

Does Growth Rate Determine the Rate of Metabolism in Shorebird Chicks Living in the Arctic?

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ABSTRACT

We measured resting and peak metabolic rates (RMR and PMR, respectively) during development of chicks of seven species of shorebirds: least sandpiper (*Calidris minutilla*; adult mass 20–22 g), dunlin (*Calidris alpina*; 56–62 g), lesser yellowlegs (*Tringa flavipes*; 88–92 g), short-billed dowitcher (*Limnodromus griseus*; 85–112 g), lesser golden plover (*Pluvialis dominicana*; 150–156 g), Hudsonian godwit (*Limosa haemastica*; 205–274 g), and whimbrel (*Numenius phaeopus*; 380 g). We tested two opposing hypotheses: the growth rate–maturity hypothesis, which posits that growth rate in chicks is inversely related to functional maturity of tissues, and the fast growth rate–high metabolism hypothesis, which suggests that rapid growth is possible only with a concomitant increase in either RMR or PMR. We have found no evidence that chicks of shorebirds with fast growth rates have lower RMRs or lower PMRs, as would be predicted by the growth rate–maturity hypothesis, but our data suggested that faster-growing chest muscles resulted in increased thermogenic capacity, consistent with the fast growth–high metabolism hypothesis. The development of homeothermy in smaller species is a consequence primarily of greater metabolic intensities of heat-generating tissues. The maximum temperature gradient between a chick's body and environment that can be

maintained in the absence of a net radiative load increased rapidly with body mass during development and was highest in least sandpipers and lowest among godwits. Chicks of smaller species could maintain a greater temperature gradient at a particular body mass because of their higher mass-specific maximum metabolic rates.

Introduction

Shorebirds, members of Charadriidae and Scolopacidae, migrate long distances in spring, typically arriving on their arctic breeding grounds in early June (Piersma et al. 1996; Schekkerman et al. 2003). After eggs hatch in July, chicks forage for themselves in an environment of relatively low ambient temperatures (T_a), strong winds, and, at times, rain, factors that promote loss of heat (West and Norton 1975; Chappell 1980; Ricklefs and Williams 2003; Schekkerman et al. 2003). Under these circumstances, one might imagine that selection favors rapid development of thermoregulation by chicks to extend foraging time before they return to the parent for brooding (Norton 1973; Krijgsveld et al. 2001). At the same time, the short growing season on the tundra during which insects are available (Schekkerman et al. 2003) imposes selection for rapid growth so that chicks can fledge before inhospitable conditions again prevail (Beintema and Visser 1989; Schekkerman et al. 1998). In support of this latter idea, chicks of arctic shorebirds grow more rapidly than chicks of confamilial species in temperate regions (Beintema and Visser 1989; Schekkerman et al. 1998).

The “tissue allocation hypothesis,” or “growth rate–maturity hypothesis” (Ricklefs 1973, 1979; Ricklefs and Webb 1985; Dietz and Ricklefs 1997; Ricklefs et al. 1998), posits that growth rate in chicks is inversely related to functional maturity of tissues. Skeletal muscle has been a focus of investigation for this hypothesis because muscle constitutes a large proportion of the mass of individual chicks and because its function is closely allied with mobility and thermogenesis, which are prominent markers of functional development. Under this hypothesis, mesenchyme cells of embryonic muscle tissue that have fused and differentiated into mature muscle fibers cannot also divide mitotically. Thus, as functional capacity of the muscle tissue increases, the proportion of embryonic cells decreases, and overall muscle growth slows (Cameron and Jeter 1971; Ricklefs 1979; O'Connor 1984; Broggi et al. 2005). The bellwether of

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support for the growth rate–maturity hypothesis has come from comparisons of growth rate and development of thermoregulation between precocial and altricial young; the latter grow rapidly but cannot thermoregulate until late in the nestling period, whereas precocial chicks grow slowly but maintain their body temperature (T_b) at moderately cold environmental temperatures for long periods, even at early developmental stages (Visser 1991). Moreover, the hypothesis is consistent with the observations that all chicks grow more slowly as development proceeds and that their thermogenic capacity per unit mass increases (Ricklefs and Weremiuk 1977; Ricklefs and Webb 1985; Choi et al. 1993). Taken together, these observations suggest an evolutionary trade-off between conflicting demands on muscle tissue; rapid growth precludes mature muscle function and vice versa. Hence, for arctic-breeding shorebirds, the hypothesis predicts that rapidly growing species will have lower thermogenic capacity than species that grow more slowly. Because skeletal muscles are primarily responsible for the generation of heat during cold stress, investigators have focused on this tissue in their tests of the hypothesis. Testing the growth rate–maturity hypothesis has proved complicated because muscle tissue of various body parts may grow at different rates and because functional maturity, not easily measured in tissue, is often indexed by water content of specific muscle groups (Starck and Ricklefs 1998). Furthermore, skeletal muscle might not be the critical tissue in the growth rate–functional maturity trade-off; bone and nervous system tissues, which are also closely associated with mobility and muscle function, might also constrain the overall growth rate of the chick.

Some authors have noted that hatchlings of arctic shorebirds grow rapidly and also have high levels of resting or field metabolism (Beintema and Visser 1989; Schekkerman et al. 1998), observations difficult to concatenate with the growth rate–maturity hypothesis. Drent and Klaassen (1989) and Klaassen and Drent (1991) argued that selection for rapid growth is intense at high latitudes and that rapid growth is possible among shorebirds only with a concomitant increase in resting metabolism, which might indicate a higher level of mature function. They further speculated that chicks of arctic-breeding species would possess enhanced thermogenic capacity during cold challenge, compared with chicks of temperate species, an attribute vital in surviving periods of cold. In their analyses, they found that day-old hatchlings of northerly-breeding shorebirds had both a faster postnatal growth rate and a higher resting metabolic rate (RMR), both corrected for mass, than did hatchlings of temperate-zone species. The linkage between fast growth and RMR was thought to be a consequence of rescaling of the internal digestive machinery in fast-growing chicks: larger liver, heart, intestines, and kidneys, organs that have high mass-specific rates of oxygen consumption (Krebs 1950; Rolfe and Brown 1997). However, when he eliminated temperate species and reanalyzed the data of Klaassen and Drent for just arctic species, Konarzewski (1994) found no

relationship between growth rate and RMR of neonates. Visser and van Kampen (1991) tested the “fast growth–high RMR” hypothesis on two strains of domestic fowl (*Gallus gallus*), one, selected for high egg production, that had relatively slow chick growth and a broiler strain selected for rapid growth. Individuals of the broiler strain did not have higher RMRs, as would be predicted by the high growth–high RMR hypothesis. Schekkerman et al. (2003) showed that chicks of the red knot (*Calidris canutus*), a species that breeds on the northern arctic tundra, had higher growth rates than chicks of other similar-sized shorebirds and that they had high daily energy expenditure, as measured by doubly labeled water, 89% above allometric predictions.

Because none of these investigators directly measured the peak metabolic rate (PMR) of chicks, support for the presence of both rapid postnatal growth and high functional capacity in arctic shorebirds, compared to their temperate relatives, remains equivocal. A tacit assumption in the fast growth–high RMR hypothesis is that RMR is positively related to PMR. Internal organs contribute significantly to RMR, as Drent and Klaassen suggest, but heat production during cold challenge is a result primarily of muscle tissue (Marsh and Dawson 1989; Hohtola and Visser 1998). Under resting conditions, all tissues are supplied with nearly equal amounts of blood, and consequently oxygen, but during cold exposure, blood is shunted to muscle because shivering requires ATP (Hinds et al. 1993; Hochachka 1994; Weibel and Hoppeler 2005).

We studied the development of temperature regulation, both RMR and PMR, of chicks of seven species of shorebirds, which ranged in neonate size from the least sandpiper (*Calidris minutilla*; mass = 4.0 g) to the whimbrel (*Numenius phaeopus*; 33.5 g), all nesting in the same location on the arctic tundra, and all but one, the lesser golden plover, belonging to the same phylogenetic clade. We tested the hypothesis, consistent with the growth rate–maturity model, that slower-growing chicks would have a higher PMR. In addition, we examined alternative hypotheses of Klaassen and Drent (1991) that rapid growth is possible only with a concomitant increase in resting metabolism and that rapidly growing chicks will have a high PMR. Further, we explored whether muscle growth rate would be positively correlated with increases in RMR and PMR, as predicted by the ideas of Klaassen and Drent, or negatively correlated, as predicted by growth–rate maturity model. A novel aspect of our work was that we continuously measured T_b during measurements on these chicks, allowing us to better understand the relationship between metabolism, T_b , and conductance.

Material and Methods

Study Area and Species

We conducted this study on the arctic tundra during June and July of the years 1995–1997 at the Churchill Northern Studies Centre, Churchill, Manitoba, Canada (58°45'N, 90°00'W), un-

der permit from the Canadian Wildlife Service, Environment, Canada. Species investigated were least sandpiper (*Calidris minutilla*; adult mass 20–22 g), dunlin (*Calidris alpina*; 56–62 g), lesser yellowlegs (*Tringa flavipes*; 88–92 g), short-billed dowitcher (*Limnodromus griseus*; 85–112 g), lesser golden plover (*Pluvialis dominicana*; 150–156 g), Hudsonian godwit (*Limosa haemastica*; 205–274 g), and whimbrel (*Numenius phaeopus*; 380 g; Dunning 1993; Visser and Ricklefs 1993). With the exception of the lesser golden plover (Charadriidae), all of these species are derived from a single radiation event that occurred at the end of the Cretaceous in less than 10 million yr (Paton et al. 2003).

Collection of Eggs; Care of Chicks

We collected eggs from nests on the tundra and transported them to the laboratory, where we placed them in incubators at an ambient temperature (T_a) of $37^\circ \pm 0.5^\circ\text{C}$. After eggs hatched, chicks were placed in small groups in cages (1 m \times 1 m) with a wire mesh bottom and a brooder lamp at one end to provide a range of T_a . They were fed a mixture of freshly caught invertebrates, chopped boiled egg, tuna, and dry food pellets, Pheasant starter type 2, prepared at the Institute for Animal Science and Health, the Netherlands. Vitamins were added to drinking water daily. Over 3 yr, we raised 256 chicks of seven species; juveniles were released on the tundra after measurements were complete. Because captive sandpiper chicks potentially grow more rapidly when exposed to colder outdoor T_a (West and Norton 1975), chicks older than 2 d were placed in 4 \times 4-m outdoor pens for several hours each day so that they could forage on tundra insects and experience their natural environment. The Institutional Animal Care and Use Committee of the University of Missouri–St. Louis approved all field and laboratory protocols.

Chick Growth

Before each metabolism trial, we measured body mass of chicks to the nearest 0.1 g. Growth data were fitted to a Gompertz model of the form $M(t) = A \exp\{-\exp[K_G(t - t_i)]\}$, where A is adult body mass, K_G is the Gompertz growth constant (1/day), proportional to the rate at which body mass approaches the asymptote (Ricklefs 1983; O'Connor 1984), $M(t)$ is body mass at age t , and t_i is the age at the inflection point, attained 36.8% of the way through the growth period. We used a nonlinear curve-fitting program that applied the Marquardt-Levenberg algorithm (Marquardt 1963) to determine parameters that minimize the sum of squares of differences between the dependent variables in the equation and observations.

Because muscle tissue is responsible for oxygen consumption under cold stress (Martin and Fuhrman 1950; Rolfe and Brown 1997; Hohtola and Visser 1998), we explored the relationship between muscle growth and metabolism. As part of an earlier

study, we had available to us measurements of lean dry mass and water content of muscles for laboratory-reared, known-age chicks from the seven species for which we had metabolism data in the present study (R. E. Ricklefs, unpublished data). Rather than kill chicks in our study, we used data from the earlier study to estimate the size and growth rate of muscle tissue. Muscle data included all muscles of one leg and muscles of the entire chest, including both pectoral and supracoracoideus muscles. Muscles were dried at 65°C to constant mass to obtain dry mass, and fat was extracted using a 1 : 5 chloroform–petroleum ether mixture to obtain lean mass. We fitted the data of muscle growth of the leg and chest using a Gompertz model. We expressed percentage of water of muscle tissue as (water content/lean wet mass) \times 100.

Measurement of Oxygen Consumption

To measure oxygen consumption ($\dot{V}O_2$), we manufactured several water-jacketed metabolic chambers of aluminum or stainless steel; chambers varied in volume between 337 and 5,749 mL. All were painted with a flat black interior paint to reduce reflected radiation (Porter 1969). The temperature of each chamber was controlled by a Neslab water bath (RTE-140; $\pm 0.1^\circ\text{C}$). A rubber gasket rendered the lid of each chamber airtight. During experiments, chicks were placed in a chamber on wire mesh above mineral oil and within a cylinder of wire mesh to prevent them from pressing against the sides of the chamber. We removed food from chicks 2 h before measurements. Once the metabolic rate of a chick had been determined, we returned it to its cage and did not measure the same chick until at least 4–5 d later.

An air compressor pushed air through two drying columns, each filled with a layer of Ascarite between two layers of Drierite, and a mass flow controller (3 L/min maximum; Tylan model FC-260) calibrated each year against a 1-L bubble meter (Levy 1964), and then into the metabolism chamber. We varied flow rates, depending on the size of the chick, so that oxygen concentration in the chamber did not fall below 20.5%. In 1995, subsamples of excurrent air passed through columns with a layer of Ascarite between two layers of silica gel, before passing through an Applied Electrochemistry (S-3AII) O_2 analyzer, the latter calibrated with dry CO_2 -free outside air. In 1996 and 1997, excurrent air passed through Teflon tubing to a dew point hygrometer (General Eastern model Hygro M4; calibrated against a National Institute of Standards and Technology standard), allowing measurement of water vapor in the air stream, and then was subsampled for analysis of oxygen concentration. Although we measured total evaporative water loss, these results will be presented elsewhere.

Our protocol consisted of first maintaining the chick at thermoneutral temperatures for 1 h, 35° – 36°C for young chicks and 30° – 32°C for older individuals, and then, during the second hour, when oxygen consumption was constant for at least 10

min, we recorded RMR. We subsequently decreased chamber temperature at a rate of 0.5°C/min, a decline in T_a that was continued until $\dot{V}O_2$ peaked (PMR) and T_b began to decrease sharply (see Ricklefs and Williams 2003). For large chicks, we elicited PMR by conducting “down” protocols with heliox, a mixture of 21% oxygen and 79% helium (Rosenmann and Morrison 1974).

We monitored chick T_b continuously with a “butt-button” constructed by threading a 40-gauge thermocouple wire through a hole in a small plastic disk and cementing the assembly in place at a 90° angle with thread and glue. We added a small bulb of epoxy to the end of the thermocouple to protect internal tissues. After the glue was dry and before measurements, the thermocouple wire was coated with Vaseline and inserted into the cloaca of the chick, 1–2 cm deep, depending on chick size. Feathers around the cloaca were then folded over the plastic disk and attached with cyanoacrylic glue, holding the thermocouple in place during the measurement. At the end of the trial, the plastic disk was detached from feathers using glue remover. We monitored T_b , T_a , dew point, and O_2 concentration of the excurrent air stream continuously with a Campbell CR10 data logger and PC208 software.

In general, when chicks reached their PMR, their T_b was ca. 35°–36°C. To see whether PMR would be higher for a chick with a T_b of 38°–40°C, for 13 trials we equilibrated chicks at thermoneutral temperatures and then immediately filled the chamber jacket with water at 5°C to elicit PMR. This “cold plunge” protocol provided an immediate cold stress to chicks before T_b had decreased. We used this protocol on chicks of least sandpipers, dowitchers, and godwits. These measurements were compared, with ANCOVA, with data for the “down” trials, but we found no significant differences and therefore combined both sets of data for analyses of metabolism and conductance.

Metabolic rate of chicks changed in response to declining T_a , violating steady state assumptions in conventional calculations of $\dot{V}O_2$ (Depocas and Hart 1957; Hill 1972). To estimate peak $\dot{V}O_2$, we calculated an instantaneous rate of oxygen consumption (Bartholomew et al. 1981): $F_{E(\text{eq})} = [F_E(t) - F_E(t-1)]/[1 - e^{(-V \times \Delta t)/V}] + F_E(t-1)$. Here $F_{E(\text{eq})}$ is the fractional equilibrium value of oxygen concentration that would be obtained if no other changes in $\dot{V}O_2$ occurred and $F_E(t)$ and $F_E(t-1)$ are the fractional oxygen concentrations at times t and $t-1$, respectively. The denominator, $1 - e^{(-V \times \Delta t)/V}$, called the Z value (Bartholomew et al. 1981), is the fraction achieved during the interval of the value of the new steady state that is reached in time Δt and is calculated as $Z = [F_E(t) - F_E(t-1)]/[F_{E(\text{eq})} - F_E(t-1)]$. This rate of approach to equilibrium is constant regardless of the magnitude of the initial perturbation and is determined by Δt , flow rate, and effective volume of the chamber (V). An important assumption in the use of instantaneous measurements of $\dot{V}O_2$ is that gases are rapidly mixed within the chamber. To facilitate rapid mixing of gases, we positioned air inlets and outlets at opposite ends of our chambers and placed

one near the top and one toward the bottom. Calculations of effective volumes from empirically derived washout curves of our chambers agreed with actual volumes within 1.5%, indicating that gases were mixing adequately. To calculate $\dot{V}O_2$, we used equation (4a) of Withers (1977), substituting $F_{E(\text{eq})}$ for F_E . To convert $\dot{V}O_2$ into heat production, we employed the factor 20.08 J/mL O_2 (Schmidt-Nielsen 1997); $\dot{V}O_2$ (mL/min) can be converted to watts using $1 \text{ W (J/s)} = 0.335 \text{ mL/min}$.

For data on mass-specific PMR, we fitted a logarithmic function, $\text{PMR/g} = Y_0 + a(1 - e^{-bx})$, where x was the proportion of adult body mass, a the asymptote in PMR/g, and b a scaling factor that describes the rate of approach to the asymptote. We evaluated the derivative of this equation as $Y' = abe^{-bx}$ at 36.8% of adult mass, the point of inflection in the Gompertz growth model, where the fastest absolute growth occurs, and compared this value among species.

Statistics

Rates of metabolism, conductance, and body mass were log transformed before statistical analyses. We compared linear regressions using ANCOVA with species as a fixed effect and log body mass as a covariate. If the interaction term was insignificant, we calculated a common slope and evaluated differences among intercepts. If the interaction term was significant, we followed Zar (1996) for multiple comparisons among slopes and calculated the test statistic $q = b_a - b_b/\text{SE}$, where SE is given by $[(S_{yx}^2)_p/2]^{1/2} \times (1/\text{SS}_a + 1/\text{SS}_b)$, where $(S_{yx}^2)_p$ is the pooled residual mean square and SS represents the sum of squares. For the percent water in muscles of the leg and chest, we used species as the main effect and body mass as covariate. For proportions, we used arcsine transformation before running statistical tests (Zar 1996). Analyses were performed using SAS, version 8.0 (Statistical Analysis System, Cary, NC), and SPSS, version 11.0 (SPSS, Chicago). Means are presented ± 1 SD.

Comparisons across species may or may not require a statistical adjustment for phylogenetic relatedness (Felsenstein 1988; Reeve and Abouheif 1999; Garland et al. 2005; Muñoz-García and Williams 2005). To reduce the complication of comparing species with different ancestries, we chose six species from the same phylogenetic clade, all of which have radiated in a relatively short period of time (Paton et al. 2003). When we tested for phylogenetic signal in our comparisons across species (Abouheif 1999), we found none.

Results

Whole-Organism Growth

Least sandpipers chicks grew most rapidly among the seven species, with a K_G value of 0.178, whereas chicks of whimbrels, with a K_G value of 0.065, grew most slowly (Fig. 1). All curve fits had an r^2 value of >0.97 . The K_G values were negatively related to adult body mass: $K_G = 0.146 - 1.98e^{-4}$ (adult body

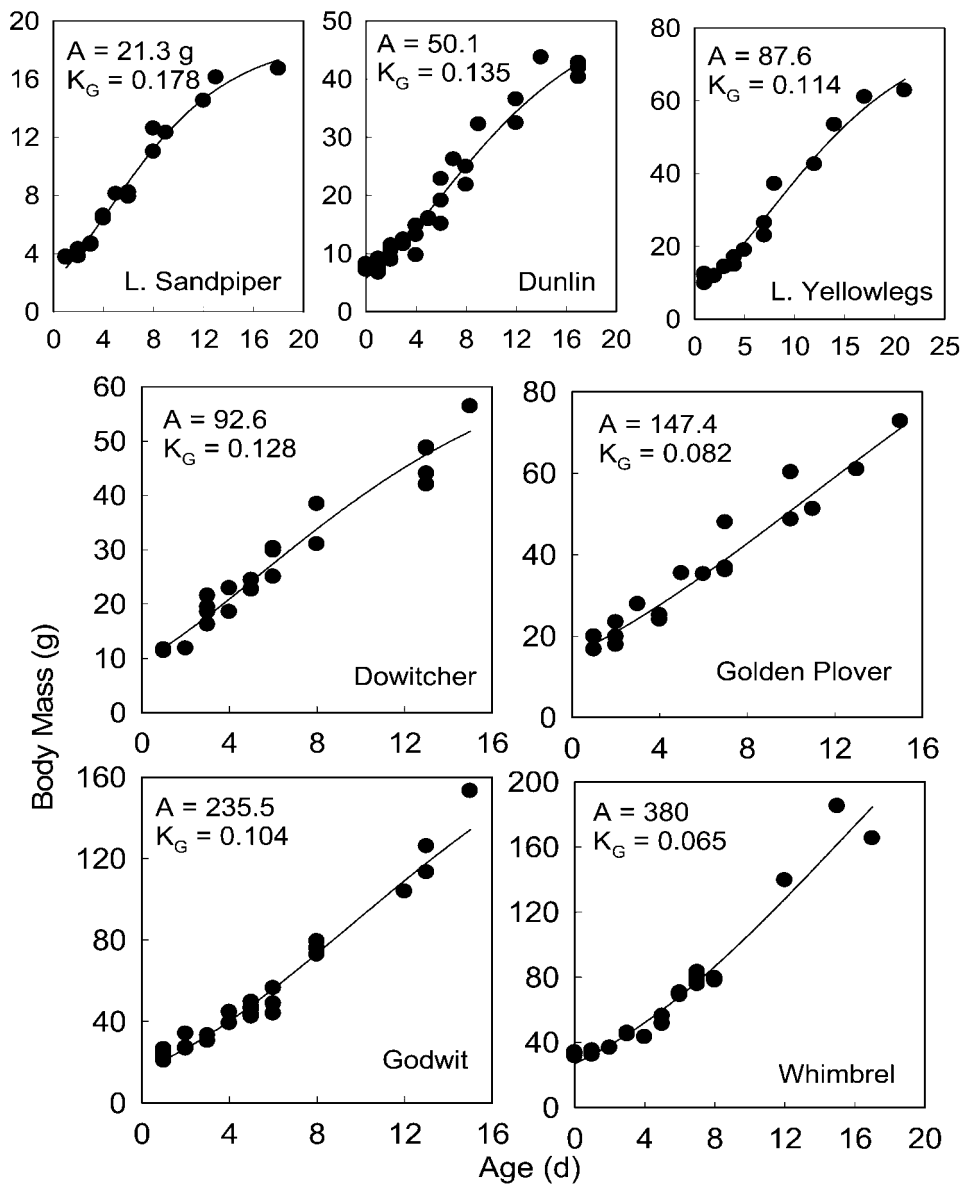


Figure 1. Growth (mass; g) of chicks of seven species of shorebirds relative to age (d). Lines were fitted with a Gompertz model. A = asymptotic mass, K_G = Gompertz growth constant (1/day).

mass, g); $r^2 = 0.65$, $F = 9.4$, $P < 0.03$, $n = 7$ —indicating that smaller species grew more rapidly than did larger species.

Resting Metabolic Rate

During the three years, we made 162 measurements on seven species of shorebird chicks. RMR increased as chicks grew, with rates of increase with respect to mass differing among species; the equations for golden plovers and least sandpipers had the highest slopes, those for dowitchers the lowest (Fig. 2; Table 1). All slopes exceeded 1.0. In an ANCOVA with log RMR as

the dependent variable, species as a main effect, and log mass as a covariate, the interaction term was significant, indicating that species differed in rate of development of RMR relative to body mass (ANCOVA: species $F = 3.1$, $P < 0.007$; intercept $F = 1,196.0$, $P < 0.0001$; log mass $F = 1,320.0$, $P < 0.0001$; species \times log mass $F = 1,320.5$, $P < 0.0001$, $n = 162$). Post hoc comparisons among slopes of the equations for RMR as a function of mass indicated that the slope of the equation for dowitchers, 1.07, differed from those of golden plovers and whimbrels, the highest slopes, 1.47 and 1.42, respectively. Chicks' T_b averaged $39.3^\circ \pm 0.9^\circ\text{C}$ during RMR trials. Although an

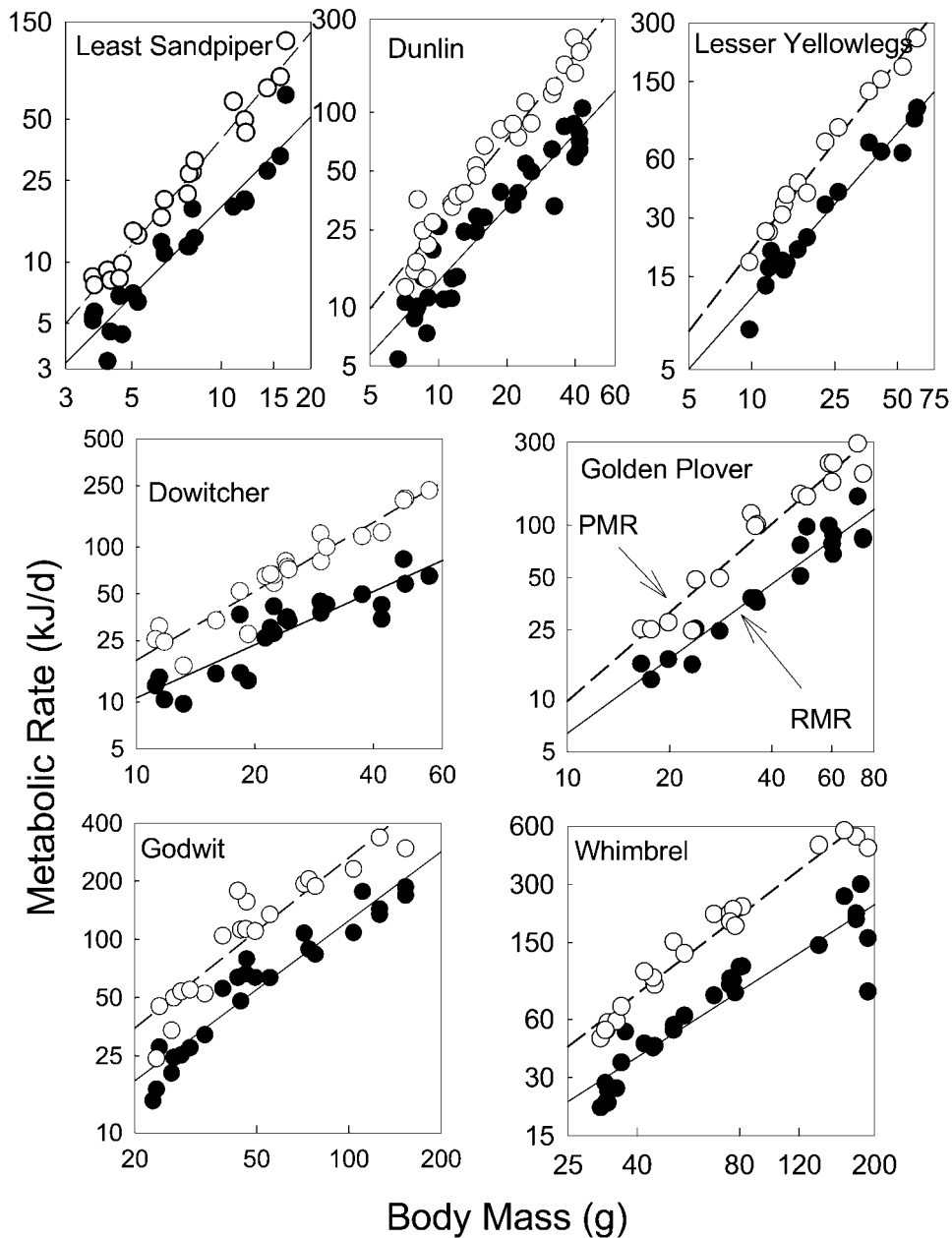


Figure 2. Resting metabolic rate ($\text{mL O}_2/\text{min}$, filled circles) and peak metabolic rate ($\text{mL O}_2/\text{min}$, open circles) as functions of body mass (g) for chicks of seven species of shorebirds.

ANOVA suggested significant differences in T_b among species during measurements of RMR ($F = 3.2$, $P < 0.005$, $n = 162$), a post hoc Tukey test and a Student-Neuman-Keuls test indicated that all species belonged to a homogeneous subset ($P > 0.05$).

Peak Metabolic Rate

The slope for the equation of PMR for least sandpipers was significantly higher than those for other species, except dunlin

and golden plover (Fig. 2; Table 1). In an ANCOVA, the interaction term was significant— $F = 2.6$, $P < 0.03$ —indicating that at least one slope differed among species. Post hoc comparisons showed that the slope for the equation for least sandpipers was significantly higher than those for other species, except dunlin and golden plover. Although dowitchers had the highest average PMR/RMR ratio (2.34) and godwits the lowest (1.95), we found no significant differences in PMR/RMR among species (ANOVA: $n = 149$, $F = 1.6$, $P > 0.15$). With spe-

Table 1: Equations for resting metabolic rate (RMR) and peak metabolic rate (PMR) for seven species of shorebirds

Species	Intercept (mL O ₂ /min)	Intercept (kJ/d)	Slope	r ²	F	N
RMR:						
Least sandpiper	-1.65	-.19	1.45	.90	148.5***	17
Dunlin	-1.59	-.12	1.27	.92	372.5***	32
Lesser yellowlegs	-1.57	-.11	1.18 ^{AB}	.95	288.6***	17
Dowitcher	-.48	-.02	1.07 ^{CE}	.79	78.2***	22
Golden plover	-2.12	-.66	1.47 ^{AC}	.90	165.7***	19
Godwit	-1.69	-.23	1.17 ^F	.87	214.5***	32
Whimbrel	-2.19	-.73	1.42 ^{BEF}	.97	599.5***	23
PMR:						
Least sandpiper	-1.55	-.09	1.70 ^{ABCD}	.97	536.5***	16
Dunlin	-1.56	-.10	1.48	.89	253.0***	31
Lesser yellowlegs	-1.53	-.07	1.41 ^A	.99	1,201***	15
Dowitcher	-1.63	-.17	1.43 ^B	.90	172.9***	21
Golden plover	-2.18	-.72	1.71 ^{EF}	.93	226.4***	17
Godwit	-1.55	-.09	1.22 ^{CE}	.86	129.3***	23
Whimbrel	-1.93	-.47	1.48 ^{DF}	.97	691.6***	20

Note: Equations are of the form $\log \text{metabolism} = a + b \log \text{mass (g)}$. For each species, equations have the same slope and statistics but different units and hence, different intercepts. Slopes with the same letter are significantly different; $P < 0.05$.

*** $P < 0.0001$ for regression.

cies combined, the mean value for the ratio $\text{PMR/RMR} = 2.11 \pm 0.5$.

Mass-Specific Peak Metabolic Rate

Mass-specific PMR increased rapidly for chicks of all species, but then the rate of increase declined as chicks matured (Fig. 3; Table 2). In this model, $\text{PMR/g} = Y_0 + a(1 - e^{-bx})$; the magnitude of b signifies the rate of increase in PMR/g, where small values of b represent a more rapid increase in PMR/g with time. Least sandpipers and dowitchers had the most rapid increase in PMR per unit tissue, whereas godwits and whimbrels had the slowest. Calculation of the derivatives of equations (Y') for these lines showed the same trends: least sandpipers had the largest increase in PMR/g at the Gompertz inflection point, followed by lesser yellowlegs and an intermediate group composed of dunlins, dowitchers, and golden plovers, and then godwits and whimbrels, with the least change. We regressed PMR/g against K_G and against residuals of K_G versus adult mass, but we found no patterns ($P > 0.7$ in all cases). We also did not detect any patterns when we regressed the derivatives of the equations for PMR/g versus percent adult mass and K_G or against residuals of K_G versus adult mass.

Whole-Organism Growth versus Metabolism

We did not find a relationship between whole-body growth rate (K_G) and slopes of lines for RMR versus body mass or for slopes of lines for PMR versus mass ($P > 0.5$). Neither was there a relationship between whole-body growth (K_G) and PMR/RMR ($P > 0.6$). Because K_G was negatively related to adult body mass, we also regressed residuals of K_G and adult mass against slopes of the equations for RMR and PMR versus body mass, but we did not find any trends ($P > 0.5$ in all cases).

Muscle Growth

Leg muscles in dunlins and least sandpipers increased in size most rapidly, with K_G values of 0.177 and 0.154, respectively, whereas leg muscles of lesser yellowlegs and dowitchers developed more slowly (Table 3). We found no significant correlations between K_G for leg or chest muscles and adult body mass, although least sandpipers had the fastest growth for chest muscles and whimbrels the slowest (Table 4; $r = -0.48$, $P > 0.2$, $n = 7$ for pectoral muscles; $r = 0.17$, $P > 0.7$, $n = 7$ for leg muscles). The percentage of water in muscles of the leg and chest decreased as chicks aged for all species (Table 4). Comparisons of slopes by ANCOVA for the equations showed no significant differences, but intercepts were significantly different for equations of percent H₂O of leg versus age ($N = 92$, $F =$

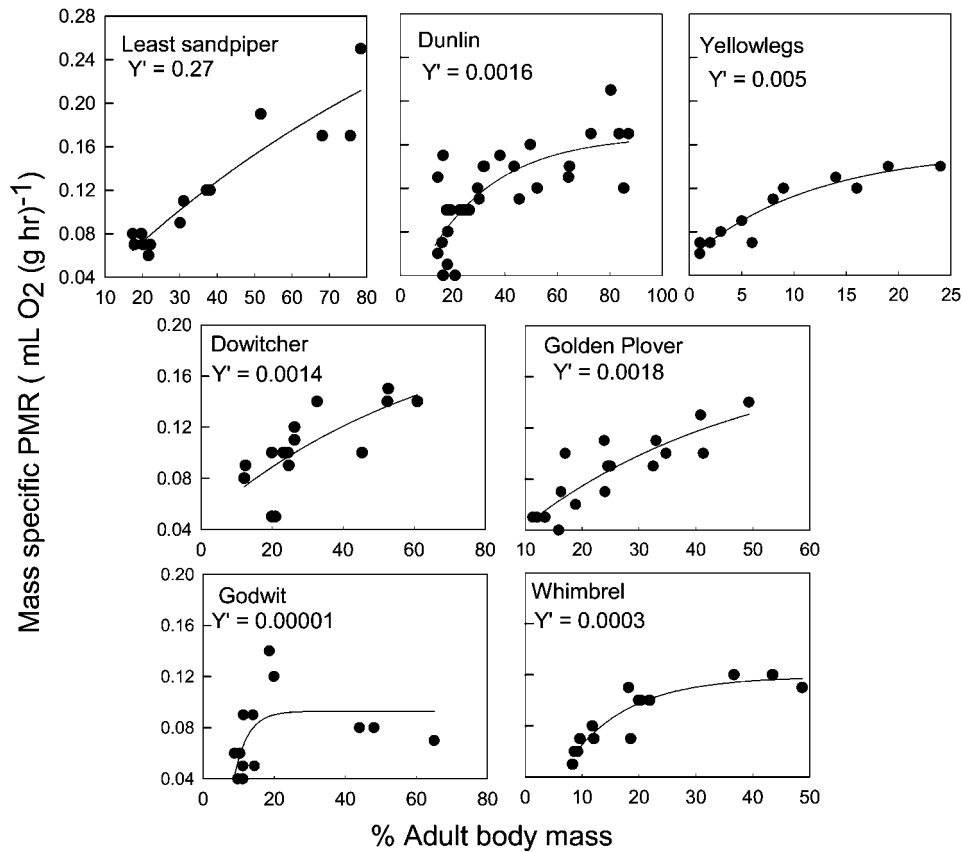


Figure 3. Mass-specific peak metabolic rate as a function of the percent of adult mass achieved for chicks of seven species of shorebirds. The derivative (Y') of equations was evaluated at 36.8% of adult mass, the inflection point of Gompertz growth.

3.8, $P < 0.003$) and of chest versus age ($N = 92$, $F = 5.2$, $P < 0.001$). Comparisons for intercepts are indicated in Table 5.

Muscle Growth versus Metabolism

Using a one-tailed test, we found evidence that species with the fastest-growing chest muscles (K_G) also had the highest slope for PMR, in support of Drent and Klaassen (1989) but in opposition to the growth rate–maturity hypothesis ($r = 0.7$, $P < 0.04$). However, this relationship was relatively weak, and therefore conclusions are tentative. We did not find any correlation between increase in RMR and growth rate of leg or chest muscles.

Conductance

When we compared C_{wet} , defined as $RMR/(T_b - T_a)$, between protocols—measurements in air or heliox—the interaction term, $\log \text{mass} \times \text{treatment}$, was insignificant ($F = 0.73$, $P > 0.3$). With the interaction term removed, C_{wet} differed significantly between treatments ($F = 1,671$, $P < 0.0001$). In heliox,

the intercept was 0.2 log units higher, or 1.58 times higher. Values for conductance in heliox were removed from analyses.

For measurements in air, we computed C_{wet} ($\text{mW}/^\circ\text{C}$; Fig. 4; Table 5). In an ANCOVA with $\log C_{wet}$ as the dependent variable, species as a fixed effect, and $\log \text{mass}$ as a covariate, the interaction term was significant, $F = 2.2$, $P < 0.05$. Post hoc

Table 2: Equations for mass-specific peak metabolic rate for seven species of shorebirds

Species	Y_0	a	b	r^2	F
Least sandpiper	.007	.42	.009	.87	38.1***
Dunlin	.002	.167	.037	.56	17.9***
Lesser yellowlegs	.049	.517	.026	.89	43.1***
Dowitcher	.046	.167	.015	.54	7.1**
Golden plover	.004	.177	.025	.76	23.3***
Godwit	-.40	.50	.26	.32	2.3 ^{NS}
Whimbrel	-.01	.136	.10	.86	37.3***

Note: Equations are of the form $\text{PMR/g} = Y_0 + a(1 - e^{-bx})$, in units of $\text{mL O}_2/(\text{g} \times \text{min})$. See Table 4 for sample sizes. NS = not significant.

** $P < 0.01$ for regression.

*** $P < 0.0001$ for regression.

Table 3: Coefficients and statistics for Gompertz equations for growth of muscles (dry mass, g) from one leg and for all muscles of the chest in seven species of shorebirds

Species	Parameters			r^2	F	K_G	N
	a	b	t_i (d)				
Leg muscles:							
Least sandpiper	.166	6.49	6.93	.82	25.1***	.154	14
Dunlin	.296	5.65	4.80	.77	32.3***	.177	22
Lesser yellowlegs	.76	12.75	8.0	.84	40.1***	.078	18
Dowitcher	.87	13.98	12.1	.95	40.0***	.072	7
Golden plover	1.36	8.68	11.23	.94	93.9***	.115	15
Godwit	2.06	6.84	8.6	.93	115***	.146	20
Whimbrel	3.02	9.22	9.17	.94	131***	.108	20
Chest muscles:							
Least sandpiper	1.3	4.2	13.93	.97	203***	.237	14
Dunlin	3.62	9.62	18.2	.97	344***	.104	22
Lesser yellowlegs	5.93	9.59	24.4	.99	854***	.104	18
Dowitcher	6.78	13.1	22.9	.96	45.4***	.076	7
Golden plover	9.09	7.55	23.2	.99	1,726***	.132	15
Godwit	15.6	11.4	23.9	.93	113***	.088	20
Whimbrel	18.7	12.4	24.7	.93	118***	.081	20

Note: t_i = age at the inflection point, 36.8% of the way through the growth period. K_G = Gompertz growth constant (1/day).

*** $P < 0.0001$.

analyses of slopes showed that least sandpipers had the lowest rate of increase in conductance among the seven species. We combined all data to generate an equation for conductance of shorebird chick with mass: $\log C_{\text{wet}}$ ($\text{mW}/^\circ\text{C}$) = $0.8 + 0.61 \log \text{mass}$ (g), $r^2 = 0.75$, $F = 381.9$, $P < 0.0001$, $n = 129$.

Temperature Limit to Homeothermy

Dividing peak metabolism by C_{wet} provides an estimate of the maximum gradient, ΔT_{max} , that a chick can maintain between its normothermic T_b and T_a (Fig. 5). We calculated equations for ΔT_{max} versus body mass from equations in Tables 1 and 5, in milliwatts. Results showed that least sandpipers and dunlins had the sharpest rise in ΔT_{max} , whereas godwits and golden plovers had the lowest. We evaluated the percentage of adult mass attained when chicks could maintain their T_b at 0°C , but this analysis yielded no general patterns. Whimbrels could maintain their T_b at freezing temperatures when they reached 25% of adult mass, golden plovers at 48%, yellowlegs at 61.2%, godwits at 82.9%, and dunlins at 92.8%. According to this analysis, dowitchers could not maintain their T_b at freezing temperatures until they reached adult mass. For all data combined, $\Delta T_{\text{max}} = 10.9 + 0.24 \times \text{mass}$ (g), $r^2 = 0.34$, $F = 61.5$, $P < 0.0001$, $n = 121$, or a 2.4°C increase in ΔT_{max} for each 10-g increase in mass.

Discussion

The physiological causes of life-history trade-offs have been and continue to be a major issue in evolutionary biology, but the role played by endogenous constraints in shaping life-history patterns remains controversial (Roff 1992; Starck and Ricklefs 1998; Zera and Harshman 2001). The adaptive significance of growth rate, which varies 30-fold among species of birds, remains unclear (Remes and Martin 2002), even though it is a fundamental component of their life history (Williams 1966; Lack 1968; Ricklefs 1973). The growth rate–maturity hypothesis suggests a trade-off between mutually exclusive phenomena, cell proliferation and mature muscle function, the latter defined by generation of heat. An alternative idea is that faster-growing species have higher thermogenic capacity, because the machinery required to grow rapidly requires a high rate of metabolism, both RMR and PMR; this is the so-called fast growth–high metabolism hypothesis.

We have measured growth, RMR, and PMR of seven species of closely related shorebirds, all breeding in the arctic, to shed light on these opposing ideas. At the whole-organism level, we have found no evidence that chicks of shorebirds with fast growth rates have lower resting rates of metabolism or lower PMR, as would be predicted by the growth rate–maturity hypothesis. The Gompertz growth constant, K_G , a metric independent of the length of the growth period, was unrelated to

Table 4: Coefficients and statistics for equations for water content of muscles of the leg and chest for seven species of shorebird chicks

Species	Intercept <i>a</i>	Slope <i>b</i>	<i>r</i> ²	<i>F</i>	<i>N</i>
Least sandpiper:					
Leg	.77 ^{AB}	-.004	.35	4.8*	11
Chest	.82 ^E	-.006	.57	11.7***	11
Dunlin:					
Leg	.77	-.002	.41	10.4**	17
Chest	.78 ^{CD}	-.003	.59	18.9***	17
Lesser yellowlegs:					
Leg	.81	-.005	.85	67.4***	14
Chest	.84	-.006	.84	60.8***	14
Dowitcher:					
Leg	.83	-.005	.83	9.7 ^{NS}	4
Chest	.82	-.004	.90	17.9*	4
Golden plover:					
Leg	.80	-.004	.78	31.2***	11
Chest	.84	-.004	.64	16.1***	11
Godwit:					
Leg	.79 ^A	-.003	.81	65.1***	17
Chest	.84 ^{DE}	-.004	.86	88.5***	17
Whimbrel:					
Leg	.82 ^B	-.004	.94	231***	18
Chest	.86 ^C	-.005	08.5	91.4***	18

Note: Equations are of the form %H₂O = *a* + *b*(age). The same letter indicates significant differences (*P* < 0.05) for post hoc comparisons after testing for overall significance of slopes and intercepts. NS = not significant.

* *P* < 0.05.

** *P* < 0.01.

*** *P* < 0.0001.

RMR or PMR. Although least sandpipers, the smallest of the species that we have measured, grew faster than other species and had among the highest increases in PMR, golden plovers had relatively slow growth, a *K_G* of 0.082, but displayed rapid increases in RMR and PMR. This lack of pattern is inconsistent with either of the hypotheses that we tested.

Among adults, some studies indicate that enhanced physiological capacities are accompanied by increased maintenance costs (Daan et al. 1990; Suarez 1996). High basal metabolic rate values are associated with large fractions of body mass accounted for by metabolically active organs, such as heart, liver, and kidney, and with high field metabolic rates. Klaassen and Drent (1991) suggested that rapid growth of shorebird chicks ought to be associated with concomitant increases in RMR because of increases in size of the internal organs necessary to support muscle tissue. While we did not find an association of rate of growth with increases in RMR or PMR, the slopes of the equations for RMR and PMR versus mass were positively related, indicating that species with the most rapid increase in RMR had similar increases in PMR, as would

be predicted by the fast growth–high metabolism hypothesis (*r*² = 0.61, *F* = 7.7, *P* < 0.04).

We found some evidence that faster-growing chest muscles resulted in increased thermogenic capacity, consistent with the fast growth–high metabolism hypothesis. Least sandpipers grew muscles of their chest rapidly and also increased their PMR at a rapid rate. Krijgsveld et al. (2001) compared muscle development and catabolic enzyme activity in chicks of the dunlin (adult mass = 50 g, neonate mass = 8 g) and whimbrel (adult mass = 380 g, neonate mass = 34 g). Dunlins had somewhat larger proportions of leg muscles than whimbrel chicks through all of the development period, and the size of their pectoral muscles increased much more rapidly, presumably associated with the earlier achievement of flight. Differences in enzyme activities per unit mass of muscle tissue were dramatic; leg muscles of small dunlin chicks had almost twice, and pectoral muscles three to four times, the citrate synthase activity of those of whimbrel chicks within the first week after hatching. Citrate synthase is an enzyme that provides an index of aerobic capacity of chicks and likely reflects the mitochondria density in muscle (Hochachka et al. 1977). The development of effective homeothermy of young chicks in smaller species is primarily a consequence of greater metabolic intensities of heat-generating tissues. It appears that natural selection can increase the metabolic intensity of rapidly growing skeletal muscles, perhaps by increasing the number of mitochondria, in contradistinction to the growth rate–maturity hypothesis.

Conductance describes the sum of properties of a chick that influence heat loss to the environment, according to the Newtonian cooling model (Scholander et al. 1950; Bakken 1976). Conductance multiplied by the gradient between *T_b* and *T_a* describes the rate of heat transfer from an animal to its environment, which must be equaled by heat production if *T_b* is to remain constant, RMR (*W*) = *C_{wet}*(*T_b* – *T_a*). Our values for *C_{wet}* showed that least sandpipers had the lowest value of conductance, whereas dowitchers had the highest.

The allometric relationship value for *C_{wet}* determined in this

Table 5: Equations for wet conductance for seven species of shorebirds

Species	Intercept	Slope	<i>r</i> ²	<i>F</i>	<i>N</i>
Least sandpiper	1.05	.34 ^{ABC}	.39	7.7**	14
Dunlin	.732	.66 ^A	.60	40.5***	29
Lesser yellowlegs	.77	.62	.73	29.9***	13
Dowitcher	.338	.97 ^B	.63	30.2***	20
Golden plover	1.02	.46	.57	15.7**	14
Godwit	.314	.91 ^C	.78	66.5***	21
Whimbrel	.44	.78	.58	22.2***	18

Note: Equations are of the form log(mW/°C) = *a* + *b*log mass (g). Values with the same letter are significantly different, *P* < 0.05.

** *P* < 0.001.

*** *P* < 0.0001 for regression.

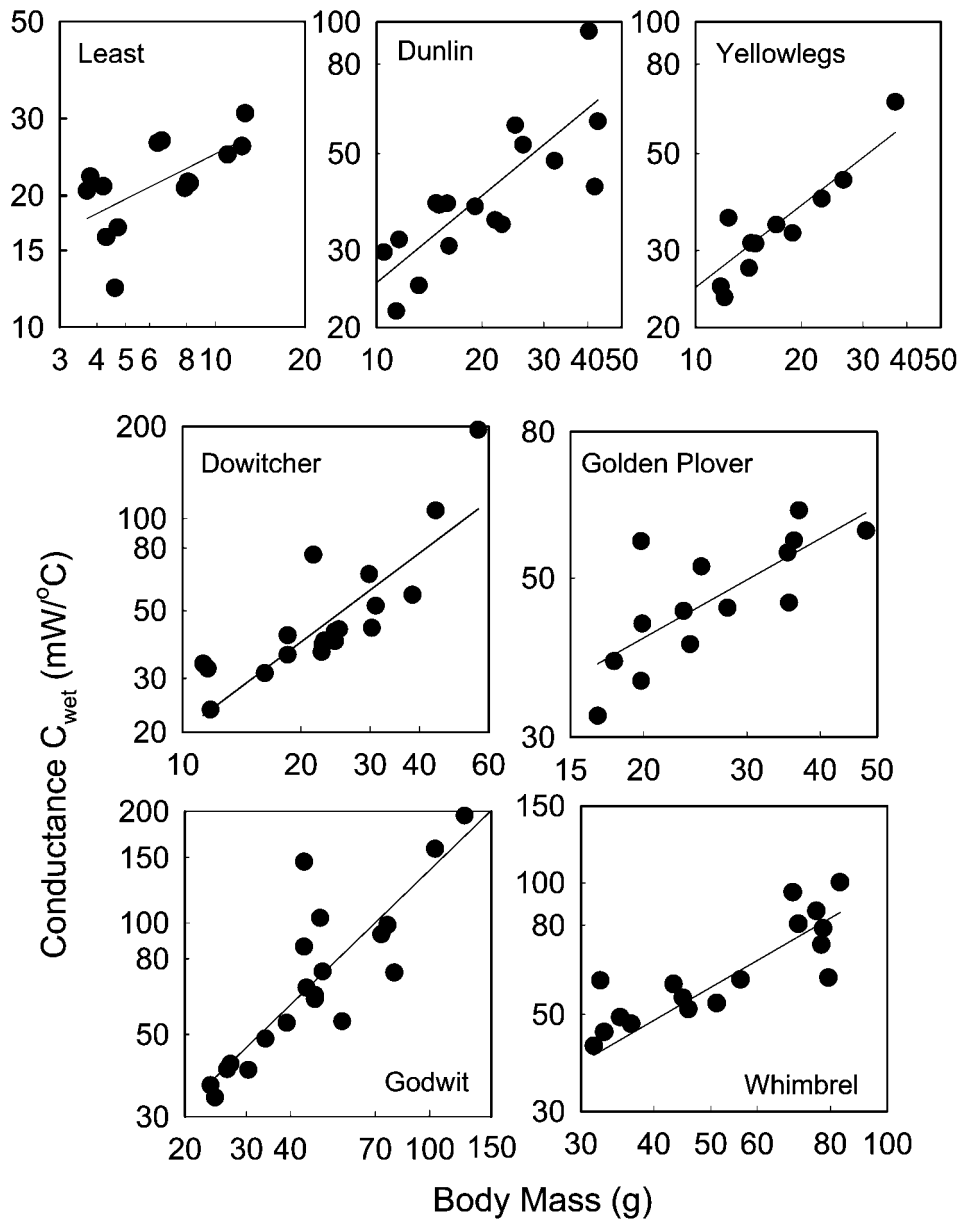


Figure 4. Wet conductance (C_{wet} , mW/°C) as a function of body mass (g) for chicks of seven species of shorebirds. *Least* = least sandpiper.

study differed considerably from that obtained by Visser and Ricklefs (1993) for chicks of five species of shorebirds that breed in the Netherlands (0.190 ± 0.057). However, this reported value is almost certainly in error, because it does not match the distribution of the data plotted in figure 4 of that publication, which would appear to have allometric slopes on the order of 0.5.

The maximum temperature gradient between a chick's body and environment (ΔT_{max}) that can be maintained in the absence of a net radiative load is a function of PMR and wet thermal conductance k , $\Delta T = PMR/k$. The value of ΔT increased rap-

idly with body mass during development, the most in least sandpipers and the least among godwits. Chicks of smaller species could maintain a greater temperature gradient at a particular body mass because of their higher mass-specific maximum metabolic rates.

Our data do not support the growth rate–maturity hypothesis and only marginally support the fast growth–high metabolism idea. With respect to the relationship between metabolism and growth rate, the most striking feature of our data is the lack of consistent patterns among these species. At this point, we need to rethink our perceptions of growth rate and metab-

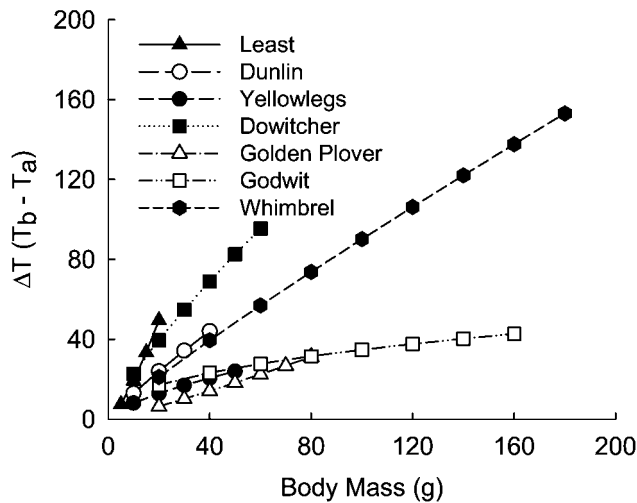


Figure 5. Estimated temperature gradient over which chicks can maintain their body temperature at peak metabolic rate (PMR), with lines and data generated from equations for PMR and wet conductance for each species. *Least* = least sandpiper.

olism in precocial birds. Why do some small species grow rapidly and yet still generate considerable heat to thermoregulate, apparently from increased mitochondria density, whereas others seem to grow more slowly and produce less heat? Answers to these questions will likely come from studies that integrate information at the molecular level with that from the whole organism. Current paradigms do not seem to be sufficient to explain the diversity of patterns between growth rate and metabolism that we see in nature.

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