

# Influence of growth rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks

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Time budgets of free-living chicks of Arctic Terns *Sterna paradisaea* and Common Terns *S. hirundo* throughout development are presented with special reference to changes in time allocation when growth rate varies. Chicks of both species were inactive most of the time observed (87%). Time allocated to the different behaviours changed during development and was generally better correlated with body mass than age. Slower growing nestlings were brooded more and allocated more time to quiescence and less time to locomotion, preening, begging and attacking (the latter two significant only for the Arctic Tern). The energetic implications of variation in time budgets with age and growth rate were considered. Parental brooding resulted in an average energy saving of nearly 40% of an individual nestling's thermoregulatory costs. Whereas thermoregulatory costs remained nearly unchanged in Arctic Tern chicks, these were negatively correlated with growth rate in Common Terns. Tentatively, we estimated a 30% reduction in a nestling's total energy requirement for a 50% reduction in average growth rate for both species.

High growth rates in birds seem to have positive effects on fitness (Coulson & Porter 1985, Richner 1989, Tinbergen & Boerlijst 1990, M. Klaassen, unpubl. dissertation, University of Groningen; however, see Tinbergen & Boerlijst 1990 for negative consequences of very high growth rates). In order to maximise growth rate, a chick should eat as much food as it is physiologically able to assimilate. However, the actual amount of food a chick receives, and thereby its growth rate, depends critically on food availability, the number of siblings in the nest and parental quality. Despite Ricklefs' (1973) conjecture that most chicks grow at some physiologically maximum rate, the intraspecific variability in avian growth rates is often considerable (e.g. Ashmole 1963, Graves 1984, Briskie & Sealy 1989, Richner 1989, Emlen *et al.* 1991, Magrath 1991, Mlody & Becker 1991, M. Klaassen, unpubl. dissertation, University of Groningen). Growth rates of chicks up to fledging may even differ by a factor of 3 (M. Kersten & A. Brenninkmeijer, unpubl.). An accurate knowledge of the relations between food intake and growth rate can be used to interpret family planning in terns, to interpret the evolutionary adaptiveness of growth rate differences (M. Klaassen, unpubl. dissertation, University of Groningen) and to model population impact on food resources.

Klaassen *et al.* (1992) raised chicks of Common Terns *Sterna hirundo* and Sandwich Terns *S. sandvicensis* in the laboratory using a graded series with different amounts of food. They found that a reduction in food intake of about

20% was accompanied by a 50% reduction in growth rate. However, the additional effects of the environment and interactions between individuals (e.g. thermoregulation, brooding) were not measured in the laboratory.

Here, we present time budgets of free-living Arctic Tern *S. paradisaea* and Common Tern chicks throughout development with special reference to the changes brought about in time allocation when growth deviates from the average growth curve for the species. By combining these time budgets and detailed energy budgets of Arctic and Common Terns exhibiting average growth rates (Klaassen 1994), the energetic consequences of growth rate differences were estimated.

## METHODS

### Growth

The study was conducted on the island of Griend (53°15'N, 5°15'E), Dutch Wadden Sea, from May to July 1989 and 1990. Several study sites were selected where both Arctic and Common Tern nests were marked. At hatching, the chicks were ringed with metal rings. Chicks were weighed to the nearest gram using a Pesola spring balance at 2-3-day intervals. Using only the data for chicks assumed to fledge (i.e. those that reached a body mass of at least 90 g), a logistic growth curve (Ricklefs 1967) was fitted to the body mass ( $M$ , g) data in relation to age ( $t$ , days) by least square analysis. A condition index was obtained by calculating residual body mass ( $M^{\text{res}}$  %):

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$$M_{res} = \frac{M - M''}{M''} \times 100\% \quad (1)$$

where  $M$  is actual body mass (g) and  $M''$  is the age-specific expected body mass (g) for each species, calculated using the logistic growth curves in Eqs. 2 and 3 (below). The residual body mass was calculated for all chicks between 3 and 25 days of age. The body mass of chicks younger than 3 days was too low to allow accurate calculations, whereas chicks older than 25 days normally show a substantial pre-fledging decline in body mass, which the logistic growth curve does not describe.

### Activity budgets

We observed 35 Arctic and 43 Common Tern chick individuals between hatching and fledging (age 0-29 days), usually over the total daylight period (from 0430h to 2230h). All observations lasting less than 50% of the daylight period were omitted from analysis. During the continuous observations of nestlings, we discriminated between parental brooding, preening, locomotion, begging, eating, attacking and being attacked. The remaining time was allocated to quiescent behaviour: standing, sitting and laying without being brooded by the parents. Observations were made from a hide, and data could be collected simultaneously from a maximum of ten chicks, using a small data logger with a resolution of one second. When body mass was not measured on the day of observation, we calculated the expected body mass by linear interpolation of the measurements on the preceding and subsequent days. For each chick observed, we measured or interpolated body mass to calculate the condition index (Eq. 1).

The percentage of time dedicated to each one of the behaviours (except for quiescence) was analysed in relation to age, body mass and condition, using multiple regression analysis (SPSS/PC+; Norusis 1988).

## RESULTS

### Growth

For Arctic Tern the logistic growth curve for chicks that reached a body mass of at least 90 g is

$$M'' = \frac{107}{1 + 9.0e^{-0.179t}} \quad (2)$$

and for Common Tern:

$$M'' = \frac{114}{1 + 6.3e^{-0.21t}} \quad (3)$$

Deviations from these average growth curves (Fig. 1) are considerable, and condition indices (Eq. 1) ranged from -72% to +40%. Chicks which develop fastest normally fledge after 21 days in Arctic and 22 days in Common Terns (Cramp 1985), but fledging age can be extended considerably. Some individuals of both species still had not fledged at 30 days of age (Fig. 1).

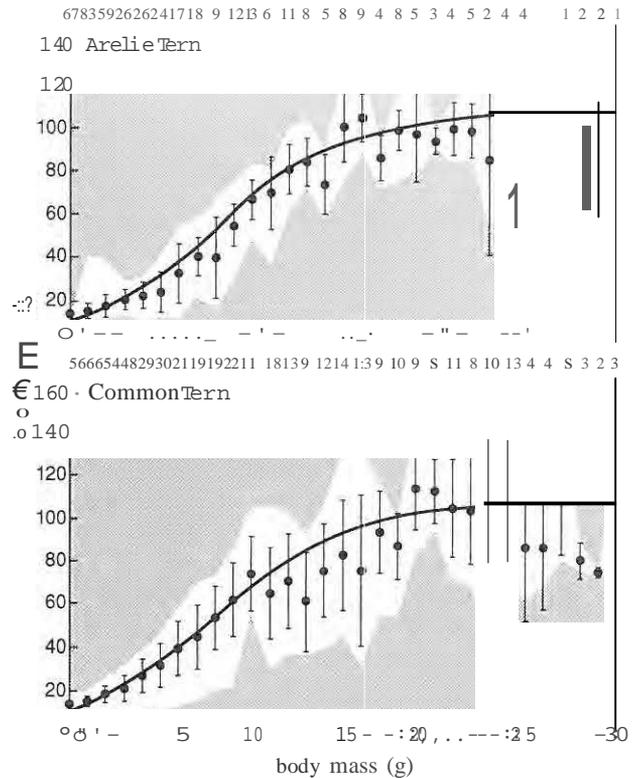


Figure 1. Change in body mass with age for Arctic (upper) and Common Tern chicks (lower) at the island of Griend for the years 1989 and 1990. Averages  $\pm$  s.d. are shown and sample sizes are given at the top of the figures, with body mass range indicated by the extent of the white area. Logistic growth curves are shown based on data from chicks that reached a body mass of at least 90 g (see text and Eqs. 2 and 3).

### Activity budgets

In total, we obtained 77 and 196 time budgets for Arctic and Common Tern chicks, respectively. The average time budget in relation to age for both species shows a striking resemblance (Fig. 2). The total average time budgets over the first 30 days of life also are virtually identical (Fig. 3). In both species, the chicks are inactive for most of the time (brooding and quiescence: 87%). Arctic Terns were brooded for more of the time than Common Terns (20% v 16%). This difference might be due to a higher average rainfall during the first week of observations for Arctic compared with Common Tern chicks, otherwise weather conditions were largely comparable.

Multiple regression analyses of the time dedicated to the different behaviours in relation to age and condition (Table 1) and body mass and condition (Table 2) revealed that parental brooding decreased and locomotion and preening increased with maturation in both species. When brooding is expressed as a function of chick age, condition index does not significantly contribute in explaining residual variation, whereas when expressed as a function of body mass, it does

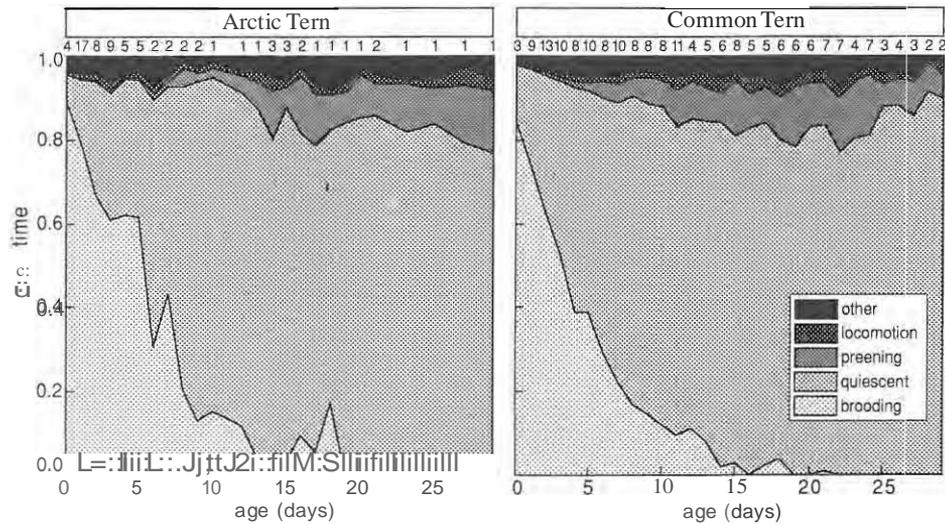


figure 2. Average time allocation in relation to age from 0 to 29 days for Arctic and Common Tern chicks. Sample sizes are given at the top of each panel. The time allocated to interactions (attacking, being attacked) was less than 1% and has been included with begging and cating in the category 'other'.

For most other behaviours, the opposite can be seen: in particular the condition index may significantly contribute to the explanation of residual variation when behaviour is expressed as a function of age. For the Arctic Tern only, attacking increased with age but not with body mass. In the same species, begging and attacking increased with condition. The equations relating time allocation to body mass and condition (Table 2) generally explain more of the variation than those using age and condition as the dependent variables (Table 1). Therefore, we used the equations from Table 2 when calculating the time allocation changes with growth rate reduction. The changes in time allocation as a result of varying growth rate are visualized in figure 4. Departing from the average growth rate, for both Arctic and Common Tern chicks, the relative changes in time allocation

over the total developmental period are calculated for chicks that grow at 50% of the average rate. Despite the lower mass-specific brooding in slow-growing chicks, the total time brooding over the developmental period is higher in the slow growers. Time allocations to all other behaviours (Table 2) either remained unchanged with a decrease in growth rate or were lower. As a result, besides brooding, quiescence was also somewhat higher in slow growers.

## DISCUSSION

### Time allocation

From the analysis of the behavioural data in relation to condition, age and body mass, it can be concluded that be-

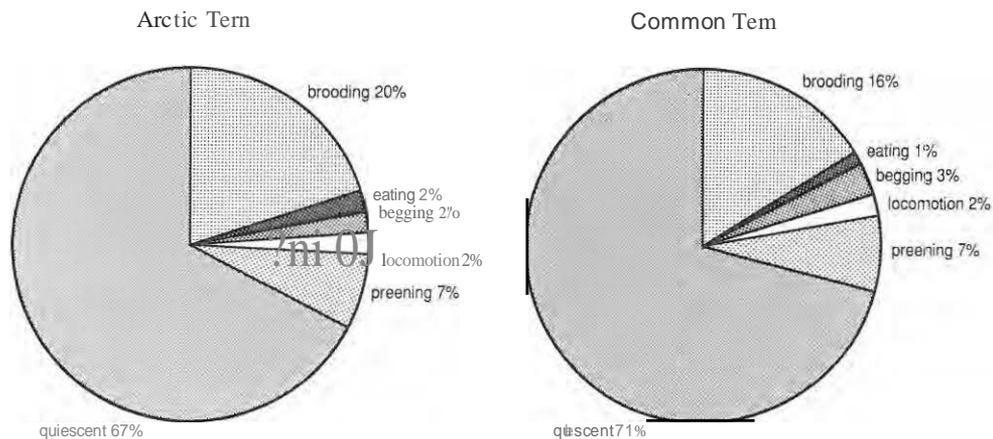


Figure 3. Average time allocation over 0-29 days of age for Arctic and Common Tern chicks. The time allocated to interactions (attacking, being attacked) was less than 1% and is not shown

Table 1. Multiple regression analyses of time allocation (%) with age (days) and condition ( $M''$ , %) for Arctic and Common Tern chicks from 3 to 25 days of age. Only constants and partial regression coefficients significantly different from zero ( $P < 0.05$ ) were entered. No significant relations were found for 'eating' and 'attacked'. No statistics were performed/or the time allocated to 'quiescence'

Behaviour type	Constant	Partial regression coefficients		
		Age	Condition	
Arctic Tern, $n = 40$ days				
Brooding <sup>†</sup>	119.1	-92.7		0.685
Begging	2.26		0.030	0.264
Locomotion	1.24	0.054	0.016	0.193
Preening		0.481		0.729
Attacking		0.004	0.001	0.337
Common Tern, $n = 151$ days				
Brooding <sup>†</sup>	83.4	-64.4		0.667
Begging				
Locomotion	1.55	0.057	0.016	0.133
Preening	3.13	0.400	0.098	0.434
Attacking				

<sup>†</sup> The  $\log_{10}$  value of age +1 was used for age.

havioural development kept pace with body mass rather than with age. This conclusion is based on the finding that a significant part of the variation in behaviour is still explained by condition when using age instead of body mass. However, brooding is an exception to this rule. This might originate from the fact that, although a chick can call for its parents, brooding is a parental behaviour. One possible scenario is that the parental motivation for brooding is governed by a fixed time program and decreases steadily after hatching. However, in disagreement with this hypothesis of a fixed time program for brooding are the observations of Richard-Yris & Leboucher (1987) in the domestic fowl *Gallus domesticus*. They found that substituting old chicks with younger ones led immediately to the appropriate maternal brooding response. Alternatively, the brooding pattern with age, or body mass and condition, might be explained with the model of Klaassen (1994), which describes time allocation to brooding as a function of parental foraging success and mass-specific thermoregulatory costs of unbrooded chicks. It is conceivable that low parental foraging success reduces growth for the obvious reason that there is less food. When parental foraging success is low, and thus chick growth rate is depressed, Klaassen's (1994) model predicts that brooding will decrease, explaining the empirically found correlation between mass-specific brooding and condition (Table 2).

Usually the second and third chicks in the nest grow at a slower rate than the first (e.g. Langham 1972). It could be argued that keeping food provisioning for the first chick high enough might occur at the expense of parental brooding for

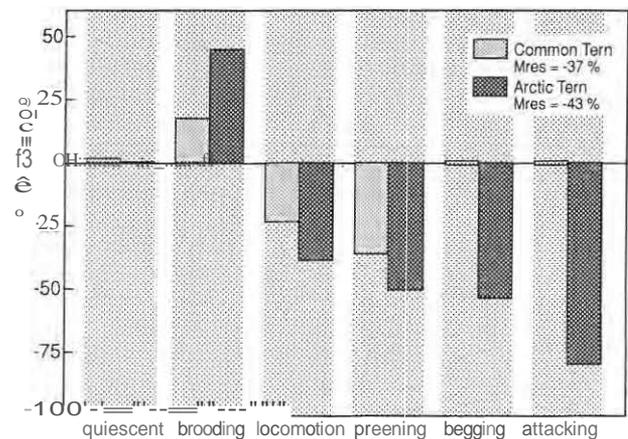


Figure 4. Time allocation changes (totalled over age 3-25 days) for Arctic and Common Tern chicks when growth rate was reduced to half the average growth rate (from 0.279 to 0.140 in Eq. 2, and from 0.242 to 0.121 in Eq. 3, which correspond with average condition index changes of -43% and -37%, respectively). Calculations were made departing from the time allocation equations in Table 2.

the younger siblings. However, for the chicks observed in this study, average time allocated to the brooding of each nestling was not significantly different for first-batched compared with later-hatched nestlings (ANCOVA using  $\log_{10}$  age: Arctic Tern  $F_{1,46} = 1.24$ , n.s.; Common Tern  $F_{2,111} = 1.92$ , n.s.). In addition, the distribution of first and later chicks

Table 2. Multiple regression analyses of time allocation (%) with body mass (g) and condition ( $M''$ , %) for Arctic and Common Tern chicks from 3 to 25 days of age. Only constants and partial regression coefficients significantly different from zero ( $P < 0.05$ ) were entered. No significant relations were found for 'eating' and 'attacked'. No statistics were performed/or the time allocated to 'quiescence'

Behaviour type	Constant	Partial regression coefficients		
		Mass	Condition	
Arctic Tern, $n = 40$ days				
Brooding <sup>†</sup>	187.8	-94.13	0.363	0.704
Begging	2.26		0.030	0.264
Locomotion		0.027		0.684
Preening	-2.71	0.142		0.662
Attacking	0.049		0.001	0.124
Common Tern, $n = 151$ days				
Brooding <sup>†</sup>	158.2	-78.23	0.374	0.683
Begging				
Locomotion	0.777	0.018		0.157
Preening		0.103		0.795
Attacking				

<sup>†</sup> The  $\log_{10}$  value was used for body mass.

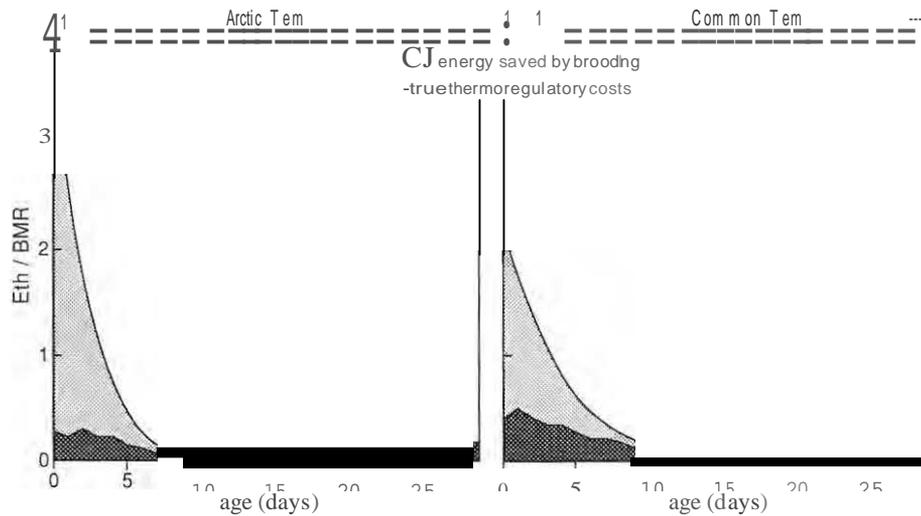


Figure 5. Thermoregulatory costs ( $E$ ) for Arctic and Common Tern chicks in relation to age, in multiples of basal metabolic rate ( $BMR$ ), at Griend when corrected for parental time allocation to brooding ( $E_{true}$ ) and when unbrooded. The difference between the thermoregulatory costs for unbrooded and brooded chicks is the energy saved by brooding.

over residual body masses above and below average is not significantly different (Arctic Tern  $X_{.2}^2 = 2.73$ , n.s.; Common Tern  $X_{.1}^2 = 1.26$ , n.s.). Thus, hatching order alone cannot explain the low parental brooding in relatively light chicks.

All behaviour that involved any kind of activity (locomotion, preening, begging, eating, attacking, being attacked) either remained unaffected or decreased with a decrease in growth rate (Fig. 4). In the domestic fowl, overall activity decreases when growth stagnates (Swiergel 1987). As to the question why activity is not zero when food is in short supply, Beach (1945) suggested that, at least in part, the function of activity is to enhance muscular development and coordination in young animals, resulting in a good physical condition which is important later in life.

#### Estimates of thermoregulatory costs and savings by brooding

Before looking at possible savings in thermoregulatory costs for the chicks as a result of parental brooding, it is necessary to estimate the thermoregulatory costs of the unbrooded nestling. From operative temperature ( $T_e$  °C; i.e. the temperature experienced including effects of wind and radiation), body temperature ( $T_b$  °C) and thermal conductance ( $h$ , kJ per day per °C; i.e. the inverse of insulation), it is possible to calculate the heat loss of an animal (Bakken 1976). At the so called lower critical temperature (LCT °C), heat loss exceeds the heat produced in basal metabolism ( $BMR$ , kJ/day) and extra heat must be produced to compensate for heat dissipation, i.e. the thermoregulatory cost.

$$E_t = h(T_b - T_e) - BMR \text{ kJ/day}, \quad (4)$$

for  $T_e < LCT$ . When  $T_e > LCT$ ,  $E_t = 0$ .

For both Arctic and Common Tern chicks, Klaassen (1993) gives equations based on empirical data describing basal metabolic rate ( $BMR = 202M + 47.04M^2 - 0.3660M^3$  and  $BMR = 1.17M + 0.038M^2 - 2.365M^3$ , respectively) and thermal conductance ( $h = 0.60M^{0.811}$  and  $h = 0.61MM^{0.8}$ , respectively) in relation to body mass. In addition, Klaassen (1994) provides hourly operative temperature measurements over 28 days prevailing at Griend. Using Eq. 4, we calculated the expected average thermoregulatory costs over all  $T_e$  estimates available for unbrooded chicks in relation to age, assuming that they remain homeothermic at 39°C body temperature (Klaassen *et al.* 1989a) and were growing according to the average growth curves (Eqs. 2 and 3 for Arctic and Common Tern chicks, respectively).  $BMR$  not only provides us with information concerning the energy expended in maintaining the basic life processes, but it also offers us a means of sealing the metabolic potential of the animal concerned; the thermoregulatory capacity for chicks is about 2  $BMR$  (Ricklefs 1989, G.H. Visser, unpubl. dissertation, University of Groningen). Expressing thermoregulatory costs for unbrooded chicks in multiples of  $BMR$  yields values as high as 3.7  $BMR$  for Arctic and 2.2  $BMR$  for Common Terns at hatching (Fig. 5). From hatching onwards, thermoregulatory costs rapidly decrease in both species, reaching a more or less stable level of  $0.1 \pm 0.05 BMR$  at 10 days of age. This demonstrates that brooding is essential for chicks of both species early in development. Not only are expenses very high, but the thermoregulatory capacity is also insufficient in young neonates. In these calculations we have disregarded the possible effect of huddling. Indeed, significant savings in thermoregulatory costs were associated with increasing the number of broodmates in altricial species (Mertens 1969, O'Connor 1975, Sullivan & Weather

1992). Also. In comparing the heat production of groups (10 to 20 subjects) with that of individual chicks of the domestic fowl, energy savings up to 15% were recorded due to huddling (Kleiber & Winchester 1933, Misson 1976). Unfortunately, no data on the effect of huddling with fewer individuals exist for semi-altricial or precocial chicks in the size range of tern chicks; therefore, we cannot account for possible thermoregulatory consequences of brood size. However, when parents were not brooding and were away from the nest site, chicks usually chose individual hiding places. We therefore suspect that huddling was only of minor importance to the thermal balance of the Arctic and Common Tern chicks in our study.

After having assessed the thermoregulatory costs of the unbrooded chick, we can now estimate the impact of brooding on the nestlings' thermoregulatory costs. Using the predicted time spent brooding in relation to body mass from Table 2, the 'true' thermoregulatory costs were calculated using the following assumptions: (1) percentage of time allocated to brooding is equal for night and day. (2) when brooding occurs, nestling thermoregulatory costs equal zero and (3) chicks are preferably brooded during the coldest hours. In addition, we had to allow for a minor extrapolation of our time budget data for chicks less than 3 days old and between 25 and 29 days of age. According to this calculation, thermoregulatory costs for the chicks are reduced by approximately 35% due to parental brooding (Fig. 5, Table 3) and never exceed 0.5 *BMR* per day. Costs will be even lower if we assume the time allocated to brooding to be higher during the night than during the day (P.H. Becker, unpubl.). The estimated energy savings by brooding presented here are largely comparable to the estimates in other larids using doubly labeled water (Klaassen *et al.* 1989b, Gabrielsen *et al.* 1992, Klaassen 1994).

Thermal conductance depends critically on body mass in chicks (e.g. Klaassen 1994, G.H. Visser, unpubl. dissertation. University of Groningen). Mass-specific basal metabolic rate is positively related with growth rate (Klaassen & Bech 1992). A lowered growth rate thus entails a decreased *BMR* on a mass-specific basis, an increased lower critical temperature and, thereby, higher thermoregulatory costs (see Eq. 4). However, although in normally developing chicks thermoregulatory capacity is about 2 *BMR* (Ricklefs 1989, G.H. Visser, unpubl. dissertation. University of Groningen). Klaassen & Bech (1992) showed that in Arctic Tern nestlings the thermoregulatory ability still developed in spite of reduced growth rate. Arctic Tern chicks in poor condition (although exclusively when not close before total starvation) had a higher metabolic capacity than equally heavy conspecifics with a higher condition and thus had a better ability to cope with cold conditions.

To show the effect of a change in growth rate on thermoregulatory cost when unbrooded, we calculated the thermoregulatory consequences associated with a growth rate reduction of 50% from the norm for each species. The method used in this calculation was essentially the same as described above (Eq. 4) for the calculation of thermoregulatory

costs in chicks growing according to the average growth curves. Only *BMR* was additionally corrected for condition differences by multiplication with  $0.98 + 0.0022M^{0.75}$ , (Klaassen & Bech 1992). The estimates of thermoregulatory costs uncorrected for brooding (Table 3) are higher for slow growing chicks compared with fast growers in both species. This is due to both a low body mass on average (high thermal conductance) and a relatively low *BMR* for a given body mass (resulting in a relatively high lower critical temperature). For Common Tern chicks, the increase is higher (48%) than for Arctic Tern chicks (15%) due to the specific differences in their basal metabolism (Klaassen 1994). Using the predicted time allocated to brooding in relation to body mass and condition from Table 2, the 'true' thermoregulatory costs were calculated using the same methodology and assumptions as used in the calculations for chicks growing according to the norm above. Due to compensatory parental brooding, the 'true' thermoregulatory costs in Arctic Tern chicks decrease slightly when growth rate slows (Table 3). In slow-growing Common Tern chicks, however, the increased energy cost for thermoregulation is not completely compensated for by the parents through brooding, and the chicks need to invest considerably more energy in thermoregulation than fast-growing conspecifics (Table 3). Brooding and foraging by the parents are mutually exclusive. Arctic Terns tend to compensate for their offspring's slow development by more brooding, thereby moderating the chick's thermoregulatory costs. Common Terns do not thereby having more time for foraging from which offspring might benefit by the resulting higher rate of food delivery to the nest. In order to shed more light on the time allocation differences to brooding, the trade off from brooding and foraging needs to be known more exactly. Nevertheless, it seems that the differences in physiology of the chicks (Klaassen 1994) and brooding behaviour relate to the typical differences in breeding habitat of the two species. Arctic Terns usually breed in more exposed habitats than Common Terns (Cramp 1985, Lemmetyinen 1974).

#### Differences in the total energy budget between fast- and slow-growing chicks

A change in growth rate results in considerable alterations in thermoregulatory costs, partly induced by concomitant changes in parental brooding behaviour, and we evaluated the impact of the other time allocation changes with variations in growth rate. First, we constructed the energy budget of a chick. Not all ingested food is digested, and part leaves the body unused in the form of pellets or faeces. The metabolisable energy intake (*ME*, kJ/day, which for tern chicks is about 80% of the gross energy intake: Massias & Becker 1990, Drent *et al.* 1992, Klaassen *et al.* 1992) must cover the energy being retained through growth as body tissue ( $E_{\text{g}}$ , kJ/day), the synthesis costs of body tissue ( $E_{\text{t}}$ , kJ/day, which is  $0.33 \times E_{\text{g}}$ , according to Ricklefs 1974), the energy necessary for all basal life processes (*BMR*, kJ/day), activity ( $E_{\text{a}}$ , kJ/day) and thermoregulation ( $E_{\text{tr}}$ , kJ/day):

Table 3. Estimated uncorrected thermoregulatory casts ( $E_h$ , kJ/30 days) and thermoregulatory casts corrected for parental brooding ( $E_{h,true}$ , kJ/30 days) for Arctic and Common Tern chicks exhibiting average growth rates and growth rates reduced to half the average (growth rate constants 0.140 and 0.121, respectively, cf. Eqs. 2 and 3)

Species	Average growth rate			50% of average growth rate		
	$E_{h,true}$			$E_{h,true}$		
	$E_u$	$E_{h,true}$	$\% E_u$	$E_u$	$E_{h,true}$	$\% E_u$
Common Tern	487	320	66%	720	507	70%

$$ME = E_{h,true} + E_{h,true} + BMR + E_{h,true} + E_{h,true} \text{ kJ/day} \quad (5)$$

We pointed out above how energy expenditure estimates for basal metabolism and thermoregulation corrected for brooding were derived for chicks growing at different rates. Energy deposited in tissue and its synthesis casts can be calculated from the growth curves taking the increase in tissue energy density ( $e_{tissue}$ , kJ/g) during development into account ( $e_{tissue} = 4.094 + 4.713 \times M/A$ , kJ/g, where M is body mass and A is asymptotic body mass, both in g; Klaassen 1994). We lack knowledge of the specific casts to accurately calculate activity casts for all the different behaviour patterns. However, we made a tentative attempt by assuming that all activity (preening, locomotion, begging, ealing, attacking, being attacked) has the same cost and that these casts are proportional to body mass. Because the activity casts for average-growing chicks are known (Klaassen 1994), the absolute activity cost changes with growth rate could be calculated as well.

To understand the overall changes in the energy budget when growth rate deviates, we compared the energy budget of chicks growing according to the norm with that of chicks that have a 50% reduced growth rate. The energy budgets (Table 4) show marked decreases of 30% in the developmental casts for slow growers in both species. However, body masses at an age of 29 days are lower in the slow-growing chicks compared with the chicks growing to the norm, and this is reflected in the synthesis and tissue cost differences between the two. Correction for these body mass discrepancies will lead to a decreased difference between the budgets for slow- and average-growing chicks (Klaassen *et al.* 1992), as all components of energy allocation in Eq. 5 are positively related with body mass. The difference of 30% reported here then might well come close to the empirical value of 20% reported by Klaassen *et al.* (1992) for laboratory-raised Common and Sandwich Tern chicks.

When food is in short supply, most energy is saved by reductions in activity and basal metabolic casts (Table 4). The origins of energy savings in the field (this study) and in the laboratory (Klaassen *et al.* 1992) might be different. The

Table 4. Estimated total energy budgets (from 0 to 29 days of age, kJ/30 days) for Arctic and Common Tern chicks exhibiting average growth rates and growth rates reduced to half the average. Indicated are the energies allocated to basal metabolism (BMR), biosynthesis ( $E_{s,i}$ ), thermoregulation corrected for parental brooding ( $E_{h,true}$ ), activity ( $E_{a,i}$ ) and body tissue ( $E_{t,i}$ ), which all add up to the metabolizable energy intake (ME, Eq. 5)

rate	Average growth rate	50% average growth %	Difference %	Difference E
<i>BMR</i>	2905	2122	-27	46
$E_{s,i}$	294	240	-18	3
$E_{h,true}$	268	233	-13	3
$E_{a,i}$	1272	552	-57	42
$E_{t,i}$	890	727	-18	10
<i>ME</i>	5629	3917	-30	100
Common Tern				
<i>BMR</i>	2913	1861	-36	60
$E_{s,i}$	305	238	-22	4
$E_{h,true}$	320	507	58	-11
$E_{a,i}$	1348	696	-48	37
$E_{t,i}$	923	720	-22	12

impression existed that the amount of activity was unaffected by growth rate in laboratory-raised chicks. Moreover, total activity cost of laboratory-raised chicks was generally lower than that of free-living chicks (respectively, 12% and 19% of ME; Drent *et al.* 1992, Klaassen 1994). Thus, activity cost reduction is probably a more important potential root of energy saving in the field than in the Laboratory when food is in short supply.

We thank the many occasional guests to the remote island of Griend for their help and company. In addition, field work was greatly alleviated by the logistic support of the 'Vereniging tot Behoud van Natuurmonumenten', 'Rijkspolitie te Water Harlingen', 'Natuur Milieu en Faunabeheer', 'Rijkswaterstaat' and Kees de Boer, Jan Veen, finally responsible for our stays at Griend, is thanked for sending us there and for his scientific support. During preparation of the manuscript, we profited from the comments of Peter Becker, RUCU Drent, Marcel Kersten, Johan van Rhijn and an anonymous referee and valuable discussions with my colleagues at the Max-Planck-Institut für Verhaltensphysiologie in Andechs.

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