ALLOCATION OF GROWTH IN FOOD-STRESSED ATLANTIC PUFFIN CHICKS

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ABSTRACT.—In long-lived seabirds that lay a single-egg clutch, allocation of growth to certain body parts may be advantageous for the chick if food is limited. To investigate this, 40 Atlantic Puffin (*Fratercula arctica*) hatchlings were distributed in seven groups that were raised on different amounts of food to 38 days of age. When food intake was reduced, growth rates were depressed for all characters measured (i.e. body mass and length of the wing, 2nd primary, forearm, head + bill, culmen, skull, tarsus, and middle toe). Head and wing parts grew preferentially relative to the other characters, and onset of growth was delayed in the primaries. All chicks accumulated significant amounts of subcutaneous fat, whereas internal fat deposits were present only in the chicks that received the most food. *Received 14 July 1995, accepted 20 March 1996.*

ONE WAY that parent birds adjust for variation in food availability is to vary clutch size (Lack 1954, 1966, 1968). In long-lived species that lay a single-egg clutch, alteration of chick growth rate apparently is the only strategy available to adjust for variation in food. Slow growth reduces daily energy requirements and allows food to be delivered at a lower rate (Lack 1968; Ricklefs 1968, 1979; Harris 1977; Nelson 1977; Drent and Daan 1980). Chick abandonment is likely when food demands cannot be met and current offspring contribute relatively little to total lifetime reproduction (Williams 1966, Goodman 1974, Drent and Daan 1980, Ricklefs 1983). Variable growth provides a basis for developmental adaptations in the chick, such as allocation of growth to parts of the body that would help reduce the nestling period and increase the chances of survival after fledging. Some seabird chicks (e.g. murres [*Uria* spp.] and Razorbills [*Alca torda*]), escape part of this dilemma by leaving the nest soon after hatching to accompany (and be fed by) their parents at sea (e.g. Lack 1968, Harris and Birkhead 1985, Ydenberg 1989). In contrast, studies of species that feed their chicks at the nest (e.g. Manx Shearwater [*Puffinus puffinus*], Harris 1966; Atlantic Puffins [*Fratercula arctica*], Tschanz 1979, Anker-Nilssen 1987; and Yellow-eyed Penguin [*Megadyptes antipodes*], van Heezik 1990) suggest that developing chicks faced with food shortages allocate resources preferentially to certain body parts.

The wide variation in chick growth rates among species of alcids has been attributed to constraints on feeding ecology, such as specialized foraging behaviors, unpredictable and patchy food distributions, and great distances between feeding and nesting sites (Lack 1968; Ricklefs 1968, 1984; Ashmole 1971; Sealy 1973; Nelson 1977; Birkhead and Harris 1985). Thus, chicks of pelagic alcids often face the problem of being fed at a low rate or even abandoned, because the contribution of an individual chick to the total lifetime reproduction of its parents is fairly small.

The burrow-nesting Atlantic Puffin is a typical alcid. It is long-lived, has delayed sexual maturity, lays one egg per clutch, and feeds mainly on pelagic fish (Harris 1984, Harris and Birkhead 1985). Chick-rearing is shared by both parents and spans 34–74 days from hatching to fledging, depending on food supply (Nettleship 1972, Harris 1984, Harris and Birkhead 1985, Barrett and Rikardsen 1992). Puffin chicks leave the nest burrow when they are about 60–80% of adult body mass (Harris and Birkhead 1985). They are at risk to abandonment by their parents because adult puffins are specialized feeders that pursue a variable and patchy food supply (Anker-Nilssen 1987, 1992; Anker-Nilssen and Øyan 1995).

Our study focused on identifying adaptations in puffin chicks that may have evolved to reduce the length of the nestling period when food supply is limited. We hypothesized that preferential allocation of growth takes place during food shortages. The allocation should favor body parts that enable the chick to reach

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the sea at an earlier physiological age or at a lower mass than "normal" and increase its chances of survival during the critical first time at sea. The characters investigated were body mass and growth of the wings, head, and feet. Fat storage also was measured because fat could serve as an energy supply during periods of erratic food availability and during the first days of independence (Lack 1968, Drent and Daan 1980, Ricklefs 1990).

STUDY AREA AND METHODS

Study area.—The study was carried out in the archipelago of Røst in northern Norway during the summers of 1990 and 1991. Chicks were collected (under license from the Directorate of Nature Management) from nest burrows on the island Hernyken (67°26'N, 11°52'E), which had approximately 55,000 occupied burrows in 1990. The puffin colony of Røst amounts to about 660,000 pairs and constitutes almost one-third of the total Norwegian population of Atlantic Puffins (Anker-Nilssen and Øyan 1995).

Chicks.—In the beginning of each June, 100 accessible nests containing an egg were checked every evening throughout the hatching period. When approximately one-third of the eggs had hatched, 20 chicks (less than 24 h old) were collected and randomly distributed between the experimental groups (see below). Chicks were collected between 23 June and 3 July in 1990 and 25 and 27 June in 1991. The first day after collection was defined as day 1, and chick mass at this day prior to their first meal was taken as the hatching mass. Chicks weighed less at hatching in 1990 than in 1991 ($t = 2.30$, df $= 37$, $P = 0.027$), but the difference was only 2 g (i.e. $<5\%$ of body mass). Therefore, data from both years were pooled for subsequent analyses.

Experimental design.—Five blocks of four one-chick cages ($21 \times 30 \times 20$ cm) were built of waterproof plywood and wire netting. Aluminum profiles with built-in heating elements made up the cross walls of the cages. The surface temperature of the profiles was regulated by a voltage regulator (Lübcke R52-220b) and kept within the range 34–37°C for the first 10 days, to compensate for brooding. During the rest of the experiment it was kept at 20–22°C to keep the chicks dry, as excreted salty water tended to accumulate on the inner walls of the cages. The room was kept dark except during a few hours of cleaning every 1–3 days, and temperature was approximately 12–15°C throughout the experiment. Disturbance was kept to a minimum.

Chicks were fed on capelin (*Mallotus villosus*) that were caught and frozen in the Barents Sea each May. Capelin were transported to Røst in blocks of 15–25 kg, which were then thawed, divided into one-day rations, and stored frozen. Individual rations were thawed in the evening before being given to the chicks as four portions supplied one by one at 0900, 1300, 1700 and 2100 (standard time). A few milligrams of Vitaplex® multivitamin were added to the morning meal every day. The experimental period ended at day 38, and at day 43 the chicks were sacrificed and frozen. All carcasses were later dissected.

In 1990, chicks were placed into two groups and given different amounts of food; diets (different amounts of capelin) were designed to simulate chick growth on Røst during a "bad" and a "good" year such that one group (group 3) always received half the amount of food as the other (group 6). One standardized equivalent (i.e. 3.33 g) of food was used as the basis for the design of the diets. One group was started with three equivalents, the other with six. In 1991, five groups were established and given 2, 4, 5, 6, and 7 equivalents, respectively, from day 1 (Table 1). At days 4, 10, and 19, chick diets were increased by a number of equivalents corresponding to their group number. Due to insufficient supplies of capelin, each chick was fed 50 g of capelin per day from the end of the experiment to day 43, resembling the "normal" age at fledging at Røst (Anker-Nilssen and Øyan 1995). Groups given equal amounts of food (group 6 in both years) acted as controls for possible differences in experimental conditions between the years. Due to a temporary problem with salted capelin being given to chicks in group 6 on days 17 to 19 in 1990, this group was excluded from further analysis.

Most chicks ate willingly throughout the experiment, except that chicks in groups 6 and 7, which were provided with the most abundant food supply, occasionally had to be force-fed during the first and last 2 to 4 days. This reluctance to feed probably was a consequence of excessive feeding, as several studies indicate much lower daily food requirements of wild puffin chicks early and late in the nestling period (Harris 1976, Harris and Hislop 1978, Ashcroft 1979, Anker-Nilssen 1987).

The quality of random samples of the capelin was determined at the Agricultural University of Norway at Ås (1990) and the State Food Control Authority at Kvål (1991) according to standard methods for water, crude fat (HCl), protein (Kjeldahl-N), and total ash content. Sample sizes were small, but there was no indication that protein and fat content of the fish differed between the two years (Table 2). The mean energetic value for the capelin was about 5.3 kJ/g of wet mass, which is well within the range of 3–11 kJ/g reported by Bradstreet and Brown (1985) and others (e.g. Barrett et al. 1987) for food brought to puffin chicks by their parents.

Measurements.—In 1990, chicks were measured every morning for the first 26 days, and thereafter every second morning. In 1991, chicks were measured each morning throughout the experimental period. All measurements were done before the first feeding of the day. Chicks were weighed to the nearest 0.2 g

TABLE 1. Amount of food (g/day and total) given to each puffin chick in the various experimental groups. The group number indicates the number of food equivalents (i.e. 3.33 g) given at the onset of the experiment.

| Group | No. of chicks | | Age of chicks (days) | | | | Total |
	1990	1991	1–3	4–9	10–18	19–37	
2	—	4	6.7	13.3	20.0	26.7	787.7
3	10	—	10.0	20.0	30.0	40.0	1,180.0
4	—	4	13.3	26.7	40.0	53.3	1,573.3
5	—	4	16.7	33.3	50.0	66.7	1,966.7
6[a]	10	4	20.0	40.0	60.0	80.0	2,360.0
7	—	4	23.3	46.7	70.0	93.3	2,753.3

[a] Group 6 excluded from analyses after day 17 in 1990. See text.

using an electronic balance. Wing length (maximum flattened chord) and, in 1991, length of the 2nd primary (from the tip to the point where the quill appears from the sheath) were measured to the nearest 1 mm using a stopped ruler. Vernier calipers were used to measure (± 0.1 mm) length of culmen, head + bill (Jones et al. 1982), tarsus, and middle toe (Tschanz 1979). Skull length was calculated by subtracting culmen length from head + bill, and length of the forearm was calculated by subtracting length of 2nd primary from total wing length (as used here "forearm" refers to the antebrachium plus the manus). All measurements were made by one person. Tarsus data from 1990 were omitted from the analyses due to a change in measuring technique.

The chicks were sexed by dissection. Sex distribution did not differ between groups ($\chi^2 = 7.07$, df = 6, $P = 0.314$; Table 3). In 1991, the amounts of deposited subcutaneous and internal posterior fat were ranked from 0 to 3 (see Jones et al. 1982). Also, the maximum thickness of the ventral subcutaneous fat depot was measured using vernier calipers to the nearest 0.1 mm, after making an incision lengthwise from the inside of the skin; internal posterior fat was excised and weighed to the nearest 0.01 g on an electronic balance. During June to August 1992, 243 adult puffins (with at least three bill grooves; Petersen [1976], Harris [1984]) were caught in mist nets at Hernyken and measured by the same person. Except for the length of 2nd primary, the same characters measured on the chicks were measured on adults.

Statistical analyses.—Most statistical calculations and tests (always two-tailed) were made using the CSS/ pc (Complete Statistical System, version 2.1) computer package. A simple statistical routine programmed in Fortran was used to calculate group means and SEs, whereas all growth curves were made using SigmaPlot (version 4.02).

Two methods were used to compare group means: (1) growth curves of group means ± 1 SE were compared directly by visual inspection; and (2) a growth index was determined for each character by comparing each of groups 2–6 with group 7, which always attained the best growth. Mean hatchling size (all groups) and final chick size in each group were converted to percentage of adult size and compared for all characters except for length of 2nd primary, forearm, and skull. Skull comparisons were omitted due to the great differences in bill proportions between adults and chicks.

RESULTS

All chicks survived until the end of the experiment. Retarded growth rates were recorded for all characters as a consequence of low food intake. Body mass was the only character in which growth was approximately proportional to the amount of food given (Fig. 1).

Wing characters.—The two groups with the lowest food supply lagged behind by day 9 in total wing length (Fig. 2). Total wing length was influenced mainly by growth of the 2nd primary, which was the only character where a delayed onset of growth was more apparent than reduced growth rate (Fig. 3). Primaries appeared to grow approximately at a constant rate

TABLE 2. Protein, fat, and caloric content of capelin (*Mallotus villosus*) fed to puffin chicks during experiments. Data are medians, with sample sizes in parentheses (each sample was derived from several fish). Energy values for 1990 were obtained from Breivik (1991).

Variable	1990	1991
Protein (% of dry mass)	60.3 (3)	60.9 (2)
Crude fat (% of dry mass)	30.8 (3)	29.8 (2)
Energy (kJ/g wet mass)	5.7 (3)	4.9 (2)

TABLE 3. Sex distribution of puffin chicks within experimental groups.

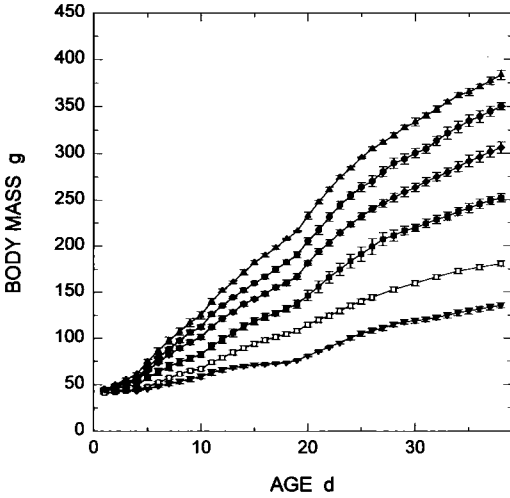| Sex | Experimental group | | | | | | Total |
	2	3	4	5	6	7	
Females	3	5	2	0	1	3	18
Males	1	5	2	4	3	1	22

FIG. 1.   Growth curves for body mass (mean ± SE) of puffin chicks in each experimental group (filled triangle pointing down, group 2; hollow square, group 3; filled square, group 4; filled diamond, group 5; filled circle, group 6; filled triangle pointing up, group 7). Sample sizes are given in Table 1.
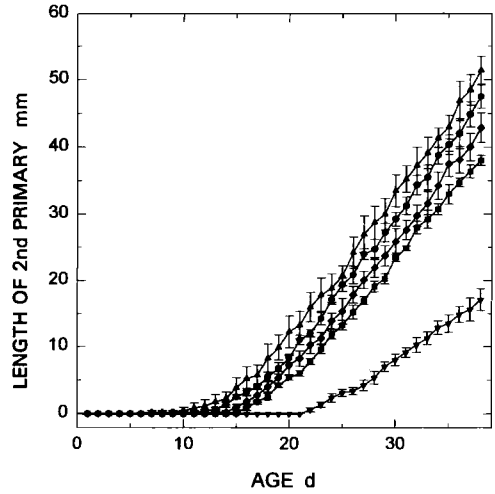

FIG. 3.   Growth curves for length of 2nd primary (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.

within each group throughout the experiment. Growth rate was almost identical in groups 4 to 7 (slope of linear regression 1.8, 1.9, 2.0 and 2.0 mm/day, respectively), but it decreased by nearly half in group 2 (1.1 mm/day). Primary quills erupted between days 11 and 14 in groups 4 to 7, whereas primaries did not erupt until

day 22 in group 2. Growth of the forearm in group 2 deviated from the others on day 6, and never obtained an asymptotic value, whereas all other groups reached almost the same asymptotic value (Fig. 4). The growth index for the forearm in group 2 (42%) was nearly half of that in the other groups (79–94%; Table 4).
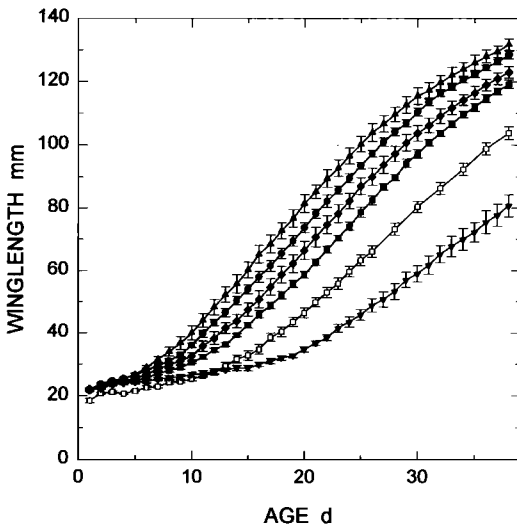
Head characters.—Culmen growth in groups

FIG. 2.   Growth curves for wing length (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.
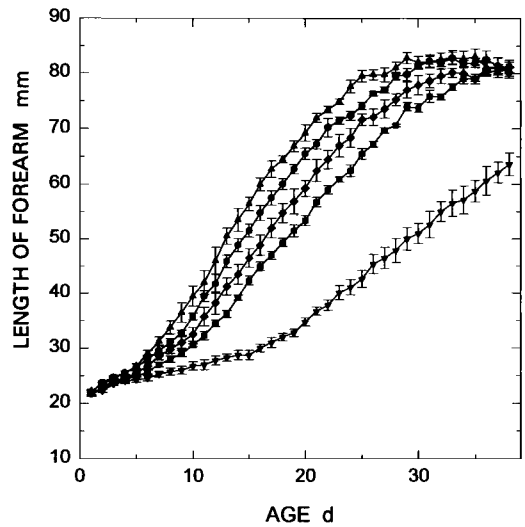

FIG. 4.   Growth curves for length of forearm (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.

TABLE 4. Growth indices for morphological characters in experimental puffin chicks. The growth index is the total amount of growth attained as a percentage of that in group 7 (the group receiving the most food), rounded to the nearest whole percentage. Within groups, preference orders are in parentheses (preference decreases with increasing numbers). Data are plotted in Figure 10. Head + bill and wing length are composites of other characters.

| Character | Experimental group | | | | | | Sum of ranks | Overall priority |
	2	3	4	5	6	7		
Skull	57 (1)	83	78 (3)	91 (1)	101 (1)	100	6.0	1
Culmen	51 (2)	56	85 (1)	85 (4.5)	96 (2)	100	9.5	2
Forearm	42 (3)	—	79 (2)	87 (3)	94 (3.5)	100	11.5	3
Middle toe	33 (4)	55	74 (4)	90 (2)	94 (3.5)	100	13.5	4
Tarsus	31 (5)	—	69 (5)	85 (4.5)	93 (5)	100	19.5	5
2nd primary	22 (7)	—	66 (6)	75 (6)	87 (6.5)	100	25.5	6
Body mass	23 (6)	39	58 (7)	74 (7)	87 (6.5)	100	26.5	7
Head + bill	54	71	81	89	97	100	—	—
Wing length	36	60	75	83	92	100	—	—

2 and 3 was markedly slower than in the other groups from day 9 onwards (Fig. 5), and their growth indices were only about half of that in group 7 (Table 4). Head characters in groups 4 to 7 grew at similar rates throughout the experiment. Skull and head + bill were the characters in which differences in growth between groups apparently was the smallest (Figs. 6 and 7). Nevertheless, group 2 still lagged behind, acquiring a growth index of about 55%, whereas groups 3 to 6 achieved between 83 and 101% for skull length and between 71 and 97% for head + bill length (Table 4).

Characters of the feet.—Both middle toe and tarsus differed greatly in growth across groups (Figs. 8 and 9). Tarsus length diminished in all groups shortly after hatching. At day 6, group 2 split from the rest and displayed markedly slower growth than the other groups for the rest of the experiment. Asymptotic values were reached by groups 4–7 for tarsus, and by groups 6 and 7 for middle toe, although at slightly different levels in each group. Growth indices varied from 31 to 94% for both characters (Table 4).

Comparisons among characters.—Characters differed in the threshold and degree of reduced growth rate. In some characters, most groups
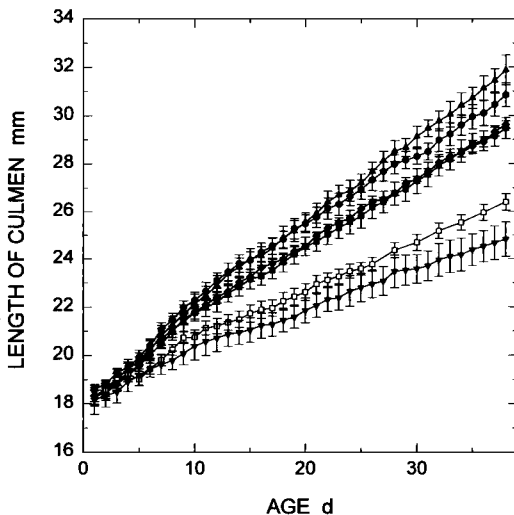

FIG. 5. Growth curves for length of culmen (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.
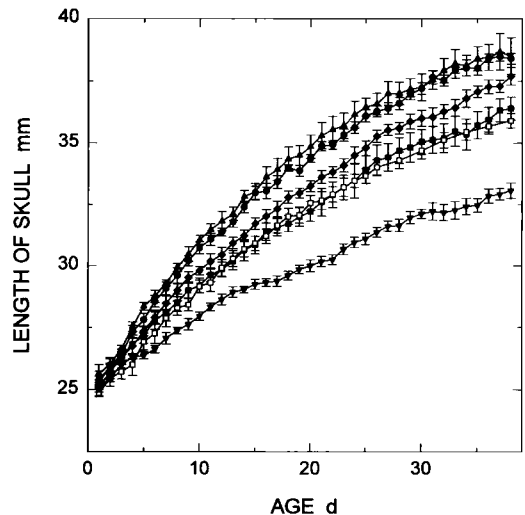

FIG. 6. Growth curves for length of skull (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.
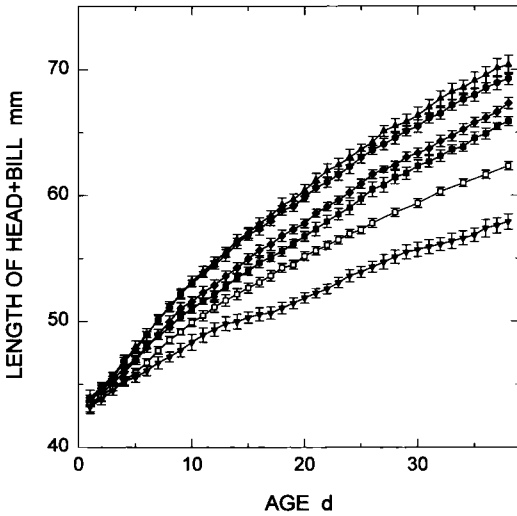
FIG. 7. Growth curves for length of head + bill (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.
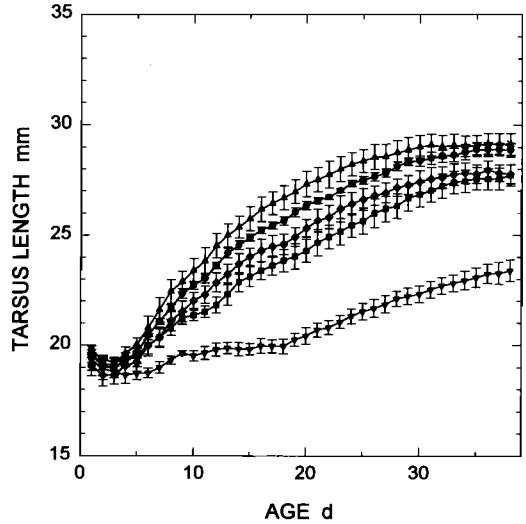

FIG. 9. Growth curves for length of tarsus (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.

exhibited very different growth rates (most evident in middle toe; Fig. 8), whereas in length of 2nd primary and culmen, retarded growth rates were pronounced only in groups 2 and 3 (Figs. 3 and 5).

Growth increased with food intake but differed among characters (Fig. 10). The effect of food intake was most pronounced for body mass,
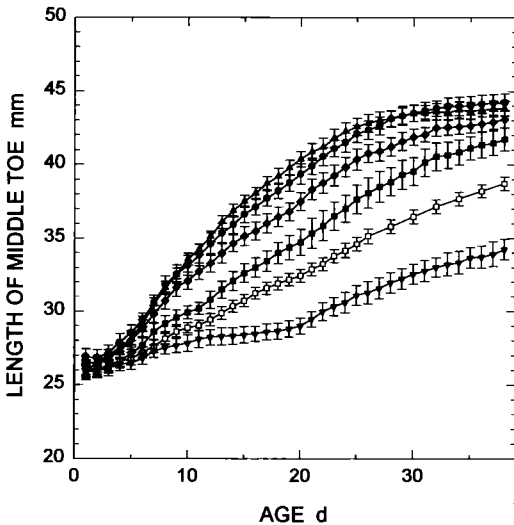

FIG. 8. Growth curves for length of middle toe (mean ± SE) in puffin chicks in each experimental group. Symbols are same as in Figure 1; sample sizes are given in Table 1.
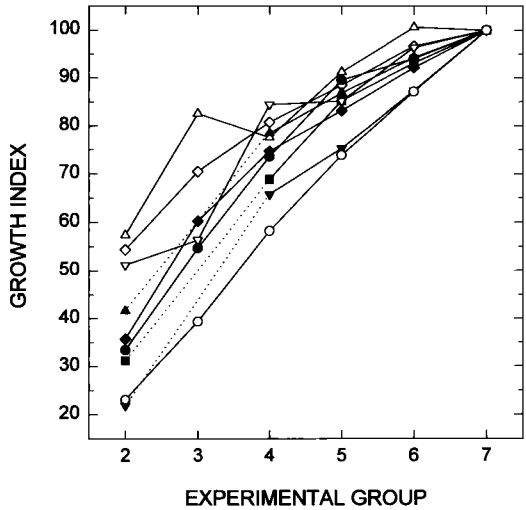

FIG. 10. Growth index (amount of total growth as percentage of growth in group 7) of morphological characters for each experimental group (hollow triangle pointing up, length of skull; hollow diamond, length of head + bill; hollow triangle pointing down, length of culmen; filled triangle pointing up, length of forearm; filled diamond, total wing length; filled circle, length of middle toe; filled square, length of tarsus; hollow circle, body mass; filled triangle pointing down, length of 2nd primary). Sample sizes are given in Table 1.

TABLE 5. Measurements of adult puffins compared with measurements of chicks (as % of adult size) at day 1 and day 38, the latter separated by experimental group.

Character	Adults			Chicks at day 1	Chicks at day 38 (by experimental group)					
	$\bar{x}$	SD	n		2	3	4	5	6	7
Body mass (g)	451.8	33.4	243	10	30	40	56	68	78	85
Wing (mm)	172.1	3.7	231	12	47	60	69	71	75	77
Culmen (mm)	45.6	1.9	230	40	54	58	65	65	68	70
Head + bill (mm)	81.0	2.1	230	54	72	77	81	83	85	87
Middle toe (mm)	45.7	1.6	55	57	75	85	91	94	97	96
Tarsus (mm)	28.8	1.0	55	68	81	—	96	97	100	101

where dependence on amount of food was almost linear. According to a simple ranking of growth indices within groups, the overall order of priority increased from body mass, primary length, tarsus, middle toe, forearm, and culmen to the skull (Table 4). Compared with adult size, the tarsus was the most developed character at hatching, followed by middle toe, head + bill, culmen, wing, and body mass (Table 5).

Fat storage.—Even the chicks that received the least amount of food deposited considerable amounts of fat. The amount of subcutaneous fat varied between scores 2 and 3, whereas internal posterior fat deposits were more variable (Table 6). The thickness of subcutaneous fat was approximately 40% higher in group 7 than in groups 2 and 3, and posterior fat deposits in group 7 were approximately 100 times greater than those in group 2.

DISCUSSION

Tradeoffs between adult survival and fecundity are important in the characterization of a bird's life history strategy (e.g. Lindén and Møller 1989, Stearns 1992, Martin 1995). The longevity, delayed onset of reproduction, and

TABLE 6. Fat deposits in puffin chicks at 43 days old, by experimental group. Fat scores ranged from 0 to 3 (see Jones et al. 1982).

Variable	Experimental group				
	2	4	5	6	7
Subcutaneous fat					
Median score	2.0	3.0	3.0	3.0	3.0
$\bar{x}$ thickness (mm)	3.6	3.6	4.1	4.4	5.1
SD thickness (mm)	0.9	0.2	0.2	0.3	0.7
Internal posterior fat					
Median score	1.0	2.0	2.5	3.0	3.0
$\bar{x}$ mass (g)	0.04	0.42	1.47	2.16	4.76
SD mass (g)	0.02	0.19	0.42	0.44	1.28

single-egg clutch of Atlantic Puffins (Hudson 1985) are traits that clearly put this species among those that give high priority to adult survival. Such species are more likely to withstand long-term environmental stresses that affect food availability. In species depending on highly unpredictable food sources, the ability of adults to breed will be sensitive to changes in prey availability. In long-lived species with clutches of one, this sensitivity may be strengthened by the fact that the single chick is expected to contribute relatively little to its parents' fitness (Clark and Ydenberg 1990). Life history theory states that risks are assumed in proportion to the adults' expectations of mortality between breeding seasons (Lindén and Møller 1989, Stearns 1992, Martin 1995), which normally is only 5–10% in Atlantic Puffins (Harris and Wanless 1991, Anker-Nilsson and Øyan 1995). Consequently, food limitation often results in poor growth, delayed fledging, and increased mortality of chicks, and may even induce the adults to abandon the nest. Such effects have been demonstrated in Atlantic Puffins and in closely related species (Harris 1978; Vermeer et al. 1979; Vermeer 1980; Lid 1981; Brown and Nettleship 1984; Anker-Nilsson 1987, 1992; Barrett et al. 1987; Martin 1989; Anker-Nilsson and Øyan 1995). Apparently, the chick will suffer from starvation unless it is able to develop adaptations that allow it to leave the nest at an earlier physiological age.

Differential growth as a response to reduced food supply has been reported in many birds, including both altricial and precocial species (Schew 1995, Schew and Ricklefs 1996). Some responses seem to be universal and probably reflect physiological constraints or adaptations that are of vital importance to all species. For instance, growth should be allocated to the nervous system and other structures that are the least able to recover from retardation (see Schew

and Ricklefs 1996). Consequently, great caution is needed before claiming that an allocation of growth is an adaptation to the particular ecology of the species in question. Nevertheless, it is important to consider any reasonable ecological explanation that could be involved, and which also may motivate further research.

Our experiment was not designed to identify the extent to which growth restrictions were merely imposed responses, i.e. a direct and unavoidable consequence of reduced supply (cf. Schew and Ricklefs 1996). The gradual retardation of growth rate for most characters among groups, as well as within groups during periods of constant food supply, indicated that imposed responses are effective in puffin chicks. Nevertheless, the heterogeneous effects of food restrictions on different characters strongly suggest that induced, adaptive variation also played an important role.

Characters of greatest importance for survival may be expected to be given preferential allocation of resources and change relatively little, or at least change less than characters of low priority. Thus, our study indicated that body mass, tarsus, and middle toe were of lower priority in puffin chicks, given their large changes in growth with varying food intake. The low-ranking value of primary length was due mainly to aspects of the growth index method, which is less applicable when a delay in onset of growth is apparent. The fact that the growth rate for primaries was approximately the same for groups 4 to 7 demonstrates that growth of primaries is given high priority when first initiated. This has been supported by other investigations. For instance, Lack and Silva (1949) found that bursting of feather sheaths in nestling European Robins (*Erithacus rubecula*) occurred independently of body mass, although in some "late developers" the bursting of feather quills was delayed two days. Harris (1966) was the first to suggest that seabirds put resources into wing development before body mass. Anker-Nilssen (1987) found that culmen lengths, but not wing lengths, of puffin fledglings were shorter in a poor than in a better year, and also suggested that puffin chicks selectively allocate energy to growth of the wings. Similarly, Gaston (1985) referred to numerous studies of alcids where the growth rate of wing feathers was unaffected by nutrition. However, he also observed that growth of remiges in underweight Thick-billed Murres (*Uria lomvia*) was

affected by their nutritional state, which also is in agreement with results of our study.

Our study indicates that growth of the head is given highest priority in food-stressed Atlantic Puffin chicks, followed by the wings and lastly the feet. A high preference for skull growth agrees with studies of Yellow-eyed Penguins (van Heezik 1990). Furthermore, Schew (1995) demonstrated that European Starlings (*Sturnus vulgaris*) and Japanese Quail (*Coturnix japonica*) maintained brain growth during periods of food restriction. These preferences probably reflect the general need for a well-developed brain and nervous system, but ecological differences between species also may be important. Nol (1986) found that the optic lobe was larger at hatching in shorebird chicks that run and catch prey soon after hatching than in those that feed by begging or pecking. Puffin chicks are independent when they leave their burrow (Harris and Birkhead 1985), and they are forced to acquire skills involved in pursuing and capturing prey very quickly. Hence, brain development should be relatively independent of fluctuations in body mass. If brain development is independent of body mass, then the effect should be more apparent in species where chicks are independent at fledging than in those where chicks are accompanied and fed by their parents for a considerable time after they leave the nest. Another reason for the allocation of energy to growth of the brain is that development of other characters probably is a function of brain development. Once adequate brain growth is accomplished, resources can be allocated to other components, such as those enabling the chick to fledge early (despite possible low body mass and poor condition), if food supply is suddenly reduced. To remain in the nest under these circumstances would represent certain death to the chick, whereas nest departure could be rewarded by survival.

Well-developed wings may be particularly important in enabling flight from the nest to the sea. Flight, in contrast to walking, makes the chick less vulnerable to predatory gulls and also shortens the time chicks are exposed to this danger. Furthermore, flight allows the chick to move farther out to sea. The time and effort needed to reach feeding areas solely by swimming probably exceeds the capacity of a chick that is already starving. Moreover, the ability to pursue and catch prey also is necessary for survival. In this context, well-developed wings

could be advantageous, because puffins use their wings for propulsion under the water. With reference to *Uria* and *Alca* species, whose remiges and rectrices develop after nest departure, Croxall and Gaston (1988) argued that swimming and finding food were unlikely to be impaired by incompletely grown flight feathers. Nevertheless, these chicks are fed by their parents long after nest departure, whereas puffin chicks are not, suggesting that well-developed wings are more important for catching prey in puffins than in the latter species. In order to capture and handle prey, the chick also may need a relatively strong and well-developed bill, which could be the reason why length of culmen ranked so high in growth allocation. We realize, however, that the apparent preferential growth of the bill also may have been an inevitable result of the bill's intimate connection with the skull (and its rapid development).

In growing birds, resources are allocated preferentially to growth of the components with the highest current functional priority, with due regard for future needs (O'Connor 1977). Ricklefs (1979) has discussed the significance of highly developed legs at hatching, which he attributed to the need for homeothermic capacity because leg muscles are the most important source of heat production early in a chick's life. This argument may explain why characters of the feet ranked so low in our study despite their relatively large size at hatching. The relative decrease in importance of leg muscles during the nestling stage for non-terrestrial species may be caused by the gradual development of other important muscles (e.g. the pectoralis), which may replace or assist the leg muscles in heat production. The importance of growth and maturation of the pectoral muscles in this connection has been emphasized for Willow Ptarmigan (*Lagopus lagopus*) by Aulie (1976).

Resources also were allocated for building up fat deposits. Despite extremely poor feeding of some chicks (i.e. groups 2 and 3), they still stored significant amounts of subcutaneous fat. Deposition of fat is documented in the Procellariiformes, which feed their single chick on a mixture of undigested food and an energy-rich oily substance (Ashmole 1971, Ricklefs et al. 1985, Ricklefs 1987). In contrast, Atlantic Puffins feed their chicks mainly on fish that have a lower energetic value. Nevertheless, our results give some support to Lack's (1968) assertion that puffin chicks build up extensive fat reserves.

In Leach's Storm-Petrel (*Oceanodroma leucorhoa*) chicks, 70–80% of the stored fat is located in subcutaneous deposits (Ricklefs 1974), which serve as a buffer against variations in food delivery rate (Ricklefs and Schew 1994). The insulatory function of these fat deposits is poorly understood but is believed to provide extra insulation in *Synthliboramphus* murrelets, which go to sea when still covered by down (Croxall and Gaston 1988). Thus, in newly fledged puffins (whose plumage often is not fully developed), deposition of subcutaneous fat may prove to be of significance. It is important to stress, however, that fat deposits were measured at day 43, when all chicks had been fed 50 g daily for five days. This rate of food supply was almost twice the former diet given to chicks in group 2, and only about half of that previously given to group 7. As demonstrated for cockerels (Osborn and Wilson 1960), it is possible that the smallest chicks stored fat because they were unable to take full advantage of the increased energy supply. Conversely, the largest chicks could have been forced to deplete their fat deposits in order to maintain growth of other body parts, as shown for European Starlings (Schew and Ricklefs 1996, Schew pers. comm.). Both effects would reduce differences in fat deposits between groups. Moreover, dissection of wild puffin chicks found dead on their way to the sea showed no signs of accumulated subcutaneous or internal fat, despite their having a larger body mass than that attained by the most poorly fed chicks in our experiment (Øyan and Anker-Nilssen unpubl. data). However, these birds may have died from starvation following depletion of fat reserves during an extended period of food shortage. A systematic examination of healthy puffin chicks captured on their way to the sea would show whether storage of subcutaneous fat, rather that internal deposits, is a general feature, or if fat deposits in our chicks resulted from the experimental feeding conditions.

We conclude that morphometric parameters in Atlantic Puffin chicks are influenced differently by food intake. In particular, when stressed for food, growth of the head is given priority over the wings, which in turn are favored over the feet. Preference probably is given to parameters that are especially important for survival if premature fledging is required due to inadequate food or parental abandonment. In an evolutionary context, preferential growth al-

location in puffins may have arisen as a consequence of frequent exposure to poor food supplies, constraints on the feeding ecology of the parents, and the subsequent risk to chicks of being abandoned.

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