PARENTAL PROVISIONING AND NESTLING DEPARTURE DECISIONS: A SUPPLEMENTARY FEEDING EXPERIMENT IN TUFTED PUFFINS (*FRATERCULA CIRRHATA*) ON TRIANGLE ISLAND, BRITISH COLUMBIA

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ABSTRACT.—I used a supplemental feeding experiment to determine whether adult Tufted Puffins (*Fratercula cirrhata*) would decrease provisioning effort in response to a reduction in nestling nutritional requirements, and to investigate the relationship between parental provisioning effort and timing of fledging. As predicted, parents of the supplemented nestlings decreased the number of provisioning trips but did not alter bill-load size or prey composition. Supplemental feeding significantly increased the growth of the culmen and tarsus but had no detectable effect on wing growth or body mass of chicks. Supplemented nestlings fledged significantly older than control nestlings. The maximum mass attained by the nestling and the age at which mass peaked also influenced timing of fledging. These results demonstrate that fledging age is influenced by both the energy provided by the parents and the nestling's developmental state and are consistent with the hypothesis that nestlings time their departure from the nest based on the costs and benefits of remaining. *Received 28 January 2003, accepted 8 January 2004.*

RESUMEN.—Utilicé un experimento de suplementación de alimento para determinar si los adultos de *Fratercula cirrhata* disminuirían su esfuerzo de aprovisionamiento como respuesta a una reducción en los requerimientos nutricionales de sus pichones y para investigar la relación entre el esfuerzo parental de aprovisionamiento y el momento del emplumamiento. Como se había predicho, los padres de los pichones a los que se le dió alimento suplementario disminuyeron el número de viajes de aprovisionamiento en lugar de alterar el tamaño de la carga llevada en el pico o la composición de presas. La suplementación de alimento incrementó significativamente el crecimiento del culmen y el tarso, pero no tuvo un efecto detectable sobre el crecimiento de las alas o el peso de los pichones. Los pichones con alimento suplementario abandonaron el nido a una edad significativamente mayor que los pichones control. El peso máximo alcanzado por el pichón y la edad a la que el peso alcanzó un pico también influenciaron el tiempo de emplumamiento. Estos resultados demuestran que la edad de emplumamiento es influenciada tanto por la energía provista por los padres como por el estadío de desarrollo del pichón, y son consistentes con la hipótesis de que los pichones establecen el momento de abandonar el nido con base en los costos y beneficios de quedarse en él.

AVIAN PARENTS MAY incur significant costs in meeting their offsprings' energetic demands during chick-rearing. In many seabird species, there are energetic costs associated with each provisioning trip (Drent and Daan 1980) and an increased risk of predation at the nesting colony (Harfenist and Ydenberg 1995). Parents are expected to regulate their effort in the current breeding attempt to maximize their lifetime reproductive success (Stearns 1992) and, thus, should not pay the costs of provisioning when the short-term energy requirements of the nestling(s) have been met. Several experimental studies have investigated regulation of food delivery by adults in birds but results are equivocal. Nestling age, nutritional demand, or both were found to regulate parental provisioning behavior in some studies of seabirds (Harris 1978; Johnsen et al. 1994; Bolton 1995; Bertram et al. 1996; Cook and Hamer 1997; Erikstad et al. 1997; Weimerskirch et al. 1997, 2000; Wernham and Bryant 1998; Harding et al. 2002), but not in others (Hudson 1979; Ricklefs 1987, 1992;

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Hamer and Hill 1994; Kitaysky 1996; Takahashi et al. 1999). Inconsistencies in results, both between and within species, may arise when incomparable types of manipulations are performed in each study (see Bertram et al. 1996), but the ability of parents to adjust provisioning effort may depend on the relationship between foraging strategies and energetic expenditure during provisioning (Johnsen et al. 1994).

Tufted Puffins (*Fratercula cirrhata*) are good candidates for such an investigation. Females lay just one egg, and young are dependent on both parents for feeding at the nest. The nestling is fed several times a day with loads of fish and invertebrates until it reaches 35% to 90% of adult size (Piatt and Kitaysky 2002), at which time it fledges and is independent. Tufted Puffins could potentially adjust parental provisioning effort by (1) changing the number of times they return to the colony with food, (2) adjusting the size of the bill load, or (3) changing the composition of prey delivered. Cook and Hamer (1997) were the first to observe food delivery during a supplemental feeding experiment of puffins to address how parents might respond to a change in nestling nutritional requirements. I used the same approach to determine the relationship between nestling demand and provisioning behavior in Tufted Puffins.

In addition to short-term adjustments in provisioning effort based on chick need, parents may influence the nestling's behavior, such as fledging age. Morbey et al. (1999) suggested that nestlings fledge when departure from the nest gives a greater expected fitness compared with remaining. Under their hypothesis, the nestling benefits by staying in the relative safety of the nest (Ydenberg 1989), if its parents continue to deliver food, but risks living off its reserves and foregoing growth at sea if the parents do not return to feed. Thus, the timing of fledging is predicted to depend on parental effort as the nestling approaches independence. The timing of fledging may also depend on the nestling's postfledging survival prospects. For example, nestlings that are young, light, or in poor condition at fledging may have a lower survival probability (Gaston 1997) and benefit more by remaining in the nest longer with continued parental provisioning than older and heavier nestlings (Morbey et al. 1999). Alternatively, nestlings may time their departure from the nest when they reach some physiological or structural readiness (Hipfner and Gaston 1999).

The first objective of the study was to determine if and how Tufted Puffins responded to variations in the nutritional requirement of nestlings by comparing feeding frequency, bill-load size, and prey species composition between nestlings that were supplemented and a group of controls. My second objective was to evaluate factors that influence nestling departure decisions, specifically to test the hypothesis that food availability (from the nestling's perspective) influences the timing of fledging.

In common with other alcids (Harris and Hislop 1978, Cairns 1987, Bertram et al. 1991, Morbey et al. 1999), Tufted Puffin parents reduce provisioning effort as the nestling approaches independence, and nestlings that remain in the nest lose mass (up to 30% of peak mass) over 1–20 days (Piatt et al. 1997, Gjerdrum 2001). If such a reduction in provisioning effort serves to encourage the nestling to fledge (Michaud and Leonard 2000), the length of time the nestling remains in the nest should be influenced by the provisioning behavior of its parents during that time. I supplemented the diet of nestlings during that period of reduced provisioning effort to experimentally increase the benefits of remaining in the nest. If fledging age is influenced by the food and energy provided by the parents, supplemented nestlings were predicted to fledge older than control nestlings. If nestlings fledge based on their state of development, supplemented nestlings were predicted to fledge earlier than controls (if supplemental feeding positively influenced nestling development), or at the same age (if supplemental feeding had no effect on development).

METHODS

I conducted a supplemental feeding experiment in 1999 and 2000 on Triangle Island, British Columbia, Canada (50°52′N, 129°05′W). Active burrows (34 in 1999, 30 in 2000) were marked and observed from a blind 50 m away. Where necessary, if the chamber could not be reached through the entrance, an access hole to the nest chamber of the burrow was dug and then covered with a wooden shingle, dirt, and grass.

To minimize investigator disturbance (Pierce and Simons 1986), excavation of burrows did not commence until I observed the first signs of hatching at the colony (when adults were first observed entering burrows with food). Nestling age was estimated

from the flattened wing length based on the age (y) to wing length (x) relationship of a group of known-age nestlings ($y = 0.07x^2 + 0.85x + 20.66$, $R^2 = 0.85$, $n = 5$; Gjerdrum 2001). All nestlings in the experiment were aged soon after hatching (<10-days old) when wing length most accurately reflects age (Rodway 1997).

Supplementary feeding.—Nestlings were paired by age and then randomly assigned to either a supplemented or control group (for both treatment groups, $n = 17$ in 1999 and $n = 15$ in 2000). In 1999, I provided each nestling in the supplemented group with 57.9 ± 16.8 g (SD) thawed herring (*Clupea* sp.) daily throughout the nestling period. Burrow tunnels were examined each day; in 1999, younger nestlings left the supplements uneaten. Any uneaten supplements were removed before additional fish were added. The herring was likely too large for the nestlings to swallow. However, older nestlings consistently ate supplements (mean age when nestlings no longer left supplements uneaten was 31.4 ± 7.8 days). In 2000, nestlings were fed 50.0 ± 17.2 g (SD) thawed sand lance (*Ammodytes* sp.) daily. Sand lance were chosen because they are much smaller than herring and were presumed to be easier for the young nestlings to swallow. Burrow tunnels were examined each day for any uneaten fish but on no occasion did I find any. In both years, I visited all burrows to standardize level of disturbance to both treatment groups, and nestlings were supplemented until fledging was confirmed.

Provisioning behavior.—Number of food deliveries made to supplemented and control nestlings were counted from the observation blind. Weather permitting, observation periods (26 observation periods totalling 88.5 h in 1999; 23 observation periods totalling 72.25 h in 2000) lasted 4 h and began at least 30 min after any human disturbance on the slope. Those periods were spread approximately equally over the daylight hours (0600–2200 hours) throughout the chick-rearing period (2 July to 21 August 1999, 27 June to 19 August 2000). I recorded the date, time, and burrow number for each feeding visit observed. In 2000, I also estimated the size and composition of bill loads delivered. Of the 582 observed feeding visits during 2000, the number, size, and species of prey were estimated for 165 of the bill loads to the 30 burrows in the experiment. Sizes of fish were estimated based on their relationship to the size of the puffin bill. Bill-load mass was estimated using species-specific length-to-mass relationships (Gjerdrum 2001). To validate bill-load composition and size estimated from the observation blind, bill loads were also intercepted using ligatures on nestlings located in a different area of the colony ($n = 67$). Rockfish (*Sebastes* sp.) and sand lance (*A. hexapterus*) dominated the diet using both techniques (rockfish: 89.2% observed and 83.7% collected; sand lance: 9.6% observed and 12.8% collected) and could easily be distinguished from one another using 8×30 binoculars. Mass was measured for 12 complete bill loads (collected immediately after delivery) and did not differ significantly from the average meal mass estimated for the 15 control nestlings in the experiment ($t = -0.13$, df = 25, $P = 0.90$).

Nestling growth and fledging behavior.—Nestlings in both the supplemented and control groups were measured every five days. Mass was measured to the nearest 1 g (for masses <100 g) or 2 g (for masses >100 g) using Pesola spring scales. I measured the flattened wing length from the wrist to the wing tip (±1 mm), length of exposed culmen (±0.1 mm), and length of tarsus (±0.1 mm) with dial calipers. All measurements were taken on nestlings at five-day intervals beginning when the adults were no longer brooding (mean age of nestlings when measurements started: 7.5 ± 4.8 days in 1999, and 5.8 ± 5.0 days in 2000) until fledging. To obtain detailed information on fledging characteristics, measurements of wing length and mass were taken at two-day intervals after nestlings reached age 40 days (considered the minimum fledging age; Vermeer and Cullen 1979).

Statistical analyses.—All analyses were performed using SPSS statistical software (SPSS Inc., Chicago, Illinois) and means are presented ±1 SD unless stated otherwise. Analyses of parental provisioning and nestling growth are confined to 2000 when nestlings ate the supplemental sand lance throughout the nestling period. In 1999, nestlings in the supplemented group ate the supplemental herring late in the nestling period, and therefore data from both 1999 and 2000 were used to examine fledging behavior. I examined years separately to account for differences in methods.

I used profile analysis to compare the variation in (1) food delivery rate and (2) nestling growth across five age classes (0–10, 11–20, 21–30, 31–40, and 41+ days after hatch). A mean value was first calculated for each nestling with multiple measurements per age category. Treatment was the grouping variable, divided into supplemented and control. Profile analysis is a special application of multivariate analysis of variance (MANOVA) where subjects are measured repeatedly on the same dependent variable and was favored over repeated measures analysis of variance (ANOVA) because the data did not meet the assumption of sphericity (Tabachnick and Fidell 2001). Profile analysis tests for parallelism (interaction between nestling age and treatment), group difference (treatment effect), and flatness (age effect). A polynomial contrast (trend analysis; Tabachnick and Fidell 2001) was used to look for significant quadratic effects of age on food delivery rate. Three nestlings in the supplemented group and four in the control group had missing data in one of the age categories and were thus eliminated from both analyses, reducing the sample size to 23 nestlings. Assumptions regarding normality of sampling distributions, homogeneity of variance–covariance matrices, linearity, and multicollinearity were met (Tabachnick and Fidell 2001).

For comparisons of bill-load size (number of prey and mass delivered per bill load) between supplemented and control nestlings, test statistics were calculated on means for individual burrows and compared using one-way ANOVA. I compared the relative proportions (by frequency of occurrence and by mass) of prey species delivered between the two treatment groups using Mann-Whitney U-tests. Proportions were first averaged for each nestling with multiple bill load estimates.

I used a multiple regression analysis to evaluate the effect of treatment (supplemented vs. control), peak mass, and age at peak mass on the fledging age for 1999 and 2000. I began with the statistical model that included treatment as a class variable, peak mass, and age at peak mass as continuous variables, and the interactions treatment × peak mass and treatment × age at peak mass. Nonsignificant interaction terms were eliminated sequentially from the model and the reduced model reanalysed (Zar 1999). Because there is an expected positive relationship between age at peak mass and fledging age (a nestling that peaks at 40 days cannot be expected to fledge younger than 40 days), I tested the significance of the slope between age at peak mass and fledging age against a hypothesized slope of one (the null hypothesis). Given the different experimental protocols across years, I analysed each year separately. Data met the assumptions of normality, linearity, and homoscedasticity (Tabachnick and Fidell 2001).

RESULTS

Feeding frequency.—Supplemented nestlings were fed significantly less often than control nestlings (Table 1; $F = 4.51$, df = 1 and 21, $P = 0.046$). Supplemented nestlings received 4.8 feeds day^{-1} compared to 6.4 feeds day^{-1} for control nestlings, given a 16-h feeding period (0600–2200 hours). When averaged over the two treatment groups, nestling age had a significant effect on feeding frequency (Wilks' lambda: $F = 6.94$, df = 4 and 18, $P = 0.001$), and a significant quadratic relationship between feeding rate and nestling age ($F = 13.10$, df = 1 and 21, $P = 0.002$) indicated a reduction in feeding frequency late in the chick-rearing period (Fig. 1). No treatment by age interaction was detected (Wilks' lambda: $F = 0.55$, df = 4 and 18, $P = 0.70$).

Bill-load size and composition.—There was no significant difference between the average number of prey items delivered per bill load to supplemented nestlings and those delivered to control nestlings (Table 1; one-way ANOVA: $F = 0.21$, df = 1 and 28, $P = 0.65$), nor was there any difference between treatment groups in

TABLE 1. Comparison of parental provisioning behavior, nestling growth, and fledging variables between supplemented and control nestlings in 1999 and 2000. Means (SD) and sample sizes are listed.

Nestling variable	1999				2000			
	Supplemented	n	Control	n	Supplemented	n	Control	n
Hatching date	27 June (3.7 days)[a]	17	27 June (3.9 days)	17	26 June (7.3 days)	15	25 June (7.6 days)	15
Feeding frequency (feeds per nestling h^{-1})[b]	—		—		0.3 (0.2)	15	0.4 (0.2)	15
Number of prey items per bill load[b]	—		—		3.4 (0.9)	15	3.2 (1.4)	15
Mass of prey per bill load (g)[b]	—		—		7.5 (2.2)	15	8.2 (3.7)	15
Peak mass (g)[c]	487.7 (61.0)	17	504.7 (67.2)	17	549.8 (32.2)	12	529.7 (52.6)	13
Age at peak mass (d)[c]	37.8 (6.9)	17	35.4 (4.7)	17	39.8 (3.1)	12	41.8 (2.7)	13
Fledge age (d)[c]	48.1 (5.2)	17	43.4 (2.5)	17	46.5 (1.0)	12	45.8 (1.4)	13

[a] Not analysed in 1999 because nestlings in that year did not eat the supplemented fish throughout the experiment.
[b] No data on bill-load size and composition were collected in 1999.
[c] In 2000, three supplemented nestlings and two controls could not be used in the analyses because they had not fledged by the end of the experiment.
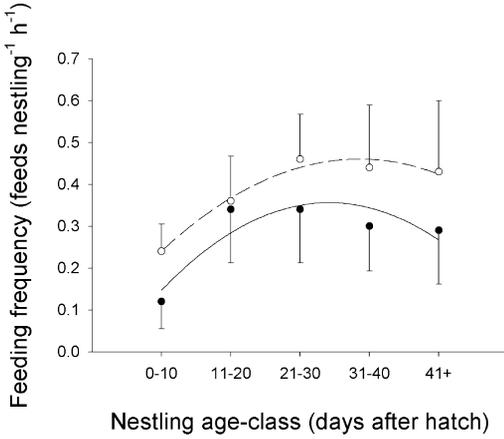
FIG. 1. Mean ± 95% confidence intervals (unidirectional) feeding frequency during five nestling age-classes for supplemented (solid points, $n = 15$) and control (open points, $n = 15$) nestlings in 2000.

the average mass of bill loads delivered (Table 1; one-way ANOVA: $F = 0.42$, df = 1 and 28, $P = 0.52$). Supplemental feeding had no detectable effect on the composition of bill loads by frequency or mass (Table 2; for all prey classes $P > 0.05$).

Nestling growth.—Culmen, tarsus, wing length, and body mass were greatest for a given age in the supplemented group compared to controls (Fig. 2A–D), although only culmen and tarsus growth differed significantly between the two treatments (culmen: $F = 4.64$, df = 1 and 22, $P = 0.04$; tarsus: $F = 6.82$, df = 1 and 22, $P = 0.02$; mass: $F = 1.61$, df = 1 and 23, $P = 0.22$; wing: $F = 1.14$, df = 1 and 23, $P = 0.30$). Analysis of culmen length showed a significant interaction between treatment and nestling age (Wilks' lambda: $F = 4.07$, df = 4 and 19, $P = 0.02$) indicating an effect of supplemental feeding only late in the chick-rearing period (Fig. 2A).

Fledging behavior.—In 1999, supplemented nestlings fledged significantly older than control nestlings (Table 1; $F = 13.55$, df = 1 and 29, $P < 0.001$). Peak mass was negatively related to fledging age ($F = 30.90$, df = 1 and 29, $P < 0.0001$). However, the effect of peak mass on fledging age was stronger for those nestlings that were supplemented (treatment by peak mass interaction: $F = 10.76$, df = 1 and 29, $P = 0.03$). The slope of the relationship between age at peak mass and fledging age was significantly less than the hypothesized slope of one ($t = -7.85$, df = 32, $P < 0.0001$). That result indicates

TABLE 2. Prey species brought to Tufted Puffin nestlings in 2000 (expressed as percentage of composition by frequency and wet mass for the major prey classes) in the supplemented ($n = 15$) and control ($n = 15$) groups. Proportions are compared using Mann–Whitney U-tests.

Prey type	Percentage of composition by frequency				Percentage of composition by wet mass			
	Supplemented	Control	U	P	Supplemented	Control	U	P
Sand lance (0) [a]	17.6	14.2	110.5	0.94	19.2	11.5	90.0	0.37
Sand lance (1+) [b]	12.3	8.2	91.0	0.39	14.4	8.8	94.0	0.46
Rockfish [c]	52.0	56.5	103.0	0.71	46.9	54.2	97.5	0.54
Squid [d]	8.5	2.6	102.0	0.68	11.1	1.9	100.0	0.62
Other invertebrates [e]	4.8	2.9	99.0	0.60	3.2	1.1	99.0	0.60
Other fish [f]	4.8	15.5	66.0	0.06	5.2	22.5	66.0	0.06

[a] *Ammodytes hexapterus* <105 mm fork length (Hatch and Sanger 1992).
[b] *Ammodytes hexapterus* >105 mm fork length (Hatch and Sanger 1992).
[c] *Sebastes* spp.
[d] *Loligo* spp.
[e] Includes euphausiids (*Thysanoessa spinifera*), unidentified worms, and larval fish.
[f] Includes salmonids (*Oncorhynchus* spp.) and sablefish (*Anoplopoma fimbria*).
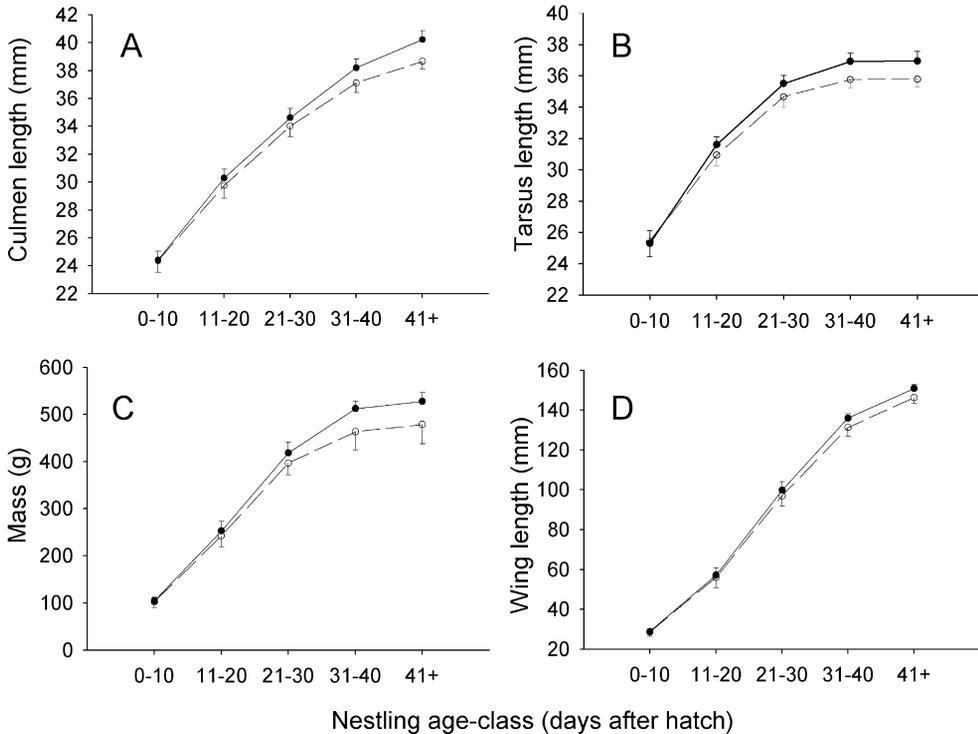
Fig. 2. Mean ± 95% confidence intervals (unidirectional) (A) nestling culmen length, (B) tarsus length, (C) mass, and (D) wing length at five nestling age-classes for supplemented (solid points, *n* = 15) and control (open points, *n* = 15) nestlings in 2000.

that nestlings that peaked young remained in the nest longer (after they reached their peak mass) than nestlings that peaked older. In 2000, supplemented nestlings fledged significantly older than control nestlings (Table 1; $F = 7.05$, df = 1 and 21, $P = 0.01$). I detected no effect of peak mass on fledging age ($F = 2.52$, df = 1 and 21, $P = 0.13$), and no interactions were significant ($P > 0.10$). Consistent with data from 1999, the slope of the regression between age at peak mass and fledging age was significantly less than the null hypothesis of one ($t = -0.22$, df = 23, $P < 0.0001$).

DISCUSSION

Parental response to manipulation of nestling nutritional requirements.—Parents of supplemented nestlings provisioned significantly less often than did parents of control nestlings. That result supports the hypothesis that parents will decrease provisioning effort in response to a reduction in their nestling's nutritional requirements. Presumably, parents perceived

the nutritional status of their nestlings either through the intensity of chick begging (Harris 1981) or through other behavioral changes in the nestling during feeding. Here, supplemental feeding of nestlings did not appear to change the prey species composition, number of prey items, or the mass of bill loads delivered by parents. Tufted Puffins may have been unable to adjust the quantity of prey or quality of bill loads if the availability of prey species is influenced by season (Vermeer 1979, Takahashi et al. 1999). Alternatively, there may be a selective advantage to birds that reduce their delivery rates if, in doing so, they also reduce the energetic costs associated with the flight to and from the feeding grounds, or their risk of predation at the colony (Harfenist and Ydenberg 1995). On Triangle Island, Bald Eagles (*Haliaeetus leucocephalus*) are known to depredate Tufted Puffins (C. Gjerdrum pers. obs.).

Of those studies designed to test the hypothesis that nestling nutritional requirements regulate the provisioning behavior of parents, few

have monitored parental behavior to answer how behavior may be modified. Similar to this study, Atlantic Puffin (*Fratercula arctica*) nestlings given supplementary food received fewer meals from their parents than did controls, but meal size and composition remained unchanged (Cook and Hamer 1997). Parents of overfed Yellow-nosed Albatross (*Diomedea chlororhynchos*) nestlings delivered smaller loads but did not change the frequency at which they fed (Weimerskirch et al. 2000). Black-browed Albatross (*D. melanophris*) parents adjusted both the size of the meal delivered and the length of the foraging trip (Weimerskirch et al. 1997). Food availability, species' foraging strategy, age, experience, and condition of the individual parents may all influence parental behavior and thus the outcome of such experiments (Chaurand and Weimerskirch 1994, Weimerskirch et al. 2000). Interestingly, Black-browed and Yellow-nosed albatross parents did not respond to their underfed nestlings by feeding more often or with larger meals (Weimerskirch et al. 1997, 2000), which suggests a limit on the ability or willingness of parents to increase effort. Although Tufted Puffin parents are able to adjust provisioning effort in response to a decrease in nestling requirements, it has not yet been established if they would respond to an increase in nutritional demand.

I examined the average mass of food consumed by both groups of nestlings to determine the extent of compensatory reduction in food delivery by parents (Bolton 1995, Cook and Hamer 1997). Control nestlings received an average of 52.5 g of food day^{-1} (8.2 g bill-load^{-1} × 6.4 feeds day^{-1}) from parental provisioning, compared with 36.0 g (7.5 g bill-load^{-1} × 4.8 feeds day^{-1}) delivered to supplemented nestlings. My supplements (~50 g day^{-1}) meant that the supplemented nestlings were receiving a total of 86 g day^{-1}, 33.5 g day^{-1} more on average than controls. Although it is unlikely that the caloric value of the thawed fish supplements was equivalent to that of food provided by parents, results from the study suggest that under unmanipulated conditions, Tufted Puffin parents are providing less food than the nestling is able to consume.

Nestling response to supplementary feeding.—As a result of supplementary feeding, nestling tarsus and culmen length increased significantly during the experiment. There was no detectable effect of treatment on wing length or mass. Growing nestlings may preferentially allocate resources to characters of greatest importance for survival (Oyan and Anker-Nilssen 1996), which here would indicate that wing length and body mass were characters of high priority. Well-developed wings may be critical for the first flight from the nest to the sea and for postfledging pursuit diving and flight (Oyan and Anker-Nilssen 1996), and numerous other studies have shown that wing growth is the variable least affected by nutrition (Hudson 1979, Gaston 1985, Bolton 1995, Oyan and Anker-Nilssen 1996). Body mass may reflect the amount of fat stores, which may serve as a buffer for a newly fledged nestling learning to feed itself (Ricklefs and Schew 1994). However, Oyan and Anker-Nilssen (1996) classified body mass as a low-priority character in terms of preferentially allocating resources in their study of growth in Atlantic Puffins. In my study, body mass was more variable than any of the structural measurements, and I may not have had the statistical power to detect any effect of supplemental feeding. Supplemented nestlings were consistently heavier than control nestlings throughout the experiment (Fig. 2C).

Nestling departure decisions.—Tufted Puffin parents decreased their food delivery rate as their nestling approached fledging and nestlings lost mass. Such a reduction in provisioning effort late in the chick-rearing period has been demonstrated for a number of alcids (Atlantic Puffin, Harris and Hislop 1978; Black Guillemot [*Cepphus grylle*], Cairns 1987; Rhinoceros Auklet [*Cerorhinca monocerata*], Bertram et al. 1991) and has implications for the nestling as it approaches independence. For example, a decrease in feeding rate may encourage the nestling to leave the nest in search of food if the parents are no longer providing the necessary nutritional requirements. If nestlings consider the net benefit of staying in the nest versus departing (Morbey et al. 1999), a nestling that continued to receive food would be expected to remain in the nest longer than one that is no longer being fed by its parents.

Here, nestlings that were supplemented delayed fledging, independent of their peak mass and age at peak mass. That result is consistent with the hypothesis that parental provisioning effort influences the timing of fledging. One potential benefit for nestlings that

fledge older is longer wings at fledging. There is a positive relationship between fledging age and wing length in Tufted Puffins (C. Gjerdrum unpubl. data). Longer wings may be a benefit for a nestling's first flight to the ocean or its first underwater dive for food (Gilchrist and Gaston 1997, Hipfner and Gaston 1999) and may be worth waiting for if the nestling continues to receive enough food to allocate to wing growth. Conversely, supplemental feeding did not affect fledging age in Atlantic Puffins (Harris 1978, Hudson 1979, Cook and Hamer 1997), and in one study, decreased the fledging age (Wernham and Bryant 1998). Rhinoceros Auklets were also found to fledge younger when given additional food (Harfenist 1995, Takahashi et al. 1999). However, none of those studies controlled for any effect of nestling peak mass or age at peak mass, which also have a strong effect on departure timing as my study has shown. Future experiments should vary the amount of supplements given to nestlings to examine the relative effects of development and parental influences on departure timing.

Reduction in parental provisioning effort late in the nestling period may instead reflect a decline in chick demand, rather than a parental decision to encourage the chick to fledge. Kitaysky (1999) demonstrated that captive Tufted Puffin chicks fed *ad libitum* voluntarily decreased their food intake starting at 34 days posthatch. Atlantic Puffins have also been shown to reject food late in the nestling period (Harris 1978). If parents here were simply responding to a decrease in their nestling's demands as they approached independence, I would have expected some rejection of the food supplements and no effect of treatment on fledging age. However, supplemented nestlings in the experiment ate all the food provided and fledged older than controls. On the basis of those results, I suggest that the reduction in provisioning effort late in the nestling period, at least in part, serves to encourage fledging.

The age and mass of the nestling prior to mass loss also had significant effects on fledging age. Younger and lighter nestlings remained in the nest longer than older and heavier nestlings, although the effect of mass was only significant in 1999 when peak mass was highly variable (coefficient of variation = 13%). Less-developed nestlings (those that reach a lower peak mass at a younger age) may remain in the nest longer

because they benefit more from the continued provisioning of their parents (Morbey et al. 1999) and have lower postfledging survival prospects than older and heavier nestlings (Gaston 1997). They may also have a higher expectation of future provisioning (Morbey et al. 1999) than a more developed nestling because parents reduce their provisioning effort as the chick matures and approaches independence. The combined results of the experiment demonstrate the importance of both nestling development and parental provisioning behavior in the timing of fledging in Tufted Puffins.

In summary, Tufted Puffin parents can adjust their level of investment based on the nutritional requirements of their nestling. Their particular foraging strategy (diurnal provisioners, multiple daily food deliveries) may help explain why they and not all seabird species have the ability to adjust provisioning effort. Future studies need to determine whether Tufted Puffins also have the ability to increase effort, and studies that span years varying in food availability could determine whether adults are able to regulate provisioning rates under less favorable conditions. This study also provides support for the hypothesis that nestlings fledge based on the costs and benefits of remaining in the nest, and experimentally demonstrates a parental role in the timing of fledging.

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