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RELATIONSHIP BETWEEN BODY COMPOSITION AND HOMEOTHERMY IN NEONATES OF PRECOCIAL AND SEMIPRECOCIAL BIRDS

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ABSTRACT.—We dissected carcasses of neonates belonging to ducks and geese (Anatidae; 8 species), shorebirds (Charadriidae and Scolopacidae; 12 species), gulls and terns (Laridae; 3 species), and nonanseriform water birds (Podicipedidae and Rallidae; 2 species) ranging in yolk-free lean wet body mass from 2.5 to 70 g. We have fitted allometric relationships between the lean wet mass of each component and the lean wet yolk-free neonatal body mass. The exponents of the relationships of the brain mass (0.73) or head mass (0.85) to neonatal body mass were significantly lower than 1. The exponents did not differ significantly from 1 for the heart, whole leg, leg bone, liver, intestines, pectoral muscles, skin, stomach, wings, feathers, yolk (wet and dry), and remainder of the body. The exponent for leg muscle mass (1.18) was significantly higher than 1. This suggests that larger chicks may have a higher potential for thermogenic heat production. At a given body mass, no differences could be detected with respect to the lean fresh leg muscle mass among ducklings, shorebirds, and the nonanseriform water birds. However, the high fractional lipid-free dry lean matter content of the leg muscles of ducklings (which might represent a high amount of contractile proteins in these muscles) could explain their observed high thermogenic heat production in response to cold stress. The exponents of feather mass and lean wet skin mass to body mass were significantly higher than 0.67 (i.e. surface-to-volume relationship of a sphere), in accordance with our previous finding that large neonates have a relatively lower minimal thermal conductance per unit surface area than smaller chicks. *Received 30 July 1993, accepted 16 December 1993.*

AFTER HATCHING, CHICKS of precocial and semiprecocial species are not fully homeothermic and often need to be brooded by a parent, especially at low ambient temperatures (e.g. Beintema and Visser 1989, Visser et al. 1989). The time the chicks spend being brooded is unavailable for feeding, for the chick as well as for the parent. From the standpoint of foraging time, it is advantageous for neonates to have a high degree of homeothermy. However, this also incurs costs in the form of higher catabolic requirements of the chicks (e.g. Ricklefs 1989, Visser and Ricklefs 1993a) and, perhaps, slower postnatal growth rate resulting from greater functional maturity of tissues (Ricklefs 1979, Ricklefs and Webb 1985). The observed level of homeothermy in the neonate reflects a balance of these costs and benefits.

In a comparison of the degree of homeothermy in precocial (i.e. self-feeding) and semiprecocial (i.e. mobile but parentally fed) neonates, Visser and Ricklefs (1993a) demonstrated that for each taxonomic unit large neonates are more homeothermic than small neonates. In addition, they showed that at a given neonatal body mass ducklings (Anatidae) have the highest degree of homeothermy, grouse and pheasants (Phasianidae) are intermediate, and shorebirds (Charadriidae and Scolopacidae) and gulls and terns (Laridae) exhibit the lowest degree of homeothermy. A comparison of metabolic rates of these neonates suggested that the following mechanisms determine the degree of homeothermy: (1) larger chicks have a more favorable ratio of heat production (i.e. peak metabolic rate under cold stress) to heat loss (minimal thermal conductance); (2) at a given body mass, species of ducks have a higher rate of cold-induced heat production than others; and (3) at a given body mass, shorebirds exhibited a higher minimal

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thermal conductance (i.e. a lower insulative capacity).

We investigated the underlying morphological basis of differences in the degree of homeothermy among neonatal birds belonging to different families. Our comparison involved 25 species in four taxonomic orders (Podicipediformes, Anseriformes, Gruiformes, and Charadriiformes). Because neonates of precocial and semiprecocial species generate heat primarily by shivering of the muscles of the leg (e.g. Choi et al. 1993), we focused on the relative size and degree of functional maturity of these muscles, which might influence peak metabolic rate. In addition, we examined differences in the down covering of the neonate in relation to thermal conductance. Finally, we characterized the energy and water reserves of the neonate in the yolk and adipose tissue in relation to metabolic requirements, to estimate the allometry of survival time of neonates under adverse weather conditions.

Methods

Species studied.—We obtained carcasses of neonates of four groups of taxa. **Geese and ducks species (Anseriformes):** Northern Pintail (*Anas acuta*; $n = 2$), Mallard (*A. platyrhynchos*; 17), Redhead (*Aythya americana*; 14), Canvasback (*A. valisineria*; 3), Canada Goose (*Branta canadensis*; 4), Oldsquaw (*Clangula hyemalis*; 4), Hooded Merganser (*Lophodytes cucullatus*; 3), Common Eider (*Somateria mollisima*; 3). **Shorebirds (Charadriidae and Scolopacidae):** Dunlin (*Calidris alpina*; 2), Least Sandpiper (*C. minutilla*; 2), Semipalmated Sandpiper (*C. pusilla*; 2), Semipalmated Plover (*Charadrius semipalmatus*; 3), Hudsonian Godwit (*Limosa haemastica*; 5), Black-tailed Godwit (*L. limosa*; 3), Stilt Sandpiper (*Micropalama himantopus*; 5), Whimbrel (*Numenius phaeopus*; 3), Red-necked Phalarope (*Phalaropus lobatus*; 3), Lesser Golden-Plover (*Pluvialis dominica*; 2), Lesser Yellowlegs (*Tringa flavipes*; 1), Northern Lapwing (*Vanellus vanellus*; 2). **Gulls and terns (Laridae):** Herring Gull (*Larus argentatus*; 5), Bonaparte's Gull (*L. philadelphia*; 7), Arctic Tern (*Sterna paradisaea*; 5). **Nonanseriform water birds (Rallidae and Podicepedidae):** American Coot (*Fulica americana*; 4), Eared Grebe (*Podiceps nigricollis*; 4).

We obtained specimens from artificially incubated eggs (Hovabator, Inc., or Pas Reform) at 37°C and a relative humidity of 60%, which resulted in a normal water loss throughout the incubation period (Ricklefs 1984, Visser and Ricklefs 1993a). The Northern Lapwing and Black-tailed Godwit eggs were collected in the vicinity of Utrecht, The Netherlands (52°06'N, 5°07'E), in the summers of 1987-1990 under license from the Ministry of Agriculture. Eggs of all other species were collected in the vicinity of Churchill, Canada (58°45'N, 94°00'W), or at the Delta Waterfowl Research Station, Canada (50°11'N, 98°20'W), in the summer of 1979.

Chicks were killed within 12 h of hatching by cervical dislocation, and weighed to the nearest 0.1 mg. Thereafter, specimens were individually placed in deflated plastic bags and immediately frozen at −20°C until further analysis.

Carcass analysis.—First, frozen chicks were thawed at room temperature. Prior to dissection, we measured the length of the down feathers in the center of the back between and somewhat posterior to the scapulae. The length of the down on the ventral side around the sternum also was measured in most species. As a first step in the dissection, feathers were plucked, and the entire skin was removed. Thereafter, the head was cut at its base, and the brain was removed (the head component is defined here as head minus the brain). Both wings were cut at the shoulders. Next, the peritoneal cavity was opened and the remaining yolk sac was removed. The pectoral muscles on both sides, heart cut at the aorta, liver, stomach (from posterior end of esophagus to exit to small intestine), and intestine were removed. From the remaining carcass one leg was cut at the hip. All leg muscles were removed from the other leg, and the remaining bone, including the foot, was treated as a separate component. The remaining parts of the body were the last component. Throughout this paper the leg-muscle component refers to the mass of the muscles of both legs. Its value was obtained by multiplying the muscle mass of one leg by 2.

After dissection, each organ was immediately placed in a tared aluminum pan and covered with wet paper to minimize evaporative water loss from the organ prior to weighing. The fresh wet mass of each organ was determined on a Sartorius or Mettler analytical balance to the nearest 0.1 mg. The dry mass of each sample was determined after drying the samples in an oven at 60°C to constant mass, generally within 48 h (Kerr et al. 1982). To extract fat, we wrapped the dry components in their pans in cheese cloth and immersed them in a 5:1 mixture of petroleum ether and chloroform for 24 h, followed by a second extraction of 24 h in fresh solvent. Samples extracted in this manner do not lose additional mass upon reextraction in a Soxhlet apparatus (Ricklefs unpubl. data). The procedure used in this study removed both structural and storage lipids. We will treat the total lipid content (storage plus structural) as equivalent to fat reserves. Thereafter, each component was dried again until constant mass to obtain the lean dry mass. Loss of water during processing was estimated by comparing the sum of the fresh masses of the dissected components to preprocessing fresh mass. In general, these losses were less than 5% of the fresh mass for neonates of the smallest species to less than 3% of the largest species. In addition, most of the loss

TABLE 1. Allometric relationships between component mass (mg) and yolk-free lean wet body mass (g) in precocial and semiprecocial neonates.[a]

Component	Exponent ± SE	Intercepts				R^2
		Anseriformes	Shorebirds	Gulls	Other water birds	
Body	1.015 ± 0.0221	251.4[A]	211.2[B]	253.3[A]	251.2[A]	0.995
Bone	1.120 ± 0.0431	39.1[A]	71.4[B]	41.6[A]	43.2[A]	0.978
Brain	0.733 ± 0.0694	87.2[A]	94.4[A]	73.6[A]	73.6[A]	0.908
Head	0.852 ± 0.0516	220.4[A]	224.9[A]	273.5[A]	192.1[A]	0.964
Heart	0.875 ± 0.0782	19.7[A]	14.1[A]	19.2[A]	14.0[A]	0.940
Intestines	0.947 ± 0.0124	40.7[A]	24.4[A]	43.5[A]	55.6[A]	0.893
Leg	1.069 ± 0.0317	91.6[A]	114.4[B]	80.3[A]	79.5[A]	0.991
Liver	1.036 ± 0.0831	33.8[A]	34.2[A]	33.9[A]	25.4[A]	0.937
Leg muscle	1.180 ± 0.0368	56.2[A]	50.6[AB]	41.2[B]	46.8[AB]	0.990
Pectoral muscle	0.919 ± 0.0892	16.8[A]	18.5[A]	18.3[A]	15.0[A]	0.905
Skin	0.991 ± 0.0630	97.5[A]	76.6[A]	88.4[A]	117.0[A]	0.965
Stomach	1.072 ± 0.0503	32.8[A]	30.3[A]	38.0[A]	60.2[B]	0.980
Wing	1.068 ± 0.0681	13.6[A]	18.1[AB]	24.4[B]	16.5[AB]	0.955
Feathers	0.894 ± 0.0693	81.2[A]	47.0[B]	62.0[AB]	46.5[B]	0.959
Lipid (body)[b]	1.091 ± 0.1116	77.7[A]	48.9[AB]	30.3[B]	42.7[AB]	0.925
Lipid (all)[c]	1.170 ± 0.1196	89.9[A]	55.8[AB]	33.7[B]	50.1[AB]	0.924
Yolk (wet)[d]	1.272 ± 0.1688	61.4[A]	59.6[A]	34.7[A]	45.6[A]	0.845
Yolk (dry)[e]	1.350 ± 0.1854	23.8[A]	22.1[A]	11.8[A]	15.8[A]	0.840
Yolk (lipid)[f]	1.504 ± 0.2115	8.93[A]	6.61[A]	3.50[A]	6.67[A]	0.841
Yolk (lean)[g]	1.248 ± 0.1953	13.6[A]	15.4[A]	8.20[A]	8.10[A]	0.788
Yolk (water)[h]	1.215 ± 0.1637	36.5[A]	37.3[A]	23.6[A]	80.4[A]	0.840

[a] Model was: component mass = aM^b (n = 25 species except for leg, where n = 23). Component mass expressed as lean wet mass except for feather component (dry mass) and components mentioned below. Intercept values for given body component with same superscripts do not differ significantly ($P > 0.01$). [b] Lipid content of main body. [c] Lipid content of body and yolk sac. [d] Wet mass of yolk sac. [e] Dry mass of yolk sac. [f] Lipid content of yolk sac. [g] Dry lean matter content of yolk sac. [h] Water content of yolk sac.

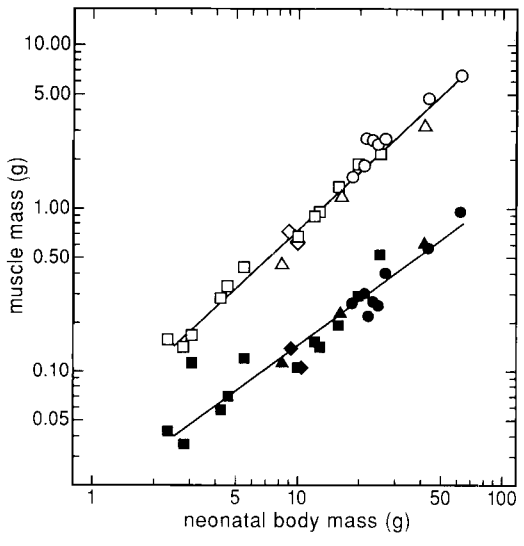

Fig. 1. Scaling of leg (open symbols) and pectoral (solid symbols) muscle mass to body mass in neonates of geese and ducks (circles), shorebirds (squares), gulls and terns (triangles), and nonanseriform water birds (diamonds). Diagonal lines represent average allometric relationships between leg or pectoral-muscle mass and neonatal body mass.

of water was from the carcass, which was exposed during the entire dissection. The muscles and internal organs were either weighed immediately after they were removed or were covered with wet paper to prevent evaporation.

We define the water content of each component as wet mass minus dry mass. The lipid mass is defined as the dry mass minus the lean dry mass, and the lean mass is defined as the wet mass minus the lipid mass. We use yolk-free lean body mass (referred to as body mass) as a standard of body mass for comparisons of different components among species and as a basis for allometric regressions.

Statistical analysis.—First, species-specific averages were calculated for each component. Analysis of covariance (ANCOVA) was used (after logarithmic transformation of component mass and total yolk-free lean wet body mass) to test whether allometric relationships differed significantly among groups (significant taxon × body mass interaction). If this factor was not statistically significant, we deleted it from the model and assumed parallel slopes. The differences in intercepts of the log-transformed values were tested with the "CONTRAST=SIMPLE" option in the MANOVA procedure of SPSS/PC+V3.0, an *a posteriori* test without preplanned comparisons, and the statistics should be evaluated conservatively (Norušis 1988). Therefore, a probability level of 0.01 was taken

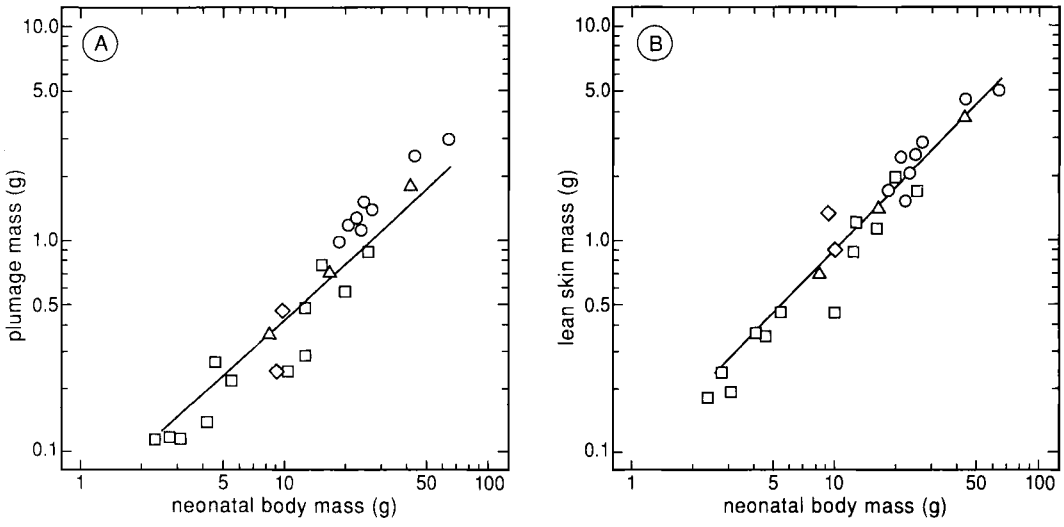

Fig. 2. Scaling of (A) plumage and (B) skin mass to body mass (for explanation of symbols, see Fig. 1). Diagonal lines represent average allometric relationships between plumage or skin mass and neonatal body mass.

to determine statistical significance. We calculated the 99% confidence limits of the slopes to test whether the allometric relationships differ from unity (isometry) or 0.67 (representing a surface-volume relationship).

Results

Scaling of body components to body mass.—We used ANCOVA to investigate the relationship of the sizes of each component (lean wet mass; mg) to body mass (g) of neonates, and whether these relationships differ between taxonomic groups. The analyses revealed that a significant interaction term existed only for the brain (for brain mass $P < 0.004$; for the other organs P-values were between 0.159 and 0.895). Subsequently, we deleted this interaction term from the model for all components (assuming a common exponent), including the brain, and tested the differences in intercepts among taxonomic groups (Table 1).

The entire model explains between 84 and 99% of the variance in component mass (Table 1). In large neonates the brain and the head are disproportionally small (exponent significantly smaller than 1). The following organs scale isometrically with body mass (exponent does not differ significantly from 1): body, heart, intestines, whole leg, leg bone, liver, pectoral muscle, skin, stomach, wing, feathers, and yolk (wet and dry). In large neonates the leg muscles are relatively large (exponent significantly greater than 1). In parallel with differences in the morphology of adults of these species, the masses of the whole leg, as well as the bone of the leg, were significantly higher for shorebird neonates compared to those of the other groups.

Scaling of leg and pectoral-muscle mass to body mass.—At a given body mass, the lean wet mass of the leg muscle is much higher than of the pectoral muscles (Fig. 1). The intercept of the allometric relationship for the leg muscle component was significantly lower for gull neonates than for duck neonates (Table 1). With respect to the allometric scaling of the leg muscle component, no differences were found between duck neonates, shorebirds, and the other nonanseriform aquatic birds (Fig. 1). Additionally, we were unable to detect significant differences among the four groups with respect to the pectoral-muscle mass (Fig. 1). ANCOVA revealed that both exponents for the relationships between wet pectoral-muscle mass and body mass, and between wet leg muscle mass and body mass differ significantly (interaction term organ type × body mass, $F_{1,46} = 19.69$, $P < 0.0001$). On average, in a 3-g neonate the leg muscles are 3.8 times as heavy as the pectoral muscles, and in a 70-g neonate 8.6 times.

Scaling of skin and plumage mass to body mass.—The allometric relationships for the mass of down feathers and the skin mass are shown in Figure 2. The exponents for the separate rela-

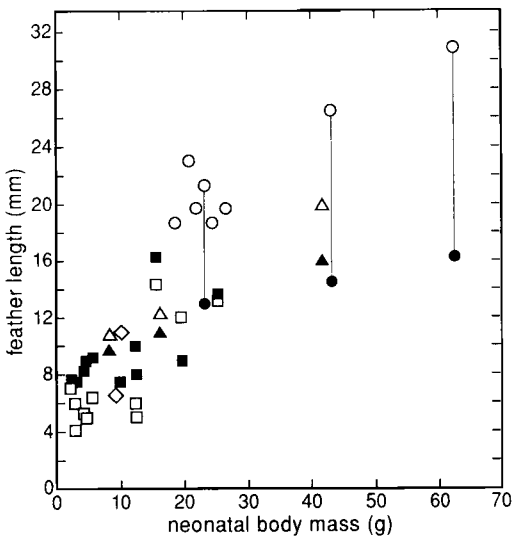

Fig. 3. Scaling of length of dorsal (open symbols) and ventral (solid symbols) feathers to body mass (for explanation of symbols, see Fig. 1). Values for dorsal and ventral feather lengths for three duck species are connected by vertical lines.

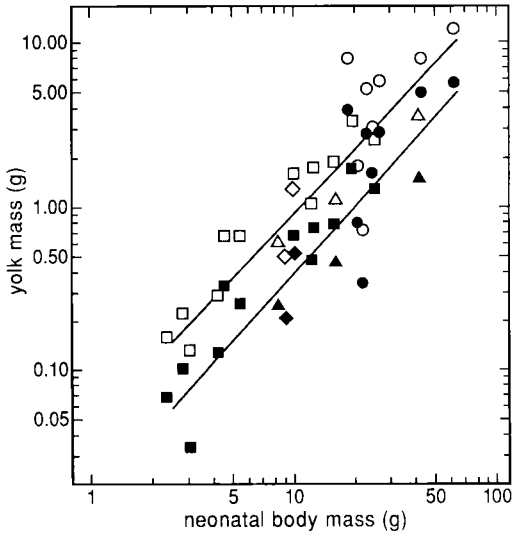

Fig. 4. Scaling of wet (open symbols) and dry (solid symbols) yolk mass to body mass (for explanation of symbols, see Fig. 1). Diagonal lines represent average allometric relationships between wet or dry yolk mass and neonatal body mass.

tionships between plumage mass and the skin mass to neonatal body mass were both significantly larger than 0.67 (surface-to-volume ratio of a sphere). Thus, larger neonates have a higher plumage and skin mass per unit of surface area. This result is consistent with the finding of Visser and Ricklefs (1993a) that larger neonates have lower surface-area-specific minimal thermal conductances than smaller neonates. The intercept for feather mass of shorebird neonates was significantly lower than that for duck neonates (Table 1). This also is consistent with the finding of Visser and Ricklefs (1993a) that the minimal thermal conductance per unit surface area of shorebirds was higher (and the insulation per unit of surface lower) than that of ducks.

Although the data set on the length of the down feathers at the dorsal (of all species) and ventral side (of 17 species only) is of limited size, it is evident that the respective lengths of down feathers on the dorsal and ventral surfaces of chicks differ in ways that vary among groups (Fig. 3). Especially, duck neonates have longer down feathers on the dorsal side of the chick as compared to the ventral side. We analyzed the ratios of dorsal and ventral feather lengths for the 17 species belonging to three taxonomic groups (ducks on average have dorsal-to-ventral length ratios of 1.79, shorebirds of 0.82, and gulls and terns of 1.16) with ANOVA. There were significant differences among the three taxonomic groups ($F_{2,14} = 27.1$, $P < 0.0001$). The relatively long dorsal down feathers in ducklings may be related to differences in the physical characteristics of plumage exposed to water and air. In contrast, in the Charadriidae (Northern Lapwing, Lesser Golden-Plover, and the Semipalmated Plover), the length of the downy feathers on the dorsal side is much shorter than on the ventral side (dorsal-to-ventral length ratio 0.6). The maximum length of the downy plumage is probably limited by its ability to remain in an upright position. Additionally, especially in small chicks, the maximum length of the downy plumage is limited because long down feathers increase the effective surface area of the chick and, thus, the heat transfer between the chick and its environment (Turner 1988).

Scaling of yolk mass to body mass.—Slopes of the allometric relationships for the wet (1.272) and dry (1.350) yolk masses exceeded unity, but not significantly (Table 1, Fig. 4). Thus, small and large neonates appear to have proportionately the same yolk reserve (4.9% of body mass for wet yolk, and 1.8% for dry yolk). We were unable to detect statistical differences for the

TABLE 2. Composition of yolk sac (water, lipid and dry lean mass; mg) in relation to fresh yolk mass (g).[a]

Factor	Exponent ± SE	Intercepts				R^2
		Anseriformes	Shorebirds	Gulls	Other water birds	
Water	0.954 ± 0.0213	559[A]	525[A]	550[A]	584[A]	99.3
Lipid	1.157 ± 0.0720	214[A]	236[A]	184[A]	188[A]	96.0
Lean	1.020 ± 0.0320	206[AB]	198[A]	248[B]	219[AB]	98.8

[a] Model was: component mass = aM^b (n = 25 species). Intercept values for same factor with same superscripts do not differ significantly ($P > 0.01$).

intercepts for the four groups, although the yolk masses of ducks and shorebirds exceeded those of gulls and nonanseriform water birds (i.e. American Coot and Eared Grebe), which are fed by their parents through at least the first two weeks after hatching.

We compared the composition of the yolk sac (water, lipid, and dry lean matter content) in relation to fresh total yolk mass (after logarithmic transformation of each component and fresh total yolk mass) among neonates of the four taxonomic groups using ANCOVA (Table 2). For none of the components (water, lipid, and dry lean matter content) did the exponent differ significantly from 1. The allometric-scaling coefficients did not differ significantly among the different taxonomic groups with respect to the water and lipid content. However, at a given yolk mass, the dry lean matter content in shorebird neonates was significantly lower than for gull and tern neonates (Table 2). On the average, yolk for all species consists of 49% water, 29% lipid, and 22% dry lean matter.

Scaling of fat reserves to body mass.—In the neonate, fat reserves are located in the yolk sac, as well as in the body (Table 1). The exponents for the relationships between amount of fat (in yolk sac and in remainder of body, respectively) to body mass were higher than 1 (1.504 and 1.091, respectively), although not significantly. In addition, at a given body mass ducklings have larger fat reserves than chicks of gulls (significant), shorebirds (not significant), and nonanseriform water birds (not significant). We used ANCOVA to test whether the exponent of the relationship between fat mass in the yolk sac and body mass (1.504) differed from the exponent of the relationship between fat mass in the body and body mass (1.091). These exponents did not differ significantly ($P = 0.85$). Assuming a common slope, which had a value of 1.385 ($F_{1,47} = 214.2$, $P < 0.0001$, $s_b = 0.0946$), we found that the intercept was significantly higher for the amount of fat in the body by a factor of 3.35 ($F_{1,47} = 39.2$, $P < 0.0001$, $R^2 = 0.84$). Thus, of all fat reserves present in the neonate 77% is located in the main body and 23% in the yolk sac.

DISCUSSION

Carcass composition in relation to thermogenic capacity.—We presume that, during the course of evolution, an optimal neonatal body composition evolved to fulfill the needs of the precocial and semiprecocial chicks at hatching and during postnatal development. Accordingly, we interpret the observed body proportions of neonates as compromises between costs and benefits of different alternatives (Visser and Ricklefs 1993b). Beintema and Visser (1989) and Visser and Ricklefs (1993a) demonstrated the importance for such chicks of regulating their body temperatures at least to some extent to provide the thermal independence necessary for foraging. Chicks of ducks had a high level of thermal independence compared to shorebirds, galliforms, and semiprecocial chicks fed by their parents (gulls and terns; Visser and Ricklefs 1993a). This mainly resulted from a high peak metabolic rate in duck neonates, which was about 250% of the level observed in pheasants, gulls, and shorebirds. Only the shorebirds had a higher thermal conductance than the other species. Thus, thermal conductance cannot solely explain the differences in homeothermy observed between the taxonomic groups.

The high level of peak metabolic rate as observed in ducklings results from a high metabolic scope (i.e. peak metabolic rate [*PMR*] minus resting metabolic rate). This could result from a high muscle mass per animal, from a high thermogenic capacity per gram muscle mass, or from both. In the neonate, most cold-induced thermogenesis is accomplished by the leg muscles, which are both larger and exhibit a greater level of mature function than pectoral

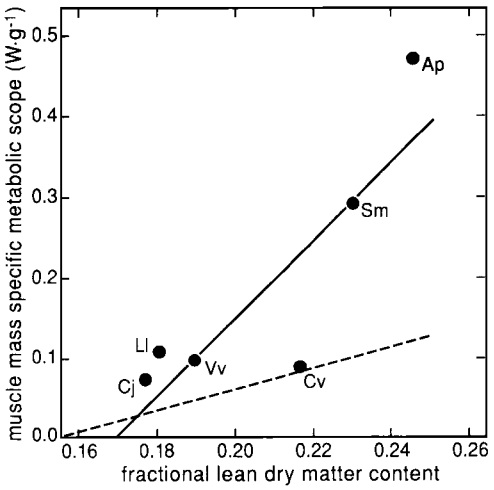

Fig. 5. Muscle-mass-specific metabolic scope in relation to fractional dry lean mass fraction of leg muscles. Values plotted for neonates of Japanese Quail (Cj), Northern Bobwhite (Cv), Northern Lapwing (Vv), Black-tailed Godwit (Ll), Common Eider (Sm), and Mallard (Ap). Diagonal line represents relationship between fractional lean dry-matter content and muscle-mass-specific metabolic scope based on data of six species. Broken line refers to intraspecific relationship for chicks of European Starling throughout their postnatal development (Ricklefs and Webb 1985).

muscles as measured by the shivering intensity (Aulie and Steen 1976, Choi et al. 1993). No significant differences in leg muscle mass could be detected among neonates of ducks, shorebirds, gulls and the other aquatic water birds (Table 1). Therefore, the high metabolic scope of ducklings must result from a much higher mass-specific thermogenic capacity. In Figure 5 we have plotted the leg muscle-mass-specific metabolic scope as a function of the fractional lean dry-matter content of the leg muscles for precocial neonates of six bird species. The data for Japanese Quail (*Coturnix japonica*) and Northern Bobwhite (*Colinius virginianus*) are taken from Choi et al. (1993). The relationship between muscle-mass-specific metabolic scope (Y) and fractional lean dry-matter content (X) can be described by:

$$Y = -0.830 + 0.049X \quad (1)$$

($F_{1,4} = 11.4$, $P = 0.028$, $r^2 = 0.68$, $s_b = 0.0145$). When extrapolating this relationship, the metabolic scope is zero at a fractional lean dry-matter content of 0.17.

Ricklefs and Webb (1985) have demonstrated in growing European Starling (*Sturnus vulgaris*) chicks a positive relationship between muscle-mass-specific metabolic scope and fractional dry-matter content (which might represent a measure for the quantity of contractile proteins in a muscle). Their regression has been entered in Figure 5 for comparison; it differs from the original regression, which was mistakenly based on the muscles from only one side of the body. Ricklefs and Webb's (1985) regression predicts a zero metabolic scope at a fractional lean dry-matter content of 0.15, which is in close agreement with the value of 0.17 found in precocial neonates. However, chicks of both duck species have a much higher metabolic scope than observed in European Starling chicks with a similar fractional lean dry-matter content. This lack of agreement is not surprising, however, because peak metabolic rate, usually measured under conditions of chronic cold stress (longer than 30–60 min), estimates aerobic capacity of the muscle rather than peak power output. Mature, functional muscles can exhibit different patterns of performance, and aerobic capacity may not be simply related to dry-matter content, but also to the presence of different fiber types in the muscle (Choi et al. 1993, Steen et al. 1989).

Yolk sac as an energy reserve.—For the neonate, the remainder of the yolk sac acts as a nutrient, energy, and water reserve (Romanoff 1944). This reserve might be especially important to precocial chicks, which must obtain their own food, because it enables the chick to survive while learning to forage (Lack 1968).

To investigate the energetic significance of the yolk sac for precocial (i.e. self-feeding) and semiprecocial (i.e. fed by their parents) neonates, we have used *PMR* values from the literature and our own data on the fat content of the yolk sac and adipose tissues of the neonate to calculate the period during which *PMR* can be sustained on the basis of these fat reserves (Table 3). We have assumed that 1 g of fat is equivalent to 39.3 kJ (Schmidt-Nielsen 1975).

Calculated survival times based on yolk alone range from 6 h (Japanese Quail) to 24 h (Northern Lapwing). Based on the total lipid reserves of the chick, these survival times range from 26 h (Arctic Tern, *Sterna paradisaea*) and 84 h (Northern Lapwing; Table 3). The relative allometric slopes of *PMR* to body mass for precocial and semiprecocial neonates (0.92), and of all fat reserves both in the yolk sac as well as

TABLE 3. Calculated survival times for neonates when at their peak metabolic rate on basis of data for fat reserves in yolk sac and body.

Species	Body mass (g)	*PMR* (W)	Lipid in yolk (g)	Lipid in body (g)	Survival time[a] (h)	Source[b]
Coturnix c. japonica	6.9	0.14	0.08	0.37	6.2 + 28.9	1,2
Sterna paradisaea	13.0	0.21	0.15	0.35	7.8 + 18.2	3,4
Larus atricilla	28.4	0.47	0.70	1.09	16.3 + 25.3	5,2
Vanellus vanellus	16.2	0.20	0.44	1.10	24.0 + 60.0	6,4
Limosa limosa	27.0	0.40	0.76	1.56	20.7 + 42.6	6,4
Anas platyrhynchos	28.8	0.98	2.02	1.47	22.5 + 16.4	7,4
Somateria mollisima	60	2.00	3.31	6.53	18.1 + 35.6	8,4

[a] First and second values represent estimated survival times on basis of fat reserves present in yolk sac and those in main body, respectively.
[b] (1) Ricklefs and Choi unpubl. data; (2) Ricklefs et al. 1978; (3) Klaassen and Bech 1992; (4) this study; (5) Dawson et al. 1972; (6) Visser and Ricklefs 1993a; (7) Koskimies and Lahti 1964; (8) Grav et al. 1988.

in the main body to body mass (1.170; Table 1), suggest that larger chicks could survive longer (scaling exponent 0.25). For the species listed in Table 3, the calculated survival times at thermoneutral conditions are about two times longer, except for duck neonates in which survival times are about four times longer. Based on an allometric scaling exponent of 0.86 for neonatal metabolic rates at themoneutrality (Klaassen and Drent 1991), an exponent of 0.31 is predicted for the survival time in relation to body mass.

Yolk sac as a water reserve.—The yolk sac not only acts as an energy reserve, but also its water content might be of importance for the chicks' survival during the first days after hatching (Romanoff 1944). For neonates this issue has not been addressed quantitatively in the ecological literature. Although the species we have studied normally develop in relatively humid habitats, we have estimated the potential contribution of the yolk sac to water budgets of Northern Lapwing and Black-tailed Godwit neonates. The water reserves in the yolk sac of the two species amounted 1.0 and 1.6 g, respectively. Rates of minimal evaporative water loss for neonates of the two species at rest were estimated to be 1.3 and 2.1 $g \cdot day^{-1}$, respectively (Visser 1991). Thus, the water of the yolk sac potentially could cover water requirements for less than one day. In addition to the water directly available from the yolk sac, metabolic water can be produced as a result of fat metabolism (1.07 g water·g fat^{-1}; Schmidt-Nielsen 1975). The total amount of neonatal lipid reserves of Northern Lapwings and Black-tailed Godwits could be estimated at 1.1 and 1.6 g, respectively, yielding 1.2 and 1.7 g metabolic water, respectively. These values suggest that these chicks should commence drinking or eating insects (with a high water content) within at least two days after hatching. On the basis of allometric scaling in neonates with respect to evaporative water loss (exponent 0.80; Visser 1991), water content of the yolk sac (exponent 1.22; Table 1), and total amount of fat reserves in the body to body mass (exponent 1.17; Table 1), we estimate larger chicks to have relatively larger water reserves compared to smaller chicks.

In conclusion, we have demonstrated that the relative sizes of body components are related in some instances to the thermal relationships of chicks to their environments. Where there is a higher peak metabolic requirement, this may be met by either larger size of the heat-producing tissue (generally the leg muscles of precocial and semiprecocial neonates) as observed in larger neonates, or greater mass-specific heat production, as observed in duck neonates.

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