Chapter 6

The energetic implications of precocial development of three shorebird species breeding in a warm environment

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Abstract

Self-feeding precocial shorebird chicks studied in temperate and arctic zones have been found to have greater energetic demands than altricial chicks, due to their greater activity and the requirement for thermoregulation. This study determines the growth and energetics of precocial shorebirds (Charadrii) in a sub-tropical environment. Chicks in this environment experience long, warm summers. We investigated the effect of body size, parental behaviour and timing of breeding on the growth and energetics of Kittlitz’s Plover, *Charadrius pecuarius*, Blacksmith Lapwing, *Vanellus armatus*, and Crowned Lapwing, *V. coronatus*, chicks (Charadriidae). The three species exhibited slower growth and longer fledging periods than arctic and temperate zone relatives of similar size. In addition, these chicks had lower energy expenditure during the prefledging period than chicks of arctic and temperate breeding shorebird species. Kittlitz’s Plovers and Crowned Lapwings breed in summer, but only Crowned Lapwings are active carers that show their chicks food. Blacksmith Lapwings are inactive carers that breed in winter. Blacksmith and Crowned Lapwings are of similar size, about four times the mass of Kittlitz’s Plovers. Kittlitz’s Plovers had a smaller growth rate coefficient and a lower resting metabolic rate and daily energetic expenditure than the larger lapwings, which is mostly a result of their small size. Taking body mass into account, however, Kittlitz’s Plover daily energy expenditure and resting metabolic rate were similar to that of the two lapwing species. Crowned Lapwings exhibited faster growth than Blacksmith Lapwings but similar daily energy expenditure. Blacksmith Lapwings compensated for the colder weather by growing more slowly, thus maintaining similar energy expenditure to the Crowned Lapwing and Kittlitz’s Plover. The small growth rate coefficient, low resting metabolic rate and low daily energy expenditure may be an adaptation of these three species to low food availability and milder ambient temperatures in their sub-tropical breeding habitats compared to shorebird chicks growing in temperate or arctic regions.
Introduction
Neonates of almost all shorebird (Charadriidae and Scolopacidae) species are classified as precocial; they leave the nest within a short period after hatching (Nice 1962, Starck & Ricklefs 1998a). Precocial development shifts the burden of collecting food from the parent to the chick. This results in greater energetic demands for the chick due to greater activity and the requirement for thermoregulation (Schekkerman et al. 1998b, Schekkerman & Visser 2001). As a consequence of exposure to environmental conditions whilst foraging, precocial chicks require thermoregulatory ability. When young, however, chick heat production is limited and chicks are unable to maintain body temperature (Visser 1993a, Ricklefs et al. 1994, Krijgsveld et al. 2001). With growth, the efficiency of thermoregulation of chicks is improved through a decreased surface area-to-volume ratio and the development of mature muscle function (Ricklefs et al. 1994). Krijgsveld et al. (2001) found that smaller Scolopacidae chicks need to invest as much energy as possible in both growth and functional maturity of tissues to maintain body temperature whilst foraging, whereas larger shorebird chicks are more capable of maintaining body temperature. Larger Scolopacidae species may reduce their daily energy requirements by slow development of functional maturity, thus enabling more energy to be channelled into growth (Krijgsveld et al. 2001). Whilst chicks are unable to maintain body temperature they allocate their time to alternate bouts of brooding and foraging (Beintema & Visser 1989a). Thus time available for foraging is limited by the requirement for brooding. Precocial shorebird chicks in the harsh environment of the Arctic exhibit greater energy expenditure and growth than predicted for precocial birds of their size (Schekkerman et al. 1998b, Schekkerman et al. 2003, Tjørve et al. submitted manuscript-b). These chicks must therefore be able to obtain sufficient food to fuel both their large energy requirements for thermoregulation and their rapid growth.

The Kittlitz’s Plover, Charadrius pecuarius, is one of the smallest shorebird species breeding in South Africa, an adult weighing about 43 g. There are 25 Vanellus species living in different environments across the globe (del Hoyo et al. 1996); 11 of these are endemic to Africa (Ward 1997, Ward et al. 1997). Two of these species, the Blacksmith Lapwing, V. armatus, and the Crowned Lapwing, V. coronatus, were chosen for the purpose of this study due to their overlapping distribution but different timing of breeding and different chick-rearing behaviour (Skead 1955, Ward 1989). Blacksmith and Crowned Lapwings are of similar adult size, 158 g and 167 g, respectively (Maclean 1993). Adult Kittlitz’s Plovers are about one quarter of the mass of these lapwings. Size differences may result in different growth and energetic expenditure patterns in Kittlitz’s Plovers compared to the lapwing species.

In the Western Cape, South Africa, Kittlitz’s Plovers and Crowned Lapwings breed during the warm, dry austral spring and summer, from August to March (Hockey & Dowie 1995, Tree 1997, Ward 1997), whereas Blacksmith Lapwings breed during the austral winter and spring, March to November (Ward et al. 1997). The natural range of Blacksmith Lapwings was the summer-rainfall area of southern Africa. Their range has undergone a major expansion in the last 50 years to include the winter-rainfall area of the Western Cape (Underhill 2004). Blacksmith Lapwings have
not adjusted their timing of breeding, so their chicks have to contend with a cold, wet environment during growth.

Shorebirds (Charadriidae and Scolopacidae) exhibit a diversity of breeding systems (Starck & Ricklefs 1998a, Székely et al. 1998). This diversity includes differences in chick-rearing behaviour (Fjeldså 1977). Blacksmith Lapwings do not actively tend their young – i.e. no feeding or showing of food, leaving chicks to search for food themselves (Hall 1964). Inactive tenders such as these may have higher chick mortality as a result of starvation due to the chicks’ inexperience in finding food and possibly the inability of adults to adequately warn chicks of potential danger due to the distance between the adults and the chicks (Ward 1989). Kittlitz’s Plovers are more attentive parents than Blacksmith Lapwings, but they do not actively assist their chicks to find food (Hockey & Dowie 1995). Crowned Lapwings actively tend their young by showing them food (Ward 1989). Active tenders, such as the Crowned Lapwing, are less territorial and generally have smaller clutches and broods than inactive tenders (Ward 1989). Mean clutch size for Kittlitz’s Plovers and Crowned Lapwings is 1.9 and 2.3 eggs, respectively, whereas mean clutch size for Blacksmith Lapwings is 3.5 eggs (Maclean 1993, Hockey & Dowie 1995, Hockey et al. 2005).

The aim of this study was to determine the impact of body size, the timing of breeding and parental behaviour on the relative growth and energetics of precocial shorebird chicks in a warm environment, and to compare these adaptations to those of shorebird species in temperate and arctic regions.

**Methods**

**Study area**

The breeding of Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings was monitored at 10 sites in the vicinity of Cape Town (34°S 18°E, Figure 6.1), South Africa, from May 2001 to April 2004. Kittlitz’s Plover breeding was monitored at two sites: Robben Island, a rocky outcrop about 10 km from Cape Town Harbour, where about 15 pairs were found on the western shores and part of the interior of the island, and a grass farm about 30 km from Cape Town where about 15 pairs attempted to breed. Blacksmith Lapwing breeding sites consisted of three golf courses where there were five to 20 pairs present during the breeding season and a car park where a single pair bred. Two of these Blacksmith Lapwing breeding sites were used by Crowned Lapwings during the summer. Crowned Lapwing breeding was monitored at two Cape Town University playing fields, a golf course, a helipad and two car parks.
Growth measurements
Broods were monitored from hatching until fledging. When first captured, chicks were measured and ringed on the right leg with an alloy (SAFRING) ring and a unique combination of colour rings. Thereafter, they were recaptured every 4–6 days during the prefledging period.

On each capture, chick mass was measured using a Pesola spring balance accurate to the nearest 0.1 g when small or 0.5 g when larger. Mean mass was determined for hatchlings and prefledglings on their last capture.

Growth curve
For each species, growth parameters were determined for the Gompertz growth model,

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

and logistic growth model,

\[ M = A / \left( 1 + e^{k \cdot (t - T)} \right) \]

In the models, the parameter \( M \) is body mass (g), \( A \) is the asymptotic mass (g), \( k \) is the growth coefficient (d\(^{-1}\)), \( t \) is the age of the chick (d) and \( T \) is age at the point of inflection (d). The fit of both growth models was compared and the better fitting model was chosen to describe the data.

The exact age of many chicks was unknown, particularly for Kittlitz's Plover chicks, because they had left the nest when first encountered. Rather than estimating
growth parameters from known age birds only, we chose to use the method based on Ricklefs (1973) and introduced by Tjørve et al. (submitted manuscript-a), thus including unknown age birds and increasing our sample size for growth parameter estimation.

Growth rate coefficients for the Gompertz model, $K_G$, or the logistic model, $K_L$, were estimated for each species from mass increments of chicks captured at least twice and that had a minimum of a five day interval between the first and the last capture. Parameter estimates were obtained from chicks which fledged successfully, to produce a curve for “normal successful” growth.

Hatching mass ($H$, g) of the different species was measured in the field, and the asymptote of body mass ($A$, g) was fixed at adult body mass – 42.5 g, 158 g and 167 g for Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings, respectively (Maclean 1993). A fixed asymptote was chosen, because parameter estimation using a free asymptote yielded unrealistic fledging masses for chicks of all three study species. These parameters ($A$, $k$ and $T$) were then used to create the growth curve.

**Energy expenditure in free-living chicks using the doubly-labelled water (DLW) technique**

Measurements of daily energy expenditure (DEE, kJ.d$^{-1}$) of chicks of the three study species were made using the doubly-labelled water (DLW) technique (Lifson & McClintock 1966; Nagy 1980, Speakman 1997, Visser & Schekkerman 1999). Visser and Schekkerman (1999) validated this method for growing shorebird chicks. Either single chicks or siblings in a two-chick family 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% D$_2$O and 60.7% H$_2^{18}$O. Both the two-sample (Nagy 1983) and single-sample (Webster & Weathers 1989) DLW protocols were used. The 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; these were flame-sealed within two to five minutes. Chicks were released after the initial blood sample was collected. The remaining experiment chicks were subjected to the single-sample protocol and were released directly after the DLW injection, and no initial blood samples were taken. Chicks from both the single and the two-sample protocols were recaptured after approximately 24 hours, and mass measurements and final blood samples were taken. Three background blood samples were taken for chicks of each of the three species.

$^{2}$H/$^{1}$H and $^{18}$O/$^{16}$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. Due to difficulties in quantitatively injecting the dose (especially in small chicks) because a small quantity of doubly-labelled water may be lost through the injection hole, the chick’s body pool water ($N$, moles) was calculated using the equation derived for shorebird chicks (modified from Schekkerman and Visser 2001),

$$N = 0.000556 \cdot M \cdot (79.86 - (9.55 \cdot (M/A))),$$
where $M$ represents the chick’s average body mass (g) over the DLW measurement (the average of the initial and final masses), and $A$ represents asymptotic body mass for the given species. Daily rates of carbon dioxide production were determined using the methods described and validated by Visser and Schekkerman (1999), Visser et al. (2000b) and Schekkerman and Visser (2001). These rates were converted to daily energy expenditure (DEE, kJ d$^{-1}$) using a factor of 27.3 kJ.l$^{-1}$ of carbon dioxide produced (Gessaman & Nagy 1988). Analyses were done in triplicate and averaged.

The 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.

In the past, the power function has been used to describe the relationship between daily energy expenditure (DEE, kJ.d$^{-1}$) and body mass ($M$, g) of shorebird chicks (e.g., Weathers & Siegel 1995, Schekkerman & Visser 2001, Schekkerman et al. 2003),

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

where $a$ and $b$ are coefficients that were estimated. The data in this study did not show linearity in log-log space for all species, thus in addition to analysing the data using the power curve, we used the modified power curve,

\[ \text{DEE} = a \cdot M^{b-(c/M)}. \]

This model was introduced in Tjørve et al. (submitted manuscript-b) to describe the energetics of Little Stint, *Calidris minuta*, chicks. The program GraphPad Prism (2003) was used for both regressions fitted in log-log space. We used the F-test to determine whether the additional term in the modified power curve was justified for the three study species. The better fitting curve was then chosen to describe the data.

We note that the DEE data contains repeated measures for chicks, and that there may be brood effects in both the DEE data and the growth data. There were no clustered deviations from the fitted curve; therefore we used the above method to give primary insights into the data. Analysis of the effects of repeated measures and brood effects may require a larger data set and this warrants investigation.

In order to compare 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. Growth indices were determined over the experiment period for each study species to determine whether chicks exhibited normal growth.

Growth rate was correlated to relative DEE (observed DEE – predicted DEE)/predicted DEE) to determine whether faster growing chicks expended more energy.

**Environmental conditions**

Hourly ambient temperature and rainfall data were obtained from the South African Weather Bureau for the general vicinity of the study areas for the three years of this study. An approximation of operative body temperature ($T_e$, °C) 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 3.5 cm diameter 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.

Resting metabolic rate determined through respirometry

Resting metabolic rate (RMR, kJ.d⁻¹) was determined for chicks at different ages during the prefledging period for all study species. Free-living chicks were captured in the morning, and experiments were carried out before 12:00 hours so that the chicks were experiencing similar conditions at the time of the experiments, thus standardising the results. Repeat measurements were completed on two Blacksmith Lapwing chicks and one Crowned Lapwing chick at intervals of at least seven days. No chick was experimented on a more than twice.

Half an hour to an hour after collection from the field, the chick’s body mass was measured to within ±0.1 g and the chick was placed in a darkened respiration chamber of appropriate size (1 l –10 l). We used the same experimental protocol employed by Lotz et al. (2003), with some modifications to ambient temperature and flow rate. The respiration chamber was placed in a temperature-controlled constant environment cabinet kept at a presumed thermoneutral temperature for the chick; i.e. between 30 °C (larger chicks) and 35 °C (smaller chicks) (Visser & Ricklefs 1993b). Temperature was measured in the chamber prior to the experiment and was monitored in the constant environment cabinet throughout the experiment. The respiration chamber was part of an open-flow indirect calorimeter. Air was pulled through the system by a pump at rates between 22.7 ml.min⁻¹ for the smallest chicks and 201.0 ml.min⁻¹ for the largest chicks. Fresh air was drawn through bev-a-line IV tubing (used for the entire respiratory setup) from outside the constant environment cabinet, through soda lime (to absorb carbon dioxide) and then through Drierite (self-indicating anhydrous CaSO₄; 10–20 mesh; to absorb water vapour). First the air was dispersed as it entered the top of the chamber, then it exited the chamber at the bottom, diagonally opposite corner of the chamber. The air was then pulled through soda lime, Drierite, and an S–3A/I Applied Electrochemistry O₂ analyser. The oxygen analyzer was set to read 20.96% O₂ when dry, CO₂-free air was flowing through the system prior to the bird being added, and we checked that the system reverted to 20.96% O₂ after each experiment. After the oxygen analyzer, the air passed through the pump and finally into a bubble flow meter for accurate measure of flow rate (Lotz et al. 2003).

Oxygen percentage values were recorded automatically on computer every 30 seconds. After an equilibration period of 40 minutes, the readings were continued for a further 50 minutes. After the experiment, the chick was weighed to within ±0.1 g.
The volume of the outlet air was converted to standard temperature (0 °C) and pressure (1013.25 hPa) dry air. A correction was made for the difference in volume of inlet and outlet air (Hill 1972), and metabolic rate, VO₂ (in ml.O₂.h⁻¹), was calculated as:

\[ VO₂ = V \cdot (F_iO₂ − F_eO₂)/(1−F_eO₂) \]

where flow rate (V) is in ml.min⁻¹, and \( F_iO₂ \) and \( F_eO₂ \) are the fractional concentrations of O₂ in the incurrent and excurrent air, respectively (Hill 1972). A moving 10 minute average was determined for O₂ consumption, and the minimum O₂ level was considered to be the resting metabolic rate. The RMR oxygen consumption values that were converted to standard temperature conditions in dry air (l.d⁻¹) were converted to energy expenditure using a conversion factor of 19.7 kJ.l⁻¹ O₂ (Visser & Ricklefs 1993b). These values were modelled using the power curve and the modified power curve. The better fitting model was chosen to produce a curve for chick resting metabolic rate for each study species.

**Energy budget estimation**

Prefledging energy budgets were constructed for each species 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 (\( E_{tis} \), kJ.d⁻¹). DEE was measured using the DLW method. \( E_{tis} \) was estimated as the daily increment of the product of body mass and energy density, using the equation (Schekkerman & Visser 2001)

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

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

DEE constitutes resting metabolism (RMR, kJ.d⁻¹), energy consumed by tissue synthesis (\( E_{syn} \), kJ.d⁻¹), and the energy costs of thermoregulation and activity (\( E_{tr + act} \), kJ.d⁻¹). Assuming a synthesis efficiency of 75%, \( E_{syn} \) was estimated as one third of \( E_{tis} \) (Weathers 1996). This is a provisional value and needs confirmation. Observed RMR determined through respirometry was used in the energy budget for the chicks of all three species. \( E_{tr + act} \) is a single estimate because there is interaction between thermoregulation and activity; heat may be lost while a chick is active, and similarly heat is generated during activity (Weathers 1996). The energy remaining after \( E_{syn} \) and RMR was the estimate for \( E_{tr + act} \).

Growth efficiency (%) during the prefledging period was estimated as the sum of the daily \( E_{tis} \) values divided by total metabolisable energy (TME, kJ), the total amount of energy metabolized during the prefledging period. 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.

Peak daily metabolisable energy (peak DME, kJ.d⁻¹) is the maximal energy demand of chicks across the prefledging period (Weathers 1992) up to the age of fledging. Precocial birds often fledge before attaining adult mass (Fjeldså 1977, Starck & Ricklefs 1998a), thus their energy requirements may continue to increase after
Section from a scientific text:

**Fledging.** Shorebirds fledge while still growing, thus peak DME of chicks in this study refers to the maximum energy demand of the chicks at fledging. Total metabolisable energy (TME) was estimated for each species. Energy budgets were calculated based on the modified power curve. Average daily metabolisable energy, ADME (kJ·g⁻¹·d⁻¹), which is TME divided by both fledging mass and the length of the prefledging period (Weathers 1992), was determined for all three study species.

**Time budget**

Time budget observations were made on six broods of Kittlitz’s Plovers for 163.5 hours, on 12 Blacksmith Lapwing broods for 50 hours and 16 Crowned Lapwing broods for a total of 99 hours. The observations made on broods of each species covered all hours of available daylight. Observations were made from a hide at a distance of 50 m to 200 m from the family, using a telescope or binoculars and behaviour was recorded continuously during observation bouts which lasted from two to six hours. Chick behaviour was recorded, distinguishing between inactive-brooding, inactive-other (including resting, sitting and standing), active-foraging, and active-other (including preening and walking or running when not foraging). The percentage of the total observation time devoted to each activity was calculated. The scatterplots of percentage time devoted to each behaviour relative to chick age was calculated. The scatterplots of percentage time devoted to each activity relative to chick age were smoothed using T4253H smoothing. Activity patterns during the day were determined by dividing observations into two-hour periods starting at 06:00 hours and ending at 20:00 hours during the summer for Kittlitz’s Plovers and Crowned Lapwings and 18:00 hours during the winter, Blacksmith Lapwings. The length of brooding and foraging bouts was calculated for each species.

**Results**

**Growth**

A single Kittlitz’s Plover chick was captured during the 2001–2002 breeding season, three captures of two chicks were made during the 2002–2003 breeding season and 77 captures of 45 chicks were made during the 2003–2004 breeding season. For Blacksmith Lapwings data from the following captures were used to construct a growth curve: 26 captures of 16 chicks from 15 broods in the 2001–2002 breeding season, 67 captures of 46 chicks from 23 broods in the 2002–2003 breeding season and 238 captures of 114 chicks from 52 broods in the 2003–2004 breeding season. For Crowned Lapwings the following data were used to construct a growth curve: 51 captures of 19 chicks from 12 broods in the 2001–2002 breeding season, 109 captures of 44 chicks from 25 broods in the 2002–2003 breeding season and 45 captures of 23 chicks from 17 broods in the 2003–2004 breeding season.

Kittlitz’s Plover chicks are small but hatchlings weigh a greater percentage of adult mass than those of Blacksmith and Crowned Lapwings (Table 6.1). Kittlitz’s Plover chicks could fly at an age of about 30 days old when their wing length exceeded 80 mm. Blacksmith Lapwing chicks could fly at an age of 40 days old and Crowned Lapwings at an age of 35 days old when their wing length exceeded 150 mm.
Fledging date for these three species was defined as the first day when wing length exceeded the abovementioned measurements or when chicks could fly at least 100 m. For all three species fledging occurred at approximately two thirds adult mass.

No formal tests were available to determine the better-fitting model for each of the study species because we used a robust regression growth analysis. The fit of the different estimated curves were compared by the p-values of the estimated growth parameters. The body mass growth for Kittlitz’s Plovers was better described by the Gompertz growth model, and that of the two lapwing species by the logistic growth model. The Gompertz growth coefficient, \(K_G\), for Kittlitz’s Plovers was 0.057 \(d^{-1}\) (Figure 6.2, Table 6.2). The logistic growth coefficients, \(K_L\), for Blacksmith and Crowned Lapwings were 0.086 \(d^{-1}\) and 0.106 \(d^{-1}\) (Figure 6.2, Table 6.2), respectively. The observed growth rate coefficient of Crowned Lapwings was larger than that of Blacksmith Lapwings (Mann-Whitney U test: \(U = 392.5, n_1 = 46, n_2 = 32\), Figure 6.2, Table 6.2).

Both the Gompertz growth rate coefficient and the logistic growth rate coefficient were determined for each species. Although the Gompertz growth model was chosen to describe the growth of Kittlitz’s Plovers and the logistic growth model was chosen to describe the growth of Blacksmith and Crowned Lapwings, the growth coefficients for the alternative model were also determined (Table 6.2).

### Table 6.1. Hatchling and pre-fledging body mass (g) for Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings in the Western Cape, South Africa. Median, mean, Range, lower quartile (L.Q.), upper quartile (U.Q.), standard deviation (SD) number of observations (n) and percent of adult body mass (g) are given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass</th>
<th>Median</th>
<th>Mean</th>
<th>Range</th>
<th>L.Q.</th>
<th>U.Q.</th>
<th>SD</th>
<th>n</th>
<th>% adult</th>
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<tbody>
<tr>
<td>Kittlitz’s Plover Hatchling</td>
<td>6.1</td>
<td>6.0</td>
<td>6.0</td>
<td>4.5 – 6.7</td>
<td>5.5</td>
<td>6.5</td>
<td>0.58</td>
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<td>Kittlitz’s Plover Prefledging</td>
<td>28.0</td>
<td>28.0</td>
<td>28.0</td>
<td>26.0 – 29.5</td>
<td>27.0</td>
<td>29.0</td>
<td>1.46</td>
<td>5</td>
<td>66</td>
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<td>11.0</td>
<td>11.0</td>
<td>9.3 – 12.2</td>
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<td>105.7</td>
<td>105.7</td>
<td>100.0 – 115.0</td>
<td>100.0</td>
<td>111.0</td>
<td>5.71</td>
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<td>67</td>
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<tr>
<td>Crowned Lapwing Hatchling</td>
<td>12.4</td>
<td>12.4</td>
<td>12.4</td>
<td>10.5 – 13.9</td>
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<td>13.1</td>
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<td>7</td>
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<td>119.0</td>
<td>117.2</td>
<td>117.2</td>
<td>102.0 – 129.0</td>
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<td>126.8</td>
<td>9.15</td>
<td>13</td>
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Figure 6.2. Increase in body mass (g) with age of Kittlitz’s Plover, Blacksmith Lapwing and
Crowned Lapwing chicks in the Western Cape, South Africa. Solid symbols represent chicks of
known age. Open symbols represent chicks of unknown hatch date that were captured twice, and
for which the age at first capture was estimated by comparing their measurements to those of
known age chicks. Symbols display the data used to fit the growth curves. Growth curve
parameters are given in Table 6.2.

Table 6.2. Growth parameters of Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing
chicks in the Western Cape, South Africa. The Lapwing species growth was described by the
logistic model, \( M = A/(1 + \exp (-k(t - T))) \), and the Kittlitz’s Plover growth was described by the
Gompertz model, \( M = A \exp (-\exp (-k(t - T))) \). In these equations \( M \) is mass (g), \( A \) is the
asymptotic mass (g), \( k \) is the growth coefficient (d−1), \( t \) is the age of the chick (d) at the time of the
observation, and \( T \) represents the age of the chick at the point of inflection (d). The number of
chicks contributing data (\( n \)), mass at hatching, \( H \), the three growth rate parameters, the lower
(L.Q.) and upper (U.Q.) quartiles and the standard deviation (SD) of the growth rate coefficient are
given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model</th>
<th>n</th>
<th>H (g)</th>
<th>A (g)</th>
<th>k</th>
<th>L.Q.</th>
<th>U.Q.</th>
<th>SD</th>
<th>T</th>
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</thead>
<tbody>
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<tr>
<td>Kittlitz’s Plover</td>
<td>Logistic</td>
<td>14</td>
<td>6.0</td>
<td>42.6</td>
<td>0.100</td>
<td>0.075</td>
<td>0.104</td>
<td>0.100</td>
<td>18.1</td>
</tr>
<tr>
<td>Blacksmith Lapwing</td>
<td>Gompertz</td>
<td>46</td>
<td>11.0</td>
<td>158.0</td>
<td>0.042</td>
<td>0.026</td>
<td>0.051</td>
<td>0.020</td>
<td>23.2</td>
</tr>
<tr>
<td>Blacksmith Lapwing</td>
<td>Logistic</td>
<td>46</td>
<td>11.0</td>
<td>158.0</td>
<td>0.086</td>
<td>0.061</td>
<td>0.102</td>
<td>0.034</td>
<td>30.1</td>
</tr>
<tr>
<td>Crowned Lapwing</td>
<td>Gompertz</td>
<td>32</td>
<td>12.4</td>
<td>167.0</td>
<td>0.058</td>
<td>0.046</td>
<td>0.067</td>
<td>0.019</td>
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<td>Crowned Lapwing</td>
<td>Logistic</td>
<td>32</td>
<td>12.4</td>
<td>167.0</td>
<td>0.106</td>
<td>0.086</td>
<td>0.130</td>
<td>0.035</td>
<td>23.9</td>
</tr>
</tbody>
</table>

Daily energy expenditure of free-living chicks

Measurements of DEE of 16 free-living Kittlitz’s Plover chicks from 15 broods,
14 free-living Blacksmith Lapwing chicks from 13 broods and 14 free-living Crowned
Lapwing chicks from 14 broods were made. Five Kittlitz’s Plover, three Blacksmith
Lapwing and six Crowned Lapwing chicks were subjected to the two-sample method.
For the single sample protocol, average time between injection of doubly-labelled
water and final sample was 22.2 hours (range = 22.0 – 22.7, SD = 0.439, n = 3) for
Kittlitz’s Plover chicks, 23.8 hours (range = 22.9 – 24.6, SD = 0.485, n = 11) for
Blacksmith Lapwing chicks, and 23.7 hours (range = 23.2 – 24.5, SD = 0.488, n = 8)
for Crowned Lapwing chicks. For the two-sampled protocol, average time between
initial and final sample was 22.8 hours (range = 17.5 – 23.8, SD = 1.86, n = 13) for
Kittlitz’s Plover chicks, 25.3 hours (range = 23.2 – 28.7, SD = 3.00, n = 3) for
Blacksmith Lapwing chicks, and 23.7 hours (range = 22.7 – 24.7, SD = 0.766, n = 6)
for Crowned Lapwing chicks.

During the experiments, one Kittlitz’s Plover lost 1.8% d−1, one remained at
constant mass, and 14 gained mass at 8.9% d−1 (SD = 9.34). The mean growth index,
observed versus average mass increase for the DLW measurement interval, for the
Kittlitz’s Plover chicks of the 16 experiments was 0.58 (median = 0.48, SD = 0.68,
range = –0.45 – 2.58). Accordingly, Kittlitz’s Plover chicks grew slower than predicted
by the fitted growth curve during the DLW measurements. Twelve of the
14 Blacksmith Lapwing chicks lost mass at an average rate of 6.2% d−1 (SD = 4.29),
and two chicks gained 4% d−1 (SD = 1.44). The average growth index for the
Blacksmith Lapwing chicks of the 14 experiments was –0.91 (median = –0.75, SD = 0.98, range = –3.09 – 0.60). Therefore Blacksmith Lapwing chicks grew slower than normal during the DLW measurements. Three of the 14 Crowned Lapwing chicks lost 1.2% d–1 (SD = 0.41), two remained at constant mass, and 10 gained mass at 6.5% d–1 (SD = 4.81). The average growth index (one being the predicted value and zero being no growth) for the Crowned Lapwing chicks of the 14 experiments was 0.71 (median = 0.50, SD = 0.84, range = –0.25 – 2.69). Accordingly, Crowned Lapwing growth during the experiments was slower than normal for the DLW measurement period. All mass losses observed were within the normal range of daily mass differences observed when comparing a chick’s mass when it has just eaten to its mass when it has not.

The daily energy expenditure data showed no outliers. The parameters of both the power curve and the modified power curve for the three species are provided in Table 6.3. The power curve with the fixed allometric scaling exponent tended to underestimate DEE in young chicks and to overestimate DEE in older chicks for the Kittlitz’s Plover and the Crowned Lapwing. The scatter of the residuals of the modified power curve were more in accordance with normal distribution along the entire body mass range than those of the power curve for these two species. The \( r^2 \) values for the modified power curve were greater than those for the power curve (Table 6.3), thus indicating that more of the variation in the data can be explained with the greater number of parameters in the former model. The modified power curve was the better fitting model to the DEE versus body mass data for the Kittlitz’s Plover and the Crowned Lapwing (F-test: Kittlitz’s Plover, \( F = 6.52, df = 13, P = 0.024 \); Crowned Lapwing, \( F = 6.04, df = 13, P = 0.029 \)) but not for the Blacksmith Lapwing (F-test: \( F = 2.096, df = 11, P = 0.176 \)). The expected relationship between DEE and body mass is a sigmoid shape, but the power curve fitted to the Blacksmith Lapwing data produces a J shape; this

<table>
<thead>
<tr>
<th>Species</th>
<th>Energy</th>
<th>Model</th>
<th>n</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>r²</th>
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<tbody>
<tr>
<td>Kittlitz’s Plover</td>
<td>DEE</td>
<td>Power curve</td>
<td>16</td>
<td>10^{1.171}</td>
<td>1.310</td>
<td>0.869</td>
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<tr>
<td></td>
<td>DEE</td>
<td>Modified power curve</td>
<td>16</td>
<td>10^{7.434}</td>
<td>–2.636</td>
<td>36.00</td>
<td>0.923</td>
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<td>RMR</td>
<td>Power curve</td>
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<td>10^{0.139}</td>
<td>0.958</td>
<td>0.796</td>
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<tr>
<td></td>
<td>RMR</td>
<td>Modified power curve</td>
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<td>10^{5.319}</td>
<td>–1.851</td>
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<td>0.832</td>
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<td>DEE</td>
<td>Power curve</td>
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<td>Modified power curve</td>
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<td>10.46</td>
<td>0.953</td>
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<td>Power curve</td>
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<td>1.132</td>
<td>0.928</td>
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<tr>
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<td>RMR</td>
<td>Modified power curve</td>
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<td>–0.225</td>
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<td>0.964</td>
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<td>Crowned Lapwing</td>
<td>DEE</td>
<td>Power curve</td>
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<td>0.943</td>
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<tr>
<td></td>
<td>DEE</td>
<td>Modified power curve</td>
<td>14</td>
<td>10^{2.101}</td>
<td>0.189</td>
<td>12.32</td>
<td>0.961</td>
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<td>Power curve</td>
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<td>10^{0.229}</td>
<td>1.168</td>
<td>0.947</td>
<td></td>
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<tr>
<td></td>
<td>RMR</td>
<td>Modified power curve</td>
<td>9</td>
<td>10^{2.169}</td>
<td>0.065</td>
<td>14.02</td>
<td>0.962</td>
</tr>
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</table>
is not biologically possible. Therefore, despite the result from the F-test, we chose to fit the modified power curve to these data.

According to the modified power curve, total DEE requirements of the three study species increased during the prefledging period (Figure 6.3). Kittlitz’s Plovers had a lower DEE than the two lapwing species. DEE of Kittlitz’s Plover chicks was 5.36 kJ.d⁻¹ on the first day after hatching, 49.8 kJ.d⁻¹ at 50% of asymptotic mass, and 57.4 kJ.d⁻¹ at fledging. Hatchling Blacksmith Lapwings had a lower DEE than Crowned Lapwings (9.64 kJ.d⁻¹ compared to 211.1 kJ.d⁻¹). At 50% of asymptotic mass DEE was 94.4 kJ.d⁻¹ for Blacksmith Lapwings and 106.6 kJ.d⁻¹ for Crowned Lapwings. At fledging, DEE of Blacksmith Lapwings was 211.1 kJ.d⁻¹ and maximum DEE of Crowned Lapwings was 189.5 kJ.d⁻¹. Mass specific peak DEE of Kittlitz’s Plovers, 1.91 kJ.d⁻¹.g⁻¹, was greater than that of Blacksmith Lapwing chicks, 1.55 kJ.d.g⁻¹, but less than that of Crowned Lapwing chicks, 1.99 kJ.d⁻¹.g⁻¹. DEE of young Crowned Lapwing chicks was greater than that of Blacksmith Lapwing chicks, but older Blacksmith Lapwing chicks had a greater DEE than older Crowned Lapwings (Figure 6.3).

Relative DEE for each chick was estimated from the modelled curve for each species and the average body mass during the experiment period. Of the 16 Kittlitz’s Plover chicks for which DEE was determined, a growth rate coefficient was determined for 11. Of the 14 chicks of each Lapwing species for which DEE was measured, the growth rate coefficient was determined for nine Blacksmith and eight Crowned Lapwings. Chicks that grew quickly had a greater relative DEE (Kittlitz’s Plover: one-tailed Spearman’s rank correlation: \( r = 0.565, P = 0.035, n = 11 \); Blacksmith Lapwing: \( r = 0.733, P = 0.0012, n = 9 \); Crowned Lapwing: \( r = 0.762, P = 0.014, n = 8 \)).

**The effect of environmental conditions on DEE**

Kittlitz’s Plover DEE measurements were taken in an average operative temperature of 21.8 °C (SD = 1.76, range = 17.4 – 23.9, n = 16), and Crowned Lapwing DEE measurements were taken in an average operative temperature of 22.9 °C (SD = 2.90, range = 17.1 – 27.3, n = 14). The average daily operative temperature during the DEE measurements of Blacksmith Lapwings was 14.1 °C (SD = 2.35, range = 10.0 – 18.1, n = 14).

Neither ambient temperature nor operative temperature improved the fit of the modified power curve to the DEE to body mass relationship of prefledging Kittlitz’s Plovers (\( P_{Ta} = 0.950, P_{Te} = 0.964 \)), Blacksmith Lapwings (\( P_{Ta} = 0.185, P_{Te} = 0.547 \)) or Crowned Lapwings (\( P_{Ta} = 0.898, P_{Te} = 0.587 \)). Therefore, the variation in DEE across the prefledging period of all three species was mostly explained by the mass of the chicks (Table 6.3).
Kittlitz’s Plover

Blacksmith Lapwing

Crowned Lapwing
Figure 6.3. The relationship between daily energy expenditure (DEE, kJ.d⁻¹) and body mass (g) described by the modified power curve and resting metabolic rate (RMR, kJ.d⁻¹) as a function of body mass (g) for Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks in the Western Cape, South Africa. The fitted modified power curve for DEE is shown by the solid line and for RMR by the dotted line (coefficients given in Table 6.3). The dashed line is the predicted RMR from Weathers and Siegel (1995). See discussion.

Resting metabolic rate
Resting metabolic rate was determined for nine Kittlitz’s Plover (6 g to 25 g), 10 Blacksmith Lapwing (13 g to 100 g) and nine Crowned Lapwing (11.3 g to 100 g) chicks at different ages during the prefledging period.

The relationship between resting metabolic rate (RMR) and body mass of all three study species was described by the modified power curve. According to the F-test, the modified power curve was the better fitting model to the RMR versus body mass data for the Blacksmith Lapwing (F-test: F = 6.82, df = 7, P = 0.035), but not for the Kittlitz’s Plover or the Crowned Lapwing (F-test Kittlitz’s Plover: F = 1.28, df = 6, P = 0.300; Crowned Lapwing: F = 2.30, df = 6, P = 0.180). The power curve fitted to Kittlitz’s Plover and Crowned Lapwing RMR data produced a J-shaped relationship between RMR and body mass. Since this is not biologically possible, we chose to fit the modified power curve to these data.

The measured RMR of Kittlitz’s Plover chicks was the lowest (26.5 kJ.d⁻¹ at fledging). Measured RMR of Crowned Lapwing chicks (141.0 kJ.d⁻¹ at fledging) was greater than that of Blacksmith Lapwing chicks (80.4 kJ.d⁻¹ at fledging) throughout the prefledging period. Kittlitz’s Plover chicks have a greater mass-specific RMR than Blacksmith Lapwing chicks: Kittlitz’s Plover chicks expended 0.781 kJ.d⁻¹.g⁻¹. Blacksmith Lapwing chicks expended 0.744 kJ.d⁻¹.g⁻¹ and Crowned Lapwing chicks expended 0.932 kJ.d⁻¹.g⁻¹ (Figure 6.3). The difference between the modelled curve for RMR and for DEE from hatching to fledging increased in all three species, but particularly for the Blacksmith Lapwing; there was an increase from no difference to 22.8 kJ.d⁻¹ in the Kittlitz’s Plover, from 4.45 kJ.d⁻¹ to 137.6 kJ.d⁻¹ in the Blacksmith Lapwing, and from 6.51 kJ.d⁻¹ to 78.2 kJ.d⁻¹ in the Crowned Lapwing (Figure 6.3).

The modified power curve used to describe the relationship between DEE and RMR with 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.

Energy budget
Peak DME and TME for Kittlitz’s Plover chicks was less than that for the two lapwing species (Figure 6.4a, Table 6.4). The peak DME and TME of Blacksmith Lapwing chicks were greater than that of Crowned Lapwing chicks (Figure 6.4b, Figure 6.4c, Table 6.4). ADME of Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings was 1.64 kJ.g⁻¹.d⁻¹, 1.07 kJ.g⁻¹.d⁻¹ and 1.09 kJ.g⁻¹.d⁻¹, respectively.
Figure 6.4. Energy budgets as a function of age for Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks in the Western Cape, South Africa. Each budget shows energy apportioned to tissue (E_{tis}), tissue synthesis (E_{syn}), thermoregulation and activity (E_{tr+act}) and resting metabolic rate (RMR).
Growth efficiencies of Kittlitz’s Plovers and Crowned Lapwings were similar: 12.9% and 12.8%, respectively. The winter-breeding Blacksmith Lapwing chicks had lower growth efficiency, 10.8%. The Kittlitz’s Plover’s total energy for growth was much lower than that of the two Lapwing species, 237.9 kJ (Table 6.4). Total energy for growth was slightly greater in Crowned than in Blacksmith Lapwings – 771.0 kJ, compared to 651.8 kJ (Table 6.4).

**Time budgets**

Newly hatched chicks less than one day old were brooded by their parents for about 29% of the time (daylight hours) in Kittlitz’s Plovers, 9% of the time in Blacksmith Lapwings and 44% of the time in Crowned Lapwings (Figure 6.5). During the first week Blacksmith Lapwings were brooded the least of the three species, 4%, compared to 26% and 34% of Kittlitz’s Plovers and Crowned Lapwings, respectively (Table 6.5). The percentage of time spent brooding declined until it ceased between six and 15 days depending on the species (Figure 6.5, Table 6.5). The percentage of time spent foraging increased and the percentage of time spent inactive but not brooding decreased in Kittlitz’s Plovers and Blacksmith Lapwings (Table 6.5). The percentage of time spent foraging decreased and the percentage of time spent inactive but not brooding increased in Crowned Lapwings (Table 6.5). Chicks of all three species spent

<table>
<thead>
<tr>
<th></th>
<th>Kittlitz’s Plover</th>
<th>Blacksmith Lapwing</th>
<th>Crowned Lapwing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak DME (kJ.d⁻¹)</td>
<td>64.5</td>
<td>235.1</td>
<td>215.2</td>
</tr>
<tr>
<td>TME (kJ)</td>
<td>1379.0</td>
<td>4526.5</td>
<td>4505.5</td>
</tr>
<tr>
<td>Predicted peak DME (kJ.d⁻¹)</td>
<td>61.5</td>
<td>172.3</td>
<td>208.5</td>
</tr>
<tr>
<td>Predicted TME (kJ)</td>
<td>1384.6</td>
<td>5007.6</td>
<td>5162.7</td>
</tr>
<tr>
<td>Relative Peak DME (% above the prediction)</td>
<td>4.8</td>
<td>36.4</td>
<td>3.2</td>
</tr>
<tr>
<td>Relative TME (% above the prediction)</td>
<td>–0.4</td>
<td>–9.6</td>
<td>–12.7</td>
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<tr>
<td>Total energy accumulated (kJ)</td>
<td>178.5</td>
<td>489.0</td>
<td>578.4</td>
</tr>
<tr>
<td>Energy of heat produced in biosynthesis (kJ)</td>
<td>59.4</td>
<td>162.8</td>
<td>192.6</td>
</tr>
<tr>
<td>Total energy for growth including biosynthesis (kJ)</td>
<td>237.9</td>
<td>651.8</td>
<td>771.0</td>
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<tr>
<td>Growth efficiency (%)</td>
<td>12.9</td>
<td>10.8</td>
<td>12.8</td>
</tr>
<tr>
<td>Total energy for growth (%)</td>
<td>17.3</td>
<td>14.4</td>
<td>17.1</td>
</tr>
<tr>
<td>Total energy for RMR (%)</td>
<td>46.4</td>
<td>40.7</td>
<td>53.9</td>
</tr>
<tr>
<td>Total energy for Eₘₑₚₜ (kJ)</td>
<td>36.3</td>
<td>44.9</td>
<td>29.0</td>
</tr>
</tbody>
</table>

*Table 6.4. Energy budget results for Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks in the Western Cape, South Africa, from the modified power curve in log-transformed space.*
Figure 6.5. Activity as a function of age of Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks in the Western Cape, South Africa. Behavioural categories include active-foraging (A-F), active-other (A-O), inactive-other (I-O) and inactive-brooding (I-B).
Table 6.5. Percentage of time spent active-foraging (A-F), active-other (A-O), inactive-brooding (I-B) and inactive-other (I-O) during the different weeks of the prefledging period for Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks in the Western Cape, South Africa.

<table>
<thead>
<tr>
<th>Week</th>
<th>Kittlitz’s Plover</th>
<th>Blacksmith Lapwing</th>
<th>Crowned Lapwing</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>55.9</td>
<td>0.4</td>
<td>26.4</td>
</tr>
<tr>
<td>2</td>
<td>65.5</td>
<td>0.5</td>
<td>18.6</td>
</tr>
<tr>
<td>3</td>
<td>83.6</td>
<td>0.6</td>
<td>2.8</td>
</tr>
<tr>
<td>4</td>
<td>87.8</td>
<td>0.2</td>
<td>0.0</td>
</tr>
<tr>
<td>5</td>
<td>89.3</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>6</td>
<td>68.7</td>
<td>0.0</td>
<td>0.1</td>
</tr>
</tbody>
</table>

A large amount of their time inactive but not brooding; chicks older than five days spent between 13% and 56% of their time inactive (Table 6.5).

Crowned Lapwing chicks spent more time foraging than Blacksmith Lapwings throughout the prefledging period (Table 6.5), and Blacksmith Lapwing chicks were brooded and otherwise inactive more than Crowned Lapwing chicks when five days old or younger (Figure 6.5, Table 6.5). Kittlitz’s Plovers spent more time brooding than Blacksmith Lapwings during the prefledging period; although they spent less time brooding than Crowned Lapwings in the first week, they spent more time brooding in the second. Brooding in Crowned Lapwing chicks older than 15 days was a result of unseasonally cold weather in the summer of 2003–2004. Random brooding events of short duration occurred in chicks close to fledging of all study species in cold temperatures.

Kittlitz’s Plover chicks spent 46% of their time brooding and 48% of their time foraging in the morning (Figure 6.6). The amount of time they spent brooding decreased during the day, and the amount of time they spent foraging increased to 73% at midday but then decreased to 44% at 16:00 hours (Figure 6.6). Kittlitz’s Plover chicks spent more time inactive in the late afternoon, when they were neither foraging nor brooding. Blacksmith and Crowned Lapwing chicks spent about 50% of their time foraging in the morning (Figure 6.6). This decreased to about 70% in the late afternoon. The amount of time chicks spent brooding or otherwise inactive increased during the day (Figure 6.6). Kittlitz’s Plover chicks had longer brooding and foraging bouts than the two lapwing species (Table 6.6). Blacksmith Lapwing and Crowned Lapwing chicks had brooding and foraging bouts that were about the same length (Table 6.6).
Figure 6.6. Daily activity of Kittlitz’s Plovers, Blacksmith Lapwing and Crowned Lapwing chicks in the Western Cape, South Africa. Behavioural categories include active-foraging (A-F), active-other (A-O), inactive-other (I-O) and inactive-brooding (I-B).
Table 6.6. Brooding and foraging bouts in minutes of Blacksmith Lapwing, Crowned Lapwing and Kittlitz’s Plover chicks in the Western Cape, South Africa. Median, mean, range, lower quartile (L.Q.), upper quartile (U.Q.), standard deviation (SD), number of observations (n) and longest bout are given.

<table>
<thead>
<tr>
<th>Species</th>
<th>Activity</th>
<th>Median</th>
<th>Mean</th>
<th>Range</th>
<th>L.Q.</th>
<th>U.Q.</th>
<th>SD</th>
<th>n</th>
<th>Longest bout</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kittlitz’s</td>
<td>Brooding</td>
<td>9.2</td>
<td>14.20</td>
<td>0.4–81.6</td>
<td>3.4</td>
<td>20.2</td>
<td>15.3</td>
<td>148</td>
<td>81.6</td>
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<tr>
<td>Kittlitz’s</td>
<td>Foraging</td>
<td>12.9</td>
<td>24.8</td>
<td>0.3–120.2</td>
<td>5.4</td>
<td>34.5</td>
<td>27.6</td>
<td>213</td>
<td>120.2</td>
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<td>Brooding</td>
<td>6.4</td>
<td>7.1</td>
<td>0.0–20.4</td>
<td>2.3</td>
<td>6.4</td>
<td>5.9</td>
<td>26</td>
<td>20.4</td>
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<tr>
<td>Blacksmith</td>
<td>Foraging</td>
<td>2.7</td>
<td>7.3</td>
<td>0.2–132.1</td>
<td>1.0</td>
<td>6.3</td>
<td>14.9</td>
<td>184</td>
<td>132.1</td>
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<tr>
<td>Crowned</td>
<td>Brooding</td>
<td>6.3</td>
<td>9.1</td>
<td>0.6–41.1</td>
<td>3.8</td>
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<td>7.8</td>
<td>57</td>
<td>41.1</td>
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<td>Foraging</td>
<td>2.9</td>
<td>5.7</td>
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<td>1.3</td>
<td>2.9</td>
<td>9.7</td>
<td>473</td>
<td>109.6</td>
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Discussion

The influence of body size on growth

The three shorebird species in this study are of different body size, thus enabling us to determine whether there is a relationship between the body size and growth rate coefficients of these species. To do this, however, the growth rate coefficients estimated with different growth models, Gompertz and logistic, need to be made comparable. Ricklefs’ (1983) conversion equation, \( K_G = 0.68 K_L \), does not always adequately describe the ratio between the Gompertz growth rate coefficient (\( K_G \)) and the observed logistic growth rate coefficient (\( K_L \)) for shorebirds. By determining both the Gompertz and logistic growth coefficients for the three study species (Table 6.2), we discovered that the Gompertz to logistic conversion factors were 0.57, 0.49 and 0.54 for Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings, respectively. Based on this finding, the conversion equation introduced by Ricklefs (1983) can only be used as a rough estimate and further investigation is required to determine the conversion factors required for other species.

For the purposes of this study, however, we used the conventional 0.68. This resulted in \( K_G \) values of 0.058 \( d^{-1} \) and 0.072 \( d^{-1} \) for Blacksmith and Crowned Lapwing chicks, respectively. The observed \( K_G \) of Kittlitz’s Plovers was 0.057 \( d^{-1} \).

Growth rate coefficients of birds have been found to decrease with increased body mass (Ricklefs 1973, Rahn et al. 1984, Beintema & Visser 1989b, Visser & Ricklefs 1993b). Adult Kittlitz’s Plovers are about one quarter of the size of adult Blacksmith and Crowned Lapwings, so this result is contrary to what one would expect from the negative relationship between growth rate coefficient and body mass observed in other shorebird species.

The \( K_G \) for shorebirds can be predicted from asymptotic mass (\( A, g \)) by using the equation \( K_G = 0.390 \cdot A^{-0.312} \) which was based on growth data from 15 shorebird species (Beintema & Visser 1989b). Using this equation, the predicted \( K_G \) of Kittlitz’s Plovers was 0.121 \( d^{-1} \) for a 42.6 g shorebird, and accordingly, Kittlitz’s Plovers grew 47% below the predicted value. The predicted \( K_G \) values for Blacksmith and Crowned Lapwing chicks were 0.080 \( d^{-1} \) and 0.079 \( d^{-1} \), respectively, and chicks of these species thus grew 28% and 9% below the predicted values for shorebirds of their size. The
three study species therefore grew slower than predicted, particularly Kittlitz’s Plover
chicks which grew at almost half the expected rate.

**The influence of body size on energy expenditure**

Small birds have a high surface area-to-volume ratio, which can result in their losing
relatively more heat to the environment than larger species in cool temperatures (Weathers 1979, Weathers 1992, Weathers & Siegel 1995). Chicks of smaller shorebird
species therefore have a relatively high overall energy expenditure as a consequence of
greater energy expenditure on thermoregulation (Schekkerman et al. 2003, Tjørve et al.
submitted manuscript-b, Krijgsveld et al. submitted manuscript).

Kittlitz’s Plover chicks had lower observed daily energy expenditure (DEE)
than Blacksmith and Crowned Lapwing chicks, which may be due to their small size.
The relative energy expenditure of the three species could be determined by
comparing their estimated peak daily metabolisable energy (DME) and total
metabolisable energy (TME) from the available data to that predicted from fledgling
body mass ($M_f$, g) and the length of the prefledging period ($t_f$, days). The predictions
were made using the equations:

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

and

\[
\text{predicted TME} = 6.65 \cdot M_f^{0.852} \cdot t_f^{0.71}
\]

(Weathers 1992). Peak DME for Kittlitz’s Plover chicks was 4.8% greater and TME
was 0.4% lower than predicted (Figure 6.4a, Table 6.4). The peak DME of Blacksmith
Lapwing chicks was 36.4% greater and the TME was 9.6% lower than predicted
(Figure 6.4b, Table 6.4). For Crowned Lapwing chicks the peak DME was 3.2%
greater and the TME was 12.7% lower than predicted (Figure 6.4c, Table 6.4).
Therefore peak DMEs of the three study species were greater than predicted, but their
TMEs were lower. The low TME may be a result of low energy expenditure for
thermoregulation in a warm climate or an adaptation to lower energy expenditure to
survive low food availability. Their growth efficiencies were similar, but the average
daily metabolisable energy (ADME) of Kittlitz’s Plover chicks was greater than that of
the two lapwing species – therefore, the smaller Kittlitz’s Plover expends more energy
for an equivalent relative growth than the larger lapwings.

Klaassen and Drent (1991) and Weathers and Siegel (1995) noted that resting
metabolic rate (RMR) in chicks tends to be greater in larger species. This relationship
was certainly true for the three study species.

**The influence of timing of breeding and parental behaviour on growth and
energy expenditure**

Foraging is associated with energy costs due to thermoregulation of chicks,
particularly if they are exposed to cold temperatures (Schekkerman & Visser 2001).
When foraging in cold temperatures, precocial chicks increase their metabolism
(Visser & Ricklefs 1993b), but the body temperature of young chicks decreases rapidly
(Norton 1970, Visser & Ricklefs 1993b) to a lower level (Krijgsveld et al. 2003a). For
example, Brown and Downs (2002) found that body temperature of Crowned
Lapwing chicks can drop to 30 °C in the laboratory. However, Krijgsveld et al. (2003a) found that regardless of age, the body temperatures of American Golden Plover, *Pluvialis dominica*, chicks in an outdoor enclosure never dropped below 35.5°C. Too severe a reduction in body temperature may reduce chick mobility and thus decrease their rate of food intake (Krijgsveld et al. 2003a). In addition, chick digestive efficiency may decrease with decreased body temperature so that foraging bouts can be limited by a digestive bottleneck (Kleiber & Dougherty 1934, Osbaldiston 1966). Chicks may therefore behaviourally limit the level to which their body temperature drops to reduce the negative influence thereof.

Brooding can potentially increase body temperature and thus mobility and digestion rate of chicks (Krijgsveld et al. 2003a). At some point, energy output outweighs energy intake thus making it more beneficial for chicks that are experiencing cool temperatures to brood than to forage. Krijgsveld et al. (2003a) found that three-day-old American Golden Plover chicks had 60% to 65% of their day available for foraging at 17°C; this decreased to ca. 40% at 12°C. American Golden Plover chicks may therefore have limited the length of their foraging bouts in favour of brooding, thereby reducing energy expenditure.

Beintema and Visser (1989b) hypothesized that cold temperatures, particularly those below 15 °C, and cold with rain are the main causes of slow growth of shorebird chicks. This was supported by Schekkerman et al. (1998b), who found that the growth rate of Curlew Sandpipers, *Calidris ferruginea*, was reduced during cold weather. In the Western Cape, Blacksmith Lapwings breed during the cold rainy winter season, whereas Crowned Lapwings breed during the warm and dry summer months (Figure 6.7). Blacksmith and Crowned Lapwings are of similar size, but Blacksmith Lapwing chicks grew at a relatively slower rate than the Crowned Lapwing. The relative RMR of Blacksmith Lapwing chicks were lower than that of Crowned Lapwing chicks, but their relative energy expenditures were similar. The slow relative growth of Blacksmith Lapwing chicks may therefore be a consequence of cold, wet weather resulting in the chicks expending relatively more energy on thermoregulation and lower food intake rates.

In arctic or temperate zones, shorebird chicks reduce energy expenditure from activity and thermoregulation by brooding (Klaassen 1994, Krijgsveld et al. 2003a). For example, Arctic Tern, *Sternula paradisaea*, and Common Tern, *S. hirundo*, chicks reduced thermoregulatory costs by 40% through brooding (Klaassen 1994). Krijgsveld et al. (2003b) found that Japanese Quail, *Coturnix c. japonica*, chicks were able to reduce their metabolic rate by 48% to 60% when switching from foraging to brooding. Behavioural thermoregulation becomes operational in shorebirds almost directly after hatching, with chicks actively seeking shade, panting or seeking brooding. This can reduce energy expenditure on thermoregulation and enable more energy to be allocated to growth and development in young chicks. The daily energy expenditure of hatchling Blacksmith Lapwings was lower than that of Crowned Lapwing hatchlings, and Blacksmith Lapwing hatchlings spent 34% more time brooding than Crowned Lapwing hatchlings. Blacksmith Lapwing hatchlings may therefore have reduced their daily energy expenditure through brooding.
Figure 6.7. Ambient temperature (°C) and monthly rainfall (mm) in Cape Town, Western Cape, South Africa, in relation to breeding periods for the three study species, Kittlitz’s Plover (KP), Blacksmith Lapwing (BSL) and Crowned Lapwing (CL), across the three years of this study (2001–2004).
Young precocial chicks do not have a fully developed thermoregulatory system (Visser & Ricklefs 1993a). For example, Brown and Downs (2002) found that complete homeothermy of Crowned Lapwings was developed at 33% to 39% of adult body mass. The development of homeothermy in chicks may increase the time available to chicks to forage by reducing their requirement to brood. In this study, the percentage of time spent foraging increased with age in all three study species. Blacksmith Lapwing chicks older than five days also spent more time brooding than Crowned Lapwing chicks, but they had greater daily energy expenditure. Therefore, despite the energetic benefits of brooding, the cool temperatures experienced by Blacksmith Lapwing chicks may have resulted in greater daily energy expenditure than Crowned Lapwing chicks once the chicks were more homeothermic.

The difference between DEE and RMR increased during the prefledging period in the three study species. The difference in the Blacksmith Lapwing was, however, 1.5 times greater than that of the Crowned Lapwing and 6.2 times greater than that of the Kittlitz’s Plover. The range expansion of Blacksmith Lapwings to the winter-rainfall region of the Western Cape (Underhill 2004) and their not changing their timing of breeding resulted in their chicks growing during the cold, wet winter months. The greater DEE compared to RMR of Blacksmith Lapwing chicks compared to that of Crowned Lapwing and Kittlitz’s Plover chicks could be a consequence of their experiencing greater energy costs from activity and thermoregulation.

The differences in relative growth rates between the three study species may be a consequence of development mode, with Crowned Lapwing chicks benefiting from being shown food by parents and Kittlitz’s Plover and Blacksmith Lapwing chicks foraging alone. With potentially lower arthropod availability in the cooler winter temperatures Blacksmith Lapwing chicks may be less efficient in foraging – particularly if the time they have available for foraging is limited by the necessity to brood. The combination of greater energy costs from thermoregulation and less efficient foraging can thus result in chicks having less energy available for growth.

The influence of breeding habitat and latitude on growth and energy expenditure

It is known that chicks of plovers and lapwings, Charadriidae, grow slower and consequently have longer prefledging periods than chicks of sandpipers, Scolopacidae (Beintema & Visser 1989b). The slow growth of Charadriidae may be an adaptation to reduce energy requirements in the food-poor, semi-arid environments in which they evolved (Székely et al. 1998, Schekkerman & Visser 2001). Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings are members of Charadriidae, therefore their slow growth rates in comparison to the predictive equation of Beintema and Visser (1989b) are possibly a consequence of their environment and evolutionary history.

The three study species mostly inhabit grasslands. Kittlitz’s Plovers inhabit dry, short grasslands, frequently close to water (Hockey & Dowie 1995). The Blacksmith Lapwing inhabits moist, short grasslands and mudflats on the edges of
dams, lakes, rivers and other water bodies (Ward et al. 1997), whereas the Crowned Lapwing favours dry, short and overburnt or overgrazed grassland (Ward 1997). Preociality in these species may be an adaptation to ground-nesting in open spaces where altricial development would increase chances of chick predation (McNabb & Olsen 1996). In addition, food availability in these environments may be limited, and preocial chicks are able to utilise food resources that would not support growth during altricial development for birds of a similar size (Visser 1998). The food items utilised by preocial shorebirds are relatively small and would make altricial feeding of chicks uneconomical. The slow growth of the three study species indicates that food availability was low or that foraging was often disturbed.

There is a large amount of variation in observed growth rate coefficients within the same species, which has been attributed to different climatic conditions and food availability. For example, observed $K_G$ values of Little Stints, *C. minuta*, were determined to be 0.0234 d$^{-1}$ (Tjørve et al. submitted manuscript-b) and 0.0281 d$^{-1}$ (Schekkerman et al. 1998a) in the Siberian Tundra in two different studies. Northern Lapwings, *V. vanellus*, are larger than Blacksmith and Crowned Lapwings, an asymptotic mass between 236 g (Beintema & Visser 1989b) and 255 g (Redfern 1983). Their $K_G$ has been recorded as 0.054 d$^{-1}$ (Beintema & Visser 1989b) and 0.079 d$^{-1}$ (Redfern 1983), which are 23.8% less and 14.0% more, respectively, than the predicted values based on their asymptotic mass. These results are therefore contradictory and illustrate the large variation in growth rates between studies which may be a consequence of different weather or food availability. The small relative growth rate of Kittlitz’s Plover chicks compared to that of Blacksmith and Crowned Lapwings may be a consequence of more limited food availability in their particular study sites or of local weather conditions.

There is a large body of work that discusses the influence of latitude on growth (e.g. Ricklefs 1968, 1976, 1984b, Klaassen 1994) and energy expenditure (e.g. Weathers 1979, Klaassen and Drent 1991). Klaassen and Drent (1991) noted that RMR in chicks tends to be higher in species from cold climates and lower in tropical species than would be expected from the bird’s mass. Kersten and Piersma (1987) suggested that natural selection could favour a low adult BMR in the tropics because this would lower the demand for food and avoid heat stress by reduced internal heat production. To explore whether the relative RMR of chicks of the three study species was lower than that of species at higher latitudes, we tested predictions for resting metabolic rate (RMR) during growth using the equation

$$RMR (kJ.d^{-1}) = 24 \cdot 10^{(-1.4852 + (1.2684 \cdot \log M) - (0.102 \cdot (\log M)^2))}$$

(Weathers & Siegel 1995) with our observed measurements. $M$ in this equation represents body mass (g). The predicted RMR values at fledging were 36.2 kJ.d$^{-1}$, 114.6 kJ.d$^{-1}$ and 129.8 kJ.d$^{-1}$ for Kittlitz’s Plover, Blacksmith Lapwing and Crowned Lapwing chicks, respectively. The observed RMR values at fledging for the three species were 73%, 71% and 92% of the predicted values for each species, respectively. The equation for all chick RMR data from the analysis of Klaassen and Drent (1991) predicted relative RMR of a chick at 34° S to be 0.904. This was similar to the relative
RMR of Crowned Lapwings but greater than that of Kittlitz’s Plovers and Blacksmith Lapwings.

The difference in relative energy expenditure between these shorebird species is probably a consequence of growth or thermoregulation. Kittlitz’s Plover chicks grew relatively slower than those of the two lapwing species, and these chicks spent less time brooding and had longer foraging bouts than those of Crowned Lapwings, which breed at the same time of the year. Kittlitz’s Plover chicks therefore seem to expend larger amounts of energy on thermoregulation. Blacksmith Lapwing chicks grow during winter and may expend more energy on thermoregulation than Crowned Lapwing chicks as a consequence.

The relatively slow growth rates and low RMRs of chicks of the three study species in the Western Cape, compared to chicks in other latitudes (Klaassen & Drent 1991), are thus most likely to be an adaptation to low food availability in a semi-arid warm environment.

The growth rate coefficients and relative growth rates of the three species of this study were generally lower than those observed in Charadriiidae species of similar size at higher latitudes (Figure 6.8). The growth rate coefficient of Kittlitz’s Plover chicks was 53% less than predicted, whereas the $K_G$ of the Little Ringed Plover, Charadrius dubius, with an asymptotic mass of 41 g, was 0.0990 d$^{-1}$ at 48 °N (Glutz von Blotzheim et al. 1975, 1977), which is 2% larger than predicted. The Ringed Plover, Charadrius hiaticula, has an asymptotic mass slightly larger than that of Kittlitz’s Plovers, 67 g, and had an observed $K_G$ of 0.108 d$^{-1}$ at 72 °N (Pienkowski 1984), which is 30% larger than predicted. The growth rate coefficients of Blacksmith and Crowned Lapwings were 72% and 91% of the predicted values, respectively. The Dotterel, Charadrius morinellus, is smaller than these two lapwing species, with an asymptotic mass of 108 g. At 57 °N their observed growth rate coefficient was 0.080 d$^{-1}$ (Thomson 1994), which is 12% larger than predicted. The relatively slower growth of Blacksmith and Crowned Lapwings compared to other Charadriidae species is likely to be a consequence of latitude and the different climate and food availability associated with latitude.

To evaluate differences in energy budgets of precocial shorebirds, we examined available data from the literature (Table 6.7). TME of Black-tailed Godwit, Limosa limosa, and Northern Lapwing, V. vanellus, chicks in the Netherlands, 53 °N, was 39% and 29%, respectively, above that predicted for their size (Schekkerman & Visser 2001). The measured TME of Red Knot chicks in Siberia, 75 °N, and Little Stint chicks in Siberia, 73 °N, was 89% and 107% above the predicted values, respectively (Schekkerman et al. 2003, Tjørve et al. submitted manuscript-b). Joest (2003) found that TME of Pied Avocet, Recurvirostra avosetta, chicks in northern Germany, 54 °N, in food-rich and food-poor environments was similar to the TME of Pied Avocet chicks in food-rich environments in Spain, 36 °N. In a food-poor environment in Spain, Pied Avocet chicks showed physiological adaptations to the unfavourable conditions by reducing their growth rates, resulting in a TME of 3856 kJ by the normal fledging age of 36 days. TME is thus increasingly greater than predicted for species with increasing latitude, and in warm climates chicks are capable of better
adapting their energy expenditure to lower food availability. This relationship between latitude and energy expenditure may be better understood by including more studies of Charadriidae species that breed at higher latitudes, e.g. the Dotterel or Ringed Plover. The inclusion of studies on Charadriidae would enable comparisons of energetics in addition to those of growth between Charadriidae and Scolopacidae.

If food availability allows brooding, it is energetically favourable (Visser & Ricklefs 1993a, Krijgsveld et al. 2003a). Chicks at higher latitudes divide their time between brooding and foraging, with very little time spent in other behaviours (Schekkerman & Visser 2001, Schekkerman et al. 2003, Tjørve et al. submitted manuscript-b). The three shorebird species of this study spent between 11% and 71% of their time inactive in behaviour other than brooding. This suggests that the thermoregulatory costs to precocial chicks in the sub-tropical environment of this study were low. A warm climate combined with lower food availability than in temperate or arctic regions, may have resulted in these precocial chicks spending time inactive.

Table 6.7. Total metabolisable energy (TME) for different shorebird species at different latitudes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Latitude</th>
<th>TME (kJ)</th>
<th>Percent predicted TME</th>
<th>Percent difference from</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red Knot</td>
<td>75°N</td>
<td>5285</td>
<td>89.0</td>
<td>1</td>
<td>1. Schekkerman et al. (2003)</td>
</tr>
<tr>
<td>Little Stint</td>
<td>73°N</td>
<td>1348</td>
<td>107.0</td>
<td>2</td>
<td>2. Tjørve et al. (submitted manuscript-b)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>8295 (food poor)</td>
<td>28.0</td>
<td></td>
<td>4. Schekkerman and Visser (2001)</td>
</tr>
<tr>
<td>Black-tailed Godwit</td>
<td>53°N</td>
<td>8331</td>
<td>39.0</td>
<td>4</td>
<td>5. this study</td>
</tr>
<tr>
<td>Northern Lapwing</td>
<td>53°N</td>
<td>6982</td>
<td>29.0</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Pied Avocet</td>
<td>36°N</td>
<td>7951 (food rich)</td>
<td>22.0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Kittlitz’s Plover</td>
<td>33°S</td>
<td>1379</td>
<td>–0.4</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Blacksmith Lapwing</td>
<td>33°S</td>
<td>4527</td>
<td>–9.6</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Crowned Lapwing</td>
<td>33°S</td>
<td>4505</td>
<td>–12.7</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>


**Conclusion**

Compared to temperate or arctic shorebird species of similar sizes, Kittlitz’s Plovers, Blacksmith Lapwings and Crowned Lapwings grew relatively slowly and had a relatively lower RMR and energy expenditure. This could be a consequence of phenotypic adaptation to a mild climate and low food availability. Kittlitz’s Plovers are considerably smaller than Blacksmith and Crowned Lapwings, and as a result they have a lower RMR and DEE. Their relatively small size and poor surface area-to-volume ratio results in a large ADME and may also result in their relatively slow growth. Blacksmith and Crowned Lapwings are of similar size and have a similar ADME. As a probable consequence of breeding in the cold, wet winter and having parents that do not assist the chicks to find food, Blacksmith Lapwing chicks grew slower and had a longer prefledging period than Crowned Lapwings.

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Weather Service. Berthe Verstapper performed the isotope analyses of the blood samples. All the field workers involved in this project are thanked for their assistance; we are particularly grateful to Gordon Scholtz, Derek Chalton, Merle Chalton, Martin Ottervanger, Margot Pennstone, Nick Pennstone and Manfred Waltner for their assistance. Kevin Winter, Department of Environmental and Geographical Science, University of Cape Town, assisted with the provision of meteorological data. Marienne de Villiers and Karen Krijgsved provided comments.