

A STATISTICAL METHOD TO ESTIMATE THE COST OF FLIGHT IN BIRDS

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Abstract.—Two approaches have been used to estimate the cost of flight in birds. The empirical approach measures costs directly or indirectly and makes allometric predictions based on body mass. The theoretical approach estimates the costs of flight based not only on mass, but on aerodynamic characteristics such as wing span and wing area.

In this paper we review different empirical techniques used to measure flight metabolism and propose two new equations to estimate the cost of flight using either mass and wing length, or weight, wing length, and wing span as estimators of flight metabolism. These new equations explain the empirical points better than a regression based on body mass alone and allow the estimation of flight metabolism using the aerodynamic characteristics of the bird.

UN MÉTODO ESTADÍSTICO PARA ESTIMAR EL COSTO ENERGÉTICO DEL VUELO EN AVES

Resumen.—Se han utilizado dos acercamientos para estimar el costo del vuelo en las aves. El acercamiento empírico mide costos directa o indirectamente y hace predicciones alométricas en base a masa corporal. El acercamiento teórico estima los costos de vuelo en base, no solo a masa corporal, sino también a características aerodinámicas tales como largo de ala, área del ala, etc. En éste artículo revisamos diferentes técnicas empíricas utilizadas para medir el metabolismo del vuelo y proponemos dos nuevas ecuaciones para estimar los costos del vuelo usando masa corporal y largo de ala, o peso, largo de ala y alcance del ala como estimadores del metabolismo del vuelo. Estas nuevas ecuaciones explican los puntos empíricos estadísticamente mejor que las regresiones basadas en masa corporal solamente y permite estimar el metabolismo del vuelo utilizando características aerodinámicas de las aves.

Flight confers great advantages, allowing birds to move rapidly over large distances, escape from predators, and pursue or capture prey in the air. It is not surprising therefore, that repeated attempts have been made to estimate flight's energetic cost. Two main approaches have been developed. The first makes predictions based upon aerodynamic theory, whereas the second employs empirical observation. In this paper, we analyze available empirical measurements of flight metabolism and extend these with regression analysis based upon variables related to a bird's aerodynamic properties, thus merging the two approaches. In this way we obtain two new equations that predict the cost of flight for a bird with given aerodynamic characteristics.

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AERODYNAMIC THEORY

Pennycuick (1969, 1975), Tucker (1973), and Greenewalt (1975) each have adapted aerodynamic theory to living birds.

In Pennycuick's (1969, 1975) model, the power required for flying has three components: induced power, (to lift the bird's weight) parasitic power, (due to a backwards force produced as a reaction to the bird's speed) and profile power (to overcome the profile drag of the wings). The final equation adds these three components, from which the cost of flight can be calculated knowing the weight and the wing span of the bird in question.

Tucker (1973) adjusted Pennycuick's (1969) equations to fit some empirical values obtained using wind tunnels. Unfortunately, only two empirical measurements were used, making extrapolation to other species questionable.

Greenewalt (1975) divided the birds in three general categories based on their aerodynamic characteristics and dimensional relationships: the "passeriform" model, the "shorebird" model and the "duck" model. The passeriform model includes birds with very high wing areas in comparison to their weights. The duck model includes birds with very small wing areas in relation to their weights. The shorebird model is intermediate.

Greenewalt's equations are derived by modifying aircraft aerodynamic theory. In general aerodynamic theory, weight is compensated by lift and drag is compensated by thrust. To this general equation Greenewalt adds friction and drag coefficients measured empirically on birds. The modifications assume that a bird's flapping wing behaves as an harmonic oscillator.

These theoretical equations estimate minimum costs at intermediate flight speeds and in general employ two kinds of variables: intrinsic properties of the bird such as body weight, flat-plate area of the body, "disk area," wing area, wing span, muscle efficiency; and extrinsic properties such as air density, speed of flight and air viscosity. All are difficult to estimate. Moreover, they have not been recorded extensively in the past by ornithologists. The standard way of preserving bird skins also precludes measurement on museum specimens. Perhaps for these reasons aerodynamic equations have not found great favor among most ornithologists to date.

EMPIRICAL METHOD

In this section we present all the available empirical data, review the limitations of these data, and explain the methods used to obtain them. We then review the allometric equations derived from these results.

Available data.—Table 1 shows all published measurements we found of flight metabolism obtained by empirical determinations. For each species we list the cost of flight metabolism in KJ/h, the total wing area of the bird, the length (chord) of the wing, the wing span, and the mass. In the case of material balance studies we show the average mass during the flight (see below).

We used the following procedures to standardize the units of measurement: In cases where there are measurements of different individuals of a given species in the same study we show the average value for mass and metabolic rate. The values for metabolic rate are converted using the equivalent of 39.5 KJ/g of fat and 20.1 KJ/l of oxygen consumed (Dawson 1974, Johnston 1970). Wing areas, wing lengths, and wing spans were obtained from the original sources when they were available. When they were not, we consulted Magnan (1922), Hartman (1961), Poole (1938), Greenewalt (1962, 1975), Roberts (1955) or measured them directly in the bird collection at the Academy of Natural Sciences of Philadelphia.

Methodological limitations of the data.—The general trend is an increase in flight metabolism with increase in mass. This is not surprising; the cost of flight must vary in relation to the mass transported. However, costs vary widely for a given mass (Fig. 1). Whether or not these are experimental errors or true differences among species is hard to determine. Such variation could also arise from the very different methodologies being used. The methods used are (based on the classification of Farner 1970):

1.—Measures of oxygen consumption in closed systems for hovering hummingbirds: this method consists of the measurement of oxygen consumption of hummingbirds that are hovering in a closed jar. Because most birds can hardly hover, this method is applicable only to hummingbirds. Sometimes it involves the use of electric grids that discourage the bird from landing. It is conceivable that such stress could increase the apparent costs of flight. Moreover, hovering is an expensive mode of flight, making comparisons with species other than hummingbirds impossible.

2.—Measurements of oxygen consumption or CO₂ production in wind tunnels: a bird is forced to fly for a given period of time inside a wind tunnel. The oxygen consumed or the CO₂ produced during flight is measured. This method permits comparisons of the costs of flight at different speeds and angles of attack. There are however, three serious disadvantages. First, no account is made of the effects of flying without progress. Second, it employs electric grids. Third, wind tunnels can be used only with trainable species, and even then, only a limited number of individuals of these “trainable” species can be taught to fly in the tunnels. For example, Torre-Bueno and Larochelle (1978) reports that only five out of 100 Starlings learned to fly in the tunnels. How these five individuals that learned to fly differed from the other 95 birds is not known.

3.—Measurements of CO₂ production during free flight using doubly-labeled water: the method itself involves an experimental error of $\pm 8\%$ and is expensive (Nagy 1980). In addition, it is necessary to catch the same individuals after the flights; often a considerable challenge. Moreover, whether the birds were in continuous flight during the period of experimentation may be difficult to ascertain. Nevertheless, this may be the best method available yet, since it is the only one that measures metabolism directly during free flight.

TABLE 1. Species, flight metabolism, variables and references.

Species	Flight metabolism (kJ/h)	Mass (g)	Wing area (cm ²)	Wing length (cm)	Wing span (cm)	Method ¹	Source
<i>Calypte costae</i>	2.54	3.0	—	—	—	C	Lasiewski (1963)
<i>Regulus regulus</i>	1.71	5.6	32.2	5.2	14.3	M	Butterfield (1952)
<i>Amazilia fimbriata</i>	4.93	5.7	—	—	—	C	Berger and Hart (1972)
<i>Setophaga ruticilla</i>	5.29	8.2	65.0	6.2	—	M	Hussell and Lambert (1980)
<i>Eulampis jugularis</i>	7.19	8.3	—	—	—	C	Hainsworth and Wolf (1969)
<i>Vermivora peregrina</i>	7.95	11.0	75.4	6.3	—	M	Raveling and Lefebvre (1967)
<i>Geothlypis trichas</i>	6.24	11.2	58.5	5.5	—	M	Hussell and Lambert (1980)
<i>Carduelis spinus</i>	10.71	12.5	73.5	7.1	21.4	M	Dolnik and Gavrilov (1973)
<i>Dendroica coronata</i>	4.9	12.9	91.0	7.4	—	M	Hussell and Lambert (1980)
<i>Erithacus rubecula</i>	6.02	16.0	80.0	7.0	22.8	M	Butterfield (1952)
<i>Erithacus rubecula</i>	5.69	16.3	81.5	7.0	22.8	M	Davis (1962)
<i>Hirundo rustica</i>	3.34	17.0	130.7	11.7	33.0	C	Kespaik (1968)
<i>Delichon urbica</i>	3.61	17.8	114.1	10.6	29.2	D	Hails (1979)
<i>Erithacus rubecula</i>	25.60	18.6	70.8	7.0	22.8	D	Tatner and Bryant (1986)
<i>Hirundo rustica</i>	4.68	18.9	146.0	11.7	33.0	D	Hails (1979)
<i>Dendroica striata</i>	4.27	19.0	126.6	7.4	—	M	Nisbet et al. (1963)
<i>Seiurus aurocapillus</i>	7.74	19.5	98.0	7.5	—	M	Hussell and Lambert (1980)
<i>Delichon urbica</i>	3.76	20.0	128.2	10.6	29.2	M	Lyuleeva (1973)
<i>Delichon urbica</i>	3.22	20.0	128.2	10.6	29.2	C	Kespaik (1968)
<i>Hirundo rustica</i>	4.77	20.0	153.8	11.7	33.0	M	Lyuleeva (1973)
<i>Melospiza melodia</i>	6.40	21.9	81.7	6.6	—	M	Helms (1959)
<i>Fringilla coelebs</i>	16.20	22.0	110.0	8.4	28.5	M	Dolnik and Gavrilov (1973)
<i>Fringilla montifringilla</i>	16.57	23.3	116.5	9.1	28.1	M	Dolnik and Gavrilov (1973)
<i>Zonotrichia albicollis</i>	13.54	26.5	108.0	7.5	—	M	Hussell and Lambert (1980)
<i>Pyrrula pyrrula</i>	20.17	29.5	134.0	8.0	25.5	M	Dolnik and Gavrilov (1973)
<i>Oenanthe oenanthe</i>	15.99	31.0	125.0	10.5	—	M	Williamson (1958, 1961)
<i>Catharus ustulatus</i>	22.89	32.0	132.2	9.9	—	M	Graber and Graber (1962)
<i>Catharus fuscescens</i>	10.7	32.3	147.0	10.2	—	M	Hussell and Lambert (1980)

TABLE 1. Continued.

Species	Flight metabolism (kg/h)	Mass (g)	Wing area (cm ²)	Wing length (cm)	Wing span (cm)	Method ¹	Source
<i>Oenanthe oenanthe</i>	10.25	34.5	125.0	10.5		M	Davis (from Nisbet 1963)
<i>Melospittacus undulatus</i>	15.36	35.0	89.7	9.8		W	Tucker (1968)
<i>Apus apus</i>	6.78	40.5	192.8	16.8	42.0	M	Lyuleeva (1973)
<i>Progne subis</i>	14.65	50.5	219.5	14.5		D	Utter and Lefebvre (1970)
<i>Coccothraustes vespertinus</i>	40.60	59.3				C	Berger et al. (1970)
<i>Sturnus vulgaris</i>	33.90	72.8	169.3	12.8	38.4	W	Torre-Bueno and Larochelle (1978)
<i>Sterna fuscata</i>	17.20	187.0	719.2	29.5	83.9	D	Flint and Nagy (1984)
<i>Columba livia</i>	85.39	254.0	461.8	22.0	67.0	M	Pearson (1964)
<i>Corvus ossifragus</i>	78.69	275.0	916.6	27.0		W	Bernstein et al. (1973)
<i>Larus atricilla</i>	69.86	350.0	1206.8	32.5		W	Tucker (1969)
<i>Columba livia</i>	92.09	384.0	698.1	22.0	67.0	D	Lefebvre (1964)
<i>Larus delawarensis</i>	78.86	427.0	1202.8	37.2		C	Berger et al. (1970)
<i>Larus marinus</i>	130.60	800.0	1142.8	47.0	172.0	M	Dolnik and Gavrilov (1973)
<i>Anas rubripes</i>	285.48	1026.0	907.9	27.1		C	Berger et al. (1970)

¹ C—Oxygen consumption in a closed system; M—Material balance study; W—Wind tunnel; D—Doubly-labeled water; O—Other.

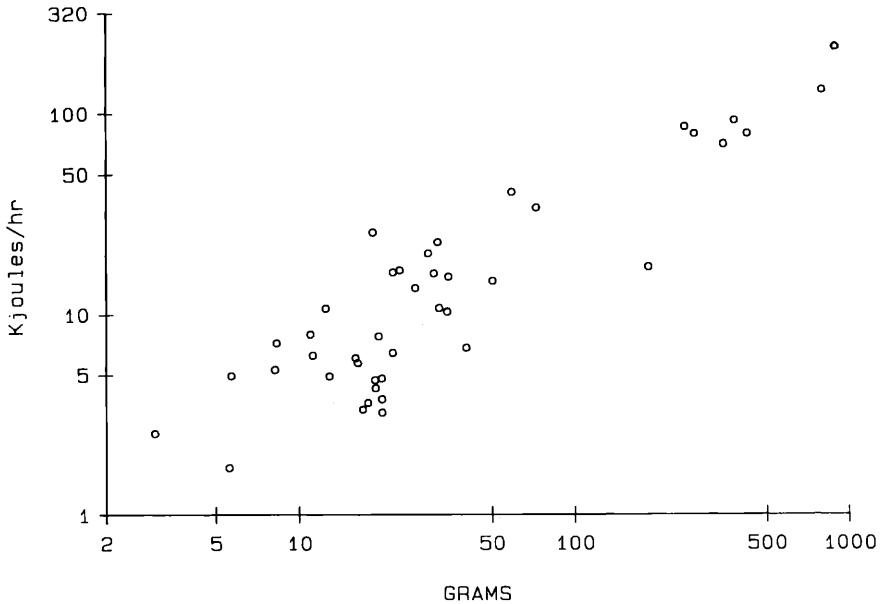


FIGURE 1. Metabolic cost of flight as a function of mass. Data compiled from sources in Table 1, converted to a common unit of measurement.

4.—Material balance studies involve determining the amount of energy used during a non-stop flight of known length and duration. The observer must know the mass of the bird before and after the flight, as well as the caloric equivalent of the mass lost. Unfortunately this method involves several assumptions that are rarely met, since it is almost impossible to catch the same individuals after the flight. Material balance involves the use of large sample sizes to compensate for small differences in mass. The method assumes that the flight is non-stop. As for method 3, non-stop flight may be difficult to demonstrate. Material balance assumes also that the difference in mass between departure and arrival is only fat consumption even though mass can also be affected by water loss. Hart and Berger (1972) show that water loss is homeostatic only below a temperature of approximately 20 C. The temperature during the flight is unknown in most cases because the altitude at which the birds are flying is either unknown or variable. Finally, it is assumed that the birds at the arrival point are the same population that departed together. This neglects the possibility that different populations with different average initial mass may mix during the migratory flight, or that light birds abandoned flight early, shrinking the apparent weight change.

Existing allometric predictions.—The first serious attempt to analyze the cost of flight was made by Nisbet et al. (1963). He analyzed the available measurements (less than a dozen) and concluded that the cost

of flight is between two and four times the resting metabolic rate (for birds in general, resting metabolic rate is approximately 1.5 times basal metabolic rate). Most of the data points used were obtained by the material balance method for birds killed or caught in some part of their migratory routes. He also included his own measurement of flight metabolism for the Blackpoll Warbler (*Dendroica striata*) (Nisbet et al. 1963). Raveling and Lefebvre (1967) reanalyzed Nisbet's data adding new measurements. The new data included those obtained for the Pigeon (*Columba livia*) using doubly-labeled water (Lefebvre 1964). They criticized Nisbet's analysis and stated that flight metabolism in birds is "hard work." Hard work is defined as the maximum amount of work that an animal can perform without incurring an oxygen debt. For domestic animals and man this is 12 times basal metabolic rate (Brody 1945, Hemingsen 1960, Wilkie 1959). Multiplying the current allometric equations for basal metabolic rate versus mass by a factor of "twelve," they showed a new equation that in fact fitted the experimental points.

In a reply, Nisbet (1967) identified problems in Raveling and Lefebvre's approach. His most important criticism was that flight is not necessarily hard work for every species and that the aerodynamic properties of birds should have an important effect on the cost of flight. This was the first published suggestion that a pure regression of flight metabolism based on body mass alone is of limited utility.

The next allometric equation came from Hart and Berger (1972). Their analysis used only measurements considered by these authors to be "accurate," including ones using wind tunnels. Their equation found flight metabolism to cost roughly 12 times basal metabolism.

Kendeigh et al. (1977) developed a new regression with several other new measurements and excluded what they called "aerial feeders" (i.e., swifts and swallows). Again, the relationship is: flight metabolism equals 12 times basal metabolic rate both for passerines and non-passerines. They excluded aerial feeders because they showed smaller values than those expected. It is significant however, that these "aerial feeders" are also species with good aerodynamic characteristics.

Hails (1979) measured flight metabolism with doubly labeled water in a swift and a swallow and compared these values with previous ones. He concluded that flight costs less for these birds due to aerodynamic characteristics.

Flint and Nagy (1984) made another analysis using only points obtained by the use of doubly labeled water. They found that the higher the aspect ratio, the lower the cost of flight. With only 5 measurements from this technique, they were unable to calculate a regression.

Table 2 shows these allometric equations. To allow direct comparison we standardized the unit of measurement using KJ for cost of flight and mass in grams. Two observations are clear from this table. First, the exponent of all the regressions is approximately 0.7. This is the same exponent of the regression of basal metabolic rate on mass, which has led to the conclusion that the cost of flight is a simple multiple of basal

TABLE 2. Existing allometric equations to estimate the cost of flight (M[kJ/h]) based on body mass (W[g]).

Author	Equation	<i>n</i>
Raveling and Lefebvre (1967)	$M = 0.91 \times W^{0.74}$	12
Hart and Berger (1972)	$M = 1.22 \times W^{0.73}$	9
Kendeigh et al. (1977):		
Passerines	$M = 1.94 \times W^{0.69}$	6
Non-Passerines	$M = 1.32 \times W^{0.69}$	11
Hails (1979)	$M = 1.78 \times W^{0.64}$	17

metabolic rate. Second, all the regressions are similar and predict similar costs of flight (roughly 12 times basal metabolic rate). These similarities among results are a consequence of using more or less the same data points.

In conclusion, the empirical approach estimates that the cost of flight is a simple function of body mass, with a value of approximately 12 times basal metabolic rate.

METHODS

Before developing our regression, we examined the published studies for obvious biases. We rejected Teal's (1969) measurements because they mixed the cost of sustained flight, of interest to us, with the cost of takeoff. His values were one order of magnitude higher than any other study. No data from hummingbirds were included in the analysis because of their different flight style.

Since body mass ranges from a few grams to a kilogram (3 orders of magnitude) we log-transformed all the data before making the analyses. With these transformed data we performed different regression analyses using the statistical package SYSTAT 3.0. The aerodynamic characteristics used were wing area, wing length, and wing span. Values of wing area and wing span were not available for all species. These species were excluded when those characteristics were used.

RESULTS

Table 3 shows the results of the different regressions: in model *a* we used a stepwise regression with mass, wing area, wing length, and wing span. Only mass and wing span significantly affected the regression. The r^2 value equaled 0.832. Sample size was limited to 20 due to a lack of wing span measurements.

In model *b* we used a stepwise regression with the same estimators used in model *a* with the exception of wing span, so as to increase the sample size to 38. The model included only mass and wing length as estimators, with an r^2 value of 0.89.

Model *c* is the classic regression of flight metabolism as a power function of body mass. The r^2 value is 0.80, and the exponent of the regression is

TABLE 3. Regressions of flight metabolism and the predictors using different models.

a Stepwise regression using mass, wing area, wing length and wing span:

$$M = 67.29 \times W^{1.763} \times S^{-2.275}$$

($n = 20$; $r^2 = 0.832$; $P < 0.0001$)

b Stepwise regression using mass, wing area, and wing length:

$$M = 3.167 \times W^{1.464} \times L^{-1.614}$$

($n = 38$; $r^2 = 0.89$; $P < 0.0001$)

c Simple regression using mass:

$$M = 0.679 \times W^{0.818}$$

($n = 39$; $r^2 = 0.80$; $P < 0.0001$)

M = Flight metabolism in KJ/h
 W = Body mass in g
 A = Wing area in cm² (both wings)
 L = Wing length in cm
 S = Wing span in cm

0.818, different from the classic exponent of 0.7 obtained by others (see above).

DISCUSSION

Model *a* states that the best characteristics to estimate the cost of flight are body mass and wing span. This is in agreement with Pennycuick's (1975) aerodynamic theory. The r^2 value is not better than that found in model *b*, which, because of the lack of wing span measurements, has an almost doubled sample size ($n = 38$). We recommend the use of this latter equation in cases when wing span is unknown.

Model *b* allows the estimation of flight metabolism using mass and wing length. Interestingly, wing area does not increase significantly the estimation power of the regression, in agreement with Pennycuick's (1975) model.

Finally, model *c* allows the estimation of the cost of flight based only on body mass. The exponent of the regression is different from the classic 0.7 exponent found in the past, however, our sample size is between two and six times higher than those regressions. The fact that our exponent differs from the 0.7 value implies that the cost of flight is not a simple multiple of basal metabolic rate.

Of the 39 measurements, six measured flight metabolism under free conditions using the doubly labeled water method. We consider them most likely to reflect true values and therefore have used them to test our regression approaches. We first recalculated model *b* without these six points, and then compared estimates from the resulting equation with the six values, thereby avoiding the circularity of Raveling and Lefebvre (see Nisbet 1967). The modified model *b* is very similar to model *b* above (symbols as in Table 3):

TABLE 4. Comparison of the doubly-labeled water method with four other methods for estimating flight metabolic rates kJ/h and with the estimates of the modified model b.

Method	Sooty tern <i>Sterna fuscata</i>	House martin <i>Delichon urbica</i>	Barn swallow <i>Hirundo rustica</i>	Purple martin <i>Progne subis</i>	Pigeon <i>Columba livia</i>	Robin <i>Erithacus rubecula</i>
Doubly-labeled water	17.2	2.9-4.2	4.7	14.6	92.0	25.6
Tucker (1973)	42.6	9.7	6.0	—	171.0	6.4
Greenewalt (1975)	33.2	6.2	5.0	—	108.0	5.6
Pennycuick (1975)	32.7	5.4	3.7	—	164.0	5.7
12 × BMR	43.3	10.5	13.6	27.5	78.4	13.3
This study	32.7	4.9	4.6	13.8	135.0	9.3

Based on Table II of Flint and Nagy (1984).

$$M = 2.23 \times W^{1.407} \times L^{-1.381}$$

($n = 32$; $r^2 = 0.90$; $P < 0.0001$)

The r^2 increases marginally, and the sample size drops to 32 due to the exclusion of the six doubly-labeled water points.

We also compared the estimates of this modified model with estimates from the other standard equations. This is shown in Table 4, based on Flint and Nagy (1984) and modified by the addition of our estimates and the doubly-labeled water measurement of Tatner and Bryant (1986) on the American Robin (*Turdus migratorius*). Table 4 does not show aerodynamic estimates for the Purple Martin due to the lack of values of wing span.

The modified model *b* is closer to the doubly labeled water estimates in five out of five cases when compared with Tucker's equations, four out of five when compared with Greenewalt's equations, four out of five when compared with Pennycuick's equations (although our estimates are closer with this model than with the others), and in four out of six cases when compared with the empirical "12 times BMR" approach.

We conclude that including aerodynamic variables in regression-based estimates of the cost of flight improves the accuracy of the estimates.

Since model *b* provides more precise estimates than previous ones for the cost of flight, and is simply calculated using easily measured characteristics of birds both in the field and in museum collections (body mass and wing length) we strongly recommend its use to estimate costs of flight.

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LITERATURE CITED

- BERGER, M., AND J. S. HART. 1972. Respiration in the hummingbird *Amazilia fimbriata* during hovering at different ambient temperatures. J. Comp. Physiol. 81:363-380.

- , ———, AND O. Z. ROY. 1970. Respiration, oxygen consumption and heart rate in some birds during rest and flight. *Z. Vergl. Physiol.* 66:201-214.
- BERNSTEIN, M. H., S. P. THOMAS, AND K. SCHMIDT-NIELSEN. 1973. Power input during flight of the fish crow. *J. Exp. Biol.* 58:401-410.
- BRODY, S. 1945. *Bioenergetics and Growth*. Reinhold, New York. Pp. 1023.
- BUTTERFIELD, W. A. 1952. A statistical note on bird weights from Lista (Norway) and Fair Isle. *Bull. Fair Isle Bird Obs.* 1:30-31.
- DAVIS, P. 1962. Robin recaptures on Fair Isle. *British Birds* 55:225-229.
- DAWSON, W. R. 1974. Appendix: conversion factors for units used in symposium. Pp. 334, in R. A. Paynter, ed. *Avian energetics*. Publications of the Nuttall Ornithological Club No. 15.
- DOLNIK, V. R., AND V. M. GAVRILOV. 1973. Energy metabolism during flight of some passerines. Pp. 288-296, in B. E. Bykhovskii, ed. *Bird migrations, ecological and physiological factors*. Halstead Press, New York.
- FARNER, D. S. 1970. Some glimpses of comparative avian physiology. *Fed. Proc.* 29:1649-1663.
- FLINT, E. N., AND K. A. NAGY. 1984. Flight energetics of free-living sooty terns. *Auk* 101:288-294.
- GRABER, R. R., AND J. W. GRABER. 1962. Weight characteristics of birds killed in nocturnal migration. *Wilson Bull.* 74:244-253.
- GREENEWALT, C. H. 1962. Dimensional relationships for flying animals. *Smithson. Misc. Collect.* 144, No. 2.
- . 1975. The flight of birds. *Trans. Am. Philos. Soc.* 65:1-67.
- HAILS, C. J. 1979. A comparison of flight energetics in hirundines and other birds. *Comp. Biochem. Physiol.* A63:581-585.
- HAINSWORTH, F. R., AND L. L. WOLF. 1969. Resting, torpid and flight metabolism of the hummingbird *Eulampis jugularis*. *Am. Zool.* 9:1100-1101.
- HART, J. S., AND M. BERGER. 1972. Energetics, water economy and temperature regulation during flight. *Proc. Int. Ornithol. Congr.* 15th:189-199.
- HARTMAN, F. A. 1961. Locomotor mechanisms of birds. *Smithson. Misc. Collect.* 143, No. 1.
- HELMS, C. W. 1959. Song and Tree sparrow weight and fat before and after a night of migration. *Wilson Bull.* 71:244-253.
- HEMINGSEN, A. M. 1960. Energy metabolism as related to body size and respiratory surfaces and its evolution. *Reports of the Steno Memorial Hospital* 9:1-110.
- HUSSEL, D. J. T., AND A. B. LAMBERT. 1980. New estimates of weight loss in birds during migration. *Auk* 97:547-558.
- JOHNSTON, D. W. 1970. Caloric density of avian adipose tissue. *Comp. Biochem. Physiol.* 34:827-832.
- KENDEIGH, S. C., V. R. DOLNIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pp. 127-204, in V. Pinowski and S. C. Kendeigh, eds. *Granivorous birds in ecosystems*. Cambridge Univ. Press.
- KESPAIK, Y. U. 1968. Heat production and heat loss of Swallows and Martins during flight. *Eesti Nsv Teaduste Akademia toimetised XVII kaoide Biologia* 2:179-190. (In Russian.)
- LASIEWSKI, R. C. 1963. Oxygen consumption of torpid, active and flying hummingbirds. *Physiol. Zool.* 36:122-140.
- LEFEBVRE, E. A. 1964. The use of doubly-labeled water for measuring energy metabolism in *Columba livia*. *Auk* 81:403-416.
- LYULEEVA, D. S. 1973. Features of swallow biology during migration. Pp. 56-69, in B. E. Bykhovskii, ed. *Bird migrations, ecological and physiological factors*. Halstead Press, New York.
- MAGNAN, A. 1922. Les caracteristiques des Oiseaux suivant le mode de vol. *Annals des Sciences Naturelles* Tomo V:125-334.
- NAGY, K. A. 1980. CO₂ production in animals: analysis of potential errors in the doubly labeled water method. *Am. J. Physiol.* 238:R454-R473.
- NISBET, I. C. T. 1967. Aerodynamic theories of flight versus physiological theories. *Bird-Banding* 38:306-308.

- , W. H. DRURY, JR., AND J. BAIRD. 1963. Weight-loss during migration. *Bird-Banding* 34:107-138.
- PEARSON, O. P. 1964. Metabolism and heat loss in pigeons. *Condor* 66:182-185.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. *Ibis* 11:525-556.
- . 1975. Mechanics of flight. Pp. 1-75, in D. S. Farner and J. R. King, eds. *Avian biology* vol. 5. Academic Press, New York and London.
- POOLE, E. L. 1938. Weights and wing areas of 143 species of North American Birds. *Auk* 55:511-517.
- RAVELING, D. G., AND E. A. LEFEBVRE. 1967. Energy metabolism and theoretical flight range of birds. *Bird-Banding* 38:97-113.
- ROBERTS, T. S. 1955. *Manual for the identification of the birds of Minnesota and neighboring states*. University of Minnesota Press.
- TATNER, P., AND D. M. BRYANT. 1986. Flight cost of a small passerine measured using doubly-labeled water: implications for energetics studies. *Auk* 103:169-180.
- TEAL, S. M. 1969. Direct measurements of CO₂ productions during flight in small birds. *Zoologica* 54:17-23.
- TORRE-BUENO, J. R., AND J. LAROCHELLE. 1978. The metabolic cost of flight in unrestrained birds. *J. Exp. Biol.* 75:223-229.
- TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Physiol.* 48:67-87.
- . 1969. The energetics of bird flight. *Sci. Am.* 220:70-78.
- . 1973. Bird metabolism during flight: evaluation of a theory. *J. Exp. Biol.* 58: 689-709.
- UTTER, J. M., AND E. A. LEFEBVRE. 1970. Energy expenditure for free flight by the purple martin. *Comp. Biochem. Physiol.* 35:713-719.
- WILKIE, D. R. 1959. The work output of animals: flight by birds and by manpower. *Nature* 183:1515-1516.
- WILLIAMSON, K. 1958. Bergmann's rule and obligatory overseas migration. *British Birds* 51:209-232.
- . 1961. The concept of "cyclonic approach." *Bird Migration* 1:235-239.

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