A incur significant costs in meeting their offsprings’ energetic demands

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 e from the flattened wing length based on the age ( ) to wing length ( ) relationship of a group of known-age nestlings (= 0.07 ^{2} + 0.85 + 20.66, R^2 = 0.85, = 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).

.—Nestlings were paired by age and then randomly assigned to either a supplemented or control group (for both treatment groups, = 17 in 1999 and = 15 in 2000). In 1999, I provided each nestling in the supplemented group with 57.9 ± 16.8 g (SD) thawed herring (*C* 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 (*A* 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 fi

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 -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).

R

[illegible].—Supplemented nestlings were fed significantly less often than control nestlings (Table 1; = 4.51, df = 1 and 21, = 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

P nd 21, F

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

.—Culmen, tarsus, wing

[illegible] ([illegible]) [illegible] 000, [illegible] ([illegible] *F* .0 , [illegible] , *P* 0.0). [illegible] (*F* . , [illegible] , *P* = 0.), [illegible] (*P* 0. 0). [illegible] (*t* 0. , [illegible] , *P* 0.000).

[illegible]

Parental response to manipulation of nestling nutritional requirements. [illegible]

[illegible] ([illegible]) [illegible]

have monitored parental behavior to answer how behavior may be modified. Similar to this study, Atlantic Puffin ( ) 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 ( ) nestlings delivered smaller loads but did not change the frequency at which they fed (Weimerskirch et al. 2000). Black-browed Albatross ( ) parents adjusted 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 [illegible] 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 [illegible]

America, no. 708 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

P , J. F., D. D. R , L. H. H , K. N . 1997. Habitat use, diet and breeding biology of Tufted Puffins in Prince William Sound, Alaska. Northwestern Naturalist 78:102–109.

P , D. J., T. R. S . 1986. The influence of human disturbance on Tufted Puffin breeding success. Auk 103:214–216.

R , R. E. 1987. Response of adult Leach's Storm-Petrels to increased food demand at the nest. Auk 104:750–756.

R , R. E. 1992. The roles of parent and chick in determining feeding rates in Leach's Storm-Petrel. Animal Behaviour 43:895–906.

R , R. E., W. A. S . 1994. Foraging stochasticity and lipid accumulation by nestling petrels. Functional Ecology 8:159–170.

R , M. S. 1997. Relationship between wing length and body mass in Atlantic Puffin chicks. Journal of Field Ornithology 68:338–347.

S , S. C. 1992. The Evolution of Life Histories. Oxford University Press, New York.

T , B. G., L. S. F . 2001. Using Multivariate Statistics. Allyn and Bacon, Boston.

T , A., M. K , Y. N , Y. W . 1999. Parental food provisioning is unrelated to manipulated offspring food demand in a nocturnal single-provisioning alcid, the Rhinoceros Auklet. Journal of Avian Biology 30:486–490.

V , K. 1979. Nesting requirements, food and breeding distribution of Rhinoceros Auklets (C) and Tufted Puffins ( ). Ardea 67:101–110.

V , K., L. C . 1979. Growth of Rhinoceros Auklets and Tufted Puffins, Triangle Island, British Columbia. Ardea 67: 22–27.

W , H., T. M , X. H . 1997. Foraging and provisioning strategies of Black-browed Albatrosses in relation to the requirements of the chick: Natural variation and experimental study. Behavioral Ecology 8:635–643.

W , H., P. A. P , L. Z . 2000. Chick provisioning by the Yellow-nosed Albatross : Response of foraging effort to experimentally increased costs and demands. Ibis 142: 103–110.

W , C. V., D. M. B . 1998. An experimental study of reduced parental effort and future reproductive success in the puffin . Journal of Animal Ecology 67:25–40.

Y , R. C. 1989. Growth–mortality trade-offs and the evolution of juvenile life histories in the Alcidae. Ecology 70:1494–1506.

Z , J. H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, Upper Saddle River, New Jersey.

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