

WATER CONTENT, THERMOGENESIS, AND GROWTH RATE OF SKELETAL MUSCLES IN THE EUROPEAN STARLING

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ABSTRACT.—We examined the relationship between function, water content, and growth rate of skeletal muscles in the European Starling (*Sturnus vulgaris*). Function was measured as the ability of nestlings to increase their rate of oxygen consumption in response to cold stress. Water content and growth rate of pectoral and leg muscles were determined for tissues dissected from a series of known-age nestlings. The maximum metabolic response to cold stress increased from 0 at 4 days of age to 4.5–5.5 cm³ O₂·g⁻¹·h⁻¹ at 15–16 days. During this period, the mass of the leg muscles increased 5-fold and that of the pectoral muscles, 12.5-fold. The water fraction (WF) of the pectoral muscles decreased from about 0.86 to 0.72, while that of the leg muscles decreased from 0.83 to 0.72.

Of the variation in metabolic response to cold stress per gram of muscle, 89% could be related to the WF of skeletal muscle by a linear relationship. Over the ages surveyed, the metabolic response varied from 0 at WF = 0.85 to an increase above resting metabolism amounting to 60 cm³ O₂·gram of pectoral and leg muscle⁻¹·h⁻¹ at WF = 0.72. Also during this period, the growth rate of both muscle masses decreased with age and proportion of water, from a mass-specific growth rate of 0.5/day at WF = 0.85 to near 0 at WF = 0.72. If these relationships represent a balance between growth rate and functional maturity in developing tissues, then even small changes in function, associated with a change in water content of only a few percent, could have large consequences for the growth rate of the individual. Received 30 August 1983, accepted 30 November 1984.

In comparisons among species of birds of the same size, the growth rate of chicks varies over an approximately 10-fold range (Ricklefs 1979b). Much of this variation is associated with the mode of development. Chicks of precocial species, which are relatively independent of their parents from an early age, grow more slowly than do those of altricial species, which depend upon their parents for food and warmth during much of their development. Such comparisons, and the observation that mass-specific growth rates of individuals slow as the individual matures functionally, led Ricklefs (1969, 1973, 1979a) to suggest that growth rate is inversely related to functional maturity at the tissue level. As a tissue differentiates and begins to function at an adult level, its proliferation by cell division and growth by cell enlargement decrease. Skeletal muscle provides a model for this constraint in that as mesenchyme cells (myoblasts) of the embryonic muscles differentiate, they fuse to form muscle fi-

bers and cease to proliferate (Holtzer 1970, Cameron and Jeter 1971).

Associated with the maturation of tissues is a decrease in content of water (Ricklefs 1967, 1979a; Bilby and Widdowson 1971; O'Connor 1977; Dunn and Brisbin 1980). In comparisons among species and in comparisons among individuals during development, the water content of a tissue has frequently been used as an index to its differentiation and functional maturity. But in spite of the general association between water content, function, and growth rate, these relationships have not been determined quantitatively. Indeed, Marsh and Wickler (1982) have questioned the use of water content as a suitable index of muscle function.

We examined the relationship between function, water content, and growth rate of skeletal muscles in the European Starling (*Sturnus vulgaris*). Skeletal muscle was chosen for two reasons: first, its pattern of development has been suggested to underlie differences in growth rate (1/time) among species of birds (Ricklefs 1979a, b); second, the function of skeletal muscle can be determined directly by simple physiological measurement. During development, increase in

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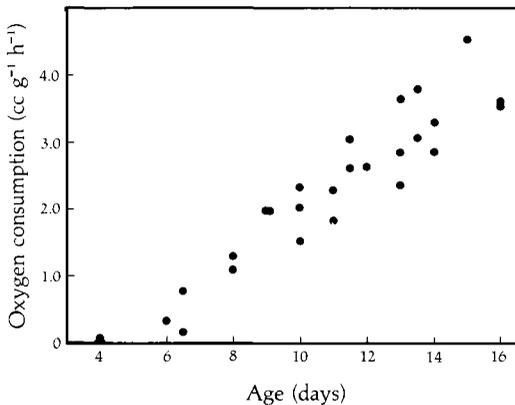


Fig. 1. Relationship between mass-specific oxygen consumption in response to cold stress and age in the European Starling. The rate of oxygen consumption is the difference between the minimum level in the thermoneutral zone and the maximum level obtained under cold stress.

function of skeletal muscle is expressed not only as increased mobility of the chick but also as increased ability to generate heat metabolically by shivering in response to cold stress (King and Farner 1961). In the altricial European Starling, metabolic response to cold is absent at hatching; as we show here, it first appears at 4–6 days of age and increases steadily until, by 12–14 days, the chick is able to maintain a constant body temperature at ambient temperatures of 20°C (Ricklefs 1979a). Concurrently, the water fraction (WF) of the leg and pectoral muscles decreases from between 0.85 and 0.90 at hatching to between 0.70 and 0.75 at fledging, and the mass-specific growth rates of these muscles decrease from between 0.60 and 0.75/day at hatching to near 0 by fledging (Ricklefs 1979a).

In this study, the development of function of skeletal muscle was determined by the elevation of oxygen consumption in response to cold stress. Each subject was sacrificed and its muscles were weighed and analyzed to determine water content. Because metabolic response to cold stress is produced almost entirely by shivering of the skeletal muscle in birds (West 1965, Calder and King 1974), this technique isolates developmental changes in skeletal muscle and allows one to examine the correlations between function, composition, and growth rate.

MATERIALS AND METHODS

Known-age nestling starlings were collected from a nest-box colony located at the Stroud Water Research Center near Kennett Square in southeastern Pennsylvania (Ricklefs and Peters 1979). All nestlings were obtained from first broods during May 1979 and May 1980. Ages of the chicks ranged between 2.5 and 20 days. Most of the nestlings were removed from their nest boxes during the late morning and transported to Philadelphia for metabolism trials. Usually 4–6 h elapsed between collecting the individual in the field and beginning the metabolism trial.

Oxygen consumption was determined in an open-flow system in which compressed dry air (incurrent air) flowed at rates of 60–1,000 cm³/min through chambers in a refrigerated incubator. Excurrent air was passed through a column of Drierite to remove water vapor, a column of soda lime to remove carbon dioxide, and a second column of Drierite. The air stream then passed through a flow meter and was subsequently sampled with a Beckman F-3 oxygen analyzer (span 19–21%). Rate of oxygen consumption (V_{O_2} , cm³/h) was calculated by the equation $V_{O_2} = \text{flow rate (cm}^3/\text{h)} \times (F_I - F_E)/(1 - F_I)$, where F_I and F_E are the fractional oxygen concentrations of the incurrent and excurrent air, respectively (Depocas and Hart 1957). Values were corrected to standard temperature (0°C) and pressure (760 mm Hg).

Metabolism trials were begun at a chamber temperature of 35°C, which was then reduced by approximately 4°C decrements at 30-min intervals until the rate of oxygen consumption reached a peak and started to decline. In 1980, for nestlings older than 9 days, compressed air was replaced at temperatures below 20°C with a mixture of 79% helium and 21% oxygen to increase the conductance of the atmosphere and thus increase cold stress (Rosenmann and Morrison 1974). The lowest temperature of the incubator was -5°C, and even with the helium atmosphere, chicks older than 16 days could not be cold-stressed beyond their maximum metabolic capacity.

For each individual, we recorded the minimum rate of oxygen consumption, presumably obtained within the thermoneutral zone, and the maximum rate of oxygen consumption under cold stress. The difference between the maximum and the minimum was used as an index to the function of skeletal muscle but also included metabolism due to circulation and respiration, which undoubtedly increased in support of muscle activity.

After the end of the metabolism trial, each of the chicks was sacrificed and frozen for later analysis. Upon thawing, we removed the pectoral muscle masses (*pectoralis* and *supracoracoideus*) and the muscles from the femur and tibia of the leg. These tissues were dried to a constant mass at 60°C and then, to remove lipids, they were extracted for 24 h in each

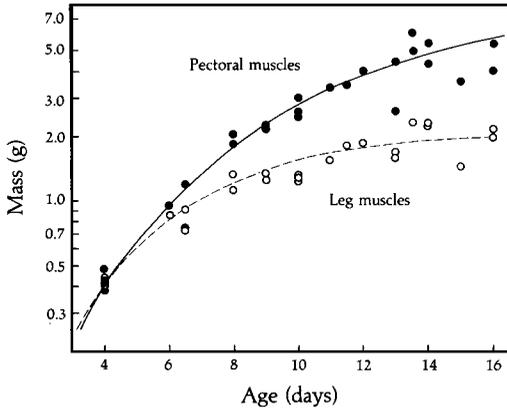


Fig. 2. Relationship between mass of the pectoral and leg muscles and nestling age in the European Starling. The curves are Gompertz equations fitted to the data (see text).

of two successive baths of a 5:1 mixture of petroleum ether and chloroform. In this paper, water content = fresh mass - dry mass; lipid content = dry mass - extracted mass; lipid-free wet mass = fresh mass - lipid; and water fraction = water content/lipid-free wet mass.

Calculations used procedures of the Statistical Analysis System (SAS, Helwig and Council 1979). Particulars of the analyses are given in the Results section.

RESULTS

The minimum level of mass-specific oxygen consumption in the thermoneutral zone was independent of age over the range 4-16 days and varied between 1.6 and 3.3 cm³·g⁻¹·h⁻¹ with an average of 2.43 cm³·g⁻¹·h⁻¹ (0.46 SD, n = 28, 4-16 days). The difference between the maximum and minimum rates of oxygen consumption increased from near 0 at 4 days of age to between 4.5 and 5.5 cm³·g⁻¹·h⁻¹ at 15-16 days (Fig. 1). Oxygen consumption in response to cold stress appeared to increase linearly during this period and undoubtedly would have continued to increase in older nestlings had we been able to achieve lower chamber temperatures in our trials.

Mass of the pectoral muscles increased from approximately 0.4 g to about 5 g, i.e. a 12.5-fold increment, between 4 and 16 days of age (Fig. 2). The leg muscles increased from approximately 0.4 g to 2.0 g, i.e. a 5-fold increment, over the same period. The relationships be-

TABLE 1. Gompertz equations fitted to the relationship between the natural logarithms of the masses of the pectoral and leg muscles and age.

	Coefficients of the Gompertz equation		
	log A	b	K
Pectoral muscle ^a			
Estimate	2.139	5.85	0.164
Standard error	0.146	0.25	0.017
Leg muscle ^b			
Estimate	0.731	4.80	0.272
Standard error	0.065	0.47	0.031

^a Overall regression statistics: F(3,25) = 542, P < 0.0001, R² = 0.98.

^b Overall regression statistics: F(3,25) = 178, P < 0.0001, R² = 0.96.

tween the logarithm of mass (M) and age (t) for each of the muscle masses were described by Gompertz equations, log[M(t)] = log(A) - b exp(-Kt), where A is the asymptote, K the growth-rate constant, and b a constant of age translation (Table 1). These calculations included data from 3 additional individuals, aged 2.5, 18, and 20 days. The mass-specific growth rate is the slope of the relationship between the logarithm of mass and age, that is, dlog(M)/dt = bK exp(-Kt), which decreases as the individual ages.

Water fractions of the leg and pectoral muscles (Fig. 3) decreased linearly over the range 4-16 days; the quadratic term of a second-order polynomial regression was not significant. Equations for the linear regressions were as follows: pectoral muscle, WF = 0.899 (0.011 SE) - 0.01153 (0.00097 SE) t, [F(1,24) = 141, P < 0.0001, R² = 0.85]; leg, WF = 0.868 (0.007 SE) - 0.00908 (0.00066 SE) t, [F(1,24) = 192, P < 0.0001, R² = 0.89].

The variation in muscle mass and proportion of water in muscle among individuals was subjected to a principal components analysis based on the matrix of correlations between 4 variables: pectoral muscle mass, leg muscle mass, water fraction of pectoral muscles, and water fraction of leg muscles (Table 2). Most of the variation in the data (88.6%) was extracted by the first factor, or principal component, and was associated with increases in muscle mass and decreases in water fraction with age. The second factor, which accounted for 8.5% of the variance, revealed a positive association be-

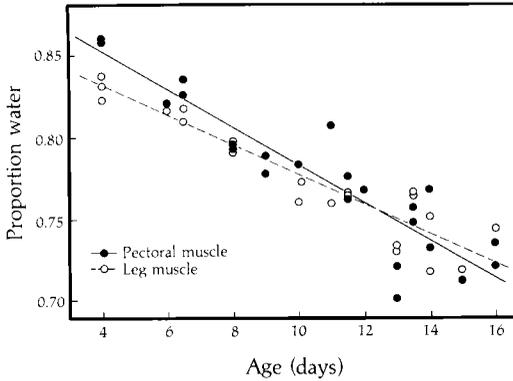


Fig. 3. Relationship between proportion of water in pectoral and leg muscles and nestling age in the European Starling. The lines are linear regressions fitted to the data.

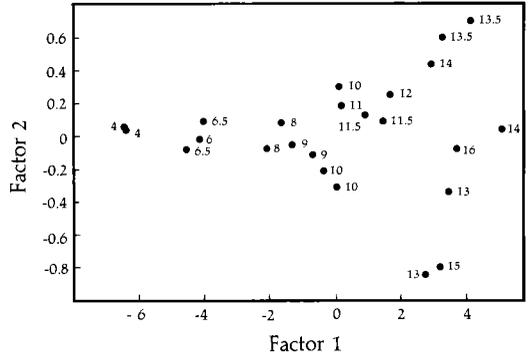


Fig. 4. Distribution of individuals with respect to the first and second factors of a principal component analysis based on the masses and water contents of the legs and pectoral muscles (see text). The number by each data point is the age of the nestling.

tween muscle mass and water fraction. Thus, at one end of factor 2 were individuals that, for their age, had relatively large muscles with high water fractions; at the other end of the scale were individuals with relatively small muscles and low water fractions. Factors 3 and 4 accounted for a negligible amount of the variance in the present analysis.

The distribution of individuals with respect to the first and second factors (Fig. 4) showed that factor 1 was strongly correlated with the age of the chick and that factor 2 represented variation among individuals of similar age, primarily among nestlings older than 9 days. The data suggest that development proceeds relatively uniformly during the first week or so of the nestling period, after which growth trajectories diverge, owing to either intrinsic genetic factors or extrinsic environmental factors, as O'Connor (1977) found for nestling Blue Tits

(*Parus caeruleus*) and House Sparrows (*Passer domesticus*).

Metabolic response to cold stress is related to the total mass of muscle and its function, defined here as the maximum increment in rate of oxygen consumption per gram of pectoral and leg muscle tissue. To relate function to water fraction in muscle tissues, we regressed the increment in rate of oxygen consumption per gram of muscle tissue against *WF* (Fig. 5). The mass-specific increment in rate of oxygen consumption was calculated as the difference between the maximum and minimum rates of oxygen consumption (cm^3/h) divided by the sum of the masses of the leg and pectoral muscles. The water fraction of the muscles is the arithmetic mean of the water fractions of the leg and pectoral muscles. Therefore, *WF* does not weight the two muscle masses according to their relative sizes. However, the water frac-

TABLE 2. Factor analysis of masses and water fractions of leg and pectoral muscles.

	Factor			
	1	2	3	4
Eigenvalues	3.543	0.341	0.084	0.033
Proportion of total	0.886	0.085	0.021	0.008
Factor pattern ^a				
Pectoral mass	0.951	0.263	0.123	0.109
Leg mass	0.936	0.318	-0.117	-0.098
Pectoral water	-0.936	0.300	0.170	-0.069
Leg water	-0.942	0.284	-0.162	0.081

^a Correlation coefficient of each of the original variables with each of the derived factors.

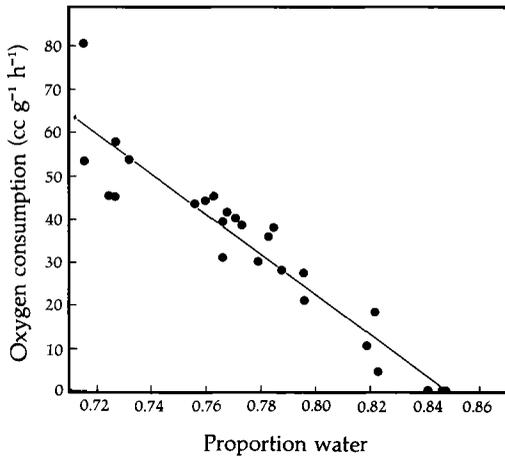


Fig. 5. Relationship between rate of oxygen consumption in response to cold stress per gram of muscle tissue and proportion of water in the muscles. The line is a linear regression fitted to the data (see text).

tions of pectoral and leg muscles of nestlings of a given age are similar, and a different method of averaging the water content would result in little difference in the final result. Metabolic capacity of muscle in response to cold stress and WF were closely related (Fig. 5). The regression equation was $V_{O_2} \text{ (cm}^3 \cdot \text{g}^{-1} \cdot \text{h}^{-1}) = 394 \text{ (26 SE) - 464 (34 SE) WF}$, [$F(1,24) = 188, P < 0.0001, R^2 = 0.89$]. Hence at $WF = 0.72$, approximately that of a 16-day-old starling, the predicted value of V_{O_2} is $60 \text{ cm}^3 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$.

The relationships of oxygen consumption to muscle mass and WF presumably parallel other developmental changes, such as somatomotor innervation and enzyme activities, that may also underlie the increase in metabolism of muscle with age. Among older nestlings, relative sizes of muscles and their water fractions varied sufficiently to examine the relationship of oxygen consumption to these variables without age as a confounding variable. To do so, we compared the residual of oxygen consumption about its trend with respect to age, to the residuals of water fraction and muscle mass about their respective trends with age in a multiple regression. To calculate residuals, the cold-induced increment in oxygen consumption and values of WF of the leg and pectoral muscle were related to age by linear regression; the masses of the leg and pectoral muscles were related to

TABLE 3. Regression of oxygen consumption on mass and water fraction of skeletal muscles based upon residuals about regression of each variable independently with age.

Variable ^a	Estimate	SE	t	P
Intercept (cm ³ O ₂ /h)	-2	7	-0.33	0.74
Pectoral mass (g)	-11	17	-0.66	0.52
Leg mass (g)	-11	44	-0.24	0.81
Pectoral water (g/g)	-1,392	503	-2.77	0.0132
Leg water (g/g)	726	604	1.20	0.25

^a Residuals of masses (g) and water fractions of leg and pectoral muscles. Dependent variable is residual of oxygen consumption (max - min). Overall regression statistics: $F(4,17) = 3.44, P = 0.031, R^2 = 0.45$.

age by Gompertz curves. We refer to the residuals as age-adjusted values.

The statistical relationship between oxygen consumption and the masses and water fractions of the skeletal muscles based upon age-adjusted values is presented in Table 3. Most of the explained sum of squares attributable to the regression model results from age-adjusted values of older rather than younger chicks because the older individuals showed more variability about the trends with age (see Figs. 2-4). Oxygen consumption was significantly related only to the water fraction of the pectoral muscles, with slope $-1,391 \text{ cm}^3 \text{ O}_2/\text{h}$. Divided by the approximately 5 g of muscle in large chicks, the slope becomes $278 \text{ (100 SE) cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, which does not differ significantly from the slope of the relationship between oxygen consumption and WF over age. Muscle mass was not a significant variable in the multiple regression because of its high correlation with WF.

The mass-specific growth rate of the leg and pectoral muscles was evaluated as the derivative of the Gompertz equation relating the logarithm of mass to age. Figure 6 compares this derivative evaluated daily to values taken from the linear regression of average WF vs. age. The specific growth rate of both the leg and pectoral muscles was about 0.35/day at a water content of about 83% (5-6 days). As the proportion of water in the muscles decreased, growth rate declined, to 0.1/day when the water fraction was 0.74 in pectoral muscles and 0.78 in leg muscles.

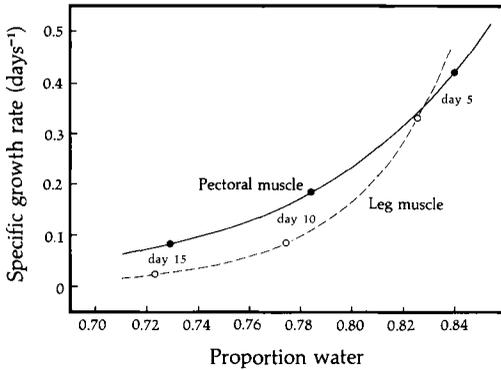


Fig. 6. Relationship between mass-specific growth rate and proportion of water in the pectoral and leg muscles of nestling European Starlings. Values were obtained from equations fitted to the relationship of each of the variables to nestling age.

DISCUSSION

This study revealed several patterns in the development of function in the skeletal muscles of starlings. First, the ability of skeletal muscles to generate heat in response to cold stress, presumably an index to the functional capacity of the muscles, was highly correlated with a decrease in the water content of the muscle tissue between 4 and 16 days of age. Second, the mass-specific growth rate of the leg and pectoral muscles was correlated with the level of water in the tissue, although the relationships for the two groups of muscles differed somewhat. Third, among nestlings of the same age, much of the variation in metabolic response to cold stress was associated with variation in the water fraction of the pectoral muscles.

Trends revealed in starlings during the development period are consistent with comparisons between species having different patterns of development. The water fractions of the legs (entire, without integument) of neonates are approximately 0.87 for altricial species vs. 0.79 for precocial species (Ricklefs 1979b). These values would correspond to mass-specific growth rates of approximately 0.60 and 0.15/day, respectively, if growth rate and water fraction of muscles bore the same relationship in precocial species as in the altricial starling (Fig. 6). The fourfold difference between altricial and precocial species predicted by this relationship is similar to the observed difference in growth

rate constants of chicks of these groups of species (Ricklefs 1979b). In contrast to the leg muscles, the water fractions of the pectoral muscles of neonates are more similar (0.89 in the starling and 0.87 in the quail); the growth rates of pectoral muscles differ much less between the starling and quail than do the growth rates of leg muscles (Ricklefs 1979a).

Muscle mass and metabolic response to cold stress have been measured in one precocial species, the Willow Ptarmigan (*Lagopus lagopus*, Aulie 1976). The metabolic response to cold stress per gram of muscle (leg plus pectoral) increased from $39 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at 1-2 days of age to $55 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at 5-6 days of age and then declined to $34 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ at 7-10 days of age. The decline during the second week of the growth period may have been related to the rapid increase in mass of the pectoral muscles, which initially have low functional capacity compared to the more mature leg muscles; the latter grow relatively slowly after hatching. The maximum metabolic response of the Willow Ptarmigan chick, $55 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, corresponds to an extrapolated muscle water fraction of approximately 0.73 in the starling (Fig. 5). Although this value may be lower than the water fraction of the leg muscles of one-week-old ptarmigan chicks, it is consistent with the parallel differences in water fraction and muscle function between altricial and precocial chicks at an early age. Because the rate of growth of the leg muscles of the ptarmigan chick between 1 and 5 days (0.09/day) is less than that of the pectoral muscles (growth rate, 0.28/day), we would predict a lower WF in the leg muscles, as observed in Japanese Quail (*Coturnix japonica*) during the first week post-hatching (Ricklefs and Marks 1985).

Marsh and Wickler (1982) measured muscle masses, enzyme activities, and metabolic responses to cold in a small passerine bird, the Bank Swallow (*Riparia riparia*). They observed that metabolic response increased abruptly, apparently between 9 and 12 days, while water content (inferred from protein levels) decreased gradually throughout development. From these results, they concluded that water content does not correlate well with muscle function. They did not, however, take into account the rapid increase in the mass of the pectoral muscles at this time and therefore did not evaluate the relationship between metabolic response per gram of muscle and water content

(cf. Fig. 5 in this paper). From their data, we estimated that fully grown nestlings (15 days) have muscle (pectoral + leg) masses of 1.5 g and a net metabolic response to cold stress of $121.5 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$ ($9 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1} \times 13.5 \text{ g}$). This gives a ratio of $81 \text{ cm}^3 \text{ O}_2 \cdot \text{h}^{-1} \cdot \text{gram}$ of muscle tissue⁻¹, which is about a third again as much as that of a starling at a similar stage of development. Such a discrepancy might be expected from the allometric scaling of metabolism to adult body size.

Although there appears to be a general relationship between water fraction and function, it clearly is affected by adult body size (Ricklefs et al. 1985), age (as shown in this study), and probably mode of development and muscle type. These considerations may limit the utility of water fraction as an index of function to comparisons of the same muscle in the same organism or to gross comparisons where the effects of other factors are reduced.

One reviewer of this paper pointed out that because large changes in water content of muscles occur before the onset of thermogenesis, *WF* cannot be used as an index of functional capacity. To clarify this misunderstanding, we emphasize that we have not suggested a causative relationship between *WF* and thermogenic capacity. Water fraction provides an index of development. Many developmental changes occur in muscles prior to the point that they can produce heat by shivering, and these changes also result in a decrease in water fraction. All we suggest here is that *WF* = 0.84 represents the point in this developmental sequence in the starling at which muscles achieve any thermogenic capacity and that heat produced per gram of muscle can be shown to increase linearly with further decrease in *WF*.

We further emphasize that developmental changes in muscle related to thermogenesis may occur without change in *WF*. For example, the water fractions of leg muscles change little during the first three weeks post-hatching in turkeys (Ranaweera and Wise 1982) and the first week in poultry (Draper 1968). During these periods, however, sodium levels decrease and potassium levels increase dramatically, apparently in relation to changes in the resting potential of muscle (Karzel 1968) and perhaps, therefore, to its contractility.

If the correlations between function and growth rate that we have described for starling skeletal muscles constitute constraints upon the

growing organism, then it should be possible to estimate the consequences of earlier or later tissue maturation on postnatal growth. For example, if the muscles of a chick of 8 days of age (*WF* = 0.80, $23 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$) were further differentiated to increase oxygen consumption twofold (*WF* = 0.75, $46 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$), i.e. about the level of an 11–12-day-old chick, the growth rates of the pectoral and leg muscles would decline from 0.23 and 0.16/day to 0.11 and 0.05/day, according to the relationships in Fig. 6. Similarly, increasing the metabolic capacity of a 4-day-old nestling ($4 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, *WF* = 0.84) to that of an 8-day-old nestling ($23 \text{ cm}^3 \text{ O}_2 \cdot \text{g}^{-1} \cdot \text{h}^{-1}$, *WF* = 0.80) would reduce the growth rates from 0.42 and 0.48/day to 0.23 and 0.16/day, i.e. by one-half to two-thirds. These calculations suggest that advancing the thermal independence of nestlings by increasing thermogenic capacity would greatly prolong postnatal development.

Whether or not the relationships described in this paper constitute basic rules of development that must be obeyed by all birds should be determined by investigating the generality of these results through comparative studies on other species with different patterns of development (e.g. Ricklefs 1979a, b). If these relationships do amount to firm rules, then it may be possible to model the development process in detail and determine the effects of evolutionary changes in development pattern on rate of growth and requirement for parental care. Such models may make it possible to interpret variation in these aspects of reproduction among species living in different environments, and to determine the consequences of development pattern for growth and energy requirements of chicks.

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LITERATURE CITED

- AULIE, A. 1976. The pectoral muscles and the development of thermoregulation in chicks of Willow Ptarmigan. *Comp. Biochem. Physiol.* 53A: 343–346.
- BILBY, L. W., & E. M. WIDDOWSON. 1971. Chemical

- composition of growth in nestling blackbirds and thrushes. *Brit. J. Nutr.* 25: 127-134.
- CALDER, W. A., & J. R. KING. 1974. Thermal and caloric relations of birds. Pp. 259-413 in *Avian biology*, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.
- CAMERON, I. L., & J. R. JETER, JR. 1971. Relationship between cell proliferation and cytodifferentiation in embryonic chick tissues. Pp. 191-222 in *Developmental aspects of the cell cycle* (I. L. Cameron, G. M. Padilla, and A. M. Zimmerman, Eds.). New York, Academic Press.
- DEPOCAS, F., & J. S. HART. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption of animals in open-circuit systems and in a short-lag, closed-circuit apparatus. *J. Appl. Physiol.* 10: 388-392.
- DRAPER, M. H. 1968. Changes in mineral and protein content of skeletal muscles from growing chicks. *J. Physiol., Lond.* 196: 85-86.
- DUNN, E. H., & I. L. BRISBIN, JR. 1980. Age-specific changes in the major body components and caloric values of Herring Gull chicks. *Condor* 82: 393-401.
- HELWIG, J. T., & K. A. COUNCIL (Eds.). 1979. *SAS user's guide*, 1979 edition. Cary, North Carolina, SAS Inst.
- HOLTZER, H. 1970. Myogenesis. Pp. 476-503 in *Cell differentiation* (O. Schjeide and J. de Vellis, Eds.). New York, Van Nostrand Reinhold.
- KARZEL, K. 1968. Changes in the resting potentials of growing chicken muscles. *J. Physiol., Lond.* 196: 86-87.
- KING, J. R., & D. S. FARNER. 1961. Energy metabolism, thermoregulation and body temperature. Pp. 215-288 in *Biology and comparative physiology of birds*, vol. 2 (A. J. Marshall, Ed.). New York, Academic Press.
- MARSH, R. L., & S. J. WICKLER. 1982. The role of muscle development in the transition to endothermy in nestling Bank Swallows, *Riparia riparia*. *J. Comp. Physiol.* 149: 99-105.
- O'CONNOR, R. J. 1977. Differential growth and body composition in altricial passerines. *Ibis* 119: 147-166.
- RANAWEERA, K. N. P., & D. R. WISE. 1982. Age associated changes in sodium, potassium and moisture contents of turkey skeletal muscles and a note on the effects of testosterone and 17-B-*oestradiol*. *Brit. Poultry Sci.* 23: 195-198.
- RICKLEFS, R. E. 1967. Relative growth, body constituents, and energy content of nestling Barn Swallows and Red-winged Blackbirds. *Auk* 84: 560-570.
- . 1969. Preliminary models for growth rates of altricial birds. *Ecology* 50: 1031-1039.
- . 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115: 177-201.
- . 1979a. Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. *Auk* 96: 10-30.
- . 1979b. Adaptation, constraint, and compromise in avian postnatal development. *Biol. Rev.* 54: 269-290.
- , D. GABALDON, & W. A. MONTEVECCHI. 1985. Postnatal development of the Northern Gannet (*Sula bassanus*), and the general relationship between growth rate and adult size in birds. *Ornis Scandinavica* in press.
- , & H. L. MARKS. 1985. Anatomical response to selection for four-week body mass in Japanese Quail. *Auk* 102: 323-333.
- , & S. PETERS. 1979. Intraspecific variation in the growth rate of nestling European Starlings. *Bird-Banding* 50: 338-348.
- ROSENMAN, M., & P. MORRISON. 1974. Maximum oxygen consumption and heat loss facilitation in small homeotherms by He-O₂. *Amer. J. Physiol.* 226: 490-495.
- WEST, G. C. 1965. Shivering and heat production in wild birds. *Physiol. Zool.* 38: 111-120.