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GROWTH AND ALLOCATION IN CAPTIVE COMMON MURRE (*URIA AALGE*) CHICKS

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ABSTRACT.—In birds, relative growth rates of morphological characters change in response to restricted food intake during development. Differential allocation of limited resources is hypothesized to reflect functional priorities for developing chicks. Body mass, wing, and flight feathers have been identified as potential priorities for seabird chicks. We used allometry to examine allocation in captive Common Murre chicks fed within a range of natural provisioning. During days 10–45 post-hatch, chicks were fed one of four diets that varied in biomass, energy content, and composition. Energy intake had a more profound effect on growth and development than diet composition; it significantly reduced absolute growth of body mass, manus, and tarsus. Between day 15 and day 20, allocation changed in all treatments: growth of manus was maintained at the expense of body mass. Chicks in more restricted treatments shifted allocation to manus at a lower body mass than those in less restricted groups, but subsequently allocated similarly. Wing loading was higher for chicks than for adult alcids, but scaled similarly. Growth of primary feathers was the most sensitive to small differences in diet composition. Our data also suggest that some changes in allocation may be ontogenetically determined rather than part of an adaptive response to reduced food intake. Received 25 June 2004, accepted 23 September 2005.

Key words: alcid, allometry, Common Murre, development, food intake, *Uria aalge*, wing loading.

Croissance et Allocation chez des Oisillons *Uria aalge*

RÉSUMÉ.—Chez les oiseaux, le taux de croissance relatif aux traits morphologiques change en réponse à une consommation de nourriture limitée au cours du développement. L'hypothèse d'une allocation différentielle des ressources, lorsqu'elles sont limitées, est avancée afin de refléter les priorités fonctionnelles des oisillons en développement. La masse corporelle, les ailes et les plumes de vol ont été identifiées comme des priorités potentielles chez les oisillons d'oiseaux marins. Nous avons utilisé l'allométrie pour examiner l'allocation chez des *Uria aalge* captifs nourris avec une gamme d'aliments naturels. Au cours des jours 10–45 suite à l'éclosion, les oisillons ont été nourris avec une des quatre diètes qui variaient en termes de biomasse, de contenu énergétique et de composition. La consommation énergétique a eu un effet plus important sur la croissance et le développement que la composition diététique, ce qui a significativement réduit la croissance absolue de

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la masse corporelle, de l'aile et du tarse. Entre le jour 15 et le jour 20, l'allocation a changé dans tous les traitements : la croissance de l'aile a été maintenue au dépend de la masse corporelle. Les oisillons soumis à des traitements plus restrictifs ont modifié l'allocation destinée à l'aile lorsque leur masse corporelle devenait plus faible que celles des oisillons dans les groupes moins restreints. L'allocation devenait similaire par la suite. La charge de l'aile était plus grande pour les oisillons que pour les adultes, mais dans un même ordre de grandeur. La croissance des plumes primaires était la plus sensible aux petites différences dans la composition diététique. Nos données suggèrent que certains changements dans l'allocation pourraient être déterminés de manière onthogénétique plutôt que d'être induits par une réponse adaptative à une consommation de nourriture réduite.

FOOD AVAILABILITY FOR developing birds is often highly variable. Chicks' developmental responses to food shortages vary among species. In some species, chicks are able to reduce metabolic rates and slow or nearly arrest growth until food becomes available again (Boersma 1986, Kitaysky 1999). In other species, chicks do not suppress growth of all body parts equally; some elements may continue to grow at near-normal rates, whereas others are substantially retarded (Boag 1987, Congdon 1990, Hario 2001, Ashton and Armstrong 2002, Dahdul and Horn 2003). Mechanistically, physiological "internal" constraints dictate patterns of relative growth (Ricklefs et al. 1998). However, the "adaptive growth" hypothesis predicts that selection should drive chicks to allocate limited resources to maintain growth of those elements that serve the most immediate needs, thereby maximizing their survival (O'Connor 1977, Ricklefs et al. 1998). This hypothesis has been used to infer that the morphological elements that are least sensitive to food restriction are the most critical to chick survival (e.g., O'Connor 1977, Øyan and Anker-Nilssen 1996). However, this hypothesis is difficult to test directly. Furthermore, there is a need for more information about the developmental responses of chicks with different juvenile life-histories to controlled variation in quality and quantity of food (but see Boag 1987, Johnston 1993, Øyan and Anker-Nilssen 1996, Schew and Ricklefs 1998, Kitaysky 1999, Dahdul and Horn 2003). Experiments quantifying how chick development is affected by levels of food restriction experienced in the wild are critical for addressing questions of developmental flexibility and constraints, and their implications for fitness.

Common Murres (*Uria aalge*) are colonially nesting seabirds. Both parents provision a

single, nest-bound chick for up to one month. Fledging age varies from about two weeks to a month, with the average near 20 days (Ainley et al. 2002, Piatt 2002). Their developmental strategy is considered intermediate between precocial and semi-precocial (Sealy 1973): chicks only attain approximately 20–25% of adult body mass by the time they fledge (Ainley et al. 2002). Fledglings cannot fly but must jump from high cliffs to reach the water, where they rely on foot propulsion to swim out to sea, escorted by the male parent for several months (Ainley et al. 2002). Food intake for Common Murre nestlings can vary both between and within years, depending on environmental conditions and parental quality (Birkhead and Nettleship 1987, Bryant et al. 1999, Kitaysky et al. 2000). Although most of the variation in chick growth rates observed in free-living Common Murres has been attributed to variation in parental provisioning, the effects of variation in food intake on growth and allocation have not been assessed experimentally.

In the literature, predictions about allocation based on juvenile life-history of seabirds fall into two major categories: (1) wing elements, primarily wing or feather length, are critical to successful fledging (Hedgren 1981, Hatch 1983, Øyan and Anker-Nilssen 1996, Hipfner and Gaston 1999, Hario 2001); and (2) energy reserves may be critical to post-hatching survival (Hatch 1983, Congdon 1990, Ydenberg et al. 1993, Gaston 1997). These hypotheses predict that when provisioning levels are not optimal, chicks should allocate limited resources preferentially to maximize wing length or body mass, respectively. In the absence of experimental evidence, these predictions remain speculative. The goal of the present study was to test the effects of limited food intake on Common

Murre chick development and to assess whether there is preferential allocation of resources to maintain growth of structural elements rather than body mass. Specifically, we sought to address (1) whether allocation (inferred from relative growth of morphological characters) changes in response to restricted food intake and (2) whether the level of restriction affects the degree of allocation.

In addition, quantity of food may not be the only factor determining resource allocation by food-restricted chicks. Parents are believed to optimize their provisioning efforts by balancing food quantity and food quality (Wright et al. 1998). Common Murres appear to selectively feed their chicks high-lipid prey items (Piatt 2002), which suggests that high lipid content is important for optimal chick growth. Therefore, we hand reared Common Murre chicks on controlled diets that varied in composition (protein and lipid content) as well as in energy content and wet biomass.

METHODS

EGG COLLECTION AND CHICK REARING

Partially incubated Common Murre eggs ($n = 28$) were collected from a colony in Cook Inlet, Alaska, in June 2000. Eggs were kept in a brooder at 37°C, except for 6 h in transit, during which temperatures never fell below 30°C. They were transported to the University of Washington, where steady incubation was resumed within 24 h of removal from nests. Eggs were incubated at 37.2°C in a Lyon TX incubator (Lyon Technologies, Chula Vista, California), at 56% relative humidity, turned once per hour. We have successfully incubated and hatched several seabird species under these conditions (Kitaysky et al. 2003). Chicks ($n = 26$) hatched between 28 July and 14 August. When chicks hatched, they were allowed to dry completely in a brooder, then measured and weighed. Chicks were transferred to artificial nests in a chamber maintained on a light cycle of 12 h light, 12 h dark, at 30°C and 80% relative humidity. At 10 days post-hatch (when chicks are capable of thermoregulating; Johnson and West 1975), we transferred the chicks to an identical chamber, but temperature was maintained at 25°C and relative humidity was 70%. These conditions were chosen to minimize

energy expenditure for thermoregulation (5–35°C is thermoneutral for adult Common Murres; Johnson and West 1975). Although this temperature may be warmer than ambient temperature at Common Murre colonies, free-living chicks are brooded throughout the nestling stage and are rarely exposed to ambient temperatures. Chicks were weighed every morning before the first feeding. This ensured that they were post-absorptive and, therefore, body mass was not affected by gut contents. Tarsus and manus (skeletal component of wing chord, not including feathers) were measured on hatch day and every five days afterward, except for day 40 post-hatch.

DIET

Food was offered to chicks five times daily. This feeding rate is at the high end of rates observed for free-living Common Murre chicks (2–5 feeds day⁻¹; reviewed in Ainley et al. 2002). For the first 10 days post-hatch, all chicks were fed whole, previously frozen fish (silverside [*Menidia menidia*]) with a multivitamin and mineral supplement. Although chicks did not receive as much food as they were capable of consuming in 24 h, food was *ad libitum* at each feeding. Chicks were handled until they refused further food. When chicks were 10 days old, feeding schedules were similar but chicks were placed on one of four controlled feeding regimens until day 45 post-hatch. Chicks were assigned to treatments sequentially by hatch order. Because the diet that parents provide for chicks in the wild varies both in quantity and quality, we were interested in examining the effects of diets that differed in biomass but were similar in energy content and composition, and vice versa. Our goal was to generate iso-energetic and iso-biomass dietary treatments using high- and low-energy forage fish provided within the reported range of variation in provisioning by free-living Common Murres (30–60 g day⁻¹; Gaston and Jones 1998). Thus, chicks received 35 g day⁻¹ silverside (a high-energy forage fish; $n = 6$), 50 g day⁻¹ silverside ($n = 7$), 35 g day⁻¹ rainbow smelt (*Osmerus mordax*, a lower-energy forage fish; $n = 6$) or 50 g day⁻¹ rainbow smelt ($n = 7$; Table 1). Although the goal of the controlled dietary treatments was to impose varying levels of food restriction, restriction

TABLE 1. Daily energy and nutrient content of dietary treatments (mean \pm SE). Composition was determined using proximate analysis, and energy content calculated based on metabolizable energy content of lipid (39.3 kJ g⁻¹) and protein (17.8 kJ g⁻¹). Different superscript letters within columns indicate significant differences among diets (Tukey's HSD multiple comparisons, $P < 0.05$).

Treatment	Energy (kJ day ⁻¹)	Water (g day ⁻¹)	Protein (g day ⁻¹)	Lipid (g day ⁻¹)
35 g day ⁻¹ smelt	187 \pm 4.5 ^a	27 \pm 0.2 ^a	5.0 \pm 0.11 ^a	2.5 \pm 0.12 ^a
35 g day ⁻¹ silverside	247 \pm 2.0 ^b	24 \pm 0.7 ^b	6.6 \pm 0.04 ^b	3.2 \pm 0.04 ^b
50 g day ⁻¹ smelt	266 \pm 6.3 ^c	39 \pm 0.3 ^c	7.1 \pm 0.15 ^b	3.6 \pm 0.17 ^b
50 g day ⁻¹ silverside	353 \pm 2.9 ^d	35 \pm 1.0 ^d	9.5 \pm 0.05 ^c	4.6 \pm 0.06 ^c
One-way ANOVA	$F = 663.21$ df = 3 and 8 $P < 0.0001$	$F = 98.61$ df = 3 and 8 $P < 0.0001$	$F = 343.83$ df = 3 and 8 $P < 0.0001$	$F = 60.74$ df = 3 and 8 $P < 0.0001$

was not immediate in all groups; and for the first few days, 50 g day⁻¹ represented a slight increase in food intake rather than a decrease (average daily food intake at day 9 post-hatch was 40 g day⁻¹). An extra feeding was sometimes required for chicks between the ages of 10 and 15 days to consume 50 g day⁻¹; however, all diets imposed limitations on chicks within a few days.

We determined composition of fish by proximate analysis (Van Pelt et al. 1997; Table 1) and calculated energy content of diets based on metabolizable energy of lipids (39.3 kJ g⁻¹) and proteins (17.8 kJ g⁻¹; Schmidt-Nielsen 1997). Silverside was 19% protein, 9% lipid, and contained 7.1 kJ g⁻¹; smelt was 14% protein, 7% lipid, and contained 5.2 kJ g⁻¹. Our goal with the 35 g day⁻¹ silverside and 50 g day⁻¹ smelt treatments was to generate iso-energetic diets, though they differed by 19 kJ day⁻¹ (<10%; Table 1).

PLUMAGE

When chicks reached 45 days of age, they were euthanized. All primary feathers (left and right wing) were measured using digital calipers. A wing from each chick was severed at the joint between the humerus and radius-ulna; most of the skin from the patagial area of the extended wing was included. Wings were pinned in the extended position, dried, and traced onto even-thickness weighing paper. The tracing was cut out and weighed and compared with a known-area cutout to estimate wing area for a single wing, then doubled to estimate total wing area (not including body mantle). Wing-

loading on day 45 post-hatch was calculated as mass \times total wing area⁻¹ (Calder 1996). Identical procedures were used to calculate wing-loading for adults of 12 alcid species (A. S. Kitaysky unpubl. data).

STATISTICAL ANALYSIS

Before analyses, data were examined for the assumptions required by parametric statistical tests (Zar 1999). If data violated these assumptions, we used equivalent nonparametric tests. One chick in the 50 g day⁻¹ smelt treatment group did not survive past day 35; it was excluded from all analyses. For all treatments, $n = 6$, except for 50 g day⁻¹ silverside, where $n = 7$.

Diet.—Differences among diets in composition (water, lipid, and protein) and energy content were tested using one-way analysis of variance (ANOVA).

Absolute growth.—We calculated average growth of morphological characters as a proportion of growth in the group with the highest energetic intake (50 g day⁻¹ silverside). Average measurement for all chicks in each group for each day was divided by the average measurement for all chicks in the 50 g day⁻¹ silverside group on the corresponding day; these proportions were then averaged for all days. We analyzed growth of mass, wing, and tarsus using two-way repeated-measures ANOVA, with food type (silverside or smelt) and amount (35 or 50 g) as factors (Fig. 1). We used Fisher's protected least-square difference (PLSD) *post hoc* tests to determine when treatments first diverged from one another.

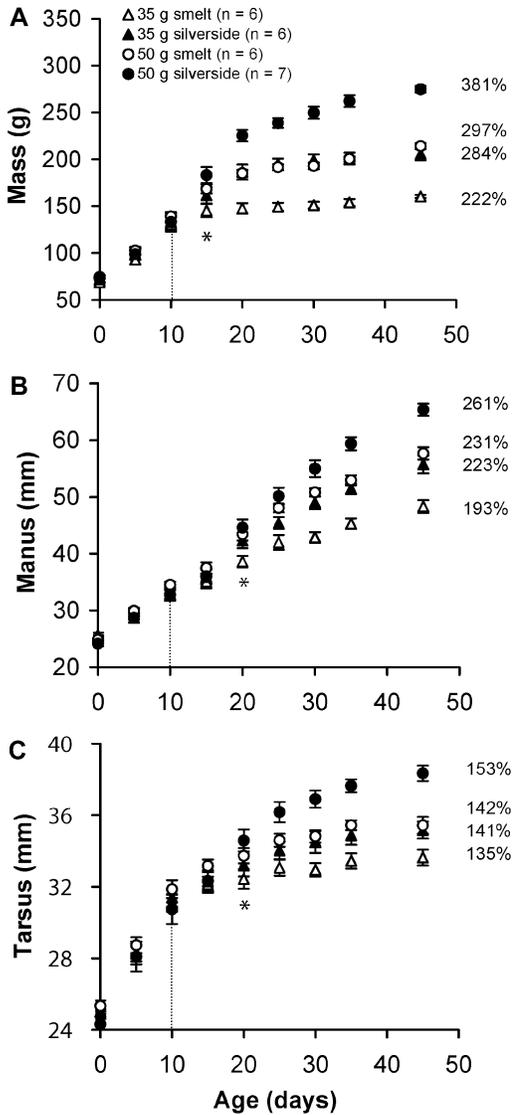


FIG. 1. Age-dependent growth of (A) body mass, (B) manus (skeletal component of wing chord), and (C) tarsus of Common Murre chicks on four different diets (g day^{-1}). Each morphological character was measured on hatch day and every five days afterward (except day 40). Dietary treatments began on day 10 and are indicated by the dotted line. The star indicates the day that measurements from different treatments first diverged. Percentages indicate final measurements (by treatment) for chicks on day 45 compared with average values for all chicks at hatching. Error bars indicate standard errors.

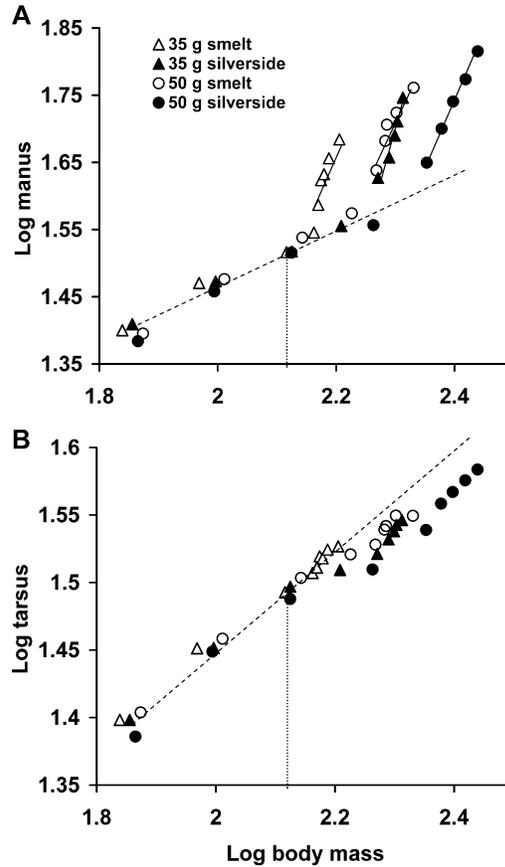


FIG. 2. Growth of skeletal elements, (A) manus and (B) tarsus, in relation to body mass of Common Murre chicks on four different diets. Each point represents the average log mass and average log skeletal element for a treatment at a single age, starting at hatch day and every five days afterward (except day 40). Dietary treatments began on day 10 and are indicated by the dotted line. The dashed line represents the unrestricted growth trajectory projected past day 10. Solid lines represent the growth trajectories of manus (from day 20 to day 45) in response to dietary treatments.

Allometry.—We plotted log manus and log tarsus against log body mass (Fig 2). Chicks in each treatment had two distinct growth trajectories for log manus: an unrestricted intake growth trajectory that did not differ among treatments and a controlled intake growth trajectory that did (Fig. 2A). To define the controlled intake trajectory, we estimated when chicks first deviated from the unrestricted growth trajectory using a box-model iterative threshold analysis to approximate the inflection point for each chick (Piatt 1990, Piatt and Methven 1992). In short, individual curves were transformed into linear relationships and different thresholds tested by sequentially replacing the independent variable (body mass) with dummy variables (0 for points below the test threshold or 1 for points above). For each iteration, least-square linear regression analysis was run, and the regression coefficient (r^2) determined. The best fit for the model, when r^2 is highest, is obtained when the test threshold is just before the inflection point (see Piatt [1990] for details). Because each data point is separated by five days (the interval on which chicks were measured), we defined the mass-at-inflection point as the midpoint between the masses on either side of the test threshold yielding the highest r^2 .

To compare the masses and ages corresponding to the trajectory switch among treatments, we used ANOVA with mass-at-inflection point or threshold age as the dependent variable and treatment as the factor. We then compared slopes and intercepts of the controlled intake trajectories (comprising all points following the inflection point as defined above) among the treatments using analysis of covariance (ANCOVA), with log manus as the dependent variable, treatment as the factor, and log body mass as the covariate (Stewart and German 1999). We used the average measurements for each treatment at each time point. For allometric analyses, the interaction term provides information about whether the slopes differ. If slopes are the same, then allocation is the same among treatments (the increment of manus growth is the same per increment of body mass gain). A significant treatment effect means that chicks are shaped differently—they have different manus lengths for a given body mass.

We used the same approach for log tarsus versus log body mass; however, because the threshold analysis indicated that for all chicks

the inflection point occurred before day 10 (when treatments began), we did not define or analyze controlled intake growth trajectories. Instead, we used ANCOVA to determine whether treatment (factor) or log body mass (covariate) explained variation in log tarsus on day 45 post-hatch (i.e., the end of the study). This allowed us to assess whether final differences in tarsus length were a result of differential allocation in response to treatments or simply body-mass dependent.

Primary flight feathers and wing-loading.—For each chick, we calculated the total length of all primaries on day 45 for each wing and took the average of both wings. Primaries of the chicks in the 35 g day⁻¹ smelt group had not erupted by day 45. Thus, we examined the effect of treatment on the remaining three groups using one-way ANOVA, and a Newman-Keuls test for *post-hoc* comparisons.

We examined effects of treatments on wing area on day 45 post-hatch using ANCOVA, with log wing area as the dependent variable, log body mass as a covariate, and treatment as a factor. If allocation to wing area changes in response to degree of food restriction, treatment will have a significant effect; if it does not, wing area will be affected only by body mass. To test whether chick wing-loading scales similarly to the allometric scaling observed in adult alcids, we compared wing-loading means for chicks in the four treatments with species-specific means for adult alcids with an ANCOVA using age (adult or chick) as a factor and log body mass as a covariate.

RESULTS

ABSOLUTE GROWTH

Dietary treatments affected growth of all morphological characters (Fig. 1 and Table 2). Both type and amount of food affected growth of body mass (food type: $F = 55.14$, $df = 1$ and 22, $P < 0.0001$; food amount: $F = 52.33$, $df = 1$ and 22, $P < 0.0001$; interaction term: $F = 0.48$, $df = 1$ and 22, $P = 0.50$). The results were similar for tarsus (food type: $F = 5.90$, $df = 1$ and 22, $P < 0.05$; food amount: $F = 9.21$, $df = 1$ and 22, $P < 0.01$; interaction term: $F = 0.15$, $df = 1$ and 22, $P = 0.71$) and for manus (food type: $F = 14.09$, $df = 1$ and 22, $P = 0.001$; food amount: $F = 24.88$, $df = 1$ and 22, $P < 0.0001$; interaction term: $F = 0.16$, $df = 1$ and

TABLE 2. Average growth of morphological characters of Common Murre chicks as a proportion of growth in the group with the highest food intake (50 g day⁻¹ silverside). Primaries were measured only on day 45; all other characters were measured every five days.

Diet treatment	Tarsus length	Manus length	Body mass	Total primary length
50 g day ⁻¹ silverside	1.00	1.00	1.00	1.00
50 g day ⁻¹ smelt	0.96	0.94	0.80	0.39
35 g day ⁻¹ silverside	0.95	0.91	0.81	0.12
35 g day ⁻¹ smelt	0.92	0.83	0.64	0.00

22, $P = 0.70$). Body mass diverged first—there were significant differences among treatment groups on day 15 (Fisher's PLSD, $P < 0.05$); manus and tarsus lengths did not differ significantly until day 20 (Fisher's PLSD, $P < 0.05$). The nearly iso-energetic groups (35 g day⁻¹ silverside and 50 g day⁻¹ smelt) never diverged from each other for any of these characters (Fisher's PLSD, $P > 0.05$; Fig. 1).

ALLOCATION

Manus.—Average slope for the unrestricted growth trajectory was 0.44. There was no difference in the age at which chicks shifted growth trajectories; the inflection point occurred between 15 and 20 days in all treatments (treatment effect: $F = 1.55$, $df = 1$ and 21, $P = 0.23$). However, chicks in different treatments shifted growth trajectories at different body masses (effect of body mass as a covariate: $F = 11.32$, $df = 1$ and 21, $P < 0.0001$; Fig. 2A). Controlled intake trajectories (from day 20 to day 45 in all treatments) had the same slope in all treatments (average slope = 2.00; test for parallelism of slopes: $F = 2.27$, $df = 7$ and 12, $P = 0.13$). Both log mass ($F = 200.86$, $df = 4$ and 15, $P < 0.0001$) and treatment ($F = 38.8$, $df = 4$ and 15, $P < 0.0001$) had a significant effect on log manus.

Tarsus.—Average slope for log tarsus versus log body mass from day 0 to day 45 post-hatch was 0.32 (Fig. 2B). On day 45 post-hatch, body-mass corrected log tarsus was not different among treatments (effect of log mass: $F = 7.49$, $df = 4$ and 24, $P = 0.01$; effect of treatment: $F = 0.94$, $df = 4$ and 24, $P = 0.44$).

Flight-feathers.—At 45 days post-hatch, primaries of chicks in the most restricted treatment (35 g day⁻¹ smelt) had not erupted at all, whereas total primary length reached ≤ 366 mm in the least restricted group (50 g day⁻¹ silverside;

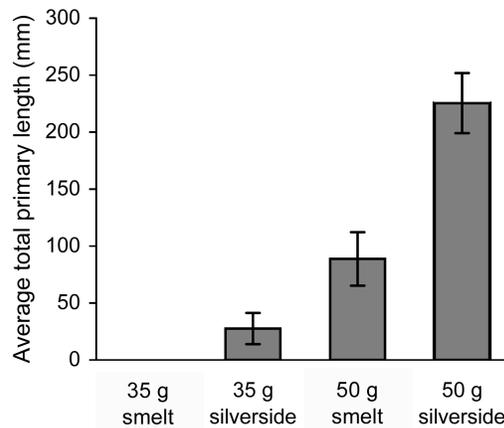


FIG. 3. Feather development of Common Murre chicks on day 45 post-hatch, by dietary treatment. Total primary feather length is the sum of all feather lengths, averaged between left and right wing for each chick. Primaries of chicks in the 35 g day⁻¹ smelt treatment group had not erupted by day 45. Error bars indicate standard errors.

Fig. 3). Total primary length was significantly different among treatments in which chicks had primaries ($F = 21.39$, $df = 2$ and 16, $P < 0.0001$; Newman-Keuls test, $P < 0.05$ for all pair-wise comparisons).

Wing area and wing-loading.—Differences in wing area among treatments were attributable solely to differences in body mass (effect of body mass: $F = 10.72$, $df = 4$ and 20, $P = 0.004$); the relationship between body mass and wing area did not differ among treatments (effect of treatment: $F = 1.45$, $df = 4$ and 20, $P = 0.26$; interaction term: $F = 0.28$, $df = 7$ and 17, $P = 0.84$). Adult alcids had lower wing-loading for their body mass than Common Murre chicks (effect of age: $F = 48.51$, $df = 1$ and 13, $P < 0.001$; Fig. 4), but scaled

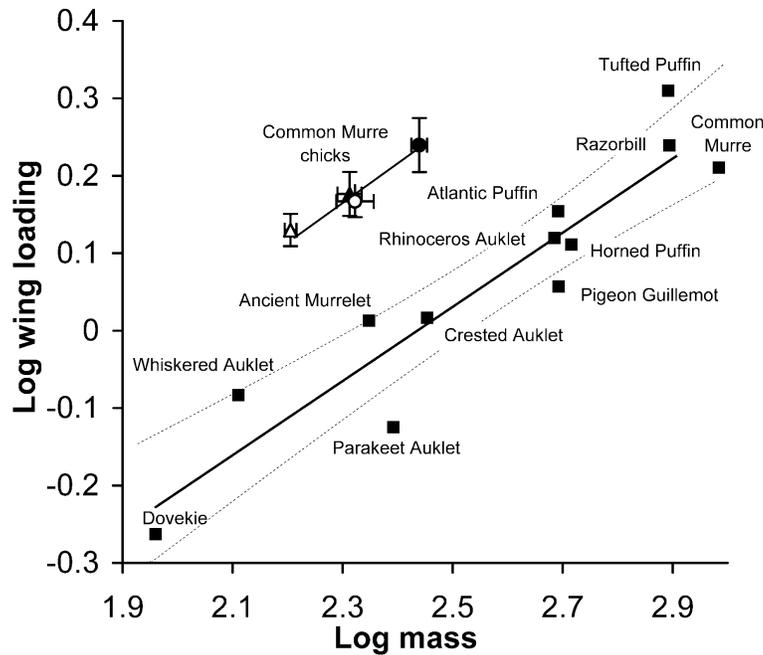


FIG. 4. Relationships between log wing loading ($\text{mass} \times \text{wing area}^{-1}$) and log body mass of Common Murre chicks on day 45 by dietary treatment (circles and triangles; $y = 0.468x - 0.907$, $r^2 = 0.97$, $n = 4$), and adult alcids (filled squares; $y = 0.479x - 1.167$, $r^2 = 0.87$, $n = 12$). Adult alcids: Razorbill (*Alca torda*), Common Murre, Dovekie (*Alle alle*), Pigeon Guillemot (*Cepphus columba*), Ancient Murrelet (*Synthliboramphus antiquus*), Parakeet Auklet (*Aethia psittacula*), Crested Auklet (*A. cristatella*), Whiskered Auklet (*A. pygmaea*), Least Auklet (*A. pusilla*), Rhinoceros Auklet (*Cerorhinca monocerata*), Atlantic Puffin (*Fratercula arctica*), Horned Puffin (*F. corniculata*), and Tufted Puffin (*F. cirrhata*). Error bars indicate standard deviations for Common Murre chicks; dashed lines indicate the 95% confidence interval for adult alcids.

allometrically (effect of body mass: $F = 84.13$, $df = 1$ and 13 , $P < 0.001$). However, slopes for adults and chicks were identical (interaction term: $F = 0.067$, $df = 1$ and 12 , $P = 0.801$).

DISCUSSION

There has been substantial speculation as to which morphological component is most critical in determining Common Murre chick survivorship and, thus, how growth is or should be prioritized (e.g., Hedgren 1981, Hatch 1983, Hipfner and Gaston 1999). We found that food restriction within the intake range observed in pre fledging chicks significantly reduced growth of all characters measured: bones, body mass, and feathers. Subsequent to food restriction, all chicks increased allocation to manus rather than body mass, regardless of the degree of

restriction; however, more restricted chicks began allocating to manus at a lower body mass than less restricted chicks. Thus, severity of food restriction did not affect allocation but affected chicks' proportions—more restricted chicks had longer manus for their body mass.

Body mass.—At the end of the study, chicks were 45 days old and weighed 150–250 g, only 15–25 % of adult body mass (~1 kg; Gaston and Jones 1998). This is likely to be lower than body masses of free-living chicks, which are reported to range from 190 g to 250 g at ~20 days. By some estimates, Common Murre chicks at sea gain 12–16 g day⁻¹ (Ydenberg 1989) and reach 95% of adult mass between 65 and 85 days post-hatch. Thus, between 30 and 45 days of age, chicks in the study were probably receiving less food than their free-living counterparts. However, patterns of growth were established

immediately after treatments began, when food intake and growth rates were still within the natural range.

Allometry.—Aside from primary feathers, body mass appears to be the character most retarded by restricted diets (Fig. 1 and Table 2). This difference in absolute growth rates suggests that chicks were not allocating to maintain body mass; more importantly, it is corroborated by the allometric analyses (Fig. 2). It is not appropriate to compare absolute growth rates of morphological characters of different dimensions and draw conclusions about allocation, because different growth rates are expected even if chicks are growing proportionally. In the simplest case, if chicks allocate such that they maintain the same proportions and grow isometrically (geometric shape is maintained regardless of absolute size; Schmidt-Nielsen 1984), then skeletal elements (which are linear) should scale to mass (which is best approximated as volumetric) to the one-third power. For example, a two-fold increase in any skeletal measurement is expected to be accompanied by an eight-fold (2^3) increase in body mass (Gould 1966). The most appropriate way to compare growth rates of these characters with different dimensions is to examine allometric relationships: log transform both characters and plot the skeletal elements against body mass (Gould 1966, Schmidt-Nielsen 1984). This approach can be used to compare growth patterns across taxa (Gould 1966), developmental stages (McLellan et al. 2002), sexes (Stewart and German 1999), or treatments (Koumoundouros et al. 2001, present study). A comparison of slopes indicates whether animals are allocating (changing shape) in the same way, whereas intercepts indicate relative shape (whether animals are the same size for a given mass; Schmidt-Nielsen 1984).

Manus.—Despite the fact that development of manus was reduced by food restriction (Fig. 1B), chicks allocated to maintain manus growth preferentially over growth of body mass (Fig. 2A). This allocation was manifested as a shift in growth trajectory. Shortly after dietary treatments began, the average slope of the relationship between log manus and log body mass more than quadrupled from 0.44 to 2.00. In contrast, if chicks had switched allocation to favor body mass, the new slope would have been shallower than in the initial trajectory. The degree of energy restriction affected the inflection point of this

shift (chicks in different treatments shifted trajectories at different body masses), but not the slope of the relationship. Thus, once chicks shifted, they allocated similarly regardless of the degree of food restriction.

There are two possible explanations for this. There may be two distinct growth trajectories for Common Murre chicks that are defined by their energy intake. In this scenario, chicks grow on one trajectory until their energetic demands exceed intake (this corresponds to a certain body mass for a given energy intake). At this point, chicks reallocate resources and begin to grow on the alternate trajectory, prioritizing manus growth. However, because chicks in all treatments switched allocation at approximately the same age (between 15 and 20 days post-hatch), the switch in allocation cannot be definitively attributed to energy restriction. Alternatively, it may be a developmentally determined shift in allocation that occurs at a certain age, regardless of food intake. Ideally, measurements would be taken daily to determine whether treatments shifted allocation at exactly the same age. In addition, a control group fed *ad libitum* for the duration of the study would have helped distinguish between ontogenetic factors and direct response to restriction. However, the 50 g day⁻¹ silverside group was consuming close to the observed maximum fed to nestlings in the wild, and it is unlikely that they exceeded energetic demands in the same window of time (15–20 days) as the lowest intake group (35 g day⁻¹ smelt). This suggests that the switch in allocation may be developmentally programmed. Changes in allocation may still be adaptive, but they may not be shaped by food intake.

Regardless of what drove the switch in growth trajectories, once on the alternate trajectory, all chicks allocated in the same way (slopes were the same), though they were at different masses when they switched trajectories. This resulted in chicks of different shapes that were scaling in the same way. Identical allocation despite differences in food intake also suggests that there is a strong ontogenetic component to the growth patterns we observed. Note that similar allocation among treatments was independent of absolute growth rates, which were vastly different.

Tarsus.—Although tarsus growth was clearly retarded by dietary restriction (Fig. 1C), it appeared to be the least vulnerable of the morphological characters we measured (Table 2).

These results agree with those of an Atlantic Puffin study that indicated that tarsus was less sensitive to food restriction than body mass or feather growth (Øyan and Anker-Nilssen 1996). When assessed in comparison with body mass, tarsus appears to respond similarly to manus in that more restricted chicks appear to have a longer tarsus for their body size (Fig. 2B); however, the trajectories are not statistically distinct. The relative insensitivity of tarsus to food restriction is primarily attributable to the fact that at hatching, tarsus is closer to adult size than any other character. For Common Murre chicks, tarsus length is primarily dictated by prehatching rather than post-hatching resource allocation, which suggests that it may be one of the highest priorities. After hatching, chicks need to devote relatively little of their resources to tarsus to attain adult size; by day 45 post-hatch, the differences among treatments are still small (Fig. 1C), and chicks in the high-intake treatment have nearly attained adult tarsus length (38–42 mm in Alaskan populations; Ainley et al. 2002). Tarsus may be a developmental priority for Common Murres either because it facilitates clinging to breeding sites that are often bare, sloped rock, or because their primary mode of locomotion for several months after fledging is swimming on the sea surface using foot propulsion (Ainley et al. 2002). A well-developed tarsus would facilitate travel between patchily distributed food sources as well as increase speed and maneuverability for avoiding predators and launching dives. The area of the foot may also be important but was not measured here.

Primary feathers.—Primary feathers were more sensitive to small dietary differences than any other morphological character measured, because they were the only character for which the 35 g day⁻¹ silverside and 50 g d⁻¹ smelt groups diverged (Figs. 1 and 3). Chicks consuming 50 g day⁻¹ smelt grew longer primaries than chicks consuming the nearly iso-energetic amount of silverside (Fig. 3). The smelt group received the same amount of lipid and protein, slightly more energy (+19 kJ day⁻¹) and substantially more water (+15 g day⁻¹) than the silverside group (Table 1). Although protein is considered critical for molt in adult passerines, it is also possible that chicks consuming 35 g day⁻¹ silverside receive less of the essential amino acids (particularly the sulfur-containing ones like cysteine), which may be the limiting factor

for feather growth (Murphy and King 1992). Under the adaptive growth hypothesis, sensitivity of primary feathers to small dietary differences would suggest that they are not a functional priority for Common Murres during this period. However, given the extremely specific nutritional requirements for feather regrowth during molt in adult birds, feather growth may simply be more tightly constrained by subtle aspects of nutrition than skeletal elements or body mass.

Wing area and wing-loading.—Common Murre chicks did not allocate to maintain an absolute “optimal” wing area or wing-loading that was independent of body mass. This is expected, because both parameters should scale allometrically (Calder 1996). We found that chicks scaled identically to adult alcids, but had higher wing-loading for their body mass (Fig. 4). Assuming that the scaling observed for adult alcids reflects a morphological balance between aerial flight (low wing-loading) and underwater flight (high wing-loading), a functional interpretation of chick wing-loading indicates that chicks are structurally suited for underwater performance, rather than aerial flight (Livezey 1988, Calder 1996).

Fledglings’ survival may depend on their ability to escape predators by diving successfully, and to forage effectively underwater. Because the mechanics of “flying” in a high-density medium like water requires reduced wing area (Pennycuik 1987), high wing-loading—both absolutely and in relation to body mass—is a trait common to birds that are adapted to underwater flying (Calder 1996). Although the fact that chicks in all treatments had high wing-loading for their body mass suggests that underwater performance exerts stronger selection pressure than aerial performance at this stage, it may reflect developmental constraints on wing or feather growth.

Most discussions of the importance of wing area and wing-loading focus on their relevance to successful fledging, which for Common Murres takes place near 20 days post-hatch (Gaston and Jones 1998), rather than 45 days post-hatch, when feather measurements were taken for the present study. However, even at 20 days post-hatch, the relationship between wing-loading and survival is not clear. Fledging Common Murres are not capable of flight but need to descend from their cliff-top breeding

sites to the water below and are often described as gliding or parachuting down on extended wings. If fledging success were solely dependent on a chick's ability to glide, wing-loading would not be critical because it would affect gliding speed but not gliding distance (Pennycuik 1987). However, most fledging Common Murre chicks flap on their way down from the colony (Hedgren 1981), presumably to generate lift to prolong the descent and land in the safety of the water. Thus, lower wing-loading (larger wing area in relation to body mass) would permit more lift and may be valuable. Despite the relatively high wing-loading at day 45, preferential allocation to manus over body mass at day 20 could reduce wing-loading and provide extra lift during fledging.

The patterns of relative growth that we observed concur with a number of studies: growth of body mass appears to be a lower priority than growth of wing components (Øyan and Anker-Nilssen 1996, Kitaysky 1999, Ashton and Armstrong 2002, Dahdul and Horn 2003). If the shift in allocation to wing is developmentally determined, it occurs at the age when chicks are preparing to fledge (just before 20 days post-hatch) and may reduce wing-loading, still providing support for the hypothesis that wing length is important for fledging or postfledging survival of Common Murres (Hedgren 1981, Hipfner and Gaston 1999). By contrast, allocation to mass gain rather than wing development has been suggested in some avian species (Congdon 1990, Bize et al. 2003). If patterns of allocation are in fact adaptive, then these differences may reflect different ecological or life-history pressures operating on different species.

Aging Common Murre chicks.—The results here clearly demonstrate that all morphological characters are vulnerable to significant retardation in response to variability in food intake. Interannual, intercolony, and inter-individual differences in chick provisioning can yield chicks that are the same age but have different sizes and shapes. Therefore, neither single morphological characters nor ratios of morphological characters can be used to accurately age Common Murre chicks.

CONCLUSION

The present study shows not only that differences in food intake have profound effects on

patterns of growth of Common Murre chicks, but that all chicks undergo fundamentally similar changes in allocation that may be independent of food intake. Ontogenetically determined changes in patterns of growth deserve further attention. In light of the adaptive growth hypothesis, our finding that chicks preferentially allocate to maintain growth of manus seems to support the hypothesis that wing length is a functional priority for Common Murre chicks. However, because it is not possible to manipulate relative growth rates, hypotheses about the adaptive value of patterns of allocation cannot be tested directly. Despite this, further research to elucidate patterns of growth over the course of development in species facing different ecological and life-history pressures is needed. Understanding the ontogenetic contribution to growth patterns as well as responses to different degrees of temporary and chronic food restriction will yield insight into the flexibility of and constraints on growth, adult phenotype, and survival of birds that regularly face fluctuations in food availability during the nestling period.

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