

GROWTH AND ENERGETICS OF TERN CHICKS FROM TEMPERATE AND POLAR ENVIRONMENTS

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ABSTRACT.—I compared the energetics of Arctic Tern (*Sterna paradisaea*) chicks from Spitsbergen and The Netherlands, Common Tern (*S. hirundo*) chicks and Sandwich Tern (*S. sandvicensis*) chicks from The Netherlands, and Antarctic Tern (*S. vittata*) chicks from King George Island. Daily energy expenditure (DEE), measured using doubly-labeled water, was only slightly higher in the chicks from the polar environments, despite the higher levels of basal metabolism (BMR) and higher costs for thermoregulation. Apparently, thermoregulatory cost as part of the DEE of the chick is only a minor item thanks to parental brooding, which may account for energy savings ranging from 40 to 80%. A simple model indicates that the magnitude of these savings is dictated by the parental time budget (i.e. the minimal foraging time needed to meet age-dependent energy requirements of chick). Basal metabolic rate in chicks of the six available studies increased with latitude. The differences could relate to a higher capacity to produce heat, which is necessary in polar environments. The basal-metabolic-rate levels in adult terns, however, do not match this latitudinal pattern for the growing chicks. Ontogenetic studies over a longer time scale would be required to clarify these discrepancies in latitudinal pattern of BMR, for which a functional explanation is given in terms of differences in migratory biology. Received 12 October 1992, accepted 4 April 1993.

THE EXTENT to which metabolic adjustments are involved in allowing the penetration of new ecological niches is a matter of current debate (Carey 1988). Comparison of the specific metabolism of different species of birds has shed light on relations between climate and lifestyle in adult birds (e.g. Ellis 1984, Bennett and Harvey 1987, Kersten and Piersma 1987, McNab 1988, Root 1988, Klaassen et al. 1990). However, the question of how young animals physiologically face their specific ecological circumstances has only rarely been addressed. Recently, Klaassen and Drent (1991) summarized evidence for ecophysiological relations in hatchling birds. I consider how the metabolism of chicks throughout development relates to climatic circumstances.

Differences in phylogeny are associated with characteristic levels of metabolism (e.g. Bennett and Harvey 1987, Klaassen and Drent 1991). Thus, climatic adaptations should be examined in closely related species. To evaluate the relationship between chick energetics and climate, I gathered data on growth and energetics of three closely related species of terns at three

widely separated study sites. Data were obtained for: Arctic Tern (*Sterna paradisaea*) chicks studied both on Spitsbergen and in The Netherlands; Common Tern (*S. hirundo*) chicks, studied in The Netherlands; and Antarctic Tern (*S. vittata*) chicks from King George Island. In addition, I present energetic features (i.e. basal metabolic rate and thermal conductance) of Sandwich Tern (*S. sandvicensis*) chicks studied in The Netherlands. To allow an even wider comparative perspective, these data from polar and temperate terns were considered along with the findings of Ricklefs and White (1981) for the tropical Sooty Terns (*S. fuscata*) studied in the Dry Tortugas, Florida (24°38'N, 82°53'W).

METHODS

Study areas and chick biometrics.—The study on Arctic Tern chicks on Spitsbergen (78°55'N, 12°00'E; hereafter Arctic Tern SP) was conducted during July and August 1986 in Ny Ålesund. The methods, as well as some results, have been presented in detail by Klaassen et al. (1989a, b, c). The study of Antarctic Terns on King George Island was conducted in December 1990 and January 1991. Two study sites were selected near the Polish station Arctowski (62°09'S, 58°28'W). In The Netherlands, growth and field energetics of Arctic Tern (hereafter identified with suffix NL) and Common Tern chicks were studied at the Wadden

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Sea island of Griend (53°14'N, 5°15'E) during June and July 1989 and 1990.

Nests at all study sites were marked and checked every second or third day from hatching onwards. At hatching, chicks were banded and from then on body mass (M) to the nearest gram and tarsus length (T) to the nearest mm were measured each time the chick was located. Logistic curves (Ricklefs 1967) were fitted to the growth data for each species at each site. For Arctic and Common terns studied in The Netherlands, growth curves were fitted to the data of fledged chicks only (for details see Klaassen et al. 1994). Growth parameters for Sandwich Terns are from laboratory-raised chicks (see Drent et al. 1992).

In Arctic SP and Antarctic terns, basal-metabolic-rate and thermal-conductance measurements were obtained for chicks taken from the field and later returned to their parents. In addition, some Arctic Tern SP chicks were taken into the laboratory and raised in captivity (see Klaassen et al. 1989c). All Arctic NL, Common and Sandwich terns subjected to basal-metabolic-rate and thermal-conductance measurements were raised in captivity from eggs collected at Griend (see Klaassen et al. 1992, Drent et al. 1992).

Energy budget.—Tern chicks are completely dependent on their parents for food intake. The daily net or metabolizable energy intake (i.e. gross energy intake minus fecal energy loss; ME ; kJ/day) is used for the production of body tissue (E_{tis} ; kJ/day) and the daily energy expenditure (DEE ; kJ/day). The daily energy expenditure can be subdivided into basal metabolism (BMR ; kJ/day), synthesis costs of body tissue and the energy used for food processing (E_{syn} ; kJ/day), thermoregulatory costs (E_{tr} ; kJ/day), and costs of activity (E_{act} ; kJ/day). In equation form:

$$ME = E_{tis} + DEE, \quad (1)$$

where

$$DEE = BMR + E_{syn} + E_{tr} + E_{act}. \quad (2)$$

Production and biosynthesis.—To estimate the production costs, growth rates and knowledge on the energy density of body tissue (e_{tis} ; kJ/g) are needed:

$$E_{tis} = (e_{tis}M)_{t+1} - (e_{tis}M)_t, \quad (3)$$

where t is age (days). Fresh Common ($n = 10$), Sandwich ($n = 17$) and Arctic tern NL ($n = 11$) casualties of various ages were collected from the field and used for carcass analysis if obviously nonstarved. For the Arctic Tern SP, however, freshly dead specimens were not found, so 11 chicks were killed. The carcasses were dried to constant mass at 70°C and analyzed for their lipid and nonlipid content by petroleum-ether extraction. Energy density of the tissues was calculated using 38 kJ/g lipid mass and 20 kJ/g nonlipid dry mass (Ricklefs 1974). The costs for the synthesis of body tissue were calculated from the production

costs assuming a synthesis efficiency ($E_{tis}/[E_{syn} + E_{tis}]$) of 75% (Ricklefs 1974):

$$E_{syn} = 0.33 E_{tis}. \quad (4)$$

E_{syn} typically is estimated by the difference in metabolizable energy of growing and nongrowing animals after correction for energy accumulated in body tissue (e.g. Ricklefs 1974, Blaxter 1989). Thereby, E_{syn} not only includes the cost of biosynthesis but also the costs of food processing, or the heat increment of feeding. However, whereas the cost for biosynthesis as such is a function of growth rate, the heat increment of feeding is a function of energy intake and food type. Thus, the estimation method of E_{syn} adopted here (Eq. 4) is theoretically inappropriate. The total of heat increment of feeding and cost of biosynthesis (E_{syn}) is expressed as a function of growth rate only (Eqs. 3 and 4) leading to underestimation of E_{syn} during periods of low growth and overestimation of E_{syn} during periods of maximum growth. In addition, the estimation method is indifferent to food type. Nevertheless, in the absence of more accurate estimation methods, I preferred to employ this simple estimate.

Daily energy expenditure.—Daily energy expenditures of free-living chicks of all species but the Sandwich Tern were measured using the doubly-labeled-water method (Lifson and McClintock 1966, Nagy 1980). Klaassen et al. (1989b) provide a description of the specific methods used in the experiments, which were identical in all species, and the calculation of the daily energy expenditure from doubly-labeled-water turnover. These calculations also take account of the minor but chronic underestimation of the daily energy expenditure using doubly-labeled-water turnover in growing animals.

Basal metabolism and thermal conductance.—Basal metabolic rate and thermal conductance were measured in units of oxygen consumption (VO_2 ; ml $O_2 \cdot g^{-1} \cdot h^{-1}$) in indirect calorimeters (see Masman and Klaassen [1987] for description of the open-flow setup used in The Netherlands and Klaassen et al. [1989c] for methods used on Spitsbergen [open and closed] and King George Island [open flow]). Dependent on the size of the chick, flow rates of 40 to 100 L/h and metabolic chambers of 2 to 17 L were used. Each session was begun only after the chick had settled down and stable readings indicated that the system had reached equilibrium. All oxygen-consumption measurements were obtained for chicks that had been kept unfed for at least 3 h, except for the Antarctic Tern. In this species, oxygen-consumption measurements for thermal conductance were conducted immediately after collection of the chick from the field. The basal-metabolic-rate measurements were always done subsequently (3 h after collection) and, thus, are comparable to the basal-metabolic-rate measurements in the other species. The basal-metabolic-rate measurements were taken at various times of the day,

ignoring possible differences between day and night metabolism that are shown to exist in adult birds (Aschoff and Pohl 1970).

Oxygen-consumption measurements were taken at constant ambient temperatures (T_a ; °C) by placing the metabolic chamber in a climatic chamber or a thermostatic water bath. In the most primitive situation, on King George, as occasion demanded, I functioned as the thermostat, and snow and the exhaust of the generator were used in temperature control. Tentative lower critical temperatures, used in setting ambient temperatures in the oxygen-consumption measurements, were estimated from the metabolic measurements of Arctic Tern SP chicks (Klaassen et al. 1989c), and by combining predictive equations for basal metabolism (Aschoff and Pohl 1970) and thermal conductance (Aschoff 1981). Basal-metabolic-rate measurements were taken at temperatures within the thermal neutral zone, at least 5°C above the presumed lower critical temperature. Measurements at ambient temperatures at least 5°C below the predicted lower critical temperature were used to estimate thermal conductance (h ; ml O₂ · g⁻¹ · h⁻¹ · °C⁻¹) according to the equation:

$$h = VO_2 / (T_b - T_a), \quad (5)$$

where T_b is the body temperature (°C) measured during or, in most cases, directly after the experiments, especially in young chicks. Body temperature was measured by inserting a small previously calibrated thermistor or thermocouple into the rectum of the bird. In cases where no body temperature was measured, an estimated value of 39°C was used. Thermal conductances below the lower critical temperature may be dependent on ambient temperature but its variation is in most cases limited. All values for oxygen consumption were calculated according to Hill (1972) and corrected to standard-temperature-and-pressure conditions. Assuming catabolism of fat and protein only, oxygen consumption was converted to heat production using 20 kJ/L O₂ (Gessaman and Nagy 1988).

Thermoregulatory costs.—To estimate the combined effects of ambient temperature, wind exposure, and solar radiation, I measured operative temperature (T_r), which is the temperature a chick would attain if it lacked metabolic heat production and water loss (Bakken 1976). The thermal environment of the Arctic Tern SP chicks was investigated measuring the core temperature of a tin cast covered with the pelt of a one-day-old chick. In The Netherlands and on King George Island, operative temperatures were estimated using hollow copper spheres painted flat black and with a diameter of 3.5 cm. To test the applicability of these spheres for approximating chick microhabitat I compared operative temperature measurements using a black sphere with operative temperature measurements using three Common Tern taxidermy mod-

els, which were made using the pelts of a small hatchling, a medium-sized chick and a large chick close to fledging. The comparison was made at a flat, open site at the Isle of Griend, The Netherlands, during spring and early summer 1990 (models medium and large in size only) and 1991 (small and large). Measurements were made under various weather conditions (Table 4 in Appendix), but never during rain. Models and the black sphere were placed on stands 1.8 m high, mostly facing into the wind, where ambient temperature (T_a ; °C) and wind speed (u , m/s; Lambrecht wind writer) were measured simultaneously at the same level. All temperature measurements were made using calibrated thermistors and stored in a Grant Squirrel (1203) data logger. Model and sphere temperatures were measured at the center. The tern chick models could also be heated and kept at a relatively constant body temperature (T_b) around 39°C (Table 4); the power needed (H , W) was also registered on the data logger. The heated models were placed in the same fashion as described above to measure the additional effect of wind on thermoregulatory costs. In addition, on a few occasions, the heated small and large models were placed in typical Common Tern chick habitat (i.e. at a small open spot in the vegetation), to assess the relevance of the wind effect on thermoregulatory expenses. When models were placed in the vegetation, wind speed was measured at 10 m. All measurements were averaged over hourly intervals before applying stepwise multiple-regression analyses using 5% significance levels (Norušis 1988). The results of these model and sphere comparisons are presented in the Appendix. They indicate that operative temperature measurements using spheres can safely be used to extrapolate from the metabolism-chamber conditions to the natural habitat in this study. Although wind can have considerable impact on the cost of thermoregulation in homeotherms (Monteith 1973; see Appendix), my measurements with heated taxidermy mounts in The Netherlands confirmed that wind speeds were low in the microhabitat frequented by the tern chicks.

The Arctic Tern SP mannequin and the spheres were placed in typical microhabitats for resting chicks, and in such a way as to guarantee maximum solar heat gain when the sun was shining and to minimize heat loss from wind. At Spitsbergen, this was on a gravel field with patchy vegetation not exceeding 10 cm in height, where recordings were obtained for 16 complete days. In The Netherlands, I used a small open spot in vegetation about 50 cm high on 28 days during the 1989 breeding season. On King George Island, the sphere was positioned behind some small rocks where operative temperatures were measured over a period of 23 days. Temperatures in spheres and mannequin were measured hourly and automatically stored in a Squirrel data logger, or plotted on a Leeds and Northrup Speedomax recorder.

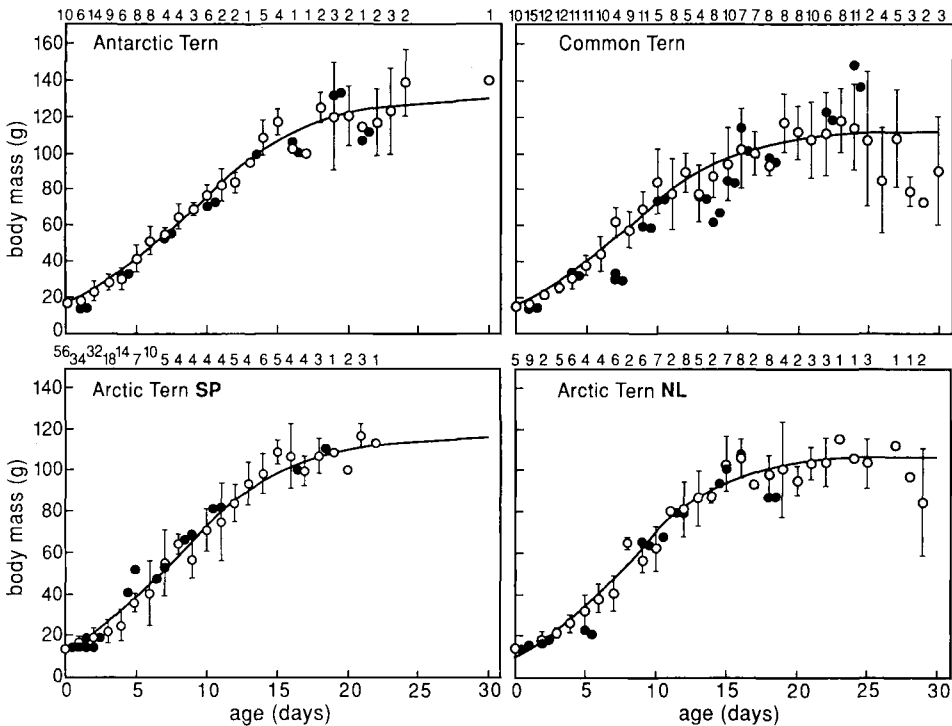


Fig. 1. Development of body mass (open symbols \pm SD) with age for Antarctic Tern, Arctic Tern SP, Arctic Tern NL and Common Tern. Logistic growth curves fitted to data points for which equations are summarized in Table 1. Sample sizes indicated at top of each panel. Arrows indicate average fledging age (Table 1). For each doubly-labeled-water measurement, body mass given by a closed symbol.

Average daily potential thermoregulatory costs (i.e. not accounting for possible parental brooding; E_{th} ; kJ/day) in the field for a specific age or body mass were calculated using all hourly operative temperature measurements (n) available at each site:

$$E_{th} = \sum_{i=1}^n E_{th(i)} / n, \quad (6a)$$

where

$$E_{th(i)} = h(T_b - T_{e(i)}) - BMR, \quad (6b)$$

and where T_b is 39°C and $E_{th(i)}$ is 0 if $h(T_b - T_{e(i)}) < BMR$. Clearly, this estimate of potential thermoregulatory cost (E_{th}) does not correspond to the real thermoregulatory costs (E_r) faced by the chick, as the energy saved by parental brooding (E_s) is not taken into account (see below).

RESULTS

Growth.—For all species, with the exception of the Arctic Tern SP, the growth data (Fig. 1) extend beyond the average fledging age (Table 1). For chicks in The Netherlands, this was pos-

sibly due to the wide variation in fledging ages of the birds sampled (congruent with large variation in growth rates; see Klaassen et al. 1994). In the Antarctic Tern, I obtained one weight for a chick beyond fledging due to the unexpected assistance of a pair of Antarctic Skuas (*Stercorarius maccormicki*) that forced the fledgling to land. Tarsus development is rapid (Table 1; T): halfway through the preflight period about 90% of its growth is already completed in all species investigated.

Carcass analysis.—For all species, body-tissue energy density was about 4.5 kJ/g at hatching, after which it steadily increased with maturation until it had approximately doubled at fledging (Fig. 2A). When energy density of body tissue is plotted as a function of the percentage of asymptotic mass, data points of all species fall along a line, a phenomenon illustrated with the inclusion of Larinae by Drent et al. (1992). However, the residuals from this predictive line show the Arctic Tern SP to be characterized by a high tissue energy density, significantly dif-

TABLE 1. Growth parameters and metabolic equations for five tern species. Arctic Terns from Spitsbergen and The Netherlands identified with suffix SP and NL, respectively. In logistic equations for body mass and tarsus growth, t is time in days, A is asymptote, and K is the growth-rate constant.

	Tern				
	Antarctic	Arctic SP	Arctic NL	Common	Sandwich
Average fledging age^a [days]					
	27	22	22	25	28
Body-mass development [g]: $M = A/(1 + be^{-Kt})$					
A (g)	133	115	107	114	219
b	6.5	8.0	9.0	6.3	11.9
K (day ⁻¹)	0.216	0.263	0.279	0.242	0.269
Tarsus development [mm]: $T = A/(1 + be^{-Kt})$					
A (mm)	18.8	16.2	16.5	21.4	30.3
b	0.41	0.29	0.30	0.60	0.70
K (day ⁻¹)	0.148	0.177	0.271	0.243	0.177
Age at 90% completed tarsus growth [days]					
	16	10	13	11	15
BMR [ml O₂·g⁻¹·h⁻¹] = $a + bM + 10^{-4}cM^2$					
a	1.99	1.25	0.42	1.17	1.41
b	0.042	0.061	0.098	0.038	0.017
c	-2.401	-4.705	-7.625	-2.365	-0.743
n	20	25	20	29	33
r^2	0.565	0.663	0.830	0.377	0.362
h [ml O₂·g⁻¹·h⁻¹·°C⁻¹] = aM^b					
a	0.61	1.21	1.26	1.28	0.72
b	-0.242	-0.486	-0.494	-0.502	-0.382
n	21	23	20	29	32
r^2	0.662	0.839	0.877	0.889	0.661
DEE [kJ/day] = aM^b					
a	0.09	0.93	1.06	0.88	
b	1.716	1.200	1.151	1.183	
n	15	16	16	27	
r^2	0.885	0.951	0.933	0.896	

^a Data from Nadler and Mix (1990) for Antarctic Tern and from Cramp (1985) for other species.

ferent from Arctic Tern NL (ANCOVA, $F_{3,44} = 3.284$, Scheffé $P < 0.05$). In contrast to the Arctic tern SP chicks, the Dutch chicks used in the carcass analyses had died of natural causes. Thus, the Dutch chicks are perhaps suspect as not yielding representative tissue energy densities. However, the Dutch data are in close accord with the determinations on the Common Tern provided by Ricklefs and White (1981) derived from chicks collected live from the field (New York). Thus, Arctic Tern SP chicks might be truly more energy rich than the other terns analyzed (as was earlier concluded by Klaassen et al. 1989b). Nevertheless, in view of the limited data, I decided to use the grand mean regression line (Fig. 2A) for calculation of production costs from the growth equations (Table 1; M) for all species, including Antarctic Tern for which no carcass analysis data are at hand.

Due to a slight increase in fat content, energy density of the dry tissue increased with 16% during development. Therefore, the 115% increase in energy density of fresh body tissue from hatching to fledging, apparently is due primarily to changes in water content. Water content, which was analyzed because these data were needed in the calculation of daily energy expenditure from doubly-labeled-water turnover rates (Klaassen et al. 1989b), shows a decrease with maturation (Fig. 2B). No significant differences were found among the tern populations (ANCOVA, $F_{3,44} = 2.454$, $P = 0.076$). Fat is deposited essentially water free and, thus, changes in fat content influence overall water content. However, the small increase in fat content during development explains only 6 of the 17% decrease in water content.

Daily energy expenditure.—For all species, dai-

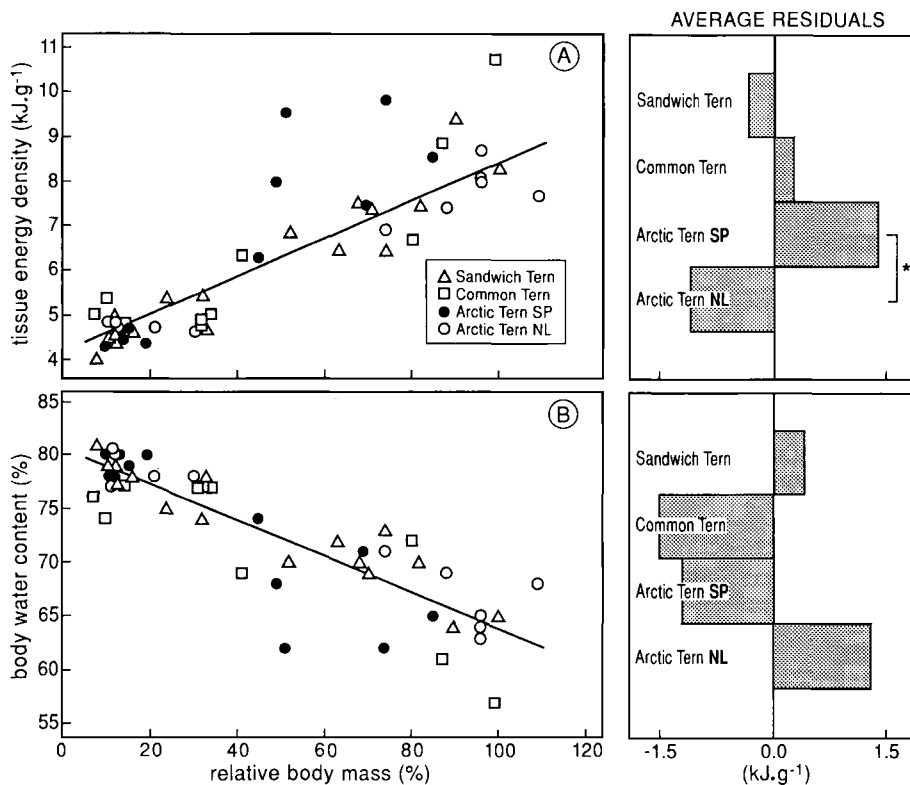


Fig. 2. Tissue energy density (A) and water content of live mass (B) as measured in analyses of Arctic SP, Arctic NL, Common and Sandwich tern chick carcasses as function of relative body mass (i.e. body mass/asymptotic body mass; A in Table 1). Least-squares regression lines through all symbols are for tissue energy density ($e_{tis} = 4.094 + 4.713M/A$ [$r^2 = 0.769$, $n = 49$]) and for water content ($F_w = 0.805 - 0.167M/A$ [$r^2 = 0.751$, $n = 49$]). For each species, mean absolute residuals from regression lines indicated. For energy density of tissue, residuals from Arctic Tern SP and Arctic Tern NL are significantly different (Scheffé $P < 0.05$).

ly energy expenditure in relation to body mass shows the same pattern (Fig. 3). To these data power functions were fitted (Table 1; *DEE*). Deviations from the composite power function (Fig. 3) were calculated as follows. For each day of life up until fledging, the smoothed energy expenditure (see Table 1; *DEE*) from each of the four studies was compared to the overall *DEE* value calculated at that body mass from the composite power function. The percentage daily deviations were averaged over the entire nestling period (right panel in Fig. 3). This diagram suggests that the Antarctic Tern expends more energy per day than would be expected from the composite curve. This is followed by the Arctic Tern from Spitsbergen, whereas the Common Tern lies slightly below (the Arctic Tern NL matching the composite curve). This trend, although suggestive, is not supported

statistically. Discriminating between species (Arctic SP and Arctic NL, Antarctic and Common terns) does not significantly enhance the proportion of the residual variation explained in the data points along the composite power function (ANCOVA, $F_{3,69} = 1.91$, $P = 0.136$).

Basal metabolic rate and thermal conductance.— In all species investigated, mass-specific basal metabolic rate in relation to body mass (Fig. 4) shows a pattern typical for semiprecocial chicks (Ricklefs 1974), a pattern that can be described by a parabolic function (Table 1; *BMR*; i.e. mass-specific basal metabolism is low at hatching, peaks about halfway through development, and then declines somewhat again).

Mass-specific thermal conductance (Fig. 4) is high at hatching and then steadily decreases during development following a power function with body mass (Table 1; *h*). For all but one

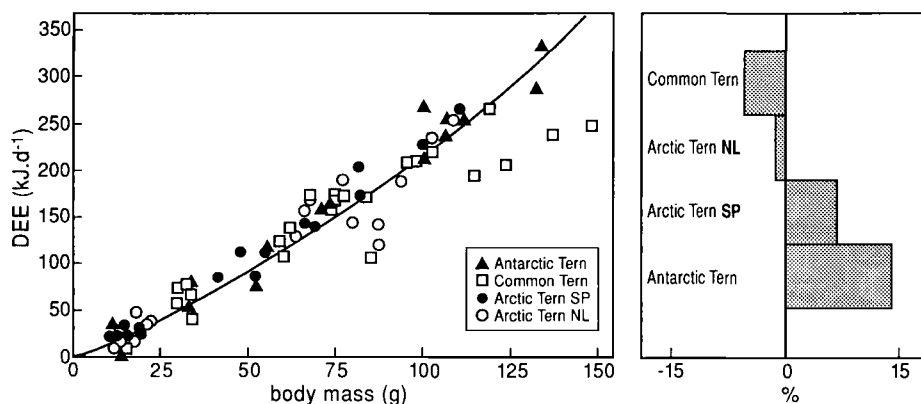


Fig. 3. Daily energy expenditure (DEE) as measured with doubly-labeled-water method for Antarctic Tern, Arctic Tern on Spitsbergen, Arctic Tern in The Netherlands, and Common Tern as a function of body mass. General least-squares power function through all data points is drawn ($DEE = 0.67M^{1.259}$ [$r^2 = 0.880$, $n = 74$]). Indicated to right is average relative difference in DEE over total developmental period (i.e. comparing the average expected DEE per species [Table 1] with the all species line [left panel]).

species the thermal-conductance values fall along the same line, the single exception being the Antarctic Tern characterized by higher values (ANCOVA, $F_{4,119} = 11.09$, Scheffé $P < 0.05$), especially later in development.

Thermoregulatory costs.—Operative temperature as a function of time of day (Fig. 5) shows large day-to-day and within-day variations. The highest values were measured around noon, clearly under the influence of solar radiation. Even at King George, the coldest environment studied with operative temperatures as low as -1°C , operative temperatures reached up to 34°C on sunny days around noon. Taking the operative temperatures for the different study sites (Fig. 5) and the species/site specific equations for thermal conductance and basal metabolism from Table 1 as points of departure, one can calculate energy expenditure for thermoregulation for each species (disregarding any parental contribution), according to Eq. 6. As shown by Figure 6A, mass-specific thermoregulatory costs are highest at hatching and decrease sharply afterwards until they more or less stabilize in all species at about 10 days of age. In Figure 6B, the total potential energy expenditures for thermoregulation until fledging are presented, showing highest costs for Antarctic Tern chicks (however, see Discussion), followed by Arctic SP, Common and Arctic tern NL chicks. Included in Figure 6B is the expected thermoregulatory cost of a Spitsbergen Arctic Tern transplanted to either Antarctica (top bar)

or The Netherlands (lower bar; see Discussion). These estimates derive from operative temperatures measured disregarding wind effects. Clearly, assessing chick thermoregulatory costs requires knowledge of the wind speed to which chicks are exposed and its effect on live chicks. However, my own measurements with taxidermy models in The Netherlands (see Appendix) indicate that wind speeds in the chick's environment were low and my thermoregulatory cost estimates are reasonable as a first approximation.

Energy budget.—All parameters necessary to compile an energy budget (Eqs. 1 and 2) are now at hand except for the activity costs that can, theoretically at least, be calculated as the remainder (Fig. 7). However, the estimated potential thermoregulatory costs exceed the energy available if basal-metabolic and biosynthetic costs are subtracted from the predicted daily energy expenditure. It is likely that the discrepancy is explained by the energy saved by the brooding behavior of the parents (Fig. 6B). As will be dealt with more fully below, the impact of parental brooding on the energy budget of a chick can be approximated, but an independent estimate of activity versus thermoregulatory costs has not been achieved.

DISCUSSION

Thermoregulatory costs and savings by brooding.—If one transplanted Arctic Terns from

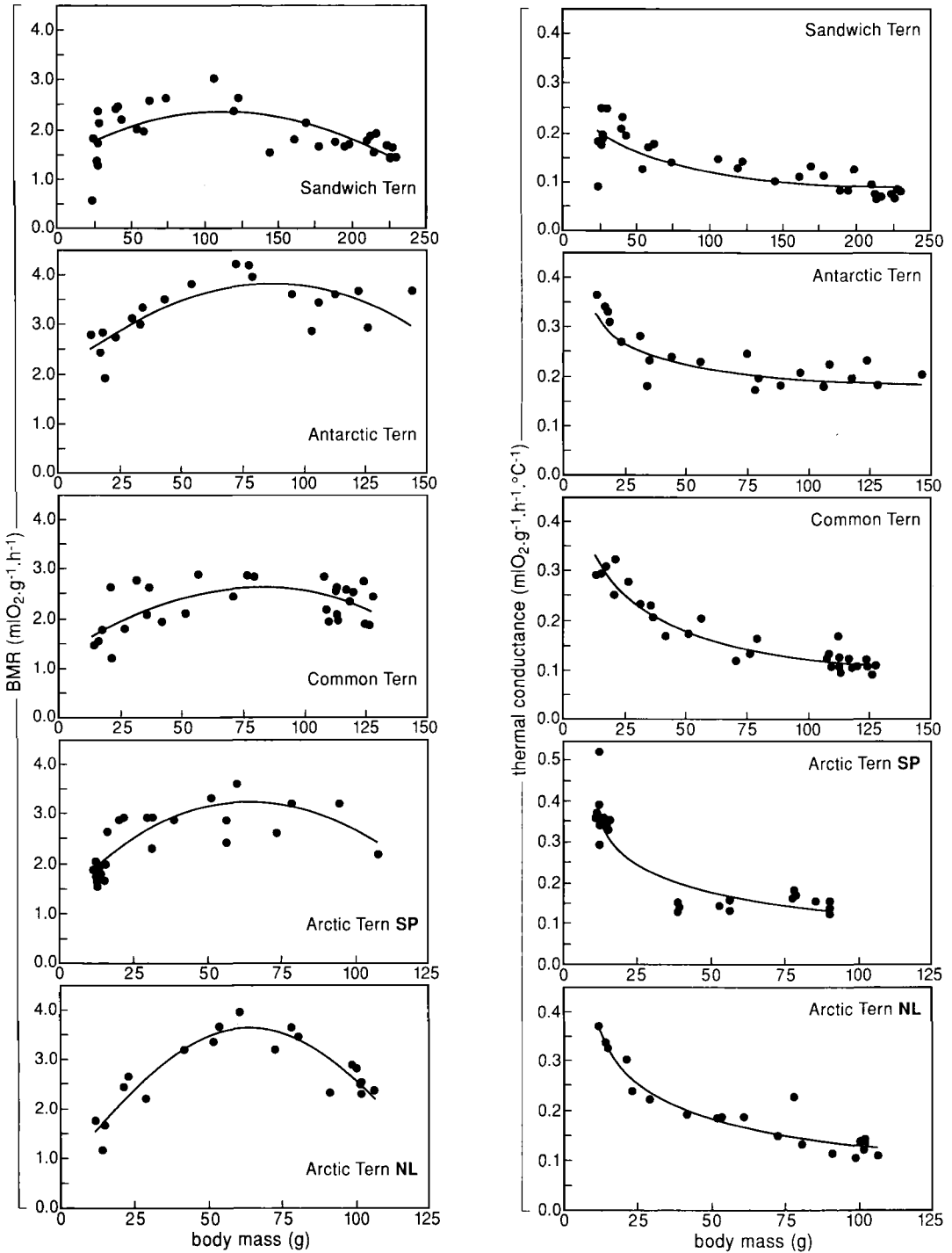


Fig. 4. Mass-specific basal metabolic rates (*BMR*; left) and mass-specific thermal conductance (*h*; right) in relation to body mass for Antarctic, Arctic SP, Arctic NL, Common and Sandwich tern chicks. Least-squares parabolas and power functions (Table 1) drawn through data points, respectively.

Spitsbergen to the opposite hemisphere and calculated total potential thermoregulatory costs over the developmental period, assuming the chick lived under the thermal regime of King George Island, there would be a relatively modest increase of only 25% (Fig. 6B). This computer-simulated exchange experiment shows that the estimated potential thermoregulatory costs for Antarctic Terns are suspiciously high (Fig. 6B); indeed, they are more than twice the potential thermoregulatory cost of the transequatorial transplant. Thermal conductance of Antarctic Tern chicks seems to be greatly overestimated, probably because they were not post-absorptive and therefore contributed an additional heat increment due to feeding, causing the inconceivably high thermoregulatory cost estimate. Experimental evidence does not support the possibility that the heat increment of feeding compensates for thermoregulatory costs (Klaassen et al. 1989c), a phenomenon that otherwise would have masked the fact that experimental birds were still processing food.

Generally, it appears that thermal conductance is dependent on body mass (Aschoff 1981, Visser 1991). If the Antarctic Tern is excluded, the remaining four species do not differ significantly and a common line of thermal conductance can be calculated ($h = 1.12 M^{-0.472}$; $r^2 = 0.832$; ANCOVA for species effect, $F_{3,99} = 0.774$, $P = 0.511$, $n = 104$). Using this common line, potential thermoregulatory costs in the Antarctic Tern would be reduced by as much as 77% to 713 kJ/fledging period.

Discussion of suspect values for thermoregulatory costs also impinges on the estimation of activity costs. Clearly, the method used to fit the calculated potential thermoregulatory costs into the energy budget underestimates both activity costs and the energy saved by brooding, and overestimates the thermoregulatory costs corrected for by parental brooding. For Antarctic Terns, this procedure led to relatively high estimates of thermoregulatory costs relative to activity costs (Fig. 7). Using the common line for thermal conductance excluding the Antarctic Tern (see above), activity costs would increase from 0.7 to 21% of total metabolizable energy intake, and attain values similar to those of the other species (Arctic Tern NL, 16%; Arctic Tern SP, 12%; Common Tern, 21%). This comparison lends additional weight to the notion that, in the absence of measurements from post-

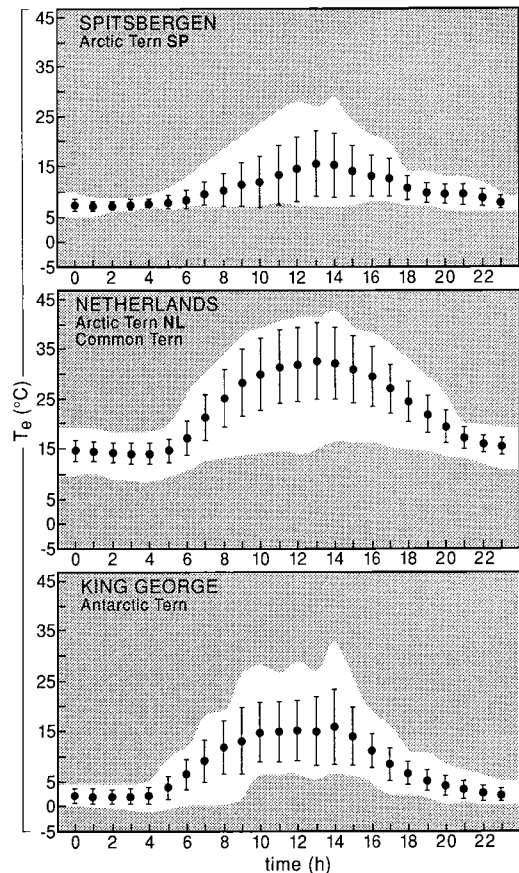


Fig. 5. Operative temperatures for tern chicks ($T_e \pm$ SD and range [unshaded area]) as function of standard local time, as measured at three study sites where field metabolic rates of tern chicks were measured.

absorptive chicks, the thermal-conductance value for the Antarctic Tern can best be extrapolated from data on the other species.

Energy savings by brooding are considerable as indicated in Figure 6B. However, many variables are involved in its calculation, making the chance of potential errors large. For comparison, time budgets provide another approach to account for the amount of thermoregulatory costs saved by parental brooding (Klaassen et al. 1994). Table 2 summarizes energetic savings due to brooding for some larids, calculated by both the energy and the time-budget approach. Both methods yield similar results, taking into account that larger species have lower potential thermoregulatory costs beyond the period of brooding due to a more favorable surface-vol-

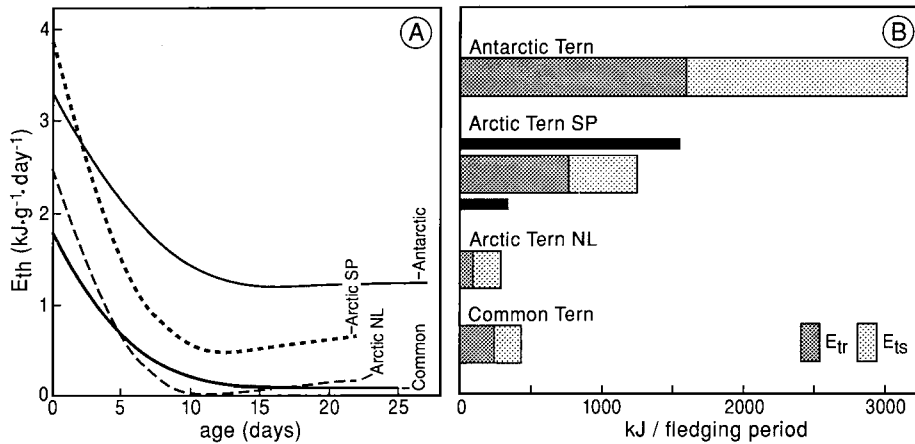


Fig. 6. Daily mass-specific potential thermoregulatory costs (E_{th} ; i.e. uncorrected for parental brooding) as function of (panel A) age for Antarctic, Arctic SP, Arctic NL, and Common tern chicks. Panel B indicates energy expenditure for potential thermoregulation (E_{th}) over total developmental period until fledging. Each bar expressing E_{th} is subdivided into part conceivably expended for thermoregulation (E_{tr}) and part saved by parental brooding (E_{ts}). Black bars indicate expected potential thermoregulatory costs for Arctic Tern SP on King George (upper) and in The Netherlands (lower). High thermoregulatory costs in Antarctic Tern might be due to methodological errors in assessment of thermal conductance (see Discussion).

ume ratio. Arctic Terns SP yield two values by the energy-budget approach (Table 2) based on only a slight difference in compiling the energy budgets from the same data base; the two values span almost the whole range of values apparent within the terns. This comparative analysis provides no absolute yardstick for interspecies distinctions, but gives some support to the idea that between one-third and two-thirds of the potential costs of thermoregulation facing the chick are defrayed by the parents. It is striking that the two heaviest species included in Table 2 experience the largest potential savings. This size-dependent trend must at least partly be due to the fact that, after the first few days of post-hatching life, chicks of these larger species attain a relatively low thermal conductance, which reduces their thermoregulatory costs when they are left alone by the parents.

Parental dilemma of whether to forage or brood.— Parental brooding and foraging are mutually exclusive. Depending on the expected foraging yield and the chick's potential thermoregulatory expenses, parents should opt for one of the two. Brooding requires only one parent; thus, the chick is (temporarily) left alone only when foraging time exceeds 50% of the maximum foraging time of a pair. Data on foraging success are not available, but I assume that, at the point of maximum chick energy requirement (cf. Fig.

7), the parents work at maximum capacity, where no time is left for brooding. Using this estimate of foraging capacity (kJ/day collected by the parents), along with the expected energy requirements of the chick under thermoneutral conditions and under fully exposed conditions, the minimal foraging rate (and thereby the maximum time allocated to brooding) can be calculated. This simple model is outlined in Figure 8, where values for the various parameters used in this model are given for Arctic Tern SP. In this model, I initially accounted for the limited metabolic capacity of neonates (Klaassen and Bech 1992). However, it appeared that this was not a critical factor limiting the time allocated to foraging (i.e. not determining the time spent brooding).

The model has several liabilities. It does not allow for other types of adult behavior. Foraging capacity may change as parental skill or food availability changes as the breeding season advances. In addition, parents may not be time limited, but may be limited in their daily energy expenditure instead, leaving more time for brooding (which is probably inexpensive). Other factors may prevent terns from foraging (e.g. darkness, fog, wind conditions; Dunn 1975), or force them to brood (e.g. predation risk, rain; wetting of insulation reduces thermal resistance to about one-half of its dry value; Webb

and King 1984). Irrespective of these drawbacks, the expected thermoregulatory costs, based on this simple model, and the thermoregulatory costs measured (Fig. 6) show a close fit (Fig. 9 for the three studies where adequate empirical estimates of thermoregulatory costs exist). In the model E_{tr} is used to estimate the metabolizable energy intake of the continuously brooded chick (ME_B). Thus, the actually measured E_{tr} and the model expectation in Figure 9 are not completely independent. It is therefore reassuring that also remarkable similarities exist between expected and true brooding-time allocations (Fig. 10).

The time allocated to brooding is only about 10% higher for Arctic Terns breeding on Spitsbergen (G. Slagsvold unpubl. data) than in The Netherlands (Klaassen et al. 1994; Fig. 10). This is a small difference in view of the large operative temperature and potential thermoregulatory cost differences between the two areas (Figs. 5 and 6B). Although the predicted time spent brooding is mostly higher than that observed in the field, the model also predicts small differences in parental brooding between the two areas amazingly well. This points out an apparent paradox: Arctic Tern chicks raised on Spitsbergen face higher thermoregulatory costs because of the harsher environment, but the parental contribution (brooding) is not raised appreciably higher than at the temperate site (The Netherlands). This must result in a higher energy expenditure for thermoregulation in the budget of chicks on Spitsbergen, which in fact is the case. Measured over the entire fledging period, the Arctic Tern chicks from Spitsbergen devote 660 kJ more to thermoregulation than their Dutch conspecifics (Figs. 6 and 7). My tentative conclusion is that the parent terns at the northern locality are constrained by their foraging demands and cannot devote more time to brooding their young, despite the energetic advantage this would provide.

The presumed priority of feeding over brooding is supported by data from intensive tabulations of parental time budgets of Arctic Terns at colonies in the northern British Isles. In situations of low fish abundance, parents are forced to lengthen their foraging trips (Monaghan et al. 1989), and the Shetland-Orkney comparison collated by Uttley (1992) clearly demonstrates how sensitive the margin of "nest time" to foraging condition is. On the Shetlands, where fish are scarce, brooding time averages only one-

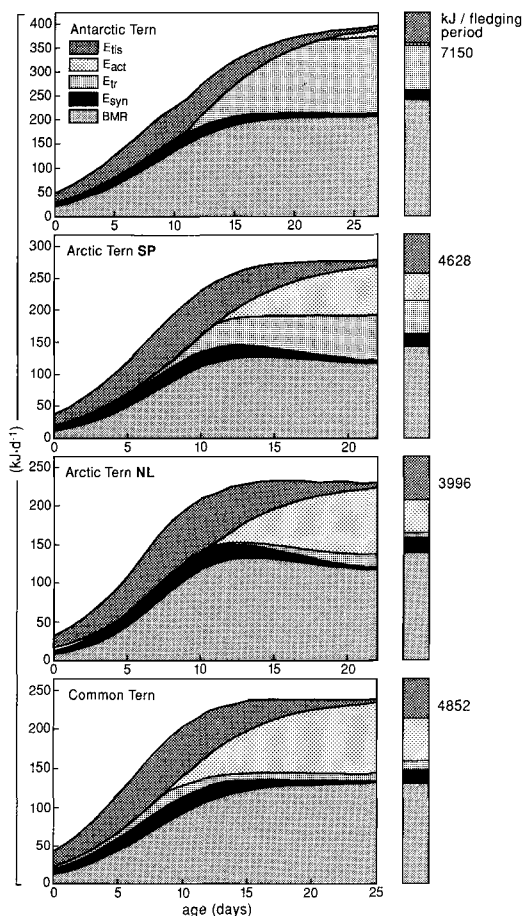


Fig. 7. Total energy budgets for chicks of Antarctic, Arctic SP, Arctic NL and Common terns indicating energy expended for basal metabolism (BMR), biosynthesis (E_{syn}), thermoregulation (E_{tr}), activity (E_{act}), and production (E_{tis}). On right side of each graph, total metabolizable energy intake over fledging period given, as is average allocation to different components of budget. Due to possible errors in methodology used for measuring thermal conductance in Antarctic Tern chicks, thermoregulatory cost estimates in this species might be too high and, consequently, activity costs too low (see Discussion).

half that observed on the Orkneys. Thus, a basic feature of the brooding model outlined here (i.e. that under conditions of low parental foraging success brooding time will decline) is in accord with these field observations. Within a colony, quality differences among parents (as deduced from differences in growth rates achieved by their offspring) are similarly reflected in their allocation of time as discussed by Klaassen et al. (1994).

TABLE 2. Reported total energetic savings by brooding up to fledging expressed as fraction of thermoregulatory expenses when unbrooded. Species ordered by asymptotic mass.

Species	Location	Percent energy saved by brooding	Method ^a	Source ^b
Arctic Tern	The Netherlands	37	1	1
Arctic Tern	The Netherlands	67	2	2
Common Tern	The Netherlands	34	1	1
Common Tern	The Netherlands	38	2	2
Arctic Tern	Spitsbergen	57	2	3, 4
Arctic Tern	Spitsbergen	39	2	2
Antarctic Tern	King George	46–81 ^c	2	2
Black-legged Kittiwake ^d	Spitsbergen	80	2	5

^a (1) Using time budgets; (2) estimating proportion of energy expenditure for unbrooded chicks that does not fit into energy budget (i.e. exceeds estimated daily energy expenditure calculated from doubly-labeled-water turnover).

^b (1) Klaassen et al. 1994; (2) this study; (3) Klaassen et al. 1989a; (4) Klaassen et al. 1989b; (5) Gabrielsen et al. 1992.

^c Highest value obtained using compilation-thermal-conductance function excluding suspicious Antarctic Tern data (see text).

^d *Rissa tridactyla*.

In the chicks of all the species investigated, at about 1 to 1.5 weeks of age, several parameters have reached values that indicate a milestone in maturation has been passed. First, a fairly stable and low mass-specific potential thermoregulatory cost is reached (Figs. 6A and 9) that, given the mass-specific limits to energy intake (Kirkwood 1983) and metabolic capacity (e.g. Klaassen and Bech 1992), increases the thermal independence of the chick. Second, 90% of tarsus growth has been completed (Table 1), indicating advanced locomotory capacity. At this point the inferred activity costs begin to contribute to the total energy expenditure. These two features reduce the need for parental attention, leaving the parents more time to forage as food requirements reach about one-half their maximum. This point is further characterized by minimal energetic savings due to brooding (Figs. 7 and 9; see also Fig. 10).

Reflections of climate in energy budget.—The energy budgets show similarities in their allocation to the different components. This phenomenon is in line with the findings of Drent et al. (1992), who summarized chick energy budgets for 28 species of birds. However, climatic adaptations may be sought in the deviations from the general pattern. Going from relatively warm to cold environments, the average daily energy expenditures get progressively higher (Fig. 3). This trend is not significant, yet, remains suggestive. Only the difference in average daily energy expenditure between Arctic Tern NL and Common Tern is not explained in this way, as both were measured in The Netherlands. Daily energy expenditure is comprised of several energetic components (Eq. 2) that, in the-

ory, could all contribute to the difference. Basal metabolism, however, is a relatively large component of the daily energy expenditure, making up about 60% on average (Fig. 7). It is this component that is higher in the Arctic Terns NL than in Common Terns.

Of the total intake of metabolizable energy, only a small proportion (ranging from 15 to 22%) is dedicated to tissue growth. Arctic Terns SP tended to have a relatively high tissue energy density (Fig. 2A) due to high fat levels. However, if one took the species-specific energy density for Arctic Terns (Klaassen et al. 1989b) instead of the composite equation used here, there would be an increase in the energy cost for tissue growth in the Arctic Tern SP of only 12% (i.e. from 20 to 22% of total metabolizable energy intake). Although of minor importance to the total energy budget, the question remains how significant this relatively high fat content is in arctic-breeding birds. Lack (1968) hypothesized that large quantities of fat in seabird chicks constitute insurance against poor feeding conditions. Alternatively, Ricklefs (1979) suggested that high fat stores are accumulated by seabird chicks as energy sinks to allow chicks to take in large quantities of energy-rich, but nutrient-poor food. That such a small proportion of the total metabolizable energy intake is used for tissue growth shows that Ricklefs' hypothesis only applies when more than two-thirds of the dry food is fat. Potential food for terns on Spitsbergen had a fat content of only about 20% (Gabrielsen et al. 1992). The relatively high fat content of Arctic Terns from Spitsbergen compared to their Dutch conspecifics favors Lack's hypothesis, as polar envi-

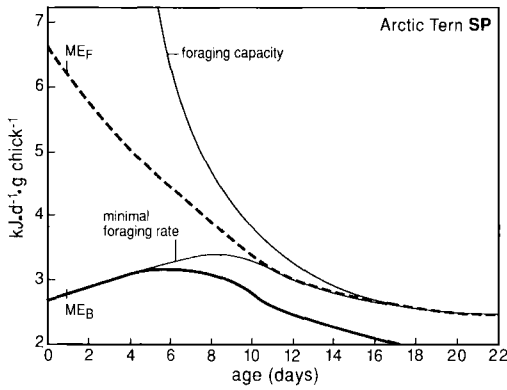


Fig. 8. Model explaining parental time allocation between foraging (expressed as minimal foraging rate) and brooding in relation to chick age, as exemplified for Arctic Tern SP (see text). Brooding involves one parent only. If total parental time allocation to foraging (f_f) less than 50%, time allocation to brooding (f_b) equals 100%; otherwise $f_b = 2(1 - f_f)$. Depending on time allocation to brooding, net energy requirement of chick varies between zero thermoregulatory costs ($f_b = 100\%$; $f_f \leq 50\%$; energy requirement of brooded chick, ME_B [kJ/day] = $ME - E_{tr}$) and maximum thermoregulatory costs ($f_b = 0\%$; $f_f 100\%$; energy requirement of unbrooded chick, ME_F [kJ/day] = $ME_B + E_{th}$). The expected minimal foraging rate equals foraging capacity (FC; 276 kJ/day [from Fig. 8]) times fraction of time allocated to foraging ($FC \cdot f_f$), which should balance the energy requirement of the chick: $f_b \cdot ME_B + (1 - f_b)ME_F = FC \cdot f_f$. Solving for f_f yields $f_f = ME_B/FC$ as long as $f_f \leq 50\%$; otherwise $f_f = (2ME_B - ME_F)/(FC + 2ME_B - 2ME_F)$. Energy requirement of brooded chick (ME_B), energy requirement of unbrooded chick (ME_F), foraging capacity and expected minimal foraging rate plotted (in terms of $\text{kJ} \cdot \text{day}^{-1} \cdot \text{g chick}^{-1}$).

ronments are characterized by more frequent harsh weather conditions than are temperate environments. However, more comparative research of closely related species from different latitudinal zones is needed to elucidate the adaptive significance of energy reserves in chicks.

Basal metabolic rate as a key energetic parameter.—As noted above, basal metabolism is a large component of the total energy budget and any change in the basal metabolism of an animal influences its total energy budget considerably. In line with the positive correlation between latitude and basal metabolism found in adult birds (Weathers 1979, Hails 1983, Ellis 1984), hatchling resting metabolism shows this trend

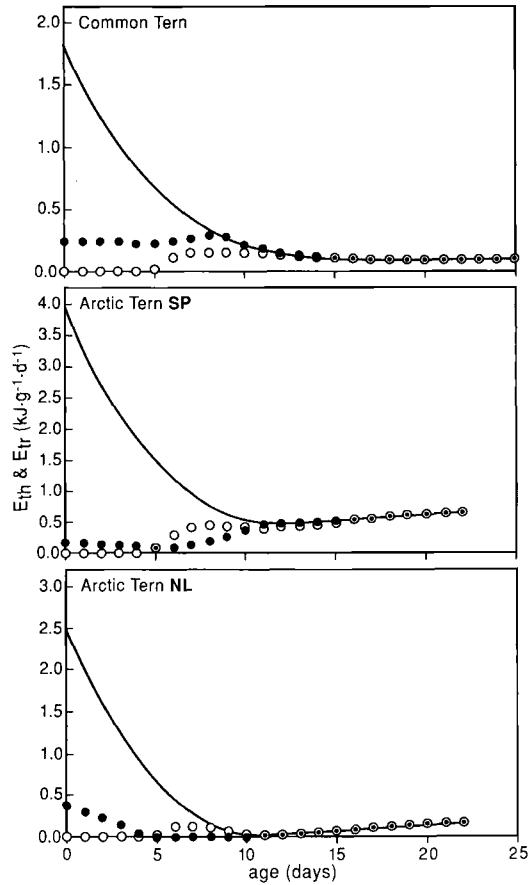


Fig. 9. Potential thermoregulatory costs (E_{th} ; solid line), thermoregulatory costs corrected for parental brooding (E_{tr} ; closed symbols), and expected thermoregulatory costs corrected for parental brooding based on model explaining parental time allocation between foraging and brooding (open symbols) in relation to chick age. Data included for Arctic SP, Arctic NL and Common terns.

as well (reviewed in Klaassen and Drent 1991). These trends are explained as climatological adaptations. In the tropics, low metabolic rates might help to reduce heat stress, while in the Arctic a high basal metabolism may be related to the higher metabolic capacities that are necessary in harsh and less predictable environments where breeding seasons are short. Also, in developing chicks there is an apparent link between basal metabolism and climate (see Fig. 11). This comparison lends additional weight from the notion that the tropical Black Noddy (*Anous minutus*; which is slightly more distantly related from the terns in Fig. 11) also has both

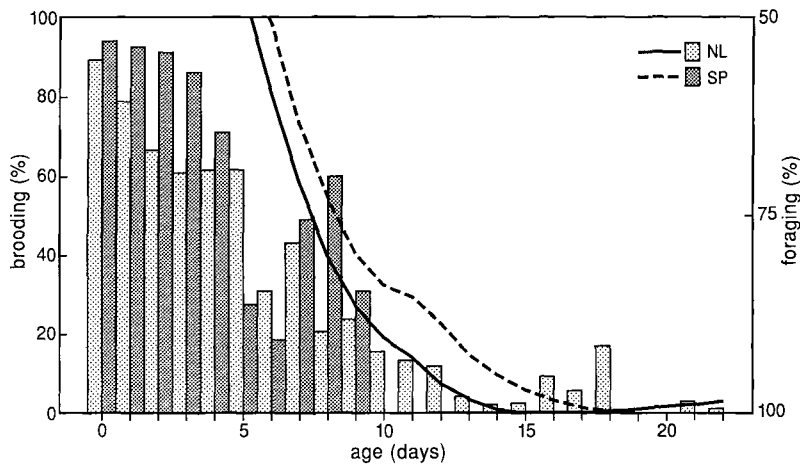


Fig. 10. Expected time allocation to brooding (one parent) and foraging (two parents) for Arctic Terns from The Netherlands (NL; solid line) and Spitsbergen (SP; dashed line) according to model described in text. For comparison, true time allocations to brooding for Arctic Tern chicks in The Netherlands (Klaassen et al. 1994) and on Spitsbergen (G. Slagsvold unpubl.) in relation to age are presented (bars).

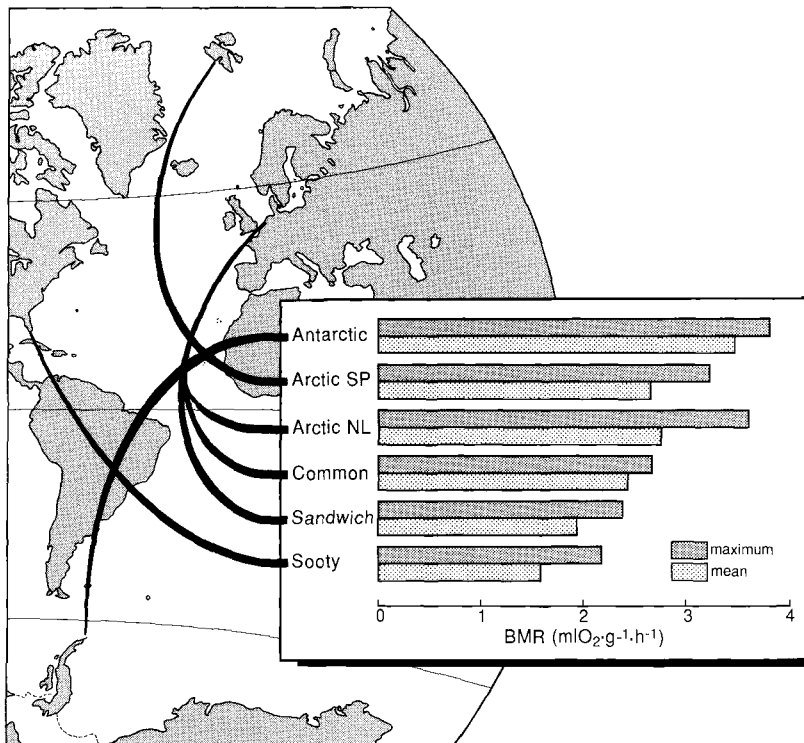


Fig. 11. Mass-specific average and maximum basal metabolism for five species of terns (of which Arctic Tern was measured at two localities) ranked in order of increasing mean operative temperature in geographic range. Definition of "maximum" is apparent from inspection of Figure 4, where highest mass-related BMR value can be read from fitted parabolic relations. Data for Antarctic, Arctic NL, Common and Sandwich terns from this study; those for Arctic Tern SP from Klaassen et al. (1989c) and for Sooty Tern from Ricklefs and White (1981).

a low mean and a low maximum basal metabolism (1.8 and 2.0 ml O₂ · g⁻¹ · h⁻¹, respectively; Pettit et al. 1984). Both the maximum and average mass-specific basal metabolic rates of Arctic Terns SP and NL differ only slightly, although the two study sites are 26° of latitude apart. Also, for the three species measured in The Netherlands, the mass-specific basal metabolic rates are reflected in the breeding distribution pattern, rather than the actual site where they were measured. This suggests that the differences in basal metabolic rate presented here are adaptive responses to climate that have been achieved in the course of evolution, and do not represent a response to local environmental conditions.

Klaassen and Drent (1991) found latitude, as well as pre- and postnatal growth rate, reflected in the basal metabolic rates of hatchlings. We presented functional explanations for these correlations, but were unable to make critical statistical tests on the data because all variables were interrelated. The basal metabolic rates presented in the current study clearly relate to latitude, the growth rates showing little variation among the species investigated (Table 1; *M*). However, this does not exclude a possible functional relationship between basal metabolism and growth rate. To examine this, chicks from related species and comparable climatological zones that exhibit different growth rates should be compared.

Even if climatic adaptations in basal metabolism appear in both adult birds and chicks, this does not mean that a compensatory metabolic adaptation, if present, necessarily exists throughout life. In Table 3, I present basal-metabolic-rate data for adult Antarctic, Arctic NL and Common terns, all measured using the same procedures described for Antarctic Tern chicks. Among adults, the Antarctic Tern has a higher metabolic rate than the other two species (ANOVA, $F_{2,21} = 3.694$, Scheffé, $P < 0.05$). Unexpectedly, adult Arctic Terns NL had a lower metabolic rate than the Antarctic Terns, and were indistinguishable from Common Terns. Although Antarctic and Arctic terns share similar breeding habitats, their wintering habits are different, which may explain their adult metabolic differences. Whereas Antarctic Terns from the Antarctic Peninsula remain in Antarctic waters (Holdgate 1963, Watson 1975) and accumulate large fat reserves before wintering (Parmelee 1988), Arctic Terns travel about 15,000 km to

TABLE 3. Basal metabolic rates (BMR; ml O₂ · g⁻¹ · h⁻¹) of adult Antarctic, Arctic NL and Common terns caught and measured during incubation period.

Species	Site	BMR ± SD (n)
Antarctic Tern	King George	3.35 ± 0.27 (5)
Arctic Tern	The Netherlands	3.08 ± 0.26 (9)
Common Tern	The Netherlands	2.93 ± 0.31 (10)

spend their winter in austral summer Antarctica (Cramp 1985). For Arctic Terns, this expensive flight may be compensated for by an energetically relatively inexpensive stay. Indeed, wintering strategies involving migration have been shown to coincide with low basal metabolic rates in North American passerine birds (Root 1988) and maintenance metabolic rates under thermoneutral conditions in waders (Klaassen et al. 1990).

Final considerations.—Although the comparative approach in my study benefitted greatly from the data of Ricklefs and White (1981) on the basal metabolism of the tropical Sooty Tern, these workers were unable to provide a total energy budget in the absence of the doubly-labeled-water technique as currently available. A prominent blind spot in my study is the lack of a complete energy budget for a tropical representative of the Sterninae. With inclusion of a tropical species, the variable growth rate would inevitably be introduced into the comparisons because it is highly correlated with latitude (Ricklefs 1968, 1976, Björnag 1979, Langham 1983, Klaassen and Drent 1991). Growth rate is important given that it can have a major influence on energy requirements (Bryant and Hails 1983, Klaassen and Drent 1991, Klaassen et al. 1992, Weathers 1992), although the ecological significance of these variations is still disputed (Ricklefs 1984).

In adult birds, thermoregulatory costs are (partly) compensated for by the heat increment of feeding (Berman and Snapir 1965, Masman 1986, Baudinette et al. 1986, Meienberger and Dauberschmidt 1992) and activity (summarized by Paladino 1985). These compensatory mechanisms can result in considerable energetic savings for thermoregulation by animals living in the cold (Webster and Weathers 1990, Masman et al. 1988). To date, the few available studies of chicks have failed to find a compensatory effect of the heat increment of feeding on thermoregulation (Kleiber and Dougherty 1934, Klaassen et al. 1989c), the compensatory effect

of activity as yet remaining uninvestigated. More research on these potentially important mechanisms for energy economization in chicks is needed.

Carey's (1988) conjecture that climatic adaptations mainly rely on behavioral adaptations is supported by my data, showing substantial effects of parental brooding on the costs of chick thermoregulation. I have presented evidence for a physiological adaptation as well, yet, am unable to show the impact of the climate associated changes in basal metabolism on survival in the different environments. Most studies dealing with climatic adaptations use correlative data. A more subtle test of the effectiveness of a given physiological trait in coping with the environment is to measure the effect of this trait as a function of the environment. For understandable reasons of logistics, such an approach is largely lacking in the study of avian climatic adaptation. It is, however, an inevitable step to take.

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APPENDIX

Summary data on ambient temperature, wind speed, and body temperature for three experiments using three different-sized taxidermy mounts of chicks are provided in Table 4.

For all three models, a close fit existed between model and sphere operative temperatures (Fig. 12), but residual variation could additionally be explained by ambient temperature and wind speed (except in the small model; Table 5). Wind direction relative to the position of the bird had no additional effect. Especially at high operative temperatures, the models yielded somewhat higher results than the sphere (Fig. 12). For calculation of thermoregulatory costs, however, especially accurate estimation of operative temperature in the low range is relevant. Thus, the simple black sphere provides a good alternative in the assessment of operative temperature for chick mannequins of all size classes, confirming Walsberg and Weathers' (1986) results.

The power consumption of heated models should be a function of the difference between body temperature and the operative temperature standardized for the wind effect (Monteith 1973, Bakken 1980). Plotting power consumption on the difference between body temperature and unstandardized operative temperature, the resulting residual variation

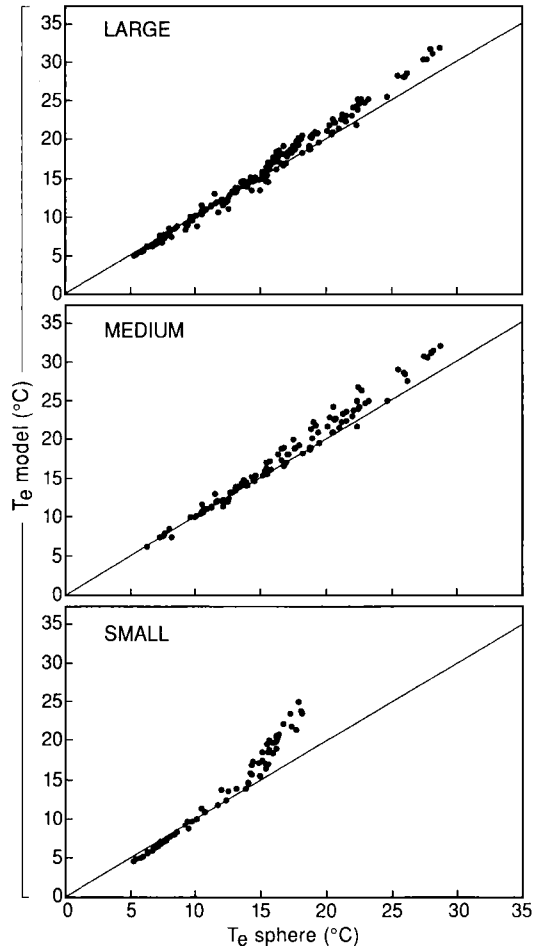


Fig. 12. Relation between operative temperature measured in black hollow copper sphere ($T_{e\text{ sphere}}$) with those measured in three Common Tern taxidermy mounts of different size ($T_{e\text{ model}}$). Iso-measure lines are drawn.

should be a function of wind speed. Following this procedure (Fig. 13) I found that the intercept of power consumption on the difference between body temperature and sphere operative temperature does not pass through the origin, which supports the finding that sphere operative temperatures underestimate those measured with the models in the high range. For all three models, the square root of wind speed significantly contributes to the explanation of the residual variation (Table 6).

Using the square root of wind speed relies on the assumption that the heat loss of the models is comparable to that of flat plates and cylinders (Monteith 1973). To test this assumption, I used least-squares analyses to estimate the power to which wind speed

TABLE 4. Mean values (range in parentheses) for ambient temperature (T_a ; °C), wind speed (u ; m/s) and body temperature (T_b ; °C) during three experiments conducted with three different-sized taxidermy mounts of Common Tern chicks. Sample size (n) indicated.

Variable	Unheated		Heated	
	On stand		On stand	In vegetation
	Small			
T_a	8.8 (5.6-11.7)		8.9 (4.9-12.4)	19.6 (13.5-27.2)
u	4.1 (2.2-6.9)		4.8 (2.8-7.2)	7.6 (0.6-12.8)
T_b	—		37.6 (34.9-39.5)	39.6 (38.4-44.9)
n	77		18	126
	Medium			
T_a	13.9 (6.6-22.2)		14.9 (6.2-26.1)	—
u	4.3 (0.8-7.6)		3.8 (0.4-9.2)	—
T_b	—		39.2 (38.5-40.0)	—
n	106		233	—
	Large			
T_a	11.8 (5.6-22.2)		14.2 (4.8-26.1)	19.6 (13.5-27.2)
u	4.2 (0.8-7.6)		3.9 (0.4-9.2)	7.6 (0.6-12.8)
T_b	—		39.0 (35.8-45.3)	39.7 (36.0-42.8)
n	183		252	126

TABLE 5. Least-squares multiple-regression lines forced through origin for operative temperature (measured in three different-sized taxidermy mounts of Common Tern chicks placed on stands) on sphere operative temperature ($T_{c\ sphere}$; °C), ambient temperature (T_a ; °C) and wind speed (u ; m/s). Squared regression coefficients given for each successively included variable in stepwise multiple-regression analysis.

	Small ($n = 77$)		Medium ($n = 106$)		Large ($n = 183$)	
	Slope	r^2	Slope	r^2	Slope	r^2
$T_{c\ sphere}$	1.742	0.9859	1.294	0.9977	1.194	0.9974
T_a	-0.829	0.9949	-0.237	0.9984	-0.040	0.9982
u	—	ns	-0.129	0.9987	-0.489	0.9980

TABLE 6. Least-squares multiple-regression lines for power consumption (measured for three different-sized taxidermy mounts of Common Tern chicks placed on stands) on difference between body and sphere operative temperature ($T_b - T_{c\ sphere}$), and square root of wind speed ($u^{0.5}$; [m/s]^{0.5}). Squared regression coefficients given for each successively included variable in stepwise multiple-regression analysis.

	Small ($n = 18$)		Medium ($n = 233$)		Large ($n = 252$)	
	Slope	r^2	Slope	r^2	Slope	r^2
Constant	-4.292	—	-2.019	—	-1.155	—
$T_b - T_{c\ sphere}$	0.150	0.5446	0.139	0.7720	0.110	0.8698
$u^{0.5}$	0.923	0.9173	0.868	0.9600	0.572	0.9620

should be taken for an optimal fit. For the medium and large model, for which enough data are available to allow this calculation, the exponents were 0.47 and 0.52, respectively, supporting the assumption.

For the models placed in the natural habitat, variation around the regression line is much less (Fig. 14) compared to the free-positioned models (Fig. 13). This is due to the fact that variations in wind speed above

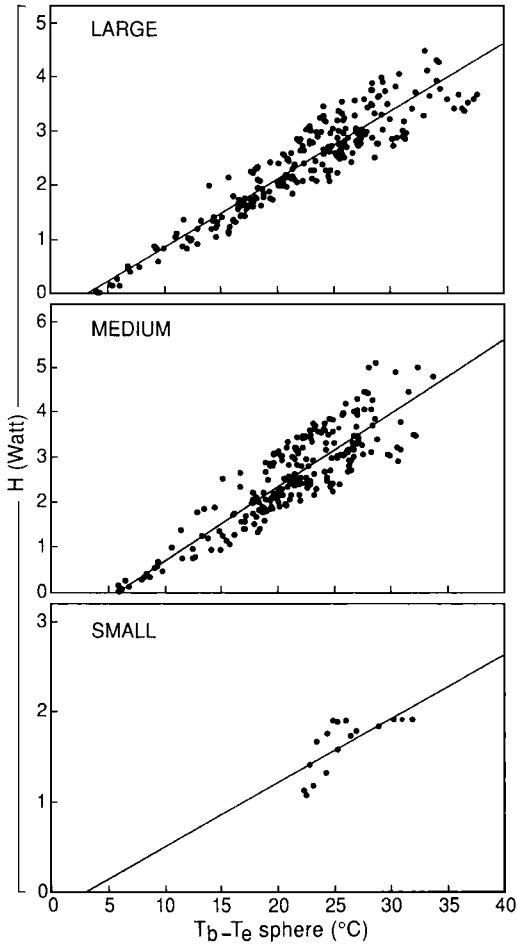


Fig. 13. Power consumption (H) of three different-sized and free-exposed taxidermy mounts of Common Terns in relation to difference between body (T_b) and operative temperature as measured with a black hollow copper sphere ($T_{e\ sphere}$). Least-squares regression lines are drawn.

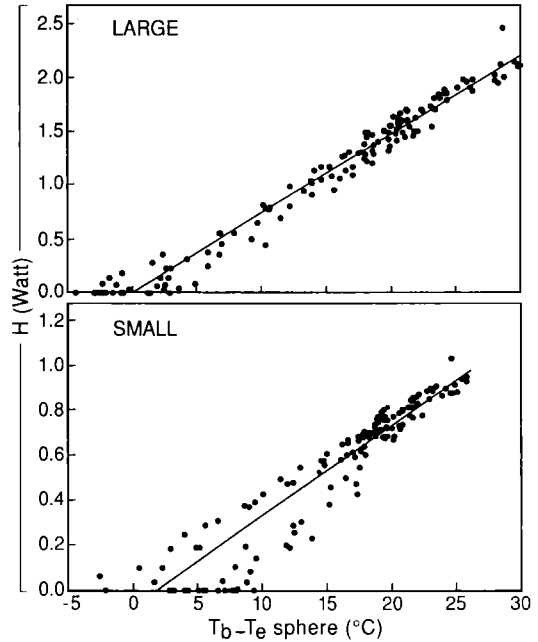


Fig. 14. Power consumption (H) of a large and small taxidermy mount of Common Tern placed in a small open spot in vegetation as related to difference between body (T_b) and operative temperature as measured with a black hollow copper sphere ($T_{e\ sphere}$). Least-square regression lines are drawn.

the vegetation did not result in large wind speed changes in the vegetation, as depicted from the power consumption of the models.

In conclusion, wind speeds are low in the natural habitat of the chicks, and operative temperature will closely resemble standardized operative temperature.