Chapter 7

Energetics of growth in semi-precocial shorebird chicks in a warm environment:
the African Black Oystercatcher,
Haematopus moquini

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Abstract

We studied prefledging growth, energy expenditure and time budgets of African Black Oystercatcher, *Haematopus moquini*, chicks on Robben Island, South Africa, and compared the growth and energetics to that of other semi-precocial and precocial shorebirds. The aim of the study was to understand the effect of parental feeding on growth and energetics of semi-precocial shorebird chicks. Chicks reached fledging mass, 463.5 g, in 40 days. The growth rate coefficient of African Black Oystercatcher chicks was 2% below the prediction limits for a shorebird species of their body mass but it was smaller than that determined for other precocial and semi-precocial shorebirds to date. Daily metabolisable energy (DME), defined as daily energy expenditure (DEE, measured with doubly-labelled water) plus energy deposited into tissue (Etis), increased with increasing body mass of the chicks. Resting metabolic rate (RMR, measured through respirometry), DME and total metabolisable energy (TME) of African Black Oystercatchers were similar to that expected for a species of their body size. The relative RMR of African Black Oystercatchers was greater than that of three precocial species in the Western Cape, but their TME was similar, their average daily metabolisable energy (ADME) was less, and they spent less time foraging (short periods of parental feeding) and more time inactive. Therefore the mode of development of African Black Oystercatcher chicks enabled them to reduce energy costs from thermoregulation and activity, and they were able to grow relatively faster than precocial, self-feeding shorebird species in similar climatic conditions in the Western Cape. The growth rate coefficient of African Black Oystercatcher chicks was smaller than that of Eurasian Oystercatcher, *H. ostralegus*, chicks, which may be a consequence of differences in body size and latitudinal effects. African Black Oystercatcher chicks up to 12 days of age experienced bouts of brooding to maintain body temperature. In general chicks spent little time being brooded and compared to the Eurasian Oystercatcher; they were simply inactive during most of the day.
Introduction
Among shorebirds we observe two different modes of development: precocial development, i.e. chicks are self-feeding and mobile soon after hatching, and semi-precocial development, i.e. chicks are mobile but parentally-fed (Nice 1962, Starck & Ricklefs 1998a). The energy expenditure of foraging and activity of self-feeding precocial species is carried by the chicks (Nice 1962, Starck & Ricklefs 1998a). As a result of the chicks’ energy allocation to activity and thermoregulation during foraging, their maximal rates of growth and development might be limited (Nice 1962), particularly in cold climates. Schekkerman et al. (2003), however, reported that the arctic breeding Red Knot, *Calidris canutus*, grew faster than temperate-breeding species. Similarly, one of the smallest arctic breeding species, the Little Stint, *C. minuta*, exhibited rapid growth (Tjørve et al. submitted manuscript-b). The fast growth and high muscular activity of these arctic breeding precocial species were associated with high energy expenditure and ultimately resulted in a shortened length of time during which chicks were dependent on parental brooding to maintain body temperature (Schekkerman et al. 2003, Tjørve et al. submitted manuscript-b). Such rapid growth is only possible if sufficient food is available. Therefore it was speculated that these species are adapted to grow rapidly in their food-rich environment. Schekkerman and Visser (2001) suggested a comparison of daily energy expenditure (DEE) of precocial and semi-precocial shorebird chicks to test the idea that energy allocation to activity and thermoregulation in precocial chicks constrains their maximal rates of postnatal growth.

Oystercatchers (Haematopidae) have semi-precocial chicks (del Hoyo et al. 1996) which are unable to find and manipulate their chosen food, i.e. mussels, limpets and invertebrates. Chicks rely on their parents for food supply until after fledging (Dircksen 1932, Groves 1984, Hockey 1984a, 1996, Lind 1965). Adult workload is therefore greatest when rearing chicks, because they need to find sufficient food to satisfy their own needs and those of their growing offspring (Hockey 1996, Leseberg et al. 2000). The chick’s energy expenditure, however, is limited to thermoregulation, movement and growth (Nice 1962).

The African Black Oystercatcher, *Haematopus moquini*, is the only species of the Haematopodidae that breeds in Africa. It populates the coast of South Africa and Namibia (Summers & Cooper 1977, Martin 1997). It breeds on the open coast and offshore islands from November to March (Leseberg et al. 2000, Tjørve & Underhill submitted manuscript-b). There, annual average temperatures are ten to twenty degrees warmer than in temperate zones where several other haematopodid species breed.

The results reported here are part of a larger study of the breeding biology of African Black Oystercatchers: e.g. Tjørve and Underhill (submitted manuscript-a, submitted manuscript-b, submitted manuscript-c) and Tjørve et al. (submitted manuscript-a). African Black Oystercatchers in the study population laid a modal clutch of two eggs (Tjørve & Underhill submitted manuscript-c), and incubation starts once the clutch is complete (Hockey 1983a). As a result, the chicks hatch synchronously and there is no measurable difference in chick size when they leave the
nest (KMCT pers. obs). Mass differences between siblings of two-chick broods of the American Black Oystercatcher, *H. bachmani*, and the Eurasian Oystercatcher, *H. ostralegus*, have been recorded to develop after two to three weeks (Safriel 1981, Groves 1984). These mass differences were attributed to sibling rivalry, where unequal food distribution resulted from dominance relations between the siblings after having left the nest (Groves 1984).Sibling rivalry affected mass at fledging, the length of the pre-fledging period and survival of sibling Eurasian and American Black Oystercatchers (Safriel 1981, Groves 1984). Similarly, we expected to observe differences in chick size to develop between sibling African Black Oystercatchers as a result of sibling rivalry.

African Black Oystercatcher chicks are parentally fed, and as a result they do not expend energy foraging. Energy can therefore be allocated into growth. The aim of this study was to determine growth rate, DEE and resting metabolic rate (RMR) of chicks of the semi-precocial African Black Oystercatcher, and to compare their growth and energy expenditure to those of other shorebird species in sub-tropical, temperate and arctic regions. Assuming that there are no digestive constraints, we predict that African Black Oystercatcher chicks grow faster than precocial wader chicks, because they do not allocate energy to foraging. We also predict that African Black Oystercatcher chicks grow faster than other semi-precocial chicks because they grow in a sub-tropical habitat where they spend less energy on thermoregulation.

**Methods**

**Study area**

Oystercatcher breeding was monitored during three consecutive austral summers, October to May, from 2001 to 2004 on Robben Island (33°47’S 18°21’E, Figure 7.1) in Table Bay about 11 km from the port of Cape Town, South Africa.

Robben Island has an area of 507 ha, and the coastline is approximately 10 km in perimeter (Figure 7.1). Most of the shoreline is rocky with varying degrees of exposure (Crawford & Dyer 2000), but there is a 400 m long section of sandy beach situated immediately south of Murray’s Bay Harbour (Figure 7.1). Robben Island is a tourist attraction, but tourists are not given free access to the island. Human disturbance by residents and tourists is greatest along the southern section of shoreline (Figure 7.1). This is the area in which tourist buses travel. Residents have access to the whole island, but most disturbances occur near the settlement.

African Black Oystercatchers were found on the narrow, 5–20 m wide upper shore, and the intertidal zone. The birds are totally dependent on the intertidal zone for their food, and most lay their clutches on the shelly and rocky areas of the upper shore.
Breeding population

Nests were found at the study site and broods were monitored from hatching until fledging. Breeding attempts were usually discovered during egg laying or incubation, although some were found as broods after hatching. In the first breeding season, 2001–2002, there were 63 breeding pairs of oystercatchers for which 68 breeding attempts, first and replacement clutches, were found as eggs, and seven were found as broods after hatching (Tjørve & Underhill submitted manuscript-c). During the second breeding season, 2002–2003, there were 68 breeding pairs, for which 85 breeding attempts, first and replacement clutches, were found as eggs and a single breeding attempt was found after hatching (Tjørve & Underhill submitted manuscript-c). There were 49 breeding pairs during the third breeding season, 2003–2004, for which 52 breeding attempts, first and replacement clutches, were found as eggs and two as broods after hatching (Tjørve & Underhill submitted manuscript-c).

Growth measurements of free-living oystercatcher chicks

Broods were monitored from hatching until fledging. When first captured, either in the nest or when first encountered on the shore, chicks were measured and ringed on the right leg with an alloy (SAFRING) ring and a unique combination of colour rings. Chick mass was measured to the nearest 0.1 or 0.5 g using a Pesola spring balance.

Body mass growth parameters were determined for the Gompertz growth function,
\[
M = A \cdot \exp \left( -\exp \left( -k \cdot (t - T) \right) \right),
\]
and the logistic growth function,
\[
M = A / \left(1 + \exp \left( -k \cdot (t - T) \right) \right).
\]
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).

Tjørve et al. (submitted manuscript-a) showed that for individual African Black Oystercatcher chicks of known age, growth parameter estimations using least squares non-linear regression resulted in an almost identical growth curve as growth parameter estimation using robust regression methods based on Ricklefs (1967). Therefore, growth rate parameters were estimated using robust regression methods described in Tjørve et al. (submitted manuscript-a). This method was used to estimate growth parameters for three precocial shorebird species by Tjørve et al. (submitted manuscript-c) to include the chicks of unknown age in the analyses.

The exact ages of 36 out of 92 chicks with sufficient data to estimate growth parameters, were unknown, because they had already left the nest when first found. The robust regression growth analysis enabled us to include these unknown age chicks in addition to the known age chicks. Mass increments of chicks captured at least twice, that had a minimum of a 10 day interval between the first and the last capture and that fledged successfully, were used in the growth analysis to produce a curve for “normal successful growth”.

Hatching mass was fixed to 39.2 g, and adult body mass to 695 g (KMCT unpubl. data) to calculate \( T \). A fixed asymptote was chosen, because parameter estimation using a free asymptote yielded unrealistic fledging masses for chicks. These parameters (\( A \), \( k \) and \( T \)) were then used to create the growth curve.

**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 African Black Oystercatchers were made using the 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 family 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% 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 12 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 \( \mu \)l blood samples were then collected from the brachial vein into glass capillary tubes, which were flame-sealed within minutes. Chicks were released after the initial blood sample was collected. The 16 chicks subjected to the single-sample protocol were released directly after the DLW
injection, and no initial blood sample was taken. All chicks were recaptured after approximately 24 hours, and blood samples and mass measurements were taken.

$^{2}H/^{1}H$ 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, 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) could not be determined for all chicks and was thus estimated using the equation derived for shorebird chicks (modified from Schekkerman and Visser 2001),

$$N = 0.000556 \cdot M \cdot (79.86 – (9.55 \cdot (M/695)),$$

where $M$ represents the chick’s average body mass (g) over the DLW measurement (the average of the initial and final masses), and 695 is asymptotic body mass (g). 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 of carbon dioxide were converted to DEE, using a factor of 27.3 kJ l$^{-1}$ of carbon dioxide produced (Gessaman & Nagy 1988). Analyses were done in triplicate and averaged.

Tjørve et al. (submitted manuscript-a) introduced the modified power curve,

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

where $a$, $b$ and $c$ are coefficients, to describe the relationship between body mass and DEE of Little Stint chicks. This model modifies the standard power curve,

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

by introducing an extra parameter, $c$, in such a way that the over-all scaling exponent $(b–(M/c))$ varies with body mass. When $c$ is zero, the modified power curve becomes the standard power curve. To keep the results of this paper as comparable as possible with those of previous studies where the power curve was used, analyses were completed using both the modified power curve and the standard power curve. The program GraphPad Prism (2003) was used for both regressions fitted in log-log space. The statistical significance of introducing the extra parameter was evaluated using an F-test (Motulsky & Christopoulos 2004). 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 (Motulsky & Christopoulos 2004).

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. The investigation of the effects of repeated measures and brood effects may require a larger data set and thus warrants investigation.

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
predicted, while a growth index of 0 denotes that chicks did not grow at all, and negative values indicate mass loss related to the predicted growth.

Environmental conditions and their impact on DEE
Hourly ambient temperature and rainfall data were obtained for Robben Island from the South African Weather Bureau for all three years of this study. In addition, weather conditions were recorded in the study area and logged every 10 minutes on a data logger (MC Systems, South Africa) throughout the breeding season. Wind speed (m.s\(^{-1}\)) was measured 40 cm above the ground with a cup anemometer (MC Systems, South Africa). An approximation of operative body temperature (\(T_e\), °C) at chick level, which integrates air temperature and the heating effect of solar 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). The impact of environmental conditions, wind speed, ambient and operative temperatures on DEE was determined through multiple linear regressions.

Resting metabolic rate determined through respirometry
Resting metabolic rate (RMR, kJ.d\(^{-1}\)) was determined using open flow respirometry for free-living chicks at different ages, i.e. from a hatchling to a fledgling. Chicks were captured during the high tide period between 07:00 and 15:00 hours; therefore, it was assumed that the chicks had been fed prior to capture.

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 – 10 l). We used the same experimental protocol as employed by Lotz et al. (2003), with modifications to the ambient temperature set and flow rates. The respiration chamber was placed in a temperature-controlled cabinet kept at a presumed thermoneutral temperature for the chick; i.e. between 30 °C (larger chicks) and 35 °C (smaller chicks) (Visser & Ricklefs 1993a). Temperature was measured in the chamber prior to the experiment and was monitored in the temperature-controlled chamber throughout the experiment. Air was pulled through the system by a pump at rates between 81.8 ml.min\(^{-1}\) for small chicks and 703.2 ml.min\(^{-1}\) for large chicks. Fresh air was drawn through a bev-a-line IV tubing (used for the entire respiratory set-up) from outside the constant environment cabinet, through soda lime (to absorb carbon dioxide), then through Drierite (self-indicating anhydrous CaSO\(_4\); 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 then into an S–3A/I Applied Electrochemistry O\(_2\) analyser. The oxygen analyzer was set to read 20.96% O\(_2\) when dry, CO\(_2\)-free air was flowing through the system prior to the bird being added, and we checked that the system reverted to 20.96% O\(_2\) 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 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 ºC) and pressure (1013.25 hPa) dry air. A correction was made for the difference in volume of inlet and outlet air (Hill 1972), so that metabolic rate, \( V_{O_2} \) (ml.O2.h\(^{-1}\)), was calculated as:

\[
V_{O_2} = V \cdot (F_{iO_2} - F_{eO_2})/(1-F_{eO_2})
\]

where flow rate (V) is in ml.min\(^{-1}\), and \( F_{iO_2} \) and \( F_{eO_2} \) are the fractional concentrations of O\(_2\) in the incurrent and excurrent air, respectively (Hill 1972). A moving 10 minute average was determined for O\(_2\) consumption, and the minimum O\(_2\) level was considered to be the RMR. RMR values were converted to energy expenditure using a conversion factor of 19.7 kJ.l\(^{-1}\) O\(_2\) (Visser & Ricklefs 1993a). These values were then converted into an energy equivalent, kJ.d\(^{-1}\). To produce a curve for chick RMR, a regression curve was fitted to the RMR data using the same method as used to model DEE.

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 estimation**

Prefledging energy budgets were estimated for African Black Oystercatcher chicks on the basis of the average body mass growth curve for free-living chicks. Metabolisable energy in growing chicks is the sum of two components: DEE and energy that is converted into tissue (\( E_{tis} \), kJ.d\(^{-1}\)). DEE was measured using the doubly-labelled water method. \( E_{tis} \) was estimated as the daily increment of the product of body mass and energy density of tissue, using the equation derived for shorebird chicks (Schekkerman & Visser 2001),

\[
E_{tis}(t) = M_t (4.38 + 3.21 (M_t/A)) - M_{t-1} (4.38 + 3.21 (M_{t-1}/A)),
\]

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 RMR, 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 through respirometry was used in the energy budget for African Black Oystercatcher chicks. Assuming a synthesis efficiency of 75\%, \( E_{syn} \) was estimated as one third of \( E_{tis} \) (Weathers 1996). This estimated value needs confirmation for African Black Oystercatchers. \( E_{tr+act} \) is a single estimate because there is interaction between them; heat may be lost while inactive, and surplus heat may be generated during activity (Weathers 1996).

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 (Fjeldså 1977, Starck & Ricklefs 1998a) thus their energy requirements may continue to increase after fledging. Shorebirds fledge at
about two thirds of adult mass; thus peak DME of the shorebird in this study refers to the energy demand of the chicks on fledging. Total metabolisable energy (TME, kJ) is the total amount of energy metabolized during the whole prefledging period. Both peak DME and TME were determined for oystercatchers from the calculated ME curve.

Growth efficiency was estimated as the percentage of total accumulated tissue during the prefledging period, divided by the TME. Total energy for growth was calculated as the sum of the percentage of total energy accumulated and that used for biosynthesis, divided by the TME. The remaining energy is what was used for RMR, locomotion and thermoregulation.

**Sibling rivalry and its impact on growth, DEE and energy budgets**

Growth measurements for 22 pairs of sibling oystercatcher chicks were obtained during the three breeding seasons. Data for 17 of these pairs had at least a 10 day interval between the first and the last measurement and were thus included in the analysis. In addition, DEE analyses were completed for seven pairs of siblings. Growth rates and DEE were compared between siblings using matched pairs t-tests to investigate the impact of sibling rivalry. Energy budgets based on the modified power curve described above and the growth of single chicks, small siblings and large siblings were determined, and the energy requirements of broods compared.

**Time budget estimation**

Time budget observations were made covering all hours of available daylight between 06:00 and 20:00 hours. Observations were made from a hide at a distance of 50 m to 200 m from the family, using a telescope or binoculars. Chick behaviour was recorded, distinguishing between inactive-brooding, active-foraging (defined here as the time taken to be given food by the parent and to consume it), active-other (including preening, walking and running to hide) and inactive-other (including resting, sitting and hiding). These were converted to percentages for each behaviour type for each observation period, the time during which the chick was observed. The scatterplots of time percentage devoted to each behaviour type were smoothed using T4253H smoothing. Activity patterns during the day were determined by dividing observations into two hour periods from 06:00 to 08:00 hours. The percentage of time spent in each activity was smoothed using techniques described above. The length of brooding and foraging (being fed) bouts were determined.

**Results**

**Growth**

In the first breeding season, 200 captures of 54 chicks from 45 broods; in the second breeding season, 208 captures of 60 chicks from 37 broods and during the third breeding season, 87 captures of 24 chicks from 14 broods were made.

Median mass of hatchlings found in the nest cup was 38.7 g (mean = 39.2, range = 34.2 – 45.5, SD = 2.71, n = 39). Chicks weighed 424.0 g (mean = 428.3,
range = 380.0 – 516.0, SD = 34.6, n = 54) on their last measurement before fledging (at 30 to 46 days). Fledglings weighed 360 – 547 g (median = 461.4, mean = 463.9, SD = 40.9, n = 49). This is 52–79% of mean adult mass for this population of African Black Oystercatchers, 695 g (KMC unpubl. data). Chicks could fly at about 40 days old, when their wing length exceeded 200 mm.

Due to the unconventional method of curve-fitting in this study, no tests were available to determine the better fitting curve, nevertheless the Gompertz growth model was chosen to describe the data.

Body mass growth of African Black Oystercatcher chicks was better described by the Gompertz growth model than the logistic model. The median Gompertz growth rate coefficient, \( K_G \), was 0.0495 d\(^{-1}\) (range 0.0238 to 0.0712, lower quartile = 0.0428, upper quartile = 0.0543, SD = 0.011, n = 92), thus body mass growth was described as

\[
M = 695 \cdot \exp (-\exp (-0.0495 \cdot (t - 21.4))),
\]

where \( M \) is body mass (g) and \( t \) is age (d) of the chick (Figure 7.2).

According to the Gompertz curve, average mass increase over the prefledging period was 10.7 g.d\(^{-1}\), and the average mass increase over the period of maximum growth, days 10 to 30, was 12.1 g.d\(^{-1}\) (Figure 7.2).

![Figure 7.2. Growth rate of African Black Oystercatcher chicks of known age (●) and estimated age (○) at Robben Island, South Africa.](image-url)
**Daily energy expenditure of free-living oystercatcher chicks**

A total of 28 DLW measurements were made on different chicks from 21 broods, including seven pairs of siblings. Mean time between injection and final sample was 23.7 hours (range = 21.5 – 24.3, SD = 0.687, n = 16) for the single sample protocol chicks. For the two-sample protocol chicks, mean time between initial and final sample was 24.1 hours (range = 23.6 – 25.0, SD = 0.39, n = 12). During the 28 experiments, 18 chicks gained mass at an average rate of 7.53% d^{-1} (SD = 5.20); three chicks neither gained nor lost mass, and seven chicks lost mass at an average rate of 2.77% d^{-1} (SD = 1.72). All mass losses observed were within the normal range of daily mass fluctuations. The average growth index was 0.45 (median = 0.53, SD = 0.87, range = –1.19 – 2.71) for the 28 oystercatcher chicks over the DLW measurement period.

Measured DEE ranged between 49.7 kJ.d^{-1} for a 37.2 g hatchling still in the nest cup (smallest) and 452.0 kJ.d^{-1} for a 455.0 g chick that was close to fledging (largest).

The daily energy expenditure data showed no outliers. The relationship describing daily energy expenditure (DEE, kJ.d^{-1}) in relation to body mass (M, g) in log-transformed space for the power curve was

\[ \text{DEE} = 1.88 \cdot M^{0.962} \]

\( (r^2 = 0.918, \text{SE}_a = 0.126, \text{SE}_b = 0.057, n = 28, \text{Figure 7.3a}) \), and for the modified power curve the relationship was

\[ \text{DEE} = 566.2 \cdot M^{0.057 - (29.0/M)} \]

\( (r^2 = 0.968, \text{SE}_a = 0.405, \text{SE}_b = 0.150, \text{SE}_c = 4.65, n = 28, \text{Figure 7.3b}) \).

The inclusion of a third term in the modified power curve improved the fit of the model describing the DEE versus body mass relationship for African Black Oystercatchers (F-test: F_{1,25} = 38.9, P < 0.001). The power curve with the fixed allometric scaling exponent tended to underestimate DEE in young chicks and overestimate DEE in older chicks. The scatter of the residuals for the modified power curve was more random along the entire body mass range than those of the power curve.

Growth rates were estimated for 22 out of the 28 birds for which DEE was measured. Relative DEE (standardised observed versus predicted DEE) was estimated for each chick. Birds that grew quickly did not have a greater relative DEE (one-tailed Spearman’s rank correlation: \( r = 0.150, P = 0.252, n = 22 \)).

According to the modified power curve that describes the relationship between DEE and body mass (Figure 7.3b), DEE of African Black Oystercatcher chicks increased from 57.0 kJ.d^{-1} in a chick on the first day after hatching to 540.2 kJ.d^{-1} in a chick that was close to fledging. At 50% asymptotic mass, 347.5 g, DEE was 485.6 kJ.d^{-1}. Total DEE across the 40 day pre-fledging period estimated from the growth curve and the modified power curve, was 14371.6 kJ.d^{-1}.
The effect of environmental conditions on DEE
The average ambient temperature was 19.1 ºC in the first breeding season, 19.4 ºC during the second breeding season and 20.4 ºC in the third breeding seasons. The average ambient temperature was 19.6 ºC (Figure 7.4). African Black Oystercatchers breed during the dry season (Figure 7.4). The average ambient temperature on Robben Island during the DEE measurements was 20.7 ºC (range = 17.0 – 23.4, SD = 1.55, n = 28). Mean wind speed was 0.6 m.s⁻¹ (range = 0.3 – 0.9, SD = 0.2, n = 19). Ambient temperature (P = 0.921), operative temperature (P = 0.995) and wind speed (P = 0.810) did not exert significant effects on DEE. No DEE experiments were performed during a period of rain. Based on the relationships between DEE and body mass and relative DEE and growth rate described above, one may assume that the variation in DEE is explained by body mass alone.

Resting metabolic rate
Resting metabolic rate of 15 different African Black Oystercatcher chicks was described by the modified power curve, which resulted in

\[ \text{RMR} = 27.48 \cdot M^{0.450 - (15.91/M)} \] (Figure 7.5).

The modified power curve was the better fitting curve to the RMR data than the power curve (F-test: F₁,₁₂ = 13.06, P = 0.004).
Figure 7.4. Ambient temperature (°C) and monthly rainfall (mm) in the vicinity of Cape Town, South Africa, across three years, from 2001-2004. The points represent the mean across the three year study and the bars represent standard deviation.
Observed RMR determined for a hatchling oystercatcher of 33.9 g was 25.9 kJ.d\(^{-1}\), and observed RMR of a 449 g chick that was close to fledging was 394.3 kJ.d\(^{-1}\). According to the modified power curve (Figure 7.5), estimated RMR of African Black Oystercatcher chicks increased during the prefledging period, from 29.2 kJ.d\(^{-1}\) in a 36.7 g hatching still in the nest cup to 352.5 kJ.d\(^{-1}\) in a 463.4 g chick of 40 days that was close to fledging. Taking body mass into account, the estimated RMR of a 40 day old chick was 0.761 kJ.d\(^{-1}\).g\(^{-1}\). As calculated from the model, total energy expenditure from RMR across the 40 day prefledging period was 8517.5 kJ.

From the models, DEE in hatchlings was 11.2 kJ.d\(^{-1}\) greater than their RMR. The difference between DEE and RMR increased to 195.2 kJ.d\(^{-1}\) in a chick of 40 days at fledging (Figure 7.6).

**Energy budget**

Based on the DEE described by the modified power curve in log-log space and growth curve, we were able to estimate a budget for the daily energy requirements as a function of the age of the chick (Figure 7.7). Peak daily metabolisable energy (DME, kJ.d\(^{-1}\)) was 629 kJ.d\(^{-1}\) for a 40 day old fledgling (Table 7.1), and total metabolisable energy (TME, kJ) over the 40 day prefledging period was 17267 kJ for African Black Oystercatcher chicks (Table 7.1). Average daily metabolisable energy, ADME (kJ.d\(^{-1}\)), which is TME divided by both fledging mass and the length of the prefledging period (Weathers 1992), was 1.02 kJ.g\(^{-1}\).d\(^{-1}\) for African Black Oystercatcher chicks.

\(E_{\text{vis}}\) and \(E_{\text{syn}}\) varied through the prefledgling period (Figure 7.7). Growth efficiency of African Black Oystercatcher chicks during this study was 16.5%. Thus the total energy estimated for growth was 22.0%, and 78.0% for RMR, locomotion and thermoregulation.

Peak DME and TME of African Black Oystercatchers determined with the power curve were greater than those determined with the modified power curve (Table 7.1). This difference is a result of the different fits of the two models: that of the power curve overestimating energy expenditure for large chicks (Figure 7.3, Table 7.1). Peak DME refers to the DME on fledging because chicks fledge at approximately three-quarters adult mass and with an increase in mass come an increase in DME.
Figure 7.5. Resting metabolic rate (RMR, kJ.d\(^{-1}\)) as a function of mass in African Black Oystercatcher chicks at Robben Island, South Africa. Data were modelled using the modified power curve (—) and the quadratic equation of Weathers and Siegel (1995, ...).

Figure 7.6. The comparison of DEE (kJ.d\(^{-1}\), •) and RMR (kJ.d\(^{-1}\), ○) data and the modified power curves that describe them (— and ..., respectively) of African Black Oystercatcher chicks at Robben Island, South Africa.
Figure 7.7. Estimated energy budget as a function of age for African Black Oystercatcher chicks at Robben Island, South Africa. Components shown are energy in tissue ($E_{\text{tis}}$), energy for tissue synthesis ($E_{\text{syn}}$), energy for thermoregulation and activity and resting metabolic rate (RMR).

Table 7.1. Energy budget results for African Black Oystercatcher chicks at Robben Island, South Africa, from the power curve and the modified power curve in log-transformed space.

<table>
<thead>
<tr>
<th></th>
<th>Power Curve</th>
<th>Modified Power Curve</th>
<th>Predicted</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak DME (kJ.d$^{-1}$)</td>
<td>772.2</td>
<td>629.1</td>
<td>635.9</td>
</tr>
<tr>
<td>TME (kJ)</td>
<td>17714.5</td>
<td>17266.7</td>
<td>17050.1</td>
</tr>
<tr>
<td>Relative Peak DME (% above the prediction)</td>
<td>21.4</td>
<td>-1.1</td>
<td></td>
</tr>
<tr>
<td>Relative TME (% above the prediction)</td>
<td>3.9</td>
<td>1.3</td>
<td></td>
</tr>
<tr>
<td>Total energy accumulated (kJ)</td>
<td>2855.0</td>
<td>2855.0</td>
<td></td>
</tr>
<tr>
<td>Energy of heat produced in biosynthesis (kJ)</td>
<td>950.7</td>
<td>950.7</td>
<td></td>
</tr>
<tr>
<td>Total energy for growth including biosynthesis (kJ)</td>
<td>3805.7</td>
<td>3805.7</td>
<td></td>
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<tr>
<td>Growth efficiency (%)</td>
<td>16.1</td>
<td>16.5</td>
<td></td>
</tr>
<tr>
<td>Total energy for growth (%)</td>
<td>21.5</td>
<td>22.0</td>
<td></td>
</tr>
<tr>
<td>Total energy for RMR (%)</td>
<td>48.1</td>
<td>49.4</td>
<td></td>
</tr>
<tr>
<td>Total energy for $E_{\text{Eth+act}}$ (%)</td>
<td>30.4</td>
<td>28.6</td>
<td></td>
</tr>
</tbody>
</table>
Sibling rivalry and its impact on growth, DEE and energy budgets

The difference in mass between siblings starts to become noticeable about two weeks after hatching (Tjørve et al. submitted manuscript-a). In total, the growth rates of 17 pairs of siblings were analysed and the larger chicks had a significantly larger growth rate coefficient than the smaller chicks (one-tailed matched pairs t-test: $t_{16} = –2.74$, $P = 0.007$, $n = 17$). However, only 14 individuals from 7 pairs of siblings were available for analysis from the 28 DLW experiments, and growth rates were known for only four of those seven pairs. In this smaller sample, the siblings did not differ in growth rate coefficient (one-tailed matched pairs t-test: $t_6 = –0.024$, $P = 0.491$, $n = 4$), DEE (one-tailed matched pairs t-test: $t_6 = –0.381$, $P = 0.380$, $n = 7$) or relative DEE (one-tailed matched pairs t-test: $t_6 = 1.65$, $P = 0.925$, $n = 7$). The lack of significance is most likely a result of the small sample size. When single chicks were compared to broods of two, they did not differ in DEE from the smaller chick (t-test: $t = 1.66$, $P = 0.06$, $n = 14$) or the larger chick (t-test: $t = 1.35$, $P = 0.10$, $n = 14$).

Single chicks had an average growth rate constant of 0.497 d$^{-1}$, which was greater than that of small and large siblings – 0.473 d$^{-1}$ and 0.495 d$^{-1}$, respectively. The peak DME determined for single chicks, small siblings and large siblings (based on their respective growth rates) were similar: 630.6 kJ.d$^{-1}$, 621.4 kJ.d$^{-1}$ and 630.1 kJ.d$^{-1}$, respectively. Therefore the total energy requirements of an average brood of two chicks was 1251.5 kJ.

Time budget

African Black Oystercatcher chicks were observed for a total of 183.4 observation hours. Newly hatched chicks were brooded by their parents for about 4% of the day (Figure 7.8). From hatching, the amount of time chicks were inactive whilst being brooded declined until it ceased at about 16 days (Figure 7.8). The average brooding bout length across the whole preflushing period was 9.53 minutes (SD = 11.42 minutes, $n = 75$), and the longest brooding bout lasted for 57.5 minutes in a one day old chick. The average foraging (being fed) bout, parental feeding, across the whole preflushing period was 1.88 minutes (SD = 3.25, $n = 634$), and the longest foraging bout lasted 36 minutes. This foraging bout was for a single chick that was continuously fed by one or the other parent. During 101.25 hours of observation, chicks less than or equal to 10 days spent an average of 91.3% (SD = 16.9) of their time inactive and being brooded and 5.6% (SD = 8.0) of their time active while foraging. During 82.15 hours of observation, chicks older than 10 days spent 85.9 % (SD = 15.2) of their time inactive and being brooded, and 6.6 % (SD = 7.3) of their time active while foraging.
African Black Oystercatcher energetics

Discussion

Growth and energy expenditure of African Black Oystercatchers

The average Gompertz growth rate coefficient, $K_G$, for body mass of African Black Oystercatcher chicks across the 40 day prefledging period, was 0.0495 d$^{-1}$. This value is close to the allometric prediction based on the equation for shorebirds (Charadriidae and Scolopacidae) by Beintema and Visser (1989b) of 0.051 d$^{-1}$ for a chick with an asymptotic body mass of 695 g; 2% below the prediction. Therefore, the growth rate coefficient of African Black Oystercatcher chicks is similar to that expected for a shorebird of their size.

As expected, daily energy expenditure (DEE) of prefledging African Black Oystercatchers increased with growth in body mass. The climate in the Western Cape is mild and fluctuations in the weather over the oystercatcher breeding season are small, therefore weather conditions did not affect DEE.

Avian postnatal metabolism was found to be more closely correlated with mass than with age (Klaassen & Bech 1992). Weathers and Siegel (1995) showed that resting metabolic rate (RMR) could be estimated to within 20% of the actual value for five passerine and 22 non-passerine species using the quadratic equation

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

where $M$ represents body mass (g). Although African Black Oystercatchers are not related to any of the species in Weathers and Siegel’s (1995) analysis, they had taken phylogenetic effects into account, and their analysis included tern species with similar chick-rearing behaviour and body mass. This equation was therefore assumed to be appropriate to predict the RMR of African Black Oystercatcher chicks. For 40 day old
African Black Oystercatcher chicks (fledglings of about 450 g) the estimated RMR was 356.1 kJ.d$^{-1}$ – i.e. 3.6 kJ.d$^{-1}$ (1%) less than the predicted peak RMR. Similarly, RMR measured across the whole prefledging period was 1% (57.6 kJ.d$^{-1}$) more than predicted (Figure 7.5).

Weathers (1992) predicted peak daily metabolisable energy (peak DME) and total metabolisable energy (TME) from fledgling body mass ($M_{fl}$, g) and 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 of African Black Oystercatcher chicks in this study was about 1% less than predicted, and the observed TME was about 1% greater than predicted. Therefore, the energy expenditure of African Black Oystercatcher chicks on Robben Island was found to be similar to that predicted for a species of its size.

**How does the growth and energy expenditure of African Black Oystercatcher chicks compare to that of other species?**

According to the Gompertz growth model, the calculated average daily mass increase over the period of maximum growth of this species was 12.1 g.d$^{-1}$. This was 78% of the maximum growth rate determined by Hockey (1984a), namely 15.6 g.d$^{-1}$. Therefore the growth rate determined in this study for African Black Oystercatcher chicks was not as fast as that of Hockey (1984a). Hockey (1984a) estimated from gross energy intake (GEI) measurements that captive African Black Oystercatcher chicks require 11578 kJ over a 40 day prefledging period. This is 5689 kJ less than that determined by DLW measurements. This difference may be partly due to the different energy requirements of captive and free-living chicks. The results of this study may therefore have implications on energy requirement estimations for this species.

Eurasian Oystercatcher, *H. ostralegus*, chick $K_G$ was recorded as 0.081 d$^{-1}$ (Kersten & Brenninkmeijer 1995). Growth rate coefficients of different species of shorebirds have been shown to decrease with increased body size (Beintema & Visser 1989b, Ricklefs 1973, Visser & Ricklefs 1993b). Therefore, the greater observed $K_G$ of Eurasian Oystercatchers may be a consequence of their smaller asymptotic body mass compared to African Black Oystercatchers.

Using the predictive equation for shorebirds by Beintema and Visser (1989b), it was determined that Eurasian Oystercatchers, with an asymptotic mass of 466 g (Starck & Ricklefs 1998b), had a growth rate coefficient 78% larger than the predicted 0.045 d$^{-1}$. Using adult mass, 530 g, as the asymptote, Eurasian Oystercatcher chicks had a growth rate coefficient 86% larger than predicted (Figure 7.9). The predictive equation for semi-precocial gulls and terns by Drent and Klaassen (1989) had a steeper slope and a larger intercept than that of Beintema and Visser (1989b) for shorebirds. Due to their semi-precocial mode of development, oystercatcher growth may follow a different trajectory to that of precocial shorebirds. Thus it may be erroneous to use the predictive equation for precocial shorebirds to compare the relative growth of oystercatchers. African Black Oystercatcher chicks, like those of
precocial shorebirds in a sub-tropical environment (Tjørve et al. submitted manuscript-a), may actually grow relatively slower than would be expected for a semi-precocial species of its size, and the relative growth of Eurasian Oystercatcher chicks may not be as fast if a relationship for semi-precocial shorebirds were used in this comparison.

Relative growth rates of precocial shorebirds are faster at higher than at lower latitudes (Tjørve et al. submitted manuscript-b, Tjørve et al. submitted manuscript-c). If this relationship holds for observed growth rate coefficients also, the smaller growth rate coefficient of African Black Oystercatcher chicks compared to that of Eurasian Oystercatcher chicks may be explained by the combined effects of the latter breeding at higher latitudes and having a smaller adult body mass.

Weathers (1979) noted that basal metabolic rate (BMR) tends to be greater in birds from cold climates and lower in tropical species than would be expected from the bird’s mass. Natural selection may favour the low resting metabolic rate (RMR) in mild environments because this lowers the demand for food (Kersten & Piersma 1987). In addition, the relative level of RMR is most likely an adaptation to a low rate of energy expenditure (Kersten & Piersma 1987). Thus we predicted that African Black Oystercatcher chicks would have a lower RMR than arctic or temperate breeding shorebirds.

![Figure 7.9](image)

**Figure 7.9.** Chick growth rate coefficient as a function of asymptotic mass for precocial shorebirds in arctic (●), temperate (■), tropical (▲) and sub-tropical (○) subregions and for semi-precocial oystercatchers (Δ). The curve represents the predictive equation of Beintema and Visser (1989b). Data in this graph were obtained from Beintema and Visser (1989b), Cairns (1982), Dement’ev and Gladov (1969), Glutz von Blotzheim (1975), Hockey (1984a), Hötker (1994), Klaassen and Drent (1991), Norton (1970, 1973), Parmelee et al. (1968), Parmelee (1970), Pienkowski (1984), Redfern (1983), Ricklefs (1973), Safriel (1975), Schekkerman (1998a, 1998b, 2001, 2003), Soikkeli (1967), Tjørve et al. (submitted manuscript-a, submitted manuscript-b, submitted manuscript-c), and this study.
The average daily energy allocation to RMR of Eurasian Oystercatchers was 0.363 kJ.d⁻¹.g⁻¹ (Kersten & Piersma 1987). This is 79% of the 0.459 kJ.d⁻¹.g⁻¹ measured in African Black Oystercatcher chicks. The RMR of hatchling Eurasian Oystercatchers was 26.4 kJ.d⁻¹ (Klaassen & Drent 1991) which was slightly less than that of African Black Oystercatchers, 28.2 kJ.d⁻¹. The calculated total RMR throughout the prefledging period of Eurasian Oystercatchers was less than that of African Black Oystercatchers, 5069 kJ (Kersten & Piersma 1987). The smaller adult size of Eurasian Oystercatchers may be one but not the only factor that causes the differences in energy metabolism between the two species.

Due to their large size, the TME of African Black Oystercatchers was larger than that of Eurasian Oystercatchers and three precocial shorebirds in the Western Cape (Kersten & Piersma 1987, Tjørve et al. submitted manuscript-c). Their ADME was, however, smaller than that of the three precocial shorebirds (Tjørve et al. submitted manuscript-c) and larger than that of Eurasian Oystercatchers (0.71 kJ.g⁻¹.d⁻¹) determined from the TME and fledgling mass in Drent and Klaassen (1989).

The relative TME of Eurasian Oystercatchers was 29% less than predicted. This result and their small RMR energy expenditure (Drent & Klaassen 1989) and rapid growth (Kersten & Brenninkmeijer 1995) indicate that chicks obtain sufficient food to sustain fast growth, but expend very little in activity. The relative energy expenditure of Eurasian Oystercatchers is less than that of African Black Oystercatchers. This difference can be partly explained by the smaller RMR energy expenditure of Eurasian Oystercatchers. African Black Oystercatchers spend little time brooding and may expend relatively more energy on thermoregulation than Eurasian Oystercatcher chicks.

**The influence of mode of development on growth and energy expenditure**

According to Ricklefs (1973, 1979) slow growth is associated with precocial development. Oystercatcher chicks, however, have precocial mobility, but are parentally fed until well after fledging (Safriel et al. 1996). Therefore, it was expected that oystercatcher chicks would be able to grow at relatively faster rates than precocial shorebird species.

African Black Oystercatcher chick growth was about the same as predicted by Beintema and Visser (1989b) for a shorebird species of its size. Using the same predictive equation, the growth rate coefficients of precocial shorebird species that breed in the same region were smaller than predicted (Tjørve et al. submitted manuscript-c). For example, the relative growth rate coefficients of Kittlitz’s Plover, *Charadrius pecuarius*, Blacksmith Lapwing, *Vanellus armatus*, and Crowned Lapwing, *V. coronatus*, chicks in the Western Cape near Cape Town were 53%, 72% and 91% of the predicted value, respectively (Tjørve et al. submitted manuscript-c). Used for comparative purposes between precocial and semi-precocial shorebird species, however, the equation suggests that the semi-precocial African Black Oystercatcher chicks grow relatively faster than precocial shorebird species in the same climatic environment.
The relative RMR at fledging of African Black Oystercatcher chicks (99%) was greater than that of Kittlitz’s Plover chicks (73%), Blacksmith Lapwing chicks (71%) and Crowned Lapwing chicks (92%) that grow in the same region (Tjørve et al. submitted manuscript-c). As observed for African Black Oystercatchers in this study, the TME values of Kittlitz’s Plover (0.4%), Blacksmith Lapwing (9.6%) and Crowned Lapwing (12.7%) chicks were close to the predicted values for their size (Tjørve et al. submitted manuscript-c). The three precocial species studied in the Western Cape had small relative RMR, large relative energy expenditure but relatively slow growth rates whereas the RMR, energy expenditure and growth rates of African Black Oystercatcher chicks were both close to predicted values. It therefore seems that in the Western Cape, semi-precocial, parent-fed chicks are able to utilise energy for growth whereas precocial, self-feeding chicks expend energy on activity and thermoregulation; thus their growth is relatively slower.

The influence of latitude on growth and energy expenditure
The TME of self-feeding precocial shorebird chicks in temperate and arctic zones was greater than predicted for birds of their body size (Schekkerman & Visser 2001, Schekkerman et al. 2003, Tjørve et al. submitted manuscript-b). The measured TME for Black-tailed Godwits, Limosa limosa, and Northern Lapwings, V. vanellus, in the Netherlands, 53 ºN, were for instance 39% and 29% greater than predicted, respectively (Schekkerman & Visser 2001). Joest (2003) found that the TME for Pied Avocets in northern Germany, 54 ºN, in a food-rich environment (8423 kJ) was greater than that of Pied Avocets in a food-rich environment in southern Spain (7951 kJ), 36 ºN. The Gompertz growth rate coefficient of Avocet chicks in northern Germany (0.0667 d –1) was 9% greater than that in southern Spain (0.0611 d –1, Joest 2003). Avocet chicks in a cold environment were able to maintain a growth rate through greater energy expenditure, possibly obtaining more food and spending larger amounts of time brooding (Joest 2003). In addition, Joest (2003) found that Avocet chicks growing in warmer environments were more adaptable to differences in food availability than chicks growing in cooler environments, which is most likely due to their lower energy expenditure on thermoregulation.

African Black Oystercatcher chicks spend little time (6%) foraging (being fed) compared to the amount of time spent foraging by precocial shorebirds. This is a result of parental provisioning (Table 7.2). This is similar to the behaviour observed by Klaassen et al. (1992) in the semi-precocial, parent-fed Arctic Terns, Sterna paridesea, and Common Terns, S. birundo. African Black Oystercatchers, however, enjoy a mild climate, and chicks spend little time being brooded, even when they are young and their thermoregulatory systems are not fully developed. Instead of brooding or foraging African Black Oystercatcher chicks spent the majority of their time (83%) inactive without being brooded. This indicates that African Black Oystercatcher chicks are able to maintain body temperature, whereas temperate- and arctic-breeding shorebirds require extensive periods of brooding (Table 7.2). Adult African Black Oystercatchers did not invest much of their time brooding their chicks, but used most
Table 7.2. Activity of African Black Oystercatcher chicks at Robben Island, South Africa, compared to other semi-precocial and precocial species. * signifies chicks older than a week. Total average time allocation over 0–29 days of age for Arctic and Common Tern chicks and over 0–37 days of age for African Black Oystercatcher chicks.

<table>
<thead>
<tr>
<th></th>
<th>Brooding</th>
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<td><strong>Parentally-fed semi-precocial species</strong></td>
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<td>Common Tern</td>
<td>16</td>
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<td>12</td>
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<tr>
<td>Arctic Tern</td>
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<td>African Black Oystercatcher</td>
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<td><strong>Temperate breeding species</strong></td>
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<td>Red Knot</td>
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<tr>
<td>Little Stint</td>
<td>36</td>
<td>63</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

1Klaassen & Bech (1992), 2Schekkerman & Visser (2001), 3Schekkerman, Tulp, Piersma & Visser (2003), Tjørve et al. (submitted manuscript-b) and this study.

of their time during the low-tide period foraging for themselves and feeding their chicks.

**Sibling rivalry and its impact on growth, DEE and energy budgets**

African Black Oystercatcher chicks hatch synchronously, within hours of each other (Hockey 1983a). As a result of sibling rivalry and parent-offspring conflicts, oystercatcher chicks start to show mass differences two to three weeks after hatching (Tjørve et al. submitted manuscript-a). The growth rate coefficients of siblings were significantly different, one chick growing faster and becoming larger than the other. A similar trend was found in siblings of American Black Oystercatchers (Groves 1984, Hazlitt et al. 2002), and Eurasian Oystercatchers (Safriel 1981).

The faster growth of one sibling means that it is capable of allocating more energy into $E_{\text{dis}}$ and $E_{\text{syn}}$ than its slower-growing sibling. $E_{\text{dis}}$ and $E_{\text{syn}}$, however, is only on average 20% of the DEE of an individual. Thus, assuming that RMR and thermoregulation costs depend only on the mass of the oystercatcher chick and not its rate of growth, even quite large differences in growth rate will not result in large differences in DEE between siblings.

The smaller chick can possibly change its behaviour when hungry, actively begging its parents for food, while the larger chick is satiated and shelters in a warm position. Consequently, the smaller sibling can expend relatively more energy than the larger sibling in thermoregulation and activity while the larger chick allocates its energy to growth, which may explain why the smaller sibling can have similar DEE as the larger chick, despite its lower mass.

Single chicks grew at about the same rate as the large sibling and marginally faster than the small sibling in two-chick broods (Tjørve et al. submitted manuscript-a). No significant differences in relative DEE were, however, observed between single chicks and the large or small siblings of two-chick broods. A larger sample size may result in significance difference.
Adult oystercatchers may adjust their feeding of chicks according to the number of chicks and the food availability of their habitat; two-chick broods requiring more parental effort than one-chick broods. Sibling rivalry can, however, reduce the energy requirements of the brood because both chicks do not grow as rapidly as single chicks, and one chick grows slower. Single chicks may therefore benefit energetically from not having to share food with a sibling.

The different sizes and hence different energy requirements of siblings may have energetic implications on the parents feeding the growing chicks. We found that an average two-chick brood requires 1251.6 kJ.d⁻¹ at 40 days when the chicks are fledging. Average single chicks require 630.6 kJ.d⁻¹ at 40 days. This value doubled, for two theoretical chicks, is 10 kJ.d⁻¹ greater than the requirements of an average two-chick brood.

**Conclusion**

African Black Oystercatcher chicks are parent-fed, semi-precocial birds that spend a large amount of time inactive without being brooded. RMR and TME of African Black Oystercatcher chicks are approximately the same as predicted for their size. Compared to self-feeding precocial shorebird species growing at the same latitude, African Black Oystercatcher chicks were better able to obtain and use energy and were able to grow at a relatively faster rate with a smaller ADME. Based on the relative growth, RMR and TME values, and assuming that relative food availability is about the same, this parent-fed semi-precocial species has gained an energetic advantage over self-feeding precocial species at the same latitude through its mode of development. Further research is required to determine whether mode of development influences shorebird energetics in cooler temperate environments. Eurasian Oystercatchers are smaller than African Black Oystercatchers and they grow at a higher latitude. The combined effects of body size and latitude may have resulted in Eurasian Oystercatchers having a larger growth rate coefficient. Their smaller ADME is most likely a consequence of their fast growth, but behaviour (brooding) and food availability may have also influenced energy expenditure.

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