ATLANTIC PUFFIN (FRATERCULA ARCTICA) PARENT-OFFSPRING BEHAVIOUR AND CONDITION UNDER VARYING NUTRITIONAL CONSTRAINTS

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by

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A thesis submitted to the
School of Graduate Studies
in partial fulfillment of the
requirements for the degree of
Master of Science

Cognitive and Behavioural Ecology Programme/Department of Psychology
Memorial University of Newfoundland

February 2011

St. John's   Newfoundland and Labrador

ABSTRACT

During the breeding season, environmental conditions can affect parental behaviour, offspring growth and survival, and the role of both parties during parent-offspring conflict. I explored the effects of environmental conditions on Atlantic puffins during the breeding season by taking advantage of yearly differences in foraging conditions and by experimentally manipulating chick diet. Chick diet and growth as well as adult stress hormones were all affected by changes in the abundance of capelin, the primary prey species of chick-provisioning puffins in the Northwest Atlantic. Chick growth was lower during poor foraging conditions as expected; however, adult stress hormones were also lower during poor foraging conditions contrary to previous findings linking low prey availability with high stress levels. Chicks fed a supplementary diet also showed an increase in mass gain rate as well as an increase in survival, while supplementary feeding had no effect on chick stress hormones. Video recordings of chicks and adults within their nesting burrows were used to examine the effects of chick condition and begging on adult provisioning behaviour. Two types of begging calls were recorded and begging was associated with poor chick condition as well as current adult provisioning behaviour. Adults did not respond to changes in begging behaviour. Use of begging calls is interpreted in the context of honest signaling models and the role of environmental conditions in the control held by adults and chicks during parent-offspring conflict is discussed.

ACKNOWLEDGEMENTS

I am incredibly grateful for the guidance and support provided by my supervisors, Anne Storey and Carolyn Walsh, during the entire process of completing this thesis. Thank-you to Greg Robertson for all of his expertise, field support, and contributions as a committee member. This manuscript benefits from comments by Anne, Carolyn, and Greg. Many people contributed to data collection in the field. Michelle, Morag, Linda, Nikita, and Erica, thanks for all the early mornings and cold blind watches. Thanks to Roz Ford for helping me figure out "the technology" and for her above average field cooking chops. Paul and Noelle also made life in the field a great experience. Paul put up with innumerable statistical questions and crazy research ideas, thanks for listening.

Beth and Ed, thank-you for your incredible guidance and patience in the genomics lab. Thanks to Don McKay for providing lab space and help with hormonal analysis. Extra special thanks to Lesley Doody for her spot punching expertise and some very very late nights in the lab. Also Lesley, thank you for your dedication to filling our bizarrely specific grocery requests, and especially for indulging our rooibos habit it the field.

Grad school just wouldn't be the same without the sometimes necessary diversions from the task at hand, so thank-you to Olivia, Elysia, Kyle, and all of the Technical Fowls for distractions on the court and at Bitter's. Finally, thanks to Amy-Lee Kouwenberg for housing and feeding me on numerous occasions, for being a great lab and teammate, for pushing me in the right direction, and being the most dependable and loving friend anyone could ask for.

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CHAPTER 1: INTRODUCTION AND CO-AUTHORSHIP STATEMENT

1.1 INTRODUCTION

Many seabirds return to well-established breeding grounds each spring to rear offspring in close proximity to persistent and abundant food sources, but what happens when these previously reliable food sources change? At the population level, food limitation shapes life history traits, population sizes, and community structure. At the individual level, food limitation influences reproductive success and survival (reviewed in Martin, 1987). Investigating the behavioural and physiological mechanisms behind these changes can help us understand the role of food availability in reproductive success and survival and predict how individuals and populations will respond to changes in food availability in the future. Furthermore, a better understanding of seabird responses to changes in food supply will increase the value of seabirds as indicators of marine food supplies as proposed by Cairns (1987).

The marine ecosystem is changing rapidly, and species that rely on marine resources can be expected to experience significant changes in food availability (Carscadden *et al.*, 2001; Croxall, 1992; Davoren & Montevecchi, 2003; Reid & Croxall, 2001). The value of seabirds as biological indicators due to behavioral and population level responses to changes in food availability has been argued previously (Cairns, 1987; Piatt et al., 2007). This thesis examines both behavioural and physiological response of the Atlantic Puffin *Fratercula arctica*, a marine predator, to natural and manipulated food constraints. Atlantic Puffins are long-lived seabirds that return to breeding colonies every spring. They are socially monogamous and usually return to the same burrow from year to year to lay a single egg (Harris & Birkhead, 1985). Timing of breeding varies between colonies and is asynchronous, but puffins in the Northwest Atlantic typically lay a single egg sometime in May and chicks hatch approximately 40 days later in June or July (Nettleship, 1972; Rodway *et al.*, 1998). Both adults incubate the egg, although the egg is frequently left alone in the protective burrow during this period. Newly hatched chicks are brooded for 6-7 days at which time chicks are able to thermoregulate on their own and are left alone in the burrow while both parents forage for food (Harris & Birkhead, 1985). Although puffins display biparental care, females invest more in the direct care of young than males: females spend more time incubating and feed chicks more often than males (Creelman & Storey, 1991).

Chick-provisioning puffins have a generalist foraging strategy and items fed to chicks include various invertebrates and fish species; however, capelin (*Mallotus villosus*) is the preferred prey species of chick-provisioning Atlantic puffins in the Northwest Atlantic (Brown & Nettleship, 1984; Montevecchi, 1993). The distribution of prey types in chick diet varies significantly from year to year and adaptive responses of chick-provisioning adults, including generalist foraging and prey switching, to changes in prey availability may explain stability in breeding success across years (Baillie & Jones, 2003; 2004; Burke & Montevecchi, 2008). Over the past two decades, changes in the timing, duration, and distribution of spawning capelin have occurred in the Northwest Atlantic (Carscadden *et al.*, 2001; 2002). These changes provide an opportunity to study the effects of changes in food availability on a species with a generalist foraging strategy during the breeding season. As Cairns (1987) and later Piatt *et al.* (2007) indicate, different species can be expected to respond differently to food shortages dependent on foraging strategies; therefore, a better understanding of the response of a species with a generalist foraging strategy, like the Atlantic puffin, can provide a valuable comparison to the responses of seabirds with specialist foraging strategies. It is also worth noting that one of the main arguments for the use of seabirds as biological indicators is that seabird data related to prey availability are easier and cheaper to obtain than traditional fisheries methods (Cairns, 1987). Puffins, in particular, show high potential for use as marine indicators as they are easy to access during the breeding season in comparison to cliff-nesting seabirds which can be difficult to access and sensitive to even short-term disturbance. Breeding parameters as well as physiological and behavioural measures can be used to assess the effects of food restrictions on seabirds. Cairns (1987) indicates that different parameters will be sensitive at differing levels of food restriction. Here, we investigated several parameters under a range of natural and manipulated food constraints.

Data were collected from two well-established puffin colonies, Great Island and Gull Island, in the Witless Bay Ecological Reserve. One aspect of the study used blood samples from adult puffins spanning over a decade (1998-2010), as well as chick growth rates and diet during years of differing food availability to assess the effects of changes in food availability on the growth of chicks and stress experienced by adult puffins during the breeding season (Chapter 2). A second aspect of the study involved supplementary feeding experiments that were used to manipulate chick food intake and study the effects of variation in food intake on chick growth, stress, begging, and adult provisioning behaviour (Chapters 3 and 4). This work involved the use of burrow cameras, small scope cameras with audiovisual recording capabilities, which allowed direct observation of chick and adult behaviour within nesting burrows. These behaviours are usually invisible to observers conducting traditional blind watches. Audio recordings paired with video taken within individual burrows allowed study of chick begging calls in conjunction with adult provisioning behaviour. The potential of chick begging calls as honest signals of chick condition is assessed and the role of environmental conditions in chick begging, adult provisioning, and chick growth and success is examined throughout this thesis.

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1.3 CO-AUTHORSHIP STATEMENT

Under the supervision of my supervisors, Dr. Anne Storey and Dr. Carolyn Walsh, I developed the research questions and design of the studies presented in this thesis. The majority of field data presented (2009-2010) was collected by myself or under my supervision. Members of the Storey/Walsh lab collected additional data opportunistically during previous field seasons. Likewise, I performed all laboratory procedures including hormone analysis and genetic sexing with help and guidance from lab members, excepting some hormone analysis completed prior to the proposal of this study. Amy-Lee Kouwenberg contributed to the analysis of hormonal data in Chapter 2. I was responsible for all other data analysis as well as the development and writing of all chapters. Committee members (Anne Storey, Carolyn Walsh, Greg Robertson) provided comments and feedback on these chapters. Dr. Anne Storey and Dr. Carolyn Walsh are co-authors on all of the data chapters and provided many contributions including fieldwork, financial support, and guidance during all phases of thesis development. Dr. Donald McKay and Amy-Lee Kouwenberg are both co-authors on Chapter 2. Dr. McKay developed the radioimmunoassay procedure described in Chapter 2 and Amy-Lee Kouwenberg helped process samples and analyze data resulting from this procedure.

CHAPTER 2: ATLANTIC PUFFIN (*FRATERCULA ARCTICA*) PHYSIOLOGICAL STRESS RESPONSE, CHICK-PROVISOINING, AND CHICK GROWTH IN YEARS OF HIGH AND LOW CAPELIN (*MALLOTUS VILLOSUS*) AVAILABLITY

2.1 ABSTRACT

Changes in prey availability have the potential to affect the behaviour and physiology of species in the marine ecosystem. We investigated the effects of capelin *Mallotus villosus* availability on Atlantic puffin *Fratercula arctica* chicks and adults in the Witless Bay Ecological Reserve, Newfoundland. Slow daily mass gain and wing growth in 2009 reflected a reduction in the proportion high quality fish in chick diet. Blood samples taken from 1998 to 2010 were used to investigate the dynamics of baseline corticosterone (CORT) levels in adult puffins across years of good and poor capelin availability in Witless Bay. In contrast to other seabirds, adults showed higher CORT levels under good foraging conditions than under poor foraging conditions. Adults showed higher CORT levels early in the breeding season and lower levels during incubation and chick rearing. Overall, females had higher CORT levels than males. We argue that caution should be used when interpreting CORT levels taken in the field and that seasonal changes as well as colony and sex differences in CORT should be considered when using CORT levels to estimate environmental stressors during the breeding season.

2.2 INTRODUCTION

Changing oceanographic and climate conditions that lead to changes in prey availability are creating challenging environments for species that rely on forage fish. (Carscadden *et al.*, 2001, 2002; Croxall *et al.*, 2002; Ranconi & Burger, 2008; Watanuki *et al.*, 2009). In some seabird species, changes in prey availability have been linked with changes in in stress hormone levels (Kitaysky *et al.*, 1999; Kitaysky et al., 2007; Doody *et al.*, 2008) as well as breeding parameters including chick diet (Baillie & Jones, 2003; Wilhelm *et al.*, 2008) and growth (Baillie & Jones, 2004). Atlantic puffins (*Fratercula arctica*) are one species experiencing changes in prey availability. We examined the effects of prey availability on stress in Atlantic puffins by first measuring chick diet and growth in years of differing prey availability to ensure that low prey availability is in fact affecting puffins during the breeding season, and second, by looking at changes in stress hormones in chick-provisioning puffins across a decade of years of differing prey availability.

Capelin (*Mallotus villosus*) is central to marine food webs in Newfoundland and has been described as the preferred prey of chick-provisioning Atlantic puffins in Atlantic Canada (Brown & Nettleship, 1984; Montevecchi, 1993). Over the past two decades, changes in the distribution as well as timing and total duration of capelin spawning in the coastal waters of Newfoundland have occurred (Carscadden *et al.*, 2002). These changes have the potential to affect the behaviour and physiology of chick-provisioning puffins as well as the condition and growth of chicks during the chick-rearing period of the breeding season. Atlantic puffins forage offshore before the arrival of capelin. When spawning capelin arrive, puffins begin to feed on inshore schools and continue to forage inshore once capelin have dispersed (Piatt, 1990). Boat surveys in Witless Bay from 1982-1984 indicate that puffins primarily occupy inshore (<30m) and bay (30-70m) regions during the breeding season and are spatially correlated with capelin within these regions (Piatt & Methven, 1986).

Although capelin is the primary prey species of chick-provisioning puffins in Newfoundland, sandlance (*Ammodytes* sp.), as well as various larval and early stage fish and invertebrates, are also components of chick diet (Rodway & Montevecchi, 1996). A flexible diet and simultaneous foraging by both parents might be expected to help buffer the effects of food stress on puffin chicks; however, deleterious effects of low capelin availability in the Northwest Atlantic have been recorded. Declining capelin abundance near the Gannet Islands in the late 1990s, as inferred from a decline in capelin in chick diet, was associated with slower mass gain of puffin chicks relative to measures from the early 1980s (Baillie & Jones, 2004). Differences in chick diet between colonies with differing capelin abundance in the Northwest Atlantic have also been noted, but hatching and fledging success remain stable (Baillie & Jones, 2003). High inter-annual variation in chick diet indicates that puffins may be resilient to changes in prey availability (Baillie & Jones, 2003, 2004). In fact, puffins may be better able to buffer the effects of low or delayed capelin availability during the breeding season than their capelin specialist counterparts, murres, for several reasons including 1) *diet*- puffins have a more generalist foraging strategy and feed chicks a more variable diet than do murres (Burke & Montevecchi, 2008), 2) *nest habitat-*

burrow nesting allows both puffin parents to forage simultaneously, while cliff-nesting requires one murre parent to remain with the chick when the other forages (Harris & Birkhead, 1985), and 3) *chick development*- puffin chicks develop more slowly and over a longer period of time (Harris & Birkhead, 1985) conceivably allowing them to resume normal growth when capelin does arrive.

Behavioural and physiological effects of capelin availability have already been noted for a related alcid, the common murre (*Uria Algae*), in Newfoundland. Regular *et al.* (2009) found that the timing of capelin arrival at Cape St. Mary's, NL, in one year predicted the average hatch time of common murre chicks the following year. This lagged effect of capelin spawning time indicates that murres can delay onset of breeding. This delay might help to ensure that chick hatching and capelin arrival coincide to provide an adequate food source during chick rearing. Late capelin arrival has also been shown to affect the stress response of common murres in the Witless Bay Ecological Reserve, where higher corticosterone levels were observed when capelin arrived later than onset of chick hatching (Doody *et al.*, 2008). Higher foraging effort and lower chick-feeding rates were also observed during this mismatch year (Wilhelm *et al.*, 2008). While murres specialize in capelin, puffins are more general foragers and might be expected to do better than murres when capelin availability is low (Burke & Montevecchi, 2008); however, changes in the type of prey fed to puffin chicks can have negative consequences. At the Gannet Islands, Labrador, chicks showed slower mass gain when fed a diet of small fish and invertebrates rather than their usual energy rich diet comprised mainly of capelin (Baillie & Jones, 2004). Baillie

& Jones (2004) demonstrated that changes in capelin availability have negative effects on puffin chicks; however, the effects of capelin availability on adult puffins in the Northwest Atlantic have not been investigated previously.

Examining the stress response of puffins under poor foraging conditions is one way to evaluate the effects of changing prey availability on chick-provisioning adults. Corticosterone (CORT) is the primary glucocorticoid in birds (Holmes & Phillips, 1976) and it is secreted in response to various physical and psychological stressors (Harvey *et al.*, 1984). This secretion mobilizes stored lipids and proteins (Belthoff & Dufty, 1998) and mediates behavioural responses when prey availability is low. Wingfield and Kitaysky (2002) argue that rises in glucocorticoid levels in response to unpredictable environmental changes help individuals avoid chronic stress by influencing behaviour and physiology during and following the unpredicted event, serving as "anti-stress" hormones. In the case of seabirds and foraging conditions, accumulating evidence indicates that corticosterone levels are high when food availability is low (Kitaysky *et al.*, 1999; Kitaysky *et al.*, 2007; Doody *et al.*, 2008). Despite this association with food abundance, the use of CORT as a direct indicator of food availability is a contentious issue in avian endocrinology due to the effects of seasonal physiological changes related to migration (Romero *et al.*, 1997) and breeding stage (Kitaysky *et al.*, 1999; Romero, 2002; Bonier *et al.*, 2009), which are difficult to isolate from the effects of food availability. In addition, the effects of food abundance on CORT sometimes interact with intrinsic factors. For example, Doody *et al.* (2008) used CORT levels and observational foraging behaviour data from 1998-

2000 to investigate the relationship between CORT levels and prey availability in the Common Murre at Witless Bay. They found that CORT levels increased in chick-provisioning adults when capelin spawning occurred later than chick hatching and that the effect was more pronounced in "high quality mates", that is, those that fed chicks at a higher than average rate. This finding indicates a positive relationship between CORT levels and provisioning rate; however, high CORT levels have also been associated with decreases in provisioning rates (Almasi *et al.*, 2008), as well as increased self-maintenance behaviour (Breuner *et al.*, 2008) further complicating the role of CORT during breeding.

In addition to seasonal variation in corticosterone levels, sex-specific behaviour and/or physiology is also linked to corticosterone levels (Lormée *et al.*, 2003; O'Reilly & Wingfield, 2003; Angelier *et al.*, 2010). Puffins, like many species in the Alcid family, exhibit biparental care (Harris & Birkhead, 1985). Both adults tend the nest and incubate the egg before hatching and continue to brood the chick until it is able to thermoregulate on its own. After the initial chick-brooding period, the safety and warmth of the burrow allows both parents to forage at the same time; however, comparison of male and female time budgets indicates that females deliver more fish meals per day than males and spend more time incubating eggs (Creelman & Storey, 1991). A sex difference in baseline CORT level might reflect this behavioural sex difference. Despite sex differences and seasonal modulation of corticosterone, associations between food abundance and stress are still detectable in some seabird species including black-legged kittiwakes (Kitaysky *et al.*, 1999) and common murres (Kitaysky *et al.*, 2007; Doody *et al.*, 2008).

Here, we used blood samples from adult Atlantic puffins collected over a decade in the Witless Bay Ecological Reserve, to investigate the effects of varying prey availability on corticosterone levels of breeding puffins. This data also allowed us to examine seasonal changes in corticosterone as indicated in other avian species (black-legged kittiwakes, Kitaysky *et al.*, 1999; starlings, Romero & Remage-Healey, 2000; tufted puffins, Williams *et al.*, 2008), as well as sex differences in corticosterone levels associated with sex-specific behaviour and physiology as indicated in other birds (black-browed albatross, Angelier *et al.*, 2010; Red-footed boobies, Lormée *et al.*, 2003; Western sandpipers, O'Reilly & Wingfield, 2003), but never before examined in Atlantic puffins. In addition, chick diet and growth rates were compared between years of varying prey availability in order to examine links between foraging conditions, chick diet, and in turn, chick growth.

2.3 METHOD

2.3.1 *Study Site*

All data collection took place on Great Island and Gull Island, Witless Bay Ecological Reserve (47º15' N, 52º46' W). Witless Bay is home to the largest Atlantic puffin colony in North America (Rodway *et al.*, 1996). The entire reserve is 31km^2 and contains four islands where numerous seabirds return to breed annually. Over 140, 000 and 123,000 pairs of ATPU nest on Gull Island and Great Island, respectively

(Cairns & Verspoor, 1980; Robertson *et al.,* 2004). Blood samples from breeding Atlantic Puffins were collected at Great Island from 1998 - 2003 and at Gull Island in 2003, 2004, 2009, and 2010. A wooden blind on the south side of Gull Island was used to conduct feeding watches in 2009. A similar blind on the southern shore of Great Island was used to conduct feeding watches in 2001 and 2002.

2.3.2 *Capelin Abundance*

In the waters surrounding Newfoundland, capelin exhibit both demersal spawning and spawning at intertidal sites on gravel beaches. Quantitative data on inshore capelin biomass is not available for the Witless Bay area; however, hydroacoustic data collected by DFO at Bellevue Beach in Trinity Bay indicates annual variation in duration of spawning and a trend towards later spawning over the past 20 years (B. Nakashima, personal communication). Bellevue Beach data are not of particular use for the current study; however, diaries containing daily records of capelin in the surrounding waters of Ferryland (approx. 26km south of Great Island) from 1998 to 2009 were supplied by DFO and were used to determine annual availability of capelin in the Witless Bay area. These capelin diaries indicate presence/absence of capelin, spawning activity, presence of dead capelin on beaches or in water, presence of live fish in water, and indirect evidence of spawning indicated by fresh capelin found in fish stomachs or reported by experienced fishers. Data from the capelin diaries are similar to Bellevue beach hydroacoustic data in years where information from both is available.

2.3.3 *Chick Diet*

Feeding watches took place from 11 July to 20 August 2009 every 1-3 days from a blind situated on a puffin slope near the southern shore of Gull Island. Watches began at sunrise and lasted for 3 hours. The time that each adult ATPU returned to the site with food, whether or not the adult entered a burrow (indicating that the food was fed to a chick) and the type of prey were recorded. Type of prey was grouped into 3 classifications: capelin, sandlance, and larval or small fish/invertebrates. The third group, larval or small fish/invertebrates, includes larval sandlance, larval sculpin, euphasiids, squid, and any small species or larval fish that were unidentifiable at a species level from our observation distance. In the case of a burrow visit where no food was visible in the adult's bill, trips were not recorded. Similar watches occurred in 2001 and 2002 on Great Island from July10th to August 6th and July 6th to August 4th, respectively. Only observations made between July 11th and August 2nd in 2009 were included in the analysis in order to match the timing of feeding watches in 2001 and 2002. Results therefore reflect chick diet during the middle chick-rearing period.

2.3.4 *Chick Growth*

Selected burrows were monitored every two days for chick hatching in order to determine chick age at time of measurement. Chicks were measured at Great Island in 2001 ($N = 19$) and 2002 ($N = 15$) and at Gull Island in 2009 ($N = 14$). All chicks were removed from the burrow twice during the breeding season, approximately 10 days apart, and mass, tarsus, and wing cord measures were taken before returning chicks to the nestbowl. These measurements were converted into daily mass gain (g/day), tarsal growth (mm/day), and wing growth (mm/day) rates.

2.3.5 *Variation in Corticosterone Levels*

Blood samples were taken from 201 adult Atlantic Puffins nesting on Great Island and Gull Island in the Witless Bay Ecological Reserve, Newfoundland, Canada, from 1998 to 2009. Samples were taken from early May to early August. Birds on Great Island were sampled in 1998 (N=32), 1999 (N=15), 2000 (N=36), 2001 (N=32), 2002 (N=7), and 2003 (N=15), while birds on Gull Island were sampled in 2003 (N=15), 2004 (N=22), 2009 (N=51), and 2010 (N=37). Puffins were caught individually by setting nooses at burrow entrances, using noose carpets, or by grubbing (reaching into occupied burrows and removing adults). Only breeding birds were sampled and only blood samples obtained within three minutes of capture were used. Blood samples taken within 3 minutes of capture are expected to reflect baseline or near baseline CORT concentrations (Romero & Reed, 2005). In some cases, and adequate sample was not taken within 3 minutes but a small sample was still collected for the sex determination procedure described below. Puffins were placed on their sides in a bag with a wing outstretched during blood sampling. Ethanol was applied to the wing at the brachial vein, where approximately 1ml of blood was drawn using a 23-gauge butterfly needle attached to a 3 cc syringe. Drops of blood were ether dispensed onto blood collection cards (1998-2004, Sigma; 2009-2010, Whatman) and allowed to dry for 24 hours, or transferred into 2mL non-heparinized blood collection tubes and left to clot before centrifuging for 5-10 minutes using a manual centrifuge and transferring serum to another 1.5mL tube.

Serum corticosterone concentrations were determined using COAT-A-COUNT Rat Corticosterone ^{125}I radioimmunoassay kits (Cat. # TKRC1, InterMedico, Markham, Ontario) using the kit's normal procedures. Blood spot corticosterone concentrations were determined using the same ^{125}I radioimmunoassay kits with modifications (as per Wilhelm, 2004; Doody *et al.*, 2008). Three different assays all following the same procedure were used to analyze bloodspot samples. First, 30μL of each assay calibrator (0, 20, 50, 100, 200, 500, 1000, or 2000 ng/ml) was applied in spots on separate blood collection cards. Cards were allowed to dry overnight before a set of 24 circles was punched from each card using a circular hole-punch with a 3.2mm diameter. Cards with blood samples were treated in the same way. In order to standardize CORT levels between assays, pooled samples were also prepared: Two sets of two punches from each of 6 cards corresponding to 6 different common murres were made. Blood samples from these murres have been used to control for variation between all assays performed in our lab, including previous assays that have included samples from Atlantic puffins. The samples used for standardization come from common murres rather than Atlantic puffins because the assay was originally developed to estimate CORT levels of murres. Next, duplicate sets of 12 punches from each calibrator and sample were placed in antibody-coated tubes labeled with the corresponding calibrator or sample. A single set of 12 punches from a sample was placed in a single tube when blood spots were not large enough to make 24 spots and the second tube remained empty. The two sets of 12 pooled sample punches were also placed in two antibody-coated tubes. Two uncoated tubes remained empty and were used to count total radioactivity. Twelve circles of the '0' calibrator were placed in an additional two uncoated tubes and were used to test non-specific binding. Next, one milliliter of ^{125}I rat corticosterone solution was added to each tube and all tubes were checked to ensure that spots were fully submerged in the solution. Tubes were covered with foil and stored at room temperature for 5 hours, at which time tubes were swirled using a multi-tube vortex mixer for six 5-second pulses. Tubes were then placed in decanting sponges and set aside. After 13 hours of room temperature incubation, all tubes, excluding uncoated total count tubes, were decanted and allowed to drain upside-down for 3 minutes. Tubes were then tapped upside-down onto absorbent paper until all punches were discharged. Corticosterone concentrations for each tube were determined using a gamma counter and in the case of duplicates, concentration scores were averaged between the two tubes associated with each sample. Corticosterone levels were standardized between the two assays using the pooled murre samples.

2.3.6 *Sex Determination*

DNA was extracted from a subset of bloodspot cards ($N = 146$) using DNeasy Blood & Tissue Kits (QIAGEN) and individuals were sexed using a CHD-based molecular method (Fridolfsson & Ellegren, 1999). Highly conserved primers (2550F and 2718R) were used resulting in females being characterized by two fragments

(CHD1W and CHD1Z) and males being characterized by one fragment (CHD1Z) following polymerase chain reactions and agarose electrophoresis.

2.3.7 *Statistical Analyses*

Logistic regression was used to analyze differences in chick diet across years. All daily growth rates were compared across years using a multivariate ANCOVA controlling for chick age. CORT comparisons across years were made using a univariate ANOVA and post hoc Tukey HSD analysis.

2.4 RESULTS

2.4.1 *Inshore Capelin Availability*

Capelin diaries indicated considerable variation in the timing and duration of inshore capelin activity across years (Table 2.1). Capelin availability for each year was considered good if direct observation of spawning activity or dead or live capelin in water or on beaches was recorded for at least 5 days between mid-June and mid-August in the capelin diary for that year. Capelin availability was considered poor when less than 5 days of capelin activity were recorded (Table 2.1). In 1998, 1999, 2000, 2001, and 2004 capelin activity was observed for between 5 and 16 days and these years were classified as good capelin years. In 2002 and 2003, capelin activity was only observed on one day and these years were classified as poor capelin years. In 2009, a complete absence of capelin activity was observed in Ferryland, while in 2010 "some" spawning activity was indicated. Both 2009 and 2010 were classified as poor capelin years.

2.4.2 *Chick Diet & Growth*

In 2009, the proportion of capelin seen during behavioural watches of chick feeds peaked on July 25th, suggesting a late inshore arrival of spawning capelin. Early in the season, chick diet was comprised primarily of invertebrates and larval fish, whereas late in the season chicks were fed mostly sandlance (Figure 2.1).

Odds of observing capelin in feeding trips were significantly lower in 2009 than in 2002 (odds ratio 0.19, $p < 0.001$) indicating a decrease in the proportion of capelin to non-capelin fish visits (Figure 2.2). Odds of observing invertebrates and larval fish in chick diet was significantly higher in 2009 than in 2001 (odds ratio 2.17, $p = 0.001$) and 2002 (odds ratio 7.09, $p < 0.001$).

Average chick age was 16.05 ± 9.32 days. Year had a significant effect on both daily mass gain ($F_{2,44} = 5.28$, $p = 0.009$) and daily wing growth rate ($F_{2,44} = 7.79$, $p = 0.001$). Daily mass gain rate in 2009 (5.25 ± 3.98 g/day) was lower than in 2001 (6.36 ± 4.95 g/day) and 2002 (5.92 ± 4.19 g/day). Daily wing growth rate was also lowest in 2009 (0.70 ± 0.49 mm/day) compared to 2001 (2.78 ± 0.34 mm/day) and 2002 (3.38 ± 0.39 mm/day; Figure 2.3).

2.4.3 *Physiological Stress*

Values obtained from the bloodspot method of CORT extraction were converted using the equation: serum (ng/ml) = (bloodspot value x .381) – 3.82 (based on CORT values from same individuals with both serum and bloodspot CORT values) to allow comparison with CORT levels determined serum assays. All CORT comparisons were made using univariate analyses of variance (ANOVA).

Overall, females had higher baseline CORT levels than males, $F_{1,144} = 4.96$, $p = 0.03$ (females 25.09 ± 1.24 ng/ml, N = 75; males 21.26 ± 1.20 ng/ml, N = 75). In order to evaluate seasonal variation in CORT levels, samples were divided into 3 breeding stage categories: egg laying (May), incubation (June) and chick rearing (July/August). Breeding stage had a significant effect on adult CORT level, $F_{2,247} = 8.37$, $p < 0.001$ (Figure 2.4). Differences in CORT levels were significant between the egg laying stage (28.63 ± 1.59 ng/ml) and incubation (20.42 ± 1.61 ng/ml) as well as the egg laying and chick rearing (21.94 ± 0.80 ng/ml) stages. CORT levels did not differ significantly between incubation and chick rearing stages.

Baseline CORT levels were higher in good capelin years than in poor capelin years ($F_{1,261} = 22.14$, $p < 0.001$); however, during the majority of good capelin years, samples came from puffins on Great Island, while during poor capelin years the majority of samples came from Gull Island puffins; therefore, a colony difference may have influenced this apparent year type difference. In fact, there was a significant effect of colony on baseline CORT levels: average CORT was higher on Gull Island than on Great Island, $F_{1,261} = 20.32$, $p < 0.001$. In 2003, a poor capelin year, and the only year where CORT levels were available for both Gull Island and Great Island, the same colony difference was shown with higher baseline CORT at Great Island, $F_{1,29} = 5.10$, $p = 0.03$ (Figure 2.5).

2.5 DISCUSSION

2.5.1 *Chick Diet & Growth*

The proportion of capelin delivered to chicks during weeks 3-6 after hatching in 2009 (18%) is the lowest proportion reported over the previous 2 decades in Witless Bay (Table 2.2). This decrease is consistent with qualitative data obtained from DFO indicating an absence of capelin spawning activity near the study area in 2009 and confirms our speculations from observations at Gull Island that adult puffins provisioned chicks with fewer capelin than in previous years. This finding corroborates our observations of fewer capelin in seabird bills, a number of dead puffin chicks found in burrows and on puffin slopes (approximately 18) and predation of puffin chicks by gulls in 2009. Increased predation likely occurred because puffin chicks spend more time near their burrow entrance when hungry, exposing them to predators (Nettleship, 1972). Baillie and Jones (2004) also found that the proportion of capelin in chick diet decreased following a decrease in capelin abundance at the Gannet Islands providing further support for the link between changes in prey base and puffin chick diet.

The effects of a decrease in forage fish with high quality food in chick diet is shown in our study by a significant decrease in daily wing growth and mass gain in 2009, when 50% of chick diet was made up of larval fish and invertebrates. Although significant variability in chick diet and short-term decreases in the primary forage species of chick-provisioning Atlantic Puffins have been recorded at many breeding sites in the Atlantic (Anker-Nilssen, 1987; Barrett & Rikardsen, 1992; Baillie & Jones, 2003; Baillie & Jones, 2004; Burke & Montevecchi, 2008), the effects of this variability in diet on chick growth is not always clear. For example, relatively slow chick growth on Bleiksøy, an island colony in Northern Norway, in the late 1980s was presumed to be the result of food stress (Barrett & Rikardsen, 1992). In contrast, puffin fledgling mass did not differ between 2004, a year when sandlance comprised 97.6% (index of relative importance, IRA) of chick diet, and 2005, when capelin comprised 92.3% (IRA) of chick diet at Funk Island, Newfoundland (Burke & Montevecchi, 2008). Fledging mass at Funk Island may not have been affected by the absence of capelin because of the high percentage of sandlance (97.6% IRA) in chick diet when capelin availability was low. In contrast, chick-provisioning puffins in Witless Bay showed an overall decrease in the amount of high quality food in chick diet in 2009. That is to say, the proportion of both capelin and sandlance in chick diet at Witless Bay decreased in 2009, a year when slow growth rates were observed. Although the proportion of capelin in chick diet was also low in 2001, sandlance dominated chick diet and growth rates were similar to 2002. Differences in overall forage fish availability rather than differences in capelin availability may explain the absence of change in fledgling mass at Funk Island in contrast to a decrease in daily wing growth and mass gain in Witless Bay in 2009. This difference also indicates that sandlance may be a more important part of puffin diet in in the Northwest Atlantic than previously thought.

The 'junk-food' hypothesis proposes that changes in the type and quality of prey a species consumes can lead to declines in productivity (Romano *et al.*, 2006). For example, Romano *et al.* (2006) fed captive black-legged kittiwake (*Rissa* *tridactyla*) and tufted puffin (*Fratercula cirrhata*) chicks diets of varying prey types and quality. Chicks fed with fish of higher lipid content gained body mass faster than those fed lower lipid diets, a finding that supports the junk-food hypothesis. The growth patterns we observed in 2009 and attributed to poor foraging conditions might be expected to affect the survival of fledglings once they leave the nest. In fact, wing length at the time of departure is especially predictive of survival during the first year of life in tufted puffins (Morrison *et al.*, 2009) making slow wing growth in this study a particularly alarming finding. In addition to growth, low quality diet can negatively affect cognitive abilities of seabird chicks and in turn may increase mortality (Kitaysky *et al.*, 2006). Though it is not a direct measure of productivity, our finding of changes in chick diet resulting in lower growth rates under difficult foraging conditions provides support for the junk-food hypothesis.

Contrary to our findings in Witless Bay, the wing growth of seabird chicks has been shown to remain relatively stable regardless of chick diet. For example, Romano *et al.* (2006) fed captive Tufted Puffin and Black-legged Kittiwake chicks 4 different diets of high to low energy density and found that daily mass gain was influenced by diet more than daily wing growth, although some significant differences between daily wing growth and final wing length between diet groups were found. Similar results for Atlantic puffin and rhinoceros auklet (*Cerohinca monocerata*) chicks have been attributed to the preferential allocation of energy to wing growth during food stress (Øyan & Anker-Nilssen, 1996; Takenaka *et al.*, 2005). It appears that despite the importance of wing development, wing growth of chicks at Gull Island in 2009 was affected by low capelin availability. In fact, this decrease is the first recorded effect of poor foraging conditions on Atlantic puffin wing growth. Øyan & Anker-Nilssen (1996) suggest that preferential allocation of energy to wing growth may allow chicks to leave the nest sooner when food supply is low. Wilhelm & Storey (2004) found that Common Murre mass growth did not differ between three years of sampling; however, wing growth was significantly higher in a poor capelin year indicating that allocation to wing growth may be prioritized so that chicks can fledge earlier when food supply is low. Early fledging might be advantageous for species that continue to provide care to chicks at sea, such as murres, but early fledging may not be as important for species like the Atlantic puffin that do not exhibit this parental care behaviour post-fledging. Although fledge dates for chicks studied at Gull Island in 2009 are unknown, slow wing growth indicates that chicks either fledged with shorter wing lengths or delayed fledging until wing length increased rather than prioritizing wing growth. If foraging conditions at Witless Bay in 2009 were more difficult than those in other studies where chick growth was compared between years of better and worse condition, then slow wing growth at Gull Island in 2009 indicates that the degree of food stress in a given breeding season may influence how growth patterns are affected and how energy is allocated during the nestling period.

2.5.2 *Corticosterone Levels of Chick-Provisioning Adults*

Changes in chick diet, growth, and survival in response to prey conditions indicate that the foraging environment does affect puffins during the breeding season and that changes in the environment have the potential to increase stress in chick-provisioning puffins. Our comparison of CORT levels between years of high and low capelin availability revealed a positive relationship between CORT and foraging conditions. This finding is contrary to many studies that indicate a negative relationship between food availability and CORT in seabirds (Kitaysky *et al.*, 1999; Kitaysky et al., 2007; Doody *et al.*, 2008). This is the first study to investigate this relationship in Atlantic puffins and suggests that the strongly supported relationship between CORT and foraging conditions may not hold for this species, or that the relationship may be obscured by other factors. Although this finding was not expected, it is not surprising in view of the considerable variability in strength and direction of relationships between CORT and stressful conditions (Bonier *et al.*, 2009). Negative relationships between experimentally induced chronic stress and CORT have been found previously, indicating that high CORT may not always indicate stressful conditions and that caution should be used when interpreting CORT levels measured in the field (Rich & Romero, 2005; Cyr & Romero, 2007).

Rich & Romero (2005) suggest that release of corticosterone is controlled by different mechanisms under normal conditions versus chronically stressful conditions: Under normal conditions, the pituitary regulates adrenocorticotropin (ACTH) release, and in turn regulates CORT concentrations, while under chronic conditions, the hypothalamus regulates arginine vasotocin (AVT) release which reduces ACTH and in turn results in lower CORT concentrations. The action of these two mechanisms under different stress conditions might explain differences in corticosterone levels under different degrees of food stress. If puffins at Gull Island experienced more difficult foraging conditions in low capelin availability years than seabirds sampled in other studies linking CORT concentrations with foraging conditions, low CORT levels might be expected. On the other hand, murres at Great Island with chicks that hatched before capelin arrival had higher CORT levels than those with later-hatching chicks during a mismatch capelin year when chick hatching began a week before spawning capelin arrived inshore, suggesting that CORT levels are elevated when an ecological problem can be solved with increased effort and suppressed when it can not.

In addition to a difference in CORT levels between good and poor capelin years, a colony difference was also shown in Witless Bay: Puffins at Great Island showed higher baseline CORT levels than puffins at Gull Island, further complicating interpretation of corticosterone levels. This difference may be the effect of an unbalanced design: most samples from good capelin years were taken at Great Island while most samples taken during poor capelin years were taken at Gull Island. However, the same colony difference in CORT levels is seen in common murres (A. Storey, pers comm., 2010) and this colony difference may reflect longer foraging distances for the Great Island birds.

There was also an overall sex difference in baseline CORT levels indicating that female puffins experience more stress during the breeding season than do males. This sex difference corresponds with observational findings that females invest more care during the breeding season, in the form of foraging and incubation, than do males

(Creelman & Storey, 1991). This finding indicates that sex differences in stress hormone levels can exist even when behavioural sex differences are minimal, as in species that exhibit bi-parental care. These hormonal differences likely depend on the degree of behavioural differences seen within a species. For example, common murres do not show a sex difference in CORT levels (Doody *et al.*, 2008). While bi-parental care is exhibited in both murres and puffins, burrow nesting allows both puffin parents to forage at the same time while cliff-nesting murres alternate foraging duties because one adult must stay with the chick at all times. According to Jones *et al.* (2002), room for negotiation over level of investment increases between parents as the importance of biparental care decreases. Since Atlantic puffins do not need to coordinate continuous brooding and both adults are able to foraging at the same time, there is more room for negotiation within breeding pairs. This flexibility in behavioural duties may explain species-specific sex differences in corticosterone levels between species that display biparental care.

Corticosterone levels decreased over the breeding season. CORT levels were highest during early breeding and lower during incubation and chick rearing. This result contrasts the seasonal pattern of increasing CORT levels over the breeding season in another long-lived seabird, the black-legged kittiwake (Kitaysky *et al.*, 1999). Short-lived passerines, on the other hand, show a similar pattern of elevated CORT levels in early breeding (Astheimer *et al.*, 1994) and CORT suppression later in breeding (Wingfield *et al.*, 1995), as do tufted puffins (Williams *et al.*, 2008). In Atlantic puffins, declining corticosterone over the breeding season might reflect foraging activities as puffins move from offshore to inshore foraging grounds upon the arrival of spawning capelin in bay areas.

Overall, differences in prey availability at Witless Bay had significant effects on both puffin chicks and adults. While a decrease in chick mass gain rate was expected during poor foraging conditions, a decrease in wing growth rate is surprising in light of the importance of wing growth and preferential allocation of energy to wing growth under poor conditions. This finding suggests that the severity of food stress in a given year might be an important factor in determining chick growth patterns and deserves further attention. Unexpectedly, adult puffins had higher CORT levels when capelin availability was high. Breeding stage, colony, and sex differences in CORT levels were also shown and are important factors to consider when using CORT levels measured in the field to draw conclusions about the stressors, intrinsic and environmental, experienced by individuals during the breeding season.

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Table 2.1: Summary of capelin diaries: observation of capelin activity in the Ferryland, Newfoundland area during the spawning season as recorded by local fishermen.

		# of days:				
Year	*Dates*	*Spawning activity observed*	*Dead capelin on beach/in water*	*Capelin in water*	*Live/dead capelin observed*	*Year Type*
1998	July 3rd - 18th	4	3	4	6	good
1999	June 20th - July 22nd	0	2	3	5	good
2000	June 1st - Aug 5th	12	2	7	16	good
2001	June 15th - Aug 15th	2	1	7	10	good
2002	June 10th - July 18th	0	0	1	1	poor
2003	June 15 - July 31st	1	0	0	1	poor
2004	June 15-July 25	5	6	4	7	good
2009	June - August	0	0	0	0	poor
2010	June-August	"some"	0	0	0	poor

Table 2.2: Proportion, based on frequency, of various prey species in chick diet at Witless Bay Ecological Reserve over the past two decades.

Year	*Colony*	*% Capelin*	*% Sandlance*	*% Other*
1993*	Great Island	44	41	15
1997**	Gull Island	34	3	63
1998**	Gull Island	45	14	41
2001	Great Island	22	48	30
2002	Great Island	52	23	26
2009	Gull Island	18	32	50

* from Rodway & Montevecchi, 1996 (total nestling period)

** from Baillie & Jones, 2003 (weeks 3 to 6 of chick rearing)

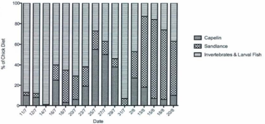


Figure 2.1: Variation in prey distribution at Gull Island during the 2009 breeding season. Proportions indicated are based on number of fish observed each day (day/month).

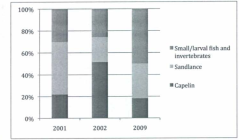


Figure 2.2: Proportion (by number) of capelin, sandlance, and small/larval fish and invertebrate species in puffin chick diet in 2001, 2002, and 2009 at Witless Bay

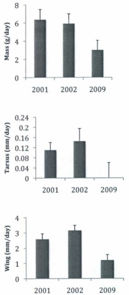
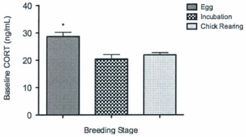
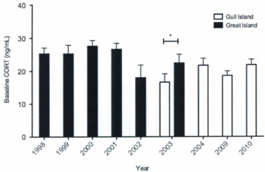


Figure 2.3: Average daily chick mass gain, tarsal growth, and wing growth with standard errors across years.



* p <.001

Figure 2.4: Average serum converted baseline CORT levels with standard error for puffins in Witless Bay during egg laying, incubation, and chick rearing breeding stages



* $p < .05$

Figure 2.5: Average serum converted baseline CORT with standard error for puffins at Gull Island and Great Island, Witless Bay

CHAPTER 3: EFFECTS OF SUPPLEMENTAL FEEDING ON ATLANTIC PUFFIN (*FRATERCULA ARCTICA*) CHICK GROWTH AND BASELINE CORTICOSTERONE LEVELS

3.1 ABSTRACT

We compared Atlantic puffin nestling growth rates, survival, and corticosterone levels between supplementary fed and control group chicks. Chicks fed a supplementary diet of one capelin per day gained mass faster than those that were not. No difference in wing or tarsal growth rate between groups was found. Contrary to previous findings in seabird chicks, food-stressed nestlings did not show increased corticosterone levels. The survival rate of chicks to the end of the experiment was higher in supplementary fed chicks. Mass gain and chick survival appeared more sensitive to changes in chick nutritional status than did physiological and skeletal growth measures and show potential as biological indicators of prey abundance.

3.2 INTRODUCTION

Although food is often more abundant for birds during the breeding season than over winter, food can limit reproductive success and chick survival (Martin, 1987). Current oceanographic and climate changes are creating especially challenging conditions for seabirds that depend on marine resources during the breeding season, and throughout the year (Carscadden *et al.*, 2001, 2002; Croxall *et al.*, 2002; Davoren & Montevecchi, 2003; Sandvik *et al.*, 2005; Ranconi & Burger, 2008; ; Watanuki *et al.*, 2009; Wolf *et al.*, 2010). Under these conditions, it is important to understand what will happen to seabird species, especially if we intend to take advantage of seabirds as potential biological indicators of fish abundance. Understanding changes in breeding parameters in response to fish abundance may be especially important as seabirds can be easily accessed and studied during the breeding season, and information gained during the chick-rearing stage is likely more sensitive to food availability than measures taken during incubation or after fledging when energy requirements are lower (as in Black-legged kittiwakes, *Rissa tridactyla*, Gill, Hatch, & Lanctot *et al.*, 2002). Breeding phenology and productivity measures including chick diet (Baillie & Jones 2003, 2004; Barrett, 2002), growth (Baillie & Jones, 2004; Barrett & Rikardsen, 1992), and adult corticosterone (CORT) levels (Kitaysky *et al.*, 2007; Doody *et al.*, 2008) have already been linked to prey availability under natural conditions. Here, we focus on the growth, survival, and stress responses of Atlantic puffin chicks (*Fratercula arctica*) to a manipulated diet in order to understand the relationships between chick condition and physiology with chick food intake. Puffin chicks are easy to monitor during the breeding season because they are restricted to their nesting burrow. This accessibility makes puffin chicks a practical group for monitoring in order to estimate changes in prey distribution and abundance.

Atlantic puffins have traditionally depended on spawning capelin as their primary prey species in the Northwest Atlantic during the breeding season (Brown & Nettleship, 1984; Montevecchi, 1993). Boat surveys in Witless Bay from 1982-1984 indicate that puffins forage close to shore and are spatially associated with capelin (Piatt & Methven, 1986). In more recent years, increasing proportions of sandlance, larval fish, and invertebrates have been seen in chick diet and slow chick growth has been recorded in Witless Bay (Chapter 2). Slow puffin chick growth and changes in chick diet have also been noted at the Gannet Islands, Labrador, where chicks received 50-70% less capelin and gained mass more slowly in 1996-1998 than 1981-1983 in response to a decrease in capelin abundance (Baille & Jones, 2004). These dietary shifts reflect changes in the distribution, timing, and total duration of capelin spawning in the coastal waters of Newfoundland over the past two decades (Carscadden et al., 2002). Comparison of puffin chick growth across years of differing prey abundance indicate a link between prey availability, chick diet, and chick growth (Chapter 2, Baillie & Jones, 2004); however, experimental manipulation of chick diet is required in order to estimate the degree of change in chick growth and survival in response to a known change in chick diet. A quantified relationship between change in diet and chick growth or survival might increase the usefulness of breeding parameters as biological indicators.

Chick growth as an indicator of prey abundance has a major advantage over fledging success in that growth measurements can be taken over a relatively short period of time enabling short research visits to colonies. Fledging success, on the other hand, requires observation over the entire hatching and fledging stages, which can each take over 20 days in Atlantic puffins due to asynchrony in hatching and fledging times (Nettleship, 1972). Cairns (1987) suggests that breeding success and chick growth are both sensitive to changes in prey availability when availability is at a poor to moderate level. Other measures related to food abundance that can be collected over a shorter period of time than growth rates might also be valuable. We investigated one physiological measure, stress, by measuring baseline CORT in chicks. Measuring hormone levels requires only one visit to a colony for only a few hours, depending on the number of samples collected.

Corticosterone is the primary glucocorticoid in birds (Holmes & Phillips, 1976) and increased CORT secretion during physical challenges may help individuals avoid chronic stress by influencing behaviour and physiology during unpredictable events, such as food limitations (Wingfield & Kitaysky, 2002). High CORT levels in adult seabirds have already been linked with food low availability (Kitaysky *et al.*, 1999, 2007; Doody *et al.*, 2008). Increased baseline CORT levels have also been shown in food-stressed seabird chicks (Nunez-de la Mora *et al.*, 1996; Kitaysky *et al.*, 2001a) and can be advantageous as they facilitate begging allowing chicks to restore their body condition by influencing adult provisioning rates (Kitaysky *et al.*, 2001b;

Quillfeldt *et al.*, 2006). The response of puffin chick CORT levels under food stress is unknown.

In this study, we used a supplementary feeding regime to compare the growth rate and stress response of fed and unfed puffin chicks on Gull Island, Witless Bay Ecological Reserve, Newfoundland. We expected that supplemental feeding would improve chick condition. More specifically, we predicted that fed puffin chicks would have faster growth rates and lower baseline CORT levels than unfed chicks. Chick mortality over the course of the experiment also led us to compare chick survival between fed and unfed chicks for the duration of the experiment.

3.3 METHOD

3.3.1 *Species and Study Site*

This study was conducted on Gull Island, Witless Bay Ecological Reserve, Newfoundland, from 10 July – 17 July 2010. Foraging conditions at the time of study were poor, as indicated by low estimates of spawning capelin in the area (Chapter 2, B. Nakashima, pers comm., 2011). Fifty active Atlantic puffin burrows on a western facing grassy slope were selected for the experiment. The location was selected for several reasons including: direct accessibility from a wooded path a safe distance puffin burrows ensuring no disturbance to other nesting areas during daily visits, a reasonable slope angle allowing safe access to burrows for the field crew during wet and slippery conditions, and a high burrow occupancy rate which decreased the time required to find active burrows and also permitted a small area of study, again decreasing the area and duration of disturbance. Puffin chicks at this site are known to be extremely sensitive to any kind of disturbance, therefore, burrows were not monitored prior to the start of the experiment and nestling age is unknown. The start date of the experiment was chosen based on mean hatch dates recorded in previous years in order to best ensure that all chicks were less than 20 days old and in the linear growth phase of development.

3.3.2 *Field Procedure*

On day one of the experiment, all fifty chicks were removed from burrows, and mass, tarsus, and wing chord measurements were made before returning chicks to the nestbowl. Each chick was randomly assigned to one of three experimental groups: 1) Supplemental feeding (SF $N = 25$), 2) Feeding control (FC $N = 10$) and 3) Control (C $N = 15$). Initial mass, wing chord, tarsus length, and estimated age did not differ between the groups (mass, $F_{2,47} = 0.47$, $p = 0.63$; wing chord, $F_{2,47} = 2.32$, $p = 0.11$; tarsus, $F_{2,47} = 2.06$, $p = 0.14$; age, $F_{2,47} = 1.45$, $p = 0.25$). Chicks in the supplemental feeding group were given one capelin weighing approximately 20g following grubbing on day one. Each supplementary capelin was placed near the nest bowl of burrows assigned to the SF group at approximately 1300h NDT daily. In the SF group, we continued to feed chicks one capelin per day for the following 6 days for a total of 7 days of supplemental feeding. In burrows assigned to the FC group, the supplemental feeding procedure was mimicked by reaching into the burrow and holding a hand close to the nest bowl before exiting the burrow. Burrows assigned to the control group remained undisturbed until the 8th day of the experiment. Puffins feed chicks several times per day with estimates indicating from 2.9 to 5.4 meals per day depending on the year of study (Wernham & Bryant, 1998). In 2010, the average feeding rate on Gull Island was only 2.3 meals per day and each meal usually consisted of a single fish or a group of larval fish or invertebrates (Chapter 3); therefore, the additional capelin per day provided to chicks in the SF group provided a considerable increase in chick food intake given the natural feeding conditions at the time of study.

On day eight of the experiment, all 50 burrows were grubbed and chick mass, tarsus, and wing chord measurements were taken. In addition, a 0.5cc blood sample was taken from the brachial vein of each chick using a 23-guage butterfly needle attached to a 3cc syringe. Blood was dispensed in drops onto blood collection cards (Whatman) and allowed to dry for 24 hours. Five chicks disappeared during the experiment and several chicks were too small to take an adequate blood sample.from the brachial vein. In addition, only samples taken in under 3 minutes were included in analysis of CORT levels as blood samples taken within 3 minutes of capture are expected to reflect baseline or near baseline CORT concentrations (Romero & Reed, 2005). These three restrictions reduced the sample size of both control groups for growth comparisons to $N = 8$ (FC) and $N = 12$ (C). Sample size for CORT level comparisons were reduced to $N = 20$ (SF), $N = 4$ (FC) and $N = 7$ (C).

3.3.3 *Baseline Corticosterone Level Determination*

Corticosterone concentrations were determined using COAT-A-COUNT Rat Corticosterone ^{125}I radioimmunoassay kits (Cat. # TKRC1, InterMedico, Markham, Ontario) with modifications for measurements using blood spot cards (as per Wilhelm, 2004; Doody *et al.*, 2008, Chapter 1). First, 30μL of each assay calibrator (0, 20, 50, 100, 200, 500, 1000, or 2000 ng/ml) was applied in spots on separate blood collection cards. Cards were allowed to dry overnight before a set of 24 circles was punched from each card using a circular hole-punch with a 3.2mm diameter. When blood spots were large enough, a set of 24 punches were made from each blood sample card. If blood spots were not large enough to allow 24 spots, 12 or 6 spots were punched. Two sets of 12 punches from each calibrator and sample were placed in antibody-coated tubes labeled with the corresponding calibrator or sample number. When 24 spots were not available, a singlicate tube containing 12 (N = 3) or 6 (N = 2) spots was paired with an empty tube. An additional two uncoated tubes remained empty and were used to count total radioactivity. Twelve circles of the '0' calibrator were placed in an additional two uncoated tubes and were used to test non-specific binding. Next, one milliliter of ^{125}I rat corticosterone solution was added to each tube and all tubes were checked to ensure that spots were fully submerged in the solution. Tubes were covered with foil and stored at room temperature for 5 hours, at which time tubes were swirled using a multi-tube vortex mixer for six 5-second pulses. Tubes were then placed in decanting sponges and set aside. After 13 hours of room temperature incubation, all tubes, excluding uncoated total count tubes, were decanted and allowed to drain upside-down for 5 minutes. Tubes were then tapped upside-down onto absorbent paper until all punches were discharged. CORT concentrations in each tube were determined using a gamma counter and concentration scores were averaged between the two tubes used for each duplicate sample. Raw scores for singlicate samples of 12 spots were used, and scores for singlicate samples of 6 spots were doubled. These values were then converted using the equation: serum (ng/ml) = (bloodspot value x .381) – 3.82 (based on CORT values from same individual puffins with both serum and bloodspot CORT values) to allow comparison with CORT levels determined using serum assays.

3.3.4 *Statistical Analyses*

We conducted all statistical tests using PASW Statistics 18.0. Analyses of variance (ANOVAs) were used to compare chick growth rates and CORT levels between treatment groups. A Fisher's exact test was used to compare survival between supplementary fed and control chicks.

3.4 RESULTS

3.4.1 *Chick Growth*

Growth measurements taken on day 1 and day 8 were used to calculate daily growth rates for tarsus, wing chord, and mass gain of each chick. There were no significant differences between FC and C groups (Table 3.1) for any of the daily growth rate parameters measured; therefore, these groups were combined for all further growth rate analyses.

No differences in daily tarsal growth ($F_{1,44} = 0.27$, $p = 0.61$) or daily wing chord growth ($F_{1,44} = 1.66$, $p = 0.21$) between supplementary fed and non-supplementary fed chicks were found. Average daily mass gain was greater in the supplementary fed group ($F_{1,44} = 4.53$, $p = 0.04$; Figure 3.1).

3.4.2 *Chick Survival*

Five chicks disappeared during the experiment. Three of these were from the control group and 2 from the feeding control group. Feeding control and control chicks were collapsed into a single non-supplemental fed group for comparison with supplemental fed. The difference in the proportion of chicks in the supplemental-fed group that survived to day 7 or the experiment (1) and the proportion of chicks in the non-supplemental fed group that survived (0.80) was significantly different ($p <$ 0.001; Fisher's exact test; Table 3.2).

3.4.3 *Corticosterone Concentrations*

Chicks in the feeding control group had significantly higher baseline CORT levels than chicks in the control group on day 7 of the experiment ($F_{1,9} = 8.08$, $p =$ 0.02); therefore, these groups were not combined as they were for growth parameter analysis, but remained separate for the overall CORT analysis. On the whole, there was no effect of group on baseline CORT levels ($F_{2,28} = 1.11$, $p = 0.34$) indicating that supplemental feeding did not reduce baseline CORT concentrations (Figure 3.2).

3.5 DISUCSSION

3.5.1 *Foraging Conditions*

The daily mass gain rate of chicks in the control group (8.57 ± 1.1 g/day) was lower than that reported on Gull Island in 1998 and those reported at the Gannet Islands in 1997 and 1998, but not 1996, a year when capelin was absent from chick diet (Baillie & Jones, 2003; Table 3.3). Daily wing growth of chicks in the control group (2.52 ± 0.37 mm/day) was also lower that reported at Gull Island in 1998 and at the Gannet Islands in 1997 and 1998 (Baillie & Jones, 2003; Table 3.3). Puffins at the Gannet Islands experienced poor foraging conditions during the years reported due to an offshore shift in capelin populations in Labrador (Baillie & Jones, 2003). Since average growth rates in our control group were lower than those reported during poor foraging conditions at the Gannet Islands, food availability at Gull Island in 2010 was assumed to be low. Reports from local fishermen collected by the Department of Fisheries and Oceans also reported low estimates of spawning capelin in the area (B. Nakashima, personal communication).

3.5.2 *Chick Growth*

Increased mass gain during supplemental feeding was consistent with previous supplementary feeding experiments on Atlantic puffins (Øyan & Anker-Nilssen, 1996; Hudson *et al.*, 1979) and other seabird species including black-legged kittiwake (Gill *et al.*, 2002), common murres (*Uria aalge*) (Benowits-Fredericks *et al.*, 2006), and rhinocerous auklets (*Cerorhincha monocerata*) (Takahashi *et al.*, 1999). This increase in mass gain is not consistent with a more recent study from Hornøya, Norway, where supplementary fed chicks showed no increase in mass gain over control chicks also following the collapse of capelin stocks (Dahl *et al.*, 2005). The absence of a mass gain affect was accounted for by a decrease in provisioning rate by parents of supplemental fed chicks. Dahl *et al.* (2005) concluded that although foraging conditions following the capelin collapse affected diet composition, they were not, in this case, significant enough to affect breeding and availability of alternative prey species allowed control puffins to maintain breeding success.

Mass gain of tufted puffin (*Fratercula cirrhata*) chicks has also been shown not to be affected by supplemental feeding (Wehle, 1983; Gjerdrum, 2004) and mass gain of horned puffin (*Fratercula corniculata*) chicks has been shown to increase when given 100g of food per day (Harding *et al.*, 2002), but remained unaffected when given 50g of food per day (Wehle, 1983). The amount of extra food provided during supplemental feeding experiments may explain differences in growth responses within species; however, Atlantic puffin chicks in Dahl *et al.*'s (2005) study described above received approximately 10g more supplemental capelin each per day compared to puffin chicks at Gull Island in 2010 and therefore the differences in growth responses to a supplementary diet between these two studies can not be explained by the amount of food given. Discrepancies in growth responses between species might be due to differences in parental behaviour during supplemental feeding. For example, tufted puffins and horned puffins both provisioned supplemental fed chicks less often than control chicks during similar feeding experiments (Harding *et al.*, 2002;

Gjerdrum, 2004) while rhinoceros auklet provisioning rates were similar between supplementary fed and control chicks (Takahashi *et al.*, 1999). Rhinoceros auklets provision chicks less often than puffins and this long provisioning interval might not leave room for provisioning rate adjustment in response to reduced food demand due to risk of starvation or unpredictable short-term food availability (Takahashi *et al.*, 1999).

Chick-provisioning Atlantic puffins feed chicks several times a day and have been shown to be able to adjust provisioning rates in response to chick food demand (Dahl *et al.*, 2005; Harris, 1983; Johnsen *et al.*, 1994; Cook & Hamer, 1997); however, under increasingly poor foraging conditions, adults may need to continue provisioning at the maximum rate permitted by prey availability in order to meet chick food demand even when chicks are receiving supplemental food. One study of puffin chick growth showed that chicks in both supplementary fed and control groups had identical growth development up until a few days prior to fledging. The total amount of food received by chicks in each group was also similar: parental provisioning in the control group was equal to parental provisioning plus supplementary food in the experimental group, indicating that parents regulated feeding in response to chick condition (Cook & Hamer, 1997). Puffins at Hornøya, Norway, showed a similar response in that parents of supplemental fed chicks decreased their provisioning rate by nearly half (Dahl *et al.*, 2005). Since supplemental fed puffins in our study did show an increase in mass gain rate, it is unlikely that parents were adjusting provisioning behaviour in response to chick condition. Adults seem to have continued feeding chicks at the maximum rate permitted by the poor foraging conditions at the colony resulting in more total food being consumed by supplemental fed chicks than control chicks.

No difference between supplementary and non-supplementary fed chicks in wing chord growth is consistent with other studies that show greater effects of mass gain over wing growth with increased food intake in seabird chicks including black-legged kittiwakes (Gill *et al.*, 2002), common murres (Benowitz-Fredericks *et al.*, 2006) and Atlantic puffins (Hudson, 1979). In the past, variation in the effects of food availability on different growth parameters has been attributed to preferential allocation of energy to higher priority characters. For example, preferential allocation to wing growth during poor foraging conditions could reduce wing-loading during fledging (Benowitz-Fredericks *et al.*, 2006). Wilhelm and Storey (2004) found that murre chicks reared in a year of low capelin availability at Great Island, Witless Bay Ecological Reserve, had overall longer wing length than those reared in years of higher capelin availability indicating that murre chicks can allocate growth during unfavorable conditions. In Atlantic puffins, preferential allocation to wing growth might facilitate early departure from the nest under poor foraging conditions, decreasing the amount of time chicks are solely dependent on their parents for provisioning (Øyan & Anker-Nilssen, 1996). Unfed puffin chicks in this study did not increase wing growth and the absence of an effect of supplemental feeding on wing growth indicates that wing growth is maintained at a relatively fixed rate independent of food intake. An effect of increased food intake on rate of mass gain but neither rate of wing growth nor tarsus growth indicates that rate of wing and tarsus growth is maintained at the cost of mass gain during food stress.

3.5.3 *Chick Survival*

Although differences in puffin chick condition between colonies with higher and lower food availability in the Northwest Atlantic have been noted previously, hatching and fledging success appear to have remained stable (Baillie & Jones, 2003). Different survival rates to day 8 of this experiment show that puffin chick survival is linked to food intake. Past differences in food availability between colonies may not have been great enough to produce differences in chick survival. In this experiment, poor foraging conditions at the time of study meant that chicks in the supplemental feeding group were receiving considerably more food energy than those that were fed only by their parents and this difference in energy intake was enough to affect chick survival. Furthermore, the short duration of this experiment does not take into account chick loss later in the breeding season. Overall chick loss may have been even higher than what was reported here. Significant differences in survival between treatment groups over this short period of time also suggests that observation of the total duration of chick hatching and fledging may not be necessary in order to detect differences in breeding success between years of differing prey availability, even if mid-season estimates of breeding success are higher or lower than those that take into account the entire fledging period. Comparisons of survival rates based on partial season and full season monitoring of puffin burrows within the same season would help determine the accuracy of partial season measures of chick survival.

3.5.4 *Corticosterone*

Higher average baseline CORT level in the feeding control group compared with the control group suggests a disturbance effect of the supplemental feeding procedure on puffin chicks. Despite the small sample sizes for control groups (C = 7, FC = 4), this result suggests that including a disturbance control group is necessary for this type of study.

Increased baseline CORT levels under food stress have been noted in black-legged kittiwake (Kitaysky *et al.*, 1999), and blue-footed booby chicks (Nunez-de la Mora *et al.*, 1996). Contrary to these negative relationships between CORT and food intake, we did not find a difference in baseline CORT levels between supplemental and non-supplemental fed puffin chicks. No effect of feeding conditions on CORT levels might be expected if chick condition did not differ between groups; however, higher daily mass gain rates in supplemental fed chicks indicates that chick condition improved with supplemental feeding.

Consistent baseline CORT levels between groups despite differences in chick condition suggest that puffin chicks might suppress CORT secretion during food shortages. Kitaysky *et al.* (2005) found similar results in tufted puffin chicks that were exposed to long and short-term food restrictions. CORT levels decreased in tufted puffin chicks that were fasted for 24h but did not decrease in control chicks. Tufted puffin chicks fed lower quality diets for a 3-week period showed lower body mass and lipid reserves as well as lower CORT levels than chicks fed higher quality diets. Although elevated CORT levels can help chicks restore their body condition by enhancing behaviours that affect adult provisioning rates, such as begging (Kitaysky *et al.*, 2001b; Quillfeldt *et al.*, 2006), chronically elevated CORT levels are detrimental to development and cognitive function (Kitaysky *et al.*, 2003). Due to the detrimental effects of elevated CORT levels, especially during early development, chicks exposed to highly variable and unpredictable feeding rates might gain greater benefits by suppressing CORT secretion during nutritional stress rather than increasing it (Kitaysky *et al.*, 2005). One benefit of not increasing CORT could be that it allows chicks to prolong time spent at the nest by causing them to maintain a low level of activity. Delaying fledging under poor foraging conditions would allow puffin chicks more time to develop before leaving their nesting burrow, increasing their chances of survival once fledged.

Tufted puffin chicks and Atlantic puffin chicks are fed less often than black-legged kittiwake chicks. For example, Gjerdrum (2004) reported a feeding rate of 6.4 meals/day for tufted puffins at Triangle Island, British Columbia while Wernham & Bryant (1998) reported feeding rates of 5.43 meals/day in 1990 and 2.91 meals/day in 1991 for Atlantic puffins on the Isle of May, Scotland. On the other hand, Braun and Hunt (1983) reported feeding rates of 2.32 meals/hour for 1st hatch and 0.88 meals/hour for 2nd hatch black-legged kittiwake chicks at St. Paul Island, Alaska. A positive relationship between food intake and CORT levels as seen in tufted puffins, or the stability of baseline CORT levels between supplemental fed and non-supplemental fed Atlantic puffin chicks as seen here, supports Kitaysky *et al.*'s (2005) prediction that chicks of species with intermittent provisioning regimes in which parents may not be able to respond to increased chick food demand should suppress CORT secretion under nutritional stress.

In summary, puffin chick mass gain rates and chick survival are clearly more sensitive to food intake than the other measures we investigated. Although adults of supplementary fed chicks may have decreased feeding rates, a difference in mass gain rates between fed and unfed puffin chicks suggests that they did not. Furthermore, Chapter 4 indicates that puffins did not adjust provisioning rates when chicks were fed supplementary fish in 2010. When taken in context with other supplemental feeding experiments, this result indicates that the ability of parents to adjust provisioning behaviour in response to manipulated chick condition is possibly dependent on current foraging conditions, as well as adult body condition (Erikstad *et al.*, 1997). Increased chick mass gain and early survival in supplemental fed chicks indicates that an increase in food intake of one capelin per day is enough to affect puffin chick condition and survival under the foraging conditions in the area at the time of study. In contrast, CORT levels were not affected by an increase of one fish per day. These results suggest that growth parameters, namely mass gain, and chick survival are better indicators of the nutritional status of puffin chicks than baseline stress levels and wing length, at least under the foraging conditions at our study site during this experiment. Wing growth rates may be reduced during very low capelin availability (Chapter 2) and could therefore be important as an indicator of extremely harsh conditions and food stress if prey abundance and availability due to distributions continues to decline. Overall, it appears that mass gain and chick survival are most important to monitor for changes in response to smaller scale changes in food availability and these factors have strong potential as biological indicators of fish abundance and distribution.

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Table 3.1: Daily growth rate means of puffin chicks with standard error (SE) for feeding control (chicks in burrows where supplemental feeding procedure was mimicked but chicks did not receive supplementary food, FC), control (chicks that did not receive supplementary food, C), and supplemental feeding (chicks fed one supplementary capelin per day, SF) groups

		FC (*N*=8)	**C** (*N*=12)	**SF** (*N*=25)
Tarsus (mm/day)	*X*	0.32	0.33	0.35
	SE	0.06	0.05	0.03
Wing Chord (mm/day)	*X*	2.63	2.52	3.07
	SE	0.46	0.37	0.26
Mass Gain (g/day)	*X*	7.77	8.57	10.49
	SE	1.30	1.06	0.70

Table 3.2: Survival rate up to 7 days by group: Control (chicks not fed supplementary food), Feeding Control (chicks in burrows where supplementary feeding procedure was mimicked but chicks did not receive supplementary food), and Supplemental Fed (chicks that received one supplemental capelin per day)

Group	***N***	***Survived (Proportion)***	***Lost (Proportion)***
Control	15	12 (0.80)	3 (0.20)
Feeding Control	10	8 (0.80)	2 (0.20)
Supplemental Fed	25	25 (1)	0 (0)

Table 3.3: Growth rate comparisons between Gull and Great Island from 1996 – 2010

	Mass gain (g/day)		**Wing growth (mm/day)**	
	Gull	*Gannets*	*Gull*	*Gannets*
1996*		7.1 (2.8)		
1997*		9 (1.8)		3.9 (0.3)
1998*	9.4 (3.2)	9.4 (2.2)	4.1 (0.4)	4.1 (0.4)
1999*				
2010	8.57 (1.1)		2.52 (0.4)	

* from Baillie & Jones (2003)

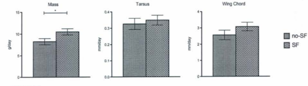

Figure 3.1: Mean daily mass gain, tarsal, and wing chord growth rates with standard errors for supplemental (N = 25) and non-supplemental fed (N = 20) chicks

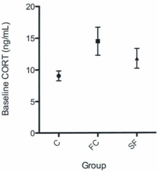

Figure 3.2: Serum converted mean baseline CORT levels and standard errors for chicks in control (C, N = 7), feeding control (FC, N = 4) and supplementary feeding (SF, N = 20) groups

CHAPTER 4: CHICK BEGGING CALL TYPES AND PARENTAL PROVISOINING IN RESPONSE TO CHICK CONDITION IN A BURROW-NESTING ALCID

4.1 ABSTRACT

Parents and offspring employ different strategies in order to maximize inclusive fitness, which can result in parent-offspring conflict. We investigated one strategy, chick begging, in the Atlantic puffin (*Fratercula arctica*) using audiovisual recordings of parent-offspring interactions in 17 burrows. Two different chick call types were identified: a medium frequency cheeping call (Type I) and a high frequency screeching call (Type II). We compared the use of these calls between and within burrows under natural conditions and following a supplementary feeding regime. A comparison of chick call types in relation to parental feeding indicated that Type I calls occur during both fish and no-fish visits to the burrow, while Type II calls occurred almost exclusively during no-fish visits. Chicks in poor body condition used more Type II calls during adult visits than chicks in better condition. Use of Type II calls decreased following supplementary feeding. This decrease did not result in a change in parental behaviour: adults continued to feed chicks the same type/quality of food at the same rate. Poor foraging conditions during the study period may explain the absence of parental response to an increase in chick condition and decrease in the use of Type II calls.

4.2 INTRODUCTION

Atlantic puffins (*Fratercula arctica*) are a long-lived seabird species with a high adult survival rate that rear only one offspring per breeding season (Harris & Birkhead 1985; Hudson 1985). In species showing these life-history characteristics, the amount of parental care provided to offspring can be understood as a tradeoff between current reproductive effort and future adult survival (Stearns 1992). When we consider the viewpoint of the offspring as well as the parent, we can expect that parent-offspring conflict will arise as offspring employ strategies to maximize inclusive fitness that compete with parental strategies during the period of parental investment (Trivers 1974). Parent-offspring conflict begins before egg-laying and is mediated through biochemical action, including hormone secretion, within the mother (Haig 1993; 1996; Müller et al. 2007). For example, maternal yolk hormone deposition has consequences for offspring development in birds (as reviewed by Müller et al. 2007). After birth, conflict is mediated primarily through behavioural action (Trivers 1974). One of the behavioural strategies employed by avian offspring is begging, a strategy commonly used by nest-bound chicks in order to obtain food from parents. Chick begging is generally thought to be an honest signal of chick condition, although dishonesty and scramble competition models can also account for the stability of begging strategies (Johnstone & Grafen 1993; Kilner & Johnstone 1997).

In a review of empirical evidence of the role of begging in offspring solicitation, Kilner and Johnstone (1997) identified three main predictions of honest signaling models: 1) begging intensity reflects offspring nutritional status, 2) parents provision offspring in relation to begging intensity, and 3) begging is costly for offspring. A major problem with these predictions is that neither prediction 2 nor 3 are exclusive to honest signaling models (Kilner & Johnstone 1997; Royle et al. 2002). For example, sibling scramble competition also predicts that the offspring that begs more will be fed the most and that begging signals must be costly (Royle et al. 2002).

The non-exclusivity of predictions in the honest signaling model creates difficulties in determining whether begging is a manipulative signal used to increase parental provisioning during parent-offspring conflict, or an honest signal that communicates chick condition to parents and is therefore advantageous to both offspring and parent. Studying chick begging and adult provisioning in the absence of sibling competition can simplify interpretation of the role of begging signals during parent-offspring conflict. Species that rear a single chick per breeding attempt provide an opportunity to do this. The role of begging signals in parent-offspring conflict amongst seabirds with a single-chick brood has included studies on several Procellariiforme species: Wilson's storm-petrels (*Oceanites oceanicus*; Quillefeldt 2002; Gladbach et al. 2009;), Cory's shearwaters (*Calonectris diomedea*; Granadeiro et al. 2000; Quillfeldt & Masello 2004; Träger et al. 2006), Manx shearwaters (*Puffinus puffinus*; Quillfeldt et al. 2004), and thin-billed prions (*Pachyptila belcheri*; Duckworth et al. 2009).

It is not surprising that burrow-nesting species have been the focus of begging behaviour studies. Since burrow-nesting seabirds only interact with their offspring in the darkness of the burrow, it is expected that auditory signals would be more effective than visual cues in communicating chick need. The majority of chick begging studies in seabirds have been based on analysis of call rates and counts under either natural or manipulated conditions (i.e., supplemental feeding or food deprivation) and provide evidence that chick begging and chick body condition are related, and that adults respond to increased begging by increasing provisioning rates when environmental conditions allow it. Some studies also incorporate analysis of the acoustic parameters of begging and indicate species-specific differences. For example, Gladbach et al. (2009) found that Wilson's storm-petrel chicks in poor condition used higher pitch begging calls and adults responded by providing larger meals. However, no relationship between acoustic parameters and chick condition or adult provisioning was found in Cory's shearwaters (Träger et al. 2006) or thin-billed prions (Duckworth et al. 2009).

The goals of this study were to: 1) identify and describe puffin chick begging call types, 2) examine the relationship between chick begging call use and chick condition, and 3) investigate parental responses to chick begging calls. In accordance with honest signaling hypotheses, we predicted that chicks in good condition would use begging signals less often than those in poor condition, that use of begging signals would decrease following supplementary feeding due to changes in chick condition, and that adults would respond to changes in chick condition and begging behaviour by adjusting their provisioning rates. Since the first goal of this study was to identify chick begging call types, we describe any call made in the presence of a foraging adult as a begging call, even though these calls might not function to affect or inform parents.

4.3 METHOD

4.3.1 *Species and Study Site*

Atlantic puffins are a burrow-nesting alcid with a single-chick brood that exhibit bi-parental care (Harris & Birkhead 1985). Audiovisual recording took place in 17 burrows at Gull Island, Witless Bay Ecological Reserve, Newfoundland, during the chick rearing stage of the 2009 ($N = 4$) and 2010 ($N = 13$) breeding seasons. Approximately 140, 000 pairs of breeding puffins return to Gull Island each spring (Robertson *et al.* 2004) and feed on capelin, *Mallotus villosus*, the preferred prey species of chick-provisioning puffins in the Northwest Atlantic (Brown & Nettleship 1984; Montevecchi 1993). In 2009 and 2010, capelin availability was low as indicated by adult provisioning behaviour (including feeding rates), and by local reports of capelin distribution (B. Nakashima, Department of Fisheries and Oceans, DFO, personal communication).

4.3.2 *Field Recording*

Four burrow scope cameras (Peep-a-Roo monochrome 1.0 diameter video probe, Sandpiper Technologies) retrofitted with omnidirectional microphones (RadioShack 33-3013) and connected to a DVR recording system (Archos AV400 Series DVR) were used to record parent-offspring interactions within active puffin burrows. Cameras were deployed in burrows and dawn to dusk recording took place for 10 days, beginning at approximately 1300h NDT on the first day and ending at approximately 1300h on the 10th day resulting in 9 full days of recording per burrow. Chicks remained undisturbed until the 4th day of videotaping when each chick being recorded was temporarily removed from the burrow at approximately 1300h and tarsus, wing chord, and mass measurements were taken. Chicks were then returned to their burrows and given one capelin (*Mallotus villosus*, approx weight – 20g). A single capelin per day was given to each chick being recorded over the following 6 days. Cameras were then removed and deployed in other active burrows where the recording and supplemental feeding procedure was repeated.

4.3.3 *Video Analysis*

Pre-supplementary feeding video footage taken from day 1 at 1300h to day 4 at 1300h and supplementary feeding video footage taken from day 7 at 1300h to day 10 at 1300h in each burrow was viewed in QuickTime Player v.6.6 (© Apple Inc.) and coded for a series of chick and adult behaviours using logger.app (© A. Earle). Only events occurring in the presence of an adult were coded and included: time of adult visit, type of visit (fish vs. no-fish), type of fish, and presence/absence of chick begging call types. Type of fish was recorded at the species level when possible but was later classified as either high-quality (capelin or sandlance, *Ammodytes spp)* or low-quality (larval fish and invertebrates). In cases where type of visit or type of fish were unclear due to obstruction of the camera lens, these parameters were coded as unknown. On average, 15.65 ± 2.57 interactions were coded per burrow.

4.3.4 *Statistical Analysis*

The proportion of each type of adult visit (food, no-food, unknown, high-quality food, low-quality food) where chicks used each type of begging call was calculated for every individual burrow before and after supplemental feeding. These proportions were used to compare use of begging call types between burrows prior to supplemental feeding and within burrows following supplemental feeding. Two-tailed paired t-tests were used to compare: 1) use of each type of begging call during food visits and during no-food visits, 2) use of long begging calls during high vs. low quality food visits and 3) number of high vs. low quality food trips per day before and after supplemental feeding. One-tailed paired t-tests were used where directional hypotheses predicted a decrease in use of begging calls and a decrease in adult burrow visits following supplemental feeding due to changes in chick condition. Relationships between chick body condition and use of begging calls, as well as associations between proportion of food type and adult provisioning per day, were analyzed using regressions. All statistical tests were performed using PASW Statistics 18.0.

4.4 RESULTS

4.4.1 *Call Types and Usage*

We identified two types of begging call types that occurred in the presence of adults. These two calls were discernible by ear, without instrumentation, but were also viewed as spectrograms using Raven Lite 1.0. Type I calls consisted of regular narrow-band call elements in the shape of an inverted U. These "cheeping" calls were repeated at regular intervals (Figure 4.1b). Type II calls were flat in shape with a gradual rise and some frequency modulation early in the call. These "long" calls had multiple harmonics and were repeated at irregular intervals (Figure 4.1b).

The total number of fish, no-fish, and unknown visits for all burrows is shown in Table 4.1. Type I calls occurred in a higher proportion of food visits than Type II calls, t 13 = 21.01, P < 0.001. There was no difference in frequency of call usage during no-food visits, t 13 = 0.99, P = 0.34. There was no difference in the proportion of food and no-food visits where Type I calls were recorded, t 12 = 1.14, P = 0.28. Type II calls occurred during a higher proportion of no-food than food visits, t 12 = -10.23, P < 0.001 (Figure 4.2). There was no difference in the proportion of parental visits with Type II calls during low quality (larval fish and invertebrates, 0.12 ± 0.08) and high quality (capelin and sandlance, 0.05 ± 0.03) food visits, t 6 =0 .88, P = 0.41. Overall, use of Type II calls appeared to vary more than use of Type I calls between fish and no-fish visits, and frequency of Type II usage was expected to change with chick condition; therefore, all following analyses focus on the use of Type II calls.

4.4.2 *Chick Condition and Type II Call Usage*

Chick body condition was calculated by dividing chick mass by tarsus length. While tarsus length increases with chick age, it is not affected by nutrition under natural conditions (Cook & Hamer, 1997). Body mass varies with feeding conditions (Baillie & Jones 2004). Therefore, dividing chick mass by tarsus length gives an index of chick condition adjusted for chick age.

Prior to supplemental feeding, chicks in poorer body condition made Type II calls during a higher proportion of no-food visits than chicks in better body condition ($R^2 = 0.30$, $P = 0.05$). This result was not true of food visits ($R^2 = 0.10$, $P = 0.30$; Figure 4.3a). Compared to chicks in better body condition, chicks in poorer body condition were more likely to use Type II calls when their parents brought high quality (capelin and sandlance) food ($R^2 = 0.40$, $P = 0.02$). There was no relationship between use of Type II calls and body condition when parents brought low quality food ($R^2 = 0.03$, $P = 0.70$; Figure 4.3b).

The proportion of visits with Type II calls decreased following supplemental feeding, t 12 = 2.03, $P = 0.03$. Use of Type II calls during no-food and unknown type visits did not decrease following supplemental feeding (no food, t 7 = 1.75, $P = 0.06$; unknown, t 7 = 1.74, $p = 0.06$; Figure 4.4).

4.4.3 *Parental Provisioning*

Prior to supplemental feeding, the number of provisioning trips (food trips) per day within burrows was higher when the proportion of low quality food, including larval fish and invertebrates, was higher in chick diet ($R^2 = 0.49$, $P = 0.02$; $N = 11$ chicks). In addition, the number of provisioning trips per day within burrows decreased as proportion of high quality food, including capelin and sandlance, increased in chick diet ($R^2 = 0.36$, $P = 0.05$; $N = 11$ chicks).

Puffin parents did not reduce their frequency of burrow visits during supplemental feeding. There was no decrease in total number of burrow visits, t 10 = 1.09, $P = 0.30$, food visits, t 10 = 0.46, $P = 0.33$, no-food visits, t 10 = 0.38, $P = 0.36$, or unknown visits, t 10 = 0.40, $P = 0.35$, per day during supplemental feeding (Table 4.2). Parents did not alter the quality of food fed to chicks during supplemental feeding. There was to no difference in proportion of low quality food trips before (0.31 ± 0.09) and after (0.38 ± 0.11) supplemental feeding, t 13 = -0.56, $P = 0.58$, nor was there a difference in number of high quality food trips before (0.56 ± 0.10) and after (0.53 ± 0.11) supplemental feeding, t 13 = 0.23, $P = 0.82$.

4.5 DISCUSSION

Of the two call types identified, there was higher variation in the use of Type II than Type I begging calls in relation to food quality and chick condition. Two distinct begging calls (rhythmic and long) have also been identified in Procellariiformes, including Wilson's storm-petrel (Quillfeldt 2002), and the structures of these calls are similar to those of Atlantic puffins. Both puffin Type I calls and petrel rhythmic calls are repeated in rapid succession at regular intervals. Type II puffin calls and petrel long calls are also similar in length and both are repeated at irregular intervals. Both types of calls differ slightly in structure between species. Type I puffin calls show an inverted U shape more similar, but shorter in duration, to petrel long calls than rhythmic calls. Type II puffin calls show a flatter shape than petrel long calls.

Despite similarities in begging call structure in petrels and puffin chicks, there are species differences that make the current study of particular interest in understanding the factors underlying variation in begging call use. Studies of begging in shearwaters (Quillfeldt & Masello, 2004) and petrels (Gladbach *et al.*, 2009; Quillfeldt, 2002) have generally focused on long calls because they occur only in the presence of adults and are displayed during every parental visit to the burrow. In contrast, puffin chicks did not always use long (Type II) calls during parental visits to the nest. This variation in call use allowed analyses of begging based on the proportion of adult visits during which chicks used each call type. A second important difference between petrels and puffins is that petrels regurgitate food during nest visits, making the quantity and type of food difficult to determine (but see Grandeiro *et al.* 2000). Puffins can return to the nest with a bill-load of whole food items, or without anything at all and the type of food fed to chicks can be determined during live observation, or better yet, from video recordings. Variation in parent visit type (food vs. no-food) and food type (high vs. low quality) allows further analyses of use of begging calls in relation to parental behaviour. Third, puffins have shorter intervals between parental visits than petrels, increasing the number of possible parental visits recorded during a day and making it easier to see changes in parental patterns with regard to chick condition and food quality and quantity.

Type II begging was used almost exclusively during parental no-food visits indicating a strong relationship between use of Type II begging calls and current adult provisioning behaviour. Still, large variation in the use of begging calls between chicks exists for both food (0 to 29 % of trips) and no-food (50 to 100 % of trips) visits. A significant correlation between chick body condition and use of Type II begging calls suggests that chick condition also plays a role in the use of these begging calls. Chicks in poor condition were more likely to use Type II calls during both no-food trips and high-quality food trips; however, this relationship did not hold for low-quality food trips. These results suggest that chicks in good condition can reduce use of Type II calls, even during no-food trips, and that chicks in poor condition can increase use of Type II calls, even when receiving high-quality food. Associations between chick body condition and begging under natural conditions have been found in other seabirds including Wilson's storm-petrel (Quillfeldt 2002; Gladbach *et al.* 2009), Cory's shearwater (Träger *et al.* 2006), Manx shearwater (Quillfeldt *et al.* 2004), and thin-billed prions (Duckworth *et al.* 2009). The relationship between begging and body condition in Atlantic puffin chicks in this study suggests that begging may exist as an honest signal of chick need in burrow-nesting seabirds other than Procellariiformes.

Experimental manipulation of chick condition showed that the use of Type II begging calls differed not only between chicks, but also within chicks. Puffin chicks reduced use of Type II begging calls during parental visits after receiving supplementary food. Similar results have been found in supplementary-fed Cory's shearwater chicks that reduced begging rates in response to increased food intake

(Granadeiro *et al.* 2000; Quillfeldt & Masello 2004), even though in one study, chick condition was not related to begging call rate prior to supplementary feeding (Granadeiro *et al.* 2000). Chicks that were deprived of food during Grandeiro *et al.*'s (2000) study did not change their begging behaviour following experimental treatment, indicating a possible maximum begging rate for chicks. Feeding conditions for shearwaters during the study, much like conditions at Gull Island during our study, were poor, and chicks may have been begging at a maximum rate prior to food deprivation and were therefore unable to increase begging following experimental treatment. Begging call rates in ring-billed gull (*Larus delawarensis*) chicks reached asymptotic levels during food deprivation (Iacovides & Evans 1998), and the same may be true for other seabirds. Although puffin chicks reduced use of Type II begging during supplementary feeding, it is unknown whether or not chicks in poor body condition would have been able to increase begging use if they were further food deprived under the already poor foraging conditions at Gull Island in 2009 and 2010.

Foraging conditions may also play a role in parental provisioning responses to begging behaviour and chick condition. At Gull Island, adult puffins with food-supplemented chicks did not decrease provisioning rates as expected, nor did they adjust the quality of food brought to chicks. Adults may have continued provisioning chicks at the maximum rate permitted by current foraging conditions in order to meet minimum chick requirements, even during supplemental feeding. The natural provisioning rate in 2009 and 2010 combined was only 2.3 visits per day. In comparison, Creelman and Storey (1991) reported provisioning rates of 1.9 meals per day for males and 2.6 meals per day for females for a combined rate of approximately 4.5 food visits per day at Gull Island in 1985, nearly double the rate observed in 2009 and 2010. Low provisioning rates along with observations by local fishermen (B. Nakashima, DFO, personal communication) indicate poor capelin availability during these study years.

Some evidence for the role of environmental conditions in parental responses to begging and chick condition come from studies of chick begging in Cory's shearwaters. Contrary to the predictions of honest signaling models, shearwater parents in one study did not reduce provisioning rates when supplementary fed chicks reduced begging rates (Grandeiro *et al.* 2000). In a more recent study, Cory's shearwater chicks that were supplementary fed also reduced begging rates, but adults did decrease provisioning rates in this case (Quillfeldt & Masello 2004). Quillfeldt and Masello (2004) suggest that the difference in parental response between these two studies was due to different conditions during the two studies. Grandeiro *et al.*'s (2000) experiment took place in a poor breeding season while Quillfeldt and Masello's (2004) study took place during a good breeding season, giving adults the ability to decrease provisioning rates in response to changes in chick behaviour. Puffins, like shearwaters, can respond to changes in chick behaviour and condition. For example, Harris (1983) showed that adult puffins increase provisioning rates in response to chick begging playbacks. Since both puffins and shearwaters can respond to changes in chick begging behaviour, it is likely that poor foraging conditions during our study period and during Granderio *et al.*'s (2000) study meant that, even with supplemental feeding, parents could not reduce their provisioning rates.

Studying begging signals in a species with a single chick brood eliminates the problem of interpreting results that may be confounded by sibling competition. In this case, however, environmental factors introduce another source of difficulty in interpreting begging and provisioning behaviour. Overall, our results indicate that environmental context is important when interpreting the behavioural responses of offspring and parents to changes in chick condition and begging. The second prediction of honest signaling models, that adults provision offspring in response to begging intensity, assumes that adults have complete control over provisioning; however, this is rarely a true assumption. Seabird chick diet and provisioning rate is highly dependent on prey availability (Barret 2002; Baillie & Jones 2003; Baillie & Jones 2004; Burke & Montevecchi 2008; Wilhelm *et al.* 2008), and is also dependent on adult condition (Erikstad *et al.*, 1997; Johnsen *et al.*, 1994). As Royle *et al.* (2002) discuss in a review of offspring begging, honest signaling is more likely to benefit offspring and parents when both parties have a high degree of control over provisioning. Therefore, honest signals are more likely to exist in single chick broods or under uniparental care, and when food availability is high. In other words, honest signals work best when chances of conflict are low. Since adults are selected to reduce parental care when conditions are bad and offspring would generally benefit from more care than adults are selected to give under these conditions, poor prey availability may increase parent-offspring conflict and reduce the effectiveness of honest signals.

In summary, two types of puffin chick begging calls were identified and use of longer Type II calls was related to parental no-food trips and poor chick condition. Use of Type II calls also decreased following supplemental feeding; however, adults did not reduce provisioning rates. In this case, the absence of adult response to changes in chick condition was probably due to foraging constraints. Therefore, variation in chick begging explained by chick condition and a change in chick diet provides evidence that begging is an honest signal in puffin chicks, despite a lack of response in provisioning behaviour by adults.

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Table 4.1: Total number of adult visits divided into visit type. The total number of burrows observed was 17. Data was not available from one burrow prior to supplementary feeding and from one burrow following supplementary feeding; therefore, sample size both prior to and following supplemental feeding is 16.

	Food Visits *N* (%)	No-Food Visits *N* (%)	Unknown Visits *N* (%)
Before SF	62 (.45)	35 (.25)	41 (.30)
After SF	65 (.51)	32 (.25)	31 (.24)
TOTAL	127 (.48)	67 (.25)	72 (.27)

Table 4.2: Number of adult visits before and after supplemental feeding. Mean number and standard error of adult visits, food visits, no-food visits, and unknown visits per day before and after supplemental feeding (SF). Sample size for all groups is 10 and significance values are based on one-tailed paired t-tests.

	Before SF	After SF	*t*	*P*
Visits/day	4.67 ± 0.59	3.90 ± 0.69	1.09	0.30
Fish visits/day	2.27 ± 0.48	1.99 ± 0.43	0.46	0.33
No-fish visits/day	0.98 ± 0.25	0.82 ± 0.31	0.38	0.38
Unknown visits/day	1.31 ± 0.34	1.19 ± 0.47	0.40	0.35

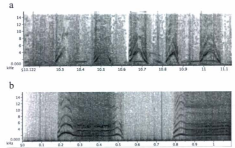

Figure 4.1: a) Type I (rhythmic) chick begging calls and b) Type II (long) chick begging call frequencies measured in kHz (y-axis) over time in seconds (x-axis). Spectrograms were produced using Raven Lite 1.0.

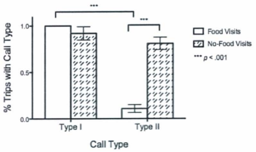

Figure 4.2: Mean proportion and standard error of food and no-food visits with Type I and Type II Calls

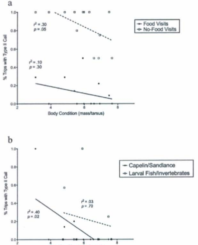

Figure 4.3: a) Proportion of adult food (solid line, closed circles) and no-food (dashed line, open squares) visits with Type II calls as a function of chick body condition on day 4 of experiment. b) Proportion of high quality (capelin and sandlance; solid line, closed circles) and low quality (larval fish and invertebrates; dashed line, open squares) provisioning trips with Type II calls as a function of chick body condition on day 4 of experiment

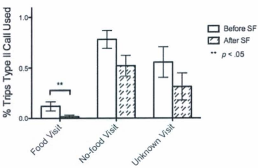

Figure 4.4: Mean proportion and standard error of food, no-food, and unknown visits with Type II calls before and after supplemental feeding (SF).

CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS

5.1 INTRODUCTION

Atlantic Puffins show variability in their breeding behaviour and condition both within and between individuals and across breeding seasons. Studying individual and group responses to changes in foraging conditions using both naturalistic and experimental studies allows us to draw conclusions about how seabirds are responding to current environmental conditions as well as how they might respond to varying degrees of change in the future.

In the preceding chapters of this thesis, responses at individual and group levels were discussed as they relate to changes in prey availability and/or chick condition. Variation in the responses of both adults and chicks to these changes indicates a dynamic relationship between parents, offspring, and environmental conditions. This final chapter summarizes the main findings and implications of the previous chapters and explores the broader significance and implications of these conclusions.

5.2 CONDITION AND SURVIVAL UNDER FOOD RESTRICTIONS

5.2.1 *Growth and survival*

Atlantic Puffins have shown an ability to compensate for poor foraging conditions by adopting a generalist foraging strategy or by prey-switching when alternative food sources are available (Baillie & Jones 2003; 2004; Barrett & Krasnov, 1996; Burke & Montevecchi, 2008). In spite of these behavioural adaptations, chick mass gain is known to decrease significantly when food availability is low (Barrett & Rikardsen, 1992; Baillie & Jones, 2004). On the other hand, studies report no relationship between foraging conditions and chick wing growth or survival (Baillie & Jones, 2003; 2004; Barrett, 2002). One of the findings in Chapter 2, that chick wing growth rate was significantly reduced during poor foraging conditions, as well as a finding in Chapter 3, that odds of survival increased significantly when chicks were supplementary fed, indicate that the degree of food restriction experienced by puffins in a given breeding season might be important in determining chick growth patterns and survival rates. As predicted by Cairns (1987), it appears that the sensitivity of breeding parameters measured was dependent on the level of food restriction experienced by puffins during each experiment. If capelin availability continues to decline, other breeding effects not previously observed might be expected to occur.

5.2.2 *Physiology*

Neither chicks nor adults showed expected increases in corticosterone levels during food restriction. These results are contrary to previous findings in several seabirds that link poor foraging conditions with increased corticosterone levels in both adults and chicks (Kitaysky *et al.*, 1999a; 1999b; 2001a; 2005; 2007; Doody *et al.*, 2008). In adult puffins, a decrease in CORT levels under poor foraging conditions was probably the result of underlying factors including intrinsic variables and colony location. In chicks, a lack of CORT response in light of evidence of changes in begging behaviour under food restriction (Chapter 4) suggests that corticosterone may not be a mechanism underlying begging behaviour as suggested by evidence from black-legged kittiwake chicks (Kitaysky *et al.*, 2001). Overall, these results imply that caution should be used when interpreting the stress response of species that rely on patchy food sources and that seabird species with generalist foraging strategies might be less susceptible to stress than foraging specialists during declines in their preferred food source.

5.3 CHANGES IN BREEDING BEHAIOUR DURING FOOD STRESS

Study of parent-offspring conflict between puffin adults and chicks has been limited, likely due to the difficulty of observing chicks and adults interacting during provisioning activities inside their burrows. Burrow scopes allow continuous monitoring of puffin behaviour inside burrows and can shed light on previously inaccessible research questions related to parent-offspring conflict. Variation and frequency in begging signals suggests that vocal communication is important in parent-offspring relationships. Chick begging behaviour varied both within and between individuals. Current parental provisioning behaviour and chick condition were both determining factors in the type and frequency of begging call displays, but adults did not respond to changes in chick begging or condition (Chapter 4). Environment was likely a limiting factor in the ability of adults to respond to changes in chick begging and condition and the control of both chicks and adults over provisioning rates was limited by the context in which parent-offspring conflict occurred.

5.4 IMPLICATIONS

Changes in chick growth (Chapter 2 & 3), behaviour (Chapter 4), and survival (Chapter 3) in response to food intake all indicate that puffin chick development is limited by food during the breeding season. Adults, on the other hand, did not show any indication of food stress other than the adoption of generalist foraging strategies when capelin availability was low. Furthermore, change in chick growth and survival appears to be dependent on the degree of food stress experienced by chicks, as predicted by Cairns (1987). Taken together, these results indicate that monitoring chicks during the breeding season can help estimate food availability and is a better indication of food availability than adult condition. Detection of changes in chick growth, behaviour, and survival may be early signs of food stress impacts on colonies. Since these changes impact future population parameters, including adult survival and population size, vigilant monitoring of chicks during the breeding season can inform conservation and protection efforts.

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