

## GROWTH AND DEVELOPMENT OF HOMEOTHERMY IN NESTLING EUROPEAN SHAGS (*PHALACROCORAX ARISTOTELIS*)

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**ABSTRACT.**—European Shag (*Phalacrocorax aristotelis*) nestlings were studied on a small island off the coast of central Norway. Increase in body mass (BM) with age ( $t$ , days) was described by the logistic equation:  $BM = 1,622 \text{ g} / [1 + e^{-0.172(t-19.9)}]$ . All growth parameters measured (body mass, and length of tarsus, wing and head) showed highest relative growth rate when the nestlings were 5–10 days old, that is, before the nestlings had achieved homeothermy. An incipient endothermic response was noted when nestlings were 9 days old, and they became homeothermic at ages of 15–18 days. Respective mass-specific resting metabolic rates for nestlings 0, 15, and 45 days old were 47, 261, and 147% of the predicted value for adult nonpasserine birds of similar body masses. Mass-specific minimal thermal conductance decreased from 366% of predicted adult value at hatching, to 220% of that predicted when nestlings were 21 days old. For nestlings 15 days old, the factorial metabolic scope (resting metabolic rate/peak metabolic rate) was only 1.5, but that increased rapidly thereafter. Rapid increase in the mass-specific RMR and decrease in minimal thermal conductance is suggested to contribute importantly to improve homeothermic ability during the first two weeks of the developmental period. At hatching, leg and pectoral muscles constituted 5.3 and 2.2%, respectively, of total wet body mass. Relative leg-muscle mass increased rapidly and had almost reached adult proportions when the nestlings were 25–30 days old. In contrast, pectoral-muscle mass increased in an almost direct proportion to the body mass during the first 30 days of the growth period, and increased rapidly thereafter. At hatching, the water fraction (water content/lipid-free wet mass) was significantly lower in the leg than in the pectoral muscles (0.920 vs. 0.931). The water fraction of leg muscles also remained lower during the entire growth period. Judging from the proportionately greater mass and higher degree of maturity of the leg compared to pectoral muscles, the former would seem to be the main site of cold-induced heat production during early development of homeothermy in European Shag nestlings. Received 30 October 2000, accepted 24 April 2001.

NEWLY HATCHED ALTRICIAL BIRDS do not respond metabolically to low ambient temperatures and are unable to maintain a large temperature gradient between their body and surroundings (Marsh and Wickler 1982, Olson 1992, Visser 1998). Therefore, during the early part of the postnatal period, most heat required for maintenance of their body temperature must be provided by parent birds. Young altricial birds usually acquire control of their body temperature during the middle part of the nestling period, when an improved ability for shivering thermogenesis allows them to produce heat faster than they lose it when cold-exposed (Marsh and Wickler 1982, Choi et al. 1993, Olson 1994). Precocial chicks, in contrast, are able to respond metabolically to low am-

bient temperatures already when they hatch (Koskimies and Lahti 1964, Steen and Gabrielsen 1986, Ricklefs 1989). Although thermoregulatory capacity varies greatly among different species, precocial chicks are usually able to maintain their body temperature over a wide range of ambient temperatures. Ability of young birds to respond metabolically to cold surroundings has been found to be closely correlated with the functional maturity of skeletal muscles (Marsh and Wickler 1982, Ricklefs and Webb 1985, Grav et al. 1988, Choi et al. 1993, Eppley and Russell 1995).

Although development of homeothermy in young birds has been the subject of many studies, information on that of large altricial birds is relatively scarce (e.g. Dunn 1976a, Evans 1984, Montevecchi and Vaughan 1989). The European Shag (*Phalacrocorax aristotelis*) is a large altricial seabird that breeds in colonies along the coasts of western Palearctic countries to

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~72°N (Cramp and Simmons 1977). We have shown in a previous study (Østnes and Bech 1997) that European Shag nestlings already have a well-developed ability to sense cold at hatching. Nonetheless, during the initial part of the development period, cold exposure causes a rapid decrease in their body temperature that only triggers a vocal response. The aim of the present study was to investigate timing of, and mechanisms involved in, achievement of homeothermy in European Shag nestlings.

#### MATERIALS AND METHODS

*Study area and material.*—Data were collected during two successive breeding seasons (June and July in 1994 and 1995) on Sklinna, a small island situated ~50 km off the coast of central Norway (65°12'N, 11°00'E). In the two seasons, a total of 334 nests were marked during the incubation period. The colony was visited on a daily basis to determine exact hatching dates of the nestlings (defined as day 0). Each nestling was identified by marking one of its legs with ink on day 0, and by marking the nestlings with electronic tags (12 mm long, 2 mm diameter, 0.09 g mass; AVID Mini Tracker, Norco, California) when they were ~6 days old. Nestlings were banded when they were ~18 days old. Weather data were obtained from a meteorological station ~500 m away from the colony.

*Growth measurements.*—Marked nestlings of known age were weighed to the nearest 1 g (0–100 g), 5 g (0–500 g), 10 g (500–1,000 g) or 25 g (1,000–2,500 g) using spring balances (Federwaage, Germany). Wing length was measured with a ruler to the nearest 1.0 mm, whereas tarsus and head lengths (from the back of the skull to the tip of the beak) were measured with a sliding caliper to the nearest 0.1 mm. For most nestlings, growth measurements were obtained several times during the growth period, and *n*-values refer to total number of measurements, not number of birds included. In addition, seven adults were caught and measured for comparison.

Data for each growth parameter were fitted to a logistic equation by nonlinear least-squares regressions (Ricklefs 1967, 1983). In 1994, we only obtained growth data during the first 27 days of the nestling period whereas growth data were obtained up to an age of 47 days in 1995. No significant differences were found in the growth of nestlings 0–27 days old between the two years (estimated asymptote: 1,407 g [2 SE = 111 g] vs. 1,325 g [2 SE = 135 g]; estimated growth constant: 0.194 [2 SE = 0.010] vs. 0.190 [2 SE = 0.025]). Thus, growth data obtained in the two years were pooled for further analysis. Relative growth rates (*R*) were calculated according to the equation of Brody (1945);

$$R = (\ln x_2 - \ln x_1) / (t_2 - t_1) \quad (1)$$

where  $x_1$  and  $x_2$  are the values at age 1 ( $t_1$ , days) and age 2 ( $t_2$ , days), respectively. We used the mean value measured for each growth parameter at a given age to calculate the *R*-values.

*Field body temperatures.*—The body temperatures ( $T_b$ ) of 21 different nestlings (age 0–11 days) were recorded whilst they were resting in their nests. Nestlings were equipped with a Co-Cu thermocouple (California fine wire, type 0.005), encased by polypropylene tubing (PP 50 or PP 160, Portex Ltd., Hythe, United Kingdom), inserted 2–4 cm into the cloaca. Thermocouples were kept in place by adhesive tape. Another thermocouple was placed close to the nest to record ambient temperature ( $T_a$ ). That thermocouple was placed in a similar environment as the nest and shaded from sunlight. Recordings of  $T_b$  and  $T_a$  were stored on a data logger (Squirrel, 12-bits, type 1203, Grant Instruments Ltd., Shepreth, United Kingdom) at 1 min intervals. When calculating the mean  $T_b$  of the nestlings, we only used values obtained after nestlings had been initially rewarmed by their parents. In addition, we only used values obtained from nestlings for which the thermocouple was still in its correct place when reinspected. Time periods for which such  $T_b$  recordings were obtained were on average 450 min (range 200–1,050 min). The  $T_a$  during those recordings was on average 9.4°C (range 7.6–10.8°C).

*Index of homeothermy.*—To determine degree of homeothermy, cooling rates of 32 nestlings (age 0–21 days) were measured in the laboratory. To maintain independent samples, each nestling was only used once, and nestlings were always taken from different nests. A thermocouple was inserted 2–5 cm into the cloaca to measure  $T_b$ . Before the start of each experiment, nestlings were warmed to a  $T_b$  of between 37.1 ± 0.3°C ( $n = 4$ ; day 0) and 39.7 ± 0.1°C ( $n = 4$ ; day 21) using an infrared heat lamp. Those values were chosen because they are close to recorded  $T_b$  values of nestlings that were brooded by their parents (see below). Nestlings were then placed in a chamber in which  $T_a$  was maintained at ~10°C (range 9.4–12.8°C). That temperature is close to the mean  $T_a$  to which nestlings are usually subjected to in the colony (see below). Measurements of  $T_b$  were obtained for a period of 45 min after cold exposure began. Recordings of  $T_b$  and  $T_a$  were stored on a data logger at 1 min intervals. The index of homeothermy (HI) was calculated by dividing the final temperature differences between the nestlings and their surroundings by the initial temperature differences, using the formula;

$$HI = (T_f - T_a) / (T_i - T_a) \quad (2)$$

where  $T_f$  and  $T_i$  are final and initial body temperatures, respectively, and  $T_a$  is ambient temperature. The index is equal to 1 when  $T_b$  is maintained with-

out change, and 0 when  $T_b$  falls to  $T_a$  within 45 min (for details, see Ricklefs 1987).

*Metabolic measurements.*—A total of 56 nestlings (age 0–45 days) were brought from the colony into a nearby field-laboratory, where we made the metabolic measurements. Each nestling was only used once. Nestlings were always taken from different nests and they were not used for other types of experiments. Nestlings were weighed to the nearest 0.1 g before and after each experiment. Because nestlings were not fasted before experiments, weight measurements obtained at the end of each experiment were used to calculate mass-specific metabolic rates. A thermocouple was inserted 2–7 cm into the cloaca to measure  $T_b$ . During experiments, nestlings were confined in metabolic chambers (volume 2–10 l), made of Plexiglas. Those chambers were placed inside a thermostatically controlled climatic chamber. Ambient temperature was recorded by a thermocouple.

Rates of oxygen consumption ( $VO_2$ ) were measured using flow-through respirometry (Withers 1977). Outside air was dried over silica gel and sucked through the metabolic chamber by an air pump (Miniport [KNF Neuberger, Freiberg-Munzingen, Germany]) at rates of 0.4–4.5 L min<sup>-1</sup>. After drying over silica gel, the actual airflow rates were measured with a calibrated flowmeter (Gilmont Instruments [Barrington, Illinois], size 2 or 3), before a fraction of the air was directed into an O<sub>2</sub> analyzer (Servomex [Crowborough, East Sussex, United Kingdom], type 244A). The O<sub>2</sub> analyzer was calibrated before each experiment using dry atmospheric air (set to 20.95% O<sub>2</sub>) and pure stock N<sub>2</sub>. Any changes in the O<sub>2</sub> reading at the end of an experiment were corrected for by assuming a linear drift. Measurements of  $VO_2$  were first obtained at thermoneutrality. For the smallest nestlings,  $T_a$  above 35°C, and for the largest nestlings,  $T_a$  above 20°C, had previously been estimated to lie within the thermoneutral zone. After 2–4 h exposure to that thermoneutral temperature, the  $T_a$  was gradually lowered at a rate of ~0.2°C min<sup>-1</sup>. When the  $T_a$  reached the lower critical temperature, nestlings responded by increasing their  $VO_2$  until the peak value was reached, after which both  $T_b$  and  $VO_2$  rapidly decreased. The experiment was then terminated. Total times that elapsed between nestlings being placed in the metabolic chamber to termination of experiments were 3–8 h, depending on age of nestlings. Recordings of O<sub>2</sub> content of the excurrent air (accuracy 0.01%) were stored, along with temperature recordings (accuracy ±0.1°C), on a Squirrel data logger at 1 min intervals. Data obtained were transferred to a computer for further analysis.

Oxygen consumption rates were calculated using equation 3a of Withers (1977). Values of mass-specific metabolic rate (MR, watts per kilogram) were subsequently calculated from the O<sub>2</sub> consumption rates,

assuming that 1 mL O<sub>2</sub> g<sup>-1</sup> h<sup>-1</sup> is equivalent to 5.5824 W kg<sup>-1</sup> and a respiratory exchange ratio of 0.79. "Resting metabolic rate" (RMR) was defined as the lowest 10 min running average value recorded during exposure to thermoneutral conditions. "Peak metabolic rate" (PMR) was similarly defined as the highest 5-min running average value recorded during cold exposure. Because it was not possible to lower  $T_a$  below -10°C, we could not obtain PMR measurements for nestlings older than 21 days.

*Thermal conductance.*—The minimal "wet" thermal conductance (MTC) was calculated according to the method originally described by Scholander et al. (1950). However, the formula described by those authors is only valid when  $T_b$  is kept constant. Because the  $T_b$  of nestlings decreased during cold exposure, we had to include a correction factor to account for the fall in  $T_b$  (see also Visser and Ricklefs 1993). Thus, the following formula was used to calculate minimal thermal conductance;

$$MTC = (PMR + A)/(T_b - T_a) \quad (3)$$

where PMR is the peak metabolic rate (watts per kilogram),  $T_b$  and  $T_a$  are the body and ambient temperatures (°C), respectively, recorded at the time that PMR was attained, and  $A$  is the correction factor for the decrease in energy content (watts per kilogram). The correction factor was calculated on the basis of the rate of fall in  $T_b$  recorded during the last 10 min period before PMR was attained, and a specific heat of 3.45 J g<sup>-1</sup> °C<sup>-1</sup> (Hart 1951).

*Muscle analyses.*—A total of 44 nestlings and 2 adults were collected and sacrificed for body-composition analysis. They were stored in air-tight plastic bags at a temperature of -20°C until being processed. All dissections were made within six months of collection. To minimize water evaporation, dissections were made while carcasses were still in a semifrozen condition. The right pectoral muscles (*M. pectoralis* and *M. supracoracoideus*) and the right leg muscles (all muscles from femur and tibia) were rapidly excised. Muscle components were immediately weighed to the nearest 0.0001 g (0–10 g), 0.001 g (10–100 g), or 0.1 g (>100 g). Fresh masses of each of the two muscle samples were doubled to obtain total muscle mass. Stomach contents were removed, weighed, and values subtracted from original body masses, to calculate the "true" wet body masses. Those body masses were used to calculate relative muscle masses (percentage).

Muscle samples were dried to a constant weight at 55°C to determine water content. Dried muscle components were placed into separate filter bags, and weighed to the nearest 0.0001 g (<8 g) or 0.001 g (>8 g) before being placed in glass containers containing a 5:1 mixture of petroleum ether and chloroform, to extract fat. That solvent mixture removes both storage lipids (triacylglycerols) and some structural lipids (phospholipids), but very little nonlipid material

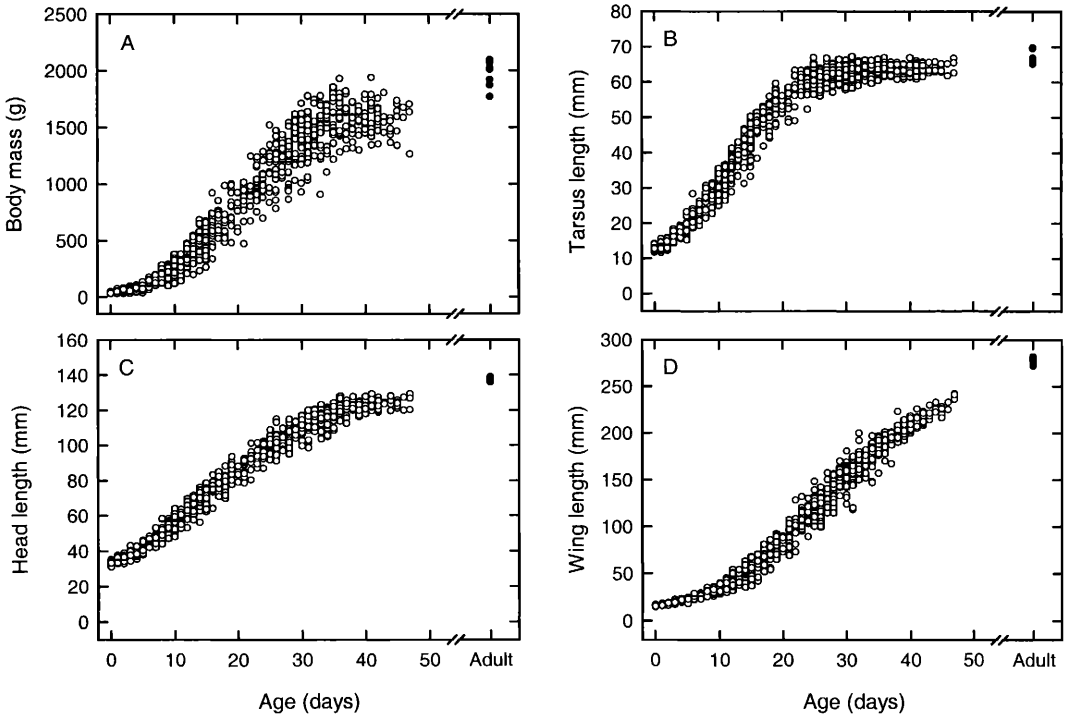


FIG. 1. Changes in (A) body mass ( $n = 1,049$ ), (B) tarsus length ( $n = 826$ ), (C) head length ( $n = 824$ ), and (D) wing length ( $n = 830$ ) of European Shag nestlings with age. Adult values (filled circles,  $n = 7$ ) are included for comparison. Curves were fitted to a logistic equation (Table 1). Growth data is based on measurements obtained from 297 different nestlings.

(Dobush et al. 1985). After lipid extraction, the bags were dried at 55°C. Lipid contents were determined from differences in masses of filter bags before and after the extraction process. Water fraction of the muscles was calculated as water fraction = water content/lipid-free wet mass (Ricklefs and Webb 1985).

**Statistics.**—Data are presented as means  $\pm$  SD. Except for growth data,  $n$  denotes number of birds investigated. Regression equations were calculated using the least-squares method. Comparisons of two means were performed using the Student's  $t$ -test. To compare more than two mean values, we used a one-way ANOVA followed by the Tukey test for pairwise comparisons. Data were tested for normality before performing statistical tests. Overall differences were considered significant for values of  $P < 0.05$ . All statistical analyses were performed using SigmaStat software (version 2.0, Jandel Scientific, Germany).

## RESULTS

**Ambient temperatures.**—The respective mean  $T_a$  in June 1994 and 1995 were 8.3°C (range 4.7–

13.8°C) and 9.4°C (range 6.6–14.2°C) and in July 12.3°C (range 8.3–20.1°C) and 11.1°C (range 7.4–17.2°C). Deviations from average temperatures computed for each of those months, based on a 30 year period, were between 0.4°C and –1.8°C.

**Growth.**—Newly hatched European Shag nestlings had a mean body mass (BM) of  $35.8 \pm 3.9$  g ( $n = 111$ ), which is  $\sim 1.8\%$  of the adult mass ( $1,965 \pm 116$  g,  $n = 7$ ). The increase in BM with age ( $t$ , days; Fig. 1A), as well as data for other measured growth parameters (Figs. 1B–D), were fitted to a logistic equation (Table 1). Asymptotic body mass (A) attained by the nestlings (1,622 g) was  $\sim 340$  g lower than mean adult mass. As indicated by inflection points of the logistic equations, various body components showed marked differences in their development patterns. However, as shown by calculated relative growth-rate values, each of the measured growth parameters showed greatest relative increase when nestlings were between 5 and 10 days old (Table 2).

TABLE 1. Logistic equations calculated for the different growth parameters measured during the growth period of nestling European Shags (see Fig. 1). Data were fitted to the logistic equation by non-linear least square regression. In the equation  $y = a/[1 + e^{-k(t - t_1)}]$ ,  $a$  is the asymptote of the curve,  $k$  is the growth constant and  $t_1$  is the age (in days) at the inflection point. The  $t_{10}$ - $t_{90}$  interval is the time (in days) required to grow from 10 to 90% of the asymptotic value.

Growth parameter	Logistic equation	$t_{10}$ - $t_{90}$	$n$
Body mass	$y = 1,622 \text{ g}/[1 + e^{-0.172(t - 19.9)}]$	25.6	1,049
Tarsus length	$y = 65.0 \text{ mm}/[1 + e^{-0.157(t - 10.2)}]$	28.0	826
Head length	$y = 134.1 \text{ mm}/[1 + e^{-0.089(t - 13.4)}]$	49.6	824
Wing length	$y = 256.8 \text{ mm}/[1 + e^{-0.109(t - 26.6)}]$	40.4	830

*Field body temperatures.*—The mean  $T_b$  recorded for 21 nestlings resting in their nests increased significantly with age, from 36.6°C at day 0 to 38.3°C at day 11 (ANOVA,  $F = 3.55$ ,  $df = 6$  and  $14$ ,  $P = 0.024$ , Fig. 2). Increase in mean  $T_b$  with age seems to be mainly due to lower fluctuations in  $T_b$  recorded for older nestlings.

*Index of homeothermy.*—Rates of body cooling were measured at a mean  $T_a$  of  $10.4 \pm 1.1^\circ\text{C}$  (range 9.4–12.8°C,  $n = 32$ ). HI increased nearly linearly with age during the first two weeks of the posthatching period (Fig. 3). When nestlings were 15–18 days old, they were able to maintain their  $T_b$  during the entire 45 min cooling period.

*Metabolic rate.*—The mass-specific RMR measured at thermoneutral conditions was lowest for the newly hatched nestlings, amounting to  $5.08 \pm 0.65 \text{ W kg}^{-1}$  ( $n = 4$ ). It increased rapidly with age during the first two weeks of development, and reached a maximum value of  $14.49 \pm 2.44 \text{ W kg}^{-1}$  ( $n = 5$ ) on day 15 (Fig. 4). For nestlings older than 15 days, RMR slowly decreased and reached a value of  $5.86 \pm 0.30 \text{ W}$

$\text{kg}^{-1}$  ( $n = 4$ ) on day 45. Respective RMR values measured for nestlings 0, 15, and 45 days old were 47, 261, and 147% of values predicted for adult nonpasserine birds of similar body masses (Aschoff and Pohl 1970).

Ability of nestlings to respond metabolically to cold surroundings improved markedly during the first three weeks of the nestling period (Fig. 5). Nestlings 0–6 days old were unable to increase their MR, even transiently, in response to a gradual lowering of  $T_a$ . Accordingly, their PMR values were close to the corresponding RMR values measured at thermoneutrality. When the nestlings were nine days old, they showed a weak (1.25-fold), transient, increase in MR in response to the lowering of  $T_a$ . Thermogenic capacity of older nestlings increased gradually with age, and nestlings 21 days old had PMR values that were on average 2.23× greater than their corresponding RMR.

TABLE 2. Relative growth rates (R-values, see Eq. 1) for various growth parameters calculated at five-day intervals during the nestling period of European Shags.

Age (days)	Body mass ([g·days] <sup>-1</sup> )	Tarsus length ([mm·days] <sup>-1</sup> )	Head length ([mm·days] <sup>-1</sup> )	Wing length ([mm·days] <sup>-1</sup> )
0–5	0.170	0.072	0.045	0.066
5–10	0.228	0.101	0.060	0.092
10–15	0.134	0.066	0.048	0.087
15–20	0.090	0.046	0.036	0.084
20–25	0.091	0.025	0.035	0.078
25–30	0.075	0.003	0.019	0.047
30–35	0.035	0.004	0.014	0.036
35–40	0.004	0.000	0.008	0.025
40–45	-0.007	0.001	0.002	0.013

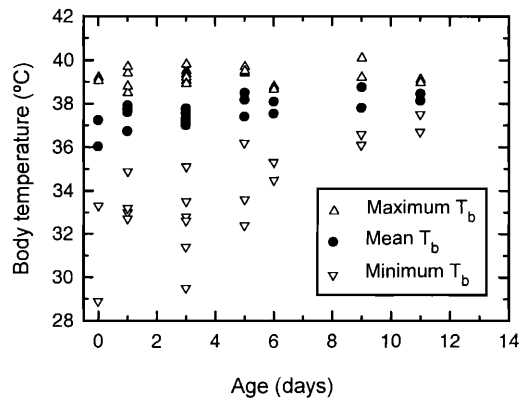


FIG. 2. Body temperatures of European Shag nestlings ( $n = 21$ ) recorded in the nest as a function of age. Average, maximum and minimum values recorded for each nestling are shown on the basis of recording periods varying from 200 to 1,050 min.

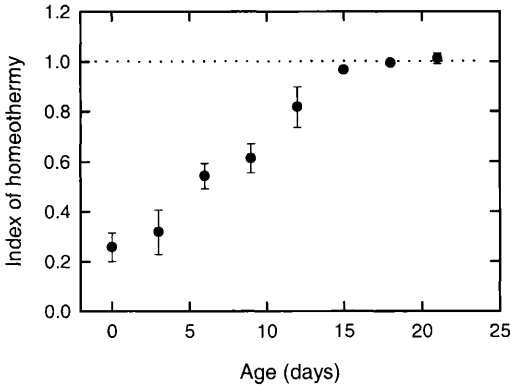


FIG. 3. Index of homeothermy (HI) as a function of age in European Shag nestlings.

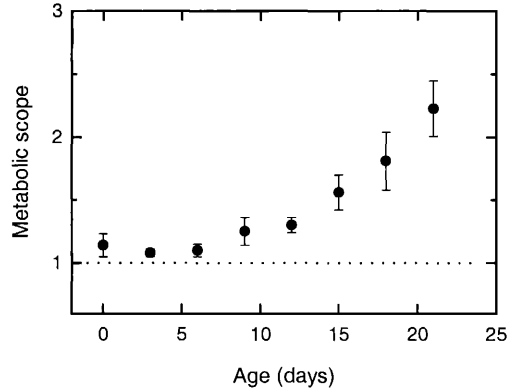


FIG. 5. Development of factorial metabolic scope (PMR/RMR) as a function of age of nestling European Shags.

The mean  $T_b$  of nestlings, measured at thermoneutral conditions, increased significantly with age (ANOVA,  $F = 18.2$ ,  $df = 13$  and  $41$ ,  $P < 0.001$ ). However, a pairwise comparison showed no significant differences in the mean  $T_b$  for nestlings older than 12 days. The mean  $T_b$  measured at thermoneutrality for nestlings 12–45 days old was  $39.0 \pm 0.59^\circ\text{C}$  ( $n = 36$ ). The mean  $T_a$  at which RMR values were obtained decreased significantly with age (ANOVA,  $F = 26.3$ ,  $df = 13$  and  $41$ ,  $P < 0.001$ ), suggesting a gradual lowering of the lower critical temperature. RMR values of newly hatched nestlings (0 days old) were measured at a mean  $T_a$  of  $34.5 \pm 0.3^\circ\text{C}$  ( $n = 4$ ), whereas those for nestlings 21–45 days old were measured at a mean  $T_a$  of  $23.8 \pm 1.11^\circ\text{C}$  ( $n = 22$ ). The  $T_b$  values generally de-

clined before the nestlings attained their PMR levels and were on average  $1.9 \pm 1.1^\circ\text{C}$  ( $n = 37$ ) below corresponding values recorded under thermoneutral conditions. The  $T_b$  of nestlings 1–9 days old decreased rapidly at  $T_a$  below the lower critical temperature and the PMR level was attained after only a slight lowering of  $T_a$ . Older nestlings were able to maintain their  $T_b$  over a wider range of  $T_a$ . In nestlings 15 and 21 days old, PMR was attained at a mean  $T_a$  of  $14.8 \pm 1.9^\circ\text{C}$  ( $n = 5$ ) and  $-5.5 \pm 5.6^\circ\text{C}$  ( $n = 37$ ), respectively.

*Thermal conductance.*—Minimal thermal conductance decreased nearly linearly with age, from  $3.51 \pm 0.62 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$  ( $n = 4$ ) for nestlings 0 days old to  $0.47 \pm 0.09 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$  ( $n = 4$ ) for nestlings 21 days old (Fig. 6). Those values are 366 and 220%, respectively, of ex-

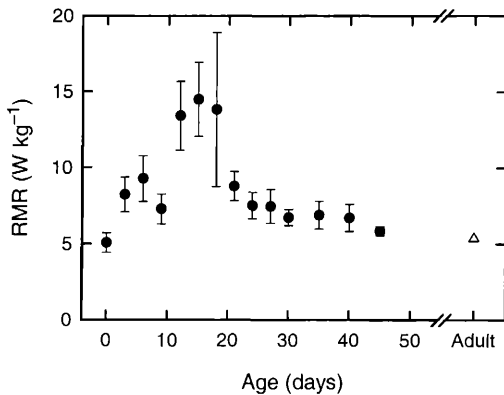


FIG. 4. Mass-specific resting metabolic rate (RMR) of European Shag nestlings as a function of age. Open triangle shows a mean value obtained for adult European Shags (Bryant and Furness 1995).

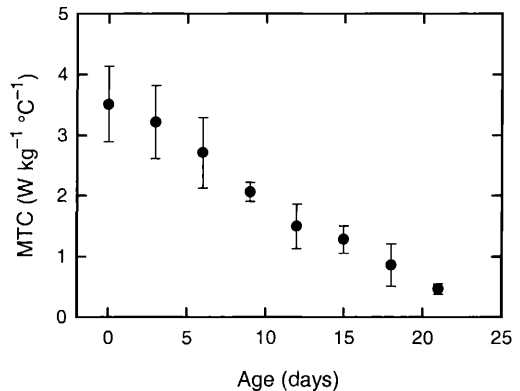


FIG. 6. Minimal thermal conductance (MTC) of nestling European Shags as a function of age.

pected values for adult nonpasserine birds of the same body mass (Aschoff 1981).

**Plumage development.**—We did not obtain any quantitative measurements of development of plumage. The newly hatched nestlings were completely naked and only gradually, during the first two weeks of age, did a downy covering develop. The first signs of external feather growth appeared in the dorsal feather tract when they were 6 days old. In nine day old nestlings, ~25 % of the body was covered by down with a length of 1–3 mm. Nestlings 15 days old were completely covered by a 10–15 mm thick downy coat.

**Muscle development.**—There were marked differences in pattern of development of the two muscle groups studied. At hatching time, leg muscles were 2.4× larger than the pectoral muscles ( $1.9 \pm 0.4$  g and  $0.8 \pm 0.2$  g, respectively;  $n = 5$ ). During the first 25–30 days of the developmental period, leg muscle mass increased rapidly, as indicated by values for newly hatched and 30 days old nestlings, which constituted  $5.7 \pm 0.8\%$  ( $n = 5$ ) and  $11.6 \pm 0.3\%$  ( $n = 3$ ), respectively, of the total wet body mass (Fig. 7A). In contrast, pectoral muscle mass increased in an almost direct proportion to body mass and thus constituted an almost constant percentage of body mass during the first 30 days of the developmental period (on average  $2.2 \pm 0.6\%$  of the total wet body mass;  $n = 37$ ). At ~30 days of age, relative growth of leg muscles ceased markedly, whereas pectoral muscles increased relatively in size (Fig. 7A). For the two adult birds investigated, relative leg muscle mass was only slightly higher than that of the pectoral muscles (14.1 vs. 12.8%). At hatching time, water fraction of the leg muscles was significantly lower than that of the pectoral muscles ( $0.920 \pm 0.013$  vs.  $0.931 \pm 0.011$ ; paired  $t$ -test,  $t = 4.21$ ,  $P = 0.014$ ,  $n = 5$ ). Water fraction of both muscle groups showed a steady decrease from hatching time onwards (Fig. 7B). However, at all times during development, water fraction of leg muscles was lower than that of pectoral muscles, indicating a higher degree of maturity of leg muscles. In contrast, in the two adult birds investigated, the mean water fractions of the pectoral and leg muscles were 0.716 and 0.742, respectively.

DISCUSSION

**Growth.**—European Shag nestlings reached an asymptotic body mass when they were 30–

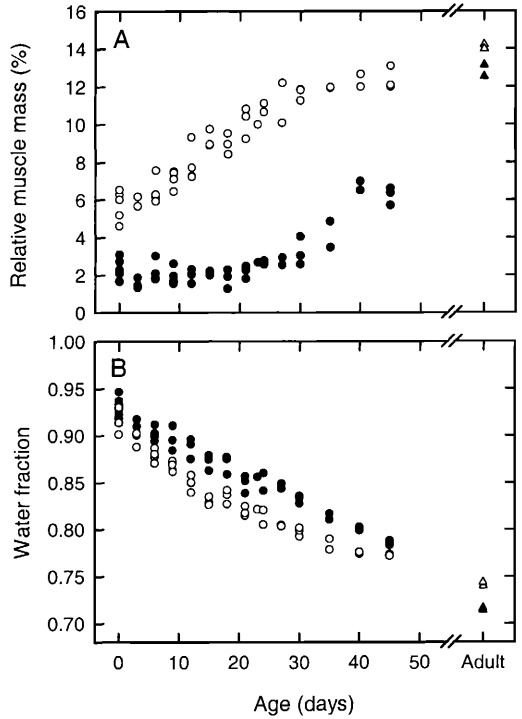


FIG. 7. Relative masses (A, expressed as a percentage of total body mass) and water fractions (B) of leg (open circles) and pectoral (filled circles) muscles of European Shag nestlings as a function of age. Similar values for leg (open triangles) and pectoral (filled triangles) of two adult birds are also included.

40 days old. During that period of postnatal development, body mass increased approximately 45-fold. The logistic growth constant ( $k = 0.172 \text{ day}^{-1}$ ), as well as the asymptotic body mass ( $a = 1,622$  g), fall within the range of values reported in other studies of the growth of nestling European Shags ( $k = 0.147\text{--}0.190 \text{ day}^{-1}$  and  $a = 1,600\text{--}1,742$  g; see Starck and Ricklefs 1998a with references therein). Starck and Ricklefs (1998b) presented an allometric relationship between the logistic  $k$ -value and the asymptotic weight, based on 557 species of birds representing all major clades of avian phylogeny. The measured  $k$ -values for European Shag nestlings are more than twice the expected values ( $0.08 \text{ day}^{-1}$ ) for a bird of that size. Members of the family Phalacrocoracidae generally seem to have high growth rates, also when compared to those for other altricial seabirds of comparable size. For example, members of the families Fregatidae ( $a = 854\text{--}1,455$

g) and Sulidae ( $a = 800\text{--}4,080$  g) have logistic  $k$ -values that range from  $0.039\text{--}0.107$  day<sup>-1</sup> (Starck and Ricklefs 1998a). European Shag nestlings, as well as those of other members of the family Phalacrocoracidae (Dunn 1975), are furthermore unusual in having an asymptotic weight well below the average adult weight. Asymptotic weight of our nestlings was only 83% of mean adult weight (1,965 g,  $n = 7$ ). That is in contrast to nestlings of other altricial and semialtricial seabirds, which normally attain weights well above the adult level before fledging (Ricklefs 1973).

Dawson and Evans (1957, 1960) proposed an energy allocation hypothesis to explain differences in growth rates seen among bird species within the altricial-precocial spectrum. That hypothesis suggests that altricial nestlings are able to allocate more energy to growth mainly owing to a reduced diversion of energy to activity and thermoregulation. If those energetic advantages of the altricial mode of development are significant, then proportion of energy allocated to growth should be highest early in the developmental period. All measured growth parameters showed highest relative growth rate before nestlings were 15 days old (Table 2), that is, in the period before the nestlings had attained homeothermy. Similar results have also been presented for another altricial bird, the Red-winged Blackbird (*Agelaius phoeniceus*; Olson 1992). Those findings are in accordance with the energy allocation hypothesis. However, marked differences existed in development of various body components. As indicated by inflection points of logistic growth curves (Table 1) and relative growth-rate values (Table 2), the tarsus had reached 50% of adult size when nestlings were 10 days old and was nearly fully grown when the nestlings were 25 days old. In contrast, the wing had reached only 50% of adult length when nestlings were 27 days old. European Shag nestlings are well able to run when they are two weeks old, whereas their capability for flight is only acquired when they are nearly fully grown. As earlier suggested, those differences in growth of different body components may be due to a competition for nutrients between various growing tissues (O'Connor 1977, Sedinger 1986).

*Development of RMR.*—The mass-specific RMR of newly hatched European Shag nes-

tlings was only 47% of the predicted value for an adult nonpasserine bird of similar body mass. A neonatal RMR substantially below the allometrically predicted adult level has previously been described both for altricial and precocial birds, but RMR values of some newly hatched precocial birds lie above the predicted adult level (Ricklefs 1989, Klaassen and Drent 1991, Weathers and Siegel 1995). Visser (1998) presented an allometric relationship between neonatal RMR and body mass. That equation, which is based on values for 120 species, spans three orders of magnitude in mass and represents all major modes of avian development. Compared to that equation, RMR of neonatal European Shags is only 75% of that expected for a neonate of that size. A very low neonatal RMR (54% of expected value) has also been reported for the Blue-eyed Shag (*Phalacrocorax atriceps*; T. L. Bucher unpubl. data cited in Visser 1998). Low neonatal RMR values found for members of the Phalacrocoracidae family is probably a reflection of their extreme degree of altriciality.

The mass-specific RMR values increased steadily during the first two weeks of age, with a peak value occurring when nestlings were 15 days old. At that age, nestlings had a RMR that was 261% of the allometrically predicted value for an adult nonpasserine bird of similar size. Such a pattern in development of RMR is known to be normal for altricial as well as precocial nestlings, although there is a tendency for a higher "overshoot" in precocial compared to altricial ones (Ricklefs 1974, Weathers and Siegel 1995). In the present study, nestlings were not fasted before they were used in the experiments, and consequently, we need to consider a possible effect of heat increment of feeding (HIF). HIF is defined as an increase in metabolic rate following ingestion of food, and may be of such a magnitude that it could constitute a significant part of the energy budget of nestlings (e.g. Janes and Chappell 1995, Chappell et al. 1997). Although we can not entirely rule out the possibility that there has been an effect of HIF on our measurements, there are two reasons why we do not consider HIF to have had any significant influence on the results. Firstly, actual time elapsed between collection of nestlings in the field and recordings of RMR during experiments was a minimum of 4 h. Because of that experimentally im-



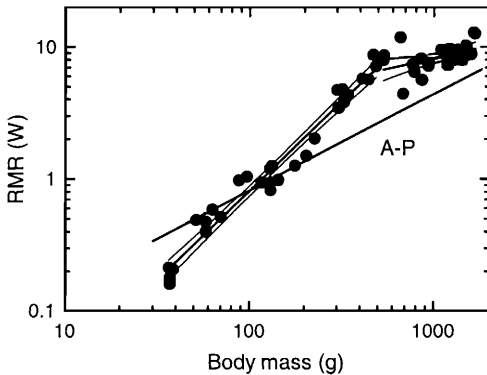


FIG. 8. Relationship between resting metabolic rate (RMR) and fresh body mass of European Shag nestlings. For nestlings 0–15 days old the relationship is described by the allometric regression  $RMR = 0.00162BM^{1.35}$ , whereas the corresponding equation for older nestlings is  $RMR = 0.923BM^{0.316}$ . Shown also is the 95% confidence interval of the estimated slopes. A scaling for adult nonpasserine birds (A–P), based on data from Aschoff and Pohl (1970), is shown for comparison.

posed food deprivation time, nestlings would have digested most of their stomach and gut content by the time RMR measurements were made. Secondly, in a previous study we did not find any correlation between stomach content and residual metabolic rate of 15 day old European Shag nestlings (Bech and Østnes 1999). The very high mass-specific RMR value found for 15 days old European Shag nestlings seems to be mainly due to a high degree of activity of energy-processing organs, notably liver and intestine (Bech and Østnes 1999).

In most precocial, semiprecocial, and semialtricial species, RMR increases with nestling body mass in a bi- or triphasic allometric linear pattern (Weathers and Siegel 1995, Dietz and Drent 1997). In contrast, for seven altricial species, at weights of <80 g, relationship between RMR and nestling body mass was found to follow a monophasic pattern, with an average allometric scaling exponent of 1.28 (Weathers and Siegel 1995). When the RMR versus body mass data for European Shag nestlings were fitted to a log–log plot, a clear biphasic pattern appeared (Fig. 8). For nestlings 0–15 days old, RMR scaled allometrically to body mass with a scaling exponent of 1.35, whereas for older nestlings the corresponding scaling exponent was only 0.32. Such a biphasic pattern in the development of RMR has also been reported for an-

another, relatively large altricial species, the White-necked Raven (*Corvus cryptoleucus*;  $a = 534$  g; Mishaga and Whitford 1983). Thus, whereas the development of RMR of small altricial species follows a monophasic pattern (Weathers and Siegel 1995), RMR of large altricial species seems to develop in a biphasic pattern similar to that found for precocial species.

*Development of homeothermy.*—On hatching, European Shag nestlings were unable to maintain their  $T_b$  when cold exposed. The high thermal conductance (366% of predicted adult level) seems to be one causative factor. Other important limiting factors are their low RMR (47% of predicted adult level) and their inability to respond metabolically to cold surroundings. Complete lack of a metabolic response to cold surroundings during the early postnatal period is a common characteristic of all altricial species so far investigated (Visser 1998). Despite the fact that European Shag nestlings have no feathers on hatching and only gradually acquire an external coat of natal down, HI increased rapidly during the first two weeks of postnatal development. At an age of 15 to 18 days, they were able to maintain their  $T_b$  at  $T_a$  that they normally experience in their natural environment ( $\sim 10^\circ\text{C}$ ). Improvement of their homeothermic ability during the first two weeks of the developmental period seems to be mainly due to a rapid increase in mass-specific RMR and a decrease in mass-specific thermal conductance. Decrease in thermal conductance noted during the initial part of the developmental period probably represents a passive effect of the rapid decrease in the surface-to-volume ratio.

Although a weak, cold-induced, metabolic response was noted when nestlings were 9 days old, the factorial metabolic scope was still only 1.5 when the nestlings were 15 days old. Despite the low metabolic scope, nestlings had a high mass-specific heat production at that age. As shown in Figure 8, RMR values exceeded expected values for adults of the same mass when nestlings were  $\sim 100$  g in weight (corresponding to an age of 5 days), and were  $2.6\times$  the predicted adult level when the nestlings were 15 days old (mean BM 512 g,  $n = 39$ ). It should be noted that even though nestlings 15–18 days old were able to maintain their  $T_b$  when exposed to  $T_a$  that they normally experience in the colony, they had to raise their metabolic

heat production to its maximum achievable rate. Thus, even at that age, they are probably not able to cope with bad weather conditions (rain, wind, or both) without protection by their parents. However, metabolic capacity of older nestlings increased rapidly, and at an age of 21 days they were able to cope with  $T_a$  well below 0°C.

Visser (1998) presented an allometric relationship for altricial birds between body mass at time of achievement of homeothermy and asymptotic body mass. According to that equation, European Shag nestlings should become homeothermic at a predicted body mass of 450 g (corresponding to an age of 13–14 days). Our nestlings achieved homeothermy at a body mass slightly above the predicted value (mean BM for 15 days old nestlings; 512 g,  $n = 39$ ). At that time ~30% of asymptotic growth had been completed. Achievement of homeothermy relatively early in the growth period has also been reported for other large altricial birds. For example, nestlings of both the Northern Gannet (*Morus bassanus*; Kirkham and Montevecchi 1982, Montevecchi and Vaughan 1989) and the Double-crested Cormorant (*Phalacrocorax auritus*; Dunn 1976a) become homeothermic at an age of ~15 days, at which time 20–25% of growth is completed. That is in contrast to small altricial species (BM < 100 g), which normally achieve homeothermy only when they are almost fully grown (see table 5.3 in Visser 1998). The main reason for the earlier achievement of homeothermy by large compared to small altricial species appears to be a more favorable surface-to-volume ratio of the former, resulting in a greater thermal inertia. That view is also supported by the fact that broods of small altricial nestlings achieve effective homeothermy at a much earlier age than isolated individuals (Dunn 1976b, 1979).

*Development of skeletal muscles.*—It is a well accepted view that shivering thermogenesis is the principal means of regulatory heat production in cold-exposed birds. Studies of young birds have mostly confirmed that general pattern (Dietz et al. 1997, Hothola and Visser 1998, Marjoniemi and Hohtola 1999). Thus, growth and maturation of skeletal muscles is an obvious prerequisite for development of homeothermy by young birds. Because of their large size, leg and pectoral muscles are the two potentially most important muscle groups in-

involved in shivering thermogenesis. Results of the present study have revealed profound differences in growth of those two muscle groups. On hatching, leg muscles were 2.4× larger than pectoral muscles. That proportional difference is less than that found in neonate precocial and semiprecocial birds that have leg muscles 4–9× larger than pectoral muscles (Visser and Ricklefs 1995). In altricial passerines, however, the masses of the two skeletal muscle groups are almost similar at hatching (Marsh and Wickler 1982, Ricklefs and Webb 1985). The rapid increase in proportion of leg muscles and delayed development of pectoral muscles is very similar to the pattern seen in highly precocial birds such as geese (Lilja 1983, Sedinger 1986, Bishop et al. 1996). Also in passerines, pectoral muscles grow very rapidly during the last part of the developmental period (Marsh and Wickler 1982, Ricklefs and Webb 1985). However, in that group of birds, growth of leg and pectoral muscles is initially almost the same. Rapid increase in proportion of leg muscles during the initial part of the developmental period and delay in development of pectoral muscles, is related to the fact that European Shag nestlings are highly cursorial relatively early in the developmental period, while ability to fly is not acquired before they are fully grown. The remarkable similarity in growth patterns of leg and pectoral muscles of the altricial European Shag and of the precocial geese indicates that development of the skeletal muscles depends more on development of locomotory ability than on position of birds within the altricial-precocial spectrum. It should also be noted that proportion of pectoral muscles did not begin to increase before leg muscles had attained their adult proportions. That supports the previously mentioned "nutrient competition" hypothesis (O'Connor 1977, Sedinger 1986), namely that nestlings allocate resources to those tissues where they are most needed at the particular moment.

The high water fraction of leg and pectoral muscles of neonate European Shags is in accordance with the general pattern seen in altricial birds (Ricklefs 1979a, b; Ricklefs and Webb 1985). A high water content has been found to be incompatible with functional maturity, and maturation of skeletal muscles is characterised by a decrease in water content, as contractile proteins and other functional elements accu-

multate in muscle tissue. It has been shown, for both altricial and precocial birds, that neonates are not capable of shivering thermogenesis before the water fraction has decreased to 0.85, which correspond to a lipid-free dry muscle mass of 15% (Ricklefs and Webb 1985, Dietz et al. 1997). Water fractions of leg and pectoral muscles of European Shag nestlings reached that "critical" level when the nestlings were 9–12 days old and 21 days old, respectively. That corresponds well with development of an incipient endothermic response noted for 9 day old nestlings. Judging from proportionally larger mass and higher degree of maturity (as indicated by water fractions) of leg muscles compared to pectoral muscles, the former would seem to be the main site of cold-induced heat production during early development of homeothermy in European Shag nestlings. If a water fraction of 0.85 should turn out to be a universal index for functional maturity of skeletal muscles in birds, then pectoral muscles will not participate in shivering thermogenesis until the nestlings are 21 days old. A contribution by pectoral muscles, however, might explain marked improvement of the thermogenic capacity of the nestlings at that age.

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