Chapter 5

Growth and energetics of a small shorebird chick in a cold environment: the Little Stint, *Calidris minuta*, on the Taimyr Peninsula, Siberia

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Abstract

The Little Stint, *Calidris minuta*, is one of the smallest shorebird species breeding in the Arctic. Their chicks are small and have a high surface area-to-volume ratio which can result in a large energy expenditure due to thermoregulation compared to larger species. We determined prefledging growth, energy expenditure and time budgets for Little Stint chicks in northwestern Taimyr, Siberia. The modified power curve was introduced to model the relationship between daily energy expenditure and body mass. Total metabolisable energy, TME, over the 15-day prefledging period was 107% greater than the allometric prediction for a bird the size of a Little Stint. Little Stint chicks also exhibited fast growth; their growth rate coefficient was 14% greater than the prediction for a bird their size. The growth of young chicks was particularly affected in cool weather which may be due to a reduction in foraging time in order to be brooded and possibly reduced foraging efficiency. Cooler weather may also reduce food availability which can impact foraging efficiency and thus the growth rate of chicks. We did not detect weather effects on energy expenditure of chicks, but lack of temperature variation during energy expenditure measurements may have prevented this. Both growth rate coefficient and energy expenditure of Little Stint chicks were greater than predicted and this is similar to that observed in other arctic shorebird species.
Little Stint growth and energetics

Introduction
Migrant shorebirds brave the low temperatures and high wind velocities of the high Arctic during the summer months, May to August (Chernov 1985, Meltofte et al. submitted manuscript). The Little Stint, *Calidris minuta*, is one of the smallest shorebirds that migrates from as far as southern Africa to the Arctic to breed, and their chicks are among the smallest self-feeding warm-blooded animals on the tundra, weighing 4.3 g upon hatching (Underhill *et al.* 1993, Schekkerman *et al.* 1998a). The highest breeding densities of Little Stints occur in the arctic tundra subzone between 72 °N and 75 °N in Siberia (Rogacheva 1992).

Little Stint chicks are self-feeding precocials (Schekkerman *et al.* 1998a) and in addition to energy needed for growth and development they also require energy for locomotion and thermoregulation whilst foraging (Starck & Ricklefs 1998a). As a result of their small size, Little Stint chicks have a large surface area compared to their body volume and thus lose heat rapidly in the cold (Schekkerman *et al.* 2003). Unlike adult birds, young chicks are incapable of maintaining their body temperature by producing sufficient heat through shivering (Dawson 1975, Visser & Ricklefs 1993a, Krijgsved et al. 2001). In addition, although the down which covers young chicks provides a measure of insulation, it is far less effective than adult plumage (Visser & Ricklefs 1993a). Therefore young chicks require brooding by their parents to insulate them from the cold and to enable their body temperatures to increase by a transfer of heat from the parent after a feeding period (Kendeigh 1969, Krijgsved *et al.* 2001). Chicks of small shorebird species grow relatively more rapidly than larger species (Beintema & Visser 1989b, Krijgsved *et al.* 2001) and Kendeigh (1969) and Krijgsved *et al.* (2001) showed that small species are capable of increasing their metabolism to a relatively higher level than large species to maintain body temperature. The fast growth of chicks of smaller species may be a result of their investing energy in growth and in mature function of tissue to its maximum capacity (Krijgsved *et al.* 2001).

Several studies of the energetics of free-living shorebird chicks have been completed in arctic and temperate zones (Schekkerman & Visser 2001, Joest 2003, Schekkerman *et al.* 2003, Visser *et al.* submitted manuscript) and these show that energy expenditure is greater in shorebirds growing at higher latitudes. We studied the growth and energetics of Little Stint chicks to explore how the energetic demands placed on them by the extreme environment of the arctic tundra and their small size affect their growth. We measured growth rate, daily energy expenditure (DEE) and time-activity budgets during the prefledging period of Little Stint chicks in the field. We compared growth and energy expenditure of Little Stints with predicted values for a species of its size and to values of other arctic and temperate-breeding shorebirds. We hypothesised that due to their small size and high surface area-to-volume ratio, Little Stint chicks have greater energy expenditure than predicted for their body size, and that environmental variation (e.g. weather) has a strong effect on their energy expenditure and time budgets and consequently impacts their growth.
Methods

Study area
Measurements were performed on birds in the vicinity of the Willem Barents Biological Station at Medusa Bay, (73°04'N 80°30'E), near Dikson on the northwestern Taimyr Peninsula, Siberia, Russia. All growth and energetics data were collected in June to August 2002 and time-budget data were collected in the summers of 2000 to 2002. The landscape of the 4 km² main study area is classified as arctic tundra (Chernov 1985), with the highest of the rolling hills reaching 39 m above sea level. The vegetation of the study area is mostly well-vegetated tundra (mosses, lichens, grasses, herbs and dwarf willows *Salix polaris*) with an area of large polygonal bogs to the east. Tulp et al. (2000), Tulp and Schekkerman (2001) and Schekkerman et al. (2004) provide a more detailed description of the study area.

Weather data
Weather conditions for the study site, including ambient air temperature (T a, °C) ca. 1 m above the ground and wind speed (m.s⁻¹) ca. 10 m above the ground, were measured and logged every five minutes. Rainfall (mm) was recorded daily.

Growth measurements
Nests were located during laying or incubation. Hatch date was estimated using floatation tests (van Paassen et al. 1984, Schekkerman et al. 2004), and nests were monitored intensively close to the predicted hatch date. Chicks were ringed and weighed either in the nest cup or when broods were encountered on the tundra. Throughout the prefledging period, chicks were recaptured when encountered to record their growth. Mass (to the nearest 0.1 or 0.5 g) was measured using Pesola spring balances. Chicks were released at the site of their capture.

Mean masses for hatchlings were determined in the nest and for prefledglings measured on their last capture at 14 to 15 days old. All chicks of known age with an accuracy of 24 hours and for which at least two measurements were taken, were used to describe growth of body mass. Growth parameters were determined for the Gompertz,

\[ M = A \cdot \exp (-\exp (-K \cdot (t - T))) \]

and logistic,

\[ M = A/(1 + \exp (-K \cdot (t - T))) \]

growth models and the fits of both growth curves were compared. In these growth models, the parameter \( M \) is body mass (g), \( A \) is the asymptotic body mass (g), \( K \) is the growth coefficient (d⁻¹), \( t \) is the age of the chick (d) at the time of the observation, and \( T \) is age at the point of inflection (d). The better fitting curve was chosen to describe the data. Chicks fledge while still increasing in mass, and it is not feasible to obtain a biologically meaningful estimate of the asymptote. The asymptote of body mass, \( A \), was therefore fixed at the mean adult body mass observed in the study area, 26.6 g (Tulp et al. 2002). The growth rate coefficient for the Gompertz curve, \( K_G \), or the logistic curve, \( K_L \), and the point of inflection were estimated for individual chicks through regression. The median values were taken as the growth rate coefficient and
point of inflection for the species. Parameter estimations were only obtained from chicks which were presumed to fledge successfully (data from chicks that were known not to fledge were removed from the analysis), to produce a curve for “normal successful” growth.

Growth of chicks may be influenced both by temperature (affecting energy expenditure and the time available for foraging instead of being parentally brooded) and by food availability. As growth of shorebird chicks follows an S-shaped curve, therefore we compared the growth rate coefficients of chicks at different ages and over different intervals by means of a growth index (growth observed / growth predicted over the same time interval from the fitted growth curve for Little Stint chicks for the 2002 breeding season (cf. Schekkerman et al. 2003)). Growth indices were determined for chicks which were captured at two to five day intervals. The growth indices were normally distributed (Kolmogorov-Smirnov test: KS = 0.05209, P > 0.10). These growth indices were used to analyse the dependence of growth rate on mid-interval date (the date midway between the first and last measurement of the chick) and ambient temperature (Tₐ, °C) during the recapture interval through linear regression. Since shorebird chicks often lose mass during the first day(s) after hatching and this is not reflected in the fitted standard growth curves (Schekkerman et al. 1998a, 1998b, Tjørve et al. submitted manuscript-a), growth indices for chicks first weighed when less than a day old (often still in the nest) tend to be lower than those for older chicks. Therefore, we analysed the growth of neonates up to 5 g and chicks greater than 5 g at the start of the recapture interval separately.

**Energetic expenditure measurements using DLW**

Daily energy expenditure (DEE, kJ.d⁻¹), defined as energy expenditure excluding that which is deposited into tissue, was measured using the doubly labelled water (DLW) technique (Lifson & McClintock 1966, Nagy 1980, Speakman 1997, Visser & Schekkerman 1999) on free-living chicks. Either single chicks or siblings in families with up to four chicks were captured, weighed to the nearest gram and then injected subcutaneously in the ventral region with 0.05 to 0.1 ml of DLW, depending on the mass of the chick. The DLW consisted of 36.7% D₂O and 59.9% H₂¹⁸O. Both two-sample (Nagy 1983) and single-sample (Webster & Weathers 1989) DLW protocols were used. The Little Stint chicks subjected to the two-sample protocol were kept warm in a well-ventilated cloth bag containing a hot water bottle after their injection for an equilibration period of approximately one hour after which four to six 10–15 μl initial blood samples were collected from the brachial vein, into glass capillary tubes, which were flame-sealed with a propane torch within minutes. These chicks were then released to their parent which stayed nearby during processing. Chicks subjected to the single-sample protocol and were released directly after the DLW injection, and no initial blood samples were taken. Broods were relocated and chicks recaptured after approximately 24 hours, and mass measurements and final blood samples were taken. Blood samples were collected from four chicks before injection with DLW to measure background isotope levels.


$^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ ratios in the blood samples were analysed with a SIRA 9 isotope ratio mass spectrometer at the Centre for Isotope Research, University of Groningen, following procedures described by Visser and Schekkerman (1999) and Visser et al. (2000a). Due to difficulties injecting exactly known quantities of DLW (especially in small chicks), the chick's body water pool ($N$, moles) was estimated using the equation for shorebird chicks (modified from Schekkerman and Visser 2001) by inserting the appropriate body mass into the function:

$$N = 0.000556 \cdot M \cdot (79.86 - (9.55 \cdot (M/26.6))),$$

where $M$ represents the chick's body mass (g) during the DLW measurement, taken as the average of the initial and final masses, and 26.6 is the asymptotic body mass (g). Daily rates of carbon dioxide production were determined using the methods described and validated for growing chicks by Visser and Schekkerman (1999), Visser et al. (2000b) and Schekkerman and Visser (2001). Rates of carbon dioxide production were converted to DEE using a factor of 27.3 kJ.l$^{-1}$ of carbon dioxide produced (Gessaman & Nagy 1988). Analyses were done in triplicate and averaged.

**Statistical analysis and a new model to establish the relationship between DEE and body mass.**

The relationship between daily energy expenditure (DEE, kJ.d$^{-1}$) and body mass, $M$ (g), in growing chicks is usually modelled using the power curve,

$$\text{DEE} = a \cdot M^b,$$

where $a$ represents a coefficient and $b$ represents the allometric scaling exponent (e.g., Weathers & Siegel 1995, Schekkerman & Visser 2001, Visser & Schekkerman 1999). The power curve can be rewritten as a straight line in log-log space,

$$\log (\text{DEE}) = A + b \cdot \log M,$$

where $A$ equals $\log a$, with $A$ (and therefore $a$) and $b$ estimated by linear regression. This model assumes a single allometric scaling exponent throughout the development period. However, this model was not appropriate for the Little Stint data (see Results).

In the past, a non-linear relationship in log-log space has been solved by applying two different power curve functions to specific phases of the postnatal period, the biphasic approach, e.g. Freeman (1967) described the resting metabolic rate of Japanese Quail, *Coturnix coturnix japonica*, using the biphasic approach and Dietz and Ricklefs (1997) used this type of analysis to determine the moment in development when metabolism changed dramatically. This biphasic approach estimates a break-point between the two models that is a mathematical artefact rather than a distinct physiological event. Weathers and Siegel (1995) found that this type of analysis did not adequately describe the metabolism of four out of 15 species included in their analysis. In addition, this method would require five estimated parameters; four for the two power curves and one for the break-point between them. We modified the original power curve by adding a third parameter so that the scaling exponent becomes $(b - (c/M))$ and varies with body mass,

$$\text{DEE} = a \cdot M^{b - (c/M)},$$

where $a$, $b$ and $c$ are coefficients to be estimated. This model is more parsimonious than the biphasic approach, with three parameters in place of five, and it overcomes
the mathematical artefact of the break-point between the two curves. The three parameters can be estimated by standard multiple linear regression software, because it can be written in the form:

$$\log (\text{DEE}) = A + b \cdot \log M + c \cdot M^{-1} \cdot \log M$$

in log-log space, where $A$ is log $a$ and $M$ is body mass (g). The parameters of this model cannot be directly compared to those of the power curve. To keep the results in this paper comparable to those of previous studies, analyses were completed using both the modified power curve and the traditional power curves. The programme GraphPad Prism (Motulsky & Christopoulos 2004) was used for both regressions. Because the power curve and the modified power curve are nested models, we used the F-test to determine which better fits the DEE data for Little Stints (Motulsky & Christopoulos 2004). The modified power curve used to describe the relationship between DEE and mass was the best-fitting model available to us at the time of the analysis. There may be another model that could better describe the data. This requires further consideration.

The DEE data were tested for outliers using Grubb’s test (Motulsky & Christopoulos 2004), and the pattern of the residuals of the regressions were tested using the Wald-Wolfowitz Runs Test (Motulsky & Christopoulos 2004). We note that the DEE data contains repeated measures for chicks and that there may be brood affects in both the DEE and the growth data. There were no clustered deviations from the fitted curve, so we used the above method to give primary insights into the data. The investigation of the effects of repeated measures and brood effects may require a larger data set and thus warrants investigation.

The impact of weather and food availability on DEE was determined through stepwise linear regression using the equation:

$$\log (\text{DEE}) = A + b \cdot \log M + c \cdot M^{-1} \cdot \log M + d \cdot T_a + e \cdot \text{wind speed} + f \cdot \text{rainfall}.$$ 

The additional explanatory variables were tested both untransformed, as done by Schekkerman and Visser (2001) and Schekkerman et al. (Schekkerman et al. 2003), and after logarithmic transformation.

**Energy budget estimation**

Prefledging energy budgets were constructed on the basis of the average body mass growth curve for free-living chicks. Metabolisable energy (ME) is the sum of two components: DEE and energy that is converted into tissue (E\text{tis}, kJ.d⁻¹). DEE measured through the DLW method constitutes resting metabolic rate (RMR, kJ.d⁻¹), energy used for assimilation of nutrients and tissue synthesis (E\text{syn}, kJ.d⁻¹), and the energy costs of thermoregulation and activity (E\text{tr+act}, kJ.d⁻¹). RMR and E\text{tr+act} were not determined separately for Little Stint chicks, but a combined value was estimated. E\text{tis} was estimated as the daily increment of the product of body mass and energy density using the equation

$$E_{\text{tis}}(t) = M_t (4.38 + 3.21 (M_t/26.6)) - M_{t-1} (4.38 + 3.21 (M_{t-1}/26.6))$$

where $M_{t-1}$ and $M_t$ are the masses (g) estimated by the logistic growth curve for days $t-1$ and $t$, and 26.6 is the asymptotic mass (g) for the species (Schekkerman & Visser 2001).
The relationship between ME and body mass was modelled using the power curve and the modified power curve. The impact of weather on ME was determined through stepwise linear regression using the modified power curve, as for the DEE.

Peak daily metabolisable energy (peak DME, kJ.d⁻¹) is the maximal daily energy demand of chicks across the prefledging period (Weathers 1992). Precocial birds often fledge before attaining adult mass (Fjeldså 1977, Starck & Ricklefs 1998a), thus their energy requirements may continue to increase after fledging. Little Stint chicks fledge at 73-92% of adult mass. Total metabolisable energy (TME, kJ) was estimated as the total amount of energy metabolized during the prefledging period. Assuming a synthesis efficiency (E_syn) of 75% (Ricklefs 1974), total energy for growth (kJ) was estimated as the sum of daily E_tis and E_syn values across the prefledging period (i.e. 1.33 \cdot [sum of daily E_tis values]). The energy used for RMR and E_tr + act was estimated by subtracting the total energy for growth from TME. Growth efficiency (%) was estimated as the sum of the daily E_tis values divided by TME.

To study the impact of the type of curve used on the estimates for peak DME and TME, energy budgets were calculated based on both the power curve and the modified power curve.

**Time budget**

Observations were made on six different broods in 2000, 2001 and 2002. Observation periods (n = 40) were scattered throughout the 24 hours of daylight and at all stages of chick development, from hatching to 17 days, and totalled 60.9 hours in bouts of 38-130 minutes (mean = 91, SD = 25 min). Chick behaviour was categorised as brooding, foraging, or other behaviours (including preening, walking and hiding at the adult’s alarm). The proportion of total observation time spent brooding was modelled in relation to age, temperature and whether it was ‘day’ (04:00 to 22:00 h) or ‘night’ (22:00 to 04:00 h) using multiple logistic regression (generalised linear models with logit link function, binomial error distribution, and total minutes per observation bout as the binomial totals).

**Results**

**Environmental conditions**

During the period that unfledged chicks were present, average ambient temperature, T_a, was 8.6°C (SD = 3.6). Rainfall during the period when unfledged chicks were present was greater than recorded in the previous two summers at the same study site. As a possible result of cool temperatures and rainfall, the peak in arthropod abundance was narrow, about a week around 20 July (Schekkerman et al. 2004).

**Chick growth**

Throughout the prefledging period, 338 captures and recaptures were made of 98 chicks from 34 broods. Fifty-nine chicks were caught at least once after they were five days old. Median hatching mass of chicks found in the nest cup was 4.3 g (mean = 4.2, range = 3.2–4.9, SD = 0.3, n = 57). Chicks fledged when 14–16 days old
(based on last capture), weighing between 19.3 and 24.4 g (mean = 22.3, SD = 1.9, n = 5). This was 73% to 92% of body mass of adult Little Stints, 26.6 g (Tulp et al. 2002).

Although no formal test was possible, the logistic growth model seemed to fit the body mass data of Little Stints as well as or slightly better than the Gompertz growth model. Body mass \( M, g \) in relation to age \( t, d \) was described as:

\[
M = \frac{26.6}{1 + \exp (-0.234 \cdot (t - 7.40))}
\]

\( (\text{SE}_{KL} = 0.006, \text{SE}_{T} = 0.169, n = 99, \text{Figure 5.1}) \).

Significant negative relationships were found between the growth index and mid-interval date (Table 5.1), indicating that there was a seasonal effect on growth. Chicks that hatched early in the breeding season grew faster than those that hatched later. Mid-interval date was negatively correlated to ambient temperature (Pearson Product Moment Correlation: \( r = -0.565, n = 89, P < 0.001 \)). The growth index was positively related to ambient temperature \( T_{a}, ^{\circ}C \) in young chicks up to two days of age, but not in older chicks (Figure 5.2, Table 5.1). The results using the different growth indices indicate that Little Stint chicks in Medusa Bay in 2002 did not grow as rapidly as has been observed in this species previously.

![Figure 5.1](image)

**Figure 5.1.** The growth of Little Stint chicks at Medusa Bay in 2002. The data points show individual measurements of chicks, and the curve is the logistic growth function, \( M = \frac{26.6}{1 + \exp (-0.234 \cdot (t - 7.40))} \), based on the medians of individual fitted curve parameters; see text for method.
Figure 5.2. Growth index over recapture intervals of Little Stint chicks at Medusa Bay in 2002, in relation to (A) mid-interval date and (B) mean ambient temperature. Filled circles and the solid line represent chicks up to two days old, and open circles and the dashed line represent chicks older than two days old.

Table 5.1. Growth index of body mass in free-living Little Stint chicks at Medusa Bay in 2002 and mid-interval date (middle date between first and last measurement), and ambient temperature, $T_a$; for more detail see text and Figure 5.2.

<table>
<thead>
<tr>
<th>Age of chicks</th>
<th>Predictor variable</th>
<th>Regression coefficients ± SE</th>
<th>( \beta )</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Constant</td>
<td>Predictor</td>
<td>( r^2 )</td>
<td></td>
</tr>
<tr>
<td>All</td>
<td>Mid-interval date</td>
<td>1.392 ± 0.195</td>
<td>-0.017 ± 0.007</td>
<td>0.061</td>
</tr>
<tr>
<td>0–2 days</td>
<td>Mid-interval date</td>
<td>1.486 ± 0.263</td>
<td>-0.041 ± 0.011</td>
<td>0.232</td>
</tr>
<tr>
<td>&gt;2 days</td>
<td>Mid-interval date</td>
<td>1.918 ± 0.408</td>
<td>-0.032 ± 0.014</td>
<td>0.116</td>
</tr>
<tr>
<td>All</td>
<td>$T_a$</td>
<td>0.731 ± 0.124</td>
<td>0.024 ± 0.014</td>
<td>0.031</td>
</tr>
<tr>
<td>0–2 days</td>
<td>$T_a$</td>
<td>0.503 ± 0.154</td>
<td>0.041 ± 0.015</td>
<td>0.135</td>
</tr>
<tr>
<td>&gt;2 days</td>
<td>$T_a$</td>
<td>1.293 ± 0.436</td>
<td>-0.043 ± 0.059</td>
<td>0.012</td>
</tr>
</tbody>
</table>

Energy expenditure

Twenty-nine measurements of DEE were made on 22 free-living chicks from eight broods. Seven chicks had two measurements made on them, at intervals of at least four days. In the 21 cases when the two-sample protocol was used, the initial blood sample was taken after an equilibration period of 0.50 to 1.27 hours (mean = 0.81, SD = 0.18). Final blood samples of these chicks were taken 24.0–24.1 hours after the initial samples were taken (mean = 24.0, SD = 0.02, \( n = 21 \)). Eight DLW measurements were taken using the single sample method; three of these were for repeated measurement chicks and five were completed on small chicks weighing less than 6 g. These chicks were sampled 24.0–24.1 hours after injection (mean 24.0,
During all experiments, chicks gained mass at an average rate of 0.82 g.d⁻¹ (range = 0.10 – 3.50, SD = 0.74, n = 29). The mean growth index over the DLW measurement interval was 0.97 (SD = 0.040, range = 0.39 – 1.39, n = 29), hence the DLW chicks grew as fast as other chicks in the field.

The DEE data showed a normal distribution with no outliers. The power curve relationship between DEE (kJ.d⁻¹) and body mass (M, g) was:

\[\text{DEE} = 0.655 \cdot M^{1.793}\] (Figure 5.3a)

\((r^2 = 0.937, \text{SE}_a = 1.256, \text{SE}_b = 1.227, n = 29)\). This power curve tended to underestimate DEE in chicks of 10 to 15 g, and to overestimate DEE in chicks heavier than 20 g (Figure 5.3a). The Runs test showed that the data did not follow the power curve (Runs test: \(n_1 = 16, n_2 = 13, n = 6, P < 0.001\)). The inclusion of an additional term to form the modified power curve significantly improved the fit (F-test: \(F = 62.0, df = 1, 26, P < 0.0001\)):

\[\text{DEE} = 10^{13.30} \cdot M^{-5.610 - \left(\frac{60.02}{M}\right)}\] (Figure 5.3b).

\((r^2 = 0.981, \text{SE}_a = 51.76, \text{SE}_b = 7.625, \text{SE}_c = 0.942, n = 29)\). The residuals of the modified power curve were evenly distributed along the fitted curve through the body mass range (Runs test: \(n_1 = 15, n_2 = 14, n = 12, P > 0.1\)).

According to the modified power curve daily energy requirements of Little Stints increased during the prefledging period, from 8.0 kJ.d⁻¹ in the first day after hatching to 128.0 kJ.d⁻¹ in a 22.4 g chick that was close to fledging (i.e. aged 15 days).

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**Figure 5.3.** The relationship between daily energy expenditure (DEE, kJ.d⁻¹) and daily metabolisable energy (ME, kJ.d⁻¹), with body mass (g) of Little Stint chicks at Medusa Bay in 2002 described by (A) the power curve and (B) the modified power curve. The solid circles and solid line represent the DEE data and the fitted allometric relationship, and the open circles and dotted line represent the ME data and the fitted allometric relationship.
The average ambient temperature at Medusa Bay during the DEE measurements was 7.8°C (range = 5.1–10.3, SD = 1.22, n = 29), mean wind speed was 7.1 m.s⁻¹ (range = 4.9–8.9, SD = 1.36, n = 29) and mean rainfall was 2.7 mm (range = 0.0–7.0, SD = 2.66, n = 29). The fit of the modified power curve was not significantly improved through the inclusion of Tₐ (P = 0.315), wind speed (P = 0.221) or rainfall (P = 0.318) during the DLW measurement. Log-transforming the weather variables before inclusion in the regression did not change the results.

**Energy budget**

The relationship between ME (kJ.d⁻¹) and body mass (M, g) can be described by the power curve,

\[ ME = 1.0859 \cdot M^{1.651} \]  (Figure 3a)

(\(r^2 = 0.943, SE_a = 1.219, SE_b = 0.078, n = 29\)). The inclusion of the additional term to form the modified power curve resulted in

\[ ME = 2.33311 \cdot M^{-4.585} - \left( \frac{50.564}{M} \right) \]  (Figure 3b)

(\(r^2 = 0.945, SE_a = 39.719, SE_b = 0.878, SE_c = 7.113, n = 29\)). According to the F-test, the power curve was the better fitting model (F-test: \(F = 2.91, df = 1, 26, P < 0.0999\)). The residuals of the power curve were, however, distributed in clumps along the fitted curve (Runs test: \(n_1 = 11, n_2 = 18, u = 8, P < 0.01\)). The residuals of the modified power curve were more evenly distributed through the body mass range (Runs test: \(n_1 = 13, n_2 = 16, u = 12, P > 0.05\)). Thus we chose to use the modified power curve for these data also.

The fit of the modified power curve was not significantly improved by the inclusion of Tₐ (P = 0.166), wind speed (P = 0.576), or rainfall (P = 0.274) over the ME measurement period or the logarithm of these variables.

Peak DME (at 15 days) of Little Stint chicks was 137.1 kJ.d⁻¹ (Figure 5.4, Table 5.2), and TME over the 15-day prefledging period was 1348.4 kJ (Table 5.2). Growth efficiency of Little Stint chicks up to 15 days old was 11%; 14% of TME was allocated to growth and 86% to RMR and Eₜₜ+ₜₚ. Peak DME and TME estimated using the power curve were greater than those estimated by the modified power curve (Table 5.2). This is a result of overestimations by the power curve in larger chicks (Figure 5.3a). Average daily metabolisable energy, (ADME), which is TME divided by both fledging mass (g) and time to fledging (d, Weathers 1992), was 3.95 kJ.g⁻¹.d⁻¹ for Little Stint chicks.
**Figure 5.4.** Prefledging energy budgets for free-living Little Stint chicks at Medusa Bay in 2002 growing at an average rate from hatching to fledging. Components shown are daily energy expenditure (DEE), energy in tissue ($E_{\text{ts}}$) and metabolisable energy intake (MEI).

**Table 5.2.** Energy budget results from the power curve and the modified power curve describing the relationship between body mass and DEE for Little Stint chicks at Medusa Bay in 2002.

<table>
<thead>
<tr>
<th></th>
<th>Power curve</th>
<th>Modified power curve</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak DME (kJ.d$^{-1}$)</td>
<td>185.9</td>
<td>137.1</td>
</tr>
<tr>
<td>TME (kJ)</td>
<td>1413.8</td>
<td>1348.4</td>
</tr>
<tr>
<td>Relative Peak DME (% above the prediction)</td>
<td>196.6</td>
<td>118.8</td>
</tr>
<tr>
<td>Relative TME (% above the prediction)</td>
<td>116.9</td>
<td>106.9</td>
</tr>
<tr>
<td>Total energy accumulated (kJ)</td>
<td>142.7</td>
<td>142.7</td>
</tr>
<tr>
<td>Energy of heat produced in biosynthesis (kJ)</td>
<td>47.5</td>
<td>47.5</td>
</tr>
<tr>
<td>Total energy for growth including biosynthesis (kJ)</td>
<td>190.2</td>
<td>190.2</td>
</tr>
<tr>
<td>Growth efficiency (%)</td>
<td>10.1</td>
<td>10.6</td>
</tr>
<tr>
<td>Total energy for growth (%)</td>
<td>13.5</td>
<td>14.1</td>
</tr>
<tr>
<td>Total energy for RMR, $E_{\text{th+act}}$ (%)</td>
<td>86.5</td>
<td>85.9</td>
</tr>
</tbody>
</table>
**Time budget**

Chicks up to one week old spent an average of 46% (SD = 23, n = 28) of their time brooding and 52% of their time foraging (SD = 22, n = 28). Chicks older than that spent 21% (SD = 27, n = 12) of their time brooding and 76% of their time foraging (SD = 27, n = 12). Other activities, including preening, walking and vigilance, were observed for only 2% (SD = 4) of the time during the first week and 3.5% thereafter. Little Stint chicks therefore spent most of their “unbrooded” time foraging.

The proportion of time brooded decreased significantly with increasing age and with increasing temperature (Table 5.3, Figure 5.5a). The regression lines in Figure 5.5a overestimates the brooding times of older chicks as few observations were made on chicks older than 12 days which effectively no longer require brooding. In addition there was a tendency for brooding time to be increased between 22:00 and 04:00 hours (Figure 5.5b), indicative of a circadian activity rhythm with sleep accommodated into night-time brooding bouts, but this was not entirely significant (P = 0.10), probably as a consequence of the small sample size for “night” relative to “day”. Interactions between age, temperature and ‘night’ proved not significant (all P > 0.13), nor were additional effects of wind (P = 0.47), or rainfall (P = 0.38), if included in a model containing age and temperature. Results were very similar if body mass was used as a predictor of brooding time instead of age (Table 5.3).

![Figure 5.5. Percentage of time Little Stint chicks at Medusa Bay in 2002 spent being brooded in relation to (A) age (d) and air temperature (°C), (logistic regression lines shown for the lowest, mean and highest air temperatures during observations); and (B) age (d) and whether broods were observed during the ‘day’ (04:00-22:00 h) or at ‘night’ (22:00-04:00 h), (regression lines shown for the mean air temperature of 7°C).](image-url)
Table 5.3. Logistic regression analysis for brooding time of Little Stint chicks at Medusa Bay in 2000, 2001 and 2002. Modelled with (A) age and (B) body mass. F-probabilities are for terms sequentially added to the model; estimates (logit proportion of time brooded) are for the final model including all variables).

<table>
<thead>
<tr>
<th>Variable added</th>
<th>df</th>
<th>Change in deviance</th>
<th>Deviance ratio</th>
<th>F-probability</th>
<th>Estimate (logit)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>constant</td>
<td>1</td>
<td>1195.0</td>
<td></td>
<td>&lt;0.001</td>
<td>1.6410</td>
<td>0.4770</td>
</tr>
<tr>
<td>age</td>
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<td>323.8</td>
<td>22.2</td>
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<td>0.0447</td>
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<tr>
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<td>285.7</td>
<td>19.6</td>
<td>&lt;0.001</td>
<td>-0.2006</td>
<td>0.0561</td>
</tr>
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<td>1</td>
<td>40.8</td>
<td>2.8</td>
<td>0.103</td>
<td>0.6000</td>
<td>0.3670</td>
</tr>
<tr>
<td>residual</td>
<td>36</td>
<td>544.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>constant</td>
<td>1</td>
<td>1195.0</td>
<td></td>
<td>&lt;0.001</td>
<td>1.775</td>
<td>0.5250</td>
</tr>
<tr>
<td>mass</td>
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<td>13.4</td>
<td>&lt;0.001</td>
<td>-0.1021</td>
<td>0.0342</td>
</tr>
<tr>
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<td>329.6</td>
<td>20.7</td>
<td>&lt;0.001</td>
<td>-0.2069</td>
<td>0.0576</td>
</tr>
<tr>
<td>‘night’</td>
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<td>55.9</td>
<td>3.51</td>
<td>0.069</td>
<td>0.704</td>
<td>0.3850</td>
</tr>
<tr>
<td>residual</td>
<td>36</td>
<td>595.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Discussion

A new function to describe energy expenditure

The modified power curve with a gradually changing allometric scaling exponent provided a significantly better fit to the daily energy expenditure (DEE) versus body mass relationship than the power curve with a constant scaling exponent. In shorebird neonates, mass-specific resting metabolic rate (RMR) is at about 50% of the level observed in adult non-passerine birds (Visser & Ricklefs 1993a). During early postnatal growth RMR increases rapidly with increasing body mass (intraspecific allometric scaling exponents being about 2 initially and about two thirds thereafter) to approach adult levels. In the past, multiphasic analyses have been performed in an attempt to describe these changes in RMR (Dietz & Ricklefs 1997), but it is unlikely that changes in the RMR versus body mass relationship occur instantly at a specific body mass. In free-living chicks, DEE versus body mass relationships may exhibit an even more pronounced pattern, because the aforementioned changes in RMR are accompanied by major behavioural changes during ontogeny, e.g. in the time spent actively foraging. Because both physiological and behavioural changes occur gradually the changes in DEE with increasing body mass are better described by a model containing gradual change in the allometric scaling exponent, like the modified power curve.

According to Tulp et al. (submitted manuscript) adult Little Stints in Medusa Bay have a DEE of 154–160 kJ.d⁻¹ during incubation and chick rearing. The modified power curve for chicks predicts a DEE of 124 kJ.d⁻¹ at adult body mass (26.6 g), ca. 20% below measured adult values. Given the differences in behaviour between adults and chicks (e.g. energy-demanding flights are not made by chicks) this seems a reasonably close match. Extrapolation of the power curve results in a difference of 145% in the opposite direction. The better fit of the modified power curve will therefore also improve the estimates for peak daily metabolisable energy (peak DME) and total metabolisable energy (TME) of Little Stint chicks (Table 5.2).
**Little Stint chick energetics**

Our estimates of prefledging metabolism in Little Stint chicks, as summarised in values for peak DME and TME can be compared to those of other birds by contrasting them to allometric predictions based on fledgling body mass \((M_f, \text{g})\) and the length of the prefledging period \(t_{fl}, \text{days}\) (Weathers 1992):

\[
\text{predicted peak DME} = 11.69 \cdot M_f^{0.9082} \cdot t_{fl}^{-0.428},
\]

and

\[
\text{predicted TME} = 6.65 \cdot M_f^{0.852} \cdot t_{fl}^{0.71}.
\]

Observed peak DME and TME of Little Stint chicks were 119% and 107% greater than predicted, respectively. Schekkerman et al. (2003) found that the observed TME of Red Knots at 75°N was 89% above the predicted value and that this large relative TME conformed to that observed in other arctic-breeding bird species. As observed in Little Stint chicks of this study, the ADME of arctic-breeding Red Knots was also large, 2.58 kJ·g⁻¹·d⁻¹ (Schekkerman et al. 2003). Therefore Little Stint chick energetics showed similar trends to that observed in other arctic-breeding birds.

Shorebird chicks in the Arctic grow rapidly in comparison to the expected growth rates for their size (Schekkerman et al. 1998a, Schekkerman et al. 1998b, Schekkerman et al. 2003), and precocial chicks in cooler temperatures exhibit greater overall energy expenditure than expected as a result of increased metabolism (Visser & Ricklefs 1993b). Krijgsveld et al. (submitted manuscript) found that the chicks of smaller arctic shorebirds had a greater mass-specific DEE than larger species, indicating a higher metabolic capacity (DEE versus RMR) than chicks of larger species. In addition, Krijgsveld et al. (submitted manuscript) argued that smaller shorebirds were simultaneously capable of rapid growth.

The fast growth and large energy expenditures of shorebird chicks at high latitudes can only be sustained through sufficient food intake. Lack (1968) suggested that that the presence of arthropods increased with latitude. Schekkerman et al. (2003) found no significant difference in arthropod availability between the arctic tundra at Cape Sterlegov, and temperate meadow. The higher intake rate of Red Knot chicks was tentatively attributed to the simpler structure of the tundra vegetation and a larger proportion of wingless or slow-moving arthropods making prey capture easier. This may also apply to Little Stint chicks.

Being brooded can reduce the heat loss of chicks to the environment and thus can reduce energy expenditure (Krijgsveld et al. submitted manuscript). The amount of time Little Stint chicks spent brooding decreased with age, and chicks were rarely observed to be brooded during the day after the age of 10 days. However, neither Little Stint chicks (this study) nor Red Knot chicks (Schekkerman et al. 2003) took full advantage of the 24-hour arctic daylight period.

*The impact of environmental conditions on energy expenditure, time budgets and growth of Little Stint chicks*

Growth rate can be influenced by bouts of cold and wet weather (Beintema & Visser 1989a). Schekkerman et al. (1998a, 2003) found that cold weather resulted in a reduction of growth rate in Curlew Sandpipers and Red Knots, respectively.
Environmental conditions (weather and arthropod availability) may affect chick energy budgets in several ways. Adverse weather may increase energy expenditure, reduce feeding time through an increase of brooding, and reduce feeding success through a diminished availability of insect prey. Although larger chicks do not suffer the same time thermoregulatory constraints as young chicks, reduced food availability can have a similar effect on their foraging efficiency and thus their growth.

We found no significant effect of ambient temperature, wind or rain on DEE or ME. The range of mean ambient temperatures during DEE measurements was small (5–10°C) compared to the range occurring at Medusa Bay over the chick-rearing period (1–17°C, unpubl. data 2000-2002). Consequently, our sample had limited power to show such effects.

Homeothermy in precocial chicks develops during the prefledging period (Visser & Ricklefs 1993ab). At low ambient temperatures the body temperature of young chicks decreases more rapidly (Norton 1970, Visser & Ricklefs 1993ba) and to a lower level (Krijgsveld et al. 2003a) whilst foraging than in warm temperatures. This reduces mobility, rate of food intake (Krijgsveld et al. 2003a) and possibly digestive efficiency (Kleiber & Dougherty 1934, Hume 2005). In periods of cold weather when energy expenditure for thermoregulation and activity is great or when intake rate is reduced through diminished prey availability, the energy expenditure of chicks can therefore be greater than their energy intake (Krijgsveld et al. 2003ba, 2003b). In this situation, chicks may seek brooding to both increase their body temperature and to reduce their net energy expenditure from thermoregulation and activity during foraging (Klaassen 1992, Krijgsveld et al. 2003a).

Besides foraging time, food intake is a function of the rate of food uptake during foraging, which will be affected mainly by food availability. In the 2002 breeding season, Little Stint chicks hatched late in relation to the seasonal peak in arthropod availability (Schekkerman et al. 2004), and there was a strong seasonal effect on chick growth; early hatching chicks grew faster than later hatching chicks. Schekkerman et al. (2004) provide a broader multi-year analysis of the relationship between growth rate of arctic shorebird chicks and arthropod abundance. They found that the surface activity of arthropods in our study area varied with both date and weather, with a mid-season peak overlain by a strong effect of ambient temperature. Arthropod availability may, therefore have affected growth of Little Stint chicks in Medusa Bay in 2002. Adverse weather can consequently exert the largest influence on Little Stint growth through the effect on food availability and the ability of chicks to uptake food.

**How does the growth of Little Stint chicks compare to other species?**

Growth rate coefficients of the different bird species described in Rahn et al. (1984), Beintema and Visser (1989b), Krijgsveld et al. (submitted manuscript) and others (Ricklefs 1973, Visser & Ricklefs 1993a) decrease with increased body size. Shorebird breeding seasons in the Arctic are limited by the short summers and it has been found that birds breeding in the Arctic, for instance Red Knots (Schekkerman et al. 2003) and Purple Sandpipers, C. maritima (Summers & Nicoll 2004), have large growth rate
coefficients. The combined effect of latitude and their small size may have resulted in Little Stint chicks exhibiting large growth rate coefficients.

The predicted Gompertz growth rate coefficient \( K_G \) for shorebird species with an asymptotic mass of 26.6 g using the equation \( K_G = 0.390 \cdot A^{-0.312} \) (Beintema & Visser 1989b) was 0.140 d\(^{-1}\). Assuming that the asymptotes are identical in the logistic and Gompertz models, \( K_L \) can be converted to \( K_G \) using the equation \( K_G = 0.68 \cdot K_L \) (Ricklefs 1983). Following this, the Little Stint chicks we studied at Medusa Bay in 2002 had a \( K_G \) of 0.159 d\(^{-1}\) which is 14% above the predicted growth for a 26.6 g shorebird.

Schekkerman et al. (1998a) found that Little Stints breeding between 72°N and 76°N in Siberia grew rapidly; a \( K_G \) of 0.210 d\(^{-1}\) at Knipovich Bay (76°N, 1990), 0.201 d\(^{-1}\) at Pronchishchev Lake (75°N, 1991) and 0.163 d\(^{-1}\) at Pyasina Delta (74°N, 1990) which gives a mean value of 0.191 d\(^{-1}\) for all three sites combined (Figure 5.6a). According to this pooled result Little Stint chicks grew 37% faster than predicted for a shorebird of 26.7 g (Schekkerman et al. 1998a). The Little Stint chicks we studied at Medusa Bay (73°N, 2002) also grew faster than predicted but not as fast as was observed by Schekkerman et al. (1998a). This may be a combined effect of Schekkerman et al. (1998a) estimating asymptotic mass for each regression compared to fixing the asymptote as in this study, the lower latitude of our study site, and the different environmental conditions experienced by the chicks in different breeding seasons.
Calidrid shorebird species that breed in the Arctic at latitudes greater than 70°N, exhibit growth rate coefficients close to or greater than predicted by the equation of Beintema and Visser (1989b, Figure 5.6b). The negative relationship between asymptotic body mass and $K_G$ described by Beintema and Visser (1989b) may explain the large growth rate coefficients of Little Stints compared to that of larger shorebird species growing at similar latitudes, e.g. Baird’s Sandpiper, $C. biardii$, (48 g) (Figure 5.6b). Some shorebird species, such as the Red Knot or Curlew Sandpiper, $C. ferruginea$, are, however, able to grow at relatively faster rates than the Little Stint, despite their larger asymptotic body mass. The Red Knot exhibited a $K_G$ of 0.163 d$^{-1}$ (Schekkerman et al. 2003), which is 86% greater than the predicted value for a shorebird with an asymptotic mass of 120 g and the Curlew Sandpiper had a $K_G$ value of 0.213 d$^{-1}$ (Schekkerman et al. 1998b), which is 88% greater than predicted for a 52 g shorebird (Figure 5.6b).

**Energy balance in the Little Stint**

The self-feeding mode of development in shorebird chicks is energetically costly because chicks need to expend energy of thermoregulation and activity in addition to growth and development. Food availability at the breeding grounds of Little Stints must, therefore, be sufficient to fulfil all of their chicks’ energy requirements in order for them to grow to fledging in the harsh Arctic environment.

Like other arctic-breeding shorebirds, Little Stint chicks exhibit faster growth than predicted for their size: their fast growth enabled fledging in about 15 days. Little Stint chicks at Medusa Bay in 2002 also exhibited greater peak DME and TME than predicted for their size. They had a larger relative energy expenditure than Red Knot chicks. Krijgsveld et al. (submitted manuscript) found that chicks of smaller arctic-breeding species had a greater energy expenditure than larger species. They argued that chicks of smaller species had a higher energetic capacity than chicks of larger species, meaning that they performed at a relatively high level making them capable of rapid growth despite a large amount of energy being expended on thermoregulation.

Large shorebirds exhibit slower growth than smaller species (Bientema and Visser 1989b); thus their breeding is limited to lower latitudes where the breeding season is longer. The growth of small shorebirds is limited by their environment. Decreasing temperatures may be associated with decreased arthropod availability and chicks may require more time brooding. The large energy expenditure due to thermoregulation in cold temperatures, limited time available for foraging and potentially lower food availability reduces the amount of energy Little Stint chicks have available for growth. Thus cold weather results in chicks experiencing a reduction in growth rate, spending more time being brooded to maintain body temperature and expending a larger amount of energy on thermoregulation and activity than during warmer weather.
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