OXYGEN CONSUMPTION AND RESPIRATORY EVAPORATION OF THE EMU AND RHEA

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The relationships between body size and rates of physiological processes have received much attention in the past. Metabolic heat production has been shown to be related to body weight by an exponential function in a large variety of organisms. The generalized relationship can be written as:

$$M = aW^b \qquad (1)$$

where M is metabolic rate, a is a constant, W is body weight, and b is an exponent which has empirical limits of 0.66 to 1.0. Equation (1) is usually written in the more convenient logarithmic form:

$$\log M = \log a + b \log W \qquad (2)$$

Lasiewski and Dawson (1967) recently reexamined the relationship between body weight and metabolic rate in birds, and demonstrated that passerine birds have a higher weight-specific metabolism than nonpasserines. The equation describing the relationship between standard metabolism and body weight of passerines is:

$$\log M = \log 129 + 0.724 \log W \qquad (3)$$

where M is heat production in kcal/day, and W is body weight in kg. Their equation for all birds except passerines spans the full size range of living birds, from 3 g hummingbird to a 100 kg ostrich, and can be written as:

$$\log M = \log 78.3 + 0.723 \log W \qquad (4)$$

with units as in equation 3. Although the data in equation (4) represent 58 species, only the Ostrich and Cassowary weighed more than 10 kg. Equation (4) is statistically indistinguishable from a comparable equation presented by King and Farner (1961) for birds weighing 0.125–10.0 kg.

The relation between avian evaporative water loss and body weight conforms to a pattern similar to that for metabolism and body weight. Bartholomew and Dawson (1953) presented data for avian species ranging from 10.8 to 147 g, showing that evaporative water loss per unit weight is inversely related to body weight. Crawford (1965) proposed a tentative equation relating these variables in birds:

$$\log E = \log 0.339 + 0.584 \log W \qquad (5)$$

where E is evaporative water loss in g/day, and W is body weight in g. Crawford's equation is based on data spanning the full size range of living birds although only 18 species were represented, and of these, only two weighed more than 180 g.

Because of the paucity of data on the physiology of large birds, we undertook the following study on rates of metabolism and evaporation in Emus and Rheas. The Emu, *Dromiceius novae-hollandiae*, stands 1.4–2.0 m tall, weighs as much as 55 kg, and inhabits open semi-arid country in Australia. The Rhea, *Rhea americana*, is the heaviest bird in the New World, weighing approximately 20 kg, and measuring 0.9 to 1.3 m in length.

MATERIALS AND METHODS

Two Emus and three Rheas were used in this study. All birds were mature individuals made available by the Zoological Society of San Diego. During periods of training and experimentation, they were housed outdoors in a 5 × 5 m pen with access to shelter. Daily rations consisted of Purina Chow, lettuce, grapes, and apples, and water was available *ad libitum.* Food was removed on evenings preceding metabolic determinations, so the birds were fasted overnight and assumed to be postabsorptive the following day. When experiments were conducted at night, food was removed in the preceding morning.

An initial training period of about 10 days was required to accustom the birds to the experimental apparatus and procedure. Thereafter, for the most part, the birds rested quietly in the experimental apparatus during determinations. The Emus were more tractable than the Rheas, and generally easier to train and handle.

The experimental procedure for determining oxygen consumption and respiratory evaporation was similar to that described by Crawford and Schmidt-Nielsen (1967) for the Ostrich. The experimental bird was lightly restrained in an open box in a darkened room. The restraining device permitted the bird to move somewhat, but not to turn around or escape. A respiratory hood (fashioned from a cylindrical Lucite tube) was fitted over the head and neck of the restrained bird. The hood was provided with a reflected rubber seal at the bottom, an exit port for air at the top, and the outside was painted with flat black paint. The hood was supported by the restraining device so that it did not rest on the bird. Room air was drawn through the tube by suction, entering past the loose-fitting rubber seal at the base of the bird's neck and exiting through the top port, and then directed into an adjoining room. Air flow through the hood was monitored with a dry gas meter, and a sample of the air passed through a drying column (Drierite), a flow meter, and a Beckman C-2 oxygen analyzer. The partial pressure of oxygen in the excurrent air from the hood was monitored until it reached a stable level and then was recorded every two minutes for a 30-minute period. The mean value of the five consecutive readings indicating the minimal oxygen consumption was used in computing standard metabolic rate. All oxygen-consumption values were converted to standard temperature and pressure. A caloric equivalent of 4.8 kcal/liter of oxygen was assumed in converting oxygen consumption to caloric units.

Respiratory evaporation was calculated from the difference in amount of water collected in the drying column during metabolic determinations and during blank runs. The amount of water vapor contained in room air was also calculated from sling psychrometric measurements of relative humidity. This technique yielded similar values to those obtained from blank runs when unaltered room air was drawn through the flow system.

Air flow through the respiratory hood was maintained at 60–80 liters/min to minimize increases in carbon dioxide or water vapor concentrations.

The mean values presented for oxygen consumption, evaporative water loss, body temperatures, and respiratory rates represent as nearly as possible birds resting in the dark in the zone of thermoneutrality in a postabsorptive state.

Body weights were determined daily during the study period by weighing the bird in the restraining device on a platform scale (± 0.2 kg).

All birds appeared healthy throughout the study and were returned to exhibition after completion of the experiments.

RESULTS AND DISCUSSION

The results obtained from this study are summarized in table 1. Oxygen consumptions of 149.9 ml O_2/min for the Emu (38.3 kg), and 114.5 ml O_2/min for the Rhea (21.7 kg) represent standard metabolic rates of 1036 and 791 kcal/day, respectively. These measured values deviate by –5 and +9 per cent, respectively, from levels predicted for birds of this size by the Lasiewski-Dawson equation for nonpasserines. Standard metabolic data are now available for the four major representatives of extant large ratite birds: the Ostrich (Crawford and Schmidt-Nielsen 1967), the Cassowary (Benedict and Fox 1927), and the Emu and Rhea. The standard metabolism of each of these large nonflying birds is similar to that expected for birds of this size from the Lasiewski-Dawson equation (fig. 1).

Evaporative water losses of 179 mg H_2O/min for the Emu and 160 mg H_2O/min for the Rhea represent 0.67 and 1.07 per cent of body weight per day, respectively. The evaporative water loss values presented for the Emu and Rhea are primarily respiratory water loss plus some cutaneous evaporation from the head and neck.

Sufficient data on evaporative water loss from birds of different sizes have accumulated to permit a more formal analysis of the relationship between avian evaporative water loss

TABLE 1. Physiological values (mean ± SD) for resting Emus and Rheas.

	Weight kg	O_2 Cons. ml/min	Evap. water loss mg/min	Body temp. °C	Resp. rate breath/min	Heart rate beats/min
Emu	38.3 ± 2.6	149.9 ± 34.8	179 ± 59.3	38.1 ± 0.3	7.1 ± 1.7	41
Rhea	21.7 ± 1.0	114.5 ± 11.9	160[a]	39.7 ± 0.1	8.5 ± 3.1	48

[a] Mean of 4 observations.

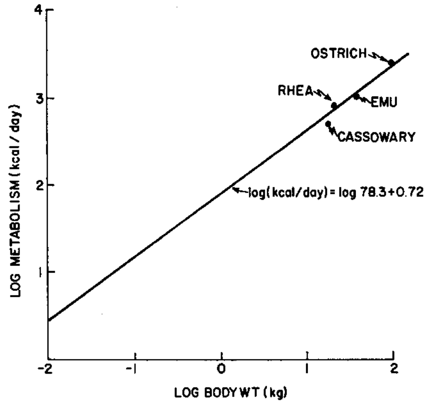

FIGURE 1. Standard metabolism of Cassowary, Rhea, Emu, and Ostrich. The line represents the Lasiewski-Dawson (1967) relationship between standard metabolism and body size in nonpasserine birds. The value for the Cassowary is from Benedict and Fox (1927); the value for the Ostrich is from Crawford and Schmidt-Nielsen (unpublished observation).

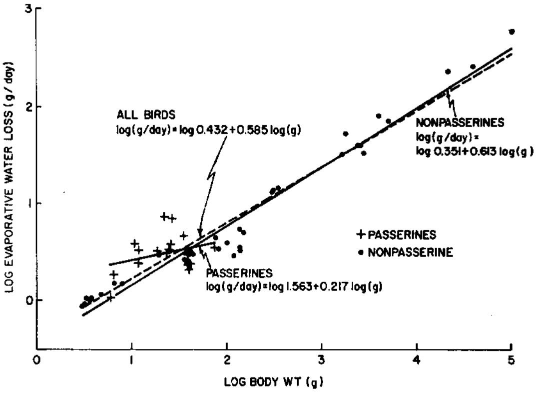

FIGURE 2. The relationships between evaporative water loss and body weight in passerine birds, nonpasserine birds, and all birds. Data are listed in table 2.

and body weight. Data from 53 species of birds are summarized in table 2 and plotted on log-log coordinates in figure 2. The values assembled represent evaporative water loss of "resting" birds at ambient temperatures within or below their respective zones of thermal neutrality. Birds included in this analysis span the full avian size range, from a 3 g hummingbird to a 100 kg ostrich. A least-squares regression line fitted to the data for all birds ($N = 53$) has the form:

$$\log E = \log 0.432 + 0.585 \log W \quad (6)$$
$$(S_{yx} = 0.182;\ S_b = 0.180;\ N = 53),$$

where E is evaporative water loss in g H_2O/day, and W is body weight in g. The data for passerines are limited and cover a narrow weight range, and the regression line fitted to these values ($N = 18$) is described by the equation:

$$\log E = \log 1.563 + 0.217 \log W \quad (7)$$
$$(S_{yx} = 0.191;\ S_b = 0.185;\ N = 18),$$

with units as in equation 6. The regression line relating evaporative water loss to body weight for all birds except passerines ($N = 35$) has the form:

$$\log E = \log 0.351 + 0.613 \log W \quad (8)$$
$$(S_{yx} = 0.152;\ S_b = 0.150;\ N = 35).$$

The data summarized in table 2 are lacking in several respects, and equations 6, 7, and 8 should be considered preliminary for the following reasons: (1) The ambient water-vapor pressures during the determinations vary widely, and this variable is an important determinant of rate of evaporation; (2) the states of nutrition and postabsorptivity, degree of physiological and psychical rest, and time of day are not always comparable, and these and other factors may influence evaporation rates; (3) the data for the three largest birds (Ostrich, Emu, Rhea) represent primarily respiratory evaporation; and (4) the data for passerines display great scatter and a markedly different regression coefficient (0.217) than the data for all birds.

There are two major sources of evaporation, skin and respiratory system. Evaporation from the skin occurs by simple diffusion, and if the water-vapor pressure gradient between the skin and air remains constant, cutaneous evaporation (E_s) should increase with body size in proportion to the increase in surface area:

$$E_s \propto W^{2/3} \quad (9)$$

The rate of evaporation from the respiratory tract is related to the vapor-pressure gradient between the environment and evaporating surfaces. If this vapor-pressure gradient and the amount of oxygen extracted during ventilation remain constant, respiratory water loss (E_r) should be proportional to the rate of ventilation, and should vary with body size as does metabolic rate:

$$E_r \propto W^{3/4} \quad (10)$$

Total evaporation ($E_t = E_r + E_s$) might then be expected to increase with body weight in the following manner:

$$E_t \propto W^n \quad (11)$$

where the value of n is between ⅔ and ¾. The empirical values of b for the three equations (6, 7, 8) relating evaporative water loss

TABLE 2. Evaporative water loss (EWL) in birds.

Species	Body weight g	Ambient temp. °C	EWL g/day	Ambient water-vapor pressure mm Hg	References
Stellula calliope	3.0	23	0.89	6.0	Lasiewski 1964
Calypte costae	3.2	23	0.93	5.5	Lasiewski 1964
Archilochus alexandri	3.3	23	1.07	6.4	Lasiewski 1964
Selasphorus sasin	3.7	23	1.07	6.4	Lasiewski 1964
Selasphorus rufus	3.8	23	1.09	6.5	Lasiewski 1964
Calypte anna	4.8	23	1.15	6.9	Lasiewski 1964
Estrilda troglodytes	6.1	25	1.10	5.7	Lasiewski *et al.* 1964
Estrilda troglodytes	6.5	25	1.87	3.4	Cade *et al.* 1965
Eugenes fulgens	6.6	25	1.51	6.3	Lasiewski and Lasiewski 1967
Lampornis clemenciae	7.9	25	1.52	6.3	Lasiewski and Lasiewski 1967
Troglodytes aedon	10.8	25	3.89	18.9	Kendeigh 1939
Taeniopygia castanotis	11.5	25	2.38	4.3	Cade *et al.* 1965
Taeniopygia castanotis	11.7	25	3.30	3.2	Calder 1964
Carpodacus mexicanus	18.8	25	3.23	6.7	Bartholomew and Dawson 1953
Patagona gigas	19.1	25	2.98	5.0	Lasiewski *et al.* 1967
Emberiza hortulana	22.0	25	7.38	8.1	Wallgren 1954
Zonotrichia leucophrys	23.2	25	3.16	6.5	Bartholomew and Dawson 1953
Passer domesticus	24.4	25	3.40	10.5	Lasiewski *et al.* 1966
Passer domesticus	26.0	25	3.74	10.5	Kendeigh 1944
Emberiza citrinella	26.4	25	7.04	7.8	Wallgren 1954
Neophema bourkii	35.3	25	2.72	5.9	Dawson 1965
Pipilo maculatus	35.4	25	4.71	9.6	Bartholomew and Dawson 1953
Pipilo aberti	38.2	25	2.94	6.0	Bartholomew and Dawson 1953
Pipilo fuscus	39.3	25	2.36	4.8	Bartholomew and Dawson 1953
Mimus polyglottos	39.6	25	2.14	4.4	Bartholomew and Dawson 1953
Richmondena cardinalis	40.0	25	2.40	3.6	Dawson 1958
Phalaenoptilus nuttallii	40.0	25.4	2.45	4.9	Bartholomew *et al.* 1962
Chordeiles acutipennis	40.2	25	3.02	6.2	Bartholomew and Dawson 1953
Neophema petrophila	40.7	25	3.30	5.9	Dawson 1965
Lanius ludovicianus	40.8	25	2.37	4.8	Bartholomew and Dawson 1953
Excalfactoria chinensis	42.7	25	3.08	6.5	Lasiewski *et al.* 1966
Toxostoma redivivum	74.7	25	3.51	7.2	Bartholomew and Dawson 1953
Chordeiles minor	75.0	25	4.50	9.4	Lasiewski and Dawson 1964
Nymphicus hollandicus	80.7	25	3.39	5.9	Dawson 1965
Otus asio sinaloensis	101.3	25	3.95	8.1	Bartholomew and Dawson 1953
Zenaidura macroura	118.7	25	2.96	6.1	Bartholomew and Dawson 1953
Platycercus zonarius	137.0	25	3.56	5.9	Dawson 1965
Otus asio quercinus	137.8	25	5.37	11.0	Bartholomew and Dawson 1953
Lophortyx californicus	138.5	25	3.30	4.0	Brush 1965
Lophortyx californicus	147.1	25	5.15	10.3	Bartholomew and Dawson 1953
Domestic Pigeon	300.0	25	13.9	9.9	Kayser 1939
Domestic Pigeon	303.7	25.2	14.1	–	Kayser 1930
Domestic Pigeon	347.0	31.5	14.6	4.04	Calder and Schmidt-Nielsen 1966
Domestic Chicken	1645.0	25	32	–	Sturkie 1965
Domestic Chicken (32 weeks)	1771.0	21–35	54.8	7.85	Medway and Kare 1957
Domestic Chicken	2430.0	25	40.8	11.9–14.3	Barott and Pringle 1946
Domestic Chicken	2510.0	23–27	40.9	9.78	Dukes 1937
Domestic Chicken	2750.0	26	34.3	15.2	Romijn and Lokhorst 1961
Domestic Chicken	4000.0	24	81.0	7.84	Romijn and Lokhorst 1961
Domestic Goose	5000.0	20	72.0	–	Benedict and Lee 1937
Rhea americana	21,500.0	26	230.4	–	Crawford and Lasiewski present study
Dromiceius novae-hollandiae	38,300.0	22	258.0	16.6	Crawford and Lasiewski present study
Struthio camelus	100,000.0	20	576.0	3.5	Crawford and Schmidt-Nielsen 1967

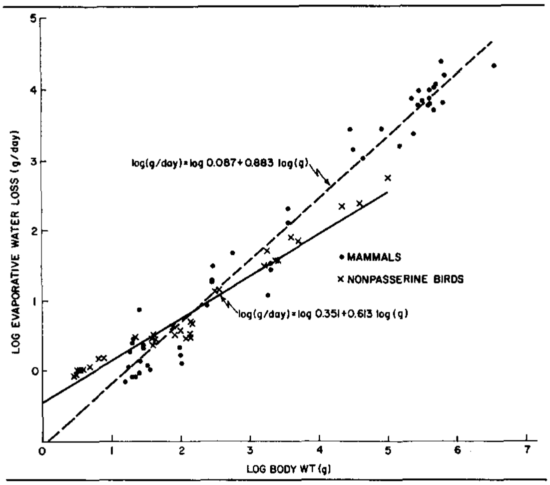

FIGURE 3. A comparison of the relationships between evaporative water loss and body weight in mammals and nonpasserine birds. The data for mammals are from Chew (1965), the equation for mammals is from Chew (personal communication).

to body weight in birds fall outside the range that might be expected on the basis of the above mentioned considerations.

Chew (1965) summarized available data on evaporative water loss of mammals ranging in weight from 15.8 g to 3630 kg. A recent reevaluation (Chew, personal communication) of mammalian data resulted in the equation:

$$\log E = \log 0.087 + 0.883 \log W \quad (12)$$

where E is evaporation in g H_2O/day and W is body weight in g, a relationship similar to that proposed by Adolph (1949) for water intake vs. body weight in mammals.

In contrast to birds, the value of the regression coefficient (0.883) for mammals is greater than might be expected from theoretical considerations. However, the difference in slope between equations 8 and 12 is not statistically significant. Before any discrepancies which may exist between evaporation in birds and mammals can be resolved, further work on the physiology of evaporative water loss is needed. Little is known about the characteristics of the exhaled air, sites of evaporation, and mechanisms of ventilation, particularly in birds. Separation of total evaporation into its cutaneous and respiratory components may clarify any physiological differences which may exist between birds and mammals.

TABLE 3. Values of evaporative water loss and standard metabolic rate predicted for nonpasserine birds of different weights.

Weight g	Evaporation g H_2O/day = $0.351g^{0.618}$	Metabolism[a] kcal/day = $78.3kg^{0.723}$	mg H_2O/ml O_2[b]
3.2	0.71	1.23	2.8
10	1.43	2.8	2.5
1000	24.1	78.3	1.5
21,700	159.0	724.6	1.1
38,300	225.2	1093.0	1.0
100,000	405.5	2187.0	0.9

[a] From Lasiewski and Dawson 1967.
[b] Assuming 1 liter O_2 = 4.8 kcal.

TABLE 4. Body temperatures (T_B) of large ratite birds.

Species	Weight kg	T_B °C	Reference
Casuarius sp.	17.6	39.0	Sutherland 1899 Benedict and Fox 1927
Rhea americana	21.7	39.7	Present study
Dromiceius novae-hollandiae	43.0	39.0	Sutherland 1899
	38.3	38.1	Present study
Struthio camelus	113	38.7	Bligh and Hartley 1965
	100	38.3	Crawford and Schmidt-Nielsen 1967

The exponents (values of b) relating standard metabolism to body weight in birds are higher than comparable exponents for avian evaporative water loss and body weight. Combination of equations predicts that the amount of water evaporated per unit oxygen consumption will decrease with increasing body weight in birds. Values of this ratio predicted for different-sized birds by equations 4 and 8 are summarized in table 3. Empirical values for the Rhea, Emu, and Ostrich of 1.4, 1.2, and 0.9 mg H_2O/ml O_2, respectively, do not differ markedly from values predicted for birds of these weights. At the other end of the avian size range, a 3.2 g Costa's Hummingbird has a mg H_2O/ml O_2 ratio of 2.1 (Lasiewski 1964), as compared with the predicted ratio of 2.8.

The mean body temperatures of the Emu and Rhea were 38.1° and 39.7°C, respectively. Comparison of these values with those available for other large ratites (table 4), and with values for smaller birds, supports the contention that the body temperatures of large ratites are lower than those for most smaller birds. McNab (1966) has recently reviewed the subject of avian body temperatures.

Resting respiratory rates of Emus and Rheas were approximately 7 and 9 breaths/min, with respective heart rates of 41 and 48 beats/min. Crawford and Schmidt-Nielsen (1967) report resting respiratory rates of 4–7/min in the Ostrich. These values are lower than respiratory and heart rates of comparable-sized mammals (Adolph 1949).

Since the relationship between body size and metabolism in mammals and nonpasserine birds does not differ significantly (Lasiewski and Dawson 1967), the lower respiratory and cardiac rates of birds raise some interesting questions regarding avian cardiovascular and respiratory physiology.

SUMMARY

The mean resting values for metabolism, evaporative water loss, body temperature, respiratory rate, and heart rate for 2 Emus (38.3 kg) and 3 Rheas (21.7 kg) obtained in this study were, respectively, 149.9 and 114.5 ml O_2/min, 179 and 160 mg H_2O/min, 38.1° and 39.7°C, 7.1 and 8.5 breaths/min, 41 and 48 beats/min.

The standard metabolism of Emus and Rheas, as well as of Cassowaries and Ostriches, does not deviate significantly from that predicted on the basis of the metabolism-weight relationships of other nonpasserine birds.

The relationships between avian evaporative water loss and body weight are analyzed and regression lines are presented. The relationship between evaporative water loss and body weight in birds and mammals is compared.

Body temperatures of large ratites are lower than those of most smaller birds. Respiratory and heart rates of Emus and Rheas are lower than those for comparable-sized mammals.

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