Physiological characteristics of arctic tern *Sterna paradisaea* chicks in relation to egg volume

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The effect of egg volume on body mass, body composition and growth rate in arctic tern *Sterna paradisaea* chicks was studied at Ny-Ålesund, on Svalbard (78°55'N, 12°00'E), in order to investigate whether differences in egg size influence the physiological characteristics of the hatchlings. The relative content of yolk and albumen in eggs did not vary in proportion to egg volume. Hatchlings from large eggs had larger body masses than hatchlings from small eggs, with 71% of the overall variation in body mass accounted for by egg volume. In newly-hatched chicks, water content, lean body and total lipid mass, as well as both leg and pectoral muscles, changed isometrically in proportion to egg volume. Hatchlings from large eggs, however, had disproportionately larger yolk sacs. The leg muscles of small chicks contained a lower proportion of water than the leg muscles of large chicks, indicating that the leg muscles of small hatchlings were functionally more mature. There was a weak, but significant, correlation between egg volume and growth rate. However, a residual analysis made to eliminate the effect of egg volume showed no correlation between hatchling body mass and growth rate. The results of the present study show that Arctic tern hatchlings from large eggs emerge with more yolk sac reserves, enabling them to better withstand periods of food-scarcity. During embryonic growth in small eggs, however, there seems to be a greater relative usage of yolk, resulting in a more developed leg musculature. This may partly compensate for the higher mass-specific heat loss in small hatchlings.

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Introduction

Intraspecific variation in egg size has been considered to be important in explaining some of the variation in the growth and survival of nestlings (Gibb 1950; Lundberg & Vaisanen 1979; Järvinen & Ylimaunu 1986; Williams 1994; Carey 1996). Thus, chicks which hatch from large eggs tend to grow faster and/or have higher survival rates than those hatched from small eggs (Parsons 1970; Schifferli 1973; Davis 1975; Järvinen & Ylimaunu 1984; Grant 1991; Magrath 1992). However, in a recent review, Williams (1994) concluded that "there is little unequivocal evidence . . . in support of a positive relationship between egg size and offspring fitness in birds." The main reason for this discrepancy is that most authors have not controlled other confounding effects, notably maternal quality. Birkhead & Nettleship (1984) estimated that 60–90% of the variation in egg size, within members of the Alcidae, is determined by maternal factors. Not only the structural size of the adult birds, but also their body condition and thus the ability of the parents to gather food, may influence egg size (Wiggins 1990). Furthermore, in the lesser black-backed gull *Larus fuscus* parental quality has been estimated to contribute more importantly to fledging success than egg size per se (Bolton 1991). However, egg size still had a significant influence on fledging success in this species because large nestlings, with greater yolk sac reserves, had higher survival rates even when reared by low quality parents (Bolton 1991). Similar studies on the shag *Phalacrocorax aristotelis* have shown positive effects of both parental quality and egg size on nestling growth (Amundsen & Stokland 1990).

Although there may be little evidence for overall changes in fitness as a consequence of egg size, Williams (1994) found that the most important effect of egg size variation on offspring fitness was found during the first few days after hatching. Such an effect could stem from a number of factors which vary, depending on whether the chicks hatch from large or small eggs. For example, large mallard *Anas platyrhynchos* ducklings are able to maintain homeothermy for a longer period than small ducklings when exposed to cold temperatures (Rhymer 1988). Such differences between newly-hatched offspring could affect their growth and survival rates. Thus, large body size may confer several advantages on hatchlings. For example, size and maturity of the metabolising and heat producing tissues, such as the skeletal muscles, may be important (Ricklefs 1983). In the American coot *Fulica americana*, Alisauskas (1986) found that hatchlings from larger eggs had a lower water index, i.e. they had a higher "functional maturity" (Ricklefs & Webb 1985). In addition, Slattery & Alisauskas (1995) reported that large egg size in the lesser snow goose *Chen caerulescens* and Ross' goose *Chen rossii* was associated with a relatively high lipid content of the newly-hatched chicks. There are also some indications that hatchlings from larger eggs might possess relatively larger yolk sac reserves, a trait which may be of special significance if the nestlings have to depend upon this reserve of metabolic substrates for a relatively long period (Birkhead & Nettleship 1984; Alisauskas 1986).

The aim of the present study was to investigate whether differences in egg size influence the body composition and physiological characteristics of arctic tern *Sterna paradisaea* hatchlings.

Materials and methods

Arctic tern chicks were studied at Ny-Ålesund, on Svalbard (78°55′N, 12°00′E), during the period 4–31 July, 1991. In the breeding colony, which covered about 0.5 km^2, 234 nests were marked during the incubation period. The nests contained either a single egg (75 nests) or two eggs (159 nests). The length (L) and breadth (B) of all 393 eggs were measured to an accuracy of 0.1 mm using a flexible ruler. The volume (V, cm^3) of the eggs was estimated according to the formula: $V = L \cdot B^2 \cdot 0.00051$ (Hoyt 1979). The colony was visited on a daily basis to determine the exact hatching dates of all the chicks.

Egg and body composition

A total of 24 fresh eggs (all from different nests) were collected for determination of the yolk and albumen contents. The eggs were boiled for 8 min and afterwards cooled in cold water. The yolk and albumen were then separated and weighed to the nearest 0.01 g, using a Mettler-balance.

A total of 15 newly-hatched chicks were collected for body composition analysis. They were taken either from single-egg clutches, or were the first chicks hatched from two-egg clutches. Only chicks collected within 1 h after hatching were used for the analyses. The chicks were brought to the laboratory of the Norwegian Polar Institute in Ny-Ålesund and immediately killed by decapitation. The following tissue samples were excised and weighed (wet weight, ww) to the nearest 0.001 g, using a Mettler-balance: (1) all muscle tissue from the right leg, (2) the right pectoral muscle and (3) the yolk sac. The masses of the two muscle samples were multiplied by two to obtain the total muscle mass. All the samples and the remaining carcasses were dried to a constant weight at 60°C to determine the water contents. Afterwards, the samples were frozen and transported to the Norwegian University of Science and Technology in Trondheim for lipid extraction.

Dried carcasses, including plumage, were first homogenised with a mortar and pestle before three subsamples, each of 0.3 g, were taken from each carcass. The entire dry yolk and muscle samples were used for lipid extraction. The samples were packed in small paper bags before lipid extraction. Lipids were extracted using 3 consecutive solutions of methanol and chloroform for 2 days each (viz. 2:1, 1:2, and finally chloroform alone). After lipid extraction the samples were dried to constant mass. The lipid content of a whole chick was calculated as the mean lipid fraction for the 3 carcass subsamples multiplied by the total dry carcass mass, and this value was added to the lipid content of dry yolk and muscle. Energy equivalents of $39.8\,kJ \cdot g^{-1}$ for lipids and $23.7\,kJ \cdot g^{-1}$ for non-lipid dry matter of the yolk sac were used when calculating the energy contents (Ricklefs 1974).

Growth analysis

Measurements of body mass (accuracy 0.05 g) at hatching (less than 24 h old) were obtained from a total of 114 chicks, of which 29 were subsequently used for the growth rate analyses. The hatching dates of these chicks varied between 10 and 20 July. No effect of hatching date on either egg volume ($r = 0.26$, $P = 0.17$) or hatching mass

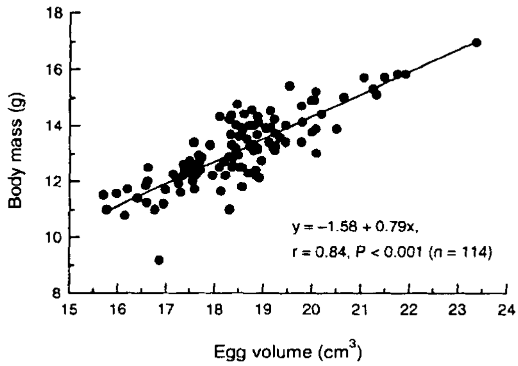

Fig. 1. Relationship of egg volume to hatchling body mass in arctic terns. Linear regression line shown.

(r = 0.01, P = 0.96) was found. All of the chicks used in the growth analyses were either from single-egg clutches or were the first chicks hatched from two-egg clutches. The identification of each chick was ensured by marking one of its legs with ink on the day of hatching and placing a metal ring on the leg on the fifth day after hatching. The body mass of the chicks was measured every day whenever possible. Some older chicks often wandered away from the nest site and could not always be found on a daily basis. Wing length was measured, with a ruler, to the nearest mm, and head length (from the back of the skull to the tip of the beak) was measured using a flexible ruler, to an accuracy of 0.1 mm.

Some chicks gained no body mass during the first two days after hatching, whereafter their body mass increased almost linearly up to an age of two weeks. Chicks more than two weeks old were characterised by declining body mass increments, until the adult mass was attained when the chicks were about 20 days old (see also Klaassen et al. 1989). Thus, the slope of the linear regression line describing the relationship between age and body mass (from 3 to 12 days of age) was taken to represent the daily body mass increment for each chick.

Statistical analysis

Student's t-test was used to test for differences between mean values. Regression lines were calculated according to the method of least squares. Pearson's correlation coefficients (r) were calculated to test for significant correlations. To determine if body composition varied allometrically with egg volume, the logarithm of each body component was regressed against the logarithm of egg volume (Ricklefs et al. 1978). Slopes equal to 1.0 indicate isometry, while slopes greater than or lesser than 1.0 indicate a proportional increase or decrease in body component with egg volume. Regression slopes were tested against the null hypothesis that slope = 1.0 using a t-test (Zar 1984). The statistical significance limit was set at $P < 0.05$. Results are presented as mean values ± standard deviations. Statistical analyses were made using SigmaStat (Jandel Scientific).

Results

Egg size and composition

The mean length and breadth values for all eggs were 40.9 ± 1.6 mm and 29.6 ± 0.8 mm, respectively, resulting in a mean estimated volume of all eggs of 18.35 ± 1.30 cm^3. In 32 of the 159 nests with two eggs we were able to determine the laying order. The volume of the first egg (A-egg: 18.68 ± 1.35 cm^3) from these two-egg clutches was significantly greater than that of the second egg laid (B-egg: 18.27 ± 1.35 cm^3; paired t-test: $P < 0.01$). However, there was no significant difference between the mean volume for the A-eggs and the mean volume (18.58 ± 1.47) for all the eggs from single-egg clutches.

The mean contents of yolk and albumen were 5.23 ± 0.39 g and 11.82 ± 1.07 g, respectively, representing 30.7 ± 2.0% and 69.3 ± 2.0% of the shell-free egg mass. There was no significant correlation between egg volume and the proportion of yolk or albumen (r = −0.31 and r = 0.31, respectively).

Body mass and composition

The overall mean body mass of the newly-hatched chicks was 13.1 ± 1.3 g (n = 114, range 9.2–17.0 g). There was a strong, positive, correlation between egg volume and body mass (r = 0.84, $P < 0.001$, Fig. 1). This relationship implies that 71% of the variation in body mass of the newly-hatched chicks is explained by egg volume. There was a weaker, but still highly significant, correlation between egg volume and one of the morphological characters, viz. the head

Table 1. Composition of newly-hatched arctic tern chicks. Shown are mean values with standard deviation (SD) and coefficient of variation (CV).

Component	*n*	Mean	SD	CV (%)
Whole Body				
Body mass (g)	15	12.59	1.16	9.2
Lean body mass (g)	12	11.80	1.15	9.7
Yolk-free body mass (g)	15	11.57	0.93	8.1
Water content (g)	12	9.87	0.94	9.5
Water content (% ww*)	12	78.5	1.1	1.4
Lipid content (g)	12	0.78	0.20	25.3
Lipid content (% ww)	12	6.2	1.4	21.8
Lipid content (% dw**)	12	28.7	5.4	18.8
Yolk				
Yolk sac (g)	15	1.02	0.40	39.6
Yolk sac (% ww)	15	8.0	2.7	33.6
Lipid in yolk sac (g)	12	0.32	0.15	46.7
Lipid in yolk sac (% ww)	12	29.8	4.9	16.3
Leg muscles				
Leg muscle mass (g)	15	0.60	0.12	20.5
Leg muscle mass (% ww)	15	4.7	0.8	16.4
Water content (%)	15	78.6	1.7	2.2
Pectoral muscles				
Pectoral muscle mass (g)	15	0.18	0.02	13.1
Pectoral muscle mass (% ww)	15	1.5	0.2	10.1
Water content (%)	15	82.6	1.5	1.8

* Wet weight
** Dry weight

length (r = 0.27, P < 0.01). Wing length at hatching was not significantly correlated with egg volume (r = 0.14, n.s.).

Body component analyses were carried out on 15 newly-hatched chicks, 12 of which were also successfully used for analyses of lipid content (Table 1). Newly-hatched chicks had a mean lipid content of 0.78 g, which represents 6.2% of the total wet body mass. The lipid content showed a much greater variability than did the body mass. The chicks hatched with a mean yolk sac weight of 1.02 g, which represents 8% of the wet body mass. The individual yolk sac weights varied very widely (Table 1). Of the two muscles studied, the leg muscle was by far the largest one at hatching time, comprising 4.7% of the wet body mass, compared to the pectoral muscles which only comprised 1.5%. Leg muscles also had a lower water content (78.6%), compared to that of pectoral muscles (82.6%). This difference was highly significant (paired t-test; P < 0.0001).

Table 2 shows the results of allometric comparisons of body components with egg volume. Dry body mass, water content, yolk-free body mass and lipid content, as well as leg and pectoral muscles, varied isometrically with egg volume. This is clearly shown because the slopes of the regression lines do not differ significantly from unity (Table 2). The slope for the yolk sac, however, was significantly higher than 1.0, pointing to a disproportionately larger yolk sac of the chicks hatched from larger eggs.

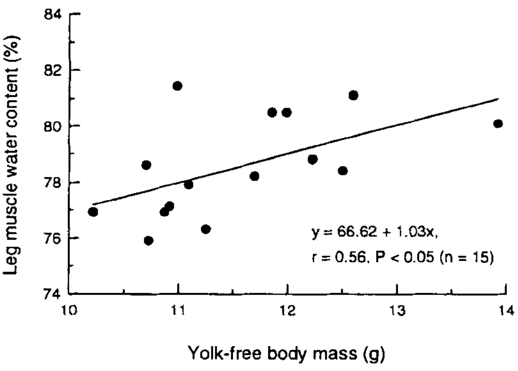

Fig. 2. Relationship of yolk-free body mass to water content (% ww) of leg muscles of newly-hatched arctic tern chicks. Linear regression line shown.

Table 2. Allometric relationships of arctic tern hatchling composition with egg volume. Intercepts (a) and slopes (b) are calculated from the regressions of log body component (g) on log egg volume (cm^3), together with the 95% confidence interval (CI) for the estimated slope.

Component	a	b	95% CI (±)	r	$t_{b=1}$	$P_{b=1}$
Body mass	−0.053	0.918	0.266	0.887	0.617	0.548
Dry body mass	−0.943	1.093	0.390	0.871	0.477	0.644
Water content	−0.035	0.797	0.416	0.771	0.978	0.351
Lean body mass	−0.046	0.889	0.296	0.885	0.751	0.470
Yolk-free body mass	0.183	0.701	0.338	0.755	1.769	0.100
Lipid content	−1.284	0.926	1.764	0.336	0.090	0.930
Yolk sac	−4.180	3.320	1.598	0.755	2.900	0.012
Leg muscles	−1.119	0.707	1.364	0.276	0.430	0.674
Pectoral muscles	−1.911	0.934	0.676	0.608	0.195	0.848

The water fraction (water mass/lean fresh body mass) of a tissue has been found to be inversely related to the functional maturity of the tissue (Ricklefs & Webb 1985). The water fraction of newly-hatched arctic tern chicks (mean value 0.84 ± 0.01, n = 12) did not differ significantly with egg volume (r = 0.44, P = 0.15). However, the water content of the leg muscles of the smaller chicks was significantly lower (Fig. 2), indicating that leg muscles of small hatchlings are functionally more mature than those of large hatchlings.

Growth

None of the chicks which hatched from the second eggs of the two-egg clutches survived and, with the exception of one chick which did survive for seven days, the majority of these chicks died within one to three days after hatching. The percentage of chicks from the first eggs of the two-egg clutches that survived for more than one week was very similar to that for the chicks from one-egg clutches, viz. 20% and 24%, respectively. Only data for chicks from one-egg clutches and the first chicks hatched from two-egg clutches were included in the growth analyses. Altogether, data were available for 29 chicks which survived until at least 12 days of age. The mean volume of the eggs from which they hatched was 18.5 ± 1.3 cm^3.

The body mass increase between 3 and 12 days of age was significantly correlated with egg volume (Fig. 3), being on average 5.3 ± 1.1 $g \cdot day^{-1}$. However, only 11% of the variation in growth rates was explained by the variation in egg volume. For each individual chick residual values for growth rate and hatchling body mass (in %), i.e. the deviations from expected values, were calculated from the equations relating growth rate to egg volume (Fig. 3) and

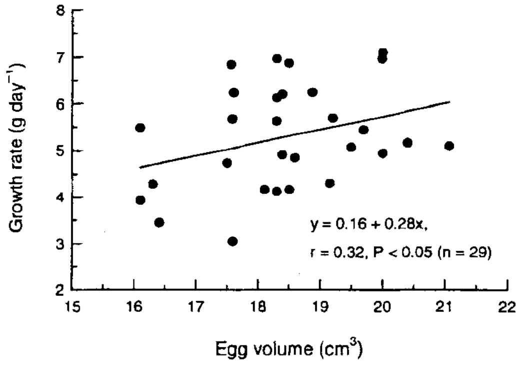

Fig. 3. Growth rates for 29 arctic tern chicks in relation to egg volume. Linear regression line shown. The probability value (P) is based on a one-tailed test, according to the hypothesis that chicks from large eggs will have the highest growth rates.

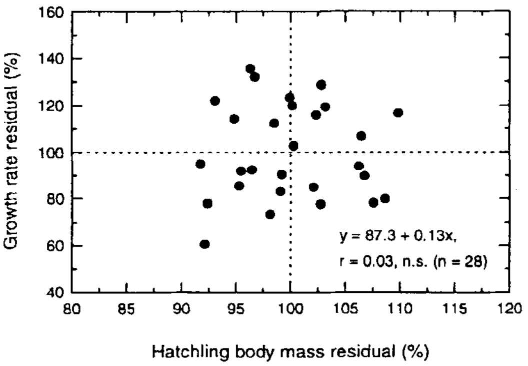

Fig. 4. Relationship between residuals of hatchling body mass and residuals of growth rate in arctic tern chicks during the first 12 days of postnatal development.

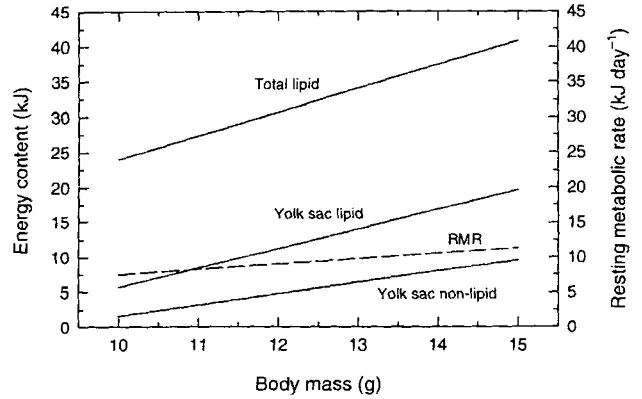

Fig. 5. The energy content of total lipid, yolk lipid and yolk non-lipid dry matter as a function of body mass (BM, g). The energy contents (solid lines) were calculated from the following regression lines: (1) Total lipid (g) = $-0.248 + 0.085 \cdot \mathrm{BM}$ ($r = 0.53$, $P < 0.05$); (2) Yolk lipid (g) = $-0.557 + 0.070 \cdot \mathrm{BM}$ ($r = 0.58$, $P < 0.05$); (3) Yolk non-lipid dry matter (g) = $-0.601 + 0.067 \cdot \mathrm{BM}$ ($r = 0.70$, $P < 0.01$). The resting metabolic rate (RMR, broken line) was calculated from a value of 1.57 $\mathrm{mlO_2 \cdot g^{-1} \cdot h^{-1}}$ for newly-hatched arctic tern chicks (Klaassen & Bech 1992) and using an energy conversion factor of 20.0 $\mathrm{kJ \cdot lO_2^{-1}}$.

hatchling body mass to egg volume ($y = -3.26 + 0.91x$, $r = 0.85$, $P < 0.001$), respectively. A comparison of the residual values showed no significant relationship between hatchling body mass and growth rate when the effect of egg volume was eliminated (Fig. 4). This shows that the growth rate differences are not an effect of the body mass of the hatchlings.

Discussion

The mean yolk content (30.7% of the shell-free egg mass) found for fresh eggs of arctic terns falls within the range of values reported for other semi-precocial species (Williams et al. 1982; Blem 1990; Carey 1996), and is very close to the value previously reported for arctic tern eggs (30.8%; Williams et al. 1982). Large arctic tern eggs contained both more yolk and albumen than small eggs, but the relative contents of yolk and albumen were similar.

From the data of the present study it is possible to estimate the amount of available energy reserves in relation to the body mass of newly-hatched arctic tern chicks. The energy content of the yolk sac (lipids and non-lipid dry matter) and of the total lipid content of the body were estimated from regression equations relating these parameters to body mass (Fig. 5) A newly-hatched chick of 10 g could potentially derive 24 kJ from the total lipid content of its body and yolk sac, 5.5 kJ of which would be derived from the yolk sac lipids. A chick of 15 g would be supplied with a total lipid-based energy content of nearly 41 kJ, almost half of which would stem from the yolk sac lipids. In addition, a chick of this size would have about 9 kJ as a potential energy source from the non-lipid matter in the yolk sac, compared to only 2 kJ for a 10 g chick. In this connection it is important to note that the solvent used for the lipid extractions washes out some structural lipids in addition to triglycerides (Dobush et al. 1985). Furthermore, it is possible that some of the fat stored in the body is unavailable for metabolic needs (Jenni & Jenni-Eiermann 1987). Thus, the regression lines presented in Fig. 5 probably overestimates the total amount of energy available for metabolic needs. However, the relative differences in energy content found between small and large chicks should be genuine.

The total energy requirement of hatchlings of different sizes is not known, but it is possible to indicate likely differences in the resting metabolic rate (RMR), using a mean value for newly-hatched arctic tern chicks of 1.57 $\mathrm{mlO_2 \cdot g^{-1} \cdot h^{-1}}$ (Klaassen & Bech 1992). Adopting this value, a 10 g and a 15 g chick would have estimated RMR values of 7.5 and 11.3 $\mathrm{kJ \cdot day^{-1}}$, respectively, during the first day after hatching. Hence, while the estimated energy consumption rate of a 15 g chick is only 1.5 times that of a 10 g chick, the available yolk sac reserves of the former are more than 3 times larger (Fig. 5). The energy content of the yolk sac of a 10 g chick corresponds to the energy needed to maintain RMR for one day whereas a 15 g chick would have enough energy in its yolk sac to maintain RMR for more than two days. Thus, the main advantages of emerging from a large egg would seem to be that the newly-hatched chick is provided with relatively larger yolk sac reserves. This could have an important impact on the survival rate during periods of nutritional stress, and might explain why the effect of egg size on offspring fitness is most pronounced during the first few days after hatching (Williams 1994).

The results of the present study have demonstrated that the composition of the fresh egg may not directly reflect the composition of the newly-hatched chick. Thus, despite a constant yolk content of the arctic tern eggs, unrelated to egg volume, hatchlings from large eggs had disproportionately larger yolk sac reserves (Table 2). This points to differences in the nutrient metabolism of small and large eggs, with a greater proportion of the yolk in small eggs being metabolised during embryonic development. A similar pattern of yolk metabolisation has been described for Japanese quail *Coturnix japonica* eggs (Ricklefs et al. 1978; Martin & Arnold 1991). Although this points to a greater fitness of larger chicks, by increasing their ability to withstand periods of food-scarcity, it does not necessarily imply that small chicks are less well off. Although a greater proportion of the yolk is metabolised during the embryonic development of small eggs, as compared to large eggs, it appears that a larger amount of energy is at the same time allocated to muscle development (Fig. 2). The lower water content, indicating a greater maturity, of the leg muscles of small chicks, may confer a thermoregulatory benefit from the relatively greater heat producing capacity of these muscles. It is interesting that Slattery & Alisauskas (1995), in their study of the two closely-related species of geese, found that the water content of the musculature of newly-hatched chicks of the smaller species, Ross' goose, was lower than that of the chicks of the larger species, lesser snow goose. The present study has shown that a similar compensatory development of muscle function can also be seen on an intraspecific level.

There was a weak, but significant, correlation between egg volume and growth rate during the first 12 days of postnatal development. The amount of yolk sac reserves is probably important for the growth of the chicks during the first few days after hatching. However, when one considers the limited amounts of metabolic substrates available in the yolk sac, the variation in yolk sac mass can hardly be expected to explain why the effect of egg volume was still significant for 12 days old chicks. Egg size is not only determined genetically, but is also related to the condition of the adult birds during the pre-laying period (Hepp et al. 1987; Meathrel et al. 1987; Blem 1990). Because the present study was primarily observational, it was not possible to distinguish between the effects of parental quality and the effects of egg volume per se on the growth rate. However, factors other than egg volume must explain most of the variation found in the growth rates, because egg volume only accounted for a small proportion (11%) of the overall variation in growth rate. This is substantiated by the fact that a residual analysis (Fig. 4) showed no effect of hatchling body mass on growth rate.

In conclusion, hatchling body mass and growth rate of arctic tern chicks were positively related to egg volume. Chicks hatched from large eggs also had disproportionately larger yolk sacs. This implies that a large chick has available yolk sac reserves to maintain the resting metabolic rate twice as long as that of a small chick. On the other hand, small chicks seem to have functionally more mature leg muscles. This possibly provides them with a relatively greater heat producing ability.

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