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Influence of body composition on the metabolic rate of nestling European shags (*Phalacrocorax aristotelis*)

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Abstract During the early development of avian nestlings, their mass-specific resting metabolic rate (RMR) changes in a biphasic pattern with the peak value often being much higher than that expected for an adult bird of similar body mass. In the present study we examined the possible influence of variations in the size of internal organs in "setting" the high RMR and peak metabolic rate (PMR) during development in a large altricial species, the European shag (*Phalacrocorax aristotelis*). Thermoneutral RMR and cold-exposure induced PMR were measured in nestlings 15 days old, the age at which the highest RMR occurred during development. Body mass averaged 414 g. Mean values of RMR and PMR were 5.75 W and 9.08 W, respectively; the RMR value corresponds to approximately 250% of the expected value for an adult non-passerine bird of similar body mass. The masses of all the organs measured (breast and leg muscles, heart, liver, intestine, and kidney) varied isometrically with total body mass. However, large chicks had a significantly lower fractional water content than small chicks, suggesting that the former had achieved a higher level of functional maturity. In contrast to what has been suggested for adult birds in general, the heart and kidney masses of shag nestlings were not significantly correlated with the metabolic rates. The intestine length, in contrast, was highly and positively correlated with both the RMR and the PMR, i.e. intestine length was a better predictor of RMR and PMR than was total body mass. In addition, liver mass was positively correlated with RMR. The results of the present study suggest that the liver in particular may play a key role in establishing the high, mass-specific RMR which is attained during development in bird chicks. Our results also support previous suggestions that early in their development, altricial chicks mainly allocate energy to the growth of 'energy-processing' organs (such as the intestine and liver) rather than to 'energy-consuming' organs.

Key words European shag · Body composition · Intestine · Liver · Metabolic rate

Abbreviations *HIF* heat increment of feeding · *PMR* peak metabolic rate · R_E respiratory exchange ratio · *RMR* resting metabolic rate · T_a ambient temperature · T_b body temperature · *TNZ* thermoneutral zone · $\dot{V}O_2$ oxygen consumption

Introduction

The metabolic rates of newly hatched chicks, whether altricial or precocial, are often lower than those of the adult birds (Ricklefs 1989; Klaassen and Drent 1991; Weathers and Siegel 1995). Consequently, during the early development, an increase in metabolic capacity occurs, as shown by an increase in the resting metabolic rate (RMR) as well as in the metabolic scope (e.g. Eppley 1984; Bech et al. 1991; Olson 1992; Choi et al. 1993; Visser and Ricklefs 1993). An increase in metabolic capacity is an obvious prerequisite for achieving homeothermy.

However, during development the resting, thermoneutral metabolic rate of the chick often exceeds the allometrically predicted equivalent value for an adult bird of similar mass (Ricklefs 1974; Klaassen and Bech 1992; Olson 1992; Dietz et al. 1995). This shows that a biphasic pattern exists in the development of the mass-specific metabolic rate. This pattern has been described for altricial as well as precocial chicks, although there is a tendency for a higher 'overshoot' in precocial and semi-precocial chicks as compared to altricial ones

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(Ricklefs 1974; Weathers and Siegel 1995). Several explanations have been proposed as a physiological basis for the high mass-specific metabolic rate recorded during development. Suggested explanations have been that it is compensation for increased heat loss from blood-filled feather quills during feather growth (Ricklefs 1974), absorption of the yolk sac (Freeman 1967; Dietz et al. 1995), disproportional growth of organs (Lilja 1983; Ricklefs 1983; Dietz et al. 1995), a greatly increased oxidative capacity of the metabolically active tissues (Dietz et al. 1995) and a direct effect of the high growth costs (Ricklefs 1974). Hence, there is still no consensus as to what is the most important factor.

The European shag (*Phalacrocorax aristotelis*) is a large altricial seabird, the nestlings of which take approximately 53 days to reach their fledging mass (Cramp and Simmons 1977). The chicks achieve homeothermy between 15 days and 20 days of age (C. Bech and J.E. Østnes, personal observation). The mass-specific RMR increases steadily during the first 2 weeks of age, with a peak value occurring at an age of approximately 15 days (C. Bech and J.E. Østnes, personal observation). At this age the chicks have an RMR which is considerably higher than the allometrically predicted equivalent value for an adult bird of similar size. The primary aim of the present study was to elucidate the physiological basis for this high RMR, and also the peak metabolic rate (PMR), in nestling European shags of this same age.

In adult birds, the RMR has been shown to be closely related to body composition (e.g. Scott et al. 1996; Piersma and Lindström 1997). For example, Daan et al. (1990) found that the metabolic rate of 22 bird species was correlated with the sum of the masses of kidney and heart. They concluded that the interspecific variation of avian RMR is a reflection of variations in the relative masses of these metabolically active organs. The *intraspecific* variation of RMR in the common kestrel (*Falco tinnunculus*), has similarly been proposed to be related to variation in the relative masses of some highly active organs (notably the heart, liver and kidney) (Daan et al. 1989), as have the seasonal changes in the metabolic rate of a long-distance migrant bird, the knot (*Calidris canutus*, Piersma et al. 1996; Weber and Piersma 1996). However, a recent study by Burness et al. (1998) illustrates that the relationship between body composition and metabolism may vary among species. These authors found that in the tree swallow (*Tachycineta bicolor*), the RMR was not correlated with masses of the same internal organs. In any case, Piersma and Lindström (1997) have recently advocated the view that the body composition of birds, as well as of mammals, is not so invariable as was hitherto believed. Indeed, the relative body composition is highly flexible and may change reversibly depending on changes in the environmental condition and ecological status of the individuals.

Little is known about the influence of relative body composition in determining the ontogenetic development of the metabolic rate in nestling birds. Dietz et al. (1995) compared the growth of several internal organs with the developmental changes in the metabolic rate of three galliform species and concluded that the initial increase in the RMR could be ascribed mainly to increases in the masses of the liver, gut and heart. However, few studies have investigated in detail the relationship in nestlings between organ size and metabolism, so the question of whether differential organ growth during development is responsible for the biphasic development of RMRs in birds is still unresolved. In consequence, the present study aimed specifically at elucidating the involvement of body composition in determining the high mass-specific metabolic rates attained during development in nestlings of the European shag.

Materials and methods

The study was carried out during the breeding season of 1994 on Sklinna (65°12′N, 11°00′E), a small island off the west coast of central Norway. The colony of European shags on this island comprised approximately 1000 breeding pairs in 1994 (Lorentsen 1994). As part of a broader study on the development of the shag, we visited part of the colony daily during the breeding season and noted the hatching dates of all the chicks.

For the present study, 16 chicks 15 days old (day of hatching termed day 0) were brought from the colony to a nearby field-laboratory, where the metabolic measurements were made. Rates of oxygen consumption ($\dot{V}O_2$) were measured using open flow-through respirometry. Outside air was dried over silica-gel and drawn through an approximately 9-l temperature-controlled metabolic chamber with a flow rate of approximately 2–3 $l\,min^{-1}$. Actual flow rates were measured with a calibrated flowmeter (Gilmont, size 2). The effluent air was dried over silica-gel and the oxygen concentration measured with an oxygen analyser (Servomex, type 244A). The oxygen analyser was calibrated using dry outside air (set to 20.95% oxygen) and pure stock nitrogen. Measurements of $\dot{V}O_2$ were first obtained within the thermoneutral zone (TNZ), which, from other tests, had been found for 15-day-old shag chicks to extend down to an ambient temperature (T_a) of about 25 °C (C. Bech and J.E. Østnes, personal observation). During the metabolic runs at thermoneutrality, we selected an initial T_a of approximately 29–30 °C, which was thus well within the TNZ. After 2–3 h exposure to this temperature, the T_a was gradually lowered, at a rate of approximately 0.25 $°C \cdot min^{-1}$. When the T_a reached the lower critical temperature, the chicks responded by increasing their oxygen uptake until the maximum metabolic rate was reached, after which both body temperature (T_b) and $\dot{V}O_2$ decreased. The experiment was then terminated and the chicks were taken out of the metabolic chamber. The total time that elapsed between the chicks being placed in the metabolic chamber and the termination of the experiments was 5–6 h. The instantaneous $\dot{V}O_2$ was calculated using the procedure of Niimi (1978) and formula 3a given by Withers (1977). The RMR was calculated from the lowest 10-min running average value of instantaneous $\dot{V}O_2$ during exposure to thermoneutral conditions. The PMR was similarly calculated from the highest 5-min running average value of instantaneous $\dot{V}O_2$ recorded during cold exposure. Metabolic rates, expressed in W, were calculated from the $\dot{V}O_2$, using a conversion factor of 20.1 kJ l^{-1} O_2 and assuming a respiratory exchange ratio (R_E) of 0.79. Any deviation between this assumed value and the actual R_E for the chicks would only influence the absolute values of the metabolic rates, not the residual values calculated. The factorial aerobic scope was calculated as the PMR divided by the RMR (IUPS 1987).

To record their T_b during the metabolic experiments, the chicks were fitted with a copper-constantan thermocouple (California fine wire, type 0.005) enclosed by polypropylene tubing (PP50), and inserted approximately 5 cm into the colon. The T_a was recorded using a similar thermocouple placed inside the metabolic chamber.

All readings of T_a and T_b as well as the voltage output from the oxygen analyser, were stored at 1-min intervals on a datalogger (Grant Squirrel, 12-bit, Type 1203). The data were later transferred into a computer for analysis.

Immediately after the completion of the metabolic experiments, the chicks were killed, weighed, and stored in air-tight plastic bags at a temperature of −20 °C until they were finally processed at the Department of Zoology in Trondheim. All dissections were made within 6 months of nestling collection. In order to minimise water evaporation, the dissections were made while the carcasses were still in a semi-frozen condition. First, the following body components were dissected out: breast muscles and leg muscles (both muscles were obtained from the right side only; total muscle mass was calculated by doubling this value), liver and heart. Thereafter, the stomach content was removed (and weighed) to obtain the true (wet) body mass. The total length of the intestine (including the duodenum, the ileum and the rectum) was then measured to the nearest 0.5 cm. All the adherent minor organs and fat were removed before the intestine was cut open and the contents removed. It was then rinsed in water and blotted dry on paper before being weighed. The heart was similarly cut open and the blood removed, whereafter it was rinsed in water and likewise blotted dry on paper. Lastly, the kidneys was taken out. All the body components were placed in tared aluminium pans and immediately weighed on a Mettler balance with an accuracy of 0.001 g. The organ components were then dried at a constant temperature of 55 °C until stable weights were attained and the masses then recorded.

Each of the dried components was placed into a filter bag. These were stitched up and weighed to the nearest 0.001 g before being placed in buckets containing a 5:1 mixture of petroleum ether and chloroform, to extract the fat. This solvent mixture mainly removes the stored lipids (triacylglycerols). However, some structural lipids (phospholipids) are also extracted, but very little non-lipid material (Dobush et al. 1985). After lipid extraction, the bags were dried at 55 °C before being re-weighed. Lipid contents were determined from the difference in the masses of the filter bags before and after the extraction process.

Values are presented as means ±1 SD and $n = 16$ in all cases. Obviation of body mass as a complicating factor was achieved by only using residual values in the correlations. For each individual, we calculated the residual values of the metabolic rates and body components as [(measured value) − (predicted value)]/(predicted value)·100, in which the predicted value was obtained from the linear regressions of log total body mass and log value of either the metabolic rate or the body component in question. All the statistical analyses were performed using SigmaStat software (version 1.0, Jandal Scientific, Germany). Significance was assumed when $P < 0.05$.

Results

During the measurements of RMR the chicks had a mean T_b of 39.4 °C (SD = 0.5, range 38.0–40.2 °C), while their mean T_b during PMR had decreased to 38.0 °C (SD = 0.9, range 35.6–38.8 °C). The T_as at which RMR and PMR were measured were 28.1 °C (SD = 1.7, range 22.8–29.6 °C) and 17.1 °C (SD = 4.2, range 12.3–24.0 °C), respectively.

The body masses of the nestlings were corrected for the stomach contents, which on average was 19.3 g (SD = 13.5, range 7.0–48.5 g). The total wet body mass of the 16 nestlings varied between 308.2 g and 583.6 g, with a mean mass of 413.6 g (SD = 70.0, Table 1). The amount of food in the stomach was not correlated with body mass ($P = 0.99$).

The mean RMR value was 5.75 W (SD = 1.64, range 3.00–8.63 W), while the mean PMR value was 9.08 W (SD = 2.98, range 4.87–14.54 W), resulting in a mean value for factorial aerobic scope (PMR/RMR) of 1.58. Expressed in rates of oxygen consumption, RMR and PMR were on average 16.8 ml min^{-1} (SD = 4.8, range 9.0–25.2 ml min^{-1}) and 26.4 ml min^{-1} (SD = 8.8, range 14.2–44.6 ml min^{-1}), respectively. Both RMR and PMR were significantly correlated with body mass. The relationship between body mass and RMR (Fig. 1) is described by the eq. $RMR(W) = 0.040 \cdot mass(g)^{1.00}$ ($r^2 = 0.33$, $P < 0.05$, SE of exponent 0.38), while the relationship between body mass and PMR is described by the eq. $PMR(W) = 0.00115\ mass(g)^{1.48}$ ($r^2 = 0.58$, $P < 0.001$, SE of exponent 0.34). The exponents of these two relationships do not differ significantly (large overlap in mean values ± 2SE).

RMR and PMR were highly interrelated, which is obvious from a visual inspection of Fig. 1. Thus, residual RMR was highly correlated with residual PMR ($r^2 = 0.77$, $P < 0.0001$). However, since the PMR can also be assumed to include the RMR, we also considered it pertinent to evaluate the relationship between the residuals of RMR and the residuals of the factorial aerobic scope. As there is no significant relationship between these two variables ($r^2 = 0.19$; $P = 0.09$), we concluded that the ability of shag nestlings to increase their metabolic rate by a certain factor above the resting level does not depend on the level of the RMR itself. The residual RMR was not correlated with stomach content ($r^2 = 0.15$, $P = 0.14$).

The body composition values for the shag nestlings are given in Table 1. Since the coefficients of variation for the dry components did not differ from those of the wet components, we used the wet component values in all the further analyses and for calculating the residual values. Most body components had coefficients of variation which were of the same magnitude as that found for total body mass, the exception being the length of the intestine. The coefficient of variation of this parameter was notably lower compared to that of the body mass (Table 1). This point is further emphasised when allometric relationships for the different body components were compared (Table 2). The allometric exponents of

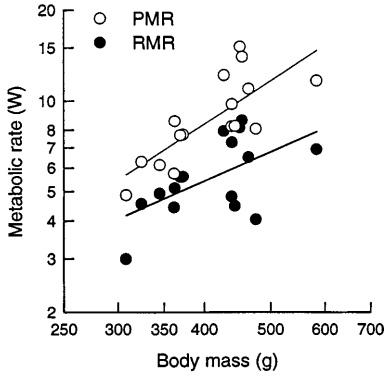

Fig. 1 Resting metabolic rates (thermoneutral, *RMR*) and peak metabolic rates (cold-induced, *PMR*) (*W*) as a function of body mass in 15-day-old European shag nestlings

Table 1 Body mass and body composition of 15-day-old European shag nestlings ($n = 16$). CV is the coefficient of variation

Parameter	Mean	SD	Range	CV
Body mass (wet, g)	413.6	70.0	308.2–583.6	16.9
Total water (g)	327.1	52.8	251.0–453.2	16.1
Total fat (g)	13.4	3.8	6.0–21.2	27.4
Lean dry mass (g)	73.2	14.4	51.2–109.2	19.2
Breast muscles				
Wet mass (g)	8.50	1.92	5.70–14.61	22.6
Dry mass (g)	1.14	0.28	0.73–2.01	24.6
Water content (%)	86.6	0.8	85.2–87.5	0.9
Leg muscles				
Wet mass (g)	38.41	7.45	26.19–59.64	19.4
Dry mass (g)	6.59	1.44	4.36–10.68	21.9
Water content (%)	82.9	0.8	81.5–84.8	1.0
Heart				
Wet mass (g)	6.42	1.07	4.82–8.35	16.7
Dry mass (g)	1.22	0.22	0.88–1.58	18.0
Liver				
Wet mass (g)	32.64	6.24	22.28–46.89	19.1
Dry mass (g)	7.76	1.45	5.02–11.17	18.7
Intestine				
Length (cm)	117.3	8.7	100.0–128.5	7.4
Wet mass (g)	13.48	2.11	10.41–19.09	15.6
Dry mass (g)	2.14	0.38	1.58–3.11	17.8
Kidney				
Wet mass (g)	12.48	2.30	9.01–16.56	18.4
Dry mass (g)	2.06	0.37	1.55–2.70	18.0

breast and leg muscles, heart, liver, kidney, and intestine masses did not differ significantly differ from 1.0 indicating an isometric variation for all these components. Thus, the variations in these components are in direct proportion to the variation in total body mass. On the other hand, the length of the intestine, in line with the lower coefficient of variation, showed a much lower allometric exponent (Table 2).

The exponent for the relationship between total dry mass and total wet body mass was significantly higher than 1.0, whereas the exponent for the relationship between water content and body mass was significantly lower than 1.0 (Table 2). Thus, the larger hatchlings had a proportionately lower fractional water content, indicating a generally higher degree of maturity. This was true also after correcting for lipid mass; thus, the larger chicks had a lower proportional water content per fat-free wet mass. When calculating the correlations of the water contents of the different body components to body mass, we found that only those of the heart and the leg muscles changed significantly, and negatively, with total body mass ($P < 0.05$ in both cases). Both the heart and leg muscles, therefore, were functionally more mature in the larger chicks. However, the residual water contents of both muscle groups were not significantly correlated with the residual metabolic rates (either RMR or PMR).

RMR residuals were significantly correlated with residual wet liver mass (Fig. 2) and residual intestinal length (Fig. 3), whereas the PMR residuals were only significantly correlated with residual intestinal length (Fig. 3). None of the residual values for other body components were correlated with either RMR or PMR. This is further emphasised by the allometric relationships found between the body components and the metabolic rates (Table 3). It is evident from an inspection of these relationships that both the wet liver mass and the intestinal length proved to be better predictors (higher r^2-values) of the variations in the RMR, than was the total wet body mass. For PMR, similarly, intestinal length was a better predictor than the body mass. A stepwise regression analysis with all absolute values of body components and intestine length as independent values of RMR revealed that only liver mass was significantly correlated with RMR and explained 56% of the variation. A similar analysis of the PMR revealed that only intestinal length was significant and explains 59% of the variation in PMR.

Discussion

The average RMR for 15-day-old shag nestlings in the TNZ was as much as 250% of the expected basal metabolic rate for an adult non-passerine bird (Aschoff and Pohl 1970). Despite this very high RMR, the nestlings were still not homeothermic, mainly due to their low metabolic scope (average PMR being only 1.58 times the average RMR) and their low thermal insulation at 15 days of age (C. Bech and J.E. Østnes, personal observation). The lack of effective homeothermy is further illustrated by the mean T_a (17.1 °C) at which PMR occurred, which was higher than the T_as (5–15 °C) to which the chicks are normally exposed in the colony

Table 2 Allometric regressions ($y = a \cdot x^b$) of log component mass on log body mass (g wet mass; $n = 16$). Also shown: the 95% confidence interval (95% CI) of the estimated slope (b), the correlation coefficients (r) and the significance levels (P) of the correlations

Parameter	log a	b	95% CI	r	P
Total dry mass (g)	−1.190	1.19	1.07–1.31	0.984	< 0.0001
Total water (g)	0.0266	0.95	0.92–0.98	0.998	< 0.0001
Total fat mass (g)	−2.670	1.45	0.81–2.09	0.770	< 0.001
Total lean dry (g)	−1.180	1.16	1.09–1.23	0.993	< 0.0001
Breast muscles (g)	−2.070	1.15	0.86–1.43	0.905	< 0.0001
Leg muscles (g)	−1.211	1.07	0.85–1.28	0.936	< 0.0001
Heart (g)	−1.454	0.86	0.57–1.16	0.842	< 0.0001
Liver (g)	−1.099	1.00	0.66–1.34	0.841	< 0.0001
Intestine (g)	−1.044	0.83	0.59–1.07	0.880	< 0.0001
Intestine (cm)	1.241	0.32	0.13–0.51	0.670	< 0.005
Kidney (g)	−1.635	1.04	0.78–1.30	0.904	< 0.0001

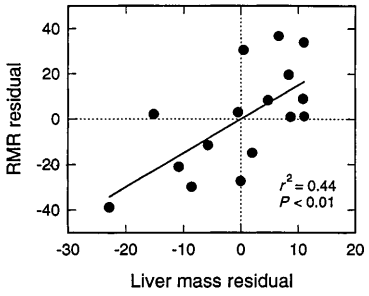

Fig. 2 Relationship between liver mass residuals and residuals of *RMR* in 15-day-old European shag nestlings

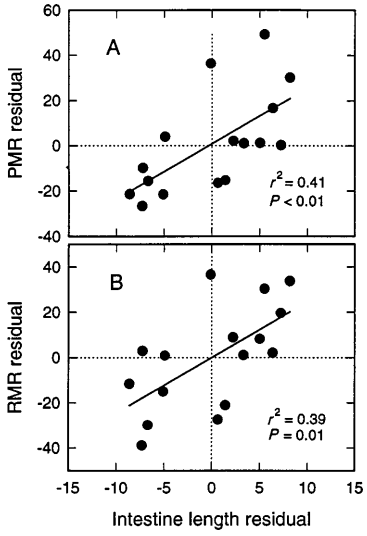

Fig. 3 Relationship between the residuals of intestine length and residuals of **A** *PMR* and **B** *RMR* in 15-day-old European shag nestlings

during the nestling period. At an age of 15 days the nestlings are thus still dependent on parental brooding. However, the nestlings will normally become homeothermic within the following week of development, due to both an increased metabolic scope and increased thermal insulation (C. Bech and J.E. Østnes, personal observation).

The main question with which the present study was concerned was to find a possible explanation for the high RMR value recorded during development. For chicks that are being fed regularly during their development, the heat increment of feeding (HIF) could potentially represent an important factor in this respect. HIF is defined as the 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 [see recent discussions in Janes and Chappell (1995) and Chappell et al. (1997)]. In the present study, we did not fast the chicks before they were used in the experiments, and consequently, we need to consider the possible effects of HIF in our measurements. However, because the actual time that elapsed between the collection of chicks in the field and the recording of metabolic rates during the experiments was 4–6 h, the shag nestlings experienced food deprivation for at least this length of time. Although we can not entirely rule out the possibility that there has been an effect of HIF in our experiments, and that the HIF may have had an influence on the levels of the recorded metabolic rates, there are two reasons why we do not consider HIF to have had any significant influence on the present results. Firstly, because of the experimentally imposed food deprivation time, the chicks would have digested most of their stomach and gut contents by the time the metabolic measurements were made. Secondly, we did not find any correlation between stomach-content and residual metabolic rate. If the heat increment of feeding had been affecting the metabolic rate, those chicks with the greatest stomach content values, assuming these to parallel the intestine content, should have had the highest metabolic rates, when the variation in body mass was accounted for. Hence, we consider that any effect of HIF will have been of only minor consequence in

Table 3 Allometric regressions ($y = a \cdot x^b$) of log metabolic rate (W) on log body component. Also shown: the fractions of variation (r^2) in RMR and PMR explained by the body component, and the significance levels (P) of the correlations. For all relationships, $n = 16$. Except where stated otherwise organ mass refers to wet mass

Parameter	RMR				PMR			
	log a	b	r^2	P	log a	b	r^2	P
Total wet body mass	−1.40	1.00	0.33	< 0.05	−2.94	1.48	0.58	< 0.001
Total dry body mass	−0.46	0.87	0.36	< 0.02	−1.41	1.22	0.57	< 0.001
Total lean dry mass	−0.41	0.88	0.34	< 0.02	−1.43	1.27	0.57	< 0.001
Total lipid mass	0.64	0.52	0.32	< 0.05	0.24	0.63	0.38	< 0.02
Total body water	−1.36	1.03	0.31	< 0.05	−2.95	1.55	0.58	< 0.001
Breast muscles	0.50	0.78	0.32	< 0.05	−0.06	1.08	0.50	< 0.01
Leg muscles	0.19	0.65	0.18	n.s.	−0.68	1.02	0.36	< 0.02
Heart	0.51	0.89	0.27	< 0.05	−0.06	1.25	0.43	< 0.01
Liver	−0.54	1.16	0.62	< 0.001	−1.05	1.32	0.64	< 0.001
Intestine	0.10	1.00	0.29	< 0.05	−0.57	1.34	0.42	< 0.01
Intestine length	−4.59	2.81	0.58	< 0.001	−6.17	3.44	0.70	< 0.0001
Kidney	0.28	0.86	0.32	< 0.05	−0.47	1.29	0.59	< 0.001

accounting for the observed variation in the metabolic rates of the shag nestlings.

Having ruled out HIF as a major contributor to the high and variable RMR in the shag nestlings, we can now pose the question: what is the role of body composition in determining the RMR level? Recently, Lilja (1997b) has measured the metabolic rate and organ masses of Japanese quail (*Coturnix coturnix japonica*) chicks during growth. He found that the metabolic rate changed in direct proportion to the changes in the combined masses of heart, liver, kidney and intestine, and concluded, therefore, that these organs had a significant influence on the RMR of the growing chicks. However, his argument was based on direct comparisons and similarities between the allometric exponents. A potentially complicating effect of total body mass, which inevitably influences both metabolic rate and the organ masses, was not accounted for. In the present study, in contrast, we used the residual values (i.e. values independent of body mass variations) when calculating our correlations. The main result derived from our study was that the RMR-residuals were influenced only by those for liver mass and the intestinal length (Figs. 2, 3). Similarly, Dietz et al. (1995) compared the 'breakpoint' of the biphasic development in the RMR with the breakpoint of several internal organs during growth in the Japanese quail, the Guinea fowl (*Numidia meleagris*) and the turkey (*Meleagris gallopavo*). These authors found that the breakpoint in the development of the digestive organs (gut and liver) roughly coincided with the breakpoint in the metabolic rate. They also pinpointed the heart as an important organ in relation to the initial increase in the metabolic rate. These results thus concur to some extent with the results of the present study, in that both studies suggest a significant contribution from the intestine and the liver. However, our results do not support the view that the RMR in chicks is influenced by heart mass. Also, a subsequent reanalysis of the data of Dietz et al. (1995) using multiple regression analyses has revealed that the liver mass explained most of the variation in RMR in Guinea fowls and turkeys (M. Dietz, personal observation). Both studies seem to provide support for the view that the RMR level of growing birds is not influenced by their heart and kidney masses. This is in contrast to the results of studies in adult birds, in which the combined kidney and heart mass has been shown to be the best predictor of the basal metabolic rate (Daan et al. 1989, 1990; but see Burness et al. 1998). Also, in a similar recent study of a mammal, the field vole (*Microtus agrestis*), heart mass proved to be a better predictor of the RMR than the body mass (Meerlo et al. 1997).

The apparent difference between chicks and adult birds in the way their organ masses influence their metabolic rates, is further illustrated by a comparison of the relative sizes of the organs in adults and nestlings. While the liver mass accounts for 7.9% of the total body mass of a 15-day-old nestling (Table 1), the liver of adult shags constitutes only 4.9% (C. Bech and J.E. Østnes, personal observation). Likewise, the intestine of a 15-day-old nestlings had already reached a length of 80% of that of the adult shag (146 cm, $n = 2$; C. Bech and J.E. Østnes, personal observation), in spite of the nestling body mass being only 22% of that of the adult (1918 g; $n = 2$). These comparisons support the view that the high RMR values of the shag nestlings are related to a rapid growth of the intestine, in combination with a relatively high liver mass.

The significant correlations found between the metabolic rates (both RMR and PMR) and intestinal length observed in the present study (Fig. 1) is especially noteworthy considering the much lower variation in intestinal length found in comparison with the mass variations of the other organs studied (Table 1). The lesser degree of variation, combined with a mass-exponent considerably less than 1.0 (Table 2), indicates that the growth of the intestine is primarily linked to chick age, rather than to body mass as such. The implication of this is that the intestine might have been growing at its maximal rate; a growth rate which then is relatively independent of the overall growth rate of the chick. This rapid initial growth of the intestine (C. Bech and J.E. Østnes, personal observation show that the intestine grows in length at an amazing rate of more than 6 cm per day during the first 15 days after hatching), supports the view that allocation of energy into the development of the gastrointestinal system is of prime importance during early development, presumably to achieve a high energy assimilation capacity and hence to promote a subsequent rapid growth rate (Lilja 1983, 1997a; Konarzewski et al. 1989, 1990; Obst and Diamond 1992). Nestlings of precocial species may differ from those of altricial species (such as the shag), in that precocial species need to prioritise growth of the locomotor apparatus immediately after hatching. In consequence, the digestive apparatus needed for nutrient uptake and processing needs either to be already present at hatching time in precocial species (Jackson and Diamond 1995) or, alternatively, the growth of the gut may be optimised with respect to other functions than growth, e.g. mobility (Ricklefs et al. 1998).

The relationship between intestinal length and metabolic rate could be direct or indirect. Although there is evidence that intestinal activity may contribute significantly to the energy budget of animals (Cant et al. 1996), it seems more likely that intestinal length is an indirect reflection of a high nutritional uptake and, in consequence, a large liver. This is supported by a comparison of the shag nestling's intestinal mass, which is only 3.3% of the total wet mass, as opposed to the liver mass, which is 7.9% (Table 1). Although one should be careful not to underestimate the impact of small organs (because organs may differ greatly in metabolic intensity), the liver is known to have a high intrinsic heat production (Krebs 1950; Scott and Evans 1992) and to undergo proliferation, or atrophy, in response to changes in energy intake (Goodman and Ruderman 1980; Hammond et al. 1994). Consequently, the variations in the RMR of

the shag nestlings are probably mainly attributable to variations in liver size, which itself is a reflection of the degree of intestinal development.

A final question remains: where is the extra heat induced during cold exposure being produced? The absence of any relationship between the residual PMR and the residuals of any of the internal organs (except intestinal length), suggests that none of the organs (including the liver) play any significant part in cold-induced heat production. Birds are generally believed to rely mainly on muscular shivering for heat production during cold exposure, although this paradigm recently has been thrown into debate and some studies appear to indicate that birds may also be capable of non-shivering thermogenesis (e.g. Duchamp et al. 1993; Marsh 1993). The relative functional maturity of the leg and breast muscles of the shag nestlings would seem to suggest that they possess the ability for shivering heat production only in the leg muscles and not in the breast muscles. This is based on the suggestion that a minimal level of maturity has to be attained (corresponding to a muscular water fraction of less than 0.85), before the muscles can contribute to shivering thermogenesis (Dietz et al. 1997), and is in line with the general view that in hatchlings the leg muscles are generally the first muscle group to develop a significant shivering thermogenesis (Hohtola and Visser 1998). However, even though the mean water content of the leg muscles of the shag nestlings (82.9%; Table 1) is below this 'functionality level', the leg muscle mass was not correlated with the PMR. On the other hand, the significant negative relationship found between body mass and the water content of the leg muscles suggests that the larger nestlings had functionally more mature leg muscles. In addition, the overall lower fractional water content of larger chicks suggests a more general maturity. It is thus plausible that the heat-producing ability during cold exposure is more a function of muscle maturity than of their absolute mass. For the 15-day-old European shag nestlings, it would thus seem that the variation in growth rate, which inevitably must have preceded the wide variation in body mass that we recorded at this age, has resulted in the larger chicks being able to allocate more energy into the maturation of the heat-producing muscles, rather than to a hypertrophy of the musculature in general. This scenario, however, might have proved to be different if other age-groups had been tested; our results do not provide any immediate explanation as to where the cold-exposure-induced heat production occurred.

In conclusion, we have shown that 15-day-old shag nestlings have a very high RMR, which seems to be a reflection of a high activity of the 'supply organs', notably the liver and the intestine. PMR, however, was only related to intestinal length. Our results do not provide evidence for the particular origin of cold-induced thermogenesis, although it seems likely that a higher functional maturity of the leg muscles in the larger chicks may be involved.

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