From an egg to a fledgling
Tjørve, Kathleen Marjorie Calf

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Prefledging energy requirements of the nocturnally-fed semi-precocial chicks of the Spotted Thick-knee,
*Burhinus capensis*

*Kathleen M.C. Tjørve, Les G. Underhill & G. Henk Visser*
Prefledging growth and energetics of Spotted Thick-knee, *Burhinus capensis*, chicks were investigated in the vicinity of Cape Town, South Africa. Because Spotted Thick-knees are nocturnal feeders during their summer breeding season it was hypothesised that their limited time available to feed would influence their growth and energetics. The growth rate coefficient, resting metabolic rate (RMR), peak daily metabolisable energy (peak DME) and total metabolisable energy (TME) of Spotted Thick-knee chicks was similar to the values predicted for birds of their size. Therefore, the potential negative impact of nocturnal feeding on chick growth may be countered by parental feeding; reducing chick energy expenditure on thermoregulation and activity, and adults potentially extending their foraging time into the day as their chicks become larger. Their relative energy requirements were greater than those of precocial shorebird chicks in the same climate of the Western Cape, but lower than those of shorebirds breeding in temperate or arctic zones. The semi-precocial mode of development of Spotted Thick-knees did not result in reduced energy expenditure or faster growth than anticipated for shorebirds in general, but their relative growth was greater than that of precocial species at the same latitude. Therefore, semi-precocial development benefits the growth of Spotted Thick-knees.
Spotted Thick-knee growth and energetics

Introduction
Weathers (1992) found that total metabolized energy over the prefledging period of birds increased with body size and age at fledging. In addition, shorebird species breeding at higher latitudes spent more energy than predicted for species of their size (Weathers 1992, Schekkerman & Visser 2001, Schekkerman et al. 2003, Tjørve et al. submitted manuscript-b). Schekkerman and Visser (2001) predicted that parentally-fed semi-precocial shorebirds would have a reduced energy expenditure compared to self-feeding precocials because the energetic burden of collecting and transporting food rests on the adult rather than the chick. Tjørve et al. (submitted manuscript-d) found that parent-fed semi-precocial African Black Oystercatcher, Haematopus moquini, chicks growing in the subtropics metabolized 3.7% more energy than predicted for a species of their body size. The mass-specific metabolic rate for this species was about the same as that determined for three precocial shorebird species growing in the same warm environment (Tjørve et al. submitted manuscript-d) although their growth rate was closer to that predicted for shorebirds in general (Tjørve et al. submitted manuscript-d).

Spotted Thick-knees, Burhinus capensis, are found throughout southern Africa (Maclean 1997). In the Western Cape, South Africa, Spotted Thick-knees breed from the end of August through to April, peaking in October and November (Maclean 1997). Spotted Thick-knee chicks are semi-precocial, adults feeding their chicks mostly insects (Hockey & Dowie 1995). The exact date at which chicks start feeding on their own is unknown, but to some degree they seem to depend on their parents until fledging (Maclean 1997). Because they feed predominantly at night (Maclean 1997) they have only about nine hours per night available for foraging at the latitude of this study. Such limited feeding time may constrain food, and thus energy, intake, and consequently chick growth.

Thick-knees have a modal clutch size of two eggs (Maclean 1997) and the chicks usually hatch synchronously (KMCT pers. obs).Sibling rivalry may occur (Hockey & Dowie 1995) and can result in one chick becoming larger and growing at a faster rate. Size difference between siblings starts to show after two to three weeks (KMCT pers. obs).

The aim of this study was to determine whether growth, DEE, RMR and total metabolisable energy intake (TME, kJ.d⁻¹) of Spotted Thick-knee chicks falls within the range observed for sub-tropical species, and whether their semi-precocial mode of development enabled chicks to grow at a faster rate than precocial species.

Methods

Study area
Spotted Thick-knee breeding was monitored at six sites in the vicinity of Cape Town (34°S 18°E, Figure 8.1), South Africa, from May 2001 to April 2004. The study sites consisted of three golf courses (one near the University of Cape Town,
Figure 8.1. The six study sites where Spotted Thick-knees were monitored in the vicinity of Cape Town, South Africa.

UCT, and two 50 km from Cape Town), two school fields and the grounds of a hospital (near UCT).

**Growth measurements**

Nests were found in the study sites and broods were monitored from hatching until fledging. Chicks were captured, measured and ringed on the right leg with an 8 mm stainless steel (SAFRING) ring and a unique combination of three colour rings. Thereafter, they were monitored at four to seven day intervals.

On each capture, chick mass was measured to the nearest 0.1 or 0.5 g using a Pesola spring balance. Mean mass was determined for hatchlings and for prefledglings on their last capture. Chicks of known age with an accuracy of 24 hours and chicks of unknown age were weighed a minimum of five days apart in order to describe growth of body mass.

Growth parameters were determined for the Gompertz growth model,

\[ M = A \cdot \exp \left( -\exp \left( -k \cdot (t - T) \right) \right) \]

and logistic growth model,

\[ M = \frac{A}{1 + \exp \left( -k \cdot (t - T) \right)} \]

In the models the parameter \( M \) is body mass (g), \( A \) is the asymptotic mass (g), \( k \) is the growth rate coefficient (d\(^{-1}\)), \( t \) is the age of the chick (d), and \( T \) is age at the point of inflection (d). The goodness of fit was compared and the better fitting model was chosen to describe the relationship between body mass and age. Because the chicks fledged while still growing, it was not possible to estimate the asymptote meaningfully, and the mean mass of adults (453.5 g) was used as the asymptote.
The exact age of many chicks was unknown because they had already left the nest when first encountered; therefore the growth of Spotted Thick-knees was modelled using methods described in Tjørve et al. (submitted manuscript-a, submitted manuscript-d).

**Energetic expenditure using the doubly-labelled water (DLW) technique**

Measurements of daily energy expenditure (DEE, kJ.d⁻¹), defined as energy expenditure of chicks excluding that which is deposited into tissue, of free-living Spotted Thick-knee chicks were made, using the DLW technique (Lifson & McClintock 1966; Nagy 1980, Speakman 1997, Visser & Schekkerman 1999). Either single chicks or siblings in families with two chicks were captured, weighed to the nearest gram and then injected subcutaneously in the ventral region or in the peritoneal cavity with 0.1 to 0.7 ml of DLW, depending on the mass of the chick. The DLW consisted of 35.6% D₂O and 60.7% H₂¹⁸O. Both the two-sample (Nagy 1983) and single-sample (Webster & Weathers 1989) DLW protocols were used. The Spotted Thick-knee chicks subjected to the two-sample protocol were kept warm in a well-ventilated cloth bag after their injection for an equilibration period of 45 min to 1 h after which initial blood samples were taken. Four to six 10–15 μl blood samples were then collected from the brachial vein, into glass capillary tubes, which were flame-sealed within minutes. These chicks were released after the initial blood samples were collected. The chicks subjected to the single-sample protocol were released directly after the DLW injection, and no initial blood samples were taken. All chicks were recaptured after approximately 24 hours, and blood samples and mass measurements were taken.

³²H/¹H and ¹⁸O/¹⁶O 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 in quantitatively injecting the dose (especially in small chicks), the chick’s body pool water (N, moles) was calculated using the equation derived for shorebird chicks (modified from Schekkerman and Visser 2001):

\[ N = 0.000556 \cdot M \cdot (79.86 - (9.55 \cdot (M/453.5)), \]

where \( M \) represents the chick’s average body mass (g) over the DLW measurement (the average of the initial and final masses), and 453.5 represents asymptotic body mass obtained from Maclean (1993). Daily rates of carbon dioxide production were determined using the methodology described and validated by Visser and Schekkerman (1999), Visser et al. (2000a) and Schekkerman and Visser (2001). These rates of carbon dioxide were converted to daily energy expenditure (DEE), using a factor of 27.3 kJ.l⁻¹ of carbon dioxide produced (Gessaman & Nagy 1988). Analyses were done in triplicate and averaged.

Tjørve et al. (submitted manuscript-b) introduced the modified power curve,
\[ \text{DEE} = a \cdot M^{b-(c/M)} \]

where \( a, b \) and \( c \) are coefficients to be estimated, to describe the relationship between body mass \((M, g)\) and \( \text{DEE} (\text{kJ.d}^{-1}) \) of Little Stint, *Calidris minuta*, chicks. This model creates a single curve by modifying the power curve,

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

such that the scaling exponent \((b-(c/M))\) varies with body mass. To keep the results of this paper as comparable as possible to those of previous studies where the power curve was used, analyses were completed using both the modified power curve and the traditional power curve. The programme GraphPad Prism (2003) was used for both regressions fitted in log-log space. Because the power curve and the modified power curve are nested, we chose to use the F-test to determine which model is the better fitting for the \( \text{DEE} \) versus body mass data for Spotted Thick-knee chicks (Motulsky & Christopoulos 2004). The \( \text{DEE} \) data were tested for outliers using Grubb’s test (Motulsky & Christopoulos 2004), and the residuals of the regressions were tested for normality using the Kolmogorov-Smirnoff test and the Shapiro-Wilk normality test (Motulsky & Christopoulos 2004).

In order to determine growth rates of experiment chicks at various stages along the growth curve, a growth index was calculated as the ratio of the observed growth of the chick and the predicted growth over the same time interval based on the fitted growth curve. Hence, a growth index of 1 means that chicks grew as fast as expected, while a growth index of 0 denotes that chicks did not grow at all, and negative values indicate mass loss.

**Resting metabolic rate determined through respirometry**

Resting metabolic rates were determined for free-living Spotted Thick-knee chicks from hatching to fledging. Chicks were captured in the morning and experiments were carried out before 14:00 hours so that the chicks experienced similar conditions at the time of the experiments. Repeat measurements were completed on two Spotted Thick-knee chicks. After being collected from the field, the chick’s body mass was measured to within \( \pm 0.1 \text{ g} \), and within half an hour to an hour the chick was placed individually in a darkened respiration chamber of appropriate size (between 1 l and 10 l). Temperature was measured in the chamber prior to the experiment and was monitored in the temperature-controlled chamber throughout the experiment. The respirometry system used in this study is further described in Tjørve *et al.* (submitted manuscript-c) and Tjørve *et al.* (submitted manuscript-d). Measured metabolic rate \( \text{VO}_2 \) (ml.O\(_2\.h^{-1}\)) values were converted to standard temperature conditions in dry air (l.d\(^{-1}\)) and, subsequently, to energy expenditure using a conversion factor of 19.7 kJ.l\(^{-1}\) O\(_2\) (Visser & Ricklefs 1993b). These values were modelled using the modified power curve in log-log space to produce a curve for chick resting metabolic rate.

The modified power curve used to describe the relationship between \( \text{DEE} \) and \( \text{RMR} \) with mass was the best-fitting model available to us at the time of the
Spotted Thick-knee growth and energetics

analysis. There may be another model that could better describe the data. This requires further consideration.

Energy budget estimation
Prefledging energy budgets were estimated for Spotted Thick-knees on the basis of the average body mass growth curve for free-living chicks. Metabolisable energy is the sum of two components: DEE and energy that is converted into tissue, Etis (kJ.d⁻¹). DEE was measured using the doubly-labelled water method. Etis was estimated as the daily increment of the product of body mass and energy density of tissue, using the equation derived for shorebird chicks

\[ E_{\text{tis}}(t) = M_t \left(4.38 + 3.21 \left(\frac{M_t}{A}\right)\right) - M_{t-1} \left(4.38 + 3.21 \left(\frac{M_{t-1}}{A}\right)\right) \]

where \(M_{t-1}\) and \(M_t\) are the masses (g) estimated by the logistic growth curve for days \(t-1\) and \(t\), and \(A\) is the asymptotic mass (g) for the species.

DEE is composed of resting metabolic rate (RMR, kJ.d⁻¹), energy consumed by tissue synthesis (E_syn, kJ.d⁻¹), and energy costs of thermoregulation and activity (E_tr + act, kJ.d⁻¹). Observed RMR determined for Spotted Thick-knee chicks through respirometry was used in the energy budget for the chicks. E_tr + act is a single estimate because there is interaction between them; heat may be lost while the chick is active, and similarly heat may be generated during activity (Weathers 1996). Assuming a synthesis efficiency of 75%, E_syn was estimated as one third of Etis (Weathers 1996). This estimated value needs confirmation.

Peak daily metabolisable energy (peak DME, kJ.d⁻¹) is the maximal energy demand of chicks across the prefledging period (Weathers 1992). Precocial birds often fledge before attaining adult mass (Fjeldsa 1977, Starck & Ricklefs 1998a) thus their energy requirements may continue to increase after fledging. Total metabolisable energy (TME, kJ) is the total amount of energy metabolized during the whole prefledging period. Both peak DME and TME were estimated for Spotted Thick-knees from the calculated ME curve.

Growth efficiency (%) was estimated as the sum of the daily Etis values, divided by TME. Total energy for growth was calculated as the sum of the total energy accumulated and the energy used to produce heat during biosynthesis. The remaining energy is what is used for RMR, locomotion and thermoregulation.

Environmental conditions and their impact on DEE
Hourly ambient temperature and rainfall data were obtained for the general vicinity of the study areas from the South African Weather Bureau for all three years of this study. An approximation of operative body temperature (T_e, ºC) at chick level, which integrates air temperature and heating effect on radiation (Bakken et al. 1985, Walsberg & Weathers 1986), was measured by recording the temperatures within a blackened copper sphere with a diameter of 3.5 cm in which a thermocouple was mounted. A similar white sphere measured ambient air temperature (Bakken et al. 1985, Walsberg & Weathers 1986). Operative and ambient temperatures were
logged every hour on a data logger (MC Systems, South Africa) during the DLW measurements. The impact of ambient and operative temperatures on DEE was estimated through stepwise linear regression.

\[ \log(\text{DEE}) = A + b \cdot \log M + c \cdot M^{-1} \cdot \log M + d \cdot T_a + e \cdot T_e. \]

The additional explanatory variables were not log-transformed, in accordance to Schekkerman and Visser (2001) and Schekkerman et al. (2003).

### Results

#### Growth

During the breeding season of 2001–2002, 25 captures and recaptures of 11 chicks from 10 broods were made; in the 2002–2003 breeding season 90 captures and recaptures of 43 chicks from 24 broods were made, and in the 2003–2004 breeding season 74 captures and recaptures of 24 chicks from 20 broods were made.

Median hatching mass of Spotted Thick-knee chicks found in the nest cup was 26.9 g (mean = 26.7, SD = 3.10, lower quartile = 24.8, upper quartile = 28.6, n = 13). Median mass of last capture before fledging was 386.3 g (mean = 379.3, SD = 43.5, lower quartile = 352.0, upper quartile = 400.0, n = 9), which is 84% of adult mass, 453.5 g (Maclean 1993). Spotted Thick-knee chicks could fly when their wing length exceeded a median length of 173 mm (mean = 168, SD = 20.2, range = 140.5-198, n = 9) at 50 to 58 days after hatching. For the purposes of this study a fledging age of 54 days was used.

Body mass growth of Spotted Thick-knee chicks was better described by the Gompertz growth model than the logistic growth model. We calculated the Gompertz growth rate coefficient, \( K_G \), of mass for individual chicks (range = 0.028 d\(^{-1}\) to 0.097 d\(^{-1}\)) and used the median growth rate value, 0.056 d\(^{-1}\) (mean = 0.056, lower quartile = 0.046, upper quartile = 0.064, SD = 0.017, n = 20) for description of the species, i.e.

\[ M = 453.5 \cdot \exp(–\exp(–0.056 \cdot (t – 18.9))), \]

where \( M \) is body mass (g), 453.5 is asymptotic body mass (g) that was set at adult body mass (Maclean 1993), and \( t \) is age (d, Figure 8.2).
Spotted Thick-knee growth and energetics

Figure 8.2. Growth in body mass (g) of Spotted Thick-knee chicks in the vicinity of Cape Town, South Africa, of known age (●), and estimated age (○).

Energy expenditure

Fifteen DLW measurements were made on Spotted Thick-knee chicks. Mean time between initial and final sample was 23.9 hours (range = 23.9 – 24.0, SD = 0.323) for the four two-sample protocol chicks. For the eleven single-sample protocol chicks mean time between injection and final sample was 23.4 hours (range = 16.8 – 24.8, SD = 2.27).

During the experiments, one chick lost mass at an average rate of 0.8% d⁻¹, the mass of one chick remained stable, and 13 chicks gained mass at an average of 7.5% d⁻¹ (SD = 6.88). The average growth index for the DLW measurement chicks was 0.97 (median = 0.60, SD = 1.59, range = –0.48 – 6.52, lower quartile = 51.1, upper quartile = 171.3) for the 15 thick-knee chicks.

The daily energy expenditure data of the 15 DLW measurements showed a normal distribution with no outliers. Two additional DLW measurements were taken on two slow-growing chicks. These data were not included in the analysis of DEE data because their growth was classed as outlier data and were removed from the growth analysis. Their growth and DEE data were, however, included in a later analysis of variation in growth and energy expenditure. The relationship between DEE (kJ.d⁻¹) and body mass (M, g) can be described by the power curve,

\[ \text{DEE} = 0.382 \cdot M^{1.262} \]  
\[ (r^2 = 0.931, \text{SE}_{B0} = 0.188, \text{SE}_{B1} = 0.095, n = 15). \]

The inclusion of the additional term to form the modified power curve improved the fit,

\[ \text{DEE} = 485.3 \cdot M^{0.036} - (27.6/M) \]  
\[ (r^2 = 0.954, \text{SE}_{B0} = 35.7, \text{SE}_{B1} = 13.6, n = 15). \]
(r² = 0.985, SE_b0 = 0.489, SE_b1 = 0.196, SE_b2 = 4.28, n = 15). The estimates of the regression coefficients of the modified power curve were closely correlated; thus the coefficients in these equations cannot be considered individually, and need to be used together to predict DEE for a given mass.

The power curve with the fixed allometric scaling exponent tended to overestimate DEE in chicks of 24 g to 47 g, and in chicks heavier than about 200 g (Figure 8.3a). The residuals of the modified power curve were evenly distributed along the fitted curve through the body mass range. An F-test showed that the modified power curve was the better fitting model to the DEE versus body mass data for Spotted Thick-knees (F-test: F = 62.0, df = 12, P < 0.0001).

![Figure 8.3](image.png)

**Figure 8.3.** Daily energy expenditure as a function of body mass in 15 Spotted Thick-knee chicks at Cape Town, South Africa, modelled with (A) the power curve and (B) the modified power curve.
According to the modified power curve, total DEE requirements of the Spotted Thick-knee increased during the prefledging period (Figure 8.3). Hatchling Spotted Thick-knees had a DEE of 20.0 kJ.d\(^{-1}\), and the DEE of a 54 day old fledgling was 381.5 kJ d\(^{-1}\). At 50% of asymptotic mass, 226.8 g, DEE of Spotted Thick-knee chicks was 319.3 kJ d\(^{-1}\).

For four chicks we obtained measurement of DEE and growth rate; however, there was no correlation between both variables (one-tailed Spearman’s rank correlation: \(r = -0.100, P = 0.437, n = 4\)). Two additional DLW experiments were carried out on slow growing chicks that took about 10 weeks to fledge. When including the growth rates and relative DEE values of these two chicks, we found that relative DEE increased with increasing growth rate (Spearman’s rank correlation: \(r = 0.886, P = 0.019, n = 6\)).

**Resting metabolic rate**

Resting metabolic rate was determined for 12 Spotted Thick-knee chicks at different ages during the prefledging period – chicks ranging in size from 38 g to 345 g. The modified power curve was used to describe the RMR of Spotted Thick-knee chicks,

\[
RMR = 1.36 \cdot M^{0.90 - (-1.58/M)} \quad (\text{Figure 8.4}).
\]

The power curve was better fitting to the RMR data than the modified power curve (F-test: \(F = 0.048, \text{df} = 9, P = 0.832\)), but the modified power curve and the power curve produced almost identical curves. To conform to methods as used by Tjørve et al. (submitted manuscript-b, submitted manuscript-c, submitted manuscript-d) the modified power curve was used in this analysis.

According to the modified power curve, peak RMR of a fledgling was 297.7 kJ.d\(^{-1}\) (Figure 8.4). Taking body mass into account, this gives a RMR for Spotted Thick-knees of 0.771 kJ.d\(^{-1}.g\)^{\(-1\)}. Estimated energy expenditure for RMR over the whole prefledging period was 8884.5 kJ.

Modelled DEE in a hatchling was 11.9 kJ.d\(^{-1}\) (38%) less than its RMR. This is most likely an artefact of the model used. The difference between DEE and RMR increased so that DEE was 83.8 kJ.d\(^{-1}\) (22%) more than RMR in a chick of 54 days at fledging (Figure 8.5).
Figure 8.4. Resting metabolic rate in relation to body mass for Spotted Thick-knee chicks in the vicinity of Cape Town, South Africa. The solid line (—) represents the modified power curve fitted to the observations and the dashed line (···) represents the quadratic equation of Weathers and Siegel (1995, ···).

Figure 8.5. The comparison of DEE data (●) and the relationship between body mass (g) and DEE (—), and RMR data (○) and the relationship between body mass (g) and RMR (···) of Spotted Thick-knee chicks in the vicinity of Cape Town, South Africa.
Energy budget

Based on the DEE described by the modified power curve, peak (maximum) DME was 426.2 kJ.d\(^{-1}\) for a 392.9 g chick of 54 days (Figure 8.6, Table 8.1). Total metabolisable energy (TME) was 17546.1 kJ for Spotted Thick-knees over a pre-fledging period of 54 days (Table 8.1). We calculated average daily metabolisable energy (ADME, kJ.d\(^{-1}\)) as TME divided by fledging mass and time to fledging (Weathers 1992). A mass specific value of 0.83 kJ.g\(^{-1}.d^{-1}\) was determined for Spotted Thick-knee chicks.

Growth efficiency is the total accumulated tissue during the pre-fledging period, divided by the TME. For Spotted Thick-knees this value was 15.2%. Total energy for growth was calculated as the sum of energy accumulated into tissue and that used for biosynthesis. For Spotted Thick-knee chicks this value was 20.3%; therefore energy for RMR, locomotion and thermoregulation was 79.7%.

The maximum DME and TME of Spotted Thick-knees determined with the power curve were considerably greater than that determined with the modified power curve, (Table 8.1). This difference is a result of the different fits of the two models; that of the modified power curve fitting the data better than the power curve for both the DEE and RMR data.

Energy budgets constructed for the median, lower quartile and upper quartile of the growth rate coefficient showed small differences (Figure 8.7). Chicks with fast growth rates had the smallest peak DME and TME (422.2 kJ.d\(^{-1}\) and 16670 kJ, respectively) and chicks with slow growth rates had the greatest peak DME and TME (445.3 kJ.d\(^{-1}\) and 20181 kJ, respectively).

![Figure 8.6. Energy budget of Spotted Thick-knee chicks in the vicinity of Cape Town, South Africa, as a function of age.](image)
Figure 8.7. Energy budget of Spotted Thick-knee chicks in the vicinity of Cape Town, South Africa, for lower quartile, median and upper quartile Gompertz growth rate coefficients, $K_G$.

Table 8.1. Energy budget results for Spotted Thick-knee chicks in the vicinity of Cape Town, South Africa, from the power curve and the modified power curve.

<table>
<thead>
<tr>
<th></th>
<th>Power curve</th>
<th>Modified Power curve</th>
<th>Predicted</th>
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<tbody>
<tr>
<td>Peak RMR (kJ.d$^{-1}$)</td>
<td>301.1</td>
<td>302.2</td>
<td>315.6</td>
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<tr>
<td>Total RMR (kJ)</td>
<td>10235.0</td>
<td>10079.8</td>
<td>10915.6</td>
</tr>
<tr>
<td>Relative Peak RMR (% above the prediction)</td>
<td>–4.6</td>
<td>–4.3</td>
<td></td>
</tr>
<tr>
<td>Relative RMR (% above the prediction)</td>
<td>–6.2</td>
<td>–7.7</td>
<td></td>
</tr>
<tr>
<td>Peak DME (kJ.d$^{-1}$)</td>
<td>750.6</td>
<td>426.2</td>
<td>481.7</td>
</tr>
<tr>
<td>TME (kJ)</td>
<td>23318.4</td>
<td>17546.1</td>
<td>18329.8</td>
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<tr>
<td>Relative Peak DME (% above the prediction)</td>
<td>55.9</td>
<td>–11.5</td>
<td></td>
</tr>
<tr>
<td>Relative TME (% above the prediction)</td>
<td>27.2</td>
<td>–4.3</td>
<td></td>
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<tr>
<td>Total energy accumulated (kJ)</td>
<td>2670.8</td>
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<td>Energy of heat produced in biosynthesis (kJ)</td>
<td>889.4</td>
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<td>Total energy for growth including biosynthesis (kJ)</td>
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<td>Growth efficiency (%)</td>
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<td></td>
</tr>
<tr>
<td>Total energy for growth (%)</td>
<td>15.3</td>
<td>20.3</td>
<td></td>
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<td>Total energy for RMR, $E_{th+act}$ (%)</td>
<td>84.7</td>
<td>79.7</td>
<td></td>
</tr>
</tbody>
</table>
Figure 8.8. Ambient temperature (°C) and monthly rainfall (mm) in the vicinity of Cape Town, South Africa, across the three year study of Spotted Thick-knees. This species breeds from August to April which is shown in this graph by “Season”.
**The effect of environmental conditions on DEE**

Average ambient temperature and rainfall data in the vicinity of Cape Town for the three years during which the study was conducted are summarized in Figure 8.8. The average ambient temperature in the vicinity of Cape Town during the three breeding seasons was 18.1 °C. The average ambient temperature during the DEE measurements of Spotted Thick-knee chicks was 19.1 °C, with a range between 13.4 °C and 29.6 °C (SD = 3.61, n = 15). Multiple linear regression showed that the variance in DEE of prefledging Spotted Thick-knees was explained mostly by the mass of the chicks because ambient (P = 0.985) and operative (P = 0.960) temperature did not exert significant effects on DEE.

**Discussion**

**Growth of Spotted Thick-knee chicks**

Age of fledging in Spotted Thick-knee chicks is 54 days. Due to this long prefledging period one would assume that they grow slowly. The median Gompertz growth rate coefficient, \( K_G \), determined from this study for Spotted Thick-knee chicks, was 0.056 d\(^{-1}\). This \( K_G \) value was larger than that determined by Tjørve et al. (submitted manuscript-a) for the semi-precocial chicks of the African Black Oystercatcher (0.0495 d\(^{-1}\)) and smaller than that of the precocial chicks of the Kittlitz’s Plover, *Charadrius pecuarius* (0.060 d\(^{-1}\)), Blacksmith Lapwing, *Vanellus armatus* (0.058 d\(^{-1}\)), and Crowned Lapwing, *V. coronatus* (0.072 d\(^{-1}\)), chicks in the same warm climate of the Western Cape (Figure 8.9). Beintema and Visser (1989b) introduced a negative relationship between asymptotic body mass and growth rate coefficient for Charadriidae and Scolopacidae. This relationship seems to hold for Spotted Thick-knees and African Black Oystercatchers also. The growth rates of the precocial species studied in South Africa (Tjørve et al. submitted manuscript-c) fell below the values predicted from the Beintema and Visser (1989b) relationship.

Consequently the \( K_G \) for Spotted Thick-knees can be predicted from the Beintema and Visser (1989b) relationship, \( K_G = 0.390 \cdot A^{-0.312} \), where asymptotic mass (\( A \), g) was set at 453.5 g. The predicted \( K_G \) for Spotted Thick-knees was 0.0578 d\(^{-1}\). Accordingly, the \( K_G \) determined for Spotted Thick-knees of this study was 4.3% smaller than predicted for their body size. This is within the prediction limits for shorebird growth.

The relative growth rate coefficient of Spotted Thick-knees was similar to that of African Black Oystercatcher chicks – 2% less than predicted (Tjørve et al. submitted manuscript-a). The growth rate coefficients of these semi-precocial chicks was not significantly different from the predicted value. The relative growth rate coefficients of Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks were 47%, 72% and 91%, respectively (Tjørve et al. submitted manuscript-c). It therefore seems that precocial shorebird species in a sub-tropical environment have relatively slower growth than semi-precocial species.
Spotted Thick-knees feed predominantly at night (Hockey & Dowie 1995); during their summer breeding season their feeding periods are therefore short, about nine hours per day. Coupled with chicks having digestive bottlenecks and the necessity to brood, the time chicks have available for feeding is limited and may constrain the growth of Spotted Thick-knee chicks. Nocturnal feeding did not seem to influence their growth rate, however, because they grew only slightly slower than predicted for their size. Chicks are parent-fed, thus reducing their energy expenditure for thermoregulation and activity. Further study is, however, required to ascertain the behavioural patterns of Spotted Thick-knees to determine whether they, like Stone Curlews, *Burhinus oedicnemus*, feed during the day when feeding large chicks (Cramp *et al.* 1983). The potential negative impact of nocturnal feeding on chick growth may therefore be countered by parental feeding to reduce chick energy expenditure, and adults extending their foraging time into the day when chicks become large.

Stone Curlews are closely related but larger than Spotted Thick-knees, with an average adult body mass of 560 g. Heinroth and Heinroth (1924–1932) found that Stone Curlew chicks had a growth rate coefficient of 0.055 d⁻¹ in captivity (Figure 8.9). This growth rate coefficient is slightly larger than that of Spotted Thick-knees and was 26% larger than predicted for a bird of its size. The growth rate coefficients of the different species described in Rahn *et al.* (1984) and Beintema and Visser (1989b) decrease with increased body size (Ricklefs 1973, Visser & Ricklefs 1993a).

Stone Curlews are found in temperate regions (Cramp *et al.* 1983), which is at a higher latitude than the sub-tropical environment where Spotted Thick-knees were studied. Growth rates of birds increase with increasing latitude (Klaassen and Drent 1991, Tjørve *et al.* submitted manuscript-b). Klaassen and Bech (1992) suggested that RMR and growth rate may be phylogenetically controlled to some extent. This result was therefore unexpected. The growth rate coefficient of Stone Curlews was, however, determined in captivity, and chicks reared in captivity usually experience no limitations of food or environmental conditions compared to free-living chicks.

**Energetics: DEE, RMR and energy budgets**

Daily energy expenditure of prefledging Spotted Thick-knees increased with growth in body mass. The climate in the Western Cape is mild, and fluctuations in the weather over the thick-knee breeding season are relatively small (Figure 8.8). These mild environmental conditions did not have a significant effect on thick-knee DEE.

Weathers (1979) stated that basal metabolic rate (BMR) in adult birds in the tropics tends to be lower than predicted from a regression of BMR on body mass for all birds, independent of their geographic distribution. Kersten and Piersma (1987) suggested that natural selection might favour relatively low BMR in the tropics because it would reduce food demand (Kersten & Piersma 1987). Food availability is thought to reduce with decreasing latitude (Lack 1968), therefore it could be beneficial to reduce energy requirements in a food-poor environment in addition to reducing the production of metabolic heat in a warm environment.

Spotted Thick-knees inhabit a warm environment; therefore it was expected that adult thick-knees would have a low BMR for their size and it was
predicted that their chicks would show a similar trend. Weathers and Siegel (1995) found that RMR can be estimated to within about 20% of the actual value by the quadratic equation

$$\log \text{RMR} = -1.4852 + 1.2684 \log M - 0.102(\log M)^2,$$

where $M$ represents body mass (g). Their analysis took into account phylogenetic effects and included a good range of species, including some tern species which are of similar size and have similar semi-precocial development to the Spotted Thick-knee. Therefore, the above equation was assumed to be appropriate for the Spotted Thick-knee. From the quadratic equation it was predicted that RMR in a hatchling would be 31.4 kJ.d$^{-1}$, and that RMR at fledging would be 315.4 kJ.d$^{-1}$. Observed hatchling RMR was within 1% of the predicted value, 31.8 kJ.d$^{-1}$, and fledgling RMR was within 4% of the predicted value, 302.2 kJ.d$^{-1}$ (Figure 8.4).

Precocial shorebirds growing in the same environment had lower observed fledgling RMR values compared to that predicted for their size – 73% for Kittlitz’s Plovers, 71% for Blacksmith Lapwings and 92% for Crowned Lapwings (Tjørve et al. submitted manuscript-c). The observed fledgling RMR of the semi-precocial African Black Oystercatcher was 99% of the predicted value (Tjørve et al. submitted manuscript-d). Therefore, it seems that the observed RMR of semi-precocial species at the same latitude, in the Western Cape, is closer to predicted values than in precocial species.

Due to their size, the TME of Spotted Thick-knees was larger than that of the three precocial shorebird species in the Western Cape (Tjørve et al. submitted manuscript-c) and smaller than that of African Black Oystercatchers (Tjørve et al. submitted manuscript-d).

Weathers (1992) predicted peak DME and TME from fledgling body mass ($M_{fl}$, g) and the length of the prefledging period ($t_{fl}$, days) using the equations

$$\text{predicted peak DME} = 11.69 \cdot M_{fl}^{0.9082} \cdot t_{fl}^{-0.428},$$

and

$$\text{predicted TME} = 6.65 \cdot M_{fl}^{0.852} \cdot t_{fl}^{0.71},$$

The observed peak DME was 11.5% less than that predicted (Table 8.1), and the observed TME was 4.3% less than that predicted (Table 8.1) for a species the size of Spotted Thick-knees.

Joest (2003) found that in Spain (36°N), Pied Avocets, *Recurvirostra avosetta*, showed physiological plasticity to the unfavourable conditions by reducing their total metabolisable energy. The slightly lower relative RMR and relative TME of Spotted Thick-knees may be, in the same way as their slightly slower growth rate, an adaptation to low food availability in a semi-arid warm environment, when compared to semi-precocial species in cooler temperate regions where food availability may be greater.

Tjørve et al. (submitted manuscript-d) concluded that the semi-precocial mode of development enabled African Black Oystercatcher chicks to have growth and energy expenditure close to that predicted for a bird of their size. Spotted Thick-knee chicks in this study exhibited growth and energy expenditure similarly
close to predicted values. The relative TME of Spotted Thick-knee chicks was, however 8.5% less than that of African Black Oystercatcher chicks (Tjørve et al. submitted manuscript-d). As observed in African Black Oystercatcher chicks, the semi-precocial mode of development seems to have offered Spotted Thick-knees energetic advantages over precocial shorebirds at the same latitude, thus enabling them to have faster relative growth.

**Conclusion**
Spotted Thick-knees are large, predominantly parentally-fed semi-precocial shorebirds. Although they are nocturnal feeders and they have limited time available to feed during the summer nights, parental feeding may reduce chick energy expenditure on thermoregulation and activity, and adults can extend their foraging time into the day as their chicks become larger. Although Spotted Thick-knee chicks did not exhibit faster growth or greater energy expenditure (RMR, peak DME and TME) than predicted, their semi-precocial mode of development benefited them with greater relative growth than precocial shorebirds at the same latitude.

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