

High growth and low corticosterone in food-supplemented Atlantic puffin *Fratercula arctica* chicks under poor foraging conditions

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ABSTRACT: Prey availability around seabird breeding colonies is often unpredictable, with prey fluctuating in both abundance and distribution. This study examined the effects of natural and experimentally altered food intake on growth and physiological condition in Atlantic puffin *Fratercula arctica* chicks during 3 breeding seasons. Previous studies have shown that food-supplemented chicks generally do not gain more mass than control chicks, because parents of food-supplemented chicks reduce their provisioning effort in response to the decreased food requirements of their offspring. In contrast, food-supplemented chicks in this study gained significantly more mass per day and had greater tarsus and wing growth than control chicks. Consistent with available information on capelin spawning, our results suggest that prey availability was generally so poor that parents could not reduce provisioning effort, even when extra food was provided. Corticosterone was significantly higher in control chicks compared with food-supplemented chicks, which is consistent with some, but not all, previous studies. Chicks had lower mass when prey availability was poor, but this was associated with high corticosterone levels only when weather conditions were also poor. These results suggest that measuring multiple fitness indices can be useful for determining overall environmental conditions and can provide insight into how puffins are adjusting to changes within their ecosystem.

KEY WORDS: Atlantic puffins · Chick growth · Corticosterone · Foraging conditions · Supplemental feeding

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INTRODUCTION

Environmental conditions around seabird breeding colonies are often unpredictable, with prey availability fluctuating in both abundance and distribution. Atlantic puffins *Fratercula arctica* raise a single offspring per year, part of a conservative strategy to maximize their long-term survival (Bókonyi et al. 2009, Breuner 2011). Having some flexibility in their parental investment, parents adjust their effort depending on their own condition and the food requirements of their offspring in response to foraging con-

ditions (Johnsen et al. 1994, Erikstad et al. 1997, 1998, 2009, Williams et al. 2008b, Rector et al. 2012).

Atlantic puffins in Newfoundland and Labrador are generalist foragers, but feed their chicks mainly capelin *Mallotus villosus*. When capelin are less available, puffins forage on sand lance *Ammodytes dubius* and larval fish. In years when prey are smaller, less abundant, or less nutritious, parents may increase the provisioning rate or the numbers of prey collected so that offspring still receive a comparable diet (Burger & Piatt 1990, Eilertsen et al. 2008, Kadin et al. 2016). Increasing provisioning rates to compen-

sate for low-quality food requires increased energy expenditure and can negatively affect adult survival and future reproductive success (Wernham & Bryant 1998, Davis et al. 2005, Breton & Diamond 2014, Elliott et al. 2014; Kress et al. 2016). If parents cannot increase provisioning effort, chick condition and fledging success may be lower (Barrett & Rikardsen 1992, Kress et al. 2016), and the risk of parental abandonment is greater (Johnsen et al. 1994, Erikstad et al. 2009). Capelin, which is more energy-dense than larval fish (Montevecchi & Piatt 1984, Lawson et al. 1998), has decreased by 90% in population abundance in offshore Newfoundland waters since the early 1990s (Buren et al. 2014, DFO 2015), and there has been a decline in size and age at spawning (Carscadden & Frank 2002). The abundance and timing of inshore capelin spawning has also shown considerable variation (Carscadden et al. 1997, Carscadden & Frank 2002, Rector et al. 2012, Regular et al. 2009, 2014, DFO 2015), influenced by seasonal sea-ice dynamics that have impacted the overall marine ecosystem (Buren et al. 2014). Consequently, proportions of capelin in the diets of puffin chicks in Witless Bay have declined, and parents have not necessarily compensated by increasing provisioning rates (Table 1).

Chick growth and physiological condition can be effective indicators of food availability during the breeding season (Cairns 1988, Piatt et al. 2007, Rector et al. 2012). When food is limited, chick mass gain can be slow while structural growth is generally maintained (Robinson et al. 2002, Moe et al. 2004). Only when food availability is extremely poor are both chick mass gain and structural growth rates lower (Øyan & Anker-Nilssen 1996, Kitaysky 1999). Secretion of corticosterone (CORT), the primary glucocorticoid in birds, can mediate trade-offs of energy allocation and resources between reproduction and survival during challenging situations (Bókony et al. 2009, Breuner 2011, Crespi et al. 2013). Traditionally thought of as a response to stress (Wingfield et al. 1998), changes in CORT levels can help maintain stability through stressful situations, performing more as an anti-stress hormone (Wingfield & Kitaysky 2002, McEwen & Wingfield 2003). Increases in CORT levels can be beneficial or costly to an individual depending on the duration and amount of CORT increase, as well as the environmental conditions and life history of the species (Romero et al. 2009, Breuner 2011). High CORT levels have been associated with decreased food availability in adult seabirds

Table 1. Frequency of capelin in Atlantic puffin *Fratercula arctica* chick diet and daily provisioning rates of parents in Witless Bay, Newfoundland and Labrador, Canada. na = no data available

Source	Island	Year	Frequency of capelin (%)	Provisioning rate (d ⁻¹)
Creelman & Storey (1991)	Gull	1985	63	4.5
Rodway & Montevecchi (1996)	Great	1993	44	na
Baillie & Jones (2003)	Gull	1997	34	na
Baillie & Jones (2003)	Gull	1998	45	na
Rector et al. (2012)	Great	2001	22	na
Rector et al. (2012)	Great	2002	52	na
Rector et al. (2012), (2014)	Gull	2009	18	2.5

(Kitaysky et al. 1999b, 2007, Doody et al. 2008, Barrett et al. 2015). For seabird chicks, the association between CORT levels and food limitations is less straightforward. Tufted puffin *F. cirrhata* chicks that were food-deprived had no elevation in CORT levels (Kitaysky et al. 2005, Williams et al. 2008a), whereas other seabird chicks had higher CORT levels when food availability was low, e.g. black-legged kittiwake *Rissa tridactyla* (Kitaysky et al. 1999a), red-legged kittiwake *R. brevirostris* (Kitaysky et al. 2001a), rhinoceros auklet *Cerorhinca monocerata* (Sears & Hatch 200), and Caspian tern *Hydroprogne caspia* (Patterson et al. 2015). Elevated CORT levels in chicks in moderately stressful situations may increase begging (Kitaysky et al. 2001b, Quillfeldt et al. 2006), resulting in increased provisioning from parents. However, if parents are unable to respond appropriately to chick begging or if chick provisioning is irregular, CORT levels may decrease or remain low to avoid the detrimental effects of chronic CORT elevations (Kitaysky et al. 2005). The variation in results may also be due to both the differing degrees of poor foraging conditions in each study and possibly species-specific adaptations in physiological responses to food shortages.

Studies that experimentally increase parental provisioning effort can measure chick response to limited food conditions. Parental provisioning effort has been increased experimentally by removing one parent (Weimerskirch et al. 1995, Takahashi et al. 1999a, 1999b), prolonging the chick-rearing period by substituting younger chicks (Johnsen et al. 1994, Bertram et al. 1996, Erikstad et al. 1997, 2009), handicapping one or both parents (Weimerskirch et al. 1995, Velando & Alonso-Alvarez 2003, Harding et al. 2009, Jacobs et al. 2013), or increasing brood size (Velando & Alonso-Alvarez 2003, Bortolotti et al. 2011). However, if parents do not have the ability to

increase effort because natural food resources are too limited, then an experimental design in which parental provisioning effort is potentially reduced by supplementing chick food intake is a more useful method to evaluate how limited food conditions influence chick growth and physiology.

Supplemental feeding experiments in previous studies have been used to reduce parental effort, demonstrating that in most situations, parents will alter their provisioning based on the food requirements of their offspring (Tveraa et al. 1998, Takahashi et al. 1999a). If supplemented food (in addition to that provided by parents) is above the necessary amount for chicks to maintain growth, then parents can reduce their provisioning. It has been demonstrated in several puffin studies that food-supplemented chicks do not gain more mass than control chicks (Hudson 1979, Wehle 1983, Cook & Hamer 1997, Wernham & Bryant 1998, Gjerdrum 2004, Dahl et al. 2005). Food-supplemented chicks initially gained more mass than control chicks in one study (Harding et al. 2002), but parents began reducing their provisioning to the food-supplemented chicks after 6 d into the experiment.

We conducted a preliminary study that indicated that food-supplemented chicks gained more mass than control chicks fed only by their parents (Rector 2011). The supplemental feeding regime appeared to be insufficient to detect any measurable effects on parental provisioning, because either the foraging conditions were really poor or not enough supplemental food was provided. There was no difference in CORT levels between the 2 groups; however, the supplemental feeding only lasted for 1 wk, which may have not been enough time for any differences to develop. The current study was modified to increase the length of time and the amount of food provided, and it was conducted over 3 breeding seasons. We predicted that: (1) mass gain would be greater in food-supplemented compared with control chicks, when prey availability was poor; (2) structural

growth would not differ between food-supplemented and control chicks; and (3) CORT levels would be higher in chicks that were fed less (control chicks and/or during poor prey availability years) than chicks that were fed more (food-supplemented chicks and/or during good foraging years).

MATERIALS AND METHODS

Study site

The study was conducted on Gull Island, in the Witless Bay Ecological Reserve, Newfoundland and Labrador, Canada (47° 15' N, 52° 46' W) during May to August 2011 through 2013. The entire reserve supports an estimated 260 000 breeding pairs of Atlantic puffins *Fratercula arctica*, with more than 140 000 pairs breeding on Gull Island (Robertson et al. 2004).

Experiment

Approximately 50 burrows with eggs were located and marked in May or June of each year. Each burrow was checked for hatching every 2 d from late June through early July. Some burrows were selected after chicks had hatched, and their ages were estimated from a regression of age on wing length of chicks of known age (as in Rodway 1997). Chicks that either died or were unreachable by the researcher were excluded from the study. All chicks were of comparable age and size in each group at the start of the experiment (Table 2). The supplemental feeding experiment began in mid-July when chicks were approximately 15–20 d old. Chicks were weighed using a 500 g Pesola scale, and wing and tarsus lengths were measured once at the beginning of the experiment and again at the end of the experiment. The growth measurements coincided with the linear growth phase (chicks continue to grow and gain mass until approximately 7–10 d before fledging [Harris & Wanless 2011]; all chicks in the experiment fledged at least 10 d after the last growth measurement). The difference between the 2 measurements was divided by the number of days in the experiment to derive a measure of daily growth.

Chicks in the experiment were either fed 2 capelin (~30 g total, provided by Fisheries and Oceans Canada [DFO]) each day (in addition to food provided by parents) or were part of an unfed control group (undisturbed or disturbed

Table 2. Age (mean \pm SE), sample size, and general linear model summary for mass, tarsus length, and wing length, indicating no difference in Atlantic puffin *Fratercula arctica* chick size between experimental groups at the start of the experiment

Year	Age (d)	N	Mass (g)		Tarsus (mm)		Wing (mm)	
			F	p	F	p	F	p
2011	17.11 \pm 0.29	44	0.52	0.597	0.22	0.805	0.37	0.693
2012	15.41 \pm 0.33	44	0.92	0.408	1.56	0.222	0.34	0.715
2013	15.19 \pm 0.51	36	2.43	0.104	2.34	0.112	1.78	0.184

by placing a hand in the burrow). At the end of the experiment, 0.5 ml of blood was taken and dropped onto a blood spot card (Whatman, GE Healthcare Life Sciences) for the CORT analysis. CORT concentrations were determined using COAT-A-COUNT Rat CORT ^{125}I radioimmunoassay kits (cat. #TKRC1, InterMedico) with modifications for measurements using blood spot cards (see Doody et al. 2008 for procedure). Intra-assay CVs were 5.50–5.89% and inter-assay CVs were 9.5–17.2%. Values between years were adjusted relative to the standardized sample in each assay for any between-year comparisons to account for the yearly assay variation; however, analyses on the non-adjusted CORT values yielded the same overall results.

Eight samples with handling times exceeding the recommended limit of 3 min (Romero & Reed 2005) were excluded from the analysis. Results remained unchanged whether these samples were included or excluded. Blood spot CORT values were converted to serum values of ng ml^{-1} (using the equation described and validated in Rector et al. 2012) when reported in the tables and figures to allow for comparisons with CORT values in other studies.

Assessment of yearly differences in capelin timing and availability

No estimates are available for inshore capelin spawning timing for the Witless Bay area; however, estimates from Bellevue Beach in Trinity Bay (80 km away, $47^{\circ}38'2''\text{N}$, $53^{\circ}45'59''\text{W}$) provided by DFO have been used previously to approximate capelin spawning in Witless Bay. In previous studies, assessments of when capelin were available to chick-rearing birds using inshore spawning information has been supported with seabird breeding data (Doody et al. 2008, Wilhelm et al. 2008, Regular et al. 2009, 2014, Rector et al. 2012, A. E. Storey et al. unpubl.). Puffins feed on capelin spawning schools and will continue to mainly forage inshore, even once capelin have dispersed (Piatt 1990, Shoji et al. 2015), which makes inshore capelin spawning activity a good estimate of available food for chick provisioning. As seen in Table 3, capelin had completely dispersed from inshore areas by mid-chick rearing in both 2011 and 2013, whereas capelin activity was distributed across the chick-rearing period in 2012. In addition, chick hatch dates were on average much later than peak spawning activity in 2013, producing a

Table 3. Mean Atlantic puffin *Fratercula arctica* chick hatch dates and inshore capelin spawning information from Fisheries and Oceans Canada (DFO)

Year	Mean chick hatch date	Peak capelin spawning	Spawning activity period
2011	1 July	5 July	26 June–20 July
2012	30 June	14 July	15 June–12 August
2013	9 July	3 & 22 July	16 June–8 July & 22–24 July

resource–breeding mismatch. Due to these yearly differences in capelin availability, we factored year into our analysis to assess for different natural feeding conditions, in addition to the different experimental feeding conditions.

Statistical analyses

The effects of the experimental feeding group and year on mass gain, tarsus growth, wing growth, and CORT were analyzed using separate univariate generalized linear models and Tukey post-hoc comparisons when appropriate. The effects of year on CORT in relation to mass gain was analyzed using an ANCOVA, and yearly relationships of mass gain, tarsus growth, and wing growth with CORT were tested using Pearson correlations. Tests of normality (Shapiro-Wilks test) for CORT values were significant, indicating that these values were not normally distributed; therefore, CORT values were log transformed for all analyses. There was no difference between the disturbed and undisturbed control groups for any of the daily growth measures or for CORT; therefore, these 2 groups were combined as the control group for all analyses. Means are expressed as ± 1 SE. All comparisons are 2-tailed, and differences were considered significant when $p < 0.05$. All statistical analyses were performed using SPSS version 23.0 (IBM).

RESULTS

Chick growth

Food-supplemented chicks gained more mass per day than control chicks ($F_{1,118} = 52.68$, $p < 0.001$). Chicks gained more mass per day in 2012, compared with 2011 and 2013 ($F_{2,118} = 10.74$, $p < 0.001$). There was no significant interaction of feeding group and year ($F_{2,118} = 0.43$, $p = 0.650$) (Fig. 1).

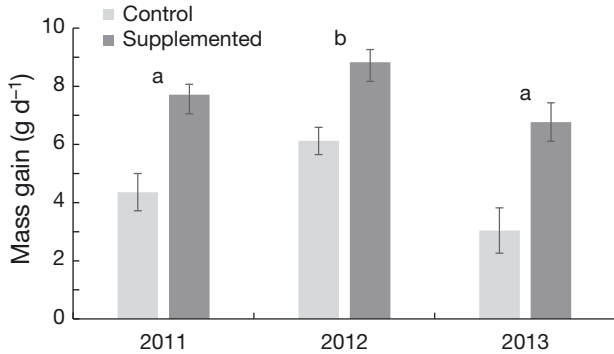


Fig. 1. Food-supplemented Atlantic puffin *Fratercula arctica* chicks gained significantly more mass (mean \pm SE) than control chicks across all years. Different lowercase letters over pairs of bars indicate a significantly lower overall mass gain in years 2011 and 2013 than in 2012. There was no significant interaction between feeding group and year

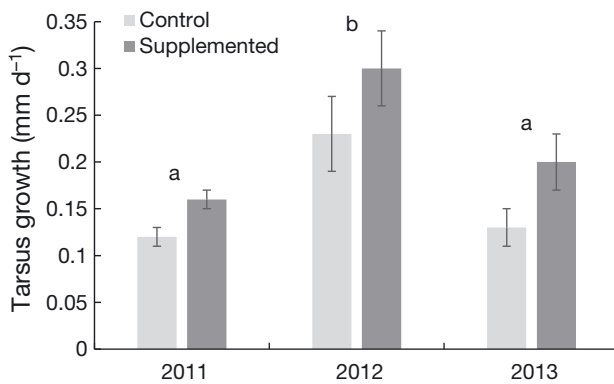


Fig. 2. Food-supplemented Atlantic puffin *Fratercula arctica* chicks had significantly greater tarsus growth (mean \pm SE) than control chicks across all years. Different lowercase letters over pairs of bars indicate a significantly lower overall tarsus growth in years 2011 and 2013 than in 2012. There was no significant interaction between feeding group and year

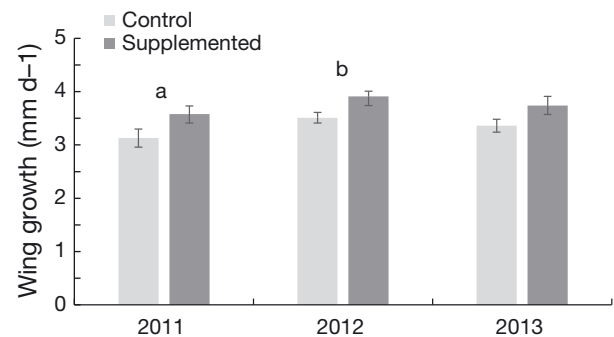


Fig. 3. Food-supplemented Atlantic puffin *Fratercula arctica* chicks had significantly greater wing growth (mean \pm SE) than control chicks across all years. Different lowercase letters over pairs of bars indicate a significantly lower overall wing growth in the year 2011 than in 2012. There was no significant interaction between feeding group and year

Food-supplemented chicks had greater tarsus growth than control chicks ($F_{1,118} = 7.41$, $p = 0.007$). Chicks had greater tarsus growth in 2012, compared with 2011 and 2013 ($F_{2,118} = 11.64$, $p < 0.001$). There was no significant interaction between feeding group and year ($F_{2,118} = 0.29$, $p = 0.750$) (Fig. 2).

Food-supplemented chicks had greater wing growth than control chicks ($F_{1,118} = 12.72$, $p = 0.001$). Chicks had greater wing growth in 2012 compared with 2011 ($F_{2,118} = 3.34$, $p = 0.039$), but there was no difference in wing growth in either 2011 or 2012 compared with 2013. There was no significant interaction between feeding group and year ($F_{2,118} = 0.03$, $p = 0.967$) (Fig. 3).

CORT

Overall, food-supplemented chicks in all years had lower CORT levels than control chicks ($F_{1,93} = 4.48$, $p = 0.037$). There was no significant difference in CORT values among years ($F_{2,93} = 0.20$, $p = 0.811$), and no significant interaction between feeding group and year ($F_{2,93} = 0.96$, $p = 0.388$) (Table 4).

Chick growth in relation to CORT

There was no significant effect of year on CORT levels after controlling for daily mass gain ($F_{2,103} = 1.15$, $p = 0.322$). Within-year relationships of CORT levels and daily mass gain showed that chick CORT levels in 2011 were negatively related to daily mass gain ($r = -0.451$, $p = 0.007$) (Fig. 4A) and tarsus growth ($r = -0.458$, $p = 0.006$) (Fig. 4B), but there was no significant correlation with wing growth ($r = -0.225$, $p = 0.193$). There was also no significant relationship between CORT levels and growth in 2012 (mass, $r = -0.131$, $p = 0.428$; tarsus, $r = -0.138$, $p = 0.402$; wing, $r = -0.079$, $p = 0.632$) or 2013 (mass, $r = -0.177$, $p = 0.326$; tarsus, $r = 0.066$, $p = 0.715$; wing, $r = -0.062$, $p = 0.734$).

Table 4. CORT levels (ng ml^{-1} , mean \pm SE) in Atlantic puffin *Fratercula arctica* chicks in the control and food-supplemented groups

Year	Control	N	Supplemented	N	All chicks	N
2011	18.39 \pm 2.32	17	14.28 \pm 1.68	18	16.27 \pm 1.44	35
2012	15.19 \pm 1.76	16	14.46 \pm 1.12	17	14.81 \pm 1.01	33
2013	18.01 \pm 2.74	15	12.13 \pm 0.92	16	14.97 \pm 1.48	31
Overall	17.20 \pm 1.31	48	13.66 \pm 0.76	51	15.38 \pm 0.76	99

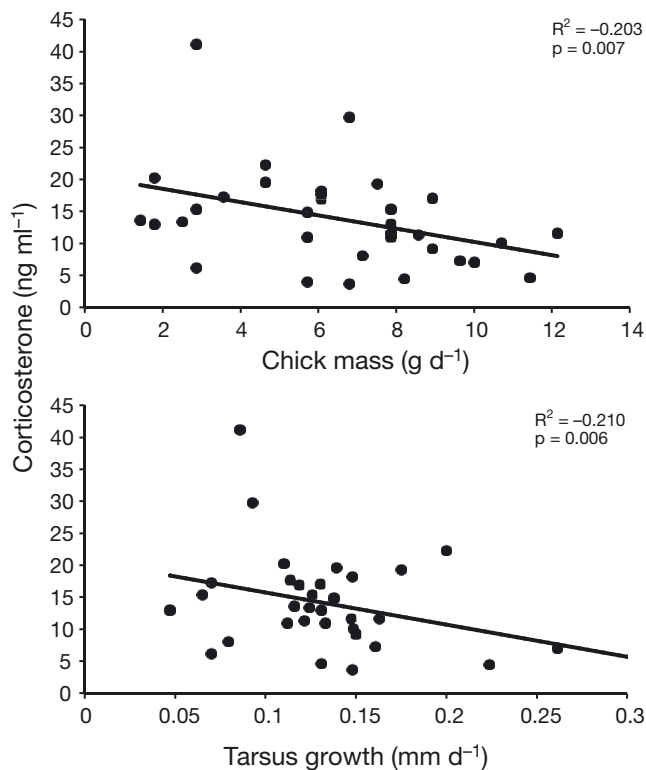


Fig. 4. Significant negative relationship in Atlantic puffin *Fratercula arctica* chicks in 2011 between CORT levels and (A) mass gain and (B) tarsus growth

DISCUSSION

Puffin chicks in this study that were provided with supplemental food had higher mass, tarsus, and wing growth and lower CORT levels than control chicks. In addition, year differences in growth corresponded with the information on capelin spawning, which suggest that prey availability was poor in 2011, good in 2012, and temporally mismatched with chick rearing in 2013. Although estimates of offshore spring capelin abundances in 2013 were double those in 2011 and 2012 (DFO 2015), they were still only 10% of what they were in the early 1990s. The abundance of capelin offshore does not necessarily translate into abundance of inshore capelin, with timing of inshore spawning relative to the chick-rearing period being a more important factor when estimating available prey for provisioning chicks (Regular et al. 2014), as the availability of key forage species is vital for successful reproduction (Hipfner 2008, Watanuki et al. 2009).

Greater mass gain in food-supplemented chicks in this study differs from other similar experiments in that puffin parents in those studies apparently re-

duced their provisioning effort in response to the supplemental feeding. Parents of food-supplemented chicks in this study, however, did not reduce their provisioning, or at least not to an extent that it eliminated the significantly higher mass gain in food-supplemented chicks. As prey availability for this colony has declined in recent years, parents may still need to work hard to feed their chicks, even when meals are supplemented. Parents may have reduced their foraging effort to some degree in the better prey year (2012), as the percent increase in daily mass gain was somewhat smaller (44%) between food-supplemented and control chicks than in 2011 (77%) and 2013 (122%). However, control chicks in 2012 still received less food from their parents (inferred from their mass gain) than control Atlantic puffin *Fratercula arctica* chicks in other supplemental feeding studies. For example, in one study (Cook & Hamer 1997), control chicks gained mass at a rate of 9.43 g d⁻¹ compared with 6.12 g d⁻¹ for control chicks in the best year (2012) of this study. Similarly, control chicks gained between 5.7 and 13.3 g d⁻¹ throughout a 25 yr monitoring study in Hornøya, Norway (Barrett 2015), in which only 3 of the worst years in that study had chicks with marginally less mass gain than the chicks in the best year of this study.

These differences in experimental studies are a consequence of variations in food supply, which is reflected in the overall declining fledging weights of puffin chicks for this colony. Researchers were no longer in the field during fledging time; however, overall fledging success can be estimated from information collected by Canadian Wildlife Services that measure recent puffin fledglings found on the mainland of Witless Bay (~10 km from the colony; see Wilhelm et al. 2013 for methods). Only 13 chicks were captured in 2011 (mean ± SE weight 210 ± 6 g, n = 3), compared to 414 chicks in 2012 (248 ± 1 g) (Wilhelm et al. 2013). In 2013, only 62 chicks were captured (236 ± 4 g), with overall post-fledge mass of chicks in 2011 and 2013 lower compared to 2012 (S. I. Wilhelm unpubl. data). Despite similar search efforts, very few stranded puffins were found in 2011 and 2013 compared to 2012, which may be an indication of fewer puffins having successfully fledged. Although conditions in 2012 were good, overall prey conditions for this colony have substantially declined in recent years, and these declining growth rates may affect future post-fledging survival and recruitment into the population (Kress et al. 2016).

Tarsus growth was lower in both 2011 and 2013 compared with 2012, and wing growth was lower in 2011 compared with 2012. Both tarsus and wing

growth were also lower in control compared with food-supplemented chicks, indicating that food scarcity was severe enough in the natural prey conditions that overall chick growth was reduced. Researchers have discussed and critiqued the use of various ratios or residuals of body mass on structural size to calculate an index of body condition (Jakob et al. 1996, Green 2001, Schulte-Hostedde et al. 2005) to determine the mass associated with energy reserves, after correcting for structural size. In this study, when food was severely limited and environmental conditions were harsh (e.g. 2011 in this study), both mass and structural size were low. The smaller size in both mass and structural components of chicks in 2011 resulted in a better body condition ratio for these chicks compared with those in 2012, despite the fact that they were clearly in worse condition (2.80 g mm^{-1} in 2011 vs. 2.76 g mm^{-1} in 2012; calculated as mass / tarsus). Thus, a different index of condition, such as CORT levels, may be a more valuable assessment of condition when environmental conditions are very poor.

In addition to the poor prey availability in 2011, weather conditions were also unfavorable, with many burrows leaking from excessive rainfall (150 mm of rain in July, Environment and Climate Change Canada). Cooler temperatures potentially made it difficult for the chicks to maintain regular body temperatures, as parents do not continuously brood chicks. When subjected to persistent cool and wet temperatures, body temperatures of chicks can drop from 38.5 to 31.1°C (Vongraven et al. 1987) and metabolism rates can increase (Wilson et al. 2004). Several thousand chicks died midseason in 2011 (M. G. Fitzsimmons pers. obs.), and a necropsy performed on a sample of chicks indicated starvation and hypothermia as the cause of death (L. Rogers pers. comm.). Low mass gain and tarsus growth were related to higher CORT in this year, although not in the other poor prey availability and mismatch year of 2013, suggesting that the association between low growth and high CORT levels in this species may occur only when their environmental conditions are extremely poor.

Our finding that CORT levels were lower in food-supplemented than control chicks differs from other studies. The puffin chicks in this colony experienced greater than normal intermittent provisioning (Table 1). Providing food supplementation to chicks at midday when parental provisioning rates are low likely reduced chick begging and energy expenditure, resulting in lower CORT levels in food-supplemented chicks compared with control chicks.

Although elevated CORT was only associated with low mass gain in 2011, chicks in both 2011 and 2013 had low mass gain. CORT level elevations can be both beneficial and costly to chicks (Kitaysky et al. 2003) and the non-linear relationship between food intake and CORT levels even within the same species suggests that multiple factors contribute to changes in CORT levels. High CORT levels in 2011 may have facilitated begging frequency and the lower mass gain may have been due to not only the low food intake, but also the greater energy expenditure to regulate body temperatures in the cool and wet conditions. Conversely, chicks in 2013 may have had suppressed CORT elevations because the parents were not responding by increasing provisioning, as the mismatch with capelin spawning limited adult foraging efforts.

In the context of previous studies, this study demonstrates that puffins have considerable flexibility in acquiring and providing food to their chicks; however, they are ultimately constrained by resources. As long as food is above some threshold level that allows chicks to maintain growth for successful fledging, adults may adjust their foraging efforts to minimize their own workload to maintain their own condition. Chick growth can be independent of food density when prey abundance is moderate to good, with parents adjusting time budgets to feed chicks adequately, as seen in several alcid seabirds (Burger & Piatt 1990, Baillie & Jones 2004, Harding et al. 2007, Burke & Montevecchi 2008, Eilertsen et al. 2008, Wilhelm et al. 2008, Regular et al. 2014). However, when prey availability falls below critical densities, parental effort is maximized, and chick growth is now controlled by food density. Puffin chick growth can be a useful indicator of low to moderate prey conditions, but provides little insight into prey density fluctuations that occur above a certain threshold of abundance. This transition from functional to uncorrelated relationships above threshold prey densities has become recognized as a fundamental characteristic of seabird-prey relationships (Piatt et al. 2007, Cury et al. 2011).

Measuring multiple fitness indices (growth, CORT, fledging success) over several years of prey fluctuations can be useful in determining how puffins are adjusting to changes within their ecosystem. Atlantic puffins in this study population have successfully endured the deteriorating foraging conditions thus far; however, long-term shortages or mismatches in prey availability with chick rearing could potentially impact future populations, as observed in other seabird breeding colonies (Barrett et al. 2006, Cury et al. 2011, Breton & Diamond 2014, Kress et al. 2016).

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