

Scaling of Respiratory Variables and the Breathing Pattern in Birds: An Allometric and Phylogenetic Approach

P. B. Frappell^{1,*}

D. S. Hinds²

D. F. Boggs³

¹Department of Zoology, La Trobe University, Melbourne, Victoria 3083, Australia; ²Department of Biology, California State University at Bakersfield, Bakersfield, California 93311-1099; ³Department of Biology, Eastern Washington University, Cheney, Washington 99004-2431

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ABSTRACT

Allometric equations can be useful in comparative physiology in a number of ways, not the least of which include assessing whether a particular species deviates from the norm for its size and phylogenetic group with respect to some specific physiological process or determining how differences in design among groups may be reflected in differences in function. The allometric equations for respiratory variables in birds were developed 30 yr ago by Lasiewski and Calder and presented as “preliminary” because they were based on a small number of species. With the expanded data base now available to reconstruct these allometries and the call for taking account of the nonindependence of species in this process through a phylogenetically independent contrasts (PIC) approach, we have developed new allometric equations for respiratory variables in birds using both the traditional and PIC approaches. On the whole, the new equations agree with the old ones with only minor changes in the coefficients, and the primary difference between the traditional and PIC approaches is in the broader confidence intervals given by the latter. We confirm the lower \dot{V}_E/\dot{V}_{O_2} ratio for birds compared to mammals and observe a common scaling of inspiratory flow and oxygen consumption for birds as has been reported for mammals. Use of allometrics and comparisons among avian groups are also discussed.

Introduction

Our understanding of the effect of body size on respiratory variables relies on the now quite old allometric analyses of Stahl (1967) for mammals and Lasiewski and Calder (1971) for birds. While Stahl’s analysis is robust and based on a large data set, the latter was initially presented as a preliminary analysis and was based on a small data set (i.e., six species). A more recent analysis (Maloney and Dawson 1994) utilising the literature (22 species) confirmed the general relationships espoused in the original study (Lasiewski and Calder 1971).

Such allometric relationships are often used by comparative physiologists either to determine predicted values of respiratory parameters for animals of a given size or to assess broader aspects of organismal design. A concerted effort over the last several decades to understand the design of the oxygen cascade has led to the paradigm that conservation in the design of the oxygen cascade occurs within broad classes of animals (Weibel et al. 1998), and conservation in the design of the oxygen cascade became a paradigm, as revealed by allometry. In the conventional view, this is evident (e.g., in mammals) in the size independence of the convection requirement (\dot{V}_E/\dot{V}_{O_2}). In other words, minute ventilation (\dot{V}_E ; mL min⁻¹) is consistently matched to oxygen consumption rate (\dot{V}_{O_2} ; mL min⁻¹), and by rearrangement of the Fick equation ($\dot{V}_E/\dot{V}_{O_2} = 1/[EO_2 \times CiO_2]$), it is apparent that extraction (EO_2) for a given inspired level of oxygen (CiO_2) has been conserved. Between broad taxonomic classes, differences in design of the gas exchanger are reflected in differences in oxygen extraction (reptiles: Tenney and Tenney 1970; Bennett 1973; Frappell and Daniels 1991; birds: Lasiewski and Calder 1971; Maloney and Dawson 1994; mammals: Stahl 1967; Frappell et al. 1992; Frappell and Baudinette 1995).

The traditional approach to the analysis of the effect of body size on respiratory variables, however, fails to account for the nonindependence of species (see, e.g., Martins and Hansen 1997; Garland et al. 1999; Garland and Ives 2000). Using phylogenetically independent contrasts, Reynolds and Lee (1996) recently reanalysed the relationship between size and \dot{V}_{O_2} in birds. The use of a phylogenetically corrected approach significantly increased the relationship between \dot{V}_{O_2} and mass to an exponent of 0.72 from the 0.67 found using the traditional method.

If the design of the respiratory system as it relates to oxygen extraction is conserved, then \dot{V}_E would be expected to maintain a consistent relationship to \dot{V}_{O_2} within broad phyletic groups. If not, then an analysis that takes account of phylogeny within

* Corresponding author; e-mail: p.frappell@zoo.latrobe.edu.au.

a class should reveal differences. If the relationship is upheld, then the components of \dot{V}_E , that is, tidal volume (V_T) and respiratory frequency (f), might also be expected to scale consistently. More precisely, it is the ventilation of the gas exchange surface that is expected to match \dot{V}_{O_2} ; hence, phyletic variations in the design of the respiratory system as it affects dead space could potentially contribute to variations that become evident in the scaling of V_T , f , and the timing of the respiratory cycle (previously unavailable for birds).

With many more measurements of respiratory variables now available, it is possible to revise and extend the allometries of respiratory variables in birds based on a larger number of species (50 species). Together with a good benchmark analysis of phylogenetic relationships for birds (Sibley and Ahlquist 1990), the object of this study was to reexamine avian respiratory variables in the context of both traditional and phylogenetically based comparisons.

Material and Methods

Data Collection

The literature was surveyed for studies on ventilation and metabolism in avian species. For each species, in all but two cases, all respiratory variables were obtained from the same study, though for five species, most notably the four cranes, measurement of \dot{V}_{O_2} was not available (Table 1). When more than one study existed for a given species, the values were averaged. Only data on unanesthetized birds breathing air at sea level (partial pressure of oxygen [PO_2] ranged from 143 to 154 mmHg) were used, but the data were gathered with a variety of measuring techniques, including mask pneumotachography and volumetric and barometric plethysmography. The studies also varied in measurement conditions (e.g., hour, illumination level, nutritional state, etc.). Where data were presented for a range of air temperatures, values were selected where both frequency and tidal volume exhibited a plateau at minimal levels but not necessarily the lowest reported values and not necessarily the lowest \dot{V}_{O_2} ; typically, values were taken at room temperature conditions ($\sim 20^\circ$ – 24°C). Data selection was aimed at obtaining what appeared to be steady state values reflecting normal resting ventilation. Two approaches were adopted to examine the relationships between the ventilatory variables and body mass: the traditional allometric approach and the PIC approach.

Traditional Approach

The traditional approach, which is the same used by earlier authors, employed least squares regression techniques following \log_{10} transformation of the data to obtain a power equation in the form $Y = aM^b$, where Y is a specific ventilatory variable and M is the body mass of the animal (kg).

Phylogenetically Independent Approach

The \log_{10} data were converted to phylogenetically independent standardised contrasts using the PDTREE module of the Phylogenetic Diversity Analysis program (PDAP), version 4 (Garland et al. 1993). Standardisation tests in PDAP-PDTREE indicated that no branch length transformations were necessary (Garland et al. 1992; see, however, "Results"). Confidence intervals at the 95% level were also obtained from PDTREE for the slope, intercept, and the overall regression (Garland and Ives 2000).

For the phylogenetically independent analysis, phylogenetic relationships (Fig. 1) were obtained ultimately from Sibley and Ahlquist (1990) using both their phylogeny and that of Reynolds and Lee (1996). A species whose phylogenetic position was unavailable was included taxonomically within a genus on the basis of the classification scheme of Sibley and Monroe (1990). If two species were involved, it was assumed that the two separated at one-half the branch length (Maddison 1989). In most cases, the generic designation was the same as for the species in question. However, for 10 species, the phylogenetic position of the specific genus was unavailable, and the species was then placed in the position of the closest genus in the classification scheme; these species are asterisked in the phylogenetic tree (Fig. 1). For two species, the position was quite clear, as they were our only representatives of that particular family (zebra finch, Passeridae) or order (hummingbirds, Trochiliformes). However, for eight species, it was more difficult to decide on their position, and judgments were made using first-tribe affinities and then, if necessary, geographical closeness, with Sibley and Monroe (1990) being used as the source of both. The judgments made follow: (1) The common pheasant (*Phasianus colchicus*) replaced the silver pheasant (*Lophura nycthemera*) in the original scheme ("original" refers to the scheme of Sibley and Monroe [1990]). (2) The four species of the geese tribe (Anserini) were grouped together assuming that the two species of *Anser* geese were more closely related to one another, then to the Canada goose (*Branta canadensis*), and then to the Muscovy duck (*Cairina moschata*). The respective branch lengths were obtained by dividing into quarters the 6.7 branch length in the original scheme between *Branta* and the two *Anas* ducks. (3) The African rosy-faced lovebird (*Agapornis roseicollis*) was assumed to take the place of the African genus *Poicephalus* in the original scheme. The barred parakeet (*Bolborhynchus lineola*) replaced another Central American genus (*Brotogeris*). (4) The spinifex pigeon (*Geopheps*) replaced *Chalaeophaps* in the original scheme based on their geographical proximity. (5) *Hesperiphona* replaced *Pinocola*, as they belong to the same tribe.

Comparisons of Orders

To decide whether the relationship of the main variables (i.e., \dot{V}_{O_2} , \dot{V}_E , V_T , and f) to body mass differed between the orders

Table 1: Respiratory variables of birds and their phylogenetic affinities

Birds	Mass (kg)	\dot{V}_{O_2} (mL min ⁻¹)	\dot{V}_E (mL min ⁻¹)	V_T (mL)	f (min ⁻¹)	T_b (°C)	T_a (°C)	P_{O_2} (mmHg)	Source
Struthioniformes:									
Struthionidae:									
Emu (<i>Dromaius novaehollandiae</i>)	40.7	111.7	3,980	846.0	4.7	38.0	25	...	Maloney and Dawson 1994
Ostrich (<i>Struthio camelus</i>)	88	415.0	7,200 ^a	1,200.0	6.0	40.0	20	159	Schmidt-Nielsen et al. 1969
Galliformes:									
Odontophoridae:									
Bobwhite (<i>Colinus virginianus</i>)	.199	4.6	135	3.1	45.0	41.2	19	143	Boggs and Kilgore 1983
Phasianidae:									
Domestic fowl (<i>Gallus gallus</i>)	1.9	27.0 ^b	590	29.3	20.5	41.6	20	159	Kassim and Sykes 1982; Gleeson 1985
Pheasant (<i>Phasianus colchicus</i>)	1.133	...	307	35.8	8.4	41.0	22	158	Boggs and Birchard 1983
Chukar (<i>Alectoris chukar</i>)	.475	6.5	150	6.44 ^a	23.3	40.4	30	159	Chappell and Bucher 1987
Blue-breasted quail (<i>Coturnix chinensis</i>)	.043	1.30 ^b	24	.35	68 ^a	159	Bernstein 1970 in Lasiewski and Calder 1971
Anseriformes:									
Anatidae:									
Mute swan (<i>Cygnus olor</i>)	9.7	109.6	1,579	533.5	3.1	39.5	18	159	Bech and Johansen 1980
Canada goose (<i>Branta canadensis</i>)	4.2	42.0	1,680	109.2	12.0	...	22	160	Funk et al. 1989
Barheaded goose (<i>Anser indicus</i>) ^c	2.36	50.2	791	66.7	11.8	42	15	146	Fedde et al. 1989
Domestic goose (<i>Anser anser</i>)	5	44.8	1,700	157.0	14.0	40.6	22	158	Scheid et al. 1989
Muscovy duck (<i>Cairina moschata</i>)	2.160	50.0	700	69.0	10.5	40.0	22	147	Jones and Holeton 1972
Black duck (<i>Anas rubripes</i>)	1.018	18.7	627	24.0	27.2	...	22	157	Berger et al. 1970
Pekin duck (<i>Anas platyrhynchos</i>)	2.438	44.3	938	79.3	14.0	40.8	22	146	Colacino et al. 1977; Jones and Holeton 1972; Black and Tenney 1980; Kiley et al. 1985
Psittaciformes:									
Psittacidae:									
Rosy-faced lovebird (<i>Agapornis roseicollis</i>)	.048	1.8	33	.95	36.2	40.4	25	158	Bucher and Morgan 1989
Barred parakeet (<i>Bolborhynchus lineola</i>)	.056	1.9	42	1.5	28.6	40.8	24	159	Bucher 1981
Green-cheeked parrot (<i>Amazona viridigenalis</i>)	.342	7.4	97	6.5	15.1	41.3	20	159	Bucher 1985
Trochiliformes:									
Trochilidae:									
Hummingbirds (<i>Selasphorus</i> spp.) ^d	.004	.55	8	.03	173.4	34.8	20	158	Bucher and Chappell 1989
Strigiformes:									
Strigidae:									
Common barn owl (<i>Tyto alba</i>)	.448	7.3	137	12.6	11.5	39.8	20	159	Souza 1988
Burrowing owl (<i>Speotyto cunicularia</i>) ^c	.163	3.6	95	2.9	31.6	39.8	20	159	Boggs and Kilgore 1983; Souza 1988
Western screech owl (<i>Otus kennicottii</i>)	.144	3.2	57	2.2	25.5	39.8	20	159	Souza 1988

Table 1 (Continued)

Birds	Mass (kg)	\dot{V}_{O_2} (mL min ⁻¹)	\dot{V}_E (mL min ⁻¹)	V_T (mL)	f (min ⁻¹)	T_b (°C)	T_a (°C)	Po ₂ (mmHg)	Source
Great horned owl (<i>Bubo virginianus</i>)	1.014	11.2	245	21.6	11.3	39.6	20	159	Souza 1988
Caprimulgidae:									
Poorwill (<i>Phalacroptilus nuttallii</i>)	.035	1.1	30	.90	34.0	39.5	20	159	Withers 1977
Columbiformes:									
Columbidae:									
Pigeon (<i>Columba livia</i>) ^c	.372	7.8	209	7.3	25.7	40.9	22	143	Bouverot et al. 1976; Williams et al. 1995
Spinifex pigeon (<i>Geophaps plumifera</i>)	.089	1.8	49	1.3	37.0	41.2	30	158	Withers and Williams 1990
Gruiformes:									
Rallidae:									
Euro coot (<i>Fulica atra</i>)	.398	7.2	199	10.0	20.0	39.3	20	159	Brent et al. 1984
Gruidae:									
Demoiselle crane (<i>Anthropoides virgo</i>)	2.2	...	1,205	48.6	24.8	39.5	24	146	Prange et al. 1985
Common crane (<i>Grus grus</i>)	4.550	...	1,784	198	9.3	39.4	24	146	Prange et al. 1985
Manchurian crane (<i>Grus japonensis</i>)	7.3	...	2,779	312.2	8.9	40.1	24	146	Prange et al. 1985
Grey crowned crane (<i>Balearica regulorum</i>)	4.6	...	2,477	101.6	24.1	38.9	24	146	Prange et al. 1985
Ciconiiformes:									
Laridae:									
Kelp gull (<i>Larus dominicanus</i>)	.980	21.1	520	29.0	19.1	41.0	20	158	Morgan et al. 1992
South polar skua (<i>Catharacta maccormicki</i>)	1.250	24.5	501	46.4	11.0	40.9	20	158	Morgan et al. 1992
Falconidae:									
American kestrel (<i>Falco sparverius</i>)	.113	3.6	63	2.1	31.9	40.4	20	159	Souza 1988
Prairie falcon (<i>Falco mexicanus</i>)	.627	7.6	149	10.9	14.2	40.5	20	159	Kaiser and Bucher 1985
Accipitridae:									
Red-shouldered hawk (<i>Buteo lineatus</i>)	.573	7.8	167	8.5	20.0	40.5	20	159	Souza 1988
Red-tailed hawk (<i>Buteo jamalensis</i>)	1.127	11.1	232	18.2	12.9	41.1	20	159	Souza 1988
Phoenicopteridae:									
Flamingo (<i>Phoenicopterus ruber</i>)	2.210	37.9	845	89.3	9.6	39.5	30	159	Bech et al. 1979
Spheniscidae:									
Little penguin (<i>Eudyptula minor</i>)	.987	11.9	219	23.5	8.6	38.5	20	159	Stahel and Nicol 1988; Johannesen and Nicol 1990
Adelie penguin (<i>Pygoscelis adeliae</i>)	4.007	44.9	751	101.4	7.8	39.3	0	158	Chappell and Souza 1988
Procellariidae:									
Storm petrel (<i>Oceanites oceanicus</i>)	.034	1.6	78	.93	81.8	39.0	20	158	Morgan et al. 1992
Giant petrel (<i>Macronectes giganteus</i>)	3.929	48.7	1,087	54.0	20.8	38.2	20	158	Morgan et al. 1992
Passeriformes:									
Corvidae:									
Fish crow (<i>Corvus assifragos</i>)	.274	8.5	223	8.2	27.3	...	20	159	Bernstein and Schmidt-Nielsen 1974

White-necked raven (<i>Corvus cryptoleucus</i>)	.480	17.0	340	10.5	32.5	42.2	22	...	Hudson and Bernstein 1981, 1983
Black-billed magpie (<i>Pica pica</i>) ^c	.165	8.9	155	3.0	52.4	41.0	24	143	Boggs et al. 1997
Hirundinidae:									
Bank swallow (<i>Riparia riparia</i>)	.014	.60	11	.09	121.8	...	20	143	Colby et al. 1987
Barn swallow (<i>Hirundo rustica</i>) ^c	.016	2.3	43	.55	79.5	40.8	25	143	Williams et al. 1995
Passeridae:									
Zebra finch (<i>Taeniopygia guttata</i>) ^c	.013	1.5	31	.35	89.8	41.5	22	143	Williams and Kilgore 1992
Fringillidae:									
Rosy finch (<i>Leucosticte arctoa</i>)	.025	1.5	25	.60	41.0	41.2	20	159	Clemens 1988
House finch (<i>Carpodacus mexicanus</i>)	.020	1.0	15	.40	38.0	40.2	20	159	Clemens 1988
Evening grosbeak (<i>Hesperiphona vespertina</i>)	.059	2.4	80	.85	95.0	...	22	158	Berger et al. 1970

Note. $\dot{V}O_2$ at STPD, other volumes at T_b , ambient pressure, and saturated.

^a Calculated from other ventilation variables.

^b $\dot{V}O_2$ taken from Bennett and Harvey (1987) and corrected to body mass given here assuming $\dot{V}O_2 \propto M^{0.75}$.

^c Timing data.

^d Broad-tailed (*Selasphorus platycercus*) and rufous (*Selasphorus rufus*).

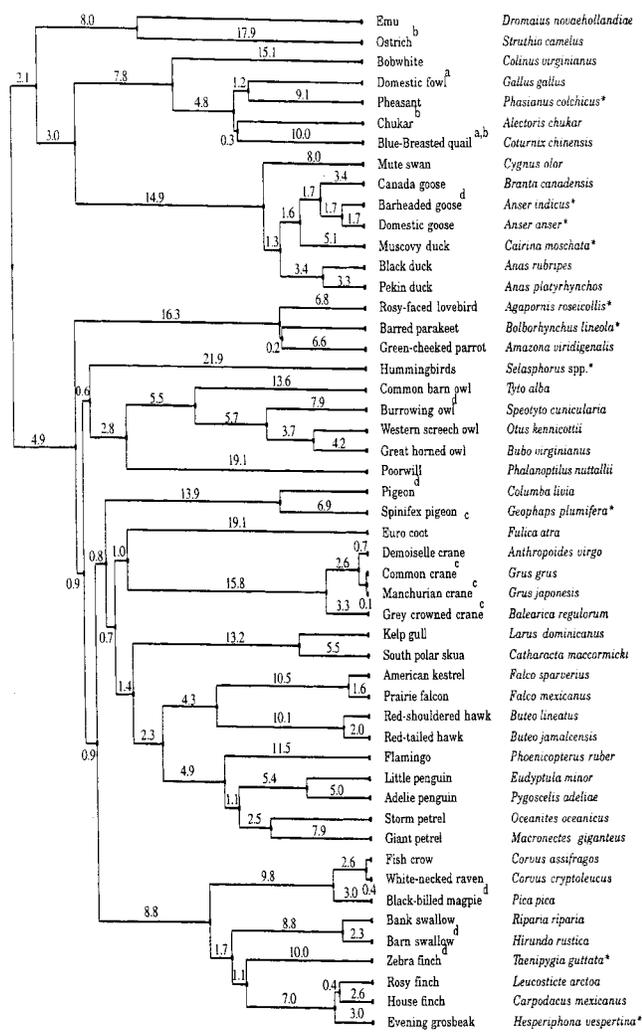


Figure 1. Hypothesized phylogenetic relationships for 50 bird species that are included in this analysis of respiratory variables. Branch lengths are $T_{50}H$ values based on DNA-DNA hybridization work (Sibley and Ahlquist 1990). *Selasphorus* spp. are broad-tailed and rufous (*Selasphorus platycercus* and *Selasphorus rufus*). Superscript letters indicate the following: a, $\dot{V}O_2$ taken from Bennett and Harvey (1987) and corrected to body mass given here assuming $\dot{V}O_2$ is proportional to $M^{0.75}$; b, ventilation variable calculated from other variables; c, no $\dot{V}O_2$ data; d, timing data. An asterisk indicates assigned by authors since genera not listed in Sibley and Ahlquist (1990) or Reynolds and Lee (1996).

of birds, stepwise multiple regression determined by the method of least squares was used. Each order containing more than one species of bird was assigned a unique dummy variable (Kleinbaum and Kupper 1978) consisting of columns of 0s with a single 1 to appropriately distinguish each species (e.g., order 1 = 100 000 000, order 2 = 010 000 000). The entry criteria for selection of significant variables was $P = 0.05$, and the sig-

nificance of the partial correlation coefficients was determined using a t -test (Zar 1984).

For the phylogenetic analysis, independent contrasts were computed for each of the unique dummy variables distinguishing each order. Stepwise regression through the origin was then used to test for the influence of order on each variable, with the standardised contrasts of log variable (e.g., V_T) as the dependent variable and the standardised contrasts of log body mass and order as the independent variables.

Results

Traditional Approach

Ventilatory variables and body mass of the 50 species of birds analysed cover a body mass range of four orders of magnitude (0.0036–88 kg); individual species and their data are given in Table 1. The slopes of the lines relating the main ventilatory variables to body mass (Fig. 1), that is, the exponents of the allometric equations (Table 2), are similar to those first presented for birds by Lasiewski and Calder (1971). However, there have been significant changes in some of the intercepts.

The effect of body mass on $\dot{V}O_2$ in the 45 species reported here (Table 2; Fig. 2A) is the same as that determined in 72 and then 254 species in which the measurement was made on resting, undisturbed birds in the zone of thermoneutrality (Lasiewski and Dawson 1967; Reynolds and Lee 1996). The 95% confidence limits presented here enclose the slopes presented in these previous analyses. However, at any body mass, our equation predicts a higher $\dot{V}O_2$ than do these basal metabolic equations (~40% at 1 kg); our 95% confidence limits do not include the earlier intercepts. This is not surprising since the data were taken for resting values and not under as controlled conditions as basal metabolic measurements are usually made. The barn swallow exhibited an exceedingly high $\dot{V}O_2$ (2.3 times expected), and its value, in the traditional sense, is considered an outlier (i.e., a value outside ± 2 standardised residuals; Fig. 2A, triangle). If the barn swallow is removed, then other species become outliers. Their subsequent removal resulted in yet other outliers, and this process was continued until finally no more outliers emerged. Since the removal of the outliers did not change the intercept or slope outside the confidence intervals obtained when including all of the birds, we have presented only the first equation obtained with all the data presented (Table 1). This is also the case for all of the respiratory variables examined below.

V_T is related to body mass (Table 2; Fig. 2B) in a similar fashion as that derived from fewer species in earlier analyses (Lasiewski and Calder 1971; Maloney and Dawson 1994). It is interesting to note that while the 95% confidence limits determined in this study overlap the exponent from earlier analyses, they are significantly higher than unity, as expected for the relationship of volumes in general to body mass (Calder 1984). At the same body mass, our equation predicted a similar

Table 2: Traditional and phylogenetically corrected relationships between avian respiratory variables and body mass (M)

Respiratory Variables	Equation	N^a	% r^2	s_{yx}	s_b	s_a	95% Confidence Limits	
							Intercept	Slope
Traditional allometry:								
\dot{V}_{O_2} (mL min $^{-1}$)	$16.3M^{.68}$	45	95	.16	.03	.03	14.5–18.4	.63–.73
\dot{V}_E (mL min $^{-1}$)	$386M^{.72}$	50	94	.18	.03	.03	340–438	.67–.78
V_T (mL)	$22.9M^{1.08}$	50	97	.17	.03	.03	20.3–25.9	1.02–1.13
f (min $^{-1}$)	$17.0M^{-.34}$	50	76	.18	.03	.03	15.0–19.3	–.39 to –.29
T_I (s)	$1.2M^{.33}$	6	96	.07	.03	.04	.9–1.5	.23–.42
T_E (s)	$1.9M^{.40}$	6	92	.11	.06	.07	1.2–2.9	.24–.56
T_{TOT} (s)	$3.1M^{.37}$	6	95	.08	.04	.05	2.2–4.3	.25–.50
V_T/T_I (mL s $^{-1}$)	$18.1M^{.63}$	6	99	.07	.03	.04	14.0–23.3	.53–.72
\dot{V}_E/\dot{V}_{O_2}	22.7	45	20.5–25.0	...
Phylogenetically corrected:								
\dot{V}_{O_2} (mL min $^{-1}$)	$15.4M^{.68}$	44	8405	.13	8.7–27.6	.59–.78
\dot{V}_E (mL min $^{-1}$)	$351M^{.71}$	49	8604	.12	199–617	.63–.79
V_T (mL)	$20.3M^{1.06}$	49	9005	.15	10.0–41.3	.96–1.17
f (min $^{-1}$)	$17.1M^{-.35}$	49	4805	.16	8.3–35.2	–.45 to –.24
T_I (s)	$1.2M^{.31}$	5	9404	.05	.9–1.6	.20–.42
T_E (s)	$1.8M^{.35}$	5	8607	.09	1.4–3.5	.02–.50
T_{TOT} (s)	$3.0M^{.33}$	5	9105	.07	2.0–4.6	.18–.48
V_T/T_I (mL s $^{-1}$)	$17.8M^{.61}$	5	9804	.05	12.9–24.4	.49–.72

Note. Body mass in kilograms. s_{yx} = standard error for the regression; s_b = standard error of the slope; s_a = standard error of the intercept.

^a For “traditional allometry,” N = number of birds species; for “phylogenetically corrected,” N = number of independent contrasts (number of bird species – 1).

value to that of Maloney and Dawson (1994), but it is higher (65% at 1 kg) than that based on the six species from the earliest analysis (Lasiewski and Calder 1971). In our analysis, three species had outlier values that were markedly reduced below (~60%) that predicted based on their body mass (ostrich, blue-breasted quail, bank swallow).

The equation determined in this study predicted a similar f at a given body mass (Fig. 2C) as that expected based on 26 species (Calder 1968). Predictions from both this equation and that of Calder (1968) are higher (26% at 1 kg) than predictions from the data set chosen on the basis of minimal frequency (Maloney and Dawson 1994). Equations in our analysis, as noted earlier, are not based on minimal frequencies but rather on overall resting, steady state ventilations as exhibited by plateaus in both f and V_T as well as \dot{V}_{O_2} (see “Discussion”). Outlier frequencies are exhibited by the grey crowned crane and Manchurian crane, with the former being elevated (2.4 times) and the latter being depressed (0.4 times) relative to that predicted based on their body mass.

\dot{V}_E , the product of V_T and f , is related to body mass with the same exponent as is \dot{V}_{O_2} (Table 2; Fig. 3A) and with a value similar to those derived on six and then 22 species (Lasiewski and Calder 1971; Maloney and Dawson 1994). Again, our equa-

tion predicted a higher \dot{V}_E for a bird of the same body mass (~35% at 1 kg). We attribute this to the inclusion of more species and to not selecting data at minimal f as did Maloney and Dawson (1994). Both the storm petrel and barn swallow exhibited outlier values that are elevated greatly over those expected (~2.3 times).

The ratio \dot{V}_E/\dot{V}_{O_2} is mass independent (Fig. 2D) as predicted since both variables are related to body mass with similar exponents (~0.7). The ratio averages 22.7 and ranges from 13.3 in the green-cheeked parrot to 48.9 in hummingbirds (Fig. 2). Both the hummingbirds and Canada goose, with a ratio of 40, fall above the 95% confidence intervals for individuals. The average ratio is similar to the 25.1 predicted for a 1-kg bird from the allometric relationships for \dot{V}_E and \dot{V}_{O_2} provided in Lasiewski and Calder (1971).

Time (s) of inspiration (T_I) and expiration (T_E) is only available for six species of birds. These are listed here in the same order as they appear in Table 1 (values are for T_I and T_E , respectively): barheaded goose, 1.88, 3.30; burrowing owl, 0.60, 0.90; pigeon, 0.74, 1.31; black-billed magpie, 0.59, 0.60; barn swallow, 0.35, 0.41; and zebra finch, 0.29, 0.37 (other data as in Table 1 with the source being the same or the first one listed).

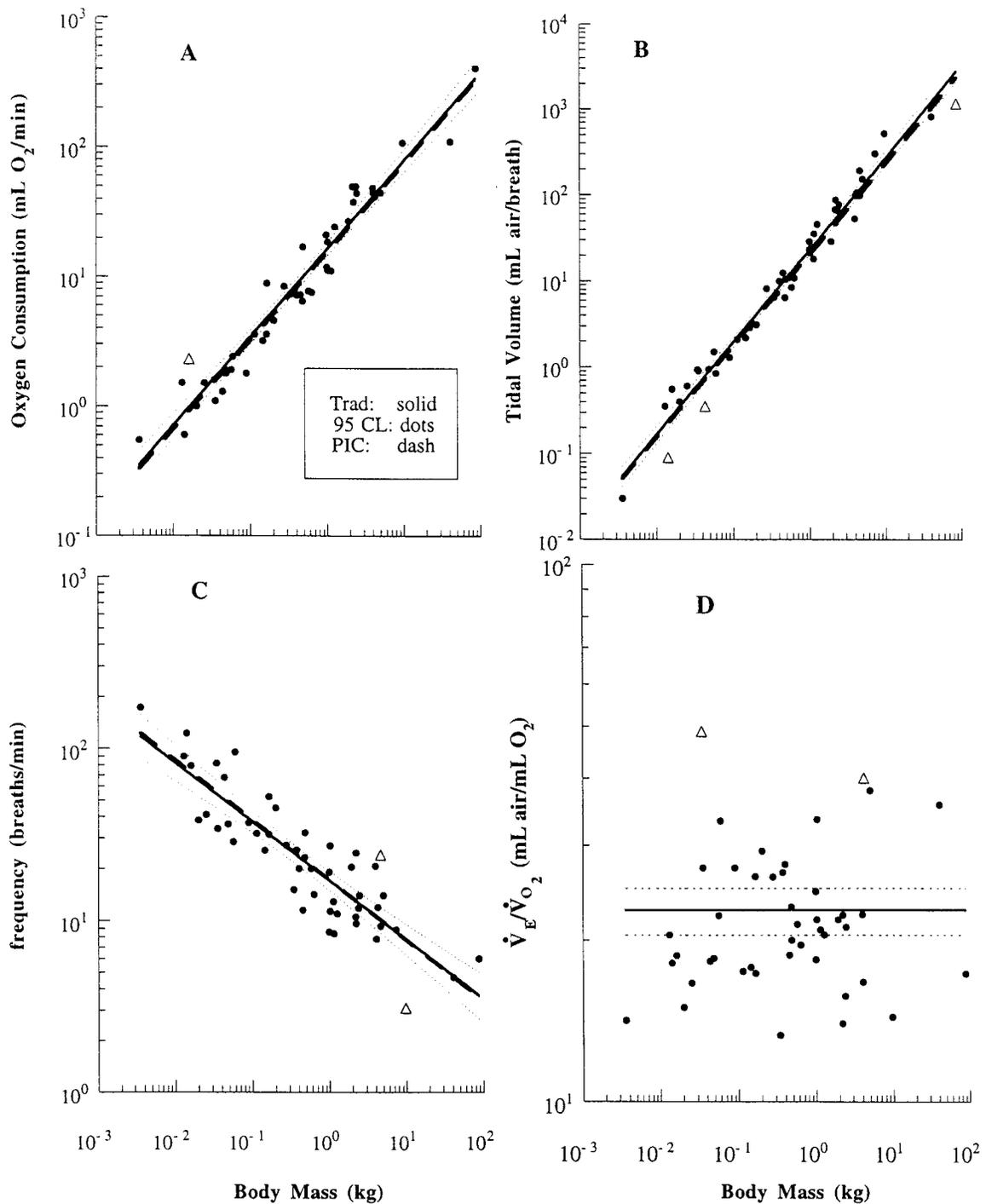


Figure 2. Relationship of ventilatory variables to body mass in birds. Variables include \dot{V}_{O_2} (A, 45 species), V_T (B, 50 species), f (C, 50 species), and \dot{V}_E/\dot{V}_{O_2} (D, 45 species). The latter relationship is mass independent. Solid and dashed lines are based on the current data obtained from traditional allometric statistics (*Trad*) and from phylogenetically independent contrasts (*PIC*), respectively. The dotted lines are the 95% confidence intervals (*CL*) for the traditional equation. The open triangles represent species (see text) whose ventilation variable falls outside acceptable limits of the traditional equation (outside of ± 2 standardised residuals).

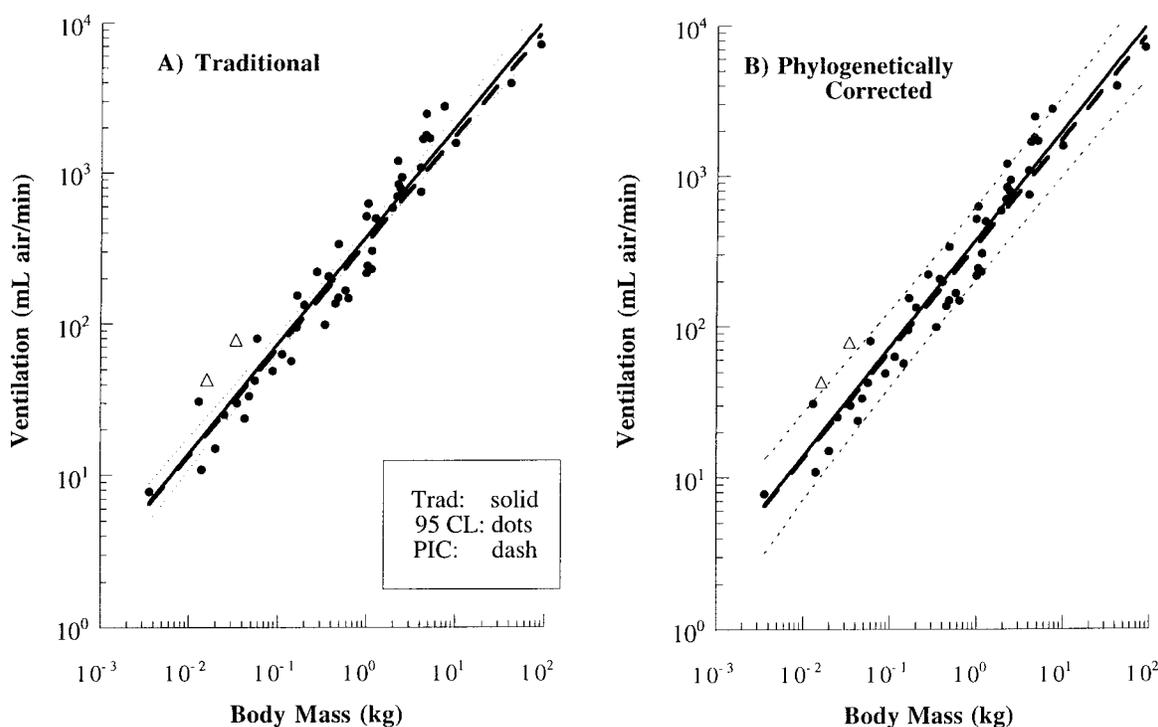


Figure 3. Relationship of \dot{V}_E to body mass in 45 bird species with 95% confidence lines (*dotted*) determined from traditional (A) and from phylogenetically corrected (B) approaches. Solid and dashed lines are based on the current data obtained from traditional allometric statistics (*Trad*) and from phylogenetically independent contrasts (*PIC*), respectively. The dotted lines are the 95% confidence intervals (*CL*) for the traditional equation in A and for the *PIC* equation in B. The open triangles represent species (see text) whose ventilation variable falls outside acceptable limits of the traditional equation (outside of ± 2 standardised residuals).

The timing variables are all affected by body mass in a similar fashion, with an average exponent close to 0.33 (Table 2; Fig. 4). At the same body mass, T_I is $\sim 38\%$ less than T_E . However, because of the small sample in this data set, this difference is not significant as indicated by overlap in the 95% confidence intervals. Both respiratory drive (V_T/T_I) and \dot{V}_{O_2} of these six species are affected by body mass in a similar fashion, with a slope of about 0.6. The slopes for both of these relationships do not differ significantly from that determined for \dot{V}_{O_2} in all 45 species.

Phylogenetically Independent Contrasts

Analyses of the respiratory variables using phylogenetically independent contrasts (PIC) resulted in equations that are very similar to those obtained using traditional means (Table 2). The effect of body mass (slopes) obtained by considering phylogeny was essentially the same as for the traditional approach for all variables considered. The elevation of the relationships varied to a slightly greater degree, with the PIC values typically being lower by 6%–11% if at all. The greatest differences between the traditional and phylogenetically independent analyses

are in the much larger standard errors and wider confidence intervals given by the latter procedure (Table 2). This is illustrated for \dot{V}_E by the distance between the dashed lines in the traditional approach (Fig. 3A) relative to the phylogenetically independent approach (Fig. 3B). For all the variables, the standard error of the slope (s_b) is almost twice as large as that obtained in the traditional procedure, while the standard error of the intercept (s_a) is four to five times greater.

In the analyses of contrasts for \dot{V}_E and V_T , there was a significant negative relationship between the absolute standardised contrast and its standard deviation (PDTREE, screen 2). This typically indicates that the branch lengths should be transformed (Garland et al. 1992). However, this was not done since, in both cases, the negative relationship was caused by a single contrast (described below) with the shortest or near shortest branch length and the largest absolute standardised contrast; removal of the single contrast eliminated the relationship. The short branch length indicates a recent divergence, and the large contrast indicates a large difference in the character.

For \dot{V}_E , the contrast was between the common and Manchurian cranes (*Grus grus*, *Grus japonensis*). Removal of one or the other or both cranes from the PIC regression resulted in

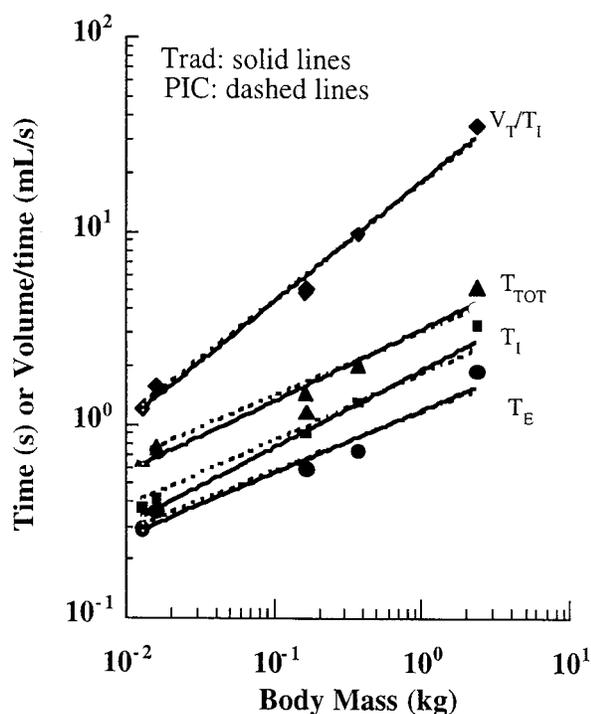


Figure 4. Relationship of respiratory drive (V_T/T_I) and times of inspiration (T_I), expiration (T_E), and total ($T_{TOT} = T_I + T_E$) to body mass as determined with traditional (*solid*) and phylogenetically corrected (*dashed*) approaches in six bird species: barheaded goose (*Anser indicus*), burrowing owl (*Speotyto cunicularia*), pigeon (*Columba livia*), black-billed magpie (*Pica pica*), barn swallow (*Hirundo rustica*), and zebra finch (*Taenipygia guttata*).

equations ($\dot{V}_E \approx 348 \text{ kg}^{0.68}$) that do not differ significantly from that given in Table 2. The decrease in slope (<4%) and in intercept (1%) results in an increase of predicted \dot{V}_E of 17% for the smallest bird (hummingbird, 3.6 g) and a decrease of 13% at the size of the largest bird (ostrich, 88 kg).

For f , the contrast was between the node of the *Grus* ssp. (common and Manchurian cranes) and the Demoiselle crane (*Anthropoides virgo*). Removal of both *Grus* ssp. or removal of only the Demoiselle crane again resulted in equations ($f \approx 17.3 \text{ g}^{-0.31}$) that do not differ significantly from that given in Table 2. The decrease in slope (11%) and increase in intercept (1%) results in a decrease of 18% for the smallest bird and increases of 20% for the largest bird. There was little difference between the phylogenetically corrected and the traditional equations for timing, T_I , T_E , T_{TOT} ($T_{TOT} = T_I + T_E$), or V_T/T_I (see Fig. 4).

Comparison of Orders

Comparison of the magnitude of a variable at a fixed body mass (i.e., intercept or elevation) reveals some differences using

the traditional approach but no differences using PIC. The latter is undoubtedly due to the larger standard deviation inherent in the phylogenetically corrected procedure.

Using the traditional equations and assuming that the slopes of the relationships were the same, V_T varied by the largest amount when comparing the various orders against one another at a fixed body mass of 1 kg (Table 3). The Galliformes are predicted to have a V_T 3.5 times larger than Struthioniformes and 2.3 times larger than birds from the other eight orders. The other eight orders showed no significant differences in V_T , although the single hummingbird was not separately compared to the other groups for this or any of the other variables; it is included in the “Others” group for all variables (Table 3). Testing for difference in slopes for all variables yielded some differences between orders, but the differences did not vary from those obtained assuming slopes were the same.

The f did not vary to the same magnitude as V_T , with Strigiformes being slightly but significantly lower than Psittaciformes and both of these orders falling some 60% below the other eight orders. \dot{V}_E of the Passeriformes and Anseriformes is about 50% above seven of the orders that had similar values. The Gruiformes exhibited the highest \dot{V}_E , which is predicted to be almost 100% higher than the seven similar orders. \dot{V}_{O_2} is similar in eight orders and is elevated the highest in the Anseriformes (54%) and followed closely by the Passeriformes (49%).

Discussion

The Use of the Traditional Equation

In spite of the variability of measurement techniques and conditions, the exponents for \dot{V}_{O_2} and ventilatory variables ana-

Table 3: Multiple regression analysis comparing effect of bird order on the elevations of traditional allometric equations that relate the main respiratory variables to body mass

Order	\dot{V}_{O_2} (mL min ⁻¹) ^a	\dot{V}_E (mL min ⁻¹) ^b	V_T (mL) ^c	f (min ⁻¹) ^d
Others	14.2	313	25.3	18.1
Passeriformes	21.1	464
Anseriformes	21.9	478
Gruiformes	...	621
Struthioniformes	16.9	...
Galliformes	59.4	...
Strigiformes	10.8
Psittaciformes	11.6

Note. Data in Table 1. Values given are those predicted for a 1-kg bird. Slopes (b) were assumed to be the same for all orders. Ordinal data compared only when two or more species were available; thus, Trochilliformes were included but were not separately compared to other groups for any of the variables, and Gruiformes were not compared for \dot{V}_{O_2} .

^a Slope (b) = 0.72.

^b Slope (b) = 0.71.

^c Slope (b) = 1.11.

^d Slope (b) = -0.36.

lysed traditionally in birds are consistent with earlier reports, though the coefficients may differ to a slight extent. Furthermore, the phylogenetically corrected regressions do not give different equations, though they broaden the confidence limits of the slope, suggesting that within a broad phyletic group, in this case the birds, the structural design of the respiratory system shows a general, consistent relationship to body size that is independent of speciation.

The widening of the 95% confidence intervals when phylogeny was incorporated has been previously noted (Reynolds and Lee 1996; Ricklefs and Starck 1996) and is due to properly accounting for the phylogenetic relationships of the species (Martins and Hansen 1997; Garland and Ives 2000). There can be no doubt that the addition of phylogenetic information has been an important conceptual step in comparative analysis by accounting for species relationships in an attempt to guarantee statistical independence. From an evolutionary perspective, this requirement is paramount (Diaz-Uriarte and Garland 1996; Martins and Hansen 1997).

On the other hand, if one is interested in broad generalisations, traditional allometry remains useful to the comparative biologist despite the inherent nonindependence and accompanying narrow confidence limits (Reynolds and Lee 1996). Nevertheless, the widening of the confidence intervals when standard PIC are utilised should act as a deterrent to those using the traditional approach to locate outlying species or clades. This study clearly demonstrates this point; when evaluated with PIC, species previously judged with allometry as outlying no longer departed from predicted values. Even so, while attributing evolutionary or adaptive significance to such outliers is undoubtedly debatable (see Garland and Adolph 1994), it does not negate the biological interest that may be warranted in such species. It should be noted that in the case of standard PIC, the species to be predicted is assumed at an unknown place on the phylogenetic tree. If instead one can say where the new species is placed on the tree, then the predicted intervals become much smaller and can be narrower than those derived from a conventional analysis (see examples in Garland and Ives 2000).

In light of the above discussion, there can be little doubt that traditional equations provide a basis for understanding physiological design by revealing size-independent variables and variables that vary systematically with body size. Such principles of design criteria (reflected in the exponents) have, to date, remained unaltered by the use of PIC. Undeniably, the use of PIC has lent support to the robustness of the design principles originally revealed with allometry. Fundamental differences in system designs as occur between broadly phyletically distinct groups remain reflected in major differences between the coefficients for the relationships between size and various parameters.

Design Criteria of the Avian Respiratory System

We began with the postulate that structural design is the basic determinant of extraction, and extraction will determine the relationship between \dot{V}_E and \dot{V}_{O_2} . Our analysis confirms a lower convection requirement (\dot{V}_E/\dot{V}_{O_2}) in birds (~23) than in mammals (~37; Table 4), supporting the view that birds have greater ability to extract oxygen (Lasiewski and Calder 1971). The ratio \dot{V}_E/\dot{V}_{O_2} determined for either birds or mammals holds despite differences in the coefficients between the traditional equations determined in the various studies relating the primary variables (\dot{V}_E and \dot{V}_{O_2}) and body mass (birds: $\dot{V}_E/\dot{V}_{O_2} = 23$, this study; 25, Lasiewski and Calder 1971; 20, Maloney and Dawson 1994; mammals: 37, Frappell et al. 1992; 35, Stahl 1967). (Maloney and Dawson did not present values for \dot{V}_{O_2} or the necessary primary values to determine \dot{V}_{O_2} from EO_2 . Therefore, we determined \dot{V}_E/\dot{V}_{O_2} for their species using the values for \dot{V}_{O_2} provided here. This seems justified given that the allometric equation for f produced with the data given here for their species did not differ from the equation they calculated [see later].) This further serves to illustrate the strength of the constraints that match supply to demand, in this case \dot{V}_E to \dot{V}_{O_2} .

The lower \dot{V}_E/\dot{V}_{O_2} ratio observed in birds compared with mammals is the result of a reduced \dot{V}_E , itself the result of a slower and deeper breathing pattern, and an increased \dot{V}_{O_2} (Table 4). Differences between the present and earlier studies for birds in the determinants of \dot{V}_E may be due to the criteria used for data selection. Maloney and Dawson (1994) systematically selected the minimal frequency at whatever T_a it could be identified. This criterion is just one suggested by Bucher (1985), who notes the folly of predicting an allometric relationship from two such relationships that have been determined with putative minimum values for each parameter chosen at different temperatures. Given the large influence of temperature on breathing pattern, Bucher is correct in suggesting that resting

Table 4: Comparison of allometric equations for respiratory variables in birds and mammals

Respiratory Variables	Birds ^a	Mammals ^b	Ratio
T_a (°C)	21.6	22.4	.96
T_b (°C)	40.1	36.5	1.10
\dot{V}_{O_2} (mL min ⁻¹)	16.3M ⁶⁸	12.9M ⁷³	1.26M ^{-.05}
\dot{V}_E (mL min ⁻¹)	385M ⁷²	518M ⁷⁴	.74M ^{-.02}
V_T (mL)	22.9M ^{1.08}	10.8M ^{1.01}	2.12M ⁰⁷
f (min ⁻¹)	17M ^{-.34}	49.1M ^{-.26}	.35M ^{-.08}
V_T/T_I (mL s ⁻¹)	18.10M ⁶³	29.00M ⁷	.62M ^{-.07}
T_I/T_{TOT}	.42	.3	1.40
\dot{V}_E/\dot{V}_{O_2}	22.74	37.8	.6
N	45	22	...

^a From this study.

^b From Frappell et al. (1992).

values should be reported to some standard temperature, but a sensible value for one parameter may not be so for another. Examination of Bucher's (1985) data for green-cheeked Amazon parrots illustrates this point. The T_a at which f was minimal (25°C) did not correspond to the T_a at which V_T was minimal (34°C), and at 34°C, f was greatly elevated as a result of heat stress. Nevertheless, both T_a 's were within the thermoneutral range for this species. Rather than rely on a temperature where one parameter was minimal, this study chose values where V_T , f , and $\dot{V}O_2$ all exhibited minimal plateaus. For the green-cheeked Amazon parrot this predominantly occurred for each parameter between 20°C and 30°C; the values at 20°C being representative of the minimal values within this range.

Maloney and Dawson's (1994) use of the minimal frequency resulted in their equation for f predicting lower frequencies than either the equation of Lasiewski and Calder (1971) or our study, which predict similar frequencies. Nevertheless, these two earlier studies determined similar coefficients for \dot{V}_E , the result of similar and lower V_T in the former and latter study, respectively, that were lower than that derived for this study.

It is interesting to note that if the same species as presented by Maloney and Dawson (1994) are selected from our data the resulting allometric equation ($f = 14.2M^{-0.29}$) does not differ significantly from that presented by these authors. This implies that minimal f tends to occur at the same T_a (though T_a was not presented by Maloney and Dawson [1994]) where $\dot{V}O_2$, V_T , and f exhibit minimal plateaus (the selection criteria in our study) but not necessarily the lowest values. Further, it is possible that in an attempt to eliminate possible measurement factors (e.g., restraint or masks) that might alter breathing pattern and elevate f , the V_T 's used by Maloney and Dawson (1994) could be positively biased by restricting the data set only to those collected by whole-body plethysmography (barometric method). In the main, minimal f tends to be associated with warmer temperatures close to the lower critical point of thermal neutrality, and the determination of V_T by the barometric method as defined by Drorbaugh and Fenn (1955) is subject to substantial errors as T_a approaches T_b and if used in association with open-flow plethysmographs (Mortola and Frappell 1998).

Breathing pattern can also change in response to thermoregulatory demands, especially at the warmer temperatures often associated with thermoneutrality. Within a species, while extraction may vary when the ventilatory system is utilised for thermoregulatory functions, it is clear that for endotherms the variation can only be slight because the relationship between \dot{V}_E and $\dot{V}O_2$ is determinant not only of sustained oxygen supply but of carbon dioxide elimination and maintenance of acid-base balance (Mortola and Frappell 2000). Indeed, a change in $\dot{V}O_2$ as a means of reducing respiratory heat and water loss is not observed to be a consistent strategy (Morgan et al. 1992).

Data on respiratory timing characteristics in birds (Table 4) are not yet available for many species, but there are some no-

table features compared to mammals. T_I 's and T_E 's tend to be more nearly equivalent in birds than in mammals, in which T_E is generally longer and is, on average, nearly twice as long as T_I (Boggs and Tenney 1984). The ratios T_I/T_{TOT} and T_E/T_{TOT} were predictable in mammals on the basis of the scaling of f and deflationary time constants. There is little comparative data on the mechanical characteristics of the avian respiratory system; therefore, such an analysis is not possible. In mammals, T_E is not just a function of deflationary time constants as they reflect passive recoil characteristics of the system. Part of the prolongation of expiration in resting mammals can be attributed to braking of the largely passively driven expiratory flow by both postinspiratory diaphragmatic activity and laryngeal adductor muscle activity that increases upper airway resistance. Furthermore, many mammals exhibit end-expiratory pauses at resting/relaxation lung volume. Shortening and ultimately eliminating this pause are the first approaches to increasing respiratory frequency in mammals, as is shortening of the pause or "nonventilatory period" in reptiles (Milsom 1988). The avian ventilatory pump is driven by intercostal muscles (with no diaphragm), and expiration is considered a largely active process more reliant on muscle contraction than elastic recoil since the highly compliant system of air sacs can offer little in that regard. Neither end-expiratory pauses, as observed in mammals, nor end-inspiratory pauses, as observed in reptiles, are seen in birds. This could be a function of mechanics alone but could also reflect the higher $\dot{V}O_2$ of birds than either reptiles or mammals and, hence, a higher sustained respiratory drive.

Despite the fact that birds consume 26% more oxygen yet extract this amount from a 35% lower amount of air passing across the gas exchange surface than mammals, it is interesting to note a common feature of mammalian and avian respiratory control systems. Mammalian respiratory physiologists have long viewed the mean inspiratory flow (V_T/T_I) as an index of respiratory drive in mammals (Milic-Emili and Grunstein 1976). In eutherians (Boggs and Tenney 1984; Frappell et al. 1992) and marsupials (Frappell and Baudinette 1995), V_T/T_I scales with body mass in the same way as metabolic rate. The analysis here (Table 4), limited to six species, also presents the same phenomenon of a common scaling of $\dot{V}O_2$ and V_T/T_I in birds. It would be interesting to determine if this pattern is extended to reptiles and then to identify the nature of the common central neural control mechanisms whose function this consistent pattern may reflect.

In sum, the basic design principles governing the respiratory system as revealed by allometry (i.e., volumes, frequencies, and rates scale in proportion to body mass with exponents of ~ 1 , $-1/4$, and $3/4$, respectively) apply to both birds and mammals. These principles, at least in birds, are further endorsed when phylogeny is considered. Fundamental differences between the two groups are revealed in the coefficients. That is, at any given body mass, birds, with respect to mammals, breathe slower and deeper, have lower ventilation, and have a greater demand for

oxygen. Presumably such differences reflect a radical change in the blueprint of the respiratory system in birds. This system, dependent on rigidity for the development of air capillaries, with a vastly increased surface area and decreased diffusion distance, and with changed mechanical properties compared to mammals, is highly efficient in terms of extracting oxygen.

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Literature Cited

- Bech C. and K. Johansen. 1980. Ventilation and gas exchange in the mute swan, *Cygnus olor*. *Respir Physiol* 39:285–295.
- Bech C., K. Johansen, and G.M.O. Maloiy. 1979. Ventilation and expired gas composition in the flamingo, *Phoenicopterus ruber*, during normal respiration and panting. *Physiol Zool* 52:313–328.
- Bennett A.F. 1973. Ventilation in two species of lizards during rest and activity. *Comp Biochem Physiol* 46A:653–671.
- Bennett P.M. and P.H. Harvey. 1987. Active and resting metabolism in birds: allometry, phylogeny and ecology. *J Zool (Lond)* 213:327–363.
- Berger M., J.S. Hart, and O.Z. Roy. 1970. Respiration, oxygen consumption and heart rate in some birds during rest and flight. *Z Vgl Physiol* 66:201–214.
- Bernstein M. and K. Schmidt-Nielsen. 1974. Ventilation and oxygen extraction in the crow. *Respir Physiol* 21:393–401.
- Bernstein M.H. 1970. The Development of Temperature Regulation in a Small Precocial Bird (Painted Quail, *Excalfactoria chinensis*). PhD diss. University of California, Los Angeles.
- Black C.P. and S.M. Tenney. 1980. Oxygen transport during progressive hypoxia in high-altitude and sea-level waterfowl. *Respir Physiol* 39:217–239.
- Boggs D.F. and G.F. Birchard. 1983. Relationship between haemoglobin oxygen affinity and the ventilatory response to hypoxia in the rhea and pheasant. *J Exp Biol* 102:347–352.
- Boggs D.F., F.A. Jenkins, and K.P. Dial. 1997. The effects of wingbeat cycle on respiration in black-billed magpies (*pica-pica*). *J Exp Biol* 200:1403–1412.
- Boggs D.F. and D.L.J. Kilgore. 1983. Ventilatory responses of the burrowing owl and bobwhite to hypercarbia and hypoxia. *J Comp Physiol* 149B:527–533.
- Boggs D.F. and S.M. Tenney. 1984. Scaling of respiratory pattern and respiratory drive in mammals. *Respir Physiol* 58:245–251.
- Bouverot P., G. Hildwein, and P.H. Oulhen. 1976. Ventilatory and circulatory oxygen convection at 4000 m in pigeon at neutral or cold temperature. *Respir Physiol* 28:371–385.
- Brent R., P.F. Pedersen, C. Bech, and K. Johansen. 1984. Lung ventilation and temperature regulation in the European coot *Fulica atra*. *Physiol Zool* 57:19–25.
- Bucher T.L. 1981. Oxygen consumption, ventilation and respiratory heat loss in a parrot, *Bolborhynchus lineola*, in relation to ambient temperature. *J Comp Physiol* 142B:479–488.
- . 1985. Ventilation and oxygen consumption in *Amazona viridigenalis*: a reappraisal of “resting” respiratory parameters in birds. *J Comp Physiol* 155B:269–276.
- Bucher T.L. and M.A. Chappell. 1989. Energy metabolism and patterns of ventilation in euthermic and torpid hummingbirds. Pp. 187–195 in C. Bech and R. E. Reinertsen, eds. *Physiology of Cold Adaptation in Birds*. Plenum, New York.
- Bucher T.L. and K.R. Morgan. 1989. The effect of ambient temperature on the relationship between ventilation and metabolism in a small parrot (*Agapornis roseicollis*). *J Comp Physiol* 159B:561–567.
- Calder W.A., III. 1968. Respiratory and heart rates of birds at rest. *Condor* 70:358–365.
- . 1984. *Size, Function, and Life History*. Harvard University Press, Cambridge, Mass.
- Chappell M.A. and T.L. Bucher. 1987. Effects of temperature and altitude on ventilation and gas exchange in chukars (*Alectoris chukar*). *J Comp Physiol* 157:129–136.
- Chappell M.A. and S.L. Souza. 1988. Thermoregulation, gas exchange, and ventilation in Adelie penguins (*Pygoscelis adeliae*). *J Comp Physiol* 157B:783–790.
- Clemens D.T. 1988. Ventilation and oxygen consumption in rosy finches and house finches at sea level and high altitude. *J Comp Physiol* 158B:57–66.
- Colacino J.M., D.H. Hector, and K. Schmidt-Nielsen. 1977. Respiratory responses of ducks to simulated altitude. *Respir Physiol* 29:265–281.
- Colby C., D.L. Kilgore, Jr., and S. Howe. 1987. Effects of hypoxia and hypercapnia on tidal volume, frequency, and ventilation of nestling and adult bank swallows. *Am J Physiol* 253:R854–R860.
- Diaz-Uriarte R. and T.J. Garland. 1996. Testing hypotheses of correlated evolution using phylogenetically independent contrasts: sensitivity to deviations from Brownian motion. *Syst Biol* 45:27–47.
- Drorbaugh J.E. and W.O. Fenn. 1955. A barometric method for measuring ventilation in newborn infants. *Pediatrics* 16:81–87.
- Fedde M.R., J.A. Orr, and H. Shams. 1989. Cardiopulmonary function in exercising bar-headed geese during normoxia and hypoxia. *Respir Physiol* 77:239–252.
- Frappell P.B. and R.V. Baudinette. 1995. Scaling of respiratory variables and the breathing pattern in adult marsupials. *Respir Physiol* 100:83–90.
- Frappell P.B. and C.B. Daniels. 1991. Ventilation and oxygen consumption in Agamid lizards. *Physiol Zool* 64:985–1001.

- Frappell P.B., C. Lanthier, R.V. Baudinette, and J.P. Mortola. 1992. Metabolism and ventilation in acute hypoxia: a comparative analysis in small mammalian species. *Am J Physiol* 262:R1040–R1046.
- Funk G.D., I.J. Valenzuela, G.N. Sholomenko, J.D. Steeves, and W.K. Milsom. 1989. Effects of changes in locomotor intensity, hypoxia and hypercapnia on locomotor-respiratory synchrony during walking/running in Canada geese. *J Exp Biol* 147:343–360.
- Garland T., Jr., and S.C. Adolph. 1994. Why not do two species comparative studies: limitations on inferring adaptation. *Physiol Zool* 67:797–828.
- Garland T., Jr., A.W. Dickerman, C.M. Janis, and J.A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. *Syst Biol* 42:265–292.
- Garland T., Jr., and A.R. Ives. 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am Nat* 155:346–364.
- Garland T., Jr., P.E. Midford, and A.R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral values. *Am Zool* 39:374–388.
- Garland T.J., P.H. Harvey, and A.R. Ives. 1992. Procedure for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol* 41:16–32.
- Gleeson M. 1985. Analysis of respiratory pattern during panting in fowl, *Gallus domesticus*. *J Exp Biol* 116:487–491.
- Hudson D.M. and M.H. Bernstein. 1981. Temperature regulation and heat balance in flying white necked ravens *Corvus cryptoleucus*. *J Exp Biol* 90:267–281.
- . 1983. Gas exchange and energy cost of flight in the white-necked raven, *Corvus cryptoleucus*. *J Exp Biol* 103:121–130.
- Johannesen H. and S.C. Nicol. 1990. Effects of cold exposure on oxygen consumption, ventilation and interclavicular air-sac gases in the little penguin (*Eudyptula minor*). *J Exp Biol* 154:397–405.
- Jones D.R. and G.F. Holeton. 1972. Cardiovascular and respiratory responses of ducks to progressive hypocapnic hypoxia. *J Exp Biol* 56:657–666.
- Kaiser T.J. and T.L. Bucher. 1985. The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation, and water loss in relation to ambient temperature in the prairie falcon, *Falco mexicanus*. *Physiol Zool* 58:748–758.
- Kassim H. and A.H. Sykes. 1982. The respiratory responses of the fowl to hot climates. *J Exp Biol* 97:301–309.
- Kiley J.P., F.M. Faraci, and M.R. Fedde. 1985. Gas exchange during exercise in hypoxic ducks. *Respir Physiol* 59:105–115.
- Kleinbaum D.G. and L.L. Kupper. 1978. *Applied Regression Analysis and Other Multivariable Methods*. Duxbury, North Scituate, Mass.
- Lasiewski R.C. and W.A. Calder, Jr. 1971. A preliminary allometric analysis of respiratory variables in resting birds. *Respir Physiol* 11:152–166.
- Lasiewski R.C. and W.R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69:13–23.
- Maddison W.P. 1989. Reconstructing character evolution on polytomous cladograms. *Cladistics* 5:365–377.
- Maloney S.K. and T.J. Dawson. 1994. Ventilatory accommodation of oxygen demand and respiratory water loss in a large bird, the emu (*Dromaius novaehollandiae*), and a re-examination of ventilatory allometry for birds. *J Comp Physiol* 164B:473–481.
- Martins E.P. and T.F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am Nat* 149:646–667.
- Milic-Emili J. and M.M. Grunstein. 1976. Drive and timing components of ventilation. *Chest* 70:S131–S133.
- Milsom W.K. 1988. Control of arrhythmic breathing in aerial breathers. *Can J Zool* 66:99–108.
- Morgan K.R., M.A. Chappell, and T.L. Bucher. 1992. Ventilatory oxygen extraction in relation to ambient temperature in four antarctic seabirds. *Physiol Zool* 65:1092–1113.
- Mortola J.P. and P.B. Frappell. 1998. On the barometric method for measurements of ventilation, and its use in small animals. *Can J Physiol Pharmacol* 76:937–944.
- . 2000. Ventilatory response to temperature changes in mammals and other vertebrates. *Annu Rev Physiol* 62:847–874.
- Prange H.D., J.S. Wasser, A.S. Gaunt, and S.L.L. Gaunt. 1985. Respiratory responses to acute heat stress in cranes (Gruidae): the effects of tracheal coiling. *Respir Physiol* 62:95–103.
- Reynolds P.S. and R.M. Lee III. 1996. Phylogenetic analysis of avian energetics: passerines and nonpasserines do not differ. *Am Nat* 147:735–759.
- Ricklefs R.E. and J.M. Starck. 1996. Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos* 77:167–172.
- Scheid P., M.R. Fedde, and J. Piiper. 1989. Gas exchange and air-sac composition in the unanaesthetised, spontaneously breathing goose. *J Exp Biol* 142:373–385.
- Schmidt-Nielsen K., J. Kanwisher, R.C. Lasiewski, J.E. Cohn, and W.L. Bretz. 1969. Temperature regulation and respiration in the ostrich. *Condor* 71:341–352.
- Sibley C.G. and J.E. Ahlquist. 1990. *Phylogeny and Classification of Birds: A Study in Molecular Evolution*. Yale University Press, New Haven, Conn.
- Sibley C.G. and B.L. Monroe, Jr. 1990. *Distribution and Taxonomy of Birds of the World*. Yale University Press, New Haven, Conn.
- Souza S.L. 1988. *The Effects of Temperature on Metabolism and Ventilation in Several Species of Raptors*. MA thesis. Riverside, University of California.

- Stahel C.D. and S.C. Nicol. 1988. Ventilation and oxygen extraction in the little penguin (*Eudyptula minor*), at different temperature in air and water. *Respir Physiol* 71:387–398.
- Stahl W.R. 1967. Scaling of respiratory variables in mammals. *J Appl Physiol* 22:453–460.
- Tenney S.M. and J.B. Tenney. 1970. Quantitative morphology of cold-blooded lungs: Amphibia and Reptilia. *Respir Physiol* 9:197–215.
- Weibel E.R., C.R. Taylor, and H. Hoppeler. 1998. The concept of symmorphosis: a testable hypothesis of structure-function relationship. *Proc Natl Acad Sci USA* 88:10357–10361.
- Williams B.R., D.F. Boggs, and D.L. Kilgore, Jr. 1995. Scaling of hypercapnic ventilatory responsiveness in birds and mammals. *Respir Physiol* 99:313–319.
- Williams B.R. and D.L. Kilgore, Jr. 1992. Ontogenetic modification of the hypercapnic ventilatory response in the zebra finch. *Respir Physiol* 90:125–134.
- Withers P.C. 1977. Respiration, metabolism, and heat exchange of euthermic and torpid poorwills and hummingbirds. *Physiol Zool* 50:43–52.
- Withers P.C. and J.B. Williams. 1990. Metabolic and respiratory physiology of an arid-adapted Australian bird, the spinifex pigeon. *Condor* 92:961–969.
- Zar J.H. 1984. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, N.J.