Special Review

GREENEWALT ON BIRD FLIGHT

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The flight of birds: The significant dimensions, their departure from the requirements for dimensional similarity, and the effect on flight aerodynamics of that departure.—Crawford H. Greenewalt. 1975. Transactions of the American Philosophical Society, New Series, vol. 65, part 4. 67 pp., 41 figs., 33 tables. $7.00.—This is a comprehensive analysis of relative sizes of birds and the relationship between size and the aerodynamics of flapping flight. The paper has three parts: The first part describes relations between body dimensions—mass, wing area, wing span, wing mass, wing length, and muscle mass—for a variety of birds. The second part describes a quantitative, aerodynamic theory that predicts the energetic requirements for flapping flight as a function of air speed, body weight, wing span, and wing surface area. The third part discusses dimensional relations in terms of the theory of the second part.

The paper is analytical, thoughtful, and thought provoking. The writing is clear for the most part, although those not familiar with conventional low-speed aerodynamics may find the paper slow going, and probably will want to use some of the texts listed in the bibliography. Unfortunately the equations are unnecessarily difficult to use, for Greenewalt does not use a consistent system of units, such as the SI system that has become conventional for this subject matter. The difficulty is compounded by table headings and text references that often do not specify units, and by the same symbol being used for different quantities. For example, in one equation the symbol W is used twice, first to symbolize weight, then to symbolize mass. Although sufficient information is given to sort these difficulties out, the extra effort required is aggravating, particularly when it could have been avoided so easily.

The paper is an excellent example of how a theory can be used to relate seemingly unconnected observations. Greenewalt's aerodynamic theory is a significant achievement in the field and makes a wealth of predictions. It cannot be reviewed comprehensively in a few pages, but I will try to give an idea of its scope by describing (1) some of the dimensional relations that Greenewalt establishes, (2) some of the consequences that flow from these relations together with the theory, and (3) the aerodynamic theory itself.

Greenewalt compares body dimensions to those of hypothetical, "dimensionally similar" birds. If two birds are dimensionally similar, then a length measurement on one is proportional to the homologous length measurement on the other. For dimensionally similar birds of the same density,

$$W = k_1 b^3 = k_2 S^{1.5},$$

or

$$\log W = \log k_1 + 3 \log b = \log k_2 + 1.5 \log S,$$

where W is body weight, b is wing span, and S is wing surface area (I use Greenewalt's symbols wherever possible in this review).

Whether actual birds are dimensionally similar may be determined by plotting, for example, the logarithm of W against the logarithm of S. Such a plot for dimensionally similar birds will have a slope of 1.5. Indeed, Greenewalt finds that birds are not dimensionally similar, and separates them into three models on the basis of regression analyses for the above plot—"passeriforms" (slope = 1.275), "shore birds" (slope = 1.4) and "ducks" (slope = 1.4). He treats hummingbirds separately (slope = 1), and finds that this group is unique in that the relations wing loading (W/S), span loading (W/b^2) and aspect ratio (b^2/S) are all approximately constant.

Greenewalt does an unusually careful job of analyzing his results statistically and points out that even though wing area and weight are related within a model, for different models, birds of the same weight may show a greater than sevenfold difference in wing area. Greenewalt provides additional information on insects and bats, and on the relations between body weight, wing weight, muscle weight, wing beat rate, and wing length.

Greenewalt then develops an aerodynamic theory that predicts the mechanical work rate (power) required for horizontal flight (relative to the air) at a particular air speed on the basis of wing span, wing area, and body weight. He selects three properties that can be calculated from this theory with which to compare passeriforms, shore birds, and ducks. These are: V_{mp}, the air speed at which the power required to sustain flight is minimum; P_{mp}/W, the power per unit weight at that air speed; and, $E_{mr}/(dW)$, the energy required per unit weight per unit distance (d) flown at the air speed (V_{mr}) for maximum range. (The subscripts $_{mp}$ and $_{mr}$ are mnemonic for "minimum power" and "maximum range," respectively.) V_{mr} is the air speed at which the ratio of power required to air speed has its minimum value—i.e. P_{mr}/V_{mr} where P_{mr} is the power required to fly at V_{mr}. Since $P_{mr}/V_{mr} = E_{mr}/d$, $E_{mr}/(dW)$ is also a minimum value—hence the maximum range subscript. Greenewalt gives simple equations (deduced from his theory) for these quantities, all of which are proportional to products of W, S, and V raised to appropriate powers. He calculates V_{mp}, P_{mp}/W and $E_{mr}/(dW)$ for birds in each of his three models and carries out a regression analysis of the logarithm of each quantity on the logarithm of weight. The resulting equations can be compared with those calculated from the model for dimensional birds, i.e. birds in which wing span is proportional to the one-third power of weight, and wing area is proportional to the two-thirds power of weight.

Greenewalt finds that among his three models, V_{mp} values for passeriforms depart most from those for dimensional birds: The larger the bird, the lower is its V_{mp} relative to that of the dimensional bird. The relation is similar but the departure is less for shore birds and is least of all for ducks. The evolutionary expalanation offered by Greenewalt is that the passeriforms have sacrificed speed for maneuverability, while shore birds and ducks, which live in more open environments, have done so to a lesser extent. Birds achieve the low values of V_{mp} largely because their wing spans differ from those of the dimensional birds.

The minimum power per unit weight (P_{mp}/W) does not change significantly with weight in the three models, although it increases with weight for the dimensional bird. The scatter of points calculated for actual birds is large, again largely because their wing spans differ from those of dimensional birds.

Finally we come to energy required per unit weight per unit distance flown. This quantity, as calculated from Greenewalt's equations, has values close to those for dimensional birds. Greenewalt reaches the interesting conclusion that the dimensional anomalies in proportions between real and dimensional birds are the result of selection for high maneuverability and time aloft in local flights (as measured by V_{mp} and P_{mp}/W), without much sacrifice of ability to fly long distances (as measured by $E_{mr}/(dW)$).

Regarding hummingbirds, Greenewalt considers the question of why the body weights of living species do not differ by more than a factor of 10. Dimensional considerations would allow a larger size ratio. On the basis of time-energy budgets, Greenewalt concludes that hummingbirds much larger than the largest existing species (with a body weight of about 20 g) would not have enough foraging time to feed themselves. Hummingbirds much smaller than the smallest existing species (weighing about 2 g) would have difficulty storing enough food to last the night.

Let us now return to the theory on which the above mentioned conclusions depend. Is it creditable? To put this question more specifically, how does the theory depend on aerodynamic and physiological principles, and does it predict measured values accurately? Let us first consider how the theory is related to aerodynamic and physiological principles.

A theory for the energetic requirements of flight may be constructed by accounting for various categories of the rate of energy use (power), and adding the resulting terms together. For example, the flight muscles do mechanical work on the wings at some rate, and various maintenance and sensory systems also require energy at some rate to keep the muscles functioning and the bird on course. The work rate of the flight muscles further subdivides rather naturally into three terms: profile power, parasite power, and induced power. These three terms arise because the velocity of the air flowing over any specified region of a flapping wing has three components: one caused by the motion of the bird's body (exclusive of the wings) through the air, a second from the motion of the flapping wings relative to the body, and a third from an air velocity component induced by the wing motion (Tucker *in* Wu et al 1975, Swimming and flying in nature, vol. 2, Plenum, p. 845). Thus a theory for flight energetics might consider four terms: profile, parasite, induced, and maintenance power. More terms could be added, for example by subdividing maintenance power. Terms can also be dropped by assigning them values of zero or by combining them with others. At least two terms must be retained to account for the characteristic U-shaped curve that describes the total power requirements of any heavier-than-air aircraft over a range of flight speeds.

Greenewalt's theory is a simple one—it separates only two terms. Greenewalt arrives at this formulation by considering the power requirement of a fixed wing aircraft with a thrust producer (e.g. a propeller) that is 100% efficient. He then multiplies each term by factors that are assumed to account for the extra power required for flapping the wings and for maintenance. Thus, Greenewalt's theory for a given bird under given conditions is of the form

$$P = a_{G,1}V^{-1} + a_{G,2}V^{2.7}.$$

Alternate theories are a three-term one offered by Pennycuick (*in* Farner and King 1975, Avian biology, vol. 5. New York, Academic Press, p. 1), namely

$$P = a_{P,1} + a_{P,2}V^{-1} + a_{P,3}V^{3},$$

and a five-term one of my own, derived from an earlier version of Pennycuick's (Tucker *in* Paynter 1974, Avian energetics, Nuttall Ornithol. Club, p. 298), namely

$$P = a_{T,1} + a_{T,2}V^{-2/3} + a_{T,3}V^{-1} + a_{T,4}V^{2} + a_{T,5}V^{5/2}.$$

The coefficients (a) are constant for a given bird under given conditions and depend on such things as air density, air viscosity, wing span, wing area, body weight, and body shape. The values of the coefficients and exponents are to some extent guesses because of lack of data, although each of the authors give rationales for the values they choose. Thus, none of the theories above can be considered to be more correct than another simply because it has a different number of terms. Some virtue, however, should attach to a theory that separates terms to the limit allowed by existing physiological and aerodynamic information, and even more if the theory can then be simplified by recombining them or showing them to be negligible. The simplicity of Greenewalt's theory results largely from minimum separation of terms rather than recombination of them or analysis of their values.

A necessary test of a theory of course is how accurately it predicts measured values. But what measured values are to be chosen? Greenewalt fits his theory to measurements of power and speed on racing pigeons flying 480 km under natural conditions (LeFebvre 1964, Auk 81: 403). Pennycuick and I fit our theories to measurements of power and speed made in wind tunnels. Unfortunately, the two sets of measurements lead to quite different results. Thus, for passeriform birds flying at speeds to maximize range, Greenewalt's theory yields the relation

$$P'_{mr} = 45.7\ m^{0.980}$$

(m is total mass in kg, P'_{mr} is the metabolic rate, distinguished from work rate by a prime, in watts at the speed for maximum range). Pennycuick's theory yields approximately

$$P'_{mr} = 102\ m^{1.067}$$

(assuming wing span in meters = 1.1 m$^{1/3}$) and my theory yields approximately

$$P'_{mr} = 94.2\ m^{0.974}$$

TABLE 1

COMPARISON OF PREDICTIONS FROM THREE THEORIES WITH MEASUREMENTS ON FIVE FLYING ANIMALS

	Percent deviation from measured values								
	Greenewalt's theory[1]			Pennycuick's theory			Tucker's theory		
Species	V_{mr}	P'_{mr}	$P'_{mr}/(WV_{mr})$	V_{mr}	P'_{mr}	$P'_{mr}/(WV_{mr})$	V_{mr}	P'_{mr}	$P'_{mr}/(WV_{mr})$
Budgerigar	15	−32	−41	11	4	−6	14	23	8
Laughing Gull	−21	−46	−32	−4	−20	−16	−11	−12	−1
Fish Crow	22	−27	−40	35	18	−12	26	22	−3
Spear-nosed Bat	34	−44	−59	49	−18	−45	38	0	−28
Flying Fox	28	−22	−39	49	23	−18	40	20	−15
Mean absolute deviation	24	34	42	30	17	19	26	16	11

[1] Wing areas, estimated from Greenewalt's data, are 0.00882, 0.102, 0.070, 0.031, and 0.180 m^2, respectively, beginning with the budgerigar. Other morphological data from Tucker 1973, previously cited. Air density = 1.2 kg/m^3.

with the same assumption. Pennycuick's theory and my own give the same metabolic rate for a 0.425 kg bird, but this rate is twice that calculated from Greenewalt's theory. The approximation equations are least squares fits to the values calculated from the actual equations for body masses between 3×10^{-3} and 10 kg, and are accurate within 16%. (Air density is 1.2 kg/meter^3 throughout this review.)

All three theories may be compared with measurements made in a wind tunnel. I have chosen three quantities to compare: (a) the air speed (V_{mr}) at which an animal can fly the maximum distance; (b) the metabolic rate (P'_{mr}) at that air speed; and, (c) the ratio $P'_{mr}/(WV_{mr})$, which is the minimum amount of metabolic energy required to fly a unit of distance at unit body weight W. P', V, and W are all expressed in the same system of units (W is a force), so $P'/(WV)$ is dimensionless. The quantities V_{mr}, P'_{mr} and $P_{mr}/(WV_{mr})$ have been measured for three birds and two bats flying in a wind tunnel (Tucker 1973, J. Exp. Biol. 58: 689, Table 2). The percentage deviations of the predictions from the three theories from these measured values are shown in Table 1.

All three theories predict V_{mr} values that are usually high. Greenewalt's theory predicts P'_{mr} values that are consistently low. Consequently, Greenewalt's values for $P'_{mr}/(WV_{mr})$ values are the lowest predicted by the three theories.

One other comparison of the theoretical predictions is interesting: the variation of $P'_{mr}/(WV_{mr})$ with body mass (m) for different species. In addition to the wind tunnel data for flying birds and bats, there are several other estimates of this quantity for other birds and for insects (Tucker 1975, Amer. Sci. 63: 413). Over a range of body masses spanning six orders of magnitude, a regression analysis of $P'_{mr}/(WV_{mr})$ on m (in kg) yields the relation

$$P'_{mr}/(WV_{mr}) = 0.529\, m^{-0.234}.$$

Greenewalt's theory for passeriforms yields

$$P'_{mr}/(WV_{mr}) = 0.362\, m^{-0.139}.$$

Pennycuick's theory for passeriforms yields approximately

$$P'_{mr}/(WV_{mr}) = 0.619\, m^{-0.070}$$

assuming wing span in meters equals 1.1 $m^{1/3}$, and my theory for passeriforms yields approximately

$$P'_{mr}/(WV_{mr}) = 0.604\, m^{-0.197}$$

with the same assumption. This last equation is most similar to that for all flying animals, although it may be that it is not the most accurate for passeriforms. As the equations for the three models differ substantially, more data, particularly for very small and very large birds, could provide a definitive test of predictions. The approximation equations are least squares fits to the values calculated from the actual equations for body masses between 3×10^{-3} and 10 kg, and are accurate within 11%.

Greenewalt points out that his theory predicts lower metabolic rates than those measured for birds flying in wind tunnels and gives the reasons why he has rejected the wind tunnel data. These are (1) that the mask and tubing attached to the birds in the wind tunnel increases aerodynamic drag, (2) that the extra weight on the bird's head would change the "angle of attack," (3) that the mask would affect the position of the bird, (4) that the mask might affect respiration, (5) that the wind tunnel width in some cases was only slightly greater than the wing span, (6) that psychological factors might influence the bird's metabolic rate, and (7) that wind tunnel results are not consistent with the performances of birds gliding or migrating in natural conditions. Corrections due to items (1), (2), (3), and (5) have been estimated elsewhere, and are either not large enough, or not in the correct direction to support Greenewalt's low predicted metabolic rates. The metabolic rate required for respiration (item 4) is estimated at only 5% of the total metabolic rate during flight (Tucker 1973, op. cit.). The "psychological factors" of item (6) are unknown. Whatever the size of their effects, the effects do not change much from day to day in the wind tunnel experiments, because the standard deviations of metabolic rate measurements under given conditions are typically less than 10% of the mean value (Tucker 1974, op. cit.).

The statement in item (7) is not supported by the cited data, which involve velocity with respect to the ground and distance covered over the ground in nature. These are not the required data for comparison with wind tunnel results or with the theories under discussion. The results and theories require the magnitude of the bird's velocity with respect to the air (air velocity) during horizontal flight and the distance covered through the air. Ground velocity is the horizontal component of the vector sum of air velocity and wind velocity (the velocity of the wind with respect to the ground) and may not be substituted for air velocity during horizontal flight. Usually ground velocity and wind velocity cannot be measured accurately and simultaneously at the same place in nature, so the air velocities of birds in natural conditions usually are not known accurately.

An example of the errors that can result from interchanging ground velocity and air velocity is Greenewalt's use of LeFebvre's data for free-flying pigeons. Thunderstorms were said to be in the region of the flight, and Pennycuick (personal communication) has calculated on the basis of weather records that the pigeons had a tail-wind of approximately 5 m/s during the flight. The tail-wind would have given the pigeons time to stop during the flight, and in fact, half of the birds had muddy feet and food in their crops when they were recaptured, proving that they had landed and fed. In addition, the birds could have taken advantage of the updrafts in the unstable atmosphere that produces thunderstorms to reduce the metabolic cost of flight. Even without accounting for updrafts, Pennycuick's figures show that the metabolic rate of the pigeons during flight, after correcting for the tail-wind, is 29% higher than Greenewalt's theory predicts. On the other hand the corrected metabolic rate is still only 77% and 81%, respectively of the values predicted by Pennycuick's theory and mine ($m = 0.4$ kg, $b = 0.66$ m, equivalent flat plate area $= 1.55 \times 10^{-3}$ m^2).

Greenewalt's dimensional arguments could be correct, whether or not his theory yields accurate values for metabolic rates, because these analyses depend on changes rather than absolute values. Then again, they could be wrong, because of the numerous untested assumptions that go into his theory, or Pennycuick's or my own for that matter. I hope that the predicting powers of these theories will be tested by measurements on animals of the diverse dimensions flying at a wide range of speeds, altitudes, and temperatures. Greenewalt's interesting evolutionary arguments perhaps are not amenable to testing, but the theory on which they are based is.

Greenewalt's monograph is a valuable contribution to our ideas on avian flight and the size of birds, well recommended to all ornithologists. Further analysis of the concepts presented by Greenewalt and, more importantly, their direct empirical testing against experimental and field observations will add considerably to our knowledge of avian flight and our understanding of relative size in birds.—*Department of Zoology, Duke University, Durham, North Carolina 27706.*