

Daily energy expenditure in precocial shorebird chicks: smaller species perform at higher levels

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Abstract We measured daily energy expenditure (DEE) during the development periods of precocial chicks of five species of Arctic shorebirds spanning a broad range in size, in order to investigate the relationships between DEE, body size, and growth rate. We also quantified the effect of weather conditions on the energy expenditure of chicks to establish the impact of cold arctic weather on their time and energy budgets. We used the doubly labeled water method to measure DEE at ambient temperatures in an outside enclosure on the subarctic tundra at Churchill, Manitoba, Canada. Growth rate was highest in the smallest species, and in general decreased with adult size, as shown by the decrease in growth rate constant and later inflection point with increasing adult body mass. DEE ranged from 14 kJ day⁻¹ in young chicks of the smaller species to 365 kJ day⁻¹ in older chicks of the larger species. From hatching onward, DEE of shorebirds was high compared to

DEE of chicks of altricial species, reflecting the high costs of locomotion and thermoregulation, and mass-specific DEE increased rapidly to adult levels. Chicks of smaller species metabolized more energy per unit mass and functioned at higher multiples of resting metabolic rate than chicks of larger species. As chicks of smaller species also had higher growth rates, and thus simultaneously invested in growth and mature function, it seems that shorebird chicks can adjust total metabolizable energy as well as its relative allocation between investment in growth and mature function. DEE was similar to cold-induced peak metabolic rates achieved by shivering thermogenesis. Because chicks were motionless during laboratory metabolism measurements, the relatively high level of DEE compared to these metabolic rates suggests that locomotion produces similar amounts of heat as shivering. Ambient temperature did not affect DEE in outdoor pens, although higher wind speed resulted in slightly increased energy expenditure. Heat produced by locomotion is possibly sufficient to sustain thermoregulation under local environments. Furthermore, when ambient temperatures are low, chicks spend more time brooding and less time foraging, which presumably counters the tendency to increase thermogenesis in response to cold.

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Zusammenfassung

Der tägliche Energieumsatz nestflüchtender Limikolenküken ist bei kleineren Arten höher.

Wir haben den täglichen Energieumsatz (DEE) während der Entwicklungsphase nestflüchtender Küken von fünf

arktischen Limikolenarten verschiedenster Größe gemessen, um die Beziehungen zwischen DEE, Körpergröße und Wachstumsrate zu untersuchen. Wir haben auch den Einfluss der Wetterbedingungen auf den Energieumsatz der Küken quantifiziert, um die Auswirkungen kalten arktischen Wetters auf ihre Zeit- und Energiebudgets zu ermitteln. Wir haben die doubly labeled water Methode angewendet, um DEE bei Umgebungstemperatur in Außengehegen in der subarktischen Tundra in Churchill, Manitoba, Kanada, zu messen. Die Wachstumsrate war bei den kleinsten Arten am höchsten und nahm allgemein mit der Adultgröße ab, wie durch die Abnahme der Wachstumskonstante und den späteren Wendepunkt mit zunehmendem adultem Körpergewicht gezeigt wurde. Der DEE reichte von 14 kJ pro Tag bei jungen Küken der kleineren Arten bis 365 kJ pro Tag bei älteren Küken der größeren Arten. Vom Schlupf an war der DEE der Limikolen hoch im Vergleich zum DEE von Küken nestlockender Arten, was die hohen Kosten für Bewegung und Thermoregulation wiederspiegelt, und der gewichtsspezifische DEE stieg rasch auf Adultniveau an. Die Küken kleinerer Arten verstoffwechselten mehr Energie pro Gewichtseinheit und hatten eine vielfach höhere Ruhestoffwechselrate als die Küken größerer Arten. Da die Küken kleinerer Arten auch höhere Wachstumsraten hatten und daher gleichzeitig in Wachstum und Ausreifung investierten, können Limikolenküken anscheinend die insgesamt verstoffwechselbare Energie sowie ihre relative Aufgliederung zwischen Investment in Wachstum und Ausreifung anpassen. Der DEE ähnelte den kälteinduzierten Höchststoffwechselraten, die durch Muskelzittern erreicht wurden. Da sich die Küken während der Stoffwechselmessungen im Labor nicht bewegten, deutet das relativ hohe DEE-Niveau im Vergleich zu diesen Stoffwechselraten darauf hin, dass Bewegung ähnlich viel Wärme wie Muskelzittern produziert. Die Umgebungstemperatur beeinflusste den DEE in Außengehegen nicht, obwohl die höhere Windgeschwindigkeit zu einem leicht erhöhten Energieumsatz führte. Die durch Bewegung produzierte Wärme reicht möglicherweise aus, um die Thermoregulation unter lokalen Umweltbedingungen aufrechtzuerhalten. Außerdem verbringen die Küken bei niedrigen Umgebungstemperaturen mehr Zeit damit, sich gegenseitig zu wärmen, und weniger Zeit mit der Nahrungsaufnahme, was vermutlich der Tendenz, die Wärmeproduktion als Antwort auf Kälte zu steigern, entgegenwirkt.

Introduction

The harsh environment of the Arctic imposes critical limits on the existence of many species. One type of limit

includes extreme physical conditions in the environment, such as low temperatures and high wind velocities (Bakken et al. 2002). Another is the brevity of the growing season (MacLean and Pitelka 1971; Nettleship 1973). The Arctic is a demanding environment for sandpipers (Scolopacidae) during the two- to three-month breeding season. Sandpiper chicks are self-feeding, and in some species weigh as little as 4 g at hatching, which places them among the smallest of endothermic animals. The precocial mode of development of sandpiper chicks presumably requires a high level of energy expenditure for locomotion and thermoregulation, particularly in the cold environments at high latitudes (e.g., West and Norton 1975; Starck and Ricklefs 1998; Schekkerman and Visser 2001; Schekkerman et al. 2003). Combined with pressure to grow rapidly during the short period of favorable conditions, shorebird chicks may operate near the limits of metabolic performance. However, few studies have measured the daily energy expenditure (DEE) of precocial chicks of any species under free-living conditions, so little is known about the effects of biotic and abiotic factors on the DEE of sandpiper chicks (e.g., Drent et al. 1992).

Schekkerman and Visser (2001) showed that levels of daily metabolized energy in chicks of Black-tailed Godwits (*Limosa limosa*) and Northern Lapwings (*Vanellus vanellus*) in temperate grassland habitats of the Netherlands were about 60 % higher than levels predicted for altricial chicks of a similar size (Weathers 1992), which have food and heat supplied by their parents. However, shorebirds in the Netherlands experience mild physical environments compared to those in many areas of the Arctic. Consistent with this difference, rates of energy metabolism in Arctic Red Knot chicks (*Calidris canutus*, Schekkerman et al. 2003) were higher than those of godwits and lapwings in the Netherlands.

Young precocial chicks, particularly those of small species that experience low environmental temperatures, lose heat rapidly during foraging (Chappell 1980; Visser and Ricklefs 1993a; Krijgveld et al. 2003a). When not actively foraging, they respond to cooling by shivering to generate heat (Dawson 1975; Hohtola and Stevens 1986), but often neither mechanism can produce enough heat to prevent body cooling (Ricklefs and Williams 2003). Therefore, foraging is regularly interrupted by periods of brooding by the parent, during which body temperature is restored to higher levels. The better a chick can maintain its body temperature, the more of its time can potentially be spent foraging. This capacity to produce heat, and thus to maintain body temperature, is primarily the product of the mass of the chick's skeletal muscle and its maximum tissue-specific metabolic rate. Thus, the capacity of the chick to generate heat increases over the growth period as the size and maturity (% of adult function) of the skeletal

muscles increase (Ricklefs 1983; Choi et al. 1993; Krijgsveld et al. 2001). In this respect, body size plays an important role in the level of energy expenditure of the chick, because smaller chicks have higher mass-specific thermal conductances (Visser and Ricklefs 1993a, b; Bakken et al. 2002).

When they are cold-stressed, chicks of small shorebird species generally increase their metabolism proportionately more than do large species (Kendeigh 1969; Williams et al. 2007). Krijgsveld et al. (2001), by measuring enzyme activity in the flight and leg muscles, found that in two species of shorebird chicks, the skeletal muscles of the smaller species (Dunlin *Calidris alpina*) had a higher functional capacity than those of the larger species (Whimbrel *Numenius phaeopus*), enabling them to increase their metabolic rate proportionately more. These results suggest that chicks of smaller species should exhibit proportionately higher mass-specific DEE in response to cold stress than chicks of larger species.

To test this, we measured DEE in outdoor enclosures, using the doubly labeled water method, throughout the growth periods of the chicks of five species of sandpipers ranging in neonatal mass from 4 to 33 g. From the smallest, the species were the Least Sandpiper (*Calidris minutilla*), Dunlin, Lesser Yellowlegs (*Tringa flavipes*), Hudsonian Godwit (*Limosa haemastica*), and Whimbrel. We also determined the effect of ambient temperature on DEE, and we related DEE to resting and peak metabolic rates as measured by Williams et al. (2007) under laboratory conditions.

Methods

Birds and housing

DEE was measured in chicks of Least Sandpiper ($n = 5$), Dunlin ($n = 7$), Lesser Yellowlegs ($n = 6$), Hudsonian Godwit ($n = 12$; repeated measurements after 12 and 24 h in 2 chicks), and Whimbrel ($n = 15$) at ages ranging from 2 to 17 days (hatch day = 0). Eggs were collected on the tundra near Churchill ($58^{\circ}45'N$, $94^{\circ}04'W$), Manitoba, Canada, in June and July during fieldwork in 1995 through 1998. Eggs were incubated at an air temperature of $37^{\circ}C$ and a relative humidity of 55 %, which was increased to 80–90 % at the first signs of hatching (starred eggshell), ca. two days before hatching. Chicks were kept for a minimum of one day in boxes in the laboratory to allow them to dry and start feeding. Heat was supplied by a light bulb, creating a range of temperatures in the box, and food and water were supplied ad libitum. For a detailed description of housing conditions, see Krijgsveld et al. (2001).

During 1995 through 1997, each chick was placed in an outside enclosure for the duration of its doubly labeled

water measurement. On nonexperimental days, the chicks were held outdoors for 4–6 h every day to every other day throughout their growth period from 1–2 days after hatching. Otherwise chicks were kept indoors. In 1998, five Whimbrel chicks in which DEE was measured additionally were held outdoors continuously from one day after hatching. Growth of chicks did not differ between years or deviate from the growth of a group held continuously indoors. Growth curves under natural conditions are unfortunately not available, but data on growth of free-living and artificially raised Golden Plover chicks in Churchill show that growth did not differ systematically between the two groups (K. L. Krijgsveld, unpublished data). DEE or ambient temperature during DEE measurements did not differ consistently between 1998 and previous years.

Two types of enclosure were used, a small one for Least Sandpiper, Dunlin, and Lesser Yellowlegs chicks up to ca. ten days of age, and a larger one for all other chicks. The small enclosure was made of fine mesh (1 cm^2) hardware cloth, 50 cm high and 2 m square, covered by a lid of hardware cloth. The large enclosure was circular with a diameter of 15–20 m, and consisted of 50 cm high chicken wire lined along the lower 20 cm with cloth sealed to the ground. A cover protected chicks from predators. A heat source creating a thermal environment of up to $41^{\circ}C$ was provided by a light bulb and a thermal blanket fitted in a wooden box ($20\text{ (h)} \times 30\text{ (d)} \times 20\text{ (w) cm}$) with an entrance of 15×15 cm. The light also served to direct the chicks to the brooder. Most chicks learned to use this brooder within a couple of hours, and all chicks entered the brooder by the second day.

Because naturally available food diminished rapidly in the enclosure, food and water were supplied daily. Food was scattered on the ground to stimulate the chicks to forage. Food consisted of pheasant starter type 2 mix (1995 and 1996; Spelderolt, Beekbergen, Netherlands) or turkey pre-starter mix (1997 and 1998; Puratone Corporation, Niverville, MB, Canada), supplemented with a mix of tuna, chicken, oatmeal, and boiled eggs, as well as with dead mosquitoes.

Egg collection was carried out under permit from the Canadian Wildlife Service. Husbandry and laboratory procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri–St. Louis, USA, and the Canadian Wildlife Service.

Growth

Growth parameters were determined by fitting logistic growth functions to individual growth data using the non-linear regression (NLR) procedure of SPSS Statistics release 12 (IBM Company). Because growth was not

followed long enough to obtain a good estimate of the asymptotic mass of each individual chick, we set the asymptote to the average weights of adults taken during the breeding season in Canada and Alaska (Least Sandpiper—Johnsgard 1981; Dunlin—Jehl and Murray 1986; Lesser Yellowlegs—Irving 1960; Hudsonian Godwit—Jehl and Smith 1970; Whimbrel—Dunning 1993).

Energy expenditure experiments

DEE was measured using the doubly labeled water method (DLW; Lifson and McClintock 1966; Nagy 1980; Speakman 1997). $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ ratios in blood samples were analyzed following procedures described in Visser and Schekkerman (1999). These authors validated the DLW method for growing shorebird chicks during 24 h trials, and showed that the relative error in DEE estimates was unrelated to the relative growth rate of the chick. For each DLW measurement in the present study, a chick was weighed and injected intraperitoneally with 0.0075 ml DLW g^{-1} in chicks of Least Sandpiper, Dunlin, and Lesser Yellowlegs, and a linearly decreasing dosage of 0.0060 ml g^{-1} at 25 g to 0.0030 ml g^{-1} at 300 g body mass was used in chicks of Hudsonian Godwit and Whimbrel. In 1995 and 1996, the DLW mixture contained 30.0 % $^2\text{H}_2\text{O}$ and 64.0 % H_2^{18}O ; in 1997 and 1998 it contained 33.8 % $^2\text{H}_2\text{O}$ and 60.6 % H_2^{18}O . After an equilibration period of 1 h, an initial blood sample was collected from the brachial vein in 4–6 glass capillary tubes each containing 10–15 μl of blood. Tubes were flame-sealed within 5 min.

After periods of 5 h 30 min to 28 h (intervals coinciding with simultaneous behavioral observations in a related study), during which time the chick was in the enclosure, the chick was weighed again and the final blood sample was taken. In a total of eight measurements on Dunlin, Hudsonian Godwit and Whimbrel, the duration varied between 5 h 20 min and 6 h 10 min (mean = 5 h 55 min); in the other 37 chicks, the duration varied between 10 h 30 min and 28 h (mean = 15 h 45 min; overall mean = 14 h, SD = 6.7). Neither interval length nor time during the diurnal cycle of activity affected DEE measurements.

Final labeled O_2 concentration as a percent of initial labeled O_2 concentration decreases as the measurement duration increases. Final O_2 concentration averaged 83 % after 6 h (SD = 2.6, n = 8), 61 % after 12 h (SD = 11.3, n = 28), and 45 % after 26 h (SD = 8.34, n = 11). Measurement duration did not affect smaller and larger species differently. Levels of DEE in the shorebird chicks were so high that a sufficient decrease in ^2H and ^{18}O could be obtained during even the short intervals. H:O ratio (fractional turnover rate of ^2H [deuterium, k_d] as a percentage of that of oxygen [k_o]) did not change with measurement duration for durations of less than 7 h versus more than 11 h, respectively, for Dunlin: mean = 62.1 %

(SD = 6.13, n = 3) versus 61.2 (6.26, 4); Hudsonian Godwit: 80.0 (3.13, 2) versus 80.1 (7.28, 12); Whimbrel: 81.4 (4.21, 3) versus 82.4 (6.60, 12).

To further evaluate the applicability of the DLW method during relatively short measurement periods (average = 12.0 h, SD = 0.62, n = 17 trials), a DLW validation experiment was conducted with chicks of Dunlin (n = 8), American Golden Plover (*Pluvialis dominicana* n = 3), Hudsonian Godwit (n = 2), and Lesser Yellowlegs (n = 3). An initial blood sample (I) was taken after an equilibration period of 1 h after injection, during which time the chick was fasting in a heated cardboard box. Next, the bird was placed in a respiration chamber and provided with access to water and food of the same type as during normal housing, with lights on at all times. Ambient temperature was set between 25 °C (for the heaviest chicks) and 35 °C (smallest chicks), representing the lower limit of the thermoneutral zone. After a measurement period of 12 h, the bird was taken out of the chamber and a first final blood sample (F12) was collected as described above. In some cases, the chick was placed back in the respiration chamber for a second 12 h measurement period, at the end of which we collected a second final sample (F24). This provided a paired comparison with the first measurement period to address the issue of differential isotope incorporation. Respirometry measurements were carried out as described in Williams et al. (2007).

For these validation experiments, no significant relationship ($P = 0.44$) could be demonstrated between the error in the DLW method (relative to gas analysis) and the duration of the DLW sampling interval. The measurements revealed that, with the application of the procedures of Visser and Schekkerman (1999), the error of the DLW method relative to the respirometry method (i.e., the accuracy) was on average +1.3 %, whereas the standard deviation (SD; i.e., the precision) was 12.0 % (GHV, unpublished). The average error and SD for short measurements were close to those observed during the 24 h trials (0 and 10.1 % respectively; Visser and Schekkerman 1999). Thus, reducing the measurement period in this study did not affect the accuracy of DLW measurements, and it decreased the precision of the estimates only slightly.

In two Hudsonian Godwits, we took final blood samples after both 12 and 24 h. DEE did not differ between the two interval lengths (after 12 and 24 h, respectively: godwit #1, 17 days old: 365 and 365 kJ day^{-1} ; godwit #2, 16 days old: 324 and 301 kJ day^{-1}).

In eight chicks, no initial blood sample was taken, only a final blood sample (i.e., single sample protocol, Ricklefs et al. 1986; Webster and Weathers 1989). Background isotope levels collected from five chicks [Dunlin, Whimbrel, and free-living American Golden Plover (*Pluvialis*

dominica; unpublished data, Jan van Gils)] were similar to each other.

DLW analysis

$^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ isotope ratios of the blood samples were determined at the Centre for Isotope Research, University of Groningen, Netherlands. Each blood sample was microdistilled using a vacuum line. ^2H was analyzed after converting the water sample to H_2 gas using a uranium oven at 800 °C, and ^{18}O was analyzed using the CO_2 equilibrium method. In the H_2 and CO_2 gases, isotope ratios were determined with a dual inlet SIRA 9 isotope ratio mass spectrometer. Analyses were done in duplicate, but a third capillary of blood was analyzed if the two measurements differed by more than 2 %. For details concerning the analytical procedure, see Visser and Schekkerman (1999).

Calculation of DEE from DLW measurements

Average background concentrations were 0.1996 atom percent for ^{18}O ($\text{SD} = 0.00023$, $n = 5$) and 0.0144 atom percent for ^2H ($\text{SD} = 0.00008$, $n = 5$). CO_2 production ($r\text{CO}_2$, liters per day) was calculated as:

$$r\text{CO}_2 = 22.4 \times [(N/2.078) \times (k_o - k_d) - 0.13 \times 0.0249 \times N \times k_d],$$

where N represents the average size of the body water pool during the measurement (mol), and k_o and k_d are the fractional turnover rates of the ^{18}O and ^2H isotopes, respectively. This equation was derived by Visser and Schekkerman (1999) from a validation study on shorebird chicks exhibiting a wide range of growth rates. In most chicks, the fractional turnover rates were calculated using the population-specific estimates for the background levels and the individual-specific isotope concentrations of the initial and the final blood samples (equations 4 and 5 in Visser and Schekkerman 1999). When we obtained only a final blood sample, we estimated the initial concentration of each isotope using the injected dose and the size of the body water pool (see below, Webster and Weathers 1989).

To minimize the effect of errors in the quantity of DLW injected, N was not estimated from isotope dilution but from the relationship between the percentage water content of the whole body and the fraction of adult mass attained by the chick (Visser and Schekkerman 1999, Schekkerman and Visser 2001). In all cases, N was calculated as the average of the estimated values at the start and end of the DLW measurement. Finally, DEE was calculated from $r\text{CO}_2$ using an energy equivalent of 27.33 $\text{kJ l}^{-1} \text{CO}_2$, which is in agreement with a protein-rich diet (Gessaman and Nagy 1988).

Environmental temperature

To relate DEE to thermal properties of the environment, we recorded environmental temperatures continuously throughout the season. A white and a black copper sphere, each having a diameter of 3.5 cm and containing a centrally positioned thermocouple, were placed 10 cm above the ground in a microhabitat characteristic of foraging shorebird chicks. The white sphere provided a measure of ambient air temperature (T_a), with the effects of wind and solar radiation largely factored out. The black sphere provided an approximation of the thermal environment with wind and solar radiation factored in, although not necessarily in the same fashion as experienced by the chick (Bakken et al. 1985; Walsberg and Weathers 1986). By subtracting the white-sphere temperature from the black-sphere temperature, we obtained a measure of radiative-conductive load independent of T_a . These estimates matched levels obtained for comparison purposes with a pyranometer (ANOVA: $F_{1, 117} = 623$, $P < 0.0001$, $r^2 = 0.84$; LI-200SA, LI-COR, Lincoln, NE, USA).

Wind speed was measured 10 cm above the ground with a cup anemometer (A100L2, Grant Instruments Ltd., Barrington, UK; minimum threshold 0.15 m s^{-1}). In addition, data on wind speed at 10 m above the ground, collected at Churchill Airport, were provided by the Winnipeg Climate Centre (Winnipeg, Canada). Local climate data were averaged over 15 min intervals and recorded with a Squirrel 1204 data logger (Grant Instruments Ltd.).

Statistics

Variations in DEE with respect to species, age, and environmental conditions were analyzed with general linear models (GLM) unless specified otherwise, using SPSS Statistics release 12 (IBM). Mass, age, and environmental variables were entered as covariates, and species as a fixed factor. For each separate analysis, the statistics for the individual covariates and factors are given, as well as the R^2 of the overall model.

Results

Size

The smallest species, Least Sandpiper, grew the fastest, whereas the larger Hudsonian Godwit and Whimbrel grew more slowly (Table 1). The growth rate constant (K_1) decreased and the inflection point increased with increasing adult body mass, following the general pattern of decreasing growth rate with increasing size first described by Ricklefs (1973). In contrast, the chicks of Lesser

Table 1 Comparison of the masses and growth rates of five species of shorebirds

Species	Body mass		K_L	t_i	n
	Neonatal	Adult			
Least Sandpiper	4	21	0.240	7.7	26
Dunlin	8	50	0.225	8.9	44
Lesser Yellowlegs	12	81	0.129	14.6	20
Hudsonian Godwit	25	255	0.170	13.9	25
Whimbrel	33	380	0.156	16.2	51

Neonatal and adult body masses (in g) are given, as well as the growth constant (K_L) and inflection point (t_i , days) determined by logistic curve fitting, and the sample size used to determine growth parameters (n individuals weighed daily)

Yellowlegs grew poorly compared to other studies on Lesser Yellowlegs (Visser and Ricklefs 1993b), and this resulted in a low growth rate constant and a late inflection point relative to their size. This did not affect the quality of the measurements of DEE (see “Methods”), although it may have contributed to the relatively low level of DEE in yellowlegs compared to the smaller Dunlin. Chick growth (here the proportional increase in mass) during DEE measurements was unrelated to ambient temperature.

DEE and time of day

DEE levels were lower when night-time hours (i.e., 22:30–3:30) comprised a larger proportion of the measurement period. This “night” effect could be accounted for by lower wind speeds at night (see below). After correcting wind speed, DEE did not show a significant variation with the fraction of the measurement that occurred during the night. This fraction was highest in chicks of Least Sandpiper and Dunlin (both 24 vs. 17 % in the other species). Thus, DEE levels in these two species were likely to have been underestimated to some degree compared to those of other species. Accordingly, we interpreted the results conservatively. Because we expected DEE to be higher in smaller species, this would not have biased our conclusions.

Daily energy expenditure

DEE ranged between 14 and 365 kJ day⁻¹. Values were lowest in chicks of Least Sandpiper and Lesser Yellowlegs, intermediate in chicks of Dunlin, and highest in chicks of Hudsonian Godwit and Whimbrel (Fig. 1). For unknown reasons, three young godwit chicks (2–3 days) had exceptionally low levels of DEE. Measurement intervals for these chicks were normal (14 h), and they showed a normal activity pattern (foraging 50 % of the time; KLK, unpublished data).

DEE of the shorebird chicks increased rapidly with age. Because chicks of the larger species weighed so much more at any given age than the smaller species, whole-body

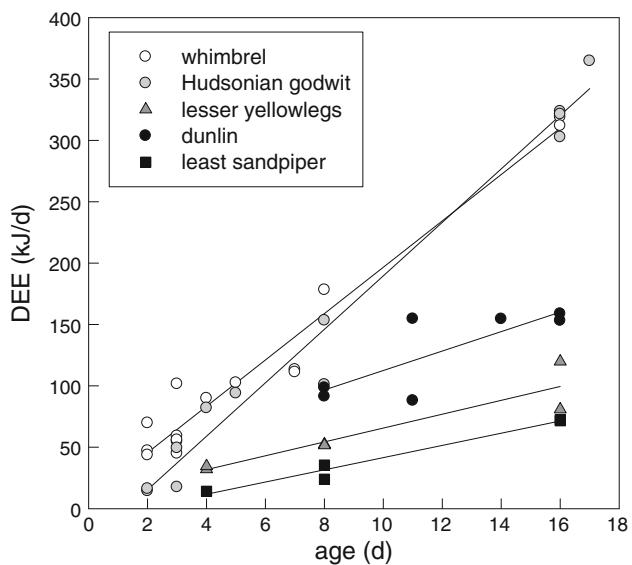


Fig. 1 Daily energy expenditure as a function of age in chicks of five species of shorebirds covering a wide range of body sizes

DEE was higher in the larger species. However, as a function of body mass, Least Sandpiper and Dunlin had higher levels of DEE than Godwit and Whimbrel (GLM: log(DEE) significantly correlated with log(mass): $F_{1,39} = 389.4, P < 0.0001$; and with species: $F_{4,39} = 27.9, P < 0.0001; R^2_{\text{model}} = 0.925$; model excludes wind speed, see below). The rate of increase in DEE with body mass did not differ significantly between species (no interaction effect between log(mass) and species: $F_{4,35} = 1.60, P = 0.20$). The common scaling exponent of this regression was 1.38 ± 0.07 SE; the intercepts were 0.10, -0.00, -0.13, -0.47 and -0.43, respectively, for Least Sandpiper, Dunlin, Lesser Yellowlegs, Hudsonian Godwit, and Whimbrel (with [Least Sandpiper, Dunlin] > [Lesser Yellowlegs] > [Godwit, Whimbrel]; based on LS means and significance of pairwise differences).

Because the exponent relating DEE to mass was greater than 1, mass-specific DEE also increased with body mass, except in the Dunlin, where the age range was probably too small to reveal an increase with mass (Fig. 2). For a given body mass, mass-specific DEE was generally higher in

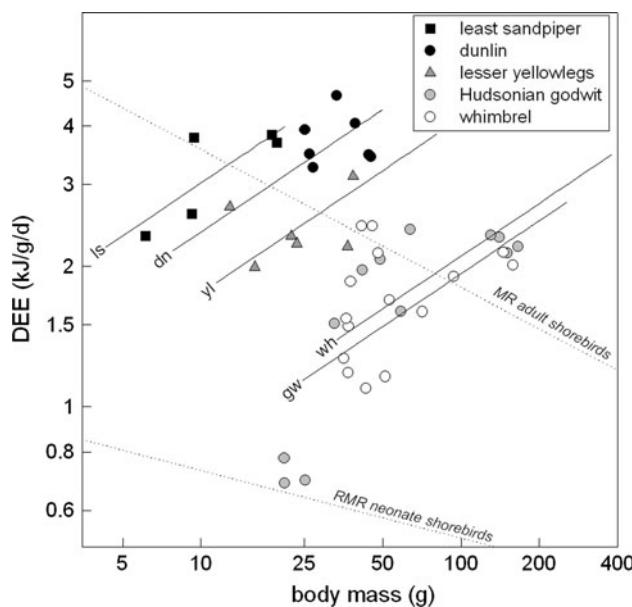


Fig. 2 Daily energy expenditure per gram of body mass as a function of body mass in chicks of five species of shorebirds representing a wide range of body sizes. Regression lines are plotted as solid lines, using a common slope for all five species ($b = 0.38$), and are extended to cover the full range of body masses from neonate to adult. Dotted lines depict the resting metabolic rate of neonatal shorebird chicks [lower line; RMR = $0.020 \times \text{mass}^{-0.145}$ (kJ g $^{-1}$ day $^{-1}$); Visser and Ricklefs 1993a] and the metabolic rate of adult shorebirds exposed to 10 °C [upper line; MR = $912 \times \text{mass}^{-0.296}$ (kJ kg $^{-1}$ day $^{-1}$); Kersten and Piersma 1987]. Levels were higher in chicks of smaller rather than larger shorebird species, and were high from hatching onward, reflecting high costs of locomotion and thermoregulation

chicks of smaller rather than larger species (GLM; $\log(\text{DEE g}^{-1})$ significantly correlated with $\log(\text{mass})$: $F_{1,36} = 33.6$, $P < 0.001$; and with species: $F_{4,36} = 33.1$, $P < 0.001$; $R^2_{\text{model}} = 0.79$, model including wind speed). Dunlin chicks showed the highest values of mass-specific DEE. Hudsonian Godwit and Whimbrel chicks had similarly low levels of mass-specific DEE. Since the within-species scaling exponent for whole-body metabolism was 1.38, mass-specific DEE increased with the 0.38 power of body mass (see McNab 1999; Hayes 2001).

Effect of ambient temperature and wind

The ambient temperature (T_a) in Churchill was high during the DEE measurements, averaging 20 °C, with a minimum of 3 °C and a maximum of 27 °C. Average T_a was below 10 °C for 5 out of 45 measurements, and it was between 10 and 20 °C for 10 measurements. Although DEE increased slightly with decreasing T_a , neither T_a nor radiative/convective load exerted significant effects on DEE.

Wind speed at chick height averaged 0.6 m s $^{-1}$ during the measurements and reached a maximum of 2.9 m s $^{-1}$.

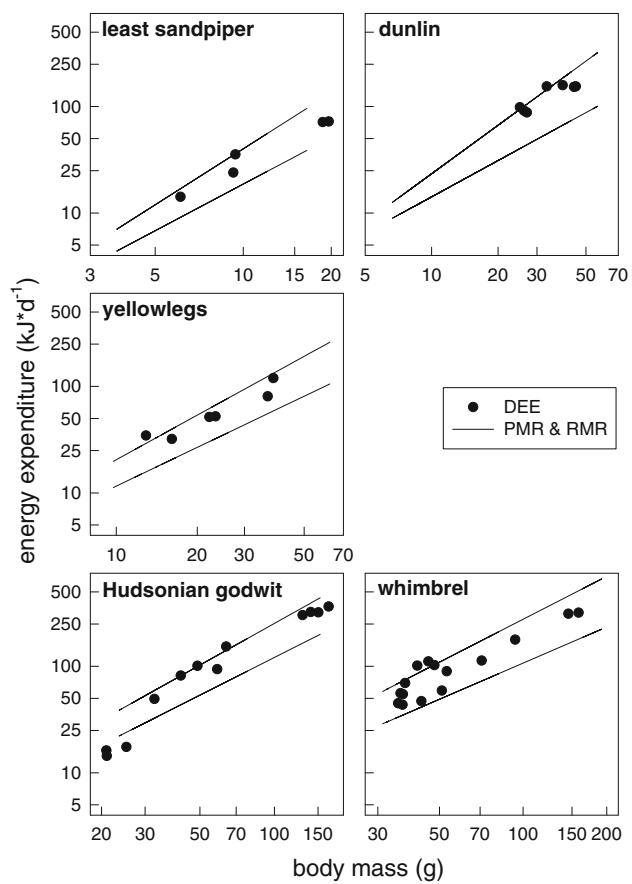


Fig. 3 Daily energy expenditure (symbols) as a function of body mass, in relation to peak and resting metabolic rate (PMR and RMR, lines) in chicks of different species of shorebirds. PMR and RMR are shown as regression lines calculated as described in Williams et al. (2007)

Wind speeds just above ground were considerably lower than wind speeds measured at 10 m above ground, which averaged 4.4 m s $^{-1}$ and reached a maximum of 10.8 m s $^{-1}$. Wind speed at ground level had a significant effect on DEE, but the increase in DEE with increasing winds was negligible [GLM: $\log(\text{DEE})$ correlated significantly with wind speed 10 cm above the ground; effect of minimum wind speed when added to the model: $F_{1,36} = 10.7$, $P < 0.01$, slope = 0.3 log(DEE) units per m s $^{-1}$; R^2_{model} increases from 0.92 to 0.94; DEE was only correlated with wind speed at ground level, not at 10 m altitude].

DEE in relation to peak and resting metabolic rate

In most species, DEE was close to, or exceeded, the peak metabolic rate (PMR) in response to cold stress measured in a flow-through respirometry system in the laboratory (Fig. 3; Williams et al. 2007). DEE was closer to PMR when chicks were small than when they were larger, especially for Least Sandpiper chicks [Fig. 4; GLM:

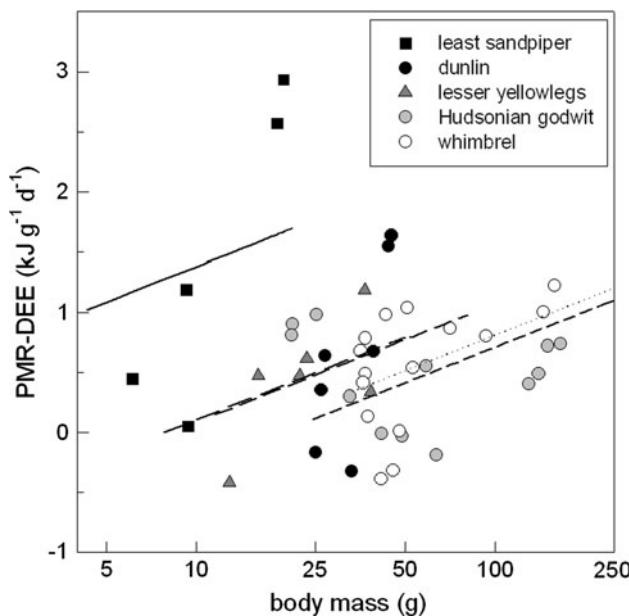


Fig. 4 DEE in relation to PMR plotted against body masses of chicks of different species of shorebirds. Values are the mass-specific peak metabolic rate minus the daily energy expenditure (PMR-DEE). Data on PMR from Williams et al. (2007). Regression lines are plotted using the common slope for all five species ($b = 0.98$) and are extended to cover the full range in body mass from neonate to fledging (increased hatching mass from smallest to largest species)

difference significantly correlated with $\log(\text{mass})$: $F_{1,39} = 6.3$, $P < 0.05$ and species: $F_{4,39} = 4.2$, $P < 0.01$; no interaction effect]. Although the difference between PMR and DEE showed a larger increase with body mass in the smaller species than in the larger species, this difference was not significant, and therefore a common slope is plotted for all five species in Fig. 4.

DEE was closely related to resting metabolic rate [RMR; linear regression DEE vs RMR (both in $\text{kJ g}^{-1} \text{day}^{-1}$): $F_{1,43} = 81.7$, $P < 0.001$, $R^2 = 0.66$]. The elevation of DEE above RMR (DEE-RMR, $\text{kJ g}^{-1} \text{day}^{-1}$) increased with body mass within species, and was larger in the smaller species than in the larger species, with Dunlin showing the highest level and Hudsonian Godwit the lowest [Fig. 5; GLM: mass-specific slope was significantly correlated with $\log(\text{mass})$: $F_{1,39} = 7.8$, $P < 0.01$ and species: $F_{4,39} = 16.7$, $P < 0.001$; overall model $R^2 = 0.63$; no interaction effect].

Discussion

Rapid development of DEE

From hatching onwards, levels of DEE of all five species of shorebird chicks were high compared to those of altricial chicks (Fig. 6). In altricial chicks, DEE was much lower than that of shorebird chicks of a similar body mass, as in

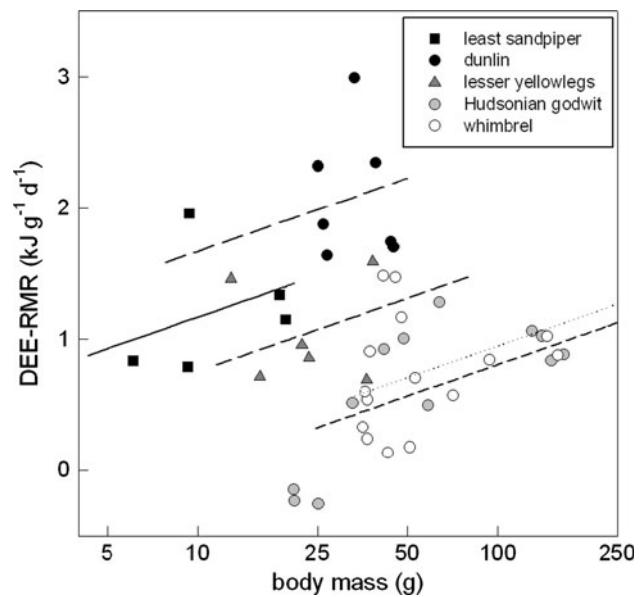


Fig. 5 DEE in relation to RMR plotted against body mass of chicks of different species of shorebirds. Values are the daily energy expenditure minus the resting metabolic rate (DEE-RMR). Data on RMR from Williams et al. (2007). Regression lines are plotted using a common slope for all five species ($b = 0.80$), and are extended to cover the full range of body masses from neonate to fledging (increased hatching mass from smallest to largest species)

for example Yellow-eyed Junco [*Junco phaeonotus*, $\text{DEE} = 0.456 \times \text{mass}^{1.656}$ (kJ/day, g); Weathers and Sullivan 1991] or Savannah Sparrow [*Passerculus sandwichensis*, $\text{DEE} = 0.943 \times \text{mass}^{1.272}$ (kJ/day, g); Williams and Prints 1986]. Neonatal DEE of these altricial chicks was similar to the neonatal RMR of shorebird chicks of a similar body mass (well below shorebird neonatal DEE; Visser and Ricklefs 1993a, b), and only at the end of the nestling period of the altricial species did their DEE reach a level close to, or just above, the neonatal DEE of shorebird chicks of comparable mass.

DEE levels obtained in this study started out well above RMR levels of neonate shorebirds as measured for a range of species by Visser and Ricklefs (1993a, b) (Fig. 2). They corresponded closely to DEE levels found in chicks of other species of shorebirds (Fig. 6), such as Black-Tailed Godwit [*Limosa limosa*; $\text{DEE} = 1.549 \times \text{mass}^{1.092}$ (kJ/day, g); Schekkerman and Visser 2001], Northern Lapwing [*Vanellus vanellus*; $\text{DEE} = 2.037 \times \text{mass}^{1.047}$ (kJ/day, g); Schekkerman and Visser 2001] and Red Knot [*Calidris canutus*; $\text{DEE} = 3.105 \times \text{mass}^{1.078}$ (kJ/day, g); Schekkerman et al. 2003]. Chicks of Avocets (*Recurvirostra avocetta*) in Germany and Spain, which have a similar neonatal body mass to Whimbrel chicks and reach a comparable fledgling mass, exhibited a mass-specific energy expenditure similar to that of Whimbrel chicks [$\text{DEE} = 2.539 \times \text{mass} - 29.94$ (kJ/day, g); Joest 2003].

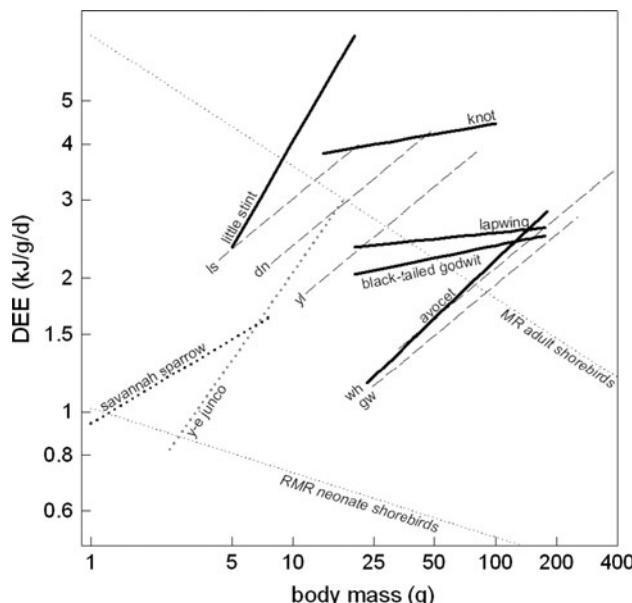


Fig. 6 Comparison of mass-specific DEE between various altricial and precocial species, plotted as a function of body mass. As Fig. 2, with data for two altricial and five precocial species added from the literature. *Dashed lines* precocial species from this study (see Fig. 2); *filled lines* other precocial species; *stippled lines* altricial species. Little Stint—Tjørve et al. (2007); Red Knot—Schekkerman et al. (2003); Northern Lapwing and Black-tailed Godwit—Schekkerman and Visser (2001); Avocet—Joest (2003); Savannah Sparrow: Williams and Prints (1986); Yellow-eyed Junco: Weathers and Sullivan (1991). For additional information see text

DEE increased rapidly with development, as indicated by the high allometric scaling exponent ($b = 1.38$) (Fig. 7). Precocial chicks invest a large proportion of their resources into developing their muscles to increase locomotory and thermoregulatory function (Starck and Ricklefs 1998, Krijgsfeld et al. 2001). Thus, it is not surprising that their metabolic function develops at a high rate, even more rapidly than that of Black-tailed Godwit and Northern Lapwing chicks ($b = 1.09$ and 1.05 , respectively; Schekkerman and Visser 2001). The scaling exponent is, however, unrelated to developmental mode. Scaling exponents for shorebird chicks do not differ consistently from those for other species, including altricial nestlings, which invest more resources into growth and less into mature function [semi-precocial Arctic Tern (*Sterna paradisaea*) and Antarctic Tern (*S. vittata*): $b = 1.31$ on average, Klaassen 1994; semi-precocial Kittiwake (*Rissa tridactyla*): $b = 0.85$, Gabrielsen et al. 1992; altricial Savannah Sparrow: $b = 1.27$, Williams and Prints 1986; altricial Yellow-eyed Junco: $b = 1.66$, Weathers and Sullivan 1991]. Thus, although DEE levels are initially high in precocial chicks, reflecting the high costs of locomotion and thermoregulation, DEE does not subsequently increase more rapidly during the course of development than in more altricial species (Fig. 7).

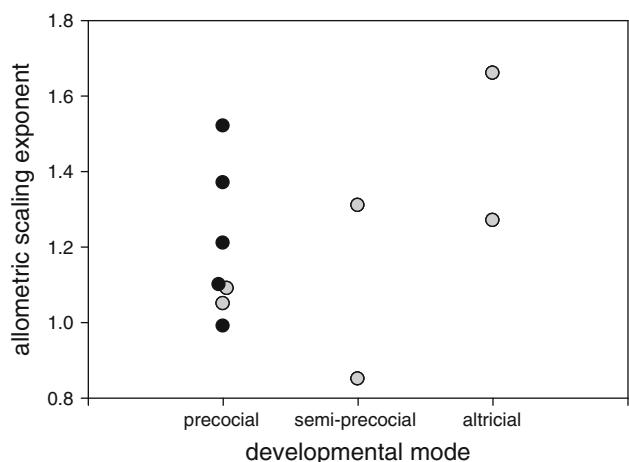


Fig. 7 Allometric scaling exponents (i.e., the slope of the relationship between mass-specific DEE and body mass) for different species of chicks. Despite higher initial levels of DEE in more precocial chicks, DEE does not increase more rapidly during the course of development than in more altricial species. *Black symbols* this study; *gray symbols* precocial Black-tailed Godwit and Northern Lapwing, semi-precocial Arctic and Antarctic Tern (avg) and Kittiwake and altricial Savannah Sparrow and Yellow-eyed Junco; all six obtained from the literature. For specifications and references see text

High DEE in small chicks

Smaller species had higher DEE levels than larger species, for a given body mass. This is in line with the generally higher metabolic intensity of smaller species (e.g., King and Farner 1961) and the fact that, for a given mass, chicks of smaller species are closer to adult size than those of larger species. Relative to the metabolic rates of both neonate and adult shorebirds, chicks of both smaller and larger species showed a high DEE from hatching onward. Relative to their RMR, however, the DEE of chicks of the smaller species exhibited greater mass-specific metabolic increments than that of chicks of larger species. In addition, the growth rates of smaller species were higher than those of larger species. Thus, chicks of small shorebird species not only performed at a relatively high energetic level, but they simultaneously grew at a high rate as well, whereas chicks of larger species performed at a lower level and grew less quickly.

This finding of a positive correlation between function and growth rate contradicts the trade-off between growth rate and mature function postulated by several authors (e.g., Dawson and Evans 1957; Ricklefs 1979; Olson 1992; Konarzewski et al. 2000), and suggests that shorebird chicks can modify the relationship between growth rate and mature function considerably. This supports the results of Krijgsfeld et al. (2001), who demonstrated that catabolic capacity (activity of the enzymes citrate synthase, pyruvate kinase, and hydroxyacyl-CoA-dehydrogenase) in the skeletal muscles of shorebird chicks, especially early in

development, was higher in the smaller and faster-growing chicks of the Dunlin than in the larger and slower-growing chicks of the Whimbrel. A possible explanation for this lies in the allometric scaling of power requirements for locomotion and the relative thermal inertia of larger chicks, which may result in a reduction in energy demands with increasing size. This is consistent with the idea that precocial chicks of larger species on the Arctic tundra are not so much restricted by low Arctic temperatures; they are mainly limited in their northern distribution by the time they need to complete growth during the short summer season. In contrast, chicks of smaller species are constrained by low Arctic temperatures, which challenge their energetic capacities and require them to work at high metabolic levels.

Little Stints (*Calidris minuta*) are similar in size to Least Sandpipers (neonatal mass both 4 g; adult mass 19–24 g vs. 21 in Least Sandpiper) and belong to the same subfamily of Calidridinae. The DEE and growth rate of chicks of Little Stints were measured in Taimyr (arctic Siberia) by Tjørve et al. (2007). The growth rates of the two species were very similar (the logistic growth constant K was 0.23 and 0.24 for Little Stint and Least Sandpiper, respectively, with inflection points of 7.4 and 7.7 days). If the functional capacity of the chicks were directly related to size and/or growth rate, one would expect a similar level of DEE in the two species. However, although the mass-specific DEE of the Little Stint was similar to that of the Least Sandpiper at hatching (both ca. 10 kJ days $^{-1}$), it increased more rapidly with size and thus reached considerably higher levels than the least sandpiper (130–140 kJ days $^{-1}$ at fledging body mass vs. 72 in Least Sandpiper). This could be related to the lower ambient temperatures at Taimyr than at Churchill (8 vs. 20 °C on average, respectively), resulting in Little Stint chicks in Siberia operating at higher energy levels. However, Dunlin chicks, which are slightly larger than Least Sandpiper chicks, and thus were expected to have a lower mass-specific DEE, also reached higher levels of mass-specific DEE than Least Sandpiper chicks under the same environmental conditions in Churchill. These results suggest that in comparison to Dunlin and Little Stint, Least Sandpiper chicks are less able physiologically to meet the energetic demands exerted by ambient conditions in the High Arctic. This could explain why its distribution is more limited in the northern regions.

Wind but not ambient temperature affects DEE

Although DEE tended to decrease slightly with increasing ambient temperature, we found no significant effect of temperature or solar radiation on DEE. For example, the DEE of three Dunlin chicks of intermediate mass, measured under the coldest local circumstances (3 °C), was

similar to the DEE of the other Dunlin chicks. The growth rate of these three chicks was, however, reduced slightly (not significantly) compared to that of the other chicks, which suggests that these chicks may have been foraging less than would be required to sustain growth, and which may have been possible as a result of artificial food provision and indoor housing. No relation between growth and ambient temperatures was observed for the other species. Tjørve et al. (2008) also found no effect of ambient or operative temperature on the DEE of chicks of Kittlitz's Plovers, Blacksmith Lapwings or Crowned Lapwings in Africa, while Schekkerman and Visser (2001) showed a decrease in DEE with increasing temperature for Godwit chicks but not for Lapwing chicks under similar weather conditions. Under Lower Arctic temperatures, Schekkerman et al. (2003) showed that DEE of Knot chicks increased with decreasing ambient temperatures, but not with wind speed.

An explanation for the observed lack of effect of ambient temperature on DEE may be that the amount of heat produced by locomotion is enough to sustain thermoregulation under most circumstances. Because ambient temperatures were relatively high during our study, this may well have been the case. Furthermore, when ambient temperatures are low, chicks spend more time brooding and less time foraging (Beintema and Visser 1989; Krijgsveld et al. 2003b). More brooding reduces energy expenditure at low temperatures (Krijgsveld et al. 2003a), which may counterbalance the effect of cold to increase thermogenesis. This may also explain why DEE was lower when night-time hours comprised a larger proportion of the measurement period, more so than the observed effect of wind speed, but no data on nocturnal brooding behavior were available to test this. When ambient temperatures are lower, chicks would need to spend more energy in order to sustain growth, and under those circumstances DEE might increase at lower ambient temperatures.

When wind speeds were higher, DEE levels did increase slightly. Bakken et al. (2002) showed that natural variation in wind speed had a substantially larger effect than T_a on the thermal conductance of shorebird chicks in Churchill. Thus, whereas the T_a values, which were relatively high for an arctic environment, may not have been low enough to exert an effect on DEE, higher wind speeds did increase DEE through reduced skin temperature and relatively high evaporative water loss (Bakken et al. 2002).

Heat production through locomotion as well as shivering

DEE was similar to cold-induced PMR. This is surprising, as DEE is generally expected to lie below PMR. Part of the explanation may be that PMR was measured by inducing

maximum thermogenic capacities, which was achieved by exposing the chicks to low temperatures (Ricklefs and Williams 2003). Several studies have shown that heat generated during locomotion substitutes thermoregulatory costs (e.g., Zerba and Walsberg 1992; Bruinzeel and Piersma 1998; Marjoniemi et al. 2001). As the chicks were not mobile in the metabolic chamber, heat had to be produced almost entirely by shivering. Especially in younger chicks, which have limited functional capacity, this is likely to have limited heat generation and thus the level of PMR in comparison to free-living chicks, where energy expenditure may be higher as a result of locomotory activity. Thus, measured PMR would be reduced below the PMR that chicks would have been able to achieve under free-living conditions where energy for locomotion adds to thermoregulation. However, small shorebird chicks are often near their limits of temperature regulation, and thus can be expected to generate heat at a near-maximal rate, without a substantial metabolic reserve.

Most animals retain, or can rapidly generate, reserve metabolic capacity (Diamond and Hammond 1992; Toloza et al. 1991; Piersma and Lindström 1997; but see Suarez et al. 1997). PMR in small shorebird chicks may be limited by developmental constraints on muscle tissue. As the chicks grew, the reserve metabolic potential increased, as indicated by the increasing difference between mass-specific PMR and DEE. This was especially true for chicks of Least Sandpiper and Dunlin, where the increase in reserve metabolic potential with body mass was largest. This is likely to be related to the rapid growth of the pectoral muscles of these species later during the chick stage (Krijgsveld et al. 2001; Marjoniemi and Hohtola 1999). The reserve metabolic potential is not used during normal foraging, especially in fair weather conditions such as in Churchill during this study, but it is stimulated in the cold metabolism chamber.

Overall, the chicks of small arctic sandpipers, which are among the smallest homeotherms, are remarkable for maintaining high levels of metabolic activity while also growing rapidly. The chicks of larger species also grow rapidly to achieve a large size during the brief Arctic growing season, but their lower thermal conductance and heat loss result in a lower daily energy expenditure per gram of body mass. Although locomotion contributes to heat production, the higher daily energy expenditure per gram of the chicks of smaller species is more closely related to thermogenic considerations than to foraging. Thus, smaller species are likely more sensitive to variations in temperature and wind speed than larger species, and these environmental conditions undoubtedly limit the northern distributions of these species.

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