RESPIRATORY AND HEART RATES OF BIRDS AT REST

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The respiratory rates of birds are inversely related to their body weights (Groebbels 1932; Salt and Zeuthen 1960). Odum (1945) noted that birds breathe at lower frequencies than do mammals of similar weights. Neither of these observations has been expressed quantitatively.

The respiratory and heart rates of mammals can be predicted from empirical equations given by Adolph (1949) and Stahl (1967) which express the resting rates as functions of body weight. The utility of comparable equations for birds prompted the collection and analysis of appropriate data. Data on respiratory and heart rates were obtained from the literature and from additional observations on 11 species.

My intention in this report is not only to provide a first approximation for such predictions, but also to recommend that collection of data on respiratory rates and heart rates be made under more rigorously standardized conditions than has been the case previously (and reported in conjunction with body weights). Reports by Odum (1945) and Lewis (1967) are models to follow in this respect.

The respiratory rate of birds is easily disturbed. In order to observe natural, resting breathing, the birds cannot be inverted, restrained, or in direct contact with any restraining device other than the cage floor (see Odum, unpublished, cited by Welty 1962: 121). The birds must be resting quietly in a thermoneutral environment, so that increased ventilation is not required for locomotor activity or thermoregulation. Body temperature cannot be hypothermic or hyperthermic. Resting body temperatures listed for a variety of species by King and Farner (1961) are useful reference points in this regard. Respiratory rates are increased to compensate for metabolic acidosis during formation of $CaCO_3$ for egg shells (Mongin and Lacassagne 1965), and data from females in lay must therefore be excluded.

METHODS

In this study respiratory frequencies were measured by direct observation and heart rates by observation of pulses in arterial catheters, using a stopwatch and hand tally. Most birds had been in captivity for several weeks. Air temperatures during the observations were 22–26°C. Smaller and more excitable birds were observed through one-way plastic windows or peep-holes in curtains while they were in cages or compartments appropriate for their sizes. The birds were not handled during the observations and were free to move within the compartments.

Unfortunately, published values for respiratory rates are not usually accompanied by complete information on the experimental situations. The selection of data used in this report consisted of excluding values when there was an indication that any one of the above criteria had not been met. However, in the absence of complete information, all of these criteria may not have been met in some cases. Equations were fitted to the data by the methods of least squares, after logarithmic transformations of the data according to the method of Simpson et al. (1960).

Standard symbols for respiratory variables (Comroe et al. 1950) will be used throughout this report. These include: f = respiratory rate or breathing frequency (breaths/min), V_T = tidal volume (ml), $\dot{V}_{O_2}$ = oxygen consumption (ml/min), W = body weight (g), $F_{I_{O_2}}$ and $F_{E_{O_2}}$ = oxygen fraction in inspired and expired air, respectively.

RESULTS AND DISCUSSION

The respiratory frequencies of 45 species of birds are given in table 1, and the relationship between respiratory rate and body weight is shown in figure 1. The regression equation for the combined data is

$$f = 182\ W^{-0.33} \qquad (1)$$

The 95 per cent confidence interval for the slope, –0.33, is ±0.04, while the 95 per cent confidence interval for the 1-gram intercept (Y-intercept), 182, is 158–214 breaths/min.

TABLE 1. Respiratory rates of resting birds (selected data).

Species	Body wt (g)	Respiratory rate (breaths/min)	Reference
Struthio camelus	100,000	5	Crawford and Schmidt-Nielsen 1967
Struthio camelus	90,000	6	Schmidt-Nielsen et al. personal comm.
Rhea americana	21,700	8.5	Crawford and Lasiewski 1968
Dromiceius novae-hollandiae	38,300	7.1	Crawford and Lasiewski 1968
Gavia immer	2,123	6.8	This study
Pelecanus erythrorhynchos	7,500	6.3	This study
P. occidentalis	3,130	8.0	Bartholomew et al. 1968
Phalacrocorax auritus	1,340	15.0	Bartholomew et al. 1968
Anser sp.	3,425	7.6	This study
Anas platyrhynchos	785	19.0	Groebbels 1932
A. platyrhynchos (Pekin)	2,608	17.0	This study
Cathartes aura	2,000	9.2	This study
Buteo buteo	658	18	Groebbels 1932
Polyborus tharus	350	15	Groebbels 1932
Gallus domesticus	5,200	13	This study
Excalfactoria chinensis	42.7	68	Lasiewski et al. 1966
Larus argentatus	930	19	This study
L. canus	388	26	Groebbels 1932
Columba livia	315	29.1	Calder and Schmidt-Nielsen 1967
Columba livia	317	28	Groebbels 1932
Columba livia	382	26	Hart and Roy 1966
Melopsitticus undulatus	38.2	69	This study
Geococcyx californianus	284.7	28.9	Calder and Schmidt-Nielsen 1967
Strix aluco	350	24	Groebbels 1932
Podargus strigoides	675	22	Lasiewski and Bartholomew 1966
Colaptes auratus	112	26	Lewis 1967
Empidonax flaviventris	10.2	74	Lewis 1967
Cyanocitta cristata	77.1	49	Lewis 1967
Corvus corone	339	20	Groebbels 1932
C. frugilegus	341	25	Groebbels 1932
C. monedula	240	26	Groebbels 1932
C. monedula	246	60.2	Groebbels 1932
Parus atricapillus	12	64	Odum 1941 (see also Welty 1962)
Troglodytes aedon	11	83	Odum 1941 (see also Welty 1962)
Dumetella carolinensis	29.4	57	Lewis 1967
Toxostoma rufum	59.2	30	Lewis 1967
Turdus merula	92	48	Groebbels 1932
T. philomelos	81	94	Groebbels 1932
T. migratorius	69.5	36.5	Lewis 1967
Hylocichla mustelina	30.5	43	Lewis 1967
Erithacus rubecula	20	97	Groebbels 1932
Sturnus vulgaris	74	92	Groebbels 1932
Passer domesticus	29.0	57	Kendeigh 1944
Passer domesticus	24.6	59	This study
Estrilda troglodytes	6.9	95	This study
Estrilda melpoda	6.9	113	This study
Serinus canaria	17	108	Groebbels 1932
Serinus canaria	16	57	Odum 1941 (see also Welty 1962)
Richmondena cardinalis	40	45	Odum 1941 (see also Welty 1962)
Melospiza melodia	20	63	Odum 1941 (see also Welty 1962)
Pyrrhula pyrrhula	23	42	Groebbels 1932
Loxia curvirostra	39.1	70	Groebbels 1932

Empirical expressions have been derived previously that relate respiratory rate to body weight in mammals. Converted to common units there are

$$f = 354 \ W^{-0.28} \quad \text{(from Adolph 1949)} \quad (2)$$

and

$$f = 322 \ W^{-0.26} \quad \text{(from Stahl 1967).} \quad (3)$$

These equations agree closely. An equation given by Mead (1960) must be rejected because it is contradicted by the figure to which it refers and by succeeding remarks in the same report.

When resting respiratory frequencies for birds and mammals are compared, the birds appear to have rates that are much lower than those of mammals, the ratio of bird :
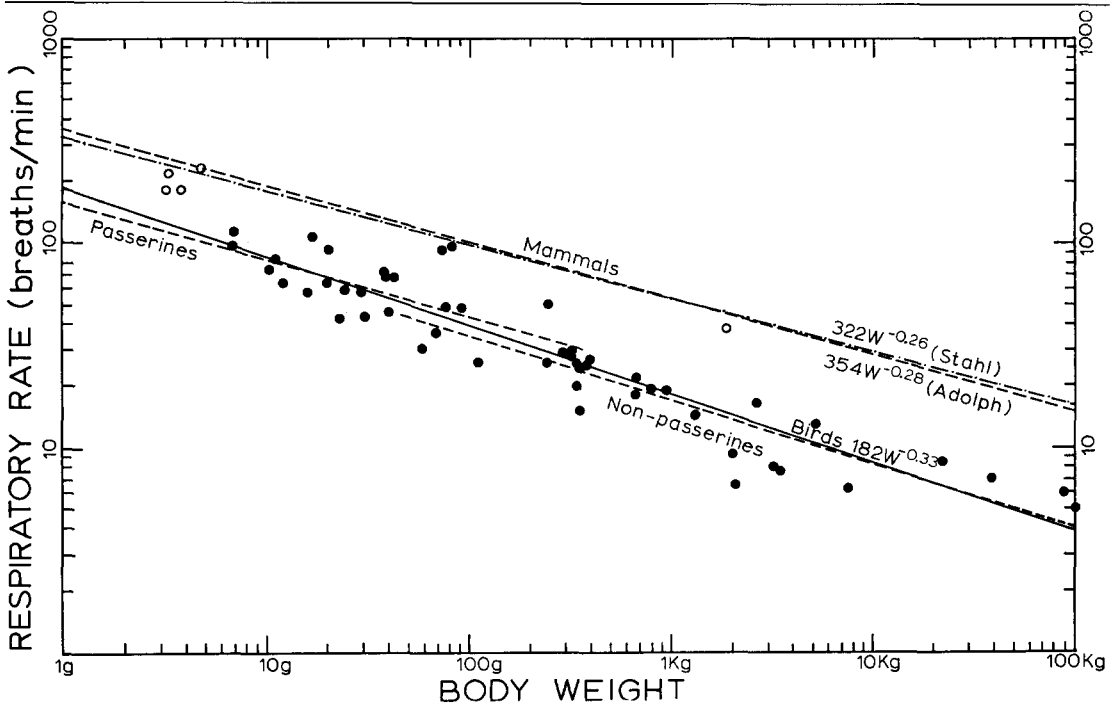
FIGURE 1. The relation between resting respiratory rate and body weight in unrestrained, resting birds, compared with lines for mammals from published equations. Shaded circles indicate respiratory rates of resting birds (data in table 1). Open circles are for restrained fowl and hummingbirds, not used in deriving the regression lines (see text).

mammal being about 0.3 to 0.6. At least some of this difference may be a result of differences in conditions under which the data were collected. Adolph's equation is based on data obtained by Guyton (1947) from restrained mammals wearing face masks. Stahl used data from standard handbooks as well as original reports including Guyton's. It may be significant that data for restrained domestic fowl (Weiss *et al.* 1963) and hummingbirds (Lasiewski 1964) fall on or near the mammal lines (fig. 1). When only the respiratory rates of some unrestrained mammals (table 2) are considered, the following equation is obtained:

$$f = 262 \ W^{-0.26}. \qquad (4)$$

However, the 95 per cent confidence intervals for this equation include the Stahl line.

The regression equations for avian and mammalian respiratory rates should be compared with regard to their slopes as well as their elevations on the ordinate in figure 1. Before this comparison is made, however, some preliminary discussion is necessary.

The power functions of these relationships, although empirically derived, should suggest basic physiological relationships if fully comparable data have been obtained for all species

for which generalization is legitimate. The interrelationships among such empirical expressions have been discussed by Adolph (1949) and Stahl (1967). Adolph stated that "It seems likely that an organism is an integrated system by virtue of the fact that none of its properties is entirely uncorrelated, but that most are demonstrably interlinked." For example, in a steady state, the oxygen consumed in a period of time must be accounted for in the volume of air inspired ($f \times V_T$) during that time and the extent to which oxygen is removed before expiration. Hence, the following must be true:

$$f \times V_T \times (F_{I_{O_2}} - F_{E_{O_2}}) = \dot{V}_{O_2}. \qquad (5)$$

That is, (breaths/min) $\times$ (ml/breath)$\times$ (per cent) = (ml O_2/min). Dimensional analysis thus provides a check for consistency between independently derived regression equations.

For mammals, empirical equations have been developed for f, V_T, and $\dot{V}_{O_2}$ as functions of body weight, and can be substituted in equation 5, as shown in table 3. The products of the powers to which W is raised to predict values for these variables should be the same on both sides of equation 5. If ($F_{I_{O_2}} - F_{E_{O_2}}$) is the same for all resting mammals (that is,

TABLE 2.   Respiratory rates of resting mammals.

Species	Body wt (g)	Resp. rate (breaths/min)	Reference
Cercaertus nanus	70	50	Bartholomew and Hudson 1962
Sorex cinereus	3.4	800	Morrison *et al.* 1953
Blarina brevicauda	(21)[a]	168	Doremus 1965
Blarina brevicauda	(21)[a]	186	Odum (in Welty 1962)
Pteropus poliocephalus	600	33	Bartholomew *et al.* 1964
Pteropus scapulatus	352	58	Bartholomew *et al.* 1964
Syconycteris australis	17.5	140	Bartholomew *et al.* 1964
Anzotrotus pacificus	21.5	120	Storer 1931
Macrodema gigas	148	55	Leitner and Nelson 1967
Marmota monax	2.62×10^3	33	Benedict and Lee 1938
Marmota monax	4.67×10^3	27.4	Benedict and Lee 1938
Castor canadensis	18.2×10^3	16	Irving and Orr 1935
Peromyscus leucopus	(22)[a]	135	Odum, in Welty 1962
Glaucomys volans	(75)[a]	91	Odum, in Welty 1962
Tamias striatus	(88)[a]	65	Odum, in Welty 1962
Citellus tridecemlineatus	157	126	Johnson 1928
C. tereticaudus	125	54	Hudson 1964
Mus musculus	39.7	120	This study
Elephas maximus	2719×10^3	4.9	Benedict 1936
Elephas maximus	3672×10^3	4.5	Benedict 1936
Camellus dromedarius	407×10^3	16	Schmidt-Nielsen *et al.* 1967
Lama guanicoe	57.8×10^3	26	Rosemann and Morrison 1963

[a] Weights from other sources.

independent of body weight, or proportional to W^0), then

$$W^{-0.28} \times W^{1.01} \times W^0 = W^{0.73} \quad (6)$$
$$\text{(from Adolph)}$$

and

$$W^{-0.26} \times W^{1.04} \times W^0 = W^{0.78} \quad (7)$$
$$\text{(from Stahl).}$$

These exponents calculated for $\dot{V}_{O_2}$ compare closely with those empirically derived ($W^{0.75}$, $W^{0.734}$, and $W^{0.76}$). The difference between the exponents as calculated from the left side of equation 5 and as empirically derived has been called the "residual mass index" by Stahl (1967).

Until the functional variables of avian respiration have been more thoroughly investigated we can only estimate indirectly the respiratory volumes in equation 5. Respiratory volumes in unrestrained pigeons and Roadrunners have been estimated from data on evaporative water loss, body temperature, and respiratory rate (Calder and Schmidt-Nielsen 1966, 1967). The assumptions underlying the estimates were that (1) in birds, which lack sweat glands, there is no significant transcutaneous water loss (*i.e.*, measured losses were all from the respiratory tract), and (2) expired air was saturated with water vapor at body temperature. The expired air

TABLE 3.   Summary of respiratory equations for mammals and birds.[a]

Respiratory rate (no./min)	Tidal volume (ml)	O₂ extraction (%)	O₂ consumption[b] (ml/min)
Mammals			
$354\ W^{-0.26}$(c)	$0.0062\ W^{1.01}$(c)		$0.057\ W^{0.75}$ (d)
$322\ W^{-0.26}$(e)	$0.0058\ W^{1.04}$(e)	$k\ W^{0.04}$(f)	$0.061\ W^{0.76}$ (e)
			$0.064\ W^{0.734}$(g)
All birds			
$182\ W^{-0.33}$	?	?	$0.124\ W^{0.668}$(h)
Nonpasserine birds			
$146\ W^{-0.31}$	?	?	$0.078\ W^{0.729}$(h)
Passerine birds			
$158\ W^{-0.28}$	?	?	$0.126\ W^{0.724}$(h)

[a] Footnotes associated with equations are shown in parentheses.
[b] Equal to the product of the three terms at the left.
[c] From Adolph (1949).
[d] From Kleiber (1961).
[e] From Stahl (1967).
[f] From Stahl (1967) according to the equation: $\Delta O_2 = (f \times V_T)/\dot{V}_{O_2}$.
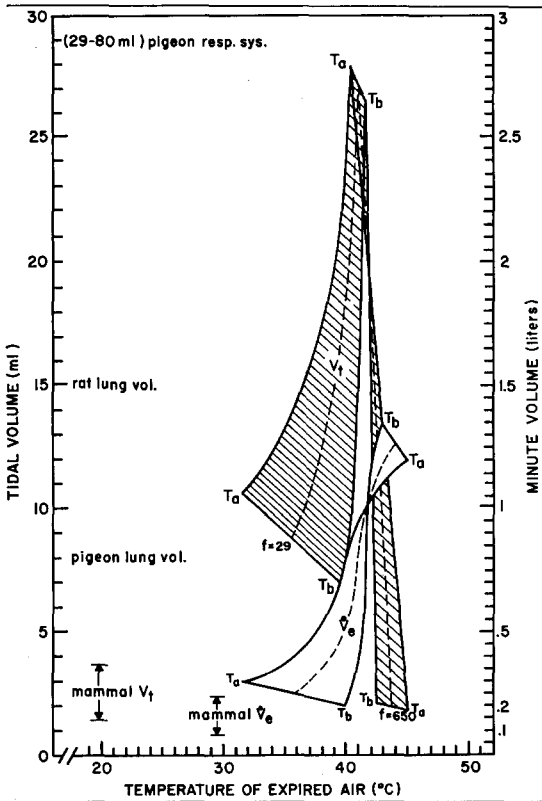[g] From Brody (1945).
[h] From Lasiewski and Dawson (1967).

FIGURE 2. Tidal volumes (V_T, hatched area) and minute volumes ($\dot{V}_e$, clear area) of the pigeon, *Columba livia*, estimated from evaporation rates during exposure to air temperatures of 30–45°C (data from Calder and Schmidt-Nielsen 1966). The broken lines indicate the volumes necessary to contain observed amounts of water vapor if the expired air had a temperature half way between air (T_a) and body (T_b) temperatures; the solid lines indicate volumes at T_a and T_b. The brackets indicate values for V_T and $\dot{V}_e \pm 1$ se for a mammal of similar weight (resting, nonpanting) as estimated from equations of Stahl (1967). Anatomical values along the left margin are from King (1966) and estimated from Tenney and Remmers (1963). The frequencies of 29 and 650 breaths/min were observed in resting and panting birds, respectively.

might be cooler if a nasal countercurrent heat exchanger exists in birds as it does, for instance, in the Kangaroo Rat (Jackson and Schmidt-Nielsen 1964). If so, then the estimates of tidal volume and minute volume can vary between values determined by body temperature and environmental air temperature. The ranges of estimated respiratory volumes in pigeons, based on these considerations, are shown in figure 2.

If the tidal volumes of birds are directly related to body weight, as in mammals, then the tidal volume of pigeons could be predicted as $0.02\ W^{1.0}$ to $0.03\ W^{1.0}$ (expired air at body temperature and environmental air tem-

perature, respectively). Other data on tidal volumes in pigeons (see Salt and Zeuthen 1960; Hart and Roy 1966) are equivalent to $0.013\ W^{1.0}$ to $0.023\ W^{1.0}$. In all cases, the volumes are more than twice those of mammals of the same weight range. The paucity and variability of data on tidal volume in other species of birds prohibit a useful regression analysis.

Lasiewski and Dawson (1967) have, however, analyzed all of the suitable data on standard metabolic rate in birds to refine our understanding of metabolism-body weight relationships. Their results were (assuming that 1 ml $O_2 = 4.8$ cal, and changing the units to conform with those used in the present analysis)

For all birds:
$$\dot{V}_{O_2} = 0.124\ W^{0.668} \qquad (8)$$
For nonpasserine birds:
$$\dot{V}_{O_2} = 0.078\ W^{0.723} \qquad (9)$$
For passerine birds:
$$\dot{V}_{O_2} = 0.126\ W^{0.724}. \qquad (10)$$

I have attempted to relate the analysis of resting respiratory rates to these equations for standard oxygen consumption. When respiratory rates of passerines and nonpasserines are treated separately, the following equations are obtained:

For nonpasserine birds:
$$f = 146\ W^{-0.31} \qquad (11)$$
For passerine birds:
$$f = 158\ W^{-0.28}. \qquad (12)$$

Equations 11 and 12 are not statistically distinguishable from each other (lower broken lines in fig. 1) but will be considered further for theoretical purposes.

Information on birds from equation 1 and equations 8 through 12 is combined for the respiratory equations in table 3. Multiplying the powers to which W is raised, we have, as in equations 6 and 7, the following equations for birds, assuming that V_T is linearly related to weight (that is, proportional to $W^{1.00}$) and the value $(F_{I_{O_2}} - F_{E_{O_2}})$ is independent of weight as in mammals.

For all birds:
$$W^{-0.33} \times W^{1.00} \times W^0 = W^{0.67} \qquad (13)$$
For nonpasserine birds:
$$W^{-0.31} \times W^{1.00} \times W^0 = W^{0.69} \qquad (14)$$
For passerine birds:
$$W^{-0.28} \times W^{1.00} \times W^0 = W^{0.72}. \qquad (15)$$

Note again the similarity of these exponents to those derived from oxygen-consumption data for each grouping (right-hand terms in table 3).

TABLE 4. Heart rates of resting birds.

Species	Body wt (g)	Heart rate (beats/min)	Reference
Pelecanus erythrorhynchos	7500	150	This study
Anser sp.	3420	113	This study
Anas platyrhynchos (Pekin)	2670	118	This study
Cathartes aura	2000	132	This study
Lophortyx californicus	138	250	Hudson and Brush 1964
Larus argentatus	930	218	This study
Columba livia	382	166	Hart and Roy 1966
Zenaidura macroura	130	135	Odum 1945
Zenaidura macroura	91.4	120	Hudson and Brush 1964
Phalaenoptilus nuttallii	40	210	Bartholomew et al. 1962
Chordeiles minor	72.5	180	Lasiewski and Dawson 1964
Archilochus colubris	4	615	Odum 1945
Colaptes auratus	112	230	Lewis 1967
Empidonax flaviventris	10.2	545	Lewis 1967
Cyanocitta cristata	77.1	307	Lewis 1967
Parus atricapillus	12	480	Odum 1945
Troglodytes aedon	11	450	Odum 1945
Cinclus mexicanus (fledgling)	40	370	Calder, unpubl.[a]
Dumetella carolinensis	28.9	427	Lewis 1967
Toxostoma rufum	59.2	303	Lewis 1967
Turdus migratorius	69.5	328	Lewis 1967
Hylocichla mustelina	30.5	363	Lewis 1967
Passer domesticus	28	350	Odum 1945
Serinus canarius	16	514	Odum 1945
Richmondena cardinalis	40	375	Odum 1945
Pipilo erythrophthalmus	40	445	Odum 1945
Spizella passerina	12	440	Odum 1945
Melospiza melodia	20	450	Odum 1945

[a] Obtained after completion of regression analysis.

Equations 13 to 15 suggest that a distinction may exist between passerine and nonpasserine birds in respiratory rates as well as in metabolic rate, as shown by Lasiewski and Dawson (1967). Hopefully, additional data will be adequately standardized and will make it possible to test this hypothesis; but statistical analyses of information now available blur this distinction and indicate the following (treating Y-intercepts and slopes for mammals as "hypothetical" values). First, the lines for respiratory rates of passerines and nonpasserines taken separately have slopes similar to those for mammals, but are distinctly separated vertically from the latter $(P < 0.001)$. Second, the lines for respiratory rates of passerines and nonpasserines are not statistically distinct vertically $(0.5 < P < 0.6)$ and so cannot be regarded as validly separated lines. And third, the line for respiratory rates of all birds is significantly different from that for mammals $(P < 0.001)$. As is the case for metabolic comparisons of all birds with mammals (Lasiewski and Dawson 1967), the weight regression slopes for respiratory rates of these classes differ significantly $(0.01 < P < 0.05)$.

The respiratory rates of birds and mammals have also been compared with respect to the ratio of heart rate to respiratory rate. It appears that the two classes do not differ greatly in this regard, although the more limited data previously available suggested a difference (see Welty 1962).

I have made a preliminary analysis of heart rates in birds in order to examine this situation further. Based on 27 points (table 4), a regression line for heart frequency (f_h, beats/min) was obtained, which is expressed by the following equation:

$$f_h = 763 \ W^{-0.23}. \qquad (16)$$

The 95 per cent confidence interval for the slope is ± 0.060, and for the Y-intercept it is 680–855 beats/min. This line is definitely lower than that for mammals, which conforms with the equation

$$f_h = 1355 \ W^{-0.25} \ (\text{from Stahl 1967}). \ (17)$$

The ratio of heart rate to respiratory rate based on these equations is 4.2 for all birds, 5.2 for nonpasserines, and 4.8 for passerines (if it is assumed that the differences in exponents are not significant). Stahl (1967) gives a comparable ratio of 4.5 for mammals. However, in the present limited analysis it may only be noted that birds have lower respiratory rates and heart rates than mammals

of the same weights, but that the ratios of rates appear to be similar in the two classes.

SUMMARY

The resting respiratory rates of birds are lower than those of mammals of the same body weights. When passerine and nonpasserine birds are considered together, the slope of the regression of respiratory rate on body weight is greater than it is in the comparable equation for mammals, and the value of the Y-intercept (ordinate) is less. When passerine and nonpasserine groups are analyzed separately, the slopes of the equations do not differ from the mammalian slope, but the values of the Y-intercepts are significantly less. More data, and standardized conditions for obtaining them, are needed to clarify these relationships.

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