A RE-EXAMINATION OF THE RELATION BETWEEN STANDARD METABOLIC RATE AND BODY WEIGHT IN BIRDS

ROBERT C. LASIEWSKI and WILLIAM R. DAWSON

An exponential relation exists between standard energy metabolism and body weight in organisms that is described by the generalized equation:

$$\text{Metabolic Rate} = a \, (\text{Body Weight})^b \tag{a}$$

where a and b are empirically derived constants. This equation can be rewritten in the more convenient logarithmic form:

$$\log \text{Metabolic Rate} = \log a + b \log \text{Body Weight} \tag{b}$$

recognizable as a mathematical expression of a straight line. Hemmingsen (1950, 1960) has reviewed the relation of energy metabolism to body size in all organisms, and argues that a b-value of 0.75 best describes the existing data for unicellular organisms, plants, poikilothermal and homeothermal animals. However, the observed limits of b are 0.63–1.0 among individual groups (Zeuthen, 1953, and others).

Despite recent increased interest in avian bioenergetics, a definitive statement concerning the relationship between metabolic rate and body weight in birds has been lacking. Several formulas for this relationship have been presented. Brody and Proctor (1932) fitted the following equation to data on avian body weight and metabolism:

$$\log M = \log 89 + 0.64 \log W \tag{c}$$

where M is in kcal/day and W is in kilograms. This expression, in which the regression coefficient (b) of 0.64 differs markedly from those obtained from mammals (0.73–0.76) by Brody and Proctor (1932), Kleiber (1932, 1947), Benedict (1938), and Brody (1945), has been generally accepted for birds until recently. King and Farner (1961) have commented that "on theoretical grounds there seems to be no reason to believe *a priori* that the relationship of metabolic rate and body weight should be very different in the homoiotherm classes." With many more metabolic values than were available previously, King and Farner re-analyzed the relationship, using more rigorous criteria for including data in their computations. They obtained the following equation:

$$\log M = \log 74.3 + 0.744 \log W \pm 0.074. \tag{d}$$

King and Farner believe that this equation is superior to that of Brody and Proctor (1932) in predicting the metabolic rates of birds weighing more than 0.1 kg. However, they concluded that it does not adequately portray the metabolism–weight relationship for smaller birds. Equation (d) is statistically indistinguishable from Kleiber's (1947) equation for mammals, and it is therefore doubtful that the metabolism–weight relationship for birds weighing more than 0.1 kg really differs from that in mammals.

King and Farner (1961) discuss the possibility that the avian relationship may be curvilinear in the lower ranges of body weight, since small birds have higher metabolic rates than predicted by their equation. Virtually all of the small birds (< 0.1 kg) are passerines, whereas all but two of the species weighing more than 0.1 kg belong to other orders. Dawson and Lasiewski have suggested (see Lasiewski, 1963; Lasiewski *et al.*, 1964) that passerines as a group show the same weight–regression coefficient as nonpasserines, but have a higher metabolism per unit weight than nonpasserines of comparable size. Documentation of this suggestion required additional data on large passerines and small nonpasserines. Now that these are available, it is

appropriate to examine further the relationship between levels of standard metabolic rate and body weight in birds.

MATERIALS AND METHODS

All of the values of standard metabolism utilized in this analysis represent measurements that conform generally to the major requirements for measuring "standard metabolic rate," as the term is generally applied to homeotherms, *i.e.*, the birds were postabsorptive, in thermoneutral surroundings, and as nearly at rest as possible. The values were obtained from three major sources: (1) table II of King and Farner (1961), which includes data on birds under near-standard conditions; (2) recently published studies or personal communications; and (3) unpublished measurements made by us in the last decade. All of the values listed in table II of King and Farner (1961) were used with the exception of those for hummingbirds, which were not obtained under standard conditions. For species in which King and Farner list separate values for males and females, we averaged both body weight and metabolic rate.

A caloric equivalent of 4.8 kcal/liter of oxygen was assumed where it was necessary to convert gaseous metabolism data to caloric values. Original measurements for the present study were performed in open flow systems using Beckman G-2 Paramagnetic Oxygen Analyzers in conjunction with multipoint recording potentiometers, as described by Dawson and Tordoff (1964). The regression lines and values for

TABLE 1
STANDARD METABOLIC RATES OF PASSERINE BIRDS

Species	Weight, kg	kcal/24 hr	Reference
Estrilda troglodytes	0.0061	2.8	Lasiewski *et al.*, 1964
			Cade *et al.*, 1965
Uraeginthus bengalis	0.0081	2.8	Lasiewski *et al.*, 1964
Troglodytes aedon	0.0090	5.3	Kendeigh, 1939
Vidua paradisea	0.0105	4.0	Terroine and Trautmann, 1927
Carduelis flammea	0.0112	5.8	Steen, 1958
Taeniopygia castanotis	0.0117	5.0	Cade *et al.*, 1965
Taeniopygia castanotis	0.0117	4.5	Calder, 1964
Pipra mentalis	0.012	6.5	Scholander *et al.*, 1950
Carduelis spinus	0.013	5.8	Gelineo, 1955
Carduelis cannabina	0.0155	7.3	Gelineo, 1955
Spizella arborea	0.0166	6.8	Present study
Junco hyemalis	0.0180	6.1	Present study
Parus major	0.0185	8.4	Steen, 1958
Melospiza melodia	0.0186	7.8	Present study
Emberiza hortulana	0.022	8.7	Wallgren, 1954
Passer montanus	0.022	8.5	Steen, 1958
Zonotrichia albicollis	0.0225	7.1	Hudson and Kimzey, 1964
Zonotrichia albicollis	0.0236	9.5	Present study
Passer domesticus			
Winter	0.0224	9.5	Fonberg, 1932
Spring	0.0235	11.0	Fonberg, 1932
Passer domesticus	0.0237	10.1	Quirring and Bade, 1943
Passer domesticus	0.0250	6.9	Miller, 1939
Passer domesticus	0.0255	6.9	Hudson and Kimzey, 1964

TABLE 1 (*Continued*)

Species	Weight, kg	kcal/24 hr	Reference
Passer domesticus	0.0260	9.4	Gelineo, 1955
Passer domesticus	0.0260	7.0	Kendeigh, 1944
Passer domesticus	0.0273	8.5	Steen, 1958
Chloris chloris	0.0245	11.1	Gelineo, 1955
Chloris chloris	0.0311	11.2	Steen, 1958
Fringilla montifringilla	0.0248	9.5	Steen, 1958
Emberiza citrinella	0.0264	9.4	Wallgren, 1954
Zonotrichia leucophrys	0.0286	8.0	King, 1964
Loxia curvirostra	0.0294	10.5	Dawson and Tordoff, 1964
Loxia leucoptera	0.0298	9.6	Dawson and Tordoff, 1964
Passerella iliaca	0.0317	11.3	Present study
Molothrus ater	0.0337	11.0	Present study
Richmondena cardinalis	0.040	12.2	Dawson, 1958
Plectrophenax nivalis	0.0418	11.4	Scholander *et al.*, 1950
Pipilo fuscus	0.0437	13.7	Dawson, 1954
Pipilo aberti	0.0468	15.0	Dawson, 1954
Hesperiphona vespertina	0.058	16.7	Dawson and Tordoff, 1959
Perisoreus canadensis	0.0645	20	Scholander *et al.*, 1950
Perisoreus canadensis	0.0712	14.3	Veghte, 1964
Cyanocitta cristata	0.0808	17.6	Misch, 1960
Corvus caurinus			
Summer	0.282	73.2	Irving *et al.*, 1955
Winter	0.306	96.7	Irving *et al.*, 1955
Corvus cryptoleucus	0.640	79.0	Present study
Corvus corax	0.850	92	Scholander *et al.*, 1950
Corvus corax	0.866	94.9	Present study

probable errors were calculated according to the least squares method of Feldstein and Hersh (1935). The "t" test was used to determine the significance of difference between slopes (a test of parallelism) by computing a pooled variance as described by Goldstein (1964:144).

RESULTS AND DISCUSSION

Birds are known to possess a marked diurnal cycle in body temperature (Chossat, 1843; Wilson, 1948; Dawson, 1954; Bartholomew and Dawson, 1954, and others), and the amplitude of the cycle is in part inversely related to body size (King and Farner, 1961; Lasiewski, 1964). Nevertheless, no clear difference exists between diurnal and nocturnal metabolic values in the data compiled in tables 1 and 2. One would expect the greatest metabolic effect of this cycle of body temperature to be found in small birds. Hudson and Kimzey (1964) note significantly higher metabolic rates for House Sparrows and White-throated Sparrows during the day than at night. However, in hummingbirds, the smallest nonpasserines, and *Estrilda troglodytes*, a very small passerine, the minimal levels of metabolism at night are indistinguishable from those occurring during the day (Lasiewski, 1963; Lasiewski *et al.*, 1964). Even in view of Hudson and Kimzey's (1964) findings, we did not feel justified in differentiating in our analysis between diurnal and nocturnal metabolic values.

We computed three least squares regression equations (e, f, g) from the avian

TABLE 2
STANDARD METABOLIC RATES OF NONPASSERINE BIRDS

Species	Weight, kg	kcal/24 hr	Reference
Apodiformes			
Stellula calliope	0.0030	1.4	Lasiewski, 1963
Calypte costae	0.0032	1.1	Lasiewski, 1963
Archilochus colubris	0.0032	1.6	Lasiewski, 1963
Archilochus alexandri	0.0033	1.3	Lasiewski, 1963
Selasphorus sasin	0.0037	1.6	Lasiewski, 1963
Selasphorus rufus	0.0038	1.5	Lasiewski, 1963
Calypte anna	0.0048	2.2	Lasiewski, 1963
Eugenes fulgens	0.0066	2.4	Lasiewski and Lasiewski, in press
Lampornis clemenciae	0.0079	2.6	Lasiewski and Lasiewski, in press
Caprimulgiformes			
Phalaenoptilus nuttalli	0.040	3.7	Bartholomew *et al.*, 1962
Nyctidromus albicollis	0.0430	7.7	Scholander *et al.*, 1950
Chordeiles minor	0.075	9.5	Lasiewski and Dawson, 1964
Strigiformes			
Micrathene whitneyi	0.0377	6.7	Ligon, D., personal comm.
Aegolius acadicus	0.1059	16.2	Collins, 1963
Aegolius acadicus	0.0855	14.5	Graber, 1962
Asio otus	0.252	19.7	Graber, 1962
Asio flammeus	0.406	26.6	Graber, 1962
Strix aluco	0.520	43	Herzog, 1930
Bubo virginianus	1.450	108	Benedict and Fox, 1927
Columbiformes			
Scardafella inca	0.0405	5.2	MacMillen and Trost, 1965
Zenaidura macroura	0.0914	13.4	Hudson and Brush, 1964
Zenaidura macroura	0.123	15.2	Riddle *et al.*, 1932
Columba palumbus	0.150	17.0	Benedict, 1938
Streptopelia decaocto	0.152	21.8	Giaja and Males, 1928
Streptopelia decaocto	0.155	18.3	Gelineo, 1955
Domestic pigeon	0.266	33.7	Gelineo, 1955
Domestic pigeon	0.300	30	Benedict, 1938
Domestic pigeon	0.311	32.9	Burckard *et al.*, 1933
Domestic pigeon	0.372	35.5	Herzog, 1930
Galliformes			
Excalfactoria chinensis	0.0427	6.0	Present study
Coturnix coturnix	0.097	23	Giaja and Males, 1928
Lophortyx californicus	0.1371	16.0	Hudson and Brush, 1964
Colinus virginianus	0.194	23.0	Present study
Domestic fowl	2.0	97.5	Benedict, 1938
Domestic fowl ♀ ♀	2.00	137	Barott and Pringle, 1941
Domestic fowl ♀ ♀	2.00	115	Dukes, 1937
Domestic fowl	2.006	130.7	Herzog, 1930
Domestic fowl ♀ ♀	2.430	164.2	Barott and Pringle, 1946
Domestic fowl ♀ ♀	2.71	124	Winchester, 1940
Penelope purpurescens	2.04	112	Benedict and Fox, 1927

TABLE 2 (*Continued*)

Species	Weight, kg	kcal/24 hr	Reference
Galliformes (Continued)			
Grax alberti	2.80	136	Benedict and Fox, 1927
Domestic turkey	3.7	184	Giaja, 1931
Gruiformes			
Grus canadensis	3.89	168	Benedict and Fox, 1927
Anthropoides paradisea	4.03	220	Benedict and Fox, 1927
Charadriiformes			
Catharacta skua	0.97	98	Benedict and Fox, 1927
Gabianus pacificus	1.21	127	Benedict and Fox, 1927
Larus hyperboreus	1.60	304	Scholander *et al.*, 1950
Falconiformes			
Falco tinnunculus	0.108	17.0	Giaja and Males, 1928
Geranoaëtus melanoleucus	2.86	106	Benedict and Fox, 1927
Aquila chrysaëtos	3.0	102	Giaja and Males, 1928
Gypaëtus barbatus	5.07	228	Benedict and Fox, 1927
Vultur gryphus	10.32	351	Benedict and Fox, 1927
Anseriformes			
Aix sponsa	0.485	65	Herzog, 1930
Branta bernicla			
Summer	1.130	108.5	Irving *et al.*, 1955
Winter	1.168	93.4	Irving *et al.*, 1955
Domestic duck	1.87	157	Giaja and Males, 1928
Chauna chavaria	2.62	142	Benedict and Fox, 1927
Domestic goose	3.3	219	Giaja, 1931
Domestic goose	5.0	280	Benedict and Lee, 1937
Domestic goose	5.89	271	Herzog, 1930
Cygnus buccinator	8.88	418	Benedict and Fox, 1927
Ciconiiformes			
Botaurus lentiginosus	0.60	56	Benedict and Fox, 1927
Guara alba	0.94	85	Benedict and Fox, 1927
Ardea herodias	1.87	128	Benedict and Fox, 1927
Mycteria americana	2.5	201	Kahl, 1962
Phoenicopterus antiquorum	3.04	215	Benedict and Fox, 1927
Jabiru mycteria	5.47	272	Benedict and Fox, 1927
Leptoptilos javanicus	5.71	307	Benedict and Fox, 1927
Pelecaniformes			
Pelecanus occidentalis	3.51	264	Benedict and Fox, 1927
Pelecanus conspicillatus	5.09	374	Benedict and Fox, 1927
Casuariformes			
Casuarius bennetti	17.6	516	Benedict and Fox, 1927
Struthioniformes			
Struthio camelus	100	2350[a]	Crawford, E. C., and Schmidt-Nielsen, K., personal comm.

[a] This value for the ostrich was computed from data provided by Crawford and Schmidt-Nielsen. They kindly allowed us to examine all of their metabolic data, and for the purposes of this paper, we selected the average of three measurements in which ostrich No. 2 sat quietly in the dark room while measurements were being made.
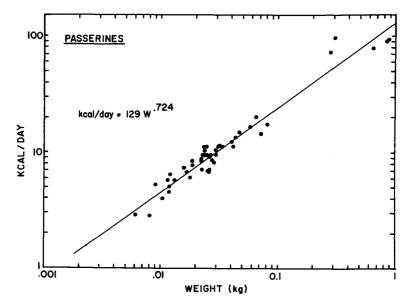
Figure 1. The relation between standard metabolic rate and body weight in passerine birds. Data are presented in table 1 (N = 48).

metabolism and body weight data assembled in table 1 (passerine birds) and table 2 (nonpasserine birds). The equation describing the relationship between standard metabolism and body weight in passerines is:

$$\log M = \log 129 + 0.724 \log W \pm 0.113 \qquad (e)$$

where M is heat production in kcal/day and W is body weight in kg. The variance indicated is one standard error of estimate, S_{yx}. The passerine values and the line described by the equation are plotted on a double logarithmic grid in figure 1.

The data for all birds except passerines yield the equation:

$$\log M = \log 78.3 + 0.723 \log W \pm 0.068 \qquad (f)$$

with the units as before. These nonpasserine data encompass the full size spectrum of living birds, ranging from small hummingbirds through the ostrich. The data and the regression line relating metabolism and body weight are plotted in figure 2.

The equation for nonpasserine birds (f) is statistically indistinguishable from the King–Farner equation for birds weighing more than 0.1 kg (d), even though equation (f) includes data from hummingbirds through the ostrich, and utilizes many more values (N = 72).

The weight–regression coefficients (b-values) of the passerine and nonpasserine equations are virtually identical, but passerines are operating at higher metabolic levels than mammals and nonpasserine birds of similar size. The wide conformance to this higher level of metabolism by representatives of an extensive array of passerine families suggests that the metabolic elevation developed early in the evolution of passerines. The significance of this development is not completely clear, but it is a common observation among ornithologists that passerines are generally more active and excitable than nonpasserines.

A regression line for all birds was derived by combining the available data for passerines and nonpasserines; this line is described by the equation:

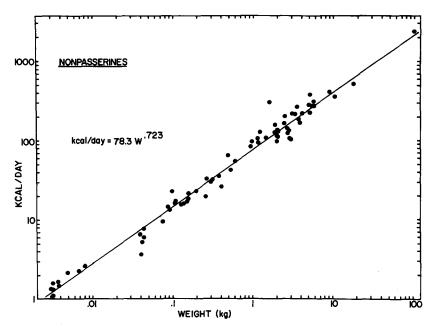$$\log M = \log 86.4 + 0.668 \log W \pm 0.086. \qquad (g)$$

Figure 2. The relation between standard metabolic rate and body weight in nonpasserine birds. Data are presented in table 2 (N = 72).

This equation is similar in both slope (b) and y-intercept (a) to the Brody–Proctor equation for birds generally (1932), and the comparable equation (7) of King and Farner (1961) for both large and small birds. This general equation for birds (g) is compared with that for passerines (e) and nonpasserines (f) in figure 3. While these comprehensive equations for birds are defensible empirically, they are markedly different from the accepted equations for metabolism–weight relationships of mammals (Benedict, 1938; Brody, 1945; Kleiber, 1947). The coincidence of b-values for passerines and nonpasserines, and the similarity between the nonpasserine equation (f) and Brody's (1945) equation for mammals (fig. 4), provides additional support for the view that the metabolism–weight relations of birds and mammals are really fundamentally similar.

The finding of a difference in the a-values of passerine and nonpasserine birds is not without precedent. Morrison (1948) demonstrated differences in the weight–specific metabolic levels of three groups of small wild mammals, rodents, insectivores, and bats. Kayser and Heusner (1964) obtained three distinct regression lines with different a-values for three groups of insects. As increased information becomes available on the metabolism of nonpasserine birds and representatives of other animal groups, further intraclass differences in metabolic level will doubtless become apparent.

SUMMARY

Three equations describing the relationship between standard metabolic rate and body weight in birds are presented. Passerine birds have a higher weight–specific
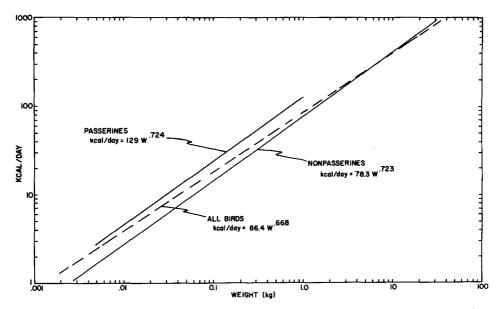
Figure 3. A comparison of the regression lines for passerine birds, nonpasserine birds, and all birds.
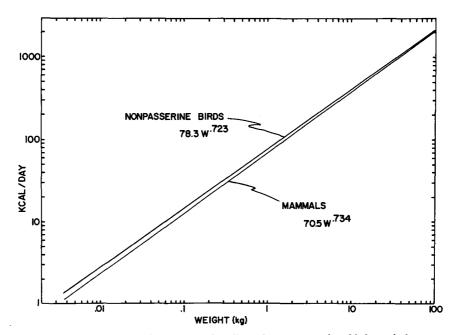

Figure 4. A comparison of the regression lines for nonpasserine birds and for mammals (Brody, 1945).

metabolic rate than nonpasserines, although the weight–metabolism regression coefficients (*b*-values) are virtually identical (0.724 and 0.723, respectively). The nonpasserine equation spans the full size range of living birds, from small hummingbirds through the ostrich, and is similar to accepted equations for mammals. An equation for all groups of birds is similar to the Brody–Proctor avian equation and the comparable equation (7) of King and Farner, but is an artifact of combining passerine and nonpasserine data.

ACKNOWLEDGMENTS

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Department of Zoology, University of California, Los Angeles, California, and Department of Zoology, University of Michigan, Ann Arbor, Michigan, 26 January 1966.