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**FOOD PROVISIONING AND GROWTH IN THE ATLANTIC PUFFIN
FRATERCULAR ARCTICA : AN EXPERIMENTAL APPROACH**

**BY
MARK COOK**

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ABSTRACT

This study provided Puffin chicks with an additional 25g of food per day during the period of maximum growth rate to determine whether: 1) adult puffins can evaluate and respond to the nutritional requirements of their chicks, and 2) whether growth parameters (rate and elevation) of structural body components are flexible in response to variable levels of nutrition.

Adult provisioning rates were significantly reduced in response to supplementary feeding, with experimental chicks receiving a mean of 2.1 feeds/d⁻¹ compared to control chicks which received 4.7 feeds/d⁻¹. There was no difference in the mean weight or energy content of the loads delivered to both groups, suggesting that the adult response to supplementary feeding took the form of a decrease in feeding frequency rather than a decrease in the size or nutritional quality of the load.

No significant differences were found between the experimental and control groups in both the growth rate of overall body size and body weight. Neither was there a difference between groups in body mass elevation (mass corrected for age). However, chicks provided with supplementary food grew significantly larger for their age than control chicks. The fact that control birds were smaller but body masses were identical between the two groups suggests that control birds were not energy limited but nutrient limited; supplementary food may have provided the additional nutrients allowing structural tissues of experimental birds to grow larger. Differences in body tissue composition, and thus differences in metabolic energy requirements, may have been indirectly responsible for the similarities in body mass between the two groups. Identical growth rates between the two groups may have been a result of constraints acting at the physiological level, which prevented any further increase in rate once maximum size was reached for a given nutrient intake. In conclusion, variation in the quality or quantity of Puffin nestling diets does effect growth patterns of structural body components. Environmental sources of morphological variation should not be neglected in studies of phenotypic variation in birds.

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3. INTRODUCTION

3.1. ADULT PROVISIONING

The regulation of food delivery by avian parents in response to nestling nutritional requirements is commonly cited in the literature, for example, work on Leach's Storm-petrel, *Oceanodroma leucorhoa* by Ricklefs (1992) and on Great Skuas, *Catharcta skua*, by Hill and Hamer (1994). The response of many avian species to supplementary feeding has been to reduce the food levels supplied to the young. This reduction in delivery rate is believed to be the result of a negative feedback cycle of sequential events involving the nutritional level of the chick, solicitation for food by the chick, parental foraging effort and delivery of food to the chick. Such a system would seem particularly important for seabirds where the resources available for chick growth may be highly variable both temporally and spatially.

Nonetheless, several studies on seabirds report conflicting evidence concerning the importance of nestling solicitation in regulating parental provisioning rate. For example, Hamer and Hill (1994) found that adult Cory's Shearwater, *Calonectris diomedea*, reduced neither their rate of food provisioning nor the meal size when the energetic requirements of their chicks were experimentally decreased. Furthermore, Hudson (1979) demonstrated that when recently hatched Puffin chicks were swapped with older, relatively faster growing chicks, both sets of foster parents continued to deliver at a rate that would be appropriate to their own chicks. Such studies suggest that either "solicitation behaviour by the chick does not convey information about nutritional status, or that parents do not or cannot act upon that information" (Ricklefs 1992). Hudson's (1979) study further suggests that the feeding rate of the puffin is regulated according to a fixed schedule determined by the stage of the breeding cycle. By contrast, Harris (1983) found that when a recording of the begging call of an extremely hungry chick was played to parent birds returning to the burrow, the adults responded by a marked and immediate increase in the delivery rate. He concluded that chicks

could communicate their nutritional requirements to the adult and that the begging call was the stimulus determining feeding rates.

The first part of this study investigates the regulation of food delivery in the Puffin. By using supplementary feeding it aims to test whether provisioning rate is controlled by parents or offspring, and whether adults alter food supply rate in response to reduced food demand at the nest. To ascertain the extent to which adult Puffins responded to supplementary feeding it was necessary to compare the rate of food provisioning and the energy content of the food loads returned to both supplementarily fed and control groups.

3.2. GROWTH RATES

Lack (1968) suggested that the rate at which adults supply food to their offspring is limited by food availability and that during the course of evolution growth rates and brood sizes are adjusted accordingly. Ricklefs (1968) developed the theory further, adding that the primary adaptation in regulating the reproductive effort is clutch size, and that adjustments to growth rates are only applicable when clutch size is small and the integer steps of adjusting brood size become too crude. In those species with a relatively large clutch size further adjustment may be attained through nestling starvation and brood reduction. This strategy is common in those species that are found in habitats where the availability of food for the brood may not be predictable at laying (O'Connor 1978). By contrast, mass growth patterns of species characterized by reduced clutch size (1-2 eggs), have been found to be highly variable (Ricklefs 1968). Such variation in avian mass growth rates have been attributed to a host of factors: variation in diet quality, quality of food, temporal patterns of food availability and temperature. Variation in these conditions may arise in relation to locality, season, habitat, weather, brood size, egg size and composition, position in the hatching sequence, age and

experience of the parents, and individual variability in the quality of parental care (Ricklefs 1983).

The theory that reducing the growth rate of nestlings from species with small clutch sizes should lead to a considerable reduction in the energy requirements of the chick (Ricklefs 1968) was later rejected by Ricklefs (1969), mainly from the results of a simple model based on allometric relationships. Ricklefs predicted that the peak energy requirements (kJ/day) reached during development would decrease by only 17% if the growth rate was reduced by as much as half. However, Klaassen *et al.* (1992), by raising Common and Sandwich Terns under laboratory conditions, have shown that a reduction in growth rate is associated with a considerable reduction in energy requirements (total gross energy intake was positively correlated with growth rate in both species). It is therefore possible that reduced growth rates have been selected to keep energy requirements as low as possible. If there is a limit to the rate at which parents can deliver food, then any reduction in chick growth rate will be advantageous to the parents by reducing the amount of food they need to deliver on any one day (Kersten & Brenninkmeijer 1995). From the chick's perspective, flexibility in energy requirements would widen the boundaries within which it could grow to fledging (Klaassen *et al.* 1992)

However, in stark contrast to his theory on mass growth rates, Ricklefs (1968) contended that although rates of many developmental process are closely linked to one another, the growth of structural body components is largely independent of the nutritional state of the chick unless food restrictions are great enough to cause starvation.

Recent studies, however, have revealed that intraspecific growth rates of structural body components are highly variable in response to levels of nutrition (Boag 1987). When experimentally manipulated, these growth rate differences are of high ecological relevance in attempting to evaluate how growth rates have evolved. Furthermore, such studies are particularly useful when the brood size is limited to a single chick, since this allows growth

rate to be related to food supply independently of the affects of brood reduction and nestling competition.

Periods of food shortage followed by others of surplus food availability are frequently encountered by the Puffin and large temporal and geographic variations in the shapes of mass growth curves, fledging mass and duration of nestling period have been documented (Nettleship 1972, Harris 1978, 1984, Barrett *et al.* 1987). The potential therefore exists in the Puffin for structural growth to vary in response to a change in food supply. The effects of food shortage, defined as a reduction in the quality and/or quantity of food supply on puffin breeding could be manifested in several ways. Growth rates may be flexible and thus slow. Even if growth rates were inflexible, changes in morphometry might result if food shortage affected the allocation of a restricted resource during development to growth of different tissues. In the worst circumstance, food shortage could ultimately result in mortality, due to desertion by adults or starvation.

The aim of the second part of this study was to determine whether experimentally induced differences in food quality causes variation in the growth pattern of structural body components in the Puffin, and if so, how these changes were manifest. However, if supplementary feeding in Puffin chicks induces a reduced rate of parental food delivery, any potential flexibility in growth patterns may be obscured because both supplementarily fed and control groups may be receiving similar energy levels. To counter the possible effects of such a system, this study was undertaken when feeding conditions were believed to be sub-optimal (Harris *person. comm.*). Under such conditions, control birds would be food limited and therefore potentially growth limited. Any potential reduction in food delivery rate to supplementarily fed chicks would occur to a lesser extent and only if the food supplement provided energy in excess of the chicks requirements.

3.3. STUDY SPECIES

The Scottish Atlantic Puffin, *Fratercula arctica grabae*, is a diurnal, pelagic seabird that weighs about 400g. In Britain it nests in underground burrows along cliff edges which it excavates with its bill and feet. Both sexes have two brood patches, but typically lay only one egg, which is incubated for between 39 and 43 days by both parents (Harris 1984). Puffins capture prey (primarily small fish and invertebrates) by pursuit diving, and feed whole prey to their semi-precocial young for between 38-44 days (Harris 1984). Puffins start breeding when between 4 and 8 years old, have an annual adult survivorship rate of about 96% and an average life expectancy of about 25 years. Where appropriate further information on their habits will be incorporated into the text; for a detailed account of the biology of the Puffin see Harris (1984).

3.4. STUDY AREA

The Isle of May is situated at the mouth of the Firth of Forth, Scotland, 8km from the Fife coast (56° 11'N, 2° 31'W) and is approximately 1 1/2km long by 1/2 km wide. It was chosen as a study site because of its proximity to a large sandeel fishery and because of its abundance of easily accessible, breeding puffins (approximately 32,000 breeding pairs).

5. RESULTS

Fledging success was high: from a total of 43 hatched eggs, only three died and by the 14 of July 24 chicks had fledged. The remaining 16 birds were healthy and were likely to fledge within the next week. All mortalities occurred when the chicks were less than 14 days post-hatching.

5.1 CHICK DIET

5.1.1. Species composition (mist-net)

A summary of the size and composition of food loads obtained from mist-netting adult puffins is given in Table 5.1. A Total of 96 loads, weighing 953g and containing 609 fish was collected. The loads contained four species of fish: sandeel *Ammodytes marinus*, sprat *Sprattus sprattus*, Atlantic herring *Clupea harengus* and rockling *Gaidropsarus spp.* No invertebrates were present.

Sandeels were by far the most common prey type, constituting 72% of all prey items, whereas herring and sprat made up only 17.5% and 6.2%, respectively (Table 5.2.). There was little variation in the species composition of food loads throughout the nestling period although rockling was depredated only towards the end of the season, whence it made up 17% of prey items, mainly at the expense of herring.

5.1.2 Prey size, prey number and load weight (mist-net)

Both the weight of the food loads and the size of the fish varied considerably between loads. Sandeels displayed the greatest size variation, ranging from post-larval specimens at 33mm to a maximum of 175mm (mean=70.67, n=404), whereas herring, sprat and rockling displayed less variation, ranging respectively from 50-82mm (mean=68.7, n=96), 65-100mm (mean=84.5, n=43) and 25-42mm (mean=31.1, n=22).

Table 5.1. Seasonal variation of food load characteristics delivered to Puffin chicks on the Isle of May in 1995. Mass per load, fish per load and fish length for each species are expressed as the mean \pm 1 S.D. Sample size is presented in parentheses. Food loads were obtained using mist-netting.

Date	Load mass (g)	Fish per load (n)	Sandeel length (mm)	Herring length (mm)	Sprat length (mm)	Rockling length (mm)
18 June-21 June	9.86 \pm 4.1 (30)	4.4 \pm 3.3 (33)	82.9 \pm 26.2 (104)	90.8 \pm 11.2 (5)	67.4 \pm 3.6 (23)	-
22 June-26 June	9.2 \pm 5.2 (33)	3.8 \pm 2.6 (33)	75 \pm 30.1 (74)	92.6 \pm 8.6 (17)	69.1 \pm 4.6 (35)	-
29 June-4 July	11.4 \pm 2.8 (21)	9.7 \pm 5.2 (21)	67.4 \pm 11 (144)	77.1 \pm 7.2 (17)	68.8 \pm 6.3 (36)	-
13 July	7.04 \pm 3.1 (11)	13.4 \pm 6.4 (11)	57.5 \pm 11 (99)	73.4 \pm 1.3 (5)	72.3 \pm 6.6 (4)	31.3 \pm 4.3 (22)
Overall	9.4 (95)	7.8 (95)	70.7 (421)	83.5 (44)	69.4 (99)	31.1 (22)

Table 5.2. Seasonal variation of prey species composition (expressed as a percentage) in the food loads delivered to Puffin Chicks on the Isle of May in 1995. Food loads were obtained using mist-netting.

Date	% Sandeel	% Sprat	% Herring	% Rockling
18 June-21 June	78	3	19	0
22 June-26 June	62	10	28	0
29 June-4 July	72	8	20	0
13 July	76	4	3	17
Overall	72	6.2	17.5	4.25

Seasonal change in mean fish length varied with respect to the species (Table 5.1.). Sandeel and sprat both displayed a marked decrease in mean lengths from 18 June to 13 July (Sandeel: 82.9-57.5mm; Sprat: 90.8-73.4mm), whereas herring steadily increased (67.4-72.3mm).

5.2 CHICK FEEDING FREQUENCY

Puffins on the Isle of May in 1995 received from 0-9 feeds per day. Supplementary feeding had a marked effect on the food provisioning rate of the adult birds (Table 5.3.). The feeding frequency during the morning peak of feeding was reduced from a mean of 1.48 feeds per 3-hour period for controls to 0.66 feeds per 3-hour period for experimental chicks ($t=-7.38$, $df=76$, $P<0.001$) (Table 5.3.). Supplementarily fed chicks therefore received only 44% of the loads delivered to control chicks during the morning peak feeding period. Differences in feeding frequency were considered with respect to group and date. There was no significant difference between dates in chick feeding frequency ($F_{(2,1)}=0.01$, $P=0.92$, ANOVA), but feeding frequency differed significantly between groups ($F_{(2,1)}=53.02$, $P<0.001$). There was no interaction between date and group ($F_{(1,1)}=0.039$, $P=0.84$).

Dawn to dusk feeding observations (Table 5.3.) also revealed a marked drop in the rate of food delivery in the experimental group (fed: mean=2.1 feeds/day⁻¹, n=10; control: mean=4.7 feeds/day⁻¹, n=74).

Table 5.3. Mean number of food loads delivered to the experimental and control Puffin chicks during the dawn to dusk and the 3-hour morning observation periods.

	Supplementarily fed	Control
<i>Feeds / 3 hours</i>	0.66	1.48
<i>Feeds / day⁻¹</i>	2.1	4.7

5.3 DAILY LOAD WEIGHT

5.3.1. Energy Content (kJ) and weight (g) of loads

There was no significant difference between mist-net and control groups in both the mean energy content (mist-net: mean=66.09 kJ/load, control: mean=68.42 kJ/load, $F_{(1,161)}=0.03$, $P=0.86$, one-way ANOVA) and the mean weight of the food loads (mist-net: mean=9.4g /load; control: 9.6 g/load, $F_{(1,180)}=0.81$, $P=0.34$) delivered by the adults. Load sizes and fish lengths estimated during feeding frequency observations were therefore deemed sufficiently accurate to be used for calculating the mean energy content and mean mass of loads delivered per day to experimental and control birds.

There was also no significant difference between supplementarily fed and control birds in both the mean energy content (fed: mean=80.74 kJ/load; control: mean=68.42 kJ/load; $F_{(1,126)}=0.15$, $P=0.7$) and mean weight (fed: mean=11.91 g/load; control: 9.6 g/load; $F_{(1,126)}$, $P=0.33$). The adult response to supplementary feeding therefore took the form of a decrease in feeding frequency rather than a decrease in the size or nutritional quality of the load.

The mean daily load weight (g/d^{-1}) delivered to control chicks ($45.02g/d^{-1}$) was almost double that of experimental chicks ($24.65g/d^{-1}$). However, with the additional daily supplement of 25g of sardine, the experimental chicks received a total of $49.7g/d^{-1}$, that is 4.5g or almost 10% more grammes of food per day than the control chicks (Table 5.4.).

Table 5.4. Daily food intake (g), mean energy content (kJ) and weight of food loads (g) delivered to experimental and control Puffin chicks. Daily food intake is expressed as both the mean daily load weight delivered by the parent and the total daily food weight received after the provision of 25g of supplementary sardine.

	Experimental	Control	Significance
<i>Mean load (kJ)</i>	80.74	68.42	ns
<i>Mean load weight (g)</i>	11.9	9.6	ns
<i>Mean daily load weight (g/d⁻¹)</i>	24.65	45.02	-
<i>Total daily intake (g/d⁻¹) (including the supplementary 25g)</i>	49.7	45.02	-

5.4 CHICK GROWTH

No significant difference in mean age was found between the two groups (mean age at first measuring:- fed: mean=13.5 days, n=20; control: mean=14.6 days, n=17; $t=-0.75$, $P=0.47$).

Additional food had a distinct effect on nestling size for a given age, causing the experimental young to grow significantly larger than the controls. A factorial multivariate analysis of variance (MANOVA) carried out between overall body size (z-values) and chick age, during the period of maximum growth, showed that supplementarily fed chicks were significantly larger than control chicks ($F_{(2,263)}=2.31$, $P<0.001$). However, there was no significant difference between the two groups in the slope of the relationship (MANOVA; $F_{(2,262)}=2.3$, $P>0.1$), revealing that the growth rates of the two groups were the same (see Figure 5.1.).

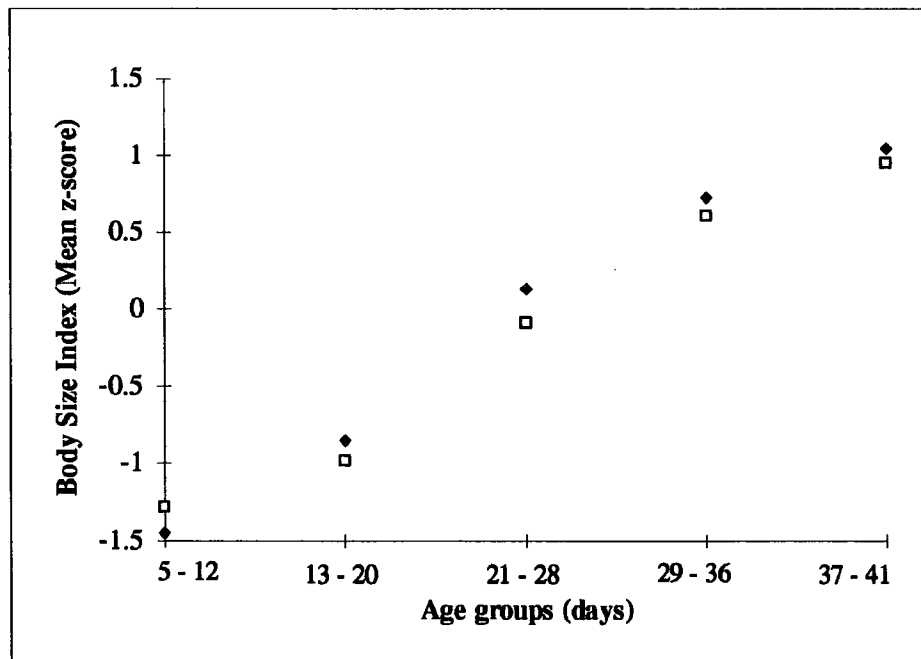


Figure 5.1. Growth in overall body size of Puffin chicks calculated from the mean z-scores of wing length, tarsus length and head+bill length. ♦ represent the experimental group, whereas □ represent the controls. Chicks are grouped in 8-day age classes.

Body mass growth curves for control and experimental young are shown in Figure 5.2. Experimental and control birds did not differ in mean mass for any given age prior to supplementary feeding (1-10 days post-hatching) or during the period of maximum growth for mass (11-21 days post-hatching). Furthermore, no significant difference was found for mass growth rate between the two groups during the period of maximum growth (exp: mean=8.31 g/d⁻¹; control: mean=8.05 g/d⁻¹; t=0.34 P=0.76) (Table 5.5.) However, once mass growth rates started to curtail, subsequent to day 25, differences in mass became apparent; mass increase was negligible for control chicks, whereas the experimental chicks continued to increase in mass and were consistently heavier than the control birds. This was reflected in mean peak weights which differed significantly between the two groups (fed: mean=318.g, n=13; control: x=305.0g, n=11; t=2.32, P<0.05) as did mean fledging weights (fed: mean=287.1, n=14; control: x=271.0, n=10; t=2.33, P<0.05) (Table 5.5.).

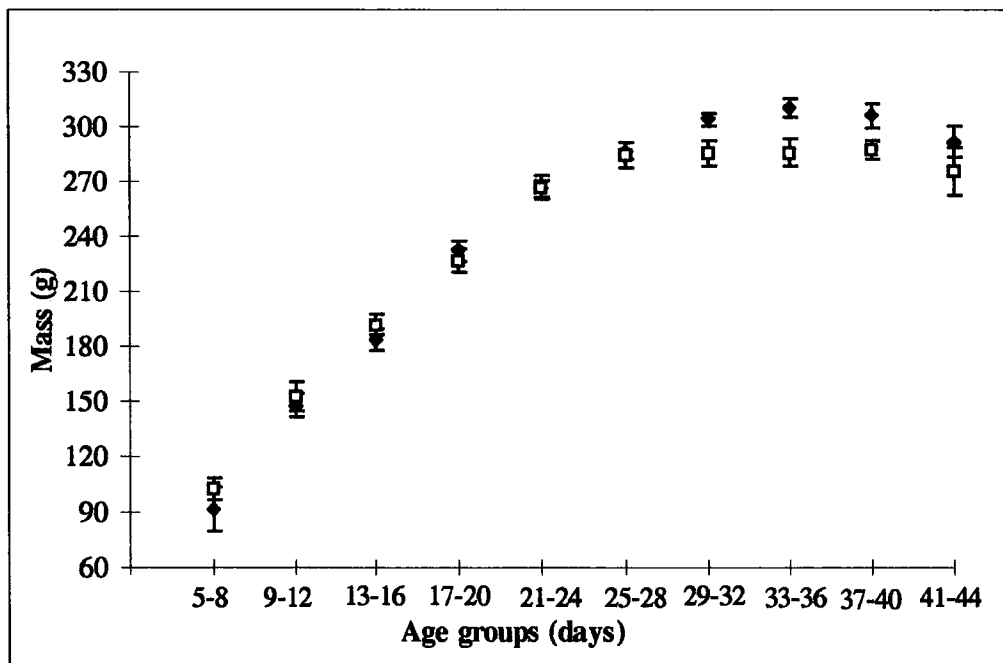


Figure 5.2. Variation in body mass as a function of age. Recorded masses \pm 1 S.E. of experimental (n=22) and control (n=17) Puffin chicks on the Isle of May, 1995. \blacklozenge represent the experimental group, whereas \square represent the controls. Chicks are grouped in 4-day age classes.

Table 5.5. Mass Growth parameters (g), and ages at peak mass and at fledging of experimental and control Puffin chicks.

	Experimental	Control	Significance
<i>Growth rate (g/day⁻¹)</i>	8.13	8.05	P=0.75
<i>Peak mass</i>	318.8	305.0	P<0.05
<i>Fledging mass</i>	287.1	271.0	P<0.05
<i>Age at peak mass (days)</i>	34.8	31.8	P=0.007
<i>Age at fledging mass(days)</i>	40.9	40.7	NS

There was also a significant difference in the age at which peak mass was reached, with control birds reaching maximum mass, on average, 3 days earlier than fed birds (control: mean=31.8 days post-hatching, n=10; fed: mean=34.8 days post-hatching, n=13; t=2.96, P=0.007). However, mean fledging ages were the same (fed: mean = 40.9 days post-hatching, n=14; control: mean=40.7 days post-hatching, n=9; t=0.18, P=0.86) (Table 5.5.) and therefore no shortening of the prefledging period took place in the supplementarily fed chicks to compensate for heavier body mass.

The logistic equations representing the form of the growth curve of the three structural body components: winglength, tarsus length and head plus bill length are shown in Table 5.6. These results are in accord with the analysis on overall body size (z-scores); asymptotic values are higher for the experimental birds indicating a larger structural size, whereas the growth rate constants (K) are identical between the two groups.

Table 5.6. Asymptotic values (A), growth rates (K) and fitted logistic equation for wing length, tarsus length and head+bill length of experimental and control puffin chicks.

Group	Body components	A (mm)	K	Equation
Experimental	Wing length	143.0	0.12	$143.0 / 1 + e^{-0.12(t-3.2)}$
	Tarsus length	28.0	0.11	$28.0 / 1 + e^{-0.11(t+6.6)}$
	Head+bill length	80.44	0.04	$80.4 / 1 + e^{-0.04(t+4.9)}$
Control	Wing length	140.2	0.12	$140.2 / 1 + e^{-0.12(t-3.6)}$
	Tarsus length	27.2	0.11	$27.2 / 1 + e^{-0.11(t+6.6)}$
	Head+bill length	74.4	0.04	$74.4 / 1 + e^{-0.04(t+6.0)}$

6. DISCUSSION

6.1. FEEDING CONDITIONS

Although the mist-net data do not give a comprehensive picture of the feeding conditions in the vicinity of the Isle of May, comparing these with data from previous years does provide some indication of the availability of food resources for Puffin chicks in 1995.

Sandeel and herring, both of relatively high calorific, lipid and protein content (Harris & Hislop 1978), were the main fish species returned to the chicks during 1995. However, sprat which has a higher calorific content (kJ g wet weight) than the other two species, was relatively rare. Studying the diet composition and feeding behaviour of Puffins on the island of St. Kilda, Harris (1984), ranked the breeding performance of these birds (based on fledging weight and nesting success) from the mid 1970's to the early 1980's and related it to the relative proportion of sprat present in the food loads. He found that in 1980, when breeding was least successful, the proportion of sprat in the diet was relatively low. During 1974-77, on the other hand, when breeding success was highest, sprat made up a large proportion of the diet. Sprat have a much higher oil content (4-14% Harris and Hislop 1978) than other species in the diet and for this reason sprat is considered to be the best food for young Puffins. It is unclear whether the relatively low proportion of sprat in the diet had any effect on the growth of Puffin chicks in 1995.

Although there was little variation in the species composition of food loads throughout the nestling period in this study (Table 5.2.), a number of authors have noted that seasonal variation in the prey species composition of fish loads is a common occurrence for the Atlantic Puffin (Harris & Hislop 1978, and Barrett & Rickardsen 1992). Since the species composition of North Sea trawl catches are comparable to those of Puffin loads of nearby colonies, it is believed that variation may result from differences in the abundance of the prey species, rather than the selection of specific prey by Puffins (Harris & Hislop 1978). In this study, since the

prey composition remained constant, it seems likely that so too did the abundance of the different prey species.

The mean length of herring increased as the season progressed, but both sandeel and sprat displayed a marked decrease in mean lengths from the 18 June to 13 July. Seasonal increases in Puffin prey size has frequently been reported (Harris and Hislop 1978; Corkhill 1973; Barrett *et al.* 1987; Wernham 1993) and have been attributed to either seasonal growth of the fish or predation by Puffins on different populations as the fish migrate into local feeding grounds (Blackburn 1979). Reports of decreases in mean fish length are less common, although Harris (1984) stated that they were likely to be the result of the larger fish moving into deeper water.

The mean weights of food loads, in contrast to mean fish length, varied little throughout the season. This is consistent with previous studies for the Isle of May (Harris 1984).

The overall mean species lengths, the mean number of fish per load, and the mean weights of the food loads (Table 5.1.), were similar to those reported by Harris (1984) for previous years on the Isle of May, when feeding conditions were considered optimal. For example, the annual mean load weights for 12 years on the Isle of May ranged from 8.2-10.4g (Harris 1984), whereas for this study it was 9.6g. Feeding rates in this study (mean of 4.7 feeds/day⁻¹) were also comparable to those recorded in previous years (range of annual mean 2.6-7.0 feeds/day for years 1976-1981).

Apart from a relatively small proportion of sprat in the diet, similarities in feeding conditions, together with data on growth rates, fledging weights, feeding activity, and proportion of chicks dying, indicate that chick production in 1995 was comparable to other years that were considered to have optimal feeding conditions.

6.2. PARENTAL RESPONSE TO SUPPLEMENTARY FEEDING

In the present study, adult provisioning rates dropped, on average, by 44% in response to supplementary feeding, suggesting that adult Puffins can evaluate and respond to the nutritional requirements of their chicks. These results are in accord with other studies on seabirds carried out by Henderson (1975), Harris (1983), Wernham (1993), and Hill and Hamer, (1994). For example, Harris (1983) found that the feeding rate of Puffin parents could be manipulated by playing recordings of the begging calls of the chick. In the same study, Harris also exchanged older chicks for younger chicks and found that the foster parents extended the feeding period to accommodate the needs of the younger chick. In contrast, experimental evidence from Hudson (1979) indicated that the parental effort (defined as any investment by the parent which increases an offspring's chance of surviving at the cost of the parent's ability to invest in other offspring) in Puffins is fixed per season, independent of the chick's current needs. However, as Werham (1993) pointed out, Hudson only recorded feeding rates for three days subsequent to switching chicks, whereas adult Puffins may take up to a week to respond to changes in the nutritional demands of their chicks.

Several studies on other pelagic feeders, of the order Procellariiformes, have also failed to find a parental response to variation in the nutritional requirements of the chick (Ricklefs, 1987, 1992, Sæther *et al.* 1993, Hamer 1994, Hamer and Hill 1993, 1994). Puffins are comparable to Procellariiformes in that they show a similar pattern of feeding (i.e. pelagic feeding, slow growth and considerable fat deposits). Lack (1968) and Ashmole (1971) viewed the fixed pattern of overfeeding and the resultant large fat deposits in Procellariiform chicks as an insurance against poor foraging success in an environment of variable oceanic conditions and temporal variation in food supply. Procellariiformes typically feed their chicks independently of one another, with intervals between meals regularly exceeding 10 days in some species (Warham 1990). The characteristically large fat reserves were therefore viewed as an emergency energy reserve for unpredictable periods between meals. However, a number

of Procellariiform species with fixed feeding rates and prodigious fat stores consistently deliver at intervals ranging between 1 and 3 days; far too short a duration to account for such large stores of fat. This questions the notion that Procellariiformes have a fixed pattern of overfeeding to insure against variable feeding conditions.

Ricklefs and Schew (1994) proposed an alternative hypothesis to account for fixed feeding patterns in Procellariiformes; rather than relating the feeding strategy to stochasticity in feeding conditions as proposed by Lack (1968) and Ashmole (1971), they believe it is a result of stochastic variation in the foraging success of each parent. Since intervals between feeds in Procellariiformes are relatively large compared to other seabirds (longer than 1 feed/day), the nutritional state of the chick may vary unpredictably between subsequent visits by an adult depending on whether or not its partner had made a visit in the intervening period. This makes it difficult for parents to adjust their provisioning rate to the nutritional needs of the chick. Thus, to ensure against the possibility of starvation, Procellariiformes supply their chicks with surplus food at a fixed rate.

Whether the feeding strategy in different seabird species is fixed or flexible may not therefore depend on the degree of variability of food supply in the respective species' feeding ranges, but ultimately on the length of the interval between successive feeds and the resulting ability of adults to recognise their chick's energy requirements.

Life history theory (Stearns 1992) states that current reproductive investment in long-lived species is more likely to be regulated by the impact of reproductive effort on future survival than in species where adult survival rate is low. In the Puffin (average life expectancy 25 years) it would therefore be advantageous to reduce the current reproductive effort to the minimum level necessary to successfully raise a chick; this would maximise the chance of future survival and therefore maximise total reproductive output. Under conditions of relatively plentiful food supply, foraging effort per unit time is lower than in periods of food shortage. Thus, under conditions of plenty, any parent that can reduce its effort in accordance with its chicks needs has a greater chance of surviving to breed again than one that over-

invests with a fixed foraging effort. Conversely, during periods of food shortage, a fixed foraging effort which supplies energy below some minimum energy level required by the chick, may result in chick starvation, whereas a flexible foraging system would allow an increase in foraging effort in line with chick demand. However, it should be expected that, because of the trade-off between current reproductive effort and future survival, any increase in effort to meet increased chick demand will have an upper limit, beyond which no further increases in effort will occur. Under such conditions the chick may reduce its growth rate or, under extreme conditions, die of starvation.

6.3. CHICK GROWTH

Although adults decreased their rate of provisioning, total food consumption rates were significantly higher among chicks given supplementary food. An investigation into growth parameters (rate and elevation) of both body weight and overall body size detected no significant difference in the growth rates of control and supplementarily fed birds during the period of maximum growth. Nor was there a difference between groups in body mass elevation (mass corrected for age). However, following several days of supplementary feeding, chicks given supplementary food were consistently larger for their age than control chicks. This was not due to any differences in size at the start of the experiment, and initiated a rapid increase in structural growth rate, followed by maintenance of elevated structural size but with a return to a similar growth rate to that shown by control chicks. It is assumed that this initial increase in growth rate was only of short duration because constraints acting at the physiological level prevented any further increase in rate. Alternatively, growth rate may represent an equilibrium between assimilation rate and mass specific metabolic requirements. Supplementary feeding may have resulted in this equilibrium being established at higher levels.

It is interesting to note that although supplementarily fed birds were indeed larger than the controls, no significant difference was detected between their age-specific body weights.

This suggests that, although control birds were not energy limited (i.e. they were receiving adequate energy supplies), they may have been limited with respect to one or more essential nutrients, for example an essential amino acid or mineral. The provision of supplementary food to the experimental chicks, may have overcome this shortfall and allowed them to grow larger. The similar weights would then be an indirect consequence of the presence of higher proportions of skeletal and muscular tissue in the supplementarily fed birds. These tissues are metabolically demanding, requiring considerable amounts of energy for their maintenance and function. Control chicks, which were structurally smaller, required less energy for tissue maintenance and the intake of an energy-rich but nutrient-poor diet in these chicks resulted in lipid deposition. By contrast, in supplementarily fed birds, energy that would otherwise be deposited as fat was utilised for tissue maintenance and burnt at a proportionally higher rate than fat reserves in the control chicks. Consequently, although the control birds were structurally smaller than their experimental counterparts, they were fatter, which may have accounted for the similarity in weight observed between the two groups.

Although growth in weight was similar during the period of maximum growth rate (up to day 25 post-hatching), differences in weight became apparent subsequent to this age. Further increases in weight were negligible for control chicks whereas supplementarily fed chicks continued to increase in weight and thus reached a significantly higher peak weight. This difference in weight between the two groups was evident until fledging. In fact, although substantial weight losses were recorded just prior to fledging in the supplementarily fed chicks, the controls remained significantly lighter, despite having lost only a small proportion of their weight. The fledging period, however, was the same for both groups, indicating that no compensatory growth occurred in the control group to achieve the same maximum weights.

A decrease in body weight in the few days prior to fledging has been reported for some avian species with infrequent and erratic feeding, for example Swallows, Gannets, Shearwaters and Puffins. Ricklefs (1968) suggests this was due to the effect of considerable

water loss when feathers and muscles mature prior to fledging. However, in many species, feeding rates decline before fledging and fat stores may be mobilized thus also contributing to the decrease in body mass. It is likely, therefore, that since control birds lost little weight before fledging, and that some weight loss will ultimately occur as a result of tissue maturation, control birds had only limited fat deposits just prior to fledging. Peak weights and growth patterns of weights for the control and supplementarily fed chicks during this study were comparable to those reported by Harris (1978) and Wernham (1993) in previous supplementary feeding experiments.

One should be aware of the fitness consequences of reduced body weights. Smaller and lighter chicks are likely to possess fewer energy reserves than their well nourished counterparts, thus being more susceptible to unfavourable weather conditions, during which thermoregulatory demands are high and food provisioning by the parents may decline (Taylor & Konarzewski 1989). Beyond fledging, retarded growth during the nestling period may be detrimental to both future survival (Coulson and Porter 1985) and reproductive success (Richner 1989). Conversely, other studies have shown that fledging weight has little if any effect on subsequent survival, for example, Oystercatchers *Haematopus ostralegus* (Kersten and Brenninkmeijer 1995), Florida Scrub Jays (Woolfenden 1978) and Sparrow Hawks *Accipiter nisus* (Newton 1986). Furthermore, Kersten and Brenninkmeijer (1995) point out that in those studies where the timing of mortality was recorded, the dependence of survival on fledging weight disappeared shortly after the young had gained independence. For instance, Blackbird *Turdus merula* fledglings with a higher fledging mass were more likely to survive for the first month, but beyond this birds had a random chance of survival and breeding. This indicated that slow growth did not necessarily result in irreversible damage. Apparently, any disadvantage associated with small size or low body weight at the time of fledging could be compensated for during a later phase (Magrath 1991). Since fledgling Puffins do not complete their growth for some time after independence (Harris 1984), it is possible that any necessary

compensatory growth can be achieved post-fledging, and that the reduced size and mass of the control chicks may not have been sufficient enough to warrant extending the growth period.

Irrespective of whether a chick's chances of survival are diminished by a reduced growth rate or fledging size, it is nonetheless in the chicks best interest to make the best of a bad job and to survive and grow even when food is limited (Kersten and Brenninkmeijer 1985).

In conclusion, variation in the quality or quantity of Puffin nestling diets does affect growth patterns of structural body components. Since chicks were measured only until fledging this study has not been able to determine whether certain avian characters undergo compensatory growth once the parental dependence has passed. If adult sizes differ as a result of differences in pre-fledging growth parameters, and if these vary consistently among colonies as a result of variation in food supply rates to chicks, then the long assumed premise that geographical morphological differences in bird populations are largely adaptive (for example, Dhondt *et al.* 1979, Zink 1983) may need re-evaluating.

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