GROWTH AND ENERGETICS OF ARCTIC TERN CHICKS
(*STERNA PARADISAEA*)

MARCEL KLAASSEN,[1,2] CLAUS BECH,[1] DIRKJAN MASMAN,[2,3] AND
GURI SLAGSVOLD[1]

[1]*Department of Zoology, University of Trondheim, N-7055 Dragvoll, Norway,*
[2]*Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands, and*
[3]*Center for Isotope Research (C.I.O.), University of Groningen,*
Westersingel 34, 9718 CM Groningen, The Netherlands

ABSTRACT.—We studied energy requirements of Arctic Tern chicks (*Sterna paradisaea*) in Ny Ålesund, Svalbard (79°N, 12°W) with special emphasis on thermoregulatory and activity costs. We used doubly labeled water to estimate energy expenditure in the field (E_{dlw}) and made laboratory measurements of the different components of total energy requirement (E_{req}). Comparison of DLW-estimates with oxygen consumption measurements showed that E_{dlw} underestimated total energy expenditure 4.5–16.0% depending on the duration of the experiment. This was probably due to incorporation of isotopes in newly synthesized tissue. Field estimates of total energy expenditure from E_{dlw} were corrected accordingly. A tern chick model was used to measure operative temperature (T_e). At midday T_e reached values up to 20°C above ambient temperature (T_a) which ranged from 3.4–9.0°C. Based on the field estimates of E_{dlw} and T_e and the laboratory measurements of basal metabolic rate and thermal conductance, we conclude that there was a considerable energy saving (456 kJ = 26% of E_{req}) during the first 10–11 days of life, due to parental brooding. After this period, when the parents stop brooding, the energy required for thermoregulation accounted for only 16% of E_{req}. From 10 days after hatching onwards, the energy needed for activity increased considerably, up to 50% of E_{req} just before fledging (Day 20). Comparison of the energy budgets of Arctic Tern chicks with the more southerly occurring closely related Common Tern (*S. hirundo*; Ricklefs and White 1981) revealed only a slightly higher energy expenditure in the Arctic Tern chicks. *Received 5 April 1988, accepted 23 November 1988.*

ENERGY expenditure of chicks living in arctic and antarctic environments has been considered to be dominated by the costs for thermoregulation. Many physiologists have focused on the ability of chicks to cope with low environmental temperatures (e.g. Maher 1964, Norton 1973, Aulie and Steen 1976, Boggs et al. 1977, Pedersen and Steen 1979, Bech et al. 1984, Jørgensen and Blix 1985, Taylor 1985, Boersma 1986). However, the abiotic environment of chicks at high latitudes and the contribution of thermoregulatory costs to their total energy expenditure have not been quantified precisely. In addition to estimating thermoregulatory costs in relation to other energy requiring processes, interspecific comparison of closely related species from different latitudes should provide a better understanding of the influence of the polar environment on chick energy requirements.

We studied energy requirements of Arctic Tern (*Sterna paradisaea*) chicks in the Arctic throughout the period from hatching to fledg-ing, with special emphasis on thermoregulatory costs. We measured field growth, operative temperature, and total energy expenditure using doubly labeled water. In addition we analyzed carcasses and measured oxygen consumption in relation to ambient temperature in chicks of different ages. From this we estimated the costs of basal metabolism, growth, thermoregulation, activity, and total energy requirements, which were compared with the Common Tern (*S. hirundo*) and the Sooty Tern (*S. fuscata*; Ricklefs and White 1981).

METHODS

We studied Arctic Tern chicks in Ny Ålesund, Svalbard (79°N, 12°W) from 12 July to 6 August 1986. The breeding biology of the Arctic Terns in Ny Ålesund has been described by Bengtson (1971) and Lemmetyinen (1972).

The colony was visited regularly and individually marked chicks of known age were weighed with a Pesola spring balance. Wing length was measured

with a ruler to the nearest mm, and tarsus and head length with a flexible ruler to 0.1 mm.

We determined body composition in 11 chicks that ranged in age from 0 to 20 days, and in 2 adult birds. If the age of the chicks was not known from hatching records, body mass and total head length were used to estimate the age from the field measurements obtained in the colony. After collection, the carcasses were weighed immediately and deep-frozen. The carcasses were analyzed for water, lipid and nonlipid dry matter content at the Department of Zoology of the University of Trondheim. We dried the carcasses at 70°C to constant weight and lipids were extracted in petroleum ether. The energy density of individual birds was calculated using energy equivalents of 38 kJ/g lipid and 20 kJ/g nonlipid dry matter (Ricklefs 1974).

Weather data were obtained from the meteorological station in Ny Ålesund. To estimate the combined effect of ambient temperature, wind exposure, and solar radiation, we measured the operative temperature (T_e) which is the temperature a chick would attain if it lacked metabolic heat production and water loss (Bakken 1976). We measured operative temperature as the core temperature (copper-constantan thermocouple) of a tin cast covered with the pelt of a 1-day-old Arctic Tern chick. This mannequin was positioned in the typical microhabitat for a resting chick, which was a gravel field with patchily distributed vegetation not exceeding 10 cm in height. Operative temperature was recorded hourly with a Leeds and Northrup Speedomax recorder during 423 out of 576 hours of investigation, of which 384 hours formed 16 complete days. The operative temperature measurements were used to extrapolate from metabolism chamber conditions to the natural habitat for all age classes, because size apparently has a negligible effect on T_e (Chappell et al. 1984, Walsberg and Weathers 1986), and the color of the chicks changes only little during development until fledging.

In the laboratory we measured oxygen consumption of postabsorptive chicks ($n = 48$) at temperatures ranging from 0 to 37°C (for methods, see Klaassen et al. 1989). Oxygen consumption was converted to energy expenditure using 20 kJ/l O_2 assuming fat metabolism. Basal metabolic rate (BMR) and thermal conductance (h) of the chicks are described as functions of body mass (M, g):

$$BMR = 0.60 + 0.029M$$
$$- 0.00023M^2 \text{ kJ} \cdot g^{-1} \cdot day^{-1} \quad (1)$$

$$h = 0.58M^{-0.486} \text{ kJ} \cdot g^{-1} \cdot day^{-1} \cdot °C^{-1} \quad (2)$$

(Klaassen et al. 1988). We calculated daily thermoregulatory costs (E_{th}) in the field from operative temperature and body mass using Eqs. 1 and 2:

$$E_{th} = h(T_b - T_e) - BMR \text{ kJ} \cdot g^{-1} \cdot day^{-1} \quad (3)$$

if $h(T_b - T_e) > BMR$, where T_b is body temperature (39°C; Klaassen et al. 1989). If $h(T_b - T_e) \le BMR$, E_{th} was assumed to be 0 kJ$\cdot g^{-1} \cdot day^{-1}$.

In the field CO_2 production was measured with doubly labeled water (DLW; Lifson and McClintock 1966, Nagy 1980). We injected 10 chicks that varied in age between 0 and 19 days with 0.14 to 0.19 ml of a mixture containing 44% of 99.84 atoms% D_2O and 56% of 90.23 atoms% $H_2^{18}O$. The amount depended on the size of the bird. A 15-μl blood sample was taken before injection, 3 h after injection (when equilibration was assumed to be complete) and every subsequent 12 h during the following 36 h. In two cases the injected chicks were not recaptured after 3 h, but were sampled 12 h after injection. Blood samples were taken from a neck vein in chicks up to 4-days-old, and from a wing vein in older chicks. Samples were sealed in a glass microcapillary. It took ca. 20 min to catch, weigh, measure, bleed, and release chicks. Blood samples were stored at 5°C until analyses by Isotope Ratio Mass Spectrometry (Masman and Klaassen 1987) at the Center of Isotope Research (C.I.O.) in Groningen.

Validation of the DLW method was obtained on three chicks of different ages, which we transported from Svalbard to Trondheim. We followed the same procedure as in the field, but between the blood samplings we measured oxygen consumption in an open flow system. Air was sucked through a 9 or 17 l metabolic chamber with a flow rate of approximately 1 l/min. The air was dried over silica-gel and oxygen concentration was determined with a Servomex 1100A oxygen analyzer. Ambient temperature in the chamber varied between 3 and 30°C. The chicks were fed *ad libitum* with fresh Torsk (*Brosme brosme*). Oxygen consumption was calculated according to Hill (1972) and converted to CO_2 production with a RQ of 0.73 as the diet consisted mainly of protein and fat.

We assumed linear mass changes in the chicks, and calculated CO_2 production from ^{18}O and D enrichments in the blood samples with eq. 21 of Lifson and McClintock (1966), which was adapted for physical fractionation effects (Lifson and Lee 1961, Lifson and McClintock 1966). Body water was calculated on the basis of the carcass analyses results. To obtain two independent estimates of CO_2 production over ca. 24 h per chick, we used each blood sample analysis only once. We calculated CO_2 production for the interval between the first and third and between the second and fourth sample after injection. In 4 cases the fourth blood sample was too low in ^{18}O to allow accurate calculation of the CO_2 production. This gave 16 independent CO_2 production estimates in 10 chicks of different ages. Carbon dioxide production was converted to total energy expenditure (E_{dlw}) using an equivalent of 25 kJ/l CO_2.
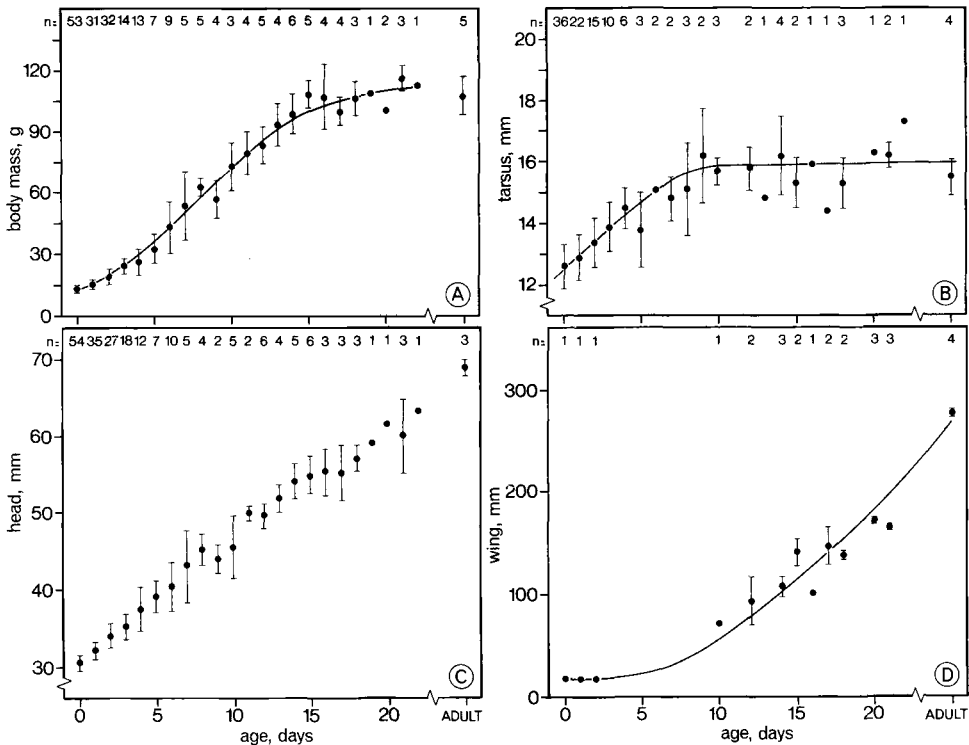
Fig. 1. Development of body mass (A), tarsus length (B), head length (C), and wing length (D) as a function of age in Arctic Tern chicks. Measurements on adults are included for comparison. The line in (A) was calculated (Eq. 4), whereas the lines in (B) and (D) were fitted by eye.

RESULTS

The increase of body mass with age (t, days) (Fig. 1A) was fitted to a logistic equation (Ricklefs 1967):

$$M = 115/(1 + 8.0e^{-0.263t}) \text{ g} \qquad (4)$$

The tarsus had a high growth rate from hatching until Day 7 when it had nearly reached adult length (Fig. 1B). Head length increased nearly linearly with age (Fig. 1C). In contrast, the wing only grew rapidly after Day 5 to Day 8, and reached 60% of adult length at fledging around Day 22 (Fig. 1D).

The carcass analyses enabled us to convert body mass gain to energy deposition and to estimate total body water content, necessary for the calculations of CO_2 production from the isotope enrichments in the blood samples. Body water content (C_w) decreased with age (Fig. 2A) following the expected pattern (Ricklefs 1974) and was described by the equation:

$$C_w = 84.6(t + 1)^{-0.091}\% \qquad (5)$$

($r = -0.875$, $P < 0.001$). The amounts of lipid and nonlipid dry mass (Fig. 2B) were accumulated with a nearly constant ratio from the third day of age onwards. About 28% of the water-free tissue was lipids. As a consequence, the increase of energy density of body tissue (C_{et}) with age (Fig. 2C) was mainly due to the decrease in water content. This increase in energy content was described by:

$$C_{et} = 3.65(t + 1)^{0.306} \text{ kJ/g wet} \qquad (6)$$

($r = 0.929$, $P < 0.001$). From the growth curve (Eq. 4) and the relationship for energy density of body tissue with age (Eq. 6), we calculated the daily cost for tissue deposition (E_{tis}). Assuming a synthesis efficiency of 75% (Ricklefs 1974), the costs for biosynthesis (E_{syn}) were derived by $E_{syn} = E_{tis}0.33$ kJ/day.

We estimated the costs for thermoregulation in the field by using the information of the
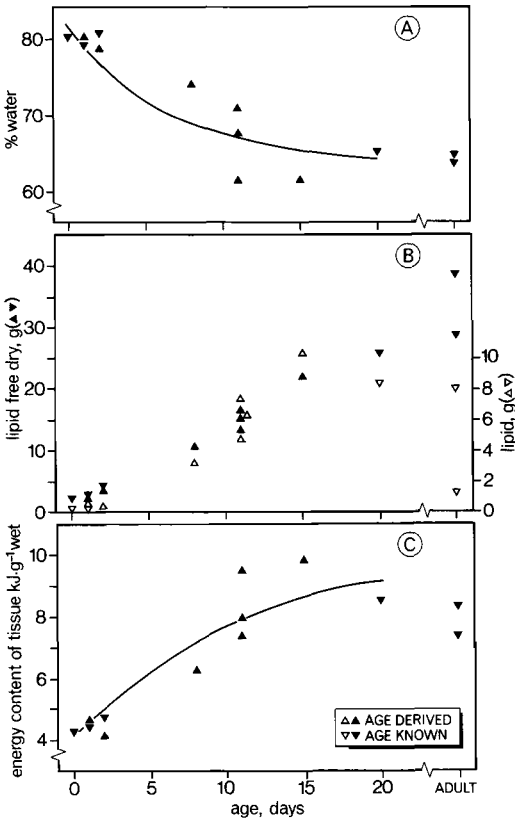
Fig. 2. Water content as percentage of total body mass (A), lipid mass (B), lipid-free dry mass (B), and energy content (C) of 11 Arctic Tern chicks and 2 adults as a function of age.

actual thermal environment, measured as T_e, and the relation between T_a and oxygen consumption established in the laboratory (Klaassen et al. 1989). Ambient temperatures in Ny Ålesund were relatively stable and ranged between 3.4 and 9.0°C over the investigation period. In contrast, the operative temperature var-

ied considerably. On cloudy days with low solar radiation the operative temperature was slightly elevated above the ambient temperature; but on clear days, operative temperature could reach values of up to 29°C (Fig. 3). The daily mass specific thermoregulatory cost was calculated from Eqs. 1–4, and assumed no brooding by the parents and a body temperature of 39°C maintained by the chicks (Klaassen et al. 1989). Mass specific thermoregulatory costs decreased rapidly over the first 7 days. From an age of ca. 10 days onwards, thermoregulatory costs stabilized around 0.6 $kJ \cdot g^{-1} \cdot day^{-1}$ (Fig. 4).

Total energy expenditure of the chicks, including basal metabolism, biosynthetic and thermoregulatory costs as well as costs for activity, was estimated by DLW. Carbon dioxide production by chicks, calculated from the measured oxygen consumption by indirect calorimetry, was systematically higher than measured by DLW (Table 1). This underestimation of the metabolic rate using DLW was less pronounced in the first (samples 1 and 3) than in the second (samples 2 and 4) part of the experiment. The errors were -4.5% (SD = 2.4) and -16.0% (SD = 9.0) for the first and second part, respectively. The field estimates of CO_2 production from DLW showed the same relatively low values for experiments started half a day after injection of the isotopes (Table 2). After correcting for the underestimations, the total energy expenditure in the field (Fig. 5) was described by:

$$E_{dlw} = 9.70(t + 1)^{1.170} \text{ kJ/day} \qquad (7)$$

($r = 0.988$, $n = 16$, $P < 0.001$).

The costs of activity (E_{act}) were calculated by subtraction of basal metabolic, biosynthetic and thermoregulatory costs from the total energy expenditure as measured with DLW.

We reconstructed total energy requirements

TABLE 1. Validation of the doubly labeled water technique. Comparison of CO_2 production estimates from doubly labeled water experiments and indirect calorimetry.

Individual	Age (days)	Initial mass (g)	Mass gain (g)	CO_2 production (mmol/day) DLW	CO_2 production (mmol/day) Indirect calorimetry	Error (%) DLW
544	5.5	41.0	6.2	151	159	−5.0
544	6.0	42.6	5.5	128	173	−26.0[a]
521	13.0	74.0	8.2	303	309	−2.0
521	13.5	69.4	16.5	289	334	−13.5[a]
502	19.0	109.0	−1.6	283	303	−6.6
502	19.5	108.0	−5.1	267	292	−8.6[a]

[a] Carbon dioxide production calculated over the second part of the experiment, see text.
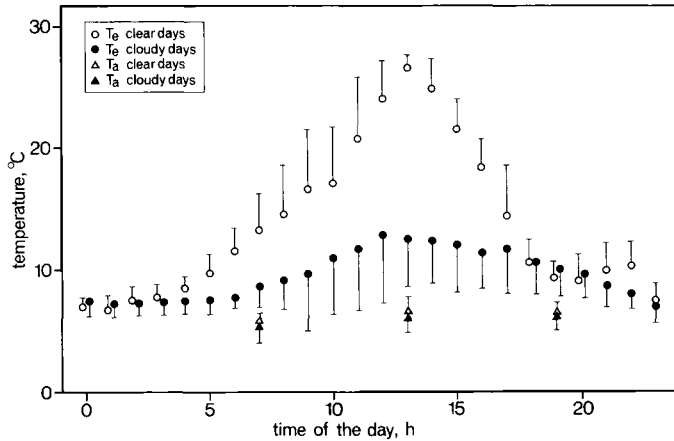
Fig. 3. Daily ambient and operative temperature (±SD) for clear (cloud cover ≤ 4/8) and cloudy (cloud cover > 4/8) days, at the Arctic Tern colony in Ny Ålesund, Svalbard, between 12 July and 6 August 1986.

(E_{req}) of Arctic Tern chicks as a function of age by integrating the data on energy costs of basal metabolism, biosynthesis, thermoregulation, activity, total energy expenditure and tissue deposition (Fig. 6).

The complete separation of BMR and costs for biosynthesis in young chicks was not possible. Hatchlings which still contain yolk, even when they are starved before BMR measurement, continue tissue growth, using the yolk as a source for metabolites (Klaassen et al. 1987). Because it is unclear whether all synthetic costs

are included in the "hatchling" BMR, the difference between total energy expenditure as measured by DLW and BMR during the first 3 days of age was assumed to consist of additional costs for synthesis in nonstarved hatchlings.

A second complication in reconstruction of the energy budget was that during the first 11 days, total energy expenditure (as calculated by the summation of BMR, synthesis, and thermoregulation) exceeded the energy expenditure estimated by DLW. This overestimate of 456 kJ or 26% of E_{req} was at least partly due to excluding the brooding behavior of the parents from the energy budget. During the first week after hatch, the chicks were thermolabile
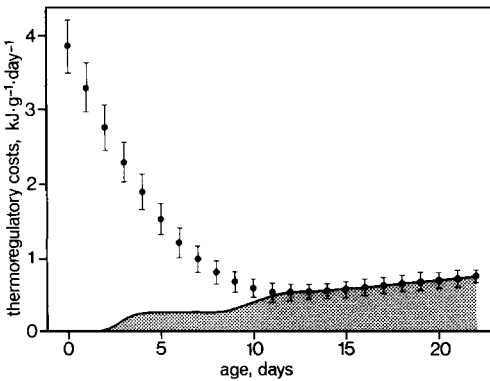

Fig. 4. Thermoregulatory costs as a function of age, calculated from operational temperature and laboratory-established relations between temperature and oxygen consumption. Indicated variation (±SD) expresses variation in measured operative temperatures (see Fig. 3). Shaded area represents the estimated actual thermoregulatory costs after accounting for parental brooding (see text).
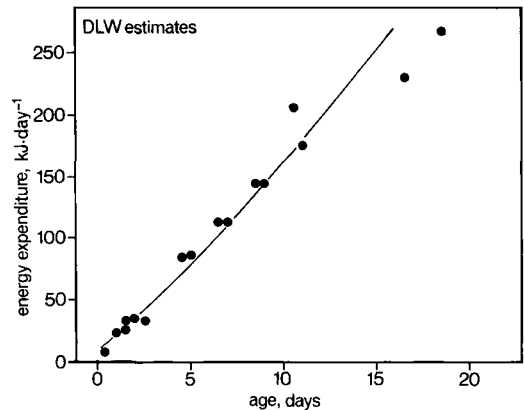

Fig. 5. Total energy expenditure measured with doubly labeled water, of free-living Arctic Tern chicks as a function of age. The corrected values are plotted (see Table 2).
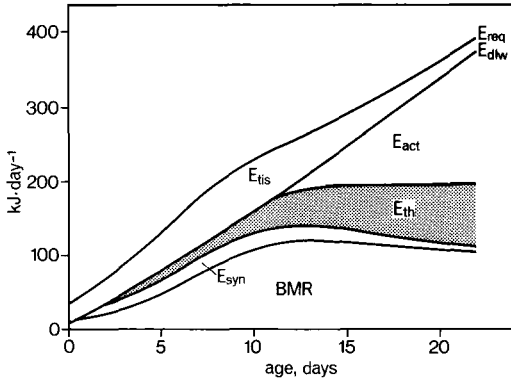
Fig. 6. Total energy requirements (E_{req}) of free-living Arctic Tern chicks in Ny Ålesund, Svalbard, from hatching until fledging. Total energy expenditure measured by DLW (E_{dlw}) is partitioned in BMR, tissue synthesis (E_{syn}), thermoregulation (E_{th}), and costs for activity (E_{act}). The accumulation of body tissue (E_{tis}) completes the total energy requirements.

TABLE 2. Field estimates of CO_2 production with doubly labeled water.

Individual	Age (days)	Initial mass (g)	Mass gain (g)	CO_2 production (mmol/day)	
				Uncorrected	Corrected[b]
12	0.5	12.7	3.8	22	23
12	1.0	15.1	1.5	36[a]	43
89	1.5	16.5	4.5	56	59
79	1.5	14.4	0.0	45	47
79	2.0	14.3	0.3	53[a]	63
1	2.5	17.9	2.0	48[a]	57
120	4.5	35.0	12.0	147	154
120	5.0	45.3	13.5	131[a]	156
86	6.5	45.2	5.3	192	201
86	7.0	48.5	12.0	170[a]	202
58	8.5	61.9	8.6	245	257
58	9.0	64.5	8.5	213[a]	254
56	10.5	81.0	1.0	349	365
56	11.0	80.0	4.0	261[a]	311
86	16.5	97.0	6.0	342[a]	407
58	18.5	109.0	3.0	453	474

[a] Carbon dioxide production calculated over the second part of the experiment, see text.
[b] Corrected according to the estimated errors for first and second part of DLW experiment, as determined in validation experiment.

(Klaassen et al. 1989) and were nearly continuously brooded by the parents (Busse 1983). In the second and third week after hatch, the parents may still brood or shelter their chicks, at least during periods of rain (Busse 1983). The thermal model is static, and not capable of selecting the most favorable microenvironment. Although we aimed for the most favorable site for our measurement, this technique probably underestimated the actual T_e encountered by chicks in the field even when not brooded by the parents. Therefore, during the first week, thermoregulatory costs were assumed to be close to zero, and increased only gradually until Day 11 (Figs. 4, 6).

The calculated energy budget of Arctic Tern chicks reveals that total energy requirements over the first 21 days of age amount to 4,442 kJ/chick. Of the total energy requirements 42% is allocated to basal metabolism, 8% to biosynthesis, 18% to thermoregulation, 9% to activity, and 23% to tissue deposition.

DISCUSSION

The use of DLW in rapidly growing animals may lead to severe errors in estimates of total energy expenditure, due to irreversible and disproportional incorporation of the isotopes in body tissue (Nagy 1980, Williams and Nagy 1985), although the method has been used widely (Fiala and Congdon 1983, Williams and

Nagy 1985, Williams and Prints 1986). Williams and Nagy (1985) argued that an underestimate of CO_2 production measured by DLW resulted from the incorporation of hydrogen but not oxygen into newly synthesized tissue. Assuming the "worst case" scenario for the Savannah Sparrow nestlings (*Passerculus sandwichensis*), Williams and Nagy (1985) calculated a possible underestimate of E_{dlw} by 25%. In the Arctic Tern chicks, measured error was up to -16.0% and well outside the range of $\pm8\%$ generally found in validation experiments in animals with fairly stable body mass (Masman and Klaassen 1987). Carbon dioxide production measurements showed that during the experiment the underestimation became more pronounced. This suggests an increasing incorporation rate of deuterium during the experiment. In the absence of more detailed studies we assume our procedure and corrections are valid.

The total energy requirements of Arctic Tern chicks changed dramatically during the second week. At this point the tarsus was virtually full grown (Fig. 1B), which indicates advanced locomotory capacity. This was confirmed by the contribution of activity costs to the total energy expenditure at Day 11. Furthermore, chicks were capable of thermoregulation at fairly low costs.
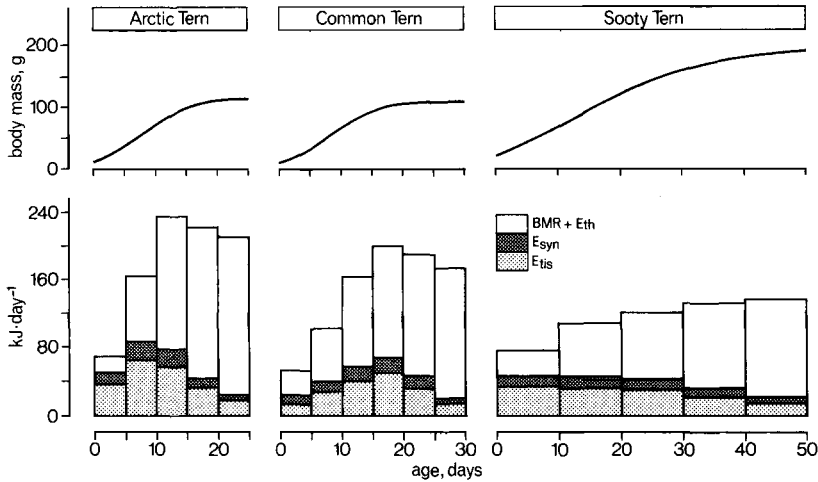
Fig. 7. Growth curves and energy requirements of Arctic, Common, and Sooty terns. Energy requirements were compiled from costs for tissue accumulation (E_{tis}), tissue synthesis (E_{syn}), and basal metabolism plus thermoregulation (BMR + E_{th}). Energy requirements for activity are excluded.

The favorable development of both locomotory and thermoregulatory capacities reduced the need of parental attention, and left more time for the parents to forage. This change occurred when the chick had reached half of its maximum energy requirement level. For the chick, these changes might be considered as a change from an altricial to a more precocial mode of life.

To evaluate the effect of the arctic environment on total energy requirements, we compared the Arctic Tern chick energy budget with the budgets of two related species studied at different latitudes (Fig. 7). Common Terns were studied on Great Gull Island, New York (41°N, 74°W), and the Sooty Terns on Bush Key, Dry Tortugas, Florida (25°N, 81°W; Ricklefs and White 1981). Activity costs were excluded from the comparison as they are unavailable for the Common and Sooty tern. Arctic and Common tern grow rapidly and have similar growth curves. The patterns of energy requirements as a function of age are also similar. Energy expenditure and deposition increase through the midpoint of development when, because of reduced tissue accumulation, they decrease slightly. The Sooty Tern grows slowly, with continuously low daily energy requirements during development.

Ambient temperatures on Great Gull Island and Bush Key were 25°C and 35°C during the day, and 17°C and 27°C during the night, re-spectively. Therefore, we assumed thermoregulatory costs were lower for both Common and Sooty tern chicks. The difference between energy requirements of Common and Arctic tern chicks was mainly a result of the differences in thermoregulatory costs, which never exceeded 0.73 times BMR or 21% of the total energy requirements in Arctic Tern chicks. The values of 21% and 18% of E_{req} for maximum and mean thermoregulatory costs may be slightly higher than the actual values because of underestimation of T_e (see above), and the possible effect of endogenous heat production during activity on thermoregulation. The heat increment of feeding did not substitute for thermoregulatory costs in Arctic Tern chicks (Klaassen et al. 1989).

In the Arctic Tern chick, there appear to be mechanisms to reduce thermoregulatory requirements. Fat content in Arctic Tern chicks was high (about 28% of wet body mass) compared to Common and Sooty tern chicks (about 22%; Ricklefs and White 1981). Fat reserves might increase insulation and serve as an energy reserve during periods of bad weather. A high metabolic capacity would also be beneficial in arctic environments to ensure enough endogenous heat production capacity for thermoregulation. The basal metabolic rate might indicate the metabolic capacity, and BMR in Arctic Tern hatchlings is indeed relatively high compared with relatives from lower latitudes (Klaassen et al. 1989).

Thus Arctic Tern chicks seem to be well prepared for the "cold Arctic" at relatively low extra expenses. However, the energy budgets used for the comparison (Fig. 7) do not cover all costs. Complete partitioning of the total energy requirements can elucidate life history strategies in related species that reproduce at different latitudes.

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The **Frank M. Chapman Memorial Fund** gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications are reviewed once a year and must be submitted no later than 15 January, with all supporting material.** Application forms may be obtained from the **Frank M. Chapman Memorial Fund Committee, Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA.**

There were no Chapman Fellowships awarded for 1988.

Chapman grants for 1988, totaling $43,954.00, with a mean of $698.00, were awarded to: Juan Amat, moulting ecology of the Red-crested Pochard (*Netta rufina*) in Spain; Gonzalo Arango, la taxonomia y las distribucion del genero *Thamnophilus* en Colombia; Todd W. Arnold, proximate and ultimate constraints on clutch size in American Coots; John M. Bates, winter survivorship in the House Sparrow (*Passer domesticus*): a morphologic and allozymic perspective; Douglas A. Bell, hybridization between the Western Gull and the Glaucous-winged Gull; William L. Benner, range expansion and rapid evolution in the House Finch *Carpodacus mexicanus*; Robert E. Bleiweiss, biochemical systematics of hummingbirds using DNA-DNA hybridization; William I. Boarman, environmental components of selection on avian song; Rhys V. Bowen, evolutionary significance of inter-specific foraging competition; Reed Bowman, mediation of asynchronous hatching and brood reduction in White-crowned Pigeons; James V. Briskie, dynamics and consequences of copulation patterns in Smith's Longspur; Neil J. Buckley, role of information transfer in the foraging behavior of Turkey Vultures *Cathartes aura*; Carolee Caffrey, cooperative breeding in American Crows: do helpers help?; Angelo P. Capparella, genetic differentiation among Patagonian birds in secondary contact; Jose Maria Cardosa da Silva, taxonomic studies of birds collected in Urucum and Corumba, Brazil; Kevin Cash, brood reduction in Swainson's Hawk; Glen Chilton, discrimination of dialects by female White-crowned Sparrows; Carla Cicero, variation in the song of the Lincoln's Sparrow (*Melospiza lincolnii*) in California; Thomas Peter Coombs-Hahn, environmental control of reproductive physiology in the Red Crossbill; Donald A. Croll, diving and energetics of the Murre; Timothy Crowe, systematics of Galliformes, Raptors, Bustards and Larks; Robert W. Dickerman, ornithological exploration of Upper Guinea lowland forest refuge; Katherine E. Duffy, the migration of owls at Cape May Point, New Jersey; David Enstrom, continuing investigation of delayed plumage maturation in Orchard Orioles; B. Patricia Escalante-Pilego, geographic variation in *Geothlypis* of Baja, California, and western Mexico; Mary C. Garvin, the role of blood parasites in mechanisms of avian sexual selection; Stephen M. Gatesy, a functional study of avian terrestrial locomotion; Rosemarie Gnam, breeding biology of the Bahama Amazon (*Amazona leucocephala bahamensis*); Pedro C. Gonzales, study of AMNH collection of Palawan birds; Martha Groom, detriments of nesting success and nest-site selection in four beach-nesting bird species; Percy N. Hebert, asynchronous hatching and parental investment in the Yellow Warbler (*Dendroica petechia*); Geoffrey E. Hill, female mate preference in relation to male carotenoid pigmentation in the House Finch; Sylvia Hope, geographic variation in call repertoire of the Steller's Jay; L. Scott Johnson, the function of territorial intrusions and mate guarding in House Wrens; Ian L. Jones, the evolution of social signals of the seabird genus *Aethia*; Michael C. Kaspari, experiments with overwintering mixed species flocks in the Sonoran Desert; Mary Katz, song variation in *Pardalotus striatus*, and its relationship to morphological variation; L. Henry Kermott, ectoparasitism of nestling House Wrens by *Protocalliphora braueri* (Diptera); Nedra Klein, geographic variation and systematics of the Yellow Warbler; Natasha B. Kotliar, a hierarchical concept of patchiness: implications for the foraging behavior of nectarivorous birds; David S. Lee, systematics of seabirds from North Carolina and the Philippines; Bruce Lyon, ecology and evolution of intraspecific brood parasitism in American Coots; Randall J. Mitchell, the effect of nectar rewards on hummingbird behavior and pollen deposition and dispersal; David C. Oren, avifauna of Maranhao State, Brazil; David Pashley, distribution of wood warblers in the Neotropics; A. Townsend Peterson, evolutionary relationships of the *Aphelocoma* Jays; Don Roberson, research on *Pterodroma* in AMNH collection; Frank G. Rozendaal, systematics of Asian-Pacific bush-warblers of the genera *Cettia, Urosphena, Tesia* and *Bradypterus* (Aves: Sylviidae); Karl-L. Schuchmann, behavior and repro-duction biology of the Tooth-billed Hummingbird (*Androdon aequatorialis*); Gilles Seutin, mechanism of species