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The morphological development of the locomotor and cardiac muscles of the migratory barnacle goose (*Branta leucopsis*)

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(With 6 figures in the text)

The masses of the locomotor and cardiac muscles of wild barnacle goose goslings, from a migratory population, were examined systematically during development and their values compared to those of pre-migratory geese. Pre-flight development was typified by approximately linear increases of body, leg, and heart ventricular mass with respect to age. Flight muscle showed an exponential increase in mass. Pectoralis muscle mass was 14·2 ± 0·3% of body mass (1297 ± 73 g, $n = 7$) in early flying goslings compared to 16·6 ± 0·3% of body mass (2318 ± 109 g, $n = 8$) in pre-migratory geese. Post-flight development was typified by stasis of leg muscle mass but hypertrophy of ventricular and pectoralis muscle mass in proportion to body mass. Ventricular mass relative to body mass showed the lowest values at 5 weeks of age (0·62 ± 0·01%) with peak values at 1 week of age (1·04 ± 0·04%). The latter may be associated with both the requirements of thermoregulation in these precocial, arctic breeding geese and the need to forage approximately 24 hours post-hatch. Peak values for leg muscle mass, relative to body mass, were found at 3 weeks of age (12·7 ± 0·36%), with lowest values in the pre-migratory geese (6·7 ± 0·21%), while peak values for pectoralis muscle mass were expressed in the pre-migratory geese with lowest values at 1 week of age (0·94 ± 0·07%). Ventricular mass was proportional to leg muscle mass up to 5 weeks of age ($M_v = 0{\cdot}38M_t^{0{\cdot}68}$, $r^2 = 0{\cdot}95$), but subsequent increase in ventricular mass was proportional to pectoralis muscle mass ($M_v = 0{\cdot}25M_p^{0{\cdot}73}$, $r^2 = 0{\cdot}81$).

Introduction

Allometric patterns of growth of locomotory muscles in migratory bird species are of potential interest in that post-hatch development can be divided into two distinct behavioural and ecological phases, pre-flight development up to fledging (which is defined here as day of first flight), and post-flight development up to departure for the migration. Both phases include large increases in body mass but the pre-flight growth is characterized by a mixture of musculo-skeletal growth and organogenesis (cf. Sedinger, 1986), while the latter is dominated by fat deposition (Ramenofsky, 1990) and a small degree of flight muscle hypertrophy associated with the energetic requirements of flight (Fry, Ferguson-Lees & Dowsett, 1972; Raveling, 1979; Marsh, 1984; Piersma & Jukema, 1990; Driedzic *et al.*, 1993). Precocial species, such as the Anatidae, are particularly interesting, as their young leave the nest after only a few days and are self-feeding (O'Connor, 1984), thus early development is based on an aquatic or cursorial locomotory lifestyle prior to fledging and preparation for the autumn migration.

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The Svalbard population of the barnacle goose (*Branta leucopsis*) flies 2,500 km from the arctic breeding grounds to winter in south-west Scotland (Owen & Gullestad, 1984; Owen & Black, 1989), thus providing the potential to study the same population of birds both before and after the migration. As part of a study of the muscle adaptations involved in physically preparing birds for the migration, this paper details the morphological changes that occur between 1 week of age and the southern migration. The results of some associated biochemical analyses have been reported elsewhere (Bishop *et al.*, 1995). Goslings hatch at the beginning of July and spend the next 12 weeks growing and preparing for the autumn migration, which normally occurs during the last week of September. They are able both to run and swim within 48 hours, and must have fully functioning hindlimb and cardiovascular musculature very soon after hatching in order to be able to forage and avoid predation. Barnacle goose goslings, on Svalbard, do not begin to fly until around 7 weeks of age (pers. obs.), and it is typical of the Anatidae that the relative growth of wing bones and muscles are very much delayed in comparison to those of the legs (Sedinger, 1986). This general pattern is also found in the semi-precocial California gull (Carrier & Leon, 1990) and the altricial bank swallow (Marsh & Wickler, 1982) and may be typical of all birds (O'Connor, 1984).

This differential development of the wing and leg musculo-skeletal systems is possible, as birds possess two locomotory muscle systems. These physically independent muscle systems are functionally dependent on the same cardiovascular system, and given that we would expect *minimum* oxygen consumption of a flying barnacle goose to be approximately twice that of the *maximum* achieved during running or swimming (Butler, 1991; Nolet *et al.*, 1992), it would be expected that the development of the heart would also reflect this functional difference. Therefore, the relative growth of the cardiac muscle and locomotory musculo-skeletal system were examined systematically in a species which undergoes a long distance migration, to study the development of the muscular capacity required to perform such a physically demanding flight.

Materials and methods

Capture of birds

Barnacle geese were caught using corral nets or small, pneumatic powered cannon nets and were captured in 2 areas on the western coast of the island of Spitsbergen, Svalbard, Arctic Norway. Goslings up to 7 weeks of age were obtained from the breeding population at Ny-Ålesund (79°55′N, 11°00′E) between 1st July and the 27th August 1991 and 1992. Pre-migratory geese were obtained from the more southerly location of Hornsund (77°10′N, 15°00′E) between 12th–23rd September 1992. Ny-Ålesund is an excellent study site which contains a large number of ringed parental birds. Thus relatively accurate ageing of goslings was possible using a combination of observing hatch dates for eggs of ringed parents and placing webtags on newly hatched goslings. In addition, each year a growth curve was calculated of age plotted against various morphometric parameters (M. J. J. E. Loonen, unpubl. data) so that unringed goslings could also be aged accurately.

Morphometric measurements

Following capture, birds were weighed and a number of measurements were made. Following terminal anaesthesia of the bird (i.p. injection of sodium pentobarbitol or inhalation of halothane), heart ventricles, pectoralis major, supracoracoideus, semimembranosus, gastrocnemius interna, and externa muscles and total leg muscle masses were measured. Ulna and tibiotarsus bones were also dissected, weighed, and measured.

Analysis of data

To understand the functional significance of the various patterns of growth seen in different tissues during development, it is necessary to look at dimensional changes with respect to both age and body mass. While muscles and bones may grow at completely different rates with respect to each other and to body mass, and with different mathematical relationships (O'Connor, 1984), the tissues are also subject to forces that are proportional to the body mass of the animal (Schmidt-Nielsen, 1984). Thus, the causes of growth may reflect both an innate maturation process and also a response to frequent use, such as muscle hypertrophy during exercise.

Data on morphometric changes were collected from 3 different seasons. The following birds were caught in Ny-Ålesund: 1991, 4 goslings at 1, 3, and 5 weeks of age but only 1 at 7 weeks; 1992, 4 goslings at 3, 5 at 5 and 3 at 7 weeks of age; 1993, 3 goslings at 7 weeks of age and 8 adults during the same period. In 1992 the following birds were caught in Hornsund, 7 pre-migratory adults (1 on 11th, 3 on 12th, 2 on 16th, and 1 on 19th of September) and 1 pre-migratory gosling on 23rd September. The main purpose of this study was to develop general conclusions about the allometric growth of the goslings with regard to the demands of specializing in a cursorial lifestyle, followed by a transition to flying. In addition, to compare the data from Ny-Ålesund with those from Hornsund, which is a separate population breeding further south on Spitsbergen, it is necessary to be able to draw general conclusions concerning development. Therefore, the data from the different years have been pooled for the analysis of age-related growth.

A number of complex growth curves has been used in the literature to describe patterns of body mass increases with age (Ricklefs, 1983). However, these equations are often inappropriate when growth of individual muscles and bones are analysed (Sedinger, 1986). In addition, migratory birds continue to increase in body mass after fledging and, therefore, do not reach a true asymptote at fledging. Therefore, the results have been subdivided into 2 ecophysiological phases.

(a) Pre-flight development from 1 week of age up to fledging at 7 weeks. However, where tissues have reached maximal size by 5 weeks of age the regression analysis is terminated.

(b) Fledging and post-flight development. Along with the 7-week-old goslings, a number of adult birds were sampled at Ny-Ålesund. Unfortunately, only a single pre-migratory gosling (estimated to be 11·5 weeks of age) was obtained along with 7 pre-migratory adults. However, all morphometric measurements of the 11·5-week-old gosling are within the range of values obtained from the pre-migratory adults, and so, when analysing the relationships of individual tissues with respect to body mass, they are referred to as pre-migratory geese.

Growth of the various limb components have been investigated to see if they vary systematically with time or with changes in body mass using either linear ($y = \mathrm{a} + \mathrm{b}x$) or power regression ($y = \mathrm{a}x^{\mathrm{b}}$) or by fitting exponential ($\log y = \mathrm{a} + \mathrm{b}x$) or logarithmic ($y = \mathrm{a} + \mathrm{b}.\log x$) curves. Regression analysis of morphological variables with respect to age was performed using least squares (or Model 1) regression, while 'reduced major axis' (or Model 2) regression was utilized for analysis with respect to body mass (Sokal & Rohlf, 1981; Rayner, 1985). Limb muscles were measured from one side of the body and multiplied by 2 to give total muscle masses. Comparisons between means were compared by unpaired 2-tailed t-test at 5% significance. Data with respect to age in weeks are presented as means ± S.E. of the means.

Results

Body mass

The general pattern of body mass changes (Fig. 1a), from day of hatch through to fledging at 7 weeks, is similar to previous studies of growth in Anatidae (Sugden, Driver & Kingsley, 1981; Lightbody & Ankney, 1984; Sedinger, 1986). Body mass (M_b, in g) is almost directly proportional to age (A, in weeks) between 1 and 5 weeks (Table I), but the rate of increase then shows a slight decline between 5 and 7 weeks of age. As the body mass exponent is close to 1, it is possible to generalize that, as an average over the three years, barnacle geese were able to assimilate approximately 217 g per week over the growth period prior to fledging. At fledging, the goslings are still very lean, with little sign of subcutaneous fat (unpubl. data). There are no data to show the type of curve describing the rate of body mass increase between 7 weeks (mean 1,297 ± 73 g, $n = 7$) and 11·5 weeks of age (2,321 g, an average increase of 79%), but it is interesting to note that a linear relationship would be equivalent to a body mass gain of approximately 227 g per week. Values for pre-migratory geese range from 1906–2864 g (mean 2318 ± 109 g, $n = 8$).

Bone length

Figure 1b shows the changes in lengths of the ulna and tibiotarsus bones with age, while increases with respect to body mass are shown in Fig. 2. The ulna shows an exponential increase in length between 1 and 5 weeks of age and fits an exponential curve which gives a reasonable prediction of values for 7-week-old goslings. The average exponential rate of increase in length up to fledging was 1·49 times per week or 1·16 times per 100 g M_b. Values for the pre-migratory geese appear to be unchanged compared to those for the 7-week-old goslings.

Length of the tibiotarsus (Fig. 2b) reaches a maximum by 5 weeks of age and the data are well described by a power curve (Table I). There are no significant changes in length between fledging (tibiotarsus = 117 mm ± 3·3; ulna = 131·5 mm ± 4·2) and the pre-migratory geese (tibiotarsus = 118 mm ± 2·3; ulna = 133 mm ± 2·3).

Sternum length (Fig. 2c) increases in a linear manner between 1 and 5 weeks of age (Table I),

TABLE I

Reduced major axis allometric equations of the form $Y = a + bA$, where A is age in weeks, or $Y = a + bM$, where M is body mass in grams

	abscissa	A	a	b	r^2
Length (mm)					
log Ulna	A	1-5	1·18	0·17 ± 0·014	0·97
log Ulna	M	1-5	1·28	0·0006 ± 0·00004	0·94
log Tibiotarsus	log A	1-5	1·80	0·37 ± 0·04	0·95
log Tibiotarsus	log M	1-5	1·00	0·35 ± 0·03	0·96
Sternum	M	1-5	23·9	0·05 ± 0·004	0·97
Mass (g)					
log Body	log A	1-5	2·31	1·06 ± 0·09	0·97
log Pectoralis	A	1-7	−0·013	0·32 ± 0·04	0·97
log Pectoralis	M	1-5	0·064	0·0013 ± 0·0001	0·96
log Supracoracoideus	A	3-7	−0·886	0·31 ± 0·06	0·88
log Supracoracoideus	M	1-5	−0·796	0·0013 ± 0·0002	0·89
log Ventricles	log A	1-5	0·326	0·74 ± 0·09	0·94
log Ventricles	log M	1-5	−1·31	0·71 ± 0·04	0·99
log Gastrocnemius	log A	1-5	0·684	1·03 ± 0·10	0·96
log Gastrocnemius	log M	1-5	−1·57	0·97 ± 0·09	0·96

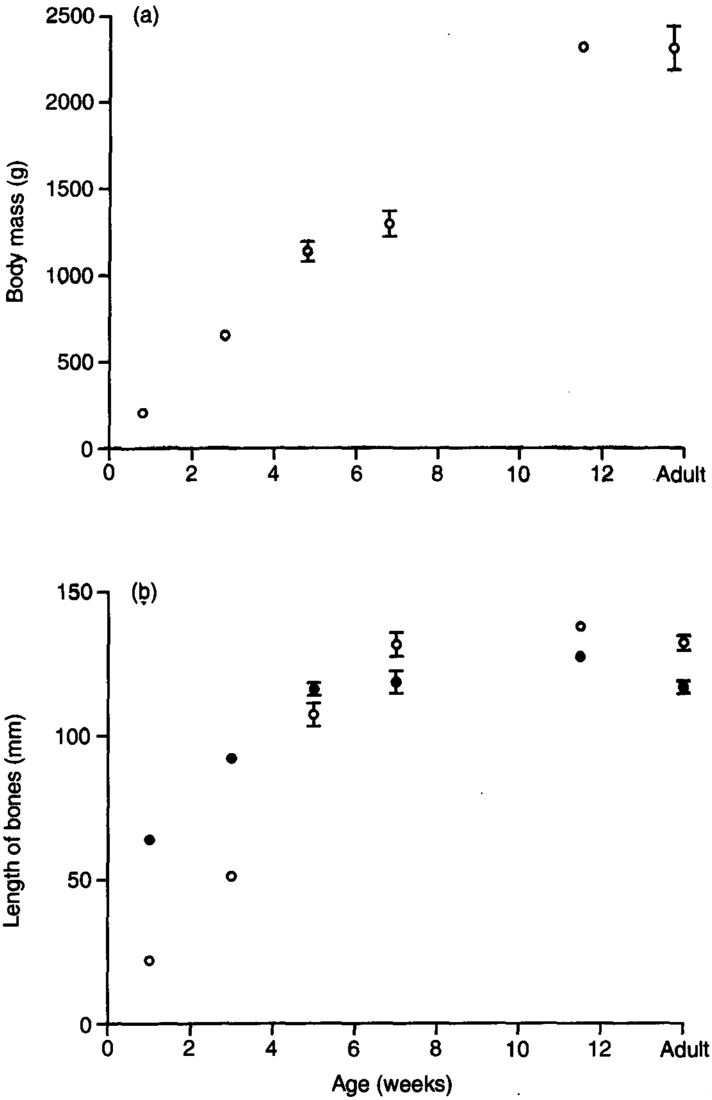


FIG. 1. Mean ± S.E. of: (a) body mass (g); and (b) length (mm) of ulna (○) and tibiotarsus (●), plotted against age of wild barnacle geese. ($n = 4$–9, except for a single individual at 11·5 weeks of age.)

but underestimates sternum size at 7 weeks. Sternum size is significantly larger in the pre-migratory geese than at fledging ($P < 0{\cdot}05$), but there appears to be no trend in sternum size with changes in body mass.

Muscle mass

Changes in muscle mass plotted against age are shown in Fig. 3 while changes with respect to

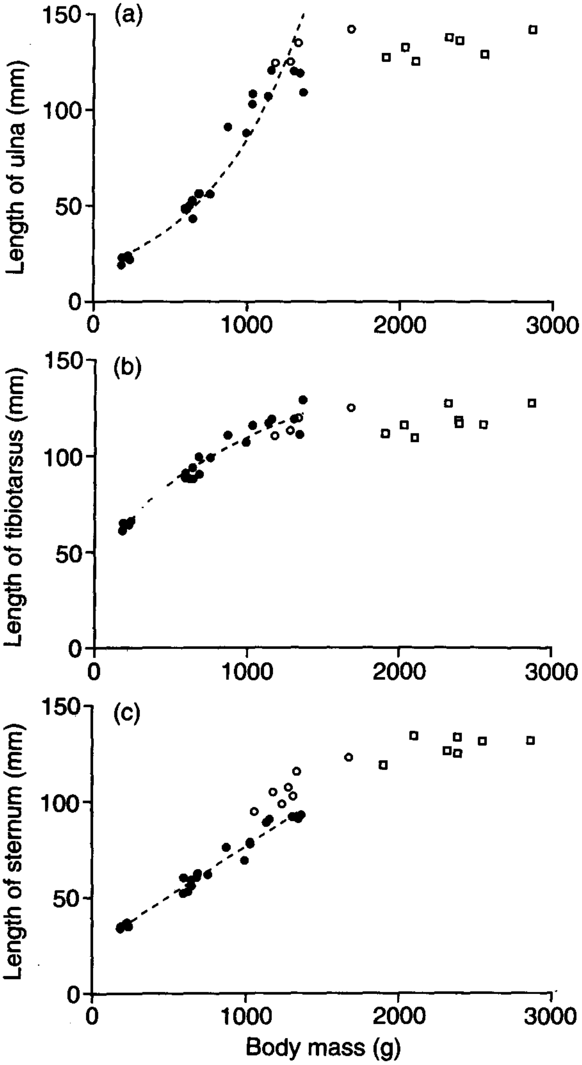


FIG. 2. Scatter diagram of the lengths (mm) of: (a) ulna; (b) tibiotarsus; and (c) sternum plotted against body mass of wild barnacle geese. Goslings of 1-5 weeks of age (●), airborne goslings of 7 weeks of age (○) and pre-migratory geese (□). Dashed line (- - -) is line of best fit applied to data from goslings of 1–5 weeks of age (see Table I and **Results**).

body mass are shown in Fig. 4. Pectoralis and supracoracoideus muscle masses increase exponentially up to 5 weeks of age (Table I), after which the growth of the wing muscles accelerates even more rapidly with respect to body mass. This is clearly a phenomenon created by a reduction in the rate of increase of body mass at this time (Fig. 1a), as pectoralis mass continues to grow at the same rate with respect to age (Fig. 3a). The exponential rate exponent up to 7 weeks of age is approximately 2·1 times as much muscle mass at the end of each week as at the beginning. At fledging, goslings had a mean pectoralis mass of 184 ± 12 g and, at this rate of

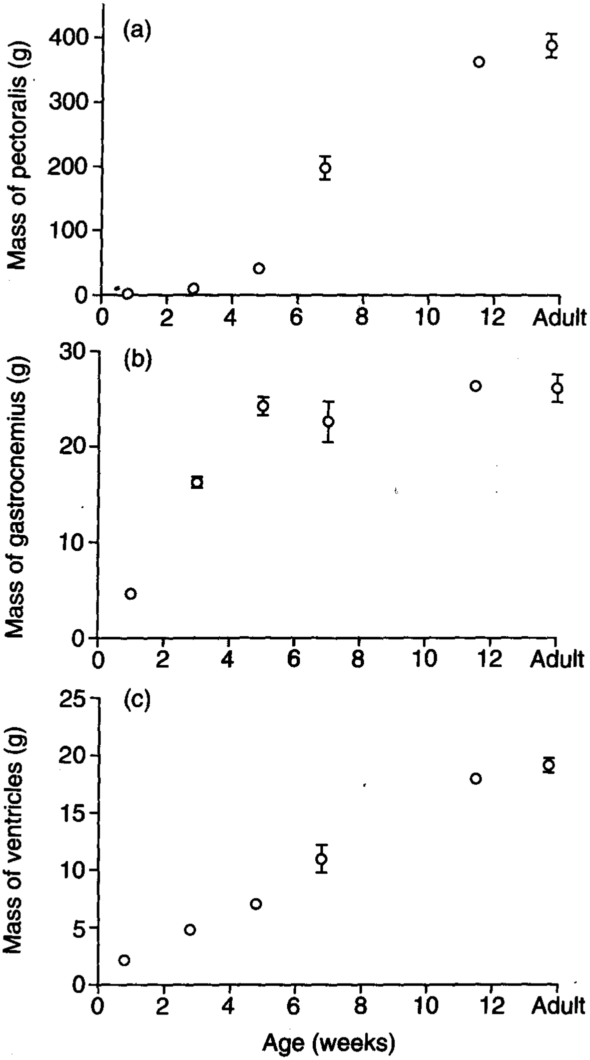
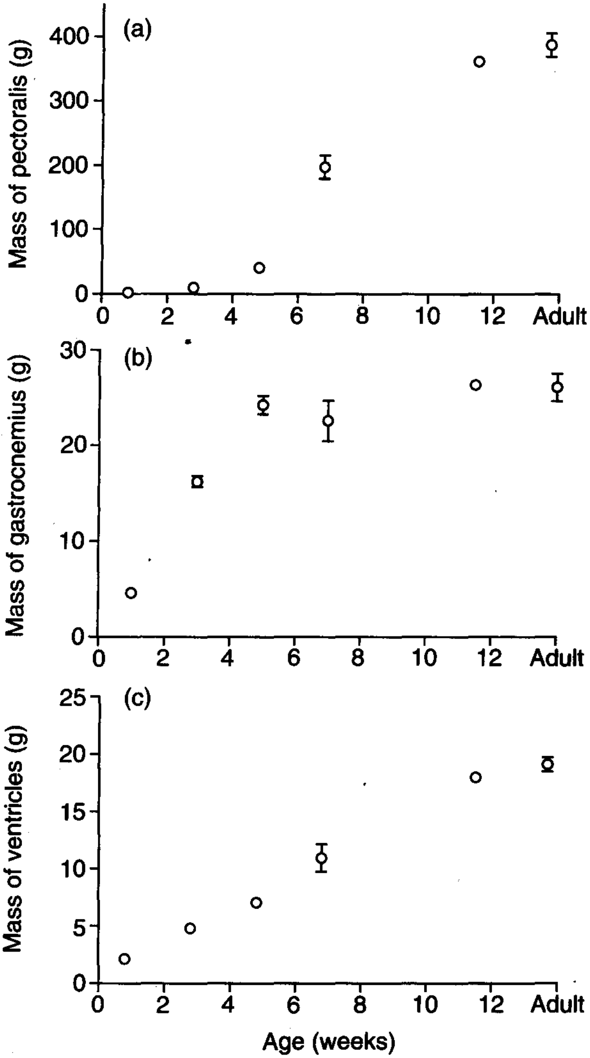


FIG. 3. Mean ± S.E. of the masses (g) of: (a) pectoralis; (b) gastrocnemius; and (c) heart ventricles plotted against age of wild barnacle geese. (*n* = 4–9, except for a single individual at 11·5 weeks of age.)

increase, pre-migratory values for pectoralis mass would be reached by 8 weeks of age. The 11·5-week-old gosling had a pectoralis mass of 362 g (an average increase of 97% compared to fledging) and pre-migratory values ranged from 336–478 g. Supracoracoideus mass at fledging was 21 ± 1·4 g, while the pre-migratory gosling had a supracoracoideus mass of 40 g and pre-migratory values ranged from 32–46 g.

Gastrocnemius muscle mass increases in direct proportion to age (Table I) and shows a very different pattern of growth to that of the wing muscles (Figs 3b & 4b). The pattern of development is well described by the power regression analysis. The gastrocnemius muscles



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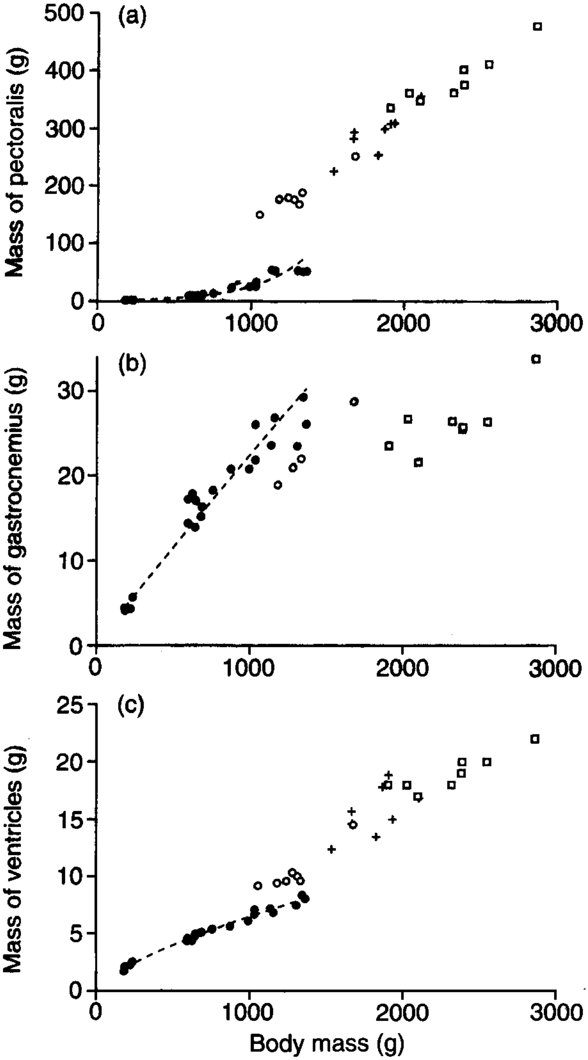

FIG. 4. Scatter diagram of the masses (g) of: (a) pectoralis; (b) gastrocnemius; and (c) heart ventricles plotted against body mass of wild barnacle geese. Goslings of 1–5 weeks of age (●), airborne goslings of 7 weeks of age (○), adults caught in Ny-Ålesund (+), and pre-migratory geese (□). Dashed line (- - -) is line of best fit applied to data from goslings of 1–5 weeks of age (see Table I and **Results**).

show only a small increase in size between fledging (22·6 ± 2·1 g) and the pre-migratory geese (26·2 ± 1·3 g). Indeed, there was little further increase in total leg muscle mass between 5-week-old goslings (134 ± 7·7 g) and the pre-migratory geese (156 ± 10·6 g), despite an average increase of 104% in body mass. For all ages the gastrocnemius and semimembranosus muscle masses (M_g and M_s, respectively) were found to be almost directly proportional to that of the total leg muscle masses ($M_g = 0{\cdot}24\, M_t^{0{\cdot}93}$, $r^2 = 0{\cdot}98$, and $M_s = 0{\cdot}08\, M_t^{0{\cdot}97}$, $r^2 = 0{\cdot}88$). Thus, measurements of semimembranosus and total leg muscle masses showed a similar relationship, with respect to age or body mass, as that found for the gastrocnemius muscle mass (Table I).

The developmental growth of the ventricles has some characteristics of both the leg and wing muscles. Ventricular mass grows steadily between 1 and 5 weeks of age and, as with the leg muscles, is well described by a power curve (Table I). In contrast to the leg muscles, which have reached a maximum pre-flight value by 5 weeks of age, the ventricles continue to increase in mass and in fact show an accelerated growth rate between 5 and 7 weeks of age. Post-fledging growth shows a similar pattern to that of the flight muscles. The pre-migratory gosling had a ventricular mass of 18 g compared to the average fledgling mass of 10·4 ± 0·7 g (an increase of 73%), while the values for the pre-migratory geese ranged from 17 to 22 g. Total heart mass can be estimated from the ventricular mass, as the mass of the atria was on average 15 ± 0·8% ($n = 17$) of the ventricular mass.

Both flight and heart muscles continue to increase in mass after fledging (Figs 4a, b). If the data from flying goslings and pre-migratory geese are analysed together, then mass of the pectoralis increases with an allometric expression of $0{\cdot}026\,M_b^{1{\cdot}24\pm0{\cdot}12}$ ($r^2 = 0{\cdot}96$), while supracoracoideus and heart exponents are $0{\cdot}006\,M_b^{1{\cdot}14\pm0{\cdot}19}$ ($r^2 = 0{\cdot}92$) and $0{\cdot}006\,M_b^{1{\cdot}03\pm0{\cdot}13}$ ($r^2 = 0{\cdot}96$), respectively. However, the above exponents for flying geese should be viewed as *maximum* estimates, as the slope of the regression may be biased by the data from the 7-week-old goslings, which are still maturing. This is further clarified by including data taken from adults caught at the same time of year as the 7-week-old goslings (Figs 4a, c). Following breeding and a complete moult of the flight feathers, during which the pectoralis and cardiac muscles atrophy (Raveling, 1979; Mainguy & Thomas, 1985; Piersma, 1988), the adult geese undergo muscle hypertrophy and regrow their flight feathers. Therefore, both groups of geese are being sampled towards the end of a growing phase and may not represent true estimates of the muscle mass adaptations required for flapping flight.

Figure 5 shows the muscle mass data plotted as percentage of body mass against body mass. There was no overlap in the data for percentage of pectoralis in the 7-week-old goslings (14·2 ± 0·3%) and the pre-migratory geese (16·6% ± 0·3), which can be divided by a line at 15%. In addition, two of the adult birds from Ny-Ålesund cluster with the goslings and six of them cluster above this 15% threshold, indicating that they may be ahead of the goslings in terms of relative development or post-breeding recovery. The allometric expressions for pectoralis, supracoracoideus, and heart mass, for geese above the 15% pectoralis threshold, are $0{\cdot}26\,M_b^{0{\cdot}94\pm0{\cdot}16}$ ($r^2 = 0{\cdot}92$), $0{\cdot}25\,M_b^{0{\cdot}66\pm0{\cdot}34}$ ($r^2 = 0{\cdot}30$), and $0{\cdot}07\,M_b^{0{\cdot}72\pm0{\cdot}26}$ ($r^2 = 0{\cdot}69$), respectively. All these M_b exponents have lower values than those which included the 7-week-old gosling data.

Peak values for percentage of total leg muscle mass are 12·7 ± 0·36% (reached at 3 weeks of age) but, by pre-migration, this figure has declined to 6·7 ± 0·21%. The relative mass of the ventricles shows a slightly more complicated pattern, with peak values at 1 week of age (1·04% ± 0·04) followed by a steady decline to reach the lowest values at 5 weeks of age (0·62% ± 0·01). They then rapidly increase towards fledging, as birds learn to fly, and are not significantly different from those of the adult birds from Ny-Ålesund (0·86%) or Hornsund (0·82%).

Changes in the masses of the ventricular and pectoralis muscles during growth are closely related to each other from the first week post-hatch, and this is clearly seen in Fig. 6a in a plot of ventricular mass against the mass of the pectoralis. Both pre-flight and post-flight development of the heart and pectoralis are well described by logarithmic equations. Lines of best fit applied to data from 1–5-week-old goslings ($M_v = 3{\cdot}8\log(M_p) + 0{\cdot}99$, $r^2 = 0{\cdot}96$) and the eight pre-migratory geese from Hornsund ($M_v = 32\log(M_p) - 65{\cdot}0$, $r^2 = 0{\cdot}82$), intersect close to the values for the

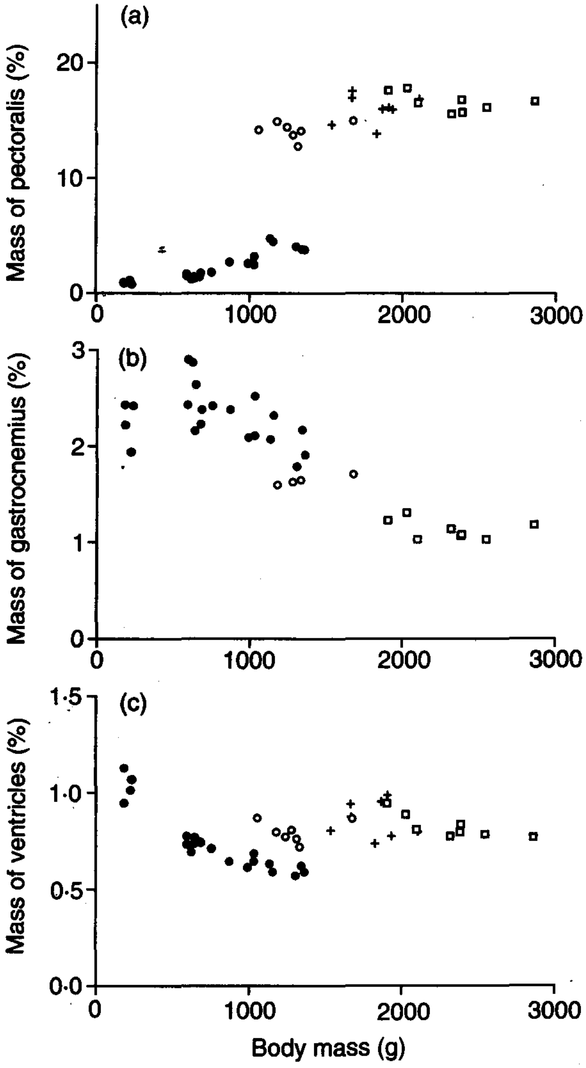

FIG. 5. Scatter diagram of percentage (%) of body mass of: (a) pectoralis; (b) gastrocnemius; and (c) heart ventricles plotted against body mass of wild barnacle geese. Symbols as in Fig. 4.

7-week-old goslings. This suggests that the period at which the birds first become airborne coincides with a complete transition in the physiological control of growth of these muscles.

Discussion

Body mass and structural growth

Increases in the length of the limb bones appears to have ceased by 7 weeks of age. This is important as it appears that by 7 weeks it is possible to predict what structural size a gosling will

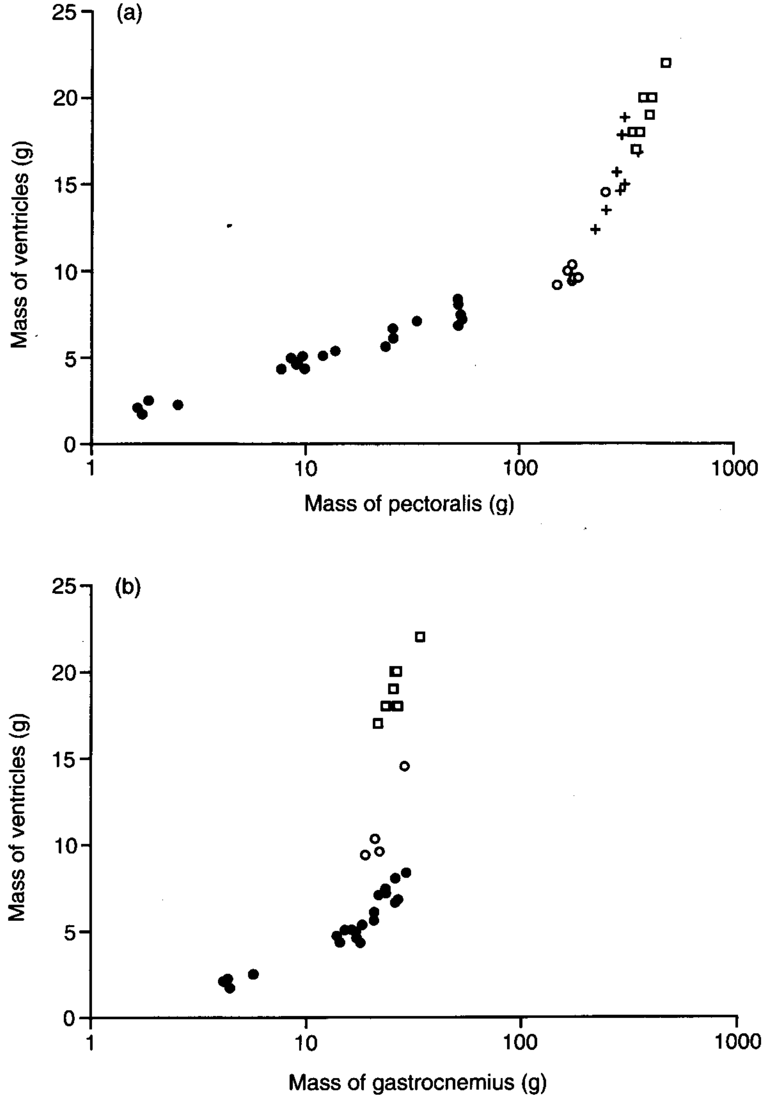

FIG. 6. Scatter diagram of the masses (g) of the heart ventricles plotted against: (a) mass of the pectoralis; and (b) gastrocnemius muscle mass of wild barnacle geese. Symbols as in Fig. 4.

be when it migrates. There appear to be differences in growth rates between years due to environmental effects (M. J. J. E. Loonen, unpubl. data; Larsson & Forslund, 1991), so that individuals born in a year with high growth rates will be bigger than birds born in a year with low growth rates. However, it is clear that general patterns of development appear unaltered between years. Certain tissues develop exponentially, while others fit an allometric power curve but, in different years, they appear to reach peak values at approximately the same age.

During early development, body mass increases in an almost linear relationship with respect to age, and therefore growth of individual tissues scaled against either age or body mass have very similar exponents, but this relationship alters after 5 weeks of age. The bones and muscles of the legs show little change in length or mass, while pectoralis and cardiac muscles continue to increase in mass with respect to age, thus changing their relative growth pattern when compared to body mass. The rate of increase in body mass must accelerate again after fledging in order to accumulate sufficient lipid stores for the migration at the end of September, although the data are insufficient to describe the pattern of lipid accumulation with respect to time. A linear relationship would require an average body mass increase of about 227 g per week between fledging and migration, of which 46 g (20%) can be accounted for by increases in masses of the pectoralis, supracoracoideus, and ventricular muscles. This compares with adult geese caught in Ny-Ålesund which, on average, only require an increase of about 167 g per week, of which 34 g (20%) can be accounted for by mass increases of these muscles.

Pre-flight development

During development, there may be conflicting selective pressures on the functional requirements of the different muscle systems. Between the ages of 1 to 6 weeks, barnacle goose goslings are unable to fly. Thus, during the initial stages of growth, barnacle geese are dependent on their hindlimbs for locomotion to avoid predation, and to forage for food. During this phase, leg bones, and muscles of the goslings increase in length and mass in direct proportion to each other and to body mass. However, by 5 weeks of age, the bones and muscles of the hindlimbs stop growing very abruptly, having reached pre-migratory size. Very large cursorial species of birds, such as the ratites, have about 25–29% of their body mass made up of leg muscles (Patak, 1988), while cursorially active species such as pheasants and rails typically have leg masses of between 11–23% (Hartman, 1961). However, while leg muscles of the barnacle geese reach 13% of body mass at 5 weeks of age, this declines to 7% in the pre-migratory geese.

Cardiac muscle provides the power to pump the blood supply to working muscles. Peak mass of the heart ventricles were measured at 1 week of age (1·04%). This may simply reflect the high mass-specific metabolic rate of small goslings relative to the older and larger geese, as a consequence of the scaling of metabolic rate with body mass (Schmidt-Nielsen, 1984). However, it may also partly reflect the large metabolic scope found in goslings during the first few days after hatch (Steen & Gabrielsen, 1986). The thermal stress experienced by arctic breeding birds, such as barnacle geese, is much greater than those of temperate species, and the ability to thermoregulate during the first few days after hatch is also greater (Untergasser & Hayward, 1972; Steen & Gabrielsen, 1986; Choi, Ricklefs & Shea, 1993).

Development of flight

There is only a small increase in total leg muscle mass between fledging and the pre-migratory geese, despite a 100% increase in body mass due to lipid deposition and flight muscle hypertrophy. Consequently, there is a large drop in the percentage of the total leg muscle mass in the older geese, and presumably a reduction in cursorial performance. However, there would be an increase in flight performance due to the consequent decrease in body mass. This disinvestment from the hindlimb musculature would seem to be an adaptation and commitment to flight as the primary form of locomotion.

That there is a fundamental shift in the pattern of growth of both the heart and the pectoralis muscle around the time of fledging is clearly seen in Fig. 6. Thus, the rapid increase in ventricular mass between 5 and 7 weeks of age appears to provide for the extra blood flow required by the pectoralis muscles at fledging, and the potential blood flow at fledging will greatly exceed the actual demand from the leg muscles. Interestingly, ventricular mass at 5 weeks of age, expressed as a percentage of the total leg muscle mass (5·2%), is similar to the ventricular mass at 7 weeks of age, when expressed as a percentage of pectoralis mass (5·5%). This relationship appears to be very consistent as the adult birds, caught in Ny-Ålesund at the same time as the 7-week-old goslings, also had a ventricular mass which was 5·3% of the mass of the pectoralis muscles.

The relationship between total leg muscle mass and the mass of the ventricles between 1–5 weeks of age ($M_v = 0{\cdot}38M_t^{0{\cdot}68}$, $r^2 = 0{\cdot}95$) has a similar mass exponent to that between the ventricular and pectoralis muscles of the pre-migratory geese ($M_v = 0{\cdot}25M_p^{0{\cdot}73}$, $r^2 = 0{\cdot}81$). Therefore, during the cursorial phase of the goslings' life, heart mass grows in proportion to the blood flow requirement of the leg muscles, while later on in development, heart mass hypertrophies in proportion to the blood flow requirements of the pectoralis muscles.

All the 7-week goslings, and adults caught at the same period, were observed in flight. One gosling was seen unsuccessfully attempting to take-off at 01:50 h on 27/8/93, but was then seen becoming airborne at 15:15 h of the same day, and was caught at 01:30 h the next day. This gosling, at 1313 g body mass, had a pectoralis mass to body mass ratio of 12·8% which was the lowest of any of the flying geese sampled (Fig. 5a), and may be close to the threshold value for take off in this species. From the present results, it can be assumed that, as most tissues are no longer increasing in mass except for the flight muscles, almost all body mass changes at 7 weeks of age are as a result of pectoralis muscle growth. Therefore, it can be estimated from the exponential growth curve for pectoralis mass growth that, 24 h earlier, the gosling would have had approximately 19 g less pectoralis muscle, giving a new pectoralis to body mass ratio of 11·5%. This would suggest that barnacle geese goslings require a pectoralis to body mass ratio of approximately 12% to be able to take-off. This is in good agreement with Marden (1987, 1990) who found that, taking all flight muscles together, birds were able to lift about six times their total flight muscle mass. If all other flight muscles are assumed to be approximately 7·5% of body mass (Hartman, 1961), then body mass of the goslings at the point of becoming airborne would be 8·3 times greater than pectoralis mass and 5·1 times greater than total flight muscle mass. The lowest percentage of pectoralis mass recorded from the flying adults caught in Ny-Ålesund was 13·9%, but there is no data on how many days previously they had first become airborne.

It is suggested that the 7-week-old goslings, and some of the post-breeding adults that are returning to the flying condition, are not yet fully adapted for sustained flying. These birds have pectoralis muscle masses below 15% (14·2% at 7 weeks of age, see page 9) compared to pre-migratory geese that always had pectoralis masses >15%. This is also consistent with the fact that the pectoralis muscle of goslings and adults caught in Ny-Ålesund around 7 weeks post-hatch had only 75% of the mass-specific activity of the aerobic enzyme citrate synthase compared to values in the pre-migratory geese (Bishop *et al.*, 1995). During the 5-week period of pre-migratory fattening, the pectoralis muscles of the barnacle geese hypertrophy in almost direct proportion with the increasing body mass. Thus, it is proposed that when making calculations of flight muscle mass-specific power outputs, at least for birds such as the Anatidae, using aerodynamic models such as that of Pennycuick (1989), the default value for flight muscle mass should relate to actual body mass and not to lean body mass.

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