

EFFECTS OF SUPPLEMENTARY FEEDING ON PROVISIONING AND GROWTH RATES OF ATLANTIC PUFFIN *FRATERCULA ARCTICA* CHICKS IN NORTH NORWAY

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Dahl H.K., Barrett R.T. & Ims R.A. 2005. Effects of supplementary feeding on provisioning and growth rates of Atlantic Puffin *Fratercula arctica* chicks in North Norway. *Atlantic Seabirds* 7(3): 133-143. *After many years of a gradual change in chick diet and a supposed deterioration in feeding conditions, chicks of Atlantic Puffins Fratercula arctica were fed 50 g supplementary food per day (capelin Mallotus villosus) to test if they grew faster than control chicks, thus indicating that conditions really were suboptimal. Growth rates were, however, approximately the same as for control chicks through a near halving of provisioning rate by the experimental parents. This suggests that feeding conditions, despite a large change in diet composition, were still adequate for normal breeding.*

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INTRODUCTION

The energetic costs of reproduction in general and provisioning of young in particular are the highest an adult bird will experience throughout its lifetime, except perhaps during migration (Bryant 1997). The high energetic costs that parents incur while provisioning young are due largely to increases in foraging time, which for auks often involve very costly flight and diving activities (Bryant 1997). Life-history theory suggests that parents should regulate their reproductive investment in each breeding attempt in order to maximize their lifetime reproductive success (Stearns 1992). One would expect long-lived species such as the Atlantic Puffin *Fratercula arctica* to be restrictive in the degree to which they exhibit increased effort in one breeding attempt, because current offspring contributes relatively little to total lifetime reproduction (Ricklefs 1983, Wooller *et al.* 1992).

Some seabird parents feed chicks at a rate independent of their chicks' current requirements (Ricklefs & Schew 1994, Takahashi *et al.* 1999), suggesting that parental effort in long-lived species may be regulated to a fixed schedule in order to maximize the survival of adults (Sæther *et al.* 1993).

However, there is growing evidence for the ability of puffins to adjust provisioning in response to their chick's need (Hudson 1979, Harris 1983, Johnsen *et al.* 1994, Cook & Hamer 1997, Erikstad *et al.* 1997, Wernham & Bryant 1998), although an individual's response to its chick's need may also depend on the current body condition of the adult, the size of the chick (and hence the prospect of survival and recruitment to the population), and temporal variation in local food availability (Johnsen *et al.* 1994, Erikstad *et al.* 1997).

Evolution has favoured the adoption by puffins of a *k* life-history strategy in order to cope with high spatial and temporal variability in marine food supplies. They show delayed maturity (first breeding when 4–8 years old), lay a single egg clutch, have high adult survival rates (*c.* 96%), have a long lifetime (an average lifespan of 25 years), and have a low fecundity rate (Harris 1984, Sandvik *et al.* 2005). Because of the buffering effect of these traits against environmental changes, numbers of Atlantic Puffins would be the least influenced in the short-term. Instead, responses would probably be manifested in changes of chick diet (species composition and the amount of fish caught), chick growth rate, delayed fledging, and under extreme food shortage, chick mortality (Harris 1978, Anker-Nilssen 1987, Barrett *et al.* 1987, Barrett & Rikardsen 1992, Baille & Jones 2003).

In the early 1980s, capelin *Mallotus villosus* and sandeel *Ammodytes* spp. dominated puffin chick diet on Hornøya, NE Norway, 70° 23' N 31° 9' E (Furness & Barrett 1985). Both capelin and sandeel have high calorific, lipid and protein contents, and are thus preferred prey species for the Atlantic Puffin (Harris & Hislop 1978, Montevecchi & Piatt 1984, Furness & Barrett 1985). Food loads consisted of few large fish and both chick growth and production were considered optimal (Barrett *et al.* 1987, Barrett 2002). As a possible consequence of the large variations and overall decline in capelin stocks in the Barents Sea (Iversen *et al.* 2006), there has since been a wide diversification in the diet of Atlantic Puffin chicks on Hornøya. By 2000, the puffins were feeding their chicks on much smaller larval and juvenile fish of a variety of species and of comparatively lower energetic values than in the early 1980s (Barrett 2002). Furthermore, load mass decreased and the number of prey items per load increased, suggesting a deterioration in the diet quality (Harris 1984).

Our study addressed the feeding behaviour and growth of adult Atlantic Puffins on Hornøya following the collapse of the capelin stock between 2000 and 2003. If food availability was low, did the adults compensate in any way to ensure normal growth of their chicks? We carried out an experiment to test whether supplementary feeding had a positive effect on puffin chick growth and survival on Hornøya in 2003.

We tested the hypothesis that the fish species in the vicinity of the colony constituted a poor chick diet such that, given that the adults were foraging at a

fixed rate, chicks fed supplementary capelin grew faster than control chicks. As several studies suggest that Atlantic Puffin adults regulate their feeding effort in relation to their chick's demand (Harris 1983, Cook & Hamer 1997, Wernham & Bryant 1998), this hypothesis would be rejected if the experimental parents decreased their feeding frequency while their chicks grew at the same rate as the control chicks. That would indicate that the availability of alternative prey species was high enough to compensate for the lack of capelin, so enabling control Puffins to maintain their breeding success.

MATERIALS AND METHODS

Puffin chick growth In mid June 2003, 44 experimental burrows and 41 control burrows with an egg or young chick were fitted with inspection lids and marked with a numbered stake. The control and experimental nests were all chosen in the same area with approximately the same burrow density, slope and distance to the cliff edge, as these parameters may each affect breeding success (Rodway *et al.* 1998). Where a chick was already present it was aged by comparing wing and culmen length with those of known-age control chicks.

The study was conducted from 15 June-5 August 2003. After the first chick had hatched, all nests were inspected every three days and all chicks were weighed to the nearest 5 g and their wing length (maximum flattened chord, including down but minus the little tuft at the end) was measured to the nearest 1 mm using a stopped ruler. The culmen was measured to the nearest 0.1 mm using vernier callipers. As the study ended before the chicks were fully grown, growth rates were compared statistically until 34 d post-hatching.

Supplementary feeding of experimental chicks Chicks were fed with recently thawed capelin. Each daily ration was cut in *c.* 3.0×0.7 cm slices, weighed on an electrical balance, and placed in small plastic bags. From the fourth to the seventh day after hatching each chick received 30 g (± 0.1 g) per day of thawed capelin, which was placed in the nest chamber. Thereafter they were given 50 g (± 0.1 g) per day, thereby approximately following the protocols of Harris (1983) and Cook & Hamer (1997). All the fish appeared to be eaten in addition to those which the adults brought, and the adults were presumed not to eat the food supplement because they do not take fish from the floor in captivity (Wernham & Bryant 1998).

Food choice Food items being brought into the colony were identified, counted and their lengths estimated (in relation to bill size) using Zeiss 10×40 binoculars. This method was used rather than catching fish-carrying adults in

mist nets in order to reduce the loss of very small food items in the vegetation, and also to reduce disturbance in the colony.

However, 26 food samples were also collected by catching fish-carrying puffins with a noose pole or at burrow entrances. They were used as controls for the visual identification and estimates of numbers and sizes of prey items. The mass of each observed food item was integrated from its estimated length based on the length/mass relationships determined from samples of the same species collected in the field from adult puffins in the same season (RTB unpubl. data). The energy content (kJ g^{-1} wet weight) of each food item was calculated using published values of fish caught in summer since prey species often have variable energy content throughout the year (Montevecchi and Piatt 1984).

Feeding frequency Comparative rates at which control and experimental chicks were fed were determined during 2-4 hour watches of 5-14 experimental burrows for a total of 39 hours. In a neighbouring area, 11-13 control burrows were simultaneously watched from another hide by another investigator, thus allowing direct comparisons to be made without having to consider variations due to weather or time of day (Harris & Hislop 1978). The observations were made from 14 June-3 August at randomly chosen hours from 0900 to 2320 hrs. A feed was recorded every time an adult with fish entered the burrow. Feeding frequency observations began at least three days after the first supplementary feeding in order to allow the adults to adjust to the experimental conditions (Hudson 1979, Harris 1983, Wernham & Bryant 1998).

The average number of feeds per hour was calculated for each chick during each watch, and each chick was assigned to a 3 day age class.

Statistical methods Analyses of growth patterns (weight, wing and culmen length) were carried out using mixed effects linear models with age, treatment group (control vs experiment) and the interaction age*treatment group as fixed effects and chick identity as a random effect nested in the treatment effect. Temporal autocorrelation between sequential measurements of the same chick was modelled as a first order process (AR-1 process). As the field season ended before the chicks were fully grown, there were few observations of the size variables for chicks older than 34 days. Any such observations were excluded from the analyses in order to achieve convergence of the numerical algorithm (restricted maximum likelihood). Logarithmic transformations (\ln) were necessary for growth variables to obtain stable variance of the residuals. All mixed model analyses were executed in PROC MIXED SAS version 6.1.

As the feeding frequency data were skewed with respect to chick age, it was not possible to take age into account using a similar analysis as that for growth pattern. Thus, a simple ANOVA model with mean feeding frequency

(number of feeds per hour) at each nest over the whole observation period was applied. No transformation was necessary for this analysis.

RESULTS

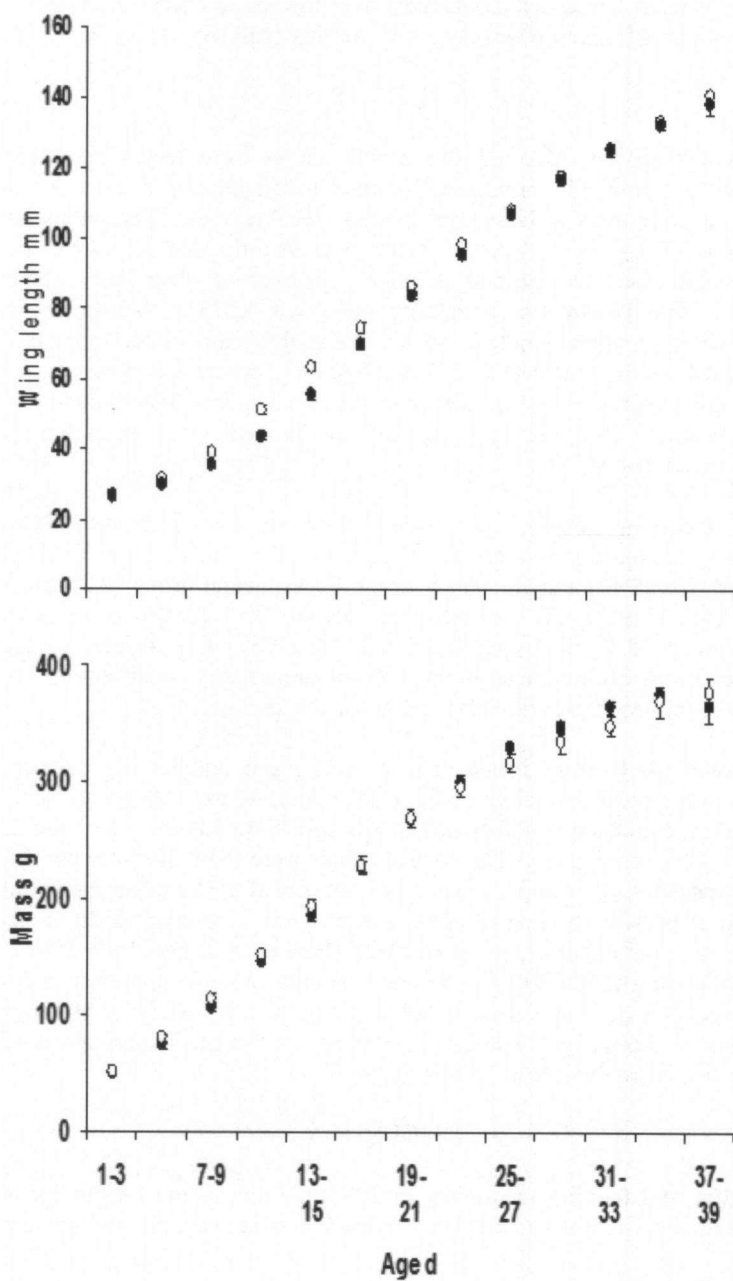
Puffin chick growth Although the growth curves were very similar (Fig. 1), there was a significant interaction between treatment and age in both wing length and body mass at least until day 34 (see Methods). The interaction on body mass ($F_{11,648} = 2.24$, $P = 0.011$) was mainly due to a tendency of experimental chicks to become relatively heavier at older age, whereas a stronger interactive effect on wing length ($F_{11,648} = 12.73$, $P < 0.001$) was due to longer wings in young control chicks. Also, the main effect treatment was significant for wing length ($F_{1,77} = 7.66$, $P < 0.007$), whereas it was not for body mass ($F_{1,77} = 0.000$, $P < 0.99$). Although the experimental chicks tended to be heavier at ages > 25 d, none of the differences in mean mass for each age class was significant (t-tests, $P > 0.05$).

Feeding frequency There was a large overall difference in feeding frequency between experimental and control chicks ($F_{1,27} = 10.87$, $P = 0.003$). The estimated overall feeding frequency in the experimental group (0.25 times per hour, 0.16-0.33 95% CI) was 60% the rate of the feeding frequency of the control group (0.42 times per hour, 0.35-0.53 95% CI). A plot of feeding frequency in the different age groups did not suggest any consistent differences among age groups in experimental or control chicks (Fig. 2).

The chicks' daily food intake The overall mean number of fish per load brought to the control chicks was 8.2 (± 0.28 SE), whereas the mean load mass (and energy equivalent) of fish was 8.1-8.8 g (48-55 kJ) for 12-15 and 20-25 day old chicks respectively. The control chicks were fed 9-10 times per day and so received 70-90 g or approximately 450-550 kJ d⁻¹. The experimental chicks were fed at 60% of the rate of control chicks and, assuming no differences in bill load size (as documented by Cook & Hamer 1997, Gjerdrum 2004), thus received 40-50 g (270-330 kJ) from their parents. With a supplementary ration of 50 g capelin per day (mean length 166.5 mm \pm 1.3 SE, $n = 50$, energetic equivalent = 5.6 kJ g⁻¹, Furness & Barrett 1985), the experimental chicks therefore ate an equivalent of 550-610 kJ d⁻¹.

DISCUSSION

Chick diet and feeding frequency In 2003, the diet of the Puffin chicks was varied and consisted of gadoid fish, sandeels, herring, capelin, and unidentified



Opposite page: figure 1. Growth rate (wing length and body mass) of experimental (dots) and control (circles) Atlantic Puffin chicks on Hornøya, 2003. Means ± 1 SE. N = 25-36 except two oldest age classes where N = 7-23.

Tegenoverliggende pagina: figuur 1. Groeisnelheid (vleugellengte en lichaamsgewicht) van bijgevoerde (punten) en 'controle-kuikens' (cirkels) van Papegaaiduiker op Hornøya, 2003. Gemiddelden ± 1 SD. N = 25-36 behalve de twee oudste leeftijdsklassen, waarbij N = 7-23.

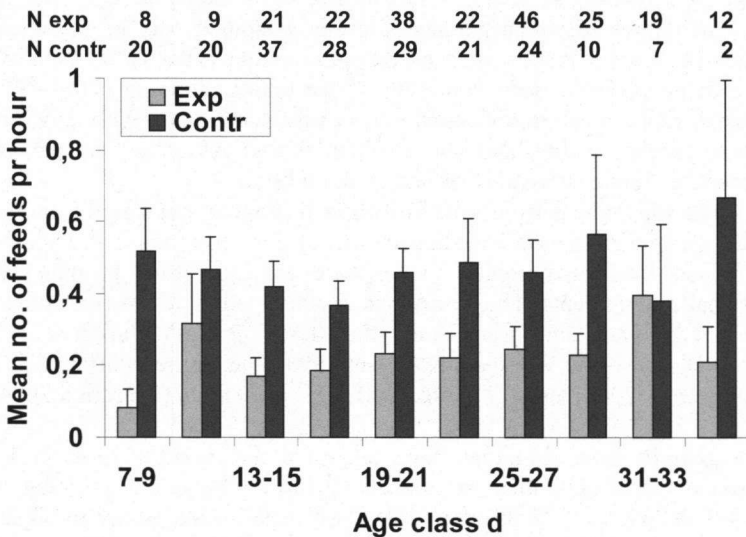


Figure 2. Feeding frequency (no. of feeds $h^{-1} \pm 1$ SE) with respect to age of experimental and control Atlantic Puffin chicks on Hornøya, 2003. N is number of chicks in each age class.

Figuur 2. Voederfrequentie (voerbeurten $h^{-1} \pm 1$ SD) in relatie tot de leeftijd van bijgevoerde en 'controle-kuikens' van Papegaaiduikers op Hornøya, 2003. N is het aantal kuikens in iedere leeftijdsklasse.

juvenile fish. Small, 0-group gadids (cod and saithe *Pollachius virens*) dominated in number, whereas small sandeels (mean length 87 mm) dominated in mass (RTB unpubl. data). The overall mean number of fish per load brought to chicks was relatively high (8.2 ± 0.28 SE), and the mean load mass (and energy equivalent) of fish was 8.1-8.8 g (48-55 kJ). A comparison with data from years dating back to 1981 showed a considerable change in diet from one dominated by large capelin and sandeels to one composed of many small larval and juvenile fish. Mean numbers of fish per load increased from 2-3 in the early

1980s to 8–10 in 2003, while the mean load mass dropped from 11–12 g to 8 g, both suggesting a gradual deterioration in the availability of high quality fish (Barrett 2002, this study).

Parental food provisioning is a readily adjustable component of reproductive effort in long-lived seabird species, and many studies have demonstrated an ability to regulate reproductive effort through adjustments of provisioning rates in response to the chick's need (e.g. Johnsen *et al.* 1994, Bolton 1995, Hamer *et al.* 1998, Granadeiro *et al.* 2000, Jodice *et al.* 2002). While the degree to which parents adjust provisioning may be influenced by species-specific constraints such as the assimilation capacity of the digestive tract (Ricklefs 1992), body condition of the adults (Johnsen *et al.* 1994) or nocturnal, single-meal provisioning habits (Takahashi *et al.* 1999), any increase probably reaches a threshold above which further investment by the parents compromises future survival (Erikstad *et al.* 1998).

The supplementary feeding on Hornøya resulted in a significant decrease in the experimental parents' feeding frequency demonstrating that adult Puffins can reduce food provisioning in response to a decrease in their chick's nutritional requirements. This corroborates other studies where conditions have been experimentally improved for e.g. the Atlantic Puffin (Johnsen *et al.* 1994, Cook & Hamer 1997, Wernham & Bryant 1998), the Horned Puffin *F. cirrhata* (Harding *et al.* 2002), and the Tufted Puffin *F. corniculata* (Gjerdrum 2004).

Chick growth Several studies have suggested that mass increase is a more sensitive measurement than the somatic growth of e.g. bill or wing length (Ricklefs & White 1975, Gaston 1985). An experimental study by Øyan and Anker-Nilssen (1996) indicated that growth of the skull is given highest priority in food-stressed puffin chicks, followed by the culmen, forearm, middle toe, tarsus, 2nd primary and, lastly, mass increase.

Despite supplementary feeding, however, there were no significant differences in mass increase during the period of maximum growth between experimental and control chicks in this study, suggesting that both sets of chicks grew near their physiological maximum rate. Harris (1978) showed that supplementary feeding of puffin chicks had a greater effect on the chick's mass at one Scottish colony, St Kilda, where feeding conditions were poor, than it had at another, the Isle of May, where feeding conditions were favourable. This suggests that puffin chick growth is limited by the maximum rate at which adults can supply food when feeding conditions are poor. The non-significant difference in mass growth rate between experimental chicks and control chicks in this study suggests that, despite a considerable change over time towards a supposedly poorer diet (Barrett 2002), the feeding conditions were still adequate for the chicks. It seems that, despite the reduction in size and increase in number

of fish fed to the chicks, the amount and quality were nevertheless high enough to maintain normal chick growth. However, the implications of any possible increase in effort required by the parents to catch a larger number of fish, such as a possible reduction in adult body condition at the end of the breeding season, remain to be investigated.

Furthermore, because change in mass is a more sensitive parameter than change in wing length (Ricklefs & White 1975, Gaston 1985, Øyan & Anker-Nilssen 1996), it is unlikely that the wings were actually longer in the young control chicks than in experimental chicks as the results suggest. The differences are most likely to be due to inconsistencies in the measurements, which were made by two different persons. That there were differences in measurements of young chicks only was probably due to the difficulty of accurately measuring downy wings, whereas the measuring method readily became standardized when the feathers erupted. The fact that supplementary-fed chicks tended to be heavier than controls towards the end of the experiment (Fig. 1; also shown by Hudson 1979, Cook & Hamer 1997, Wernham & Bryant 1998), however, suggests that experimental chicks were willing to eat more food than their parents would normally have provided at the end of the season, which in turn may accord some post-fledging survival advantages (Hamer *et al.* 1991).

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EFFECT VAN BIJVOEDERING OP VOEDEREN EN GROEISNELHEID VAN KUIKENS VAN PAPEGAAIDUIKER *FRATERCULA ARCTICA* IN NOORD-NOORWEGEN

Na vele jaren van een geleidelijke verandering in het dieet van kuikens van Papegaaiduikers *Fratercula arctica* en een veronderstelde achteruitgang in feeding conditions, werden kuikens bijgevoerd met 50 g lodde capelin *Mallotus villosus* per dag om te controleren of ze sneller groeiden dan de 'controle-kuikens'. Daarmee zou , thus indicating that conditions really were suboptimal. Growth rates were, however, approximately the same as for control chicks through a near halving of provisioning rate by the experimental parents. This suggests that feeding conditions, despite a large change in diet composition, were still adequate for normal breeding.

REFERENCES

- Anker-Nilssen T. 1987. The breeding performance of Puffins *Fratercula arctica* on Røst, Northern Norway in 1979-1985. Fauna Norv. Ser. C, Cinclus 10: 21-38.

- Baille S. M. & Jones I.L. 2003. Atlantic Puffin (*Fratercula arctica*) chick diet and reproductive performance at colonies with high and low capelin (*Mallotus villosus*) abundance. *Can. J. Zool.* 81: 1598-1607.
- Barrett R.T. 2002. Atlantic Puffin *Fratercula arctica* and Common Guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. *Mar. Ecol. Prog. Ser.* 230: 275-287.
- Barrett R.T., Anker-Nilssen T., Rikardsen F., Valde K., Røv N. & Vader W. 1987. The food, growth and fledging success of Norwegian Puffin chicks *Fratercula arctica* in 1980-1983. *Ornis Scand.* 18: 73-83.
- Barrett R.T. & Rikardsen F. 1992. Chick growth, fledging periods and adult mass loss of Atlantic Puffins *Fratercula arctica* during years of prolonged food stress. *Colonial Waterbirds* 15: 24-32.
- Bolton, M. 1995. Experimental evidence for regulation of food delivery to Storm Petrel *Hydrobates pelagicus* nestlings: The role of chick body condition. *Animal Behaviour* 50: 231-236.
- Bryant D.M. 1997. Energy expenditure in wild birds. *Proc. Nutr. Soc.* 56: 1025-1039.
- Cook M.I. & Hamer K.C. 1997. Effects of supplementary feeding on provisioning and growth rates of nestling Puffins *Fratercula arctica*: evidence for regulation of growth. *J. Avian Biol.* 28: 56-62.
- Erikstad K.E., Asheim M., Fauchald P., Dahlhaug L. & Tveraa T. 1997. Adjustment of parental effort in the Puffin; the roles of adult body condition and chick size. *Behav. Ecol. Sociobiol.* 40: 95-100.
- Erikstad K.E. Fauchald P. Tveraa T. & Steen H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecol.* 79: 1781-1788.
- Furness R.W. & Barrett R.T. 1985. The food requirements and ecological relationships of a seabird community in North Norway. *Ornis Scand.* 16: 305-313.
- Gaston A.J. 1985. Development of the young in the Atlantic Alcidae. In: *The Atlantic Alcidae* (eds Nettleship D.N. & Birkhead T. R.) pp. 319-354. Academic Press, Toronto.
- Gjerdrum C. 2004. Parental provisioning and nestling departure decisions: supplementary feeding experiment in Tufted Puffins (*Fratercula cirrhata*) on Triangle Island, British Columbia. *The Auk* 121: 463-472.
- Granadeiro J.P., Bolton M., Silva M.C., Nunes M. & Furness R.W. 2000. Responses of breeding Cory's Shearwater (*Calonectris diomedea*) to experimental manipulation of chick condition. *Behav. Ecol.* 11: 274-281.
- Hamer K.C., Furness R.W. & Caldow R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. *J. Zool. Lond.* 223: 175-188.
- Hamer K.C., Lynnes A.S. & Hill J.K. 1998. Regulation for chick provisioning rate in Manx Shearwaters: experimental evidence and implications for nestling obesity. *Functional Ecol.* 12: 625-630.
- Harding A.M.A., Pelt T.I.V., Piatt J.F. & Kitaysky A.S. 2002. Reduction of provisioning effort in response to experimental manipulation of chick nutritional status in the Horned Puffin. *The Condor.* 104: 842-847.
- Harris M.P. 1978. Supplementary feeding of young Puffins, *Fratercula arctica*. *J. Anim. Ecol.* 47: 15-23.
- Harris, M.P. 1983. Parent-young communication in the Puffin *Fratercula arctica*. *Ibis* 125: 109-114.
- Harris M. 1984. *The Puffin*. T. & A.D. Poyser, Calton.
- Hudson, P.J. 1979. The parent-chick feeding relationship of the Puffin, *Fratercula arctica*. *J. of Anim. Ecol.* 48: 889-898.
- Harris, M.P., and J.R.G. Hislop. 1978. The food of young Puffins *Fratercula arctica*. *J. Zool. Lond.*, 185: 213-236.
- Iversen S.A., Fossum P., Gjøsæter H., Skonen M. & Toresen R. (eds.). 2006. Havets ressurser og miljø. Fisken og Havet, særnr. 1. Inst. Mar. Res., Bergen.

- Jodice P.G.R., Roby D.D., Hatch S.A., Gill V.A., Lancot R.B. & Visser G.H.. 2002. Does food availability affect energy expenditure rates of nestling seabirds? A supplemental-feeding experiment with Black-legged Kittiwakes (*Rissa tridactyla*). *Can. J. Zool.* 80: 214-222.
- Johnsen I., Erikstad K.E. & Sæther B.-E.. 1994. Regulation of parental investment in a long-lived seabird, the Puffin *Fratercula arctica*: an experiment. *Oikos* 71:273-278.
- Montevecchi W.A. & Piatt J. 1984. Composition and energy contents of mature inshore spawning Capelin (*Mallotus villosus*): implications for seabird predators. *Comp. Biochem. Physiol.* 78A: 15-20.
- Ricklefs R.E. 1983. Comparative avian demography. *Current Ornithol.* 1: 1-32.
- Ricklefs R.E. 1992. The role of parents and chick in determining feeding rates in Leach's Storm-petrel. *Animal Behaviour* 43: 895-906.
- Ricklefs R.E. & Schew W.A. 1994. Foraging stochasticity and lipid accumulation by nestling petrels. *Functional Ecol.* 8: 159-170.
- Ricklefs R.W. & White, S.C. 1975. A method of constructing nestling growth curves from brief visits to seabird colonies. *Bird Banding* 45: 135-140.
- Rodway M.S., Chardine J.W. & Montevecchi W.A. 1998. Intra-colony variation in breeding performance of Atlantic Puffins. *Colonial Waterbirds* 21: 171-184.
- Sandvik H., Erikstad K.E., Barrett R.T. & Yoccoz N.G. 2005. The effect of climate on adult survival in five species of North Atlantic seabirds. *J. Anim. Ecol.* 74: 817-831.
- Sæther S.E., Andersen R. & Pedersen H.C. 1993. Regulation of parental effort in a long-lived seabird: an experimental manipulation of the cost of reproduction in the Antarctic Petrel *Thalassocia antarctica*. *Behav. Ecol. Sociobiol* 33: 147-150.
- Stearns, S.C. 1992. The evolution of life histories. Oxford Univ. Press, New York.
- Takahashi, A., Kuroki M., Niizuma Y. & Watanuki Y. 1999. Parental provisioning in unrelated to manipulated offspring food demand in a nocturnal single-provisioning alcid, the Rhinoceros Auklet. *J. Avian Biol.* 30: 486-490.
- Wernham C.V. & Bryant D.M. 1998. An experimental study of reduced parental effort and future reproductive success in the Puffin, *Fratercula arctica*. *J. Anim. Ecol.* 67: 25-40.
- Wooller R.D., Bradley J.S. & Croxall J.P. 1992. Long-term population studies of seabirds. *Trends in Ecol. and Evol.* 7: 111-114.
- Øyan H.S. & Anker-Nilssen T. 1996. Allocation of growth in food-stressed Atlantic Puffin chicks. *The Auk* 113: 830-841.