is also within the 95 % fiducial limits. The choice of the exponents is to some extent arbitrary, and it is possible that future expansion of the data will require the values chosen here to be amended. However, there is only a small amount of scope for varying them, without either violating equations 5 or going outside the fiducial limits of the regression coefficients.

#### *Practical frequency prediction*

To change proportionality 9 into a predictive equation, an estimate is needed of the constant of proportionality. Fig. 1 shows a double-logarithmic plot of the observed wingbeat frequencies from Table 3 against the expression on the right-hand side of proportionality 9. The fitted line is a reduced major axis line (Rayner, 1985). This is the same as the 'standard major axis' line of Hofman (1988), who also supplies formulae for finding the slope, and the standard deviation of the slope. The constant of proportionality is estimated to be 1.08, so the equation for predicting the wingbeat frequency of an unknown bird from its mass, span and area is:

$$f = 1.08 (m^{1/3} g^{1/2} b^{-1} S^{-1/4} \rho^{-1/3}) . \quad (10)$$

The correlation coefficient from Fig. 1 is 0.947, which is significant well beyond the 1 % probability level, in spite of the modest number of data points (32). The slope of the line is 1.04, and is not significantly different from 1 ( $t$ -test). The dimensionless multiplier (1.08) is entirely empirical, as dimensional analysis makes no prediction about this.

#### *Potential for extrapolation*

Fig. 1 displays a very satisfactory fit between the derived equation and the field data, but the latter cover only a limited spectrum of bird species. If equation 10 has the degree of generality which the method of derivation implies, it should be less sensitive to extrapolation than a fitted line based on regression analysis alone. The prediction is that if other observers contribute measurements on passerines, bats and insects, and combine them with the measurements in Table 3, equation 10 will continue to give a good fit to the expanded data, subject to some reservations due

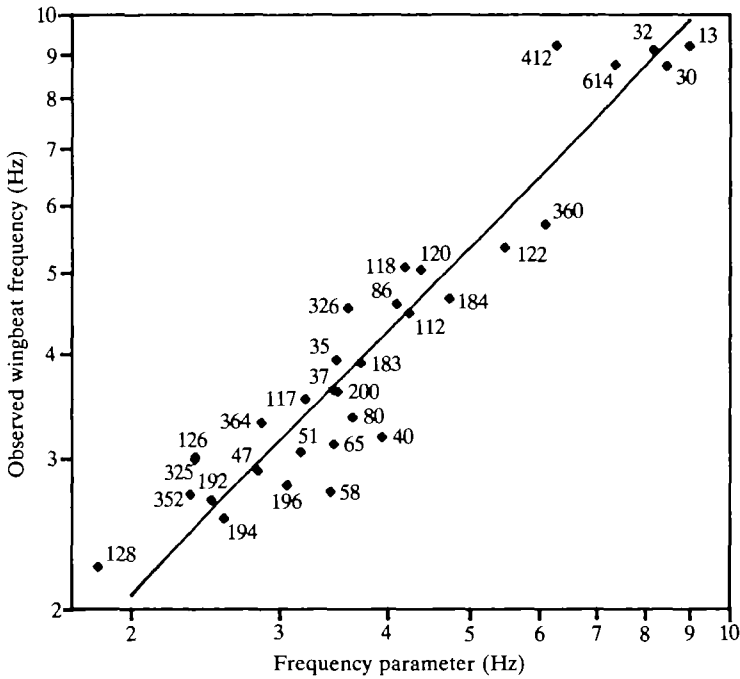


Fig. 1. Double-logarithmic plot of observed wingbeat frequency from Table 3 *versus* 'frequency parameter' (the expression on the right-hand side of proportionality 9). Slope of standard major-axis line 1.04. Correlation coefficient 0.947 for 32 points (significant  $P < 0.01$ ). Slope not significantly different from 1 ( $t$ -test). Species numbers as in Table 1.

to the treatment of wing moment of inertia. Since so few measurements have been made of the moment of inertia of bird wings, it is difficult to assess how much error is likely to arise from using proportionality 6 to incorporate it. The chance of introducing a systematic error would no doubt be greater in a larger sample, including animals whose wings are constructed on different mechanical principles. One might provisionally expect that proportionality 6 would be more likely to apply within a major taxon than between such taxa. If the sample were to be augmented by pooling the present data with others on, say, various insects, it would be very desirable to get some measurements of moment of inertia.

It should be noted that it is not practical to extend the present data by culling observations of mass, wing span, wing area and wingbeat frequency from the literature. Although vast quantities of such data can be unearthed by diligent search, the original observers in most cases did not define with sufficient precision how these variables were defined or measured. Examination of the numbers often reveals that the definitions, whatever they were, differed from those used here. To determine how far equation 10 can be extrapolated, the present data would have to be augmented by collecting further observations especially for the purpose, using exactly the same definitions for the variables.

*Wingbeat wavelength*

The wingbeat wavelength ( $\lambda$ ) is defined as:

$$\lambda = V/f, \quad (11)$$

where  $V$  is the airspeed and  $f$  is the wingbeat frequency.  $\lambda$  is the distance flown in one wingbeat cycle. To find how wingbeat wavelength varies in different birds, one may note from Pennycuick (1975) that the minimum power speed (or maximum range speed) is expected to depend on physical variables in the following way:

$$V \propto m^{1/2} g^{1/2} b^{-1} \rho^{-1/2}, \quad (12)$$

if it is assumed that the disc area and the equivalent flat plate area of the body are each proportional to  $b^2$ . Dividing proportionality 12 by proportionality 9 gives the following for the wavelength:

$$\lambda \propto m^{1/6} S^{1/4} \rho^{-1/6}. \quad (13)$$

Neither gravity nor the wing span appears in proportionality 13, because each of these variables affects both the speed and the wingbeat frequency in the same manner, and therefore cancels. The values of wavelength from Table 3 are plotted against the expression on the right-hand side of proportionality 13 in Fig. 2. The correlation coefficient is 0.788 for 30 points, which is significant at the 1% probability level. The slope is 0.817, which is not significantly different from 1 ( $t$ -test). It should be remembered that the wavelength estimates in Table 3 were obtained by combining separate observations of airspeed and wingbeat frequency, made on different birds on different occasions. Although this is not expected to bias the estimated wavelengths, it might account for the greater scatter in Fig. 2 as compared to Fig. 1.

*Advance ratio*

Ellington (1984) uses a dimensionless variable called the 'advance ratio' ( $J$ ), to represent the ratio of the airspeed due to forward motion to that due to flapping, as 'seen' at some fixed point on the wing.  $J$  is defined as:

$$J = \lambda/\phi b, \quad (15)$$

where  $\phi$  is the 'stroke angle', that is the angle through which the wing is rotated at the shoulder during the downstroke. Measurements cannot be given for advance ratio as such, because stroke angle could not be measured by the methods used in this study, but values for the ratio of wavelength to span (denoted by  $H$ ) are listed in the last column of Table 3. These numbers would be the same as Ellington's advance ratio for a bird that beats its wings through a stroke angle of 1 radian. The stroke angle measured for the double-crested cormorant by Pennycuick (1989b) was not far from 1 radian, and values for other species in the sample, though not measured, are not likely to differ from this by more than a factor of 2 in either direction.

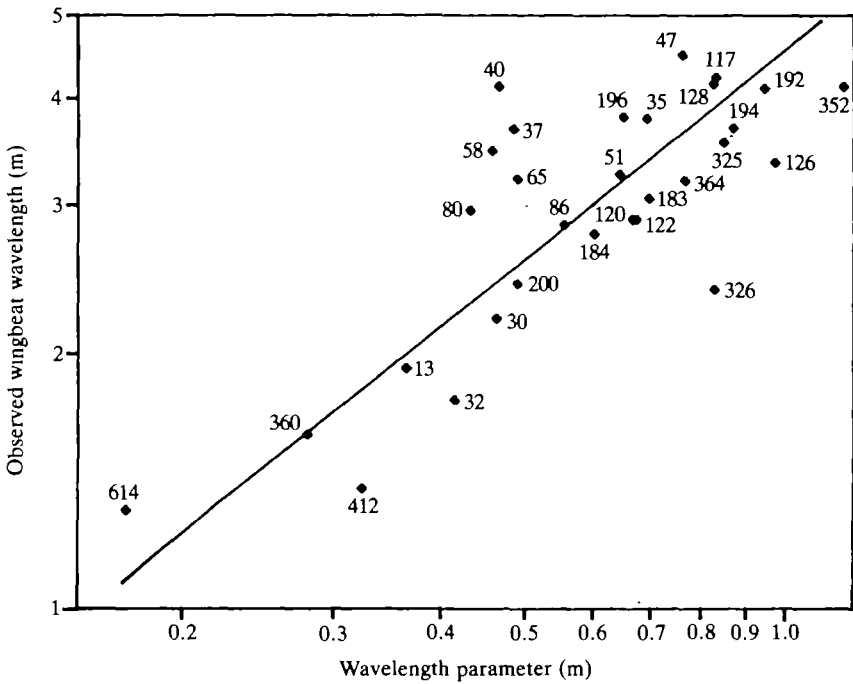


Fig. 2. Double-logarithmic plot of observed wingbeat wavelength from Table 3 versus 'wavelength parameter' (the expression on the right-hand side of proportionality 14). Slope of standard major-axis line 0.817. Correlation coefficients 0.788 for 30 points (significant  $P \ll 0.01$ ). Slope not significantly different from 1 ( $t$ -test). Species numbers as in Table 1.

*Allometry of frequency and wavelength*

In geometrically similar birds, the wing span would vary with the one-third power, and the wing area with the two-thirds power of the mass. Hence, from proportionality 9, the wingbeat frequency would vary inversely with the one-sixth power of the mass. From proportionality 13, the wingbeat wavelength would vary with the one-third power of the mass, that is directly with the linear dimensions. The wavelength:span ratio would be independent of the mass. If the stroke angle were independent of the mass, then so also would be the advance ratio. These allometric trends have applications to very broad questions, such as the upper limit to the mass of flying birds, but are not much help for predicting the wingbeat frequencies or wavelengths of individual species, because of the wide departures from geometric similarity seen in birds of different adaptive types.

*Adjustment of the flight muscles*

Equation 10 permits the effect on wingbeat frequency to be predicted for variations of wing span, wing area, gravity and air density, in addition to the body mass. Three of these five variables (gravity, wing span and wing area) may be considered fixed as far as an individual bird is concerned. Gravity is usually

perceived as constant, since only one planet is currently available to field observers, although no such restrictions need constrain the theorist (Pennycuick, 1987*b*). Wing span and area are usually considered to vary only in the sense of evolutionary change, although it is possible that some birds that moult biennially may change their wing shape and size between the breeding and migration seasons.

The remaining two variables, body mass and air density, are liable to change by a large amount in an individual bird in the course of one flight. For example the mass of a long-distance migrant may decline by a factor of two as fuel is used up, and a high-flying migrant may encounter density changes of similar magnitude. These changes alter the 'natural' wingbeat frequency, according to equation 10. The implication is that maximum efficiency would only be obtained by the flight muscles if their intrinsic speed were changed to suit, an adjustment which can be traced to the rate constants that govern the attachment and detachment frequencies of myosin crossbridges (Pennycuick, 1990). The muscles of growing animals certainly 'slow down' in this sense to match the animal's increasing size, but it seems unlikely that such an adjustment could be made by a migrating bird on a time scale of hours or minutes. In some circumstances, birds avoid the need to reduce wingbeat frequency by flapping intermittently (either bounding or flap-gliding) but this expedient is only helpful if more muscle power is available than is required. Further insight into the way that birds adjust their wingbeat frequency in flight (if they do) will have to await direct observation of migrants in flight, or experiments on birds trained to fly in a hypobaric wind tunnel.

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