



AN ABSTRACT OF THE THESIS OF

Scott Jennings for the degree of Master of Science in Wildlife Science presented on March 17, 2015.

Title: Provisioning, Growth and Survival of Adélie Penguin Chicks at Cape Crozier, Ross Island, Antarctica.

Abstract approved:

---

Katie M. Dugger

Understanding the factors that contribute to or limit reproductive success is a fundamental objective of the field of ecology, providing insight into the ways ecosystems function and facilitating better management of natural resources. Behaviors that benefit offspring often increase costs to parents, and thus parents must adjust their level of investment under different conditions to maximize their fitness. Investigating the ways in which individual animals vary parental investment in response to changing environmental conditions is critical to predicting population responses to natural or anthropogenic changes in environmental conditions.

I studied the relationships between provisioning, growth, and survival of Adélie Penguins at a very large, high latitude breeding colony where intraspecific competition for food is thought to limit reproductive rates and colony growth through density dependent processes. I measured three aspects of provisioning, which previous research has shown or suggested might represent variation in parental investment, with increased presumed benefits to chicks coming at an energetic cost to parents. These measurements of parental provisioning effort included: 1) the overall amount of food delivered; 2) the type of food delivered; and 3) the frequency of food delivery. I measured mass and skeletal growth, determined chick sex via molecular methods, and evaluated daily survival probability using quantitative methods which allowed for imperfect resighting probability. I collected data during two breeding seasons, one of which appeared to be relatively typical in terms of growth rates and breeding success (Austral summer of 2012-

13; “2012”), and one characterized by apparent food limitation and depressed chick growth rates and reproductive success (Austral summer of 2013-14; “2013”). I compared provisioning, growth and survival at the level of individual penguin families in order to gain a more direct perspective of how trade-offs in parental investment may impact offspring growth and survival, and ultimately how they affect reproductive success.

I found that 1) male penguin chicks gained on average  $15.6 \text{ g d}^{-1}$  more, and grew bill length  $0.05 \text{ mm d}^{-1}$  faster than female chicks. Growth rates of flipper, tibiotarsus, and foot length were similar between the sexes, and these overall patterns in growth rate were consistent between the two years of the study. In addition 2) the relationships between growth rates and the amount and type of food delivered were different for different morphological features (mass vs. skeletal growth), and also between the sexes. Across most morphological measurements, growth rates of males during 2013 (believed to be the more challenging year) were more sensitive to variation in the provisioning parameters. These differences led me to conclude that during 2013, when there was a greater interval between feedings, parents had to deliver a higher quality (lipid-rich) diet and a greater quantity of food to male chicks in order to maintain their faster growth rate. Contrary to many previous findings for this species, 3) survival rates declined throughout the entire chick-rearing period for both sexes and during both years. This temporal pattern in survival could be related to competition for food at the very large colony where this study took place, with competition increasing throughout the season as chicks grew and require more food. Patterns of decline in survival probability were different between the sexes, but the differences were not consistent between two years of study. In both years the probability of a male surviving from about 10 days post-hatch to the end of the chick provisioning period was similar, at around 0.36; for females however, this probability was 0.68 in 2012 but only 0.17 in 2013. Finally, 4) survival probability could not be predicted directly by growth rates, but was predicted by the size of chicks when they made a critical transition from the guard to the crèche stage at approximately 2-3 weeks old (higher survival with larger size at crèching). Chick size when making this transition was best predicted by growth rates and the age when chicks transitioned to the crèche stage.

These results increase our understanding of the relationships between trade-offs in parental investment and offspring growth and survival. The Southern Ross Sea is a relatively simple ecosystem and Adélie penguins are constrained to breed within the short austral summer, yet my results suggest that alternative parental investment strategies may exist under different environmental conditions for this long-lived seabird. These results also provide critical information to help facilitate sound management of the Ross Sea ecosystem as that system undergoes natural and anthropogenic changes.

©Copyright by Scott Jennings

March 17, 2015

All Rights Reserved

Provisioning, Growth and Survival of Adélie Penguin Chicks at Cape Crozier, Ross  
Island, Antarctica

by

Scott Jennings

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Presented March 17, 2015

Commencement June 2015

Master of Science thesis of Scott Jennings presented on March 17, 2015.

APPROVED:

---

Major Professor, representing Wildlife Science

---

Head of the Department of Fisheries and Wildlife

---

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

---

Scott Jennings, Author

## ACKNOWLEDGMENTS

A great many people and institutions made this project possible, and to them I owe my gratitude. The field portion of my research was funded by NSF grant ANT-0944411 awarded to Oregon State University and Point Blue Conservation Science, Petaluma, CA, USA. I received additional support from the Department of Fisheries and Wildlife, Oregon State University, via TA-ships and the M. A. Ali Graduate Chair Award in Fisheries Biology.

I am so grateful to my major advisor, Dr. Katie M. Dugger. Katie provided incredible mentorship. She taught me how to bring quantitative tools to bear on field observations, and she provided support and encouragement when needed, but also challenged me to expand the bounds of my scientific skills. She taught me to sort through the uninformative clutter to find the fundamental message hidden in the data. She kept me focused and made sure that it was always the data telling me what they mean, and not *vice versa*. She has been patient yet efficient in providing feedback, and that feedback has always helped me improve as a scientist.

My graduate research was part of a long term study involving many collaborators from multiple states and countries, and each of them has made a meaningful contribution to this project. Drs. David Ainley and Grant Ballard taught me everything I know about penguins, and so much more. David has spent more time in Adélie Penguin colonies than perhaps anyone else. These books are not only an excellence source of information about Adélie penguins, but when viewed in chronological sequence they also provide a unique sense of both the ways a field of study can change over 2 decades time, and also how the thought process evolves in a researcher working on a single species for that span of time. To have the opportunity work in the field with someone possessing such a deep understanding of a species and the ecosystem in which it lives has been a remarkable experience. This deep understanding that David has cultivated has greatly inspired my development as a researcher. Grant has been an incredible mentor and friend, since before I even became involved with the Adélie Penguin project. From him I have learned a range of topics, from how to catch a penguin, to how to manage data, to how to judge



evidence for or against a hypothesis, that you should always use more rocks than you think to tie down your tent, and the best places at Cape Crozier to go skiing. He has taught me the importance of loving the work you do, and that having fun does not mean you aren't doing good work, but rather helps ensure it.

Additional CO-PI's, other collaborators, and field assistants have provided advice, guidance suggestions, inspiration, encouragement, and great friendship both in the field and at home: Annie Schmidt, Annie Pollard, Amelie Lescroël, Melanie Massaro, Arvind Varsani, Megan Elrod, Jean Pennycook, and David Gremellet. Without the advice and guidance of these people, my project would have looked very different than what it does now. In particular, Arvind Varsani gave time, energy and lab space and resources for molecular determination of chick sexes; and was even very patient with me as I blundered my way through a day of pipetting and PCR in his lab.

The staff and contractors of the US Antarctic Program provided amazing logistic support, without which we would not be able to do the work we do. Peggy Malloy kept us happily well-fed in the field. The pilots, techs, and other staff of PHI Inc. provided safe, efficient, beautiful and fun helicopter transport to remote field sites under often challenging conditions. The radio operators at MacOps kept us in contact with the world and gave us someone besides ourselves and the penguins to talk to. And so many other dedicated people in the McMurdo galley, Carpenter shop, Heavy machinery shop, and elsewhere helped make this project possible.

The members of the Dugger labs have provided a great community of people to discuss ideas and work through problems: Peter Kappes, Kevyn Groot, Liz Mulligan, Cheryl Horton, Lee Foster, Chad Marks-Fife, Kevin Buffington, Chris Malachowski, Erin Harrington, Megan Zarzychi, and Anne Mini.

I also thank the members of my Graduate Committee, Drs. Don Lyons and Lorenzo Ciannelli, for excellence discussion and suggestions which improved this project. In particular, Don's insight into growth of seabird and other chicks, and Lorenzo's instruction in mixed modeling, helped tremendously. I also thank Dr. Stevan J. Arnold for serving as Graduate Council Representative.

My parents and family have always supported my decisions in life, providing advice and support at every step, and giving me the opportunity to follow my heart and dreams to live a wonderful life. Abbey has been an integral part of my life balance during school. She ensures I got out to a park or to hike a trail every day (twice), and makes me laugh with nearly everything she does.

And finally, my wife Libby, I couldn't have done any of this without you. You have encouraged and supported me, given me guidance in all things from statistical analysis to providing me with a new perspectives on how Adélies might be raising their chicks. You gave honest feedback at every stage to help me focus my ideas and keep my project on track. You have provided friendship, love, and always a good laugh through the ups and downs of this crazy process.

## AUTHOR CONTRIBUTIONS

Grant Ballard and David Ainley contributed to this project at most stages, including acquiring funding, assisting with study design and development, and editorial review of chapters. Arvind Varsani conducted molecular sexing and reviewed Chapter 2.

# TABLE OF CONTENTS

	<u>Page</u>
Chapter 1 GENERAL INTRODUCTION .....	1
BACKGROUND .....	2
Tradeoffs in reproduction .....	2
The evolution of our understanding of seabird foraging as it relates to raising young .....	2
Provisioning and growth of avian young- with an emphasis on seabirds .....	5
Offspring sex and parental investment.....	6
THE ADÉLIE PENGUIN .....	7
Study location and this project as part of ongoing research.....	8
Adélie Penguin chick growth.....	10
Chapter 2 SEX-BASED DIFFERENCES IN ADÉLIE PENGUIN (PYGOSCELIS ADELIAE) CHICK GROWTH RATES .....	14
ABSTRACT.....	15
INTRODUCTION .....	16
STUDY AREA AND METHODS .....	18
Field work .....	18
Analysis .....	18
RESULTS .....	20
DISCUSSION .....	22
REFERENCES .....	25
Chapter 3 THE INFLUENCE OF DIET, ADULT AGE AND PROVISIONING BEHAVIOR ON CHICK GROWTH IN ADÉLIE PENGUINS .....	32
ABSTRACT.....	33
INTRODUCTION .....	34
METHODS .....	37
Morphological measurements .....	38
Penguin weighbridge .....	39
Feather collection.....	40
Analysis .....	40
RESULTS .....	42
Data summary .....	42
All chicks .....	43

## TABLE OF CONTENTS (Continued)

	<u>Page</u>
WB subset .....	45
KA subset.....	46
DISCUSSION .....	46
REFERENCES .....	52
Chapter 4 TRADE-OFFS IN OFFSPRING-REARING BEHAVIOR: UNDERSTANDING THE RELATIONSHIPS BETWEEN GROWTH, BROOD-GUARDING, AND OFFSPRING SURVIVAL IN THE ADÉLIE PENGUIN .....	68
ABSTRACT.....	69
INTRODUCTION .....	70
METHODS .....	73
Field methods.....	73
Analysis .....	75
Growth rates and crèche timing .....	75
Survival .....	76
RESULTS .....	77
Growth rate and crèche-timing .....	78
Survival.....	79
DISCUSSION.....	83
REFERENCES .....	89
Chapter 5 GENERAL CONCLUSIONS .....	99
PRIMARY FINDINGS.....	100
CONTRIBUTION AND FINDINGS IN THE CONTEXT OF A CHANGING ROSS SEA ..	101
BIBLIOGRAPHY .....	105

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
Figure 1.1. Map of the Ross Sea, showing land (dark gray), ice shelf (permanent glaciers on the sea; stippling), the 500 m (black) and 1000 m (light gray) bathymetric contours, the Adélie Penguin colony at Cape Crozier, Ross Island (star), and the approximate extent of the Ross Sea polynya in December (adapted from Smith et al. 2007; dashed line). For reference, the shelf break in the Ross Sea occurs at approximately 800m.....	13
Figure 2.1 Schematic illustrating the location of morphological measurements collected from male and female Adélie Penguin chicks during Austral summers of 2012-13 and 2013-14 on Ross Island, Antarctica. Bill was measured to the nearest hundredth mm and remaining measurements to the nearest mm. Dashed line indicates humeral head on underside of the flipper. ....	29
Figure 2.2 Estimated average growth rates, with 95% confidence intervals for mass, and length of bill, flipper and tibiotarsus for male and female Adélie Penguin chicks during the Austral summers of 2012-13 (2012) and 2013-14 (2013) on Ross Island, Antarctica. Estimates include mean values for other important variables in best model for each measurement (see text for details). Note different units and scales for y axes. Foot growth is not shown due to lack of support for an effect of sex. ....	30
Figure 2.3 Estimated mean values for $\delta^{15}\text{N}$ , and 95% confidence intervals, for male and female Adélie Penguin chicks during the Austral summers of 2012-13 and 2013-14 on Ross Island, Antarctica. $\delta^{15}\text{N}$ is a proxy for the proportion of fish in the diet; see Chapter 3 for details. ....	31
Figure 3.1. Morphological measurements collected during the austral summers of 2012-13 and 2013-14 on Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Dashed line indicates distal edge of the humeral head which can be palpated on the underside of the flipper.....	64
Figure 3.2. Estimated growth rates (mass, bill, flipper and tibiotarsus; and 95% confidence intervals) for measurements of $\delta^{15}\text{N}$ for Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (“2012”) and 2013-14 (“2013”). Estimates are from the best model, across the range of observed values for $\delta^{15}\text{N}$ (larger value = greater proportion of diet comprised of fish) calculated separately for females and males during both years of the study. Includes data from all chicks combined (i.e. WB and KA subsets; see text for details). Note different units and scales for y-axes. ....	65
Figure 3.3. Estimated growth rates (flipper, tibiotarsus, foot; and 95% confidence intervals) for measurements of average food delivered per day per chick (FOOD) for Adélie Penguin chicks in the Weighbridge data subset at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (“2012”) and 2013-14 (“2013”). Estimates are from the best model, across the range of observed values for FOOD, calculated for females during the two years of the study, and with mean values for all other continuous variables in the model. Note: the model included an additive sex effect, thus growth rates for males had the same slope but greater intercept than for females. ....	66

## LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
Figure 3.4. Relationship between estimated growth rates (flipper, tibiotarsus, foot) and foraging trip duration (FTD) for Adélie Penguin chicks in the Weighbridge data subset at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (“2012”) and 2013-14 (“2013”). Estimates are from best model, across the range of observed foraging trip duration (FTD) values, calculated for females during the two years of the study, and with mean values for other continuous covariates in the model. Dashed lines are 95% confidence intervals.....	67
Figure 4.1. Model averaged estimates of daily survival probability for male and female Adélie Penguin chick at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (2012) and 2013-14 (2013). Error bar width is greater for males. Dashed line indicates mean crèche date (day 67 in both years; Nov 1= day 1). .....	98

## LIST OF TABLES

<u>Table</u>	<u>Page</u>
Table 2.1 Parameter estimates and 95% confidence intervals for the sex effect on growth from the best model (i.e., lowest AIC <sub>c</sub> ) for each morphological measurement of Adélie Penguin chicks during Austral summers of 2012-13 and 2013-14 on Ross Island, Antarctica. Plus signs denote additive effects and asterisks denote interactions. Sex was not supported as an important factor associated with for foot growth.....	28
Table 2.2 Average daily growth rate estimates (with 95% CI) from best model (i.e., model with lowest AIC <sub>c</sub> ) relating growth rates of morphological characteristics and mass to sex, year, brood size, chick hatching order; and sample sizes (n) for male and female Adélie Penguin chicks measured, and weighed during Austral summers of 2012-13 (2012) and 2013-14 (2013) on Ross Island, Antarctica. Sex was not supported as an important variable for foot growth so only means by year (best model results) are reported. ....	28
Table 3.1. Correlation between relative hatch day and all growth rates (added a posteriori), and the period of linear growth (days post-hatch) for morphological measurements collected from Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. P-value is for correlation.....	57
Table 3.2. Names and brief description of covariates used to model Adélie Penguin chick growth at Cape Crozier, Ross Island, Antarctica. ....	57
Table 3.3. Number of Adélie Penguin chicks measured for each data subset, sex, and year of the study, at Cape Crozier, Ross Island, Antarctica.....	57
Table 3.4. Correlation between pairs of continuous covariates measured for Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. See Table 3.2 for covariate descriptions.....	58
Table 3.5. Model selection results for growth of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, including all models accounting for 90% of the AIC <sub>c</sub> weight and the intercept-only model. Results include 3 subsets of the data (All, WB, KA) and growth of 5 morphological measurements (Mass, Flipper, Tibiotarsus, Foot, Bill); see text for details. Footnotes for each set of results indicates the random effect structure included in the model set, the AIC <sub>c</sub> value of the best-supported model, and an indication of the % process variance explained by best model (either R <sup>2</sup> value for models with fixed effects only; or result of variance component analysis for mixed models). K is number of model parameters, Δ AIC <sub>c</sub> is the difference in corrected AIC values of each model from the best-supported model. AIC <sub>c</sub> Wt. is the relative AIC <sub>c</sub> weight for each model, and -2lnL is negative 2 times the log-likelihood. ....	59
Table 3.6. Coefficient estimates, standard errors, and 95% CI for the best supported model explaining growth of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Growth rates were modeled for each of 5 morphological measurements and 3 data subsets (see text for details). 95% CI for mixed models (identified by bold text) were obtained by bootstrapping. Spaces are blank for covariates not included in the best-supported model for a particular data subset and morphological measurement. ....	63



## LIST OF TABLES (Continued)

<u>Table</u>	<u>Page</u>
Table 4.1. Names and descriptions of covariates considered in models to estimate daily survival of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Also include whether covariate was used for modeling survival ( $\phi$ ), resighting probability ( $p$ ), or both. ....	94
Table 4.2. Model selection results for determining factors related to the size and age at which Adélie Penguin chicks enter the crèche at Cape Crozier, Ross Island, Antarctica. K is number of model parameters, $\Delta$ AICc is the difference in corrected AIC values of each model from the best-supported model. AICc Wt. is the relative AICc weight for each model, and $-2\ln L$ is negative 2 times the log-likelihood. ....	95
Table 4.3. Model selection results for determining the best model structure for estimating resighting probability of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2.....	95
Table 4.4. Model selection results from the first stage of survival modeling: determining factors related the survival probability of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2.....	96
Table 4.5. Model selection results from the second stage of survival modeling: determining factors related the survival of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2.....	96
Table 4.6. Model selection results from the third stage of survival modeling: determining the best time constraint for estimates of survival of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2.....	96
Table 4.7. Model selection results from the fourth stage of survival modeling: determining relationships between growth rates (mass, flipper, tibiotarsus) and daily survival probability of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2 .....	97
Table 4.8. Model selection results from the fifth stage of survival modeling: determining relationships between size (mass, flipper, tibiotarsus) and age when entering the crèche stage and subsequent daily survival probability of Adélie Penguin chicks during the entire crèche period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2.....	97

## Chapter 1

### GENERAL INTRODUCTION

Scott Jennings

## BACKGROUND

### *Tradeoffs in reproduction*

Much research effort has been directed towards understanding trade-offs in the allocation of time, energy, and effort of free-living organisms. Trade-off theory is fundamental to ecology, and trade-offs associated with reproduction are central to the mechanisms of natural selection (Reznick 1985, Stearns 1989). To maximize lifetime reproductive success, individuals make energetic and time-budget trade-offs between provisioning offspring, protecting offspring, self-maintenance, and retaining the ability to undertake future reproduction (Cam et al. 1998, Riou et al. 2012). Certain broad patterns in reproductive trade-offs that were predicted by early theory have been supported by empirical research. For example, species with higher productivity generally have more precocial young (higher investment in number of offspring, less in offspring care), and longer life spans often correspond with lower productivity in any single year (higher investment in parent survival, less in short term fecundity; Starck and Ricklefs 1998, Sibly et al. 2012).

### *The evolution of our understanding of seabird foraging as it relates to raising young*

A chief limitation on the growth rate of any population is the rate at which individuals can gather resources needed to raise offspring. The marine environment presents a range of ecological factors which shape reproductive trade-offs. Seabirds, with life-history characteristics that generally include long life and low annual reproduction, have been an important group of animals for understanding limits to individual productivity and population growth. The concept of “provisioning” can be defined in various ways including the amount of food parents bring to offspring, the rate at which it is delivered, or some combination of both. A primary limitation for the amount or rate of provisioning by seabirds is the fact that parents must forage over wide areas of sea but must bring food back to offspring at a centrally-located nest (Ashmole 1971). Our early understanding of resource availability in the oceans led researchers to conclude that small clutch sizes and slow chick growth rates, characteristic of many seabirds, resulted from the overall low density and unpredictable patchiness of their prey (Ashmole 1963, Lack 1968). However, later researchers emphasized that certain areas of the oceans are

extremely productive, and showed that seabirds are adapted to exploit these productive areas (Ricklefs 1990). These details were not entirely unknown or ignored by Ashmole and others, but recent technological advancements, allowing more accurate remote sensing of the oceans and tracking of individual animals at sea, have allowed a growing appreciation for both the predictability of marine resources and the degree to which seabirds take advantage of this predictability (Weimerskirch 2007).

Several recent studies have challenged the notion that seabirds breed at the energetic boundary of what is possible given their environment, and replaced it with a more nuanced understanding that breeding seabirds operate with some flexibility within an energetic envelope that is somewhat broader than was previously thought. For example, seabird parents which are supplementally-fed or that are more proficient foragers expend less effort on provisioning but increase brood-guarding effort (Jodice et al. 2002, Lescroël et al. 2010). It is perhaps not particularly surprising that individuals will reduce parental investment when finding themselves with more energy. However research has also shown that this flexibility operates in the opposite direction too, and several seabird species have the capacity to increase the energy spent on foraging and successfully raise experimentally-enlarged broods (e.g., Ydenberg and Bertram 1989, VanderWerf 1992). Researchers now believe that seabirds generally maintain a small clutch size in order to prevent “overinvesting” in a large brood (Erikstad et al. 1997), the raising of which may result in physiological stress great enough to negatively affect adult survival if resources unexpectedly become limited (reviewed by Ricklefs 1990).

Working to understand the bounds of the energetic envelope within which seabirds operate, and the degree of flexibility they have to change energetic allocations within that envelope, has been a focus of much recent seabird research. Early work assumed no negative energy budget on the part of parents (Ricklefs 1983), but more recent studies revealed that as food resources fluctuate, parent seabirds can either expend more energy to maintain chick growth, but sacrifice their own condition, or they can keep energy expenditure the same, maintain their own condition, but sacrifice chick growth and perhaps chick survival (e.g., Kitaysky et al 2000). A range of responses along the spectrum between these extremes has been observed. For example, while Shy Albatross

(*Thalassarche cauta*) do not adjust provisioning (rate and/or amount of food delivered to chicks) based on chick needs (Hedd et al. 2002), in many other species provisioning appears to vary depending on chick needs, or a combination of chick needs and parent condition. For example, Black-browed (*Diomedea melanophrys*) and Grey-headed Albatross (*D. Chrysostoma*), and Thin-billed Prions (*Pachyptila belcheri*) adjust the amount fed to chicks based on chick condition (Weimerskirch et al. 1995, Waugh et al. 2000). Additionally, Puffins (species not provided, presumably *Fratercula arctica*; Erikstad et al. 1997) and Antarctic Petrels (*Thalassoica Antarctica*; Tveraa et al. 1998b) adjust provisioning based on both their own condition and that of the chicks.

Many studies have focused on the tube-nosed seabirds (Procellariiformes) and fascinating generalizations have emerged in this group of organisms. Many of these species mediate the trade-offs between chick provisioning and parental self-maintenance by alternating short chick-provisioning foraging trips, from which energy flow to chicks greatly increases but parent condition deteriorates, with longer trips to restore their own (i.e., the parent's) condition (Weimerskirch 1998, Weimerskirch et al. 2003). An increase in energy expenditure during a given breeding season may cause a decrease both in current parent condition and decreased survival in subsequent years (Jacobsen et al. 1995; Kitaysky et al. 2000). However, short-term periods of high physiological stress may not have lasting effects on survival or proper physiological function (Ricklefs and Wikelski 2002), and the temporary negative energy balance that bimodal foraging facilitates appears to allow seabird parents to sustain chick provisioning over the long provisioning periods characteristic of many Procellariiformes.

The conditions under which these behaviors exist among certain specialized seabird species remain poorly understood. In the high-latitude penguins for example, the relatively short breeding season (Ainley 2002) results in unique trade-offs between provisioning for growth versus guarding chicks against predation and weather. Bimodal foraging trips have been described in some studies of these species, but even within species the behavior is not observed in all populations and there has yet to emerge a generalizable understanding of the importance of bimodal foraging trips in this seabird group (Croxall et al. 1999, Barlow and Croxall 2002, Ballard et al. 2010a). Parent

penguins go into energetic debt during the breeding season (Watanuki et al. 2002, Ballard et al. 2010a), but it remains unclear how this behavior benefits chicks under different environmental conditions

*Provisioning and growth of avian young- with an emphasis on seabirds*

A considerable body of research has investigated juvenile growth rates of avian species. Two broad lines of inquiry have focused on 1) the extent to which avian growth rates are determined primarily by parents' ability to provide food to young (Lack 1968), and 2) the ways in which differences in growth rates between species are the result of the evolutionary histories and current ecological conditions facing particular species (Ricklefs 1968, 1984). Within species, comparisons have also been made in the trade-offs between brood size, provisioning rates, and brood-guarding to maximize the survival of individuals within broods (e.g., Nur 1984). In many bird species, nestling weight and brood size are negatively related, indicating parents must make tradeoffs between number of offspring produced and their likelihood of survival (Nur 1984, Tinbergen and Boerlijst 1990, Chapman et al. 2011).

Seabirds are characterized by small broods in comparison to other avian taxa, and parent-offspring trade-offs, rather than within-brood conflict or brood-reduction, have been a focus of much seabird research (but the latter has also received some attention, see e.g., Torres and Drummond 1999). Because the ratio of marginal benefits versus costs of brood size reduction are too low with clutches of only 1 or 2 eggs, there has been a growing appreciation of the variability in seabird chick growth rates, and how parents might adjust chick growth rates to maximize their lifetime fitness under different circumstances (Drent and Daan 1980).

A primary and unsurprising factor determining growth rates is the amount of food parents deliver to the chicks (Ricklefs 1968, Lyons and Roby 2011). A consistent finding among many studies is that when foraging costs to parents are increased, either through environmental fluctuation or experimental manipulation, both provisioning rate (mass of food per unit time), and chick growth rates decline (Weimerskirch et al. 2000). However, there is not always a simple positive relationship between provisioning and growth (e.g.,

Bertram et al 1991), and several additional factors are important. Characteristics of parents can also influence food delivery, either through inherent differences in size or other physical characteristics (e.g., Leo 1998), or through experience gained with more time spent foraging or more breeding attempts (e.g., Daunt et al 2007). The importance of total food delivery has been further refined in studies investigating the type of food delivered (e.g., the "junk food hypothesis"; Jodice et al 2006). A consistent result among many such studies is a positive relationship between chick growth rates and the lipid content of their diet (Golet et al. 2000, Wanless et al. 2005). Other aspects of diet type, such as the importance of protein content, various types of lipid (i.e. fatty acids), and other minor nutrients have received little attention.

#### *Offspring sex and parental investment*

With the advent of DNA-based sexing techniques, studies investigating how seabirds might vary provisioning and other parental care (guarding or brooding) based on the sex of offspring and parents are now possible and of recent research interest. In sexually size dimorphic species, the larger sex must grow faster or for a longer period of time. When these differences in growth occur while offspring are still entirely or partially nutritionally-dependent upon parents, then there can be a greater cost to parents of raising offspring of the larger sex (Trivers and Willard 1973). However, the fitness contribution of these offspring may not be greater in all circumstances, and thus parents may not always be willing to invest the extra effort in the more expensive sex. A consistent pattern is emerging across a range of dimorphic mammal and bird species that environmental conditions are an important factor in determining sex-biased investment (Weladji et al 2003; Martins 2004). Parents generally invest more in the larger and more expensive sex during times of higher resource availability, because these offspring are more likely to benefit from this increased investment later in life (e.g., Common Murre [*Urea aalge*]; Cameron-MacMillan et al. 2006). In contrast, when resources are limited, investment in the less expensive sex may be favored because the fitness of this sex may not be as negatively affected by low provisioning (e.g., Black-legged Kittiwake [*Rissa trydactyla*]; Merkling et al. 2012). This pattern appears to be consistent across species with both male-and female-biased sexual size dimorphism (Hipkiss et al. 2002).

## THE ADÉLIE PENGUIN

Except where otherwise cited, the following overview of Adélie Penguin (*Pygoscelis adeliae*) ecology and breeding biology is based on Dr. David Ainley's long-term research and insight, most of which has been compiled into two volumes (Ainley et al. 1983, Ainley 2002).

The Adélie Penguin is a pagophilic, or ice-obligate species that occupies a circumpolar range within the sea ice zone around the coast and nearby islands of the Antarctic continent, and sub-Antarctic islands up to about 57°S. This species congregates for breeding in snow-free, coastal locations. Most of the 161 known Adélie Penguin colonies contain between 1,000 and 50,000 pairs, while only six breeding colonies are larger than 100,000 pairs.

After pair-bonding in the Austral Spring (October – November), pairs lay 1 or (usually) 2 eggs. The male usually takes the first incubation shift, after which parents alternate incubation duties with 1 to 2 week foraging trips for the duration of the 34-day incubation period (Taylor 1962). After the chicks hatch, parents' foraging trips shorten to 1-4 days and for the initial 15-30 days one parent remains at the nest to guard the chicks. In most situations both parents eventually forage simultaneously, at which time chicks gather in groups called crèches, which provide protection from predation and adverse weather (Davis 1982). At approximately 55 days old, chicks fledge and leave the colony for the ocean where they will remain for several years before returning to undertake their own reproductive effort (Ainley 2002).

Sea ice forms an important substrate for primary productivity in the rich Southern Ocean food web (Arrigo and Thomas 2004), and sea ice concentration (SIC) is perhaps the most important environmental variable affecting Adélie Penguin foraging ecology (Watanuki et al. 2002, 2010, Emmerson and Southwell 2008, Beaulieu et al. 2010). In the Ross Sea, parents return to nest sites with more overall food in years of intermediate SIC (Ballard et al. 2010a), while fish may comprise a greater proportion of diet when SIC is lower (Ainley et al. 1998, 2003). The diet of Adélie Penguins foraging over continental slope areas, such as Western Antarctic Peninsula, is comprised largely of Antarctic Krill



(*Euphausia superba*), and contains relatively few fish (Chapman et al. 2010, Lyver et al. 2010). Most studies of Adélie Penguin chick diet and energetics have taken place in these areas. In contrast, in the southern Ross Sea (overlying continental shelf rather than slope), penguin diets are comprised of a combination of Crystal Krill (*Euphausia crystalorophia*, hereafter “krill”) and Antarctic Silverfish (*Pleurogramma antarcticum*, hereafter “fish”; Ainley et al 1998; Polito et al 2002). The importance of diet composition to Adélie Penguin chick growth is further discussed below.

#### *Study location and this project as part of ongoing research*

The Ross Sea lies within the Pacific sector of the Southern Ocean and is one of the southern-most reaches of ocean on the planet. The Ross Sea is the largest continental shelf system in the Southern Ocean and as such it is among the most productive marine ecosystems in this part of the world (Arrigo et al. 1998). It is a relatively deep continental shelf system, with average depths around 500 m (Figure 1.1; Smith et al. 2007). Changes in sea ice concentration (SIC) within and between years are perhaps the largest influence on biological communities in the Ross Sea. The Ross Sea Polynya, a large area of reduced sea ice concentration (SIC) in the southern Ross Sea formed by strong southerly winds blowing off the continent, has a large role in the influence of SIC on Ross Sea ecology (Figure 1.1). This polynya is present to some extent just to the north-east of Ross Island throughout the winter months, and it expands to include much of the Ross Sea by the end of summer. Where the polynya exists throughout winter, there is a complete mixed layer in early spring, which results in substantial nutrient concentrations near the surface at the beginning of the growing season (Smith et al. 2007). This causes a strong spring-time pulse of primary productivity, with a large standing stock of phytoplankton generally present by mid-December (Smith and Gordon 1997, Smith and Donaldson 2014), when Adélie Penguin chicks begin hatching.

Approximately 33- 38% of the world Adélie Penguin population breeds in the Ross Sea, and the four colonies of the Southeastern Ross Sea metapopulation represent the southern-most breeding population of the species (LaRue et al. 2013, Lyver et al. 2014). The data for my graduate work was collected at Cape Crozier (77°31’S, 169°23’E), the largest Adélie Penguin colony on Ross Island with over 270,000 breeding

pairs (Lyver et al. 2014). Other colonies comprising this metapopulation are Cape Royds (c. 3000 pairs), Cape Bird (c. 75,500 pairs), and Beaufort Island (c. 39,000 pairs; Lyver et al. 2014). Cape Crozier is adjacent to the portion of the Ross Sea polynya which remains ice free in winter, and this proximity to the rich, early season productivity is thought to be related to the very large size of this colony (Ainley 2002). The size of the Cape Crozier colony is an important component in interpreting the results of this study.

The research described here was part of a larger project conducted by an international team of researchers studying Adélie Penguins in the Ross Sea (more info and publication list at [www.penguinscience.com](http://www.penguinscience.com)). Initial work by this team investigated differences in population trends of the four colonies on and near Ross Island (Ainley et al. 2004), described foraging behavior and diet relative to colony size, intra- and inter-specific competition, and sea ice conditions (Ainley et al. 1998, 2003, 2004, 2006), and also conducted methodological investigations of the effects of instrument and flipper band attachment on Adélie Penguin demographics (Ballard et al. 2001, Dugger et al. 2006). This team went on to examine Adélie Penguin ecology in the context of large scale habitat and environmental factors (Ainley et al. 2005), including the species role in the overall Ross Sea ecosystem (Ainley et al. 2006, 2007, 2011, Ballard et al. 2011) and details of metapopulation dynamics among the four southern Ross Sea colonies, such as movement, survival and diet related to colony size and environmental variability (Ballance et al. 2009, Dugger et al. 2010, 2014). Winter migration and habitat use (Ballard et al. 2010b), as well as the differences in demographic rates (survival and breeding success) related to individual quality (Lescroël et al. 2009, 2010) were also investigated.

This long term project provided context for my research, and some results of this work have particular bearing on the questions I investigated. Chick mass at 5 weeks post-fledging was strongly related to colony size, with the heaviest chicks raised at the smallest colony (Cape Royds), and the lightest chicks raised at the largest (Cape Crozier; Dugger et al. 2014, Whitehead et al. 2015). At Cape Crozier, Adélie Penguins were shown to make trade-offs between chick provisioning and maintenance of parent condition, and these trade-offs depended on parent mass both at the beginning of the

season and before individual foraging trips, as well as on environmental conditions (i.e., sea ice concentration; Ballard et al. 2010a). In addition, food delivery and chick mass measured at the colony scale were highest during years of intermediate sea ice concentration (Ballard et al. 2010a). Adélie Penguins with higher reproductive success were also more proficient foragers, taking shorter trips to bring back the same amount of food and thus spending more time at the nest than birds with poorer success (Lescroël et al. 2010).

These results provide context for investigating the ways in which behaviors that increase costs to parents might benefit young, particularly since colony size has increased steadily since this previous work was conducted, reaching current historical highs (Lyver et al. 2014). To date, these differences in provisioning behaviors have been compared only coarsely to population level (cross-sectional) chick growth (Dugger et al. 2014, Whitehead et al. 2015) and survival. Here I build upon these results to understand growth and survival implications of different provisioning at the scale of individual penguin pairs and chicks, at the largest colony in this metapopulation.

#### *Adélie Penguin chick growth*

Adélie Penguin chicks weigh 90 g at hatching and gain 50-125 g d<sup>-1</sup> (mean 100-105) to reach a fledging weight of 2.5-3.25 kg approximately 50-55 days after hatching (Volkman and Trivelpiece 1980, Salihoglu et al. 2001, Ainley 2002). As expected, chick growth is generally positively related to provisioning rate (Clarke et al. 2002). Energetic models suggest that even a 4% decrease in provisioning rate can decrease growth and affect recruitment probability (Chapman et al. 2011). However, Adélie Penguin chicks require 21.3-33.6 kg of total food to successfully fledge (compiled by Chapman et al. 2010, also see Salihoglu et al. 2001). This nearly 33% range in reported values, compared to the narrow range suggested by the energetic models indicate that this species has a complicated ecology, perhaps with several unconsidered sources of variation in annual growth.

The relationship between diet composition and Adélie Penguin chick growth has also been investigated, although only at the scale of colony-means (cross-sectional). The

average energy densities of krill and fish are  $4.62 \text{ kJ g}^{-1}$  and  $5.2 \text{ kJ g}^{-1}$ , respectively (Ainley et al. 2003), though there is high variance around these means for both prey types based on age and maturity class (Volkman and Trivelpiece 1980, Chapman et al. 2010, 2011). Recent work has shown that adult Adélie Penguins may preferentially choose higher lipid foods when provisioning chicks (Chapman et al. 2010), and that this can be important for chick growth (Ainley et al. 2003). Indeed, models for Adélie Penguins, parameterized with data from the western Antarctic Peninsula (wAP) indicate the addition of fish, specifically Antarctic Silverfish of Age Class 3 or older, to an all-krill diet will increase fledging weight by an average of 117 g, a difference that had positive consequences on survival and recruitment to the breeding population (Chapman et al. 2011).

Many previous studies of Adélie growth have taken place at relatively small colonies (1,800 -8,000 pairs) in lower latitudes, where growth rates and fledging sizes may be different (Volkman and Trivelpiece 1980), and where intraspecific competition may be less important (e.g., Ballance et al. 2009), than at larger and/or more southerly colonies. Both latitude and colony size affect patterns of chick growth. Populations breeding at higher latitudes generally grow faster, and reach an asymptotic size (Ricklefs 1968) at a smaller and/or younger age than populations in lower latitudes (Volkman and Trivelpiece 1980). When growth reaches an asymptote, the individual's foraging proficiency must only meet maintenance costs (not growth), and thus a smaller, earlier asymptote may be advantageous in the short breeding seasons of higher latitudes (Volkman and Trivelpiece 1980).

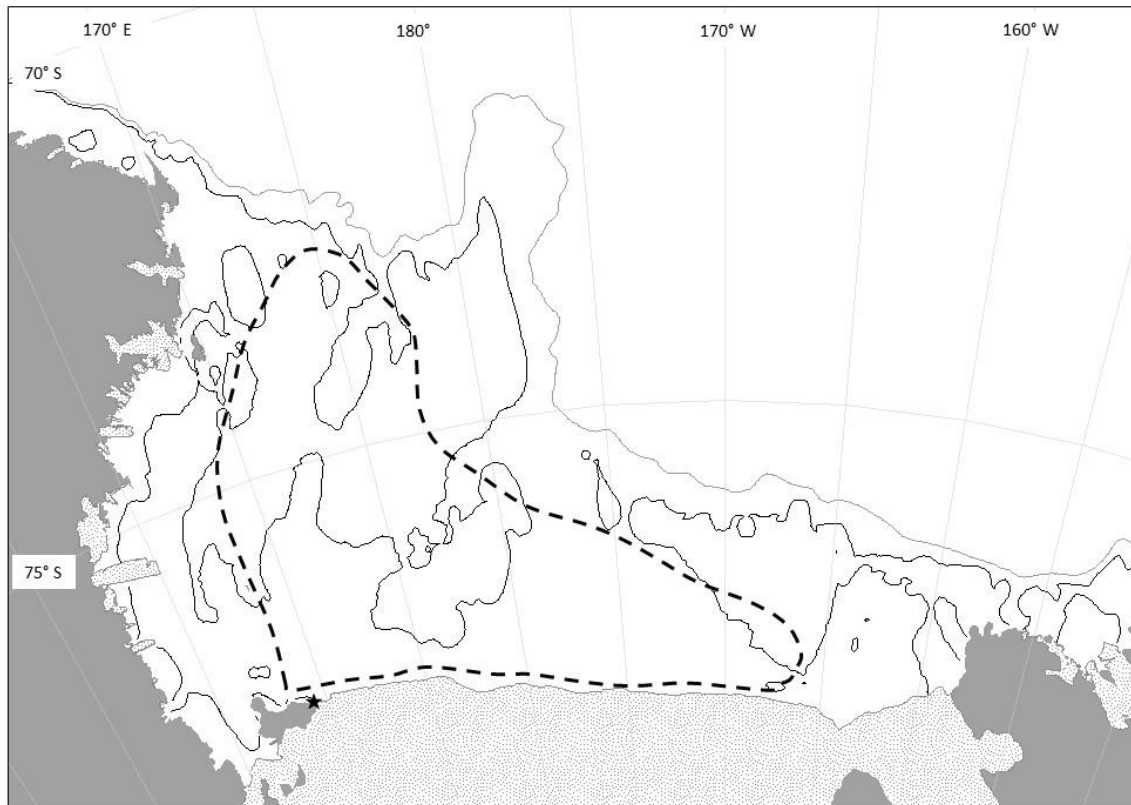
The large range in reported food loads delivered to chicks may also reflect difficulties in concurrently measuring provisioning and growth rates in wild, free-living populations. Previous researchers have estimated provisioning and/or prey requirements based on 1) direct measures of chick growth combined with prey energy content and measurements of chick metabolic rate (Culik et al. 1990, Janes 1997); 2) measures of change in mass of adults before and after foraging trips (Chappell et al. 1993, Ballard et al. 2010a); or 3) by measuring mass of adult stomach contents (Ainley et al. 2003). Values for provisioning and growth have often been averaged across penguin pairs and

chicks (cross-sectional studies), so that the direct relationships between provisioning and growth cannot be evaluated at the individual pair level. However, Clarke et al. (2002) found a positive relationship between provisioning (measured directly through the entire season) and a single measure of chick size (fledging mass) from chicks of those parents.

While the fledging weight of Adélie Penguins has been shown to differ by sex, the relationships between sex, provisioning, and growth rate have yet to be evaluated simultaneously for this species. Previous work relating Adélie growth and provisioning rates yielded important insights into chick food requirements at the population level (Chapman et al. 2011; Clarke et al. 2002; Salihoglu et al. 2001). However, the direct measurement of provisioning rates and chick growth at the level of the individual pair is still lacking. Investigation at this scale is required to better understand the relationships between provisioning and growth across the range of individual variation.

Considering what is known about avian life-history trade-offs, seabird ecology, and more specifically Adélie Penguin breeding biology, I investigated the relationships between offspring provisioning, growth and survival in this long-lived, colonial nesting seabird. I characterized differences in growth rate between male and female chicks, something that had yet to be done for this species (Chapter 2). I then investigated the relationships between chick growth rates and the type and overall amount of provisioned food (Chapter 3). Finally I investigated whether growth rates or the age and size of chicks at an important transition (from brood-guarding to crèche period) could predict survival probability (Chapter 4). These chapters were written as standalone manuscripts intended for publication in peer-reviewed journals. However, to save space and improve readability of this thesis document, in certain cases methodologies common to multiple chapters are only described once, and the reader is referred back to that description.

Figure 1.1. Map of the Ross Sea, showing land (dark gray), ice shelf (permanent glaciers on the sea; stippling), the 500 m (black) and 1000 m (light gray) bathymetric contours, the Adélie Penguin colony at Cape Crozier, Ross Island (star), and the approximate extent of the Ross Sea polynya in December (adapted from Smith et al. 2007; dashed line). For reference, the shelf break in the Ross Sea occurs at approximately 800m.



## Chapter 2

### SEX-BASED DIFFERENCES IN ADÉLIE PENGUIN (*PYGOSCELIS ADELIAE*) CHICK GROWTH RATES

Scott Jennings, Arvind Varsani, Katie M. Dugger, Grant Ballard, David G. Ainley

## ABSTRACT

Sexually size dimorphic species must show some difference between the sexes in the growth parameters (growth rate and/or length of growing period). This can cause the sexes to be impacted by environmental variability in different ways, and understanding these differences allows a better understanding of patterns in productivity between individuals and populations, which can ultimately allow better management of natural resources and prediction of the impacts of changing environments. We investigated differences in growth rate between male and female Adélie Penguin (*Pygoscelis adeliae*) chicks during two breeding seasons at Cape Crozier, Ross Island, Antarctica. Adélie Penguins are a slightly dimorphic species, with males averaging larger than females in mass (~11%) and bill (~8%) and flipper length (~3%). Mass and length of flipper, bill, tibiotarsus, and foot were measured at 5-day intervals for 45 male and 40 female individually-marked chicks. Chick sex was molecularly determined from feathers. We used linear mixed effects models to estimate daily growth rate as a function of chick sex, while controlling for hatching order, brood size, year, and individual variation in parental pairs. Accounting for season and hatching order, male chicks gained mass an average of 15.6 g d<sup>-1</sup> faster than females. Growth in bill length showed a similar pattern, and the calculated size difference at fledging was similar to that observed in adults. There was no evidence for sex based differences in growth of other morphological features. The differences in growth rate we observed have potentially important implications for juvenile survival, recruitment rates, and ultimately population-level processes.



## INTRODUCTION

Sexual size dimorphism (SSD) is common in a wide range of animal taxa and is thought to result from different selective forces operating on males and females for their different reproductive or ecological roles (Blanckenhorn 2005, Teder 2014). In many vertebrate species, the evolution of SSD has been linked to social mating systems and sexual selection, with greater SSD observed in polygynous than monogamous species (Plavcan and van Schaik 1997, Dunn et al. 2001). However, these selective forces may also derive from natural selection, and efforts are ongoing to determine the relative importance of these factors (Olsen et al. 2013).

Seabird species show both male- and female-biased SSD, and the direction of dimorphism has been linked to a range of behaviors and other ecological factors. It has been suggested that differences in the magnitude of SSD between certain seabird species is related to aerial- vs. ground-based displays by males of each species (Serrano-Meneses and Székely 2006). Additionally, it has been suggested that SSD in mass and wing morphology result from foraging niche divergence of males and females, perhaps reducing intersexual competition for resources in these central-place foraging species (Shaffer et al. 2001).

Achievement of sexual size dimorphism may involve two non-exclusive processes: the larger sex may grow faster, or may grow for a longer period of time, or there could be some combination of the two. A range of combinations of growing faster and growing longer have been observed in birds. In several avian species, chicks of the larger sex grow faster and fledge larger (e.g., Yellow-headed Blackbird [*Xanthocephalus xanthocephalus*]; Richter 1983; Wandering Albatross [*Diomedea exulans*]; Weimerskirch et al. 2000). However, in at least one other bird species the sexes grow at similar rates but the larger sex grows for a longer time period (e.g., Common Tern [*Sterna hirundo*]; Becker and Wink 2003).

Growth rates are an important component of life history (Arendt 1997), providing mechanisms for a range of ecological trade-offs between fast and slow growth. Faster-growing individuals may out-compete siblings for food and may be less susceptible to

predation (Ricklefs 1984). Faster growth may also facilitate fledging or achieving mature size sooner (Lack 1968), which can increase survival in the post-fledging period via faster acquisition of adult foraging capabilities (Marchetti and Price 1989), or more time spent foraging before the onset of winter (Harris et al. 2007). However, in many species offspring do not grow at the maximum rate possible, indicating there may be some costs associated with fast growth (Arendt 1997). Indeed, recent research has indicated that fast growth may come at the expense of resistance to oxidative stress or reductions in other immune functions (Alonso-Alvares et al. 2007, Kim et al. 2010). Faster-growing individuals also may be disproportionately affected during times of resource limitation due to their greater absolute food requirements (Ricklefs 1984). Additionally, faster-growing offspring may be more costly for parents to rear, the hypothesized reason for the slow growth typical of Procellariiformes (Warham 1990).

Dimorphism in growth rates may result in different selective pressures acting on males and females (Clutton-Brock et al. 1985). There is also growing evidence for plasticity in growth rates (Dmitriew 2011), and the degree of plasticity may vary between sexes in dimorphic species (Badyaev 2002). For example, captive-reared Zebra Finches (*Taeniopygia guttata*), male nestlings grow at a higher rate than females at low feeding levels, but this pattern reversed at higher feeding levels (Martins 2004). Taken together, these factors indicate that a better understanding of the differences in growth rates between the sexes can aid our understanding of patterns of productivity in individuals and populations.

The Adélie Penguin (*Pygoscelis adeliae*) is a mildly dimorphic species with adult males averaging slightly larger than females in mass (mean [SD] = 5.0[0.8] kg vs. 4.6[0.7] kg), flipper length (210.9 [6.5] mm vs. 203.8 [6.8] mm) and bill length (35.6 [2.8] mm vs. 32.9 [2.4] mm; Ainley and Emison 1972). Sex-based differences in the size at fledging have been reported in this species (Beaulieu et al. 2009, Chapman et al. 2010), but differences in growth rate have yet to be evaluated. Here we examined, for the first time in this species, sex-based differences in chick mass and skeletal growth rates. We also evaluated the evidence for skewed sex ratio at hatching, and conducted an *a posteriori* investigation of potential differences in diet between male and female chicks.

## STUDY AREA AND METHODS

### *Field work*

Data were collected during the Austral summers of 2012-13 and 2013-14 (hereafter “2012” and “2013”, to reflect the year at the beginning of the summer) at Cape Crozier, Ross Island, Antarctica. This study was part of a larger effort that used individually marked, known-age penguins to investigate reproductive ecology and demography (more info at [www.penguinscience.com](http://www.penguinscience.com)). The nests used in this study were chosen systematically from these known birds to represent a range of parental (i.e., age, breeding quality) and nest site (interior or edge of subcolonies) characteristics. Incubated nests were checked every 1-3 d to determine hatching day.

Morphological measurements began at 10 d post-hatching for first-hatched chicks. Second-hatched chicks, if present, were also measured at this time, to reduce disturbance to the nest of returning just 1 or 2 days later. We collected 5 morphological measurements on chicks including: mass, measured to the nearest 25 g using a spring scale; bill length measured (hundredth of a mm) with digital calipers from the most distal extent of skin on the side of the upper mandible to the tip of the bill; flipper length measured along the underside of the flipper from the distal edge of the humeral head to the tip of the flipper; foot length measured to the end of the longest (middle) toe excluding the toenail, with the tibiotarsus-tarsometatarsus joint held against the stop of a flush stop ruler; and tibiotarsus length was measured with the leg held in a natural position, with the femur-tibiotarsus joint held against the stop of a flush stop ruler, and measured to the sole of the foot (Fig 2.1). Flipper, foot, and tibiotarsus lengths were measured to the nearest mm. We also collected 5-10 feathers from between the belly and upper leg, and individually marked each chick with a T-bar fish tag (Floy Tags Inc., USA). Thereafter, we repeated morphological measurements on 5-d intervals for the remainder of the 50-55 d chick rearing period.

### *Analysis*

Sex was determined using DNA extracted from the collected feathers. We used *CHD*-gene targeted PCR using primer pair 2550F (5'-GTT ACT GAT TCG TCT ACG

AGA-3') and 2718R (5'-ATT GAA ATG ATC CAG TGC TTG-3'; Fridolfsson and Ellegren 1999). DNA was extracted from the feather calamus (~5mm) using the Extract-N-Amp™ Blood kit (Sigma-Aldrich, USA) following the manufacturer's instructions. 4µl of the DNA extract was used as a template in a 25µl polymerase chain reaction (PCR) using KAPA Blood PCR Mix B (Kapa Biosystems, USA) with the *CHD*-gene primer pair 2550F and 2718R. The *CHD*-gene 2550F and 2718R primer pair derived amplicons for Z and X chromosomes (~600bp and 700bp respectively) enabled us to designate the sex, i.e., only a ~600bp amplicon indicated male (ZZ) and both a ~600bp and ~700bp amplicon indicated female (ZW).

We employed a 2-step process to model growth as a function of sex, while controlling for other factors. First, we fitted linear models to the measurements of each chick separately to obtain a daily growth rate for each chick. We fit linear models to the linear phase of growth only, which represented a different length of time for each morphological measurement (mass and flipper=10-40 d post hatch; tibiotarsus and foot=10-35 d; bill=10-55 d). We modeled the growth of each morphological parameter separately, and the slope coefficients from these models were taken as the daily growth rates for each morphological measurement for each chick.

We then modeled each morphological measurement separately by fitting linear, mixed effects models with daily growth rate as the response variable and sex, hatching order (A or B), brood size (1 or 2) and season as fixed effects. Nest ID was included as a random effect to account for lack of independence between siblings. We used random intercept only for the structure of our random effect, because this variable had too few levels (only 1 or 2 chicks per nest) to allow slope estimation. We examined the relative importance of the fixed effects by fitting candidate models with all possible main effects of the variables under consideration. Qualitative comparisons based on field observations suggested differences in growth rates between the two years of the study, so we also considered models with the interactions between year and the remaining covariates. We used maximum-likelihood methods when determining best-supported fixed effect model structure (Zuur et al. 2009).

We also conducted an *a posteriori* evaluation of the proportion of chick diet comprised of higher-lipid fish (versus krill) as a possible explanation for observed sex- or year-based differences in chick growth rates. We used stable isotope analysis of a portion of the feathers collected to evaluate  $\delta^{15}\text{N}$  isotope for each chick. Full methods for stable isotope analysis are described in Jennings (2015, Chapter 3). We compared models with the main effect for sex alone, the additive sex and year effects and the interaction between year and sex, and also included the intercept-only model.

We compared Akaike information criterion values with a correction for small sample sizes ( $\text{AIC}_c$ ) and Akaike Weights ( $\text{AIC}_c$  wts) to evaluate models, and generally the model with the lowest  $\text{AIC}_c$  and highest  $\text{AIC}_c$  wt was selected as having the most support (Burnam and Anderson 2002). We evaluated the direction and strength of the effect of sex on growth by examining the estimated coefficients and assessing whether 95% confidence limits overlapped zero. We calculated profile likelihood confidence intervals because the sampling distribution of variance estimates from mixed models may be asymmetric and sample sizes in this study were relatively small (Zuur et al. 2009). In all analyses the categorical covariates were coded as Sex: Male=1 and Year: 2013=1. Analysis was conducted in R version 3.1.1 (R Core Team 2014) and the lme4 (Bates et al. 2014) and lmerTest packages (Kuznetsova et al. 2014).

## RESULTS

We detected no differences in sex ratio by hatching order or brood size ( $X^2$  [2, N = 113 chicks] = 0.72; P = 0.20), or between seasons ( $X^2$  [1, N = 113 chicks] = 0.45; P = 0.50). The best-supported model for mass and flipper growth rates included Sex, Year, Hatching order, Brood size, and the interaction between Year and Hatching order ( $\text{AIC}_c$  wts. = 0.37 and 0.60, respectively). For mass growth the 95% confidence interval on the Sex effect did not overlap zero, suggesting that males gained mass at a faster rate than females in both years (Table 2.1). The interaction between Year and Hatching order indicated second-hatched chicks grew slower than first-hatched, and this pattern was stronger in 2013 ( $\beta$  = -23.3; SE = 9.9; 95% CI = -43.1 to -2.4). For flipper growth, there was only weak evidence for a positive effect of Sex on growth rate ( $\beta$  = 0.30; SE = 0.22; CI = -1.2 to 0.73; Table 2.2).

The best-supported model for bill and tibiotarsus growth included only Sex and Year ( $AIC_c$  wts. = 0.53 and 0.40, respectively). For bill growth, there was strong evidence for faster growth in males (see Table 2.1) and slower growth in both sexes during 2013 (2013  $\beta$  = -0.08; SE = 0.02; CI = -0.12 to -0.04). However for tibiotarsus the 95% confidence interval associated with the coefficients of both estimates slightly overlapped zero (Sex: see Table 2.1; 2013  $\beta$  = -0.33; SE = 0.18; 95% CI = -0.67 to 0.03), suggesting neither factor had a very strong effect. For foot growth, the best-supported model contained Year only ( $AIC_c$  wt. = 0.33), with the 95% confidence interval on the estimate of the year effect slightly overlapping zero ( $\beta$  = 0.21; SE = 0.11; 95% CI = -0.02 to 0.43).

While accounting for Year, Brood size and Hatching order, male Adélie Penguin chicks gained mass at an average rate of 15.6 g d<sup>-1</sup> (95% CI: 5.6-25.5 g d<sup>-1</sup>) faster than females (Table 2.2, Figure 2). Across the duration of the linear growth period of mass (10 to 40 days old) this dimorphism in growth rates led to a difference in estimated average size (at day 40) of 468 g. This estimated size difference is similar to the differences in observed mass of the few chicks we measured in the final days before fledging (13 males, 15 females), where males were on average 430 g larger. Bill growth-rate (controlling for year) was also faster in males, and while the magnitude of the difference may seem relatively small (0.05 mm d<sup>-1</sup>, 95% CI: 0.02-0.09; Table 2.3, Fig 2.2), the percent difference in growth rates between males and females was actually greater for bill growth than mass growth. We found little evidence for the effect of sex on growth rates of flipper, tibiotarsus, or foot lengths (Table 2.1, 2.2, Figure 2.2).

In the *a posteriori* investigation of the proportion of chick diet comprised of fish, the best supported model contained just the main effect for sex. The coefficient for the sex effect in this model provided good evidence that male chicks were provisioned with more fish than female chicks ( $\beta$  = 0.26; 95% CI: 0.07 to 0.45; Figure 3). The second-ranked model contained the additive sex and year effect ( $\Delta AIC_c$  = 1.9, but since this model had one additional parameter, we concluded that year was an uninformative parameter (Arnold 2010), and that there was no support for year-based differences in the amount of fish fed to chicks (i.e.  $\delta^{15}N$ ).

## DISCUSSION

We detected faster growth rates of mass and bill length in male Adélie Penguin chicks than in females. This difference in growth rates could have important implications for the reproductive ecology of this species, particularly at the very large colony where this study was conducted and where competition for food is thought to be limiting colony growth (Lyver et al. 2014). An increase in fledging mass (after 50-55 d growth) of only 117 g increased the probability of recruitment in this species (Chapman et al. 2011). The difference in growth rates we observed was large enough to result in males being on average approximately 450 g heavier than females in the final 10 days before fledging. Thus, this difference is biologically-significant, with the potential to cause differential survival between the sexes during both the pre-fledging and post-fledging periods.

The rate of bill length growth between males and females also differed. Since bill growth was slow ( $0.22 \text{ mm d}^{-1}$  for females), the observed  $0.05 \text{ mm d}^{-1}$  difference in growth rate was comparable to the difference in mass growth rates between the sexes, despite the seemingly small magnitude of this difference. Indeed, because bill growth continued for the duration of the 50-55 d chick rearing period, unlike other skeletal measurements (see below), by fledging age the bills of male chicks were on average 2.3 mm longer than female bills (as calculated from the best-supported model for bill growth; male = 24.4 mm; female = 21.9 mm). This difference is similar to the difference in average adult bill lengths at Cape Crozier (male = 24.3 vs. female = 22.6 mm; Ainley and Emison 1972, Ainley and Ballard unpub. data), indicating that Adélie Penguin chicks nearly achieve adult dimorphism in bill size by fledging age. The growth of flipper, tibiotarsus, and foot length were all similar between males and females. However, there is dimorphism in flipper length in adults (Ainley and Emison 1972), and thus it seems likely that males continue growing flipper length longer than females.

Our *a posteriori* analysis of diet composition revealed that the diet of male chicks had a greater proportion of fish than that of female chicks. The diets of adult and chick Adélie Penguins in the southern Ross Sea is comprised almost entirely of a combination of Crystal Krill (*Euphausia crystalorophia*) and Antarctic Silverfish (*Pleurogramma antarcticum*; Ainley 2002). Silverfish has been shown to have a higher lipid content than

krill and thus provide a more calorically-dense food for penguin chicks (Ainley et al. 2003, Chapman et al. 2010). Thus, the difference in diet composition between male and female chicks is a possible mechanism for the sex-based differences in growth rates that we detected.

In Adélie Penguins, chicks hatch 1-2 d apart, and we observed that the first-hatched chick is often bigger and grows faster, possibly by outcompeting its sibling for food (also reported by Ainley 2002). Singleton chicks have also been reported to grow faster than those from two-chick broods, likely due to greater overall access to food (Ainley and Schlatter 1972). Given these patterns in growth, the results reported here could be due to the sex of first-hatched or singleton chicks being male biased. However, we detected no evidence of skewed sex ratios by hatching order or brood size, indicating that the differences in growth we report are not simply due to greater access to food for singleton chicks or a competitive advantage based solely on hatching-order-induced size differences.

The faster growth observed in male chicks may be a byproduct of adult SSD, rather than a feature providing a selective advantage during the growth phase. A rapid increase in both number and size of fat cells is largely responsible for mass growth in Adélie Penguin chicks. The ability to both deposit and later mobilize these fat reserves could provide selective advantage to individuals coping with such a short breeding season (Raccurt et al. 2008). Considering our results in this context, it may be that males have a greater capacity for increasing the mass of adipose tissue. The mechanisms for this possible difference in growth capacity are unclear, but if true, this capacity could benefit males later in life during several stages of reproductive effort when long-term fasting is required (more so in males than females; Ainley 2002). Male Adélie Penguins arrive at the colony earlier in the season than females in order to secure territories, which allows for less pre-breeding foraging time and requires longer distance traveled over more extensive spring ice floes (Ainley et al. 1983). Males also take a larger proportion of the incubation duty, and generally lose a larger proportion of their mass during the breeding effort (Ballard et al. 2010). The development of fat cells in male penguin chicks may not necessarily provide any advantage during the growing period, but rather may be a



developmental process expressed during growth that is important for breeding males later in life. Thus males may gain selective advantage in multiple ways by having a greater capacity for acquiring and storing energy reserves.

We have shown that offspring sex is an important factor in determining some components of growth in Adélie Penguin chicks (mass, bill length), and unimportant in others (flipper, tibiotarsus, foot). This is the first study to our knowledge to document sex-based differences in offspring growth rates in this species. The identification of these growth rate differences provides a greater understanding of the ways in which ecological factors may impact the two sexes differently. Ultimately these results increase our understanding and ability to predict how populations may respond to fluctuating environmental or other factors.

#### ACKNOWLEDGMENTS

We would like to thank Libby Porzig, Annie Schmidt, Annie Pollard, Amelie Lescroël, Melanie Massaro, Megan Elrod and Jean Pennycook for their assistance with field work, and additionally Melanie Massaro for contributing funds for a portion of the molecular sexing. We also thank Donald Lyons and Lorenzo Ciannelli for valuable discussions that helped greatly with this research. The US Antarctic Program provided logistic support; financial support was provided by NSF grants *ANT- 0944411*. S. Jennings received additional support from Oregon State University, Fisheries and Wildlife Department (M. A. Ali Graduate Chair Award in Fisheries Biology). All penguin chick capture, handling, and data collection methods performed during this study were approved under appropriate Antarctic Conservation Act permits from the National Science Foundation Office of Polar Programs and Oregon State University's Institutional Animal Care and Use Committee. This is Point Blue Conservation Science Contribution No. XXXX. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## REFERENCES

- Ainley, D. G. 2002. *The Adelie Penguin: Bellwether of Climate Change*. Columbia University Press, New York, New York, USA.
- Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. *The Condor* 105:95–106.
- Ainley, D. G., and W. B. Emison. 1972. Sexual size dimorphism in Adelie Penguins. *Ibis* 114:267–271.
- Ainley, D. G., R. E. LeResche, and W. J. L. Sladen. 1983. *Breeding Biology of the Adelie Penguin*. Page 240.
- Ainley, D. G., and R. P. Schlatter. 1972. Chick raising ability in Adelie Penguins. *Auk* 89:559–566.
- Alonso-Alvares, C., S. Bertrand, B. Faivre, and G. Sorci. 2007. Increased susceptibility to oxidative damage as a cost of accelerated somatic growth in zebra finches. *Functional Ecology* 21:873–879.
- Arendt, J. D. 1997. Adaptive Intrinsic Growth Rates: An Integration Across Taxa. *The Quarterly Review of Biology* 72:149–177.
- Arnold, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- Badyaev, A. V. 2002. Male and Female Growth in Sexually Dimorphic Species : Harmony , Conflict , or Both ? 11–33.
- Ballard, G., K. Dugger, N. Nur, and D. Ainley. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405:287–302.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <URL: <http://CRAN.R-project.org/package=lme4>>.
- Beaulieu, M., A.-M. Thierry, T. Raclot, Y. Le Maho, Y. Ropert-Coudert, H. Gachot-Neveu, and A. Ancel. 2009. Sex-specific parental strategies according to the sex of offspring in the Adelie penguin. *Behavioral Ecology* 20:878–883.
- Becker, P. H., and M. Wink. 2003. Influences of sex, sex composition of brood and hatching order on mass growth in common terns *Sterna hirundo*. *Behavioral Ecology and Sociobiology* 54:136–146.

- Blanckenhorn, W. U. 2005. Behavioral Causes and Consequences of Sexual Size Dimorphism. *Ethology* 111:977–1017.
- Burnam, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York.
- Chapman, E., E. Hofmann, D. Patterson, C. Ribic, and W. Fraser. 2011. Marine and terrestrial factors affecting Adélie Penguin *Pygoscelis adeliae* chick growth and recruitment off the western Antarctic Peninsula. *Marine Ecology Progress Series* 436:273–289.
- Chapman, E. W., E. E. Hofmann, D. L. Patterson, and W. R. Fraser. 2010. The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie Penguin (*Pygoscelis adeliae*) chick growth: A modeling study. *Deep Sea Research Part II: Topical Studies in Oceanography* 57:543–558.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? *Biological reviews of the Cambridge Philosophical Society* 86:97–116.
- Dunn, P. O., L. A. Whittingham, T. E. Pitcher, S. Evolution, N. Jan, and P. O. Dunn. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55:161–175.
- Fridolfsson, A.-K., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* 20:116–121.
- Harris, M. P., M. Frederiksen, and S. Wanless. 2007. Within- and between-year variation in the juvenile survival of Common Guillemots *Uria aalge*. *Ibis* 149:472–481.
- Kim, S.-Y., J. C. Noguera, J. Morales, and A. Velando. 2010. Quantitative genetic evidence for trade-off between growth and resistance to oxidative stress in a wild bird. *Evolutionary Ecology* 25:461–472.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Bojesen. 2014. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. <http://CRAN.R-project.org/package=lmerTest>.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Western Printing Services, Bristol.
- Lyver, P. O., M. Barron, K. J. Barton, D. G. Ainley, A. Pollard, S. Gordon, S. McNeill, G. Ballard, and P. R. Wilson. 2014. Trends in the breeding population of Adélie penguins in the Ross Sea, 1981-2012: a coincidence of climate and resource extraction effects. *PloS One* 9:e91188.

- Marchetti, K., and T. Price. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews* 64:51–70.
- Martins, T. L. F. 2004. Sex-specific growth rates in zebra finch nestlings: a possible mechanism for sex ratio adjustment. *Behavioral Ecology* 15:174–180.
- Olsen, B. J., R. Greenberg, J. R. Walters, and R. C. Fleischer. 2013. Sexual dimorphism in a feeding apparatus is driven by mate choice and not niche partitioning. [http://sbe.umaine.edu/olsen/reprints/Olsen et al 2013 - SWSP bill dimorphism\\_BehEco.pdf](http://sbe.umaine.edu/olsen/reprints/Olsen%20et%20al%202013%20-%20SWSP%20bill%20dimorphism_BehEco.pdf).
- Plavcan, J. M., and C. P. van Schaik. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American journal of physical anthropology* 103:37–68.
- R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Raccurt, M., F. Baudimont, J. Tirard, B. Rey, E. Moureaux, A. G  lo  n, and C. Duchamp. 2008. Growing in Antarctica, a challenge for white adipose tissue development in Adelie penguin chicks (*Pygoscelis adeliae*). *American journal of physiology. Regulatory, integrative and comparative physiology* 295:R1671–R1679.
- Richter, W. 1983. Balanced Sex Ratios in Dimorphic Altricial Birds: The Contribution of Sex-Specific Growth Dynamics. *The American Naturalist* 121:158–171.
- Ricklefs, R. E. 1984. The Optimization of Growth Rate in Altricial Birds. *Ecology* 65:1602–1616.
- Serrano-Meneses, M.-A., and T. Sz  kely. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113:385–394.
- Shaffer, S. A., H. Weimerskirch, and D. P. Costa. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* 15:203–210.
- Team, R. C. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Teder, T. 2014. Sexual size dimorphism requires a corresponding sex difference in development time: a meta-analysis in insects. *Functional Ecology* 28:479–486.

Warham, J. 1990. The Petrels: their ecology and breeding systems. Academic Press, San Diego, CA.

Weimerskirch, H., C. Barbraud, and P. Lys. 2000. Sex differences in parental investment and chick growth in wandering albatrosses : fitness consequences. *Ecology* 81:309–318.

Zuur, A. F., E. N. Ieno, N. Walker, A. a. Saveliev, and G. M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R.

Table 2.1 Parameter estimates and 95% confidence intervals for the sex effect on growth from the best model (i.e., lowest AIC<sub>c</sub>) for each morphological measurement of Adélie Penguin chicks during Austral summers of 2012-13 and 2013-14 on Ross Island, Antarctica. Plus signs denote additive effects and asterisks denote interactions. Sex was not supported as an important factor associated with for foot growth.

Morphological measurement	Best-supported model <sup>a</sup>	Estimate for sex effect	95% Conf. Interval lower	upper
Mass (g d <sup>-1</sup> )	sex + brood size + hatch order*year	15.60	5.66	25.52
Flipper (mm d <sup>-1</sup> )	sex + year	0.30	-0.12	0.73
Bill (mm d <sup>-1</sup> )	sex + brood size + hatch order*year	0.05	0.02	0.09
Tibiotarsus (mm d <sup>-1</sup> )	sex + year	0.26	-0.08	0.60
Foot (mm d <sup>-1</sup> )	year	-	-	-

<sup>a</sup> all models included nest ID as a random effect

Table 2.2 Average daily growth rate estimates (with 95% CI) from best model (i.e., model with lowest AIC<sub>c</sub>) relating growth rates of morphological characteristics and mass to sex, year, brood size, chick hatching order; and sample sizes (n) for male and female Adélie Penguin chicks measured, and weighed during Austral summers of 2012-13 (2012) and 2013-14 (2013) on Ross Island, Antarctica. Sex was not supported as an important variable for foot growth so only means by year (best model results) are reported.

	2012		2013	
	Male	Female	Male	Female
n	23	21	37	32
Mass (g d <sup>-1</sup> )	99.89 (89.95-109.81)	84.29 (71.34-97.24)	67.24 (52.69-81.8)	51.64 (37.09-66.2)
Flipper (mm d <sup>-1</sup> )	4.88 (4.45-5.3)	4.58 (4.04-5.11)	4.02 (3.42-4.62)	3.72 (3.12-4.31)
Bill (mm d <sup>-1</sup> )	0.27 (0.24-0.31)	0.22 (0.19-0.25)	0.19 (0.15-0.23)	0.14 (0.10-0.18)
Tibiotarsus (mm d <sup>-1</sup> )	3.13 (2.78-3.47)	2.86 (2.54-3.19)	2.8 (2.45-3.15)	2.54 (2.19-2.89)
Foot (mm d <sup>-1</sup> )	1.06 (0.88-1.23)		1.27 (1.04-1.49)	

Figure 2.1 Schematic illustrating the location of morphological measurements collected from male and female Adélie Penguin chicks during Austral summers of 2012-13 and 2013-14 on Ross Island, Antarctica. Bill was measured to the nearest hundredth mm and remaining measurements to the nearest mm. Dashed line indicates humeral head on underside of the flipper.

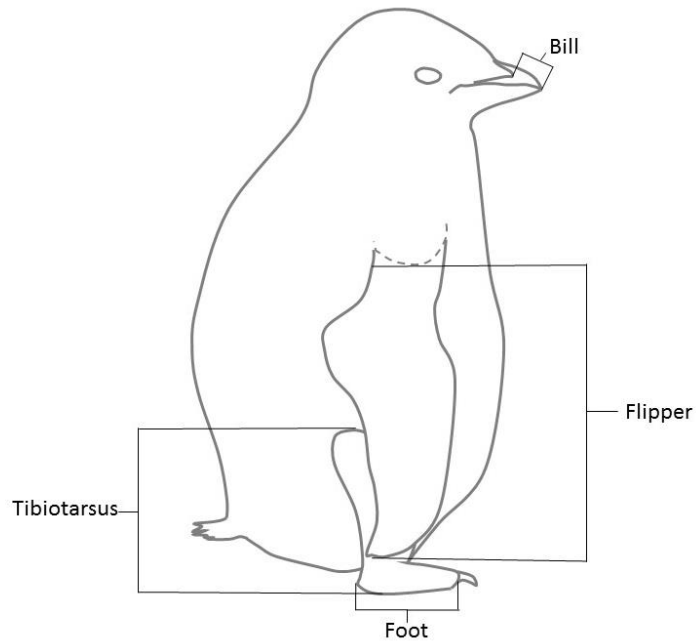


Figure 2.2 Estimated average growth rates, with 95% confidence intervals for mass, and length of bill, flipper and tibiotarsus for male and female Adélie Penguin chicks during the Austral summers of 2012-13 (2012) and 2013-14 (2013) on Ross Island, Antarctica. Estimates include mean values for other important variables in best model for each measurement (see text for details). Note different units and scales for y axes. Foot growth is not shown due to lack of support for an effect of sex.

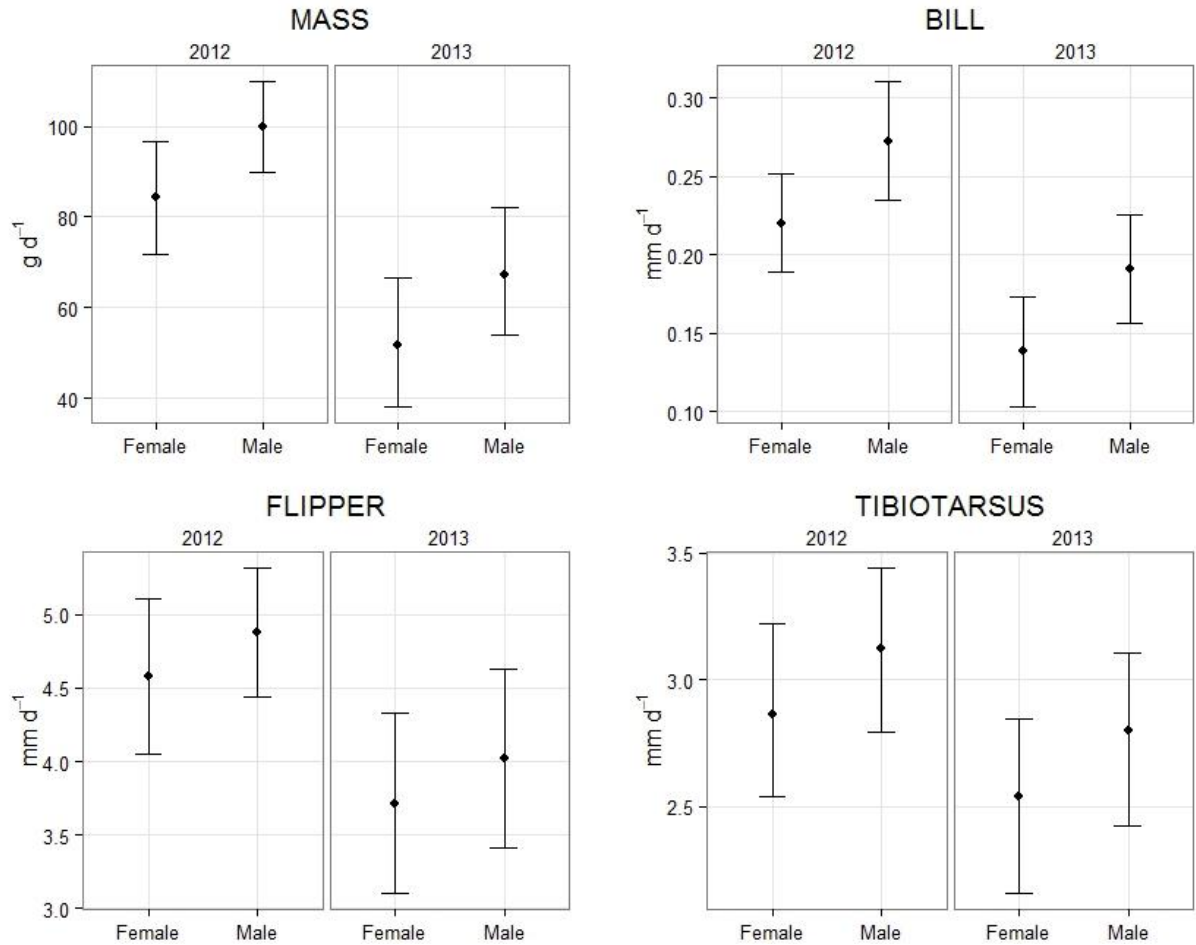
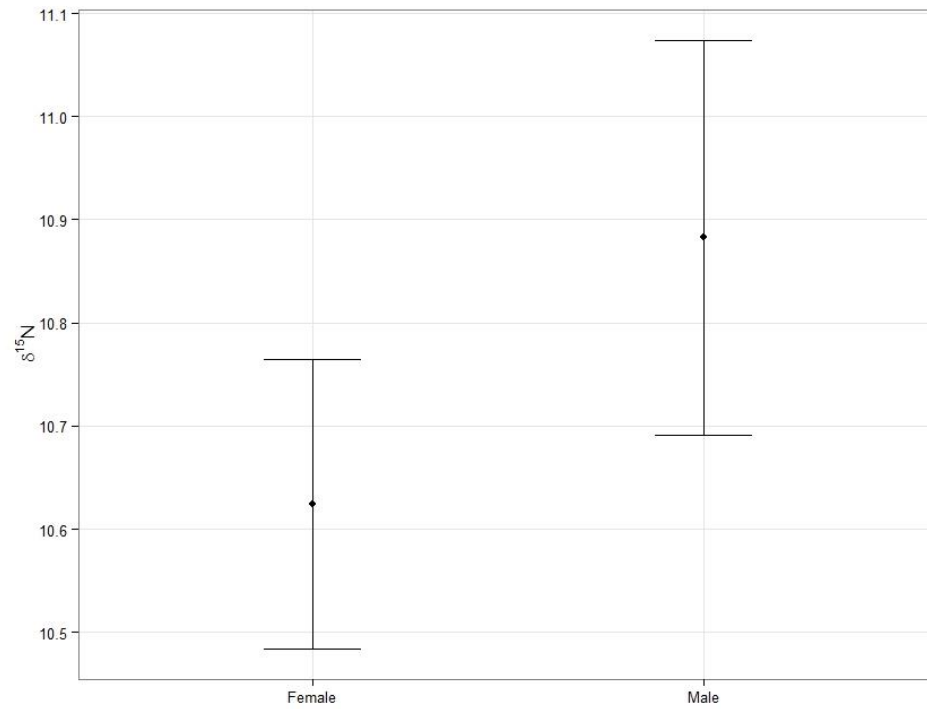


Figure 2.3 Estimated mean values for  $\delta^{15}\text{N}$ , and 95% confidence intervals, for male and female Adélie Penguin chicks during the Austral summers of 2012-13 and 2013-14 on Ross Island, Antarctica.  $\delta^{15}\text{N}$  is a proxy for the proportion of fish in the diet; see Chapter 3 for details.





## Chapter 3

# THE INFLUENCE OF DIET, ADULT AGE AND PROVISIONING BEHAVIOR ON CHICK GROWTH IN ADÉLIE PENGUINS

Scott Jennings

## ABSTRACT

During the offspring provisioning period, individual animals must make trade-offs in how they allocate time, energy, and other resources to maximize their reproductive success. Often, behaviors which increase offspring condition come at a cost to parent condition. Understanding how these trade-offs influence juvenile growth is important for building our knowledge of the factors limiting this important life stage. I investigated the relationships between provisioning and chick growth of Adélie Penguins nesting at a very large, high latitude colony, where competition for food is thought to limit chick growth and colony size through density-dependent processes. I measured three aspects of provisioning, which previous research indicated represent variation in costs to parents: average food delivered per day, type of prey delivered, and the frequency of food delivery. I measured mass and skeletal growth for the duration of the chick-rearing period during two seasons, the first of which was normal in terms of chick growth and reproductive success, but the second of which was characterized by apparent food limitation, slow chick growth and poor reproductive success at the colony scale. Growth of male chicks was more sensitive to variation in provisioning, but only during the apparent food-limited year. Mass growth appeared to be more sensitive to variation in the quality of prey (higher lipid), while skeletal growth appeared to be more sensitive to variation in average daily food delivered. There was no evidence for a relationship between parent age and chick growth rates. These results suggest that variation in parental investment strategies may have a stronger influence on chick growth in times of apparent resource limitation, and that this influence may not be the same for male and female offspring. The observed variation in growth rates between males and females was large enough to lead to size differences that may have important implications for recruitment. These results will improve our understanding of how population processes respond to changing environmental conditions.

## INTRODUCTION

The period of juvenile growth is an important life stage with implications for survival and fitness later in life (Le Galliard et al. 2005). Parental investment is the extent to which the behaviors of a parent benefit a single offspring at the expense of the parent's residual reproductive output (Clutton-Brock 1991). During juvenile growth, the extent and quality of parental care can modulate the effects of environmental variability on offspring condition and quality, but often at a cost to parents. Factors such as food availability, predation pressure, and weather variability affect energy expenditure by provisioning parents, providing a mechanism for trade-offs between parent and offspring condition (Stearns 1989). The ability of individual parents to navigate these trade-offs can have a strong impact on juvenile growth, and provides the basis for variation in individual fitness of parents.

Parental investment may vary in one or more of several components, including offspring defense, amount and type of food delivered, or the degree to which investment is divided between siblings. This variation can be dependent on factors intrinsic (e.g., parent condition or age; offspring needs) or extrinsic (e.g., environmental conditions, predation pressure, competition) to the parents and offspring (Erikstad et al. 1997, Bårdsen et al. 2011). For instance, younger parents may be more likely to maintain their own condition for future reproductive efforts than older parents, or a reduction in resources may alter the way in which provisioned food is divided among sibling offspring (Clutton-Brock 1991, Daunt et al. 2001, Bunce et al. 2005). In addition, the interactions between intrinsic and extrinsic factors can further complicate trade-offs in parental investment. Theory suggests that parents in better condition, or with greater access to resources, should invest more in offspring of the sex which would benefit most from that marginal increase in resources (Trivers and Willard 1973). For example, in many vertebrate species parents invest more in female offspring in times of resource limitation, because males raised under poor conditions (resulting in poorer quality adults) may be less able to compete for mates, and thereby miss breeding opportunities; whereas even females raised under poor conditions may almost always reproduce (e.g., Red Deer [*Cervis elaphus*], Clutton-Brock et al. 1981; Rhesus Monkeys [*Macaca mulatta*], Berman

1988; Blue-footed Booby [*Sula nebouxii*], Velando 2002). However, in other species these relationships may not exist or may be reversed (Pronghorn Antelope [*Antilocapra americana*], Byers and Moodie 1990; Western Bluebirds [*Sialia mexicana*], Leonard et al. 1994). Thus, while the Trivers-Willard hypothesis remains a valuable starting point for investigations of parental care, variation in parental investment is complex and likely varies across species, as well as among individuals within species. Seabirds serve as informative model organisms for studying the impacts of variation in parental investment because, as central-place foragers during the breeding season, many of these species face unique ecological constraints which can limit demographic processes (Ashmole 1971). Coincidentally, central place foraging also facilitates the relatively efficient collection of data on reproductive behavior of a large number of individuals that are facing the same environmental conditions.

Recent observational and experimental work has indicated substantial variability in seabird parental investment (Weimerskirch et al. 1997, Tveraa et al. 1998a, Phillips and Croxall 2003). As food resources fluctuate, parent seabirds may make adjustments in the energy allocated to rearing chicks; they can either expend more energy to maintain chick growth and (possibly) sacrifice their own condition, or they can keep energy expenditure the same and maintain their own condition, but sacrifice chick growth, and perhaps chick survival (Kitaysky et al. 2000). For seabirds in general, the amount of food delivered per unit time decreases as foraging trip duration increases, because parents utilize more of the resources acquired for their own maintenance during longer trips (Weimerskirch et al. 1994, Granadiero et al. 1998). In some species this pattern is so pronounced that parents undertake a bimodal foraging strategy: on short foraging trips parents sacrifice their own condition to provide food at a more rapid rate to their chicks, whereas on long foraging trips parents regain their own condition, but the amount of food delivered to chicks per day declines (e.g., Granadeiro et al. 1998, Tveraa et al. 1998b, Weimerskirch et al. 2003). However, there is substantial variability in the degree to which parent condition, offspring condition, and environmental conditions may influence the amount of parental care provided by adults, both within and between species (Weimerskirch et al. 1995, Tveraa et al. 1998b, Waugh et al. 2000).

Understanding the relationships between variation in parental investment and offspring growth can inform our understanding of the proximate and ultimate drivers of variation in investment trade-offs. We investigated these relationships in a high-latitude population of Adélie Penguins (*Pygoscelis adeliae*). For this population in particular, there exists a relatively simple set of factors among which trade-offs in parent investment must be made. Additionally rapid offspring growth must be maintained in order for chicks to fledge before the onset of winter. Adélie Penguins deliver food loads ranging from 200-1,200 g collected on foraging trips lasting 1-3 days, and parents generally sacrifice their own condition (i.e. lose more mass) to deliver more food to chicks at a faster rate (Clarke et al. 2002, Ballard et al. 2010). Adults display a pattern of declining amounts of food delivered per unit time with increasing trip length, and a bimodal foraging strategy has been observed in some, but not all studies (Watanuki et al. 2002, Ballard et al. 2010).

The diet of adults and chicks of this population during the chick-provisioning period has only 2 main components: Crystal Krill (*Euphausia crystalorophia*) and Antarctic Silverfish (*Pleurogramma antarcticum*; Ainley et al. 1998, Polito et al. 2002). Silverfish has a higher lipid content than krill, and Adélie Penguins may preferentially choose higher lipid foods (Chapman et al. 2010), which can be important for chick growth (Ainley et al. 2003). Despite the demonstrated benefits of higher-lipid diet to chick growth, the continued importance of krill to Adélie Penguin population dynamics (Trivelpiece et al. 2011, Kohut et al. 2014) suggests a potentially higher parental cost associated with provisioning chicks with predominantly fish. Differences in relative abundance (Ainley et al. 2006, Smith et al. 2007), predator-avoidance capabilities (O'Brien 1987), and density of aggregations (O'Brien 1987, Fuiman et al. 2002) between krill and fish may all contribute to the relative efficiency at which penguins can acquire a sufficient biomass of each prey type to maintain chick growth. It is also possible that Silverfish use ocean habitats in a temporal or spatial way that make penguins preying on them more accessible to larger predators (i.e., leopard seals [*Hydrurga leptonyx*], orca [*Orcinus orca*]), thereby increasing predation risk for adults who feed chicks primarily fish.

The goals of this study were to investigate the relationships between chick growth rate and parental investment in Adélie Penguins, and to test the relative importance of different aspects of provisioning behavior in predicting chick growth rates. I considered 3 aspects of chick provisioning to represent tradeoffs between costs to parents and benefits to chicks: 1) the proportion of fish in the diet provisioned to chicks (more fish in the diet represents higher parental investment in reproduction); 2) the total amount of food delivered to chicks (increased food delivery represents increased parental investment); and 3) the length of foraging trips (shorter feeding intervals represents greater parental investment). For each question I predicted that a greater investment would be correlated with more rapid chick growth: 1) the proportion of fish in the diet would positively relate to chick growth rates; 2) longer feeding intervals (measured by foraging trip duration) would be correlated with slower chick growth rates; and 3) increased amounts of food delivered daily to chicks would be positively correlated with chick growth rates. I also evaluated whether older parents might invest more heavily in their offspring by testing a fourth prediction: 4) that there is a positive relationship between chick growth rates and parent age.

## METHODS

The Adélie Penguin is an ice-obligate species, existing only where sea ice is present for most of the year and breeding in coastal colonies throughout the Antarctic continent and sub-Antarctic islands north to 57° S latitude (Ainley 2002). Parents lay one or, more commonly, two eggs and regularly raise both chicks at least to crèching (Ainley 2002). Incubation lasts 33 days, and after hatching the chicks are guarded by at least one parent for the first 2-3 weeks. Thereafter both parents forage simultaneously to meet the increased demands of the chicks. At this point the chicks enter the crèche stage, with the chicks from several adjacent nests gathering into a single group for protection from the elements and predation (the “crèche”). Chicks are fed for approximately 55 days from hatch, before they fledge from the colony.

I collected data during the Austral summers of 2012-13 and 2013-14 (hereafter referred to as “2012” and “2013” reflecting the calendar year at the start of the season) at Cape Crozier, Ross Island, Antarctica, the largest colony in a 4-colony meta-population

located on or adjacent to Ross Island. My research was part of a larger effort to investigate Adélie Penguin reproductive ecology and meta-population demographics (more info at [www.penguinscience.com](http://www.penguinscience.com)). The larger, long-term study featured a population of individually-marked, known-age and known-breeding-history individuals at multiple colonies and I collected data on some of these birds at Cape Crozier during 2013. Additionally, some parts of the long-term study include the operation of a penguin weighbridge at Cape Crozier to estimate food delivery by parents to nests (more detail below). The weighbridge does not include any known-age individuals, and thus “known-age” (KA) and “weighbridge” (WB) represent two different populations of parent penguins, about which different information is known and collected. The chicks used in this study were associated with nests that were selected during early- to mid-incubation and monitored throughout the breeding season. These nests were selected systematically from both parent populations to represent a range of parental (i.e., age, breeding quality; KA subset only) and nest site (interior or edge of subcolonies) characteristics.

#### *Morphological measurements*

I monitored nests every 1-3 d during incubation to determine hatching day for all eggs present in the nest. At 10 d post-hatching for the first-hatched chick I began to collect morphological measurements and individually marked each chick with a T-bar fish tag (Floy Tags Inc., USA). If present, the second-hatched chick was also measured and tagged on this day to reduce disturbance to the nest caused by returning only one or two days later. I collected several morphological measurements including: mass, measured to the nearest 25 g using a spring scale; bill length (hundredth of a mm), measured with digital calipers from the most distal extent of skin on the side of the upper mandible to the tip of the bill; flipper length (mm), measured from the distal edge of the humeral head, to the tip of the flipper; foot length (mm), measured to the end of the longest (middle) toe excluding the toenail, with the tibiotarsus-tarsometatarsus joint pressed against the stop of a flush stop ruler; tibiotarsus length (mm), measured with the leg held in a natural position, with the femur-tibiotarsus joint held against the stop of a flush stop ruler, and measured to the sole of the foot (Figure 3.1). I collected this range of morphological measurements because I believed there may be different relationships

between the explanatory variables of interest and growth rates of different morphological features (e.g., mass vs. skeletal growth). Thereafter, I repeated morphological measurements on 5-d intervals for the remainder of the 50-55 d chick rearing period, and fish tags were removed at the end of the monitoring period (>50d).

### *Penguin weighbridge*

To measure variability in average food delivered and average foraging trip length between nests, I utilized a penguin weighbridge which is operated as part of ongoing long-term research at Cape Crozier. A fence surrounding a sub-colony of approximately 200 nests funneled penguin movement over a weight scale coupled with a direction sensor and Radio Frequency Identification (RFID) antenna which detected Passively Interrogated Tags (PIT) implanted in adult birds (for full weighbridge design and usage see: Ballard et al. 2001, 2010). The weighbridge was operated from early egg-laying (early November) through the majority of chick-rearing period (late January). I identified nests with at least one PIT tagged parent (using a handheld PIT tag reader) during the laying period for inclusion in my study.

The weighbridge automatically recorded the identity, direction of travel, mass (kg), date, and time for each PIT tagged individual crossing the scale and triggering the PIT tag reader. I assumed no parental digestion of stomach contents during the relatively short visits (~50%<1 day; 16%<2 days) to the nest (Clarke et al. 2002); thus, the amount of food delivered to the nest was calculated as the difference in parent mass between an incoming trip and the subsequent outgoing trip (Ballard et al. 2001). Because I lacked a method to estimate distribution of food between siblings, I assumed it was evenly distributed between chicks. This assumption was consistent with previous observations of equal division of food loads amongst siblings in Adélie Penguins except in circumstances of resource limitation (Spurr 1975, Lishman 1985). I calculated daily provisioning rate to each chick (FOOD) as total food delivered to the nest divided by the duration of the foraging trip (to the nearest tenth of a day) and the number of chicks present in the nest at the time of the incoming crossing. I averaged foraging trip duration (FTD) across the entire season for each nest, thus FTD values are equal for siblings. If both adults from a



nest were PIT tagged, I combined their trip lengths to obtain a single, average FTD for the nest.

### *Feather collection*

Stable isotope values from feather material can provide information on diet within ~2 weeks prior to, and during, feather growth (Bearhop et al. 2010). Adélie Penguin chicks have three separate feather generations during the period of parental care (Taylor 1962). I collected samples from the second, thicker downy plumage (grown at 12-17 days) and the juvenile plumage (replaced at 25-35 days and similar in structure and color to adult feathers), which represent diet provided to the chicks during the provisioning period. Five to 10 feathers (depending on feather size/plumage generation) were collected from the cleft between the abdomen and leg on each chick. The ratio of  $^{15}\text{N}$  to  $^{14}\text{N}$  nitrogen isotopes in these feathers, relative to that in a standard sample ( $\delta^{15}\text{N}$ ; units as a proportion: ‰), was determined using a PDZ Europa ANCA-GSL elemental analyzer and a PDZ Europa 20-20 isotope ratio mass spectrometer (analysis conducted by the Stable Isotope Facility, UC Davis, USA). I focused on  $\delta^{15}\text{N}$  because previous work has shown distinct differences in  $\delta^{15}\text{N}$  values between fish and krill in this part of the southern ocean (Burns et al. 1998, Hodum and Hobson 2000), and a relationship between  $\delta^{15}\text{N}$  and the proportion of fish in the diet has been detected at the colony scale on Ross Island (Ainley et al. 2003). A subset of feathers from each chick was used to determine sex by molecular means (Griffeths et al. 1998; Jennngs 2015, Chapter 2).

### *Analysis*

Using only data collected during the linear growth phase (a time span specific to each morphological measurement; Table 3.1), I fit linear models to the repeated measurements of each morphological measurement over time, for each chick. The linear phase of growth for each measurement was identified via comparison of  $R^2$  values and visual inspection of lines fit by linear model to the measurement data at incrementally-increasing age intervals. Within each morphological measurement, the duration of the period of linear growth was similar between individuals. The slope coefficient from each model was taken as the daily growth rate for each measurement for each chick.

I then used linear mixed effects models to explore the relationships between daily growth rate and the explanatory variables of interest (Table 3.2). The analysis was conducted in three iterations based on the three subsets of the data, which had different types of information available to address my questions of interest. In the first iteration, because I had isotope values from chicks in both the KA and WB parent groups, data for all chicks combined were used to evaluate the relationships between growth rate and  $\delta^{15}\text{N}$ . Next I used the Weighbridge (WB) subset of data to evaluate the relationships between growth rates and FOOD, FTD, and  $\delta^{15}\text{N}$ . Finally, I used the Known-Age (KA) data subset to evaluate the relationships between chick growth and parent age (PA) and  $\delta^{15}\text{N}$ . In all 3 iterations I also considered the effect of chick Sex, Year (KA subset excluded because I only collected data during 2013 for this group), Hatching order, and Brood size. I also checked for correlation between any continuous covariates which might be included together in the same model.

Development of the candidate model sets was informed by the predictions being tested, field observations, and a previous analysis focused on variation in growth rates between the sexes (Jennings 2015; Chapter 2). I considered all combinations of additive effects to test the importance of variables both singly and relative to each other, and also fit models with some year- and sex-based interactions which I hypothesized might be important. I included chick Sex and Year as fixed effects, and included Nest and Hatching order as random effects to account for lack of independence between chicks from the same nest, or with the same hatching order. Because of limitations in overall sample size and number of observations within each level of the nest variable, I restricted analysis of random effects to estimation of variation in the intercept only.

I fit models using Maximum Likelihood Estimation to evaluate fixed effects, and compared AIC values corrected for small sample size (AICc) to select the model with the best combination of additive main effects and interactions (Burnam and Anderson 2002). Mixed effects models were the starting point for this part of the analysis. However, if the variance for a particular random effect was estimated as zero, or very small relative to the residual variance, then the random effect was removed and the model was rerun using Restricted Maximum Likelihood (REML) to verify the lack of variation attributable to

the random effect, before proceeding with the model selection process. For growth of each morphological character, random effects not supported in the analysis of all data combined were excluded from analysis of the WB and KA data subsets.

I used  $R^2$  values to evaluate the explanatory power of linear models with fixed effects only. For the mixed effects models I used a variance component analysis where the total process variance was estimated as the total residual variance from the intercept-only model using REML. The estimated residual variance from the best model (using REML) reflected the amount of unexplained process variance unaccounted for by the model covariates. Thus, the percent of the total process variance explained by covariates in the best model was estimated using the following equation (Olson et al. 2004):

$$((\text{Resid. Var}_{\text{intercept only}} - \text{Resid. Var}_{\text{best model}}) / \text{Resid. Var}_{\text{intercept only}}) * 100$$

To determine the relative importance of variables in the best model, I evaluated the magnitude and sign of the model coefficients, along with the degree to which 95% confidence intervals for these coefficients overlapped zero. To aid interpretation of the effect of explanatory variables which were of direct interest to my predictions, I also plotted estimated growth rates for each year and each sex across values representing the observed range for these variables, while holding the other variables in that model at their mean values. To aid interpretation of model results, I also summarized variability (means  $\pm$  sd) in average FOOD, average FTD, and  $\delta^{15}\text{N}$  by Year, Parent age and chick Sex. All analysis was conducted in R version 3.1.1 (R Core Team 2014) and the lme4 package (Bates et al. 2014).

## RESULTS

### *Data summary*

I measured growth of 34 chicks in 2012 and 43 chicks in 2013, including 42 chicks in the Weighbridge subset (WB) across both years, and 35 in the Known-Age subset in the 2013 (KA; Table 3.2). I observed slower overall chick growth rates (Figs 3.2-4), and fewer 2-chick broods, during the 2013 season (% broods with 2 chicks: 2012=83%; 2013=44%) for the nests I monitored in this study.

There was no difference in  $\delta^{15}\text{N}$  values between the 2 years ( $10.7 \pm 0.4$  and  $10.8 \pm 0.4$  ‰; two sample t-test, two-sided p-value= 0.28), but average trip lengths (FTD) were longer in the 2013 ( $31.3 \pm 9.4$  vs.  $47.8 \pm 16.6$  hrs; two sample t-test, two-sided p-value=0.03). Although the average food delivered per day (FOOD) was statistically different between the 2 years (2012:  $160.5 \pm 96.7$  vs. 2013:  $257.3 \pm 139.6$  g d<sup>-1</sup>; two sample t-test, two-sided p-value= 0.01), this significance was driven by a large number of small values in 2012. Only a single particularly large (but still biologically-reasonable) value in 2013 was outside the range of values from 2012. I chose  $r \geq 0.60$  as the correlation threshold precluding inclusion of two variables in the same model and none of the correlations between continuous covariates were deemed great enough to preclude inclusion of both covariates in the same model (Table 3.4). A separate analysis identified relative hatch date (calculated separately for each year of the study) as an important factor explaining variation in the age at which chicks entered the crèche stage (Jennings 2015, Chapter 4). Thus while hatch day was not included in the analysis of growth rates described below, an *a posteriori* evaluation of these relationships revealed no correlation between relative hatch date and any of the 5 growth rates (Table 3.1). In all analyses the categorical covariates were coded as Sex: Male=1 and Year: 2013 =1.

#### *All chicks*

I used data from all chicks together to evaluate the relationship between growth rate and  $\delta^{15}\text{N}$  value, with  $\delta^{15}\text{N}$  serving as a proxy for the fish to krill ratio in the diet. Higher values of  $\delta^{15}\text{N}$  suggest more fish in the diet. The best-supported model for mass growth contained the 3-way interaction between Sex, Year, and  $\delta^{15}\text{N}$  for the fixed effects component of the model, and random effects for nest and hatching order (Table 3.5). This model explained 19.3% of the observed process variation in mass growth rates. The coefficient in this model for the effect of  $\delta^{15}\text{N}$  was positive and the 95% confidence interval overlapped zero only slightly, indicating at least weak support for the hypothesis that more fish in the diet resulted in increased growth rates (Table 3.6). Thus, there was some evidence that for females in 2012, an increase of 1 ‰ in  $\delta^{15}\text{N}$  was associated with a 24.3 g d<sup>-1</sup> increase in mass growth rate. However, there was stronger evidence for such a relationship for males in the second year. The coefficient for the 3-way Year:Sex: $\delta^{15}\text{N}$

interaction was large, positive and with 95% CI's that did not overlap zero, indicating higher growth for males in 2013 when there was more fish in the diet (higher values of  $\delta^{15}\text{N}$ ), but no such effect for females (Table 3.6). Thus, the estimated mass growth rates in the second year were slower for males than females only at very low values of  $\delta^{15}\text{N}$ , and during 2013 an increase of 1 ‰ in  $\delta^{15}\text{N}$  was associated with an increase in male mass growth rate of 59.3 g d<sup>-1</sup>. These results suggest that male growth in the second year was more sensitive to variation in  $\delta^{15}\text{N}$  than was female growth during that year or growth of both sexes in the first year (Figure 3.2).

The best-supported models for growth rates of flipper and tibiotarsus also contained the 3-way interaction between Sex, Year, and  $\delta^{15}\text{N}$  for the fixed effects component, but had a random effect for nest only (Table 3.5). The flipper and tibiotarsus models explained 25.6% and 12.0% of the observed variation in these growth rates, respectively. The coefficients in these models showed similar general patterns to those in the model of mass growth. Thus, only for male chicks during year 2 was there strong evidence for an effect of  $\delta^{15}\text{N}$  on growth, where a 1 ‰ increase in  $\delta^{15}\text{N}$  was associated with an increase in flipper and tibiotarsus growth rates of 2.45 mm d<sup>-1</sup> and 0.80 mm d<sup>-1</sup>, respectively.

For bill growth, the best-supported model contained fixed effect structure only, but still contained the 3-way interaction of year, sex and  $\delta^{15}\text{N}$  (Table 3.5). This model explained 39.3% of the observed variation in bill growth rates. In this model, the direction of effects were similar to those for the other growth rates, but all 95% confidence intervals overlapped zero, including the 3-way interaction (Table 3.6). Thus there was only weak evidence for the effect of an interaction between Year, Sex, and  $\delta^{15}\text{N}$  on bill growth rates (Figure 3.2). This is confirmed by the competitive model ( $\Delta\text{AICc}=1.6$ ) with interactions between Year and Sex, and the additive effects of  $\delta^{15}\text{N}$ . In this competitive model the Sex and Sex:Year covariates had 95% Confidence intervals excluding zero, but the confidence intervals for the  $\delta^{15}\text{N}$  coefficient include zero, suggesting  $\delta^{15}\text{N}$  was less important than Year and Sex in predicting bill growth.

Finally, for foot growth, the best supported model contained only the fixed effect for  $\delta^{15}\text{N}$  and the random effect for nest. This model explained only 4.9% of the observed variation in foot growth, and although the  $\delta^{15}\text{N}$  coefficient was positive, 95% confidence intervals strongly overlapped zero, thus  $\delta^{15}\text{N}$  only explained a very small amount of the variation in foot growth rates.

#### *WB subset*

Growth measurements for the Weighbridge (WB) subset of the data were used to evaluate the importance of average food delivered per day (FOOD) and average foraging trip duration (FTD), relative to  $\delta^{15}\text{N}$ , in predicting chick growth rates. This data subset included data from both years of the study. WB-specific variables (FOOD and FTD) were included in the best-supported model for growth of flipper, tibiotarsus, and foot (Table 3.5). For these 3 morphometric measurements, the best-supported model included the additive effects of Sex,  $\delta^{15}\text{N}$ , and FTD and the Year:FOOD interaction. There was no support for random effects of nest or hatching order for these 3 morphometric measurements, so these best-supported models included fixed effects only. There was no support for the importance of FOOD or FTD in predicting growth of mass or bill length (Table 3.5).

For flipper growth, the model coefficients for the main effects of both FOOD and FTD were slightly negative with 95% confidence intervals broadly overlapping zero, but the coefficient for the Year:FOOD interaction was positive (recall categorical covariate coding: 2013=1) and 95% confidence interval did not overlap zero (Table 3.6). In addition, this best model for flipper growth explained 43.3% of the observed variation in the data. Thus there was strong evidence for a positive effect of FOOD on flipper growth during 2013 only, where an increase in FOOD of  $10 \text{ g d}^{-1}$  was associated with an increase in flipper growth rate of  $0.06 \text{ mm d}^{-1}$  (Figure 3.3).

The best models for tibiotarsus and foot growth explained 39.1% and 45.8% of the observed variation in the data, respectively. In general the patterns in model coefficients for the best-supported models for tibiotarsus and foot growth were similar to those in the best flipper growth model (Table 3.5). The coefficients for the Year:FOOD

interaction in the best tibiotarsus and foot models were positive, and 95% confidence intervals did not overlap zero. Thus more FOOD was associated with increased growth of tibiotarsus and foot lengths in 2013 only, where an increase in FOOD of  $10 \text{ g d}^{-1}$  was associated with an increase in tibiotarsus and foot growth rates of  $0.04 \text{ mm d}^{-1}$  and  $0.03 \text{ mm d}^{-1}$ , respectively (Figure 3.3).

#### *KA subset*

Growth measurements for chicks in the Known-Age (KA) subset of the data were used to evaluate the importance of Parent Age, relative to  $\delta^{15}\text{N}$ , in predicting chick growth rates. It is important to recall that this subset only included data from 2013 (second year of the study). Parent Age was only supported as an important variable in predicting flipper growth rates, and was not included in top models for growth of any of the other morphological measurements. The best-supported model for flipper growth rates contained a random effect for nest and fixed effects for the interaction between sex and  $\delta^{15}\text{N}$ , and the additive effect of parent age (Table 3.5). The effect of parent age on flipper growth was negative, contrary to predictions, and the 95% confidence interval overlapped zero, suggesting there was only a weak effect of parent age on flipper growth rates (Table 3.6). It is of note that the estimated relationships between male and female growth rates and  $\delta^{15}\text{N}$  were the same for this data subset as they were when data from all chicks was considered. This is perhaps not surprising, because there were fewer WB than KA chicks during the second year of the study, and thus the patterns in the all-chicks data would be expected to closely match those in the KA subset. For mass, tibiotarsus and bill growth, the best-supported models contained only the Sex: $\delta^{15}\text{N}$ , and for foot growth the intercept-only model was best-supported (Table 3.5).

## DISCUSSION

This study supported the predicted positive correlation between growth rates and the proportion of fish in chick diets, but this correlation was conditional on chick sex and year of the study, such that a higher-fish diet appeared most important for males during 2013. Similarly, I found some support for the predicted positive correlation between growth rate and average food delivered per day, but again only in the second year of the

study, and only for the 3 measures of skeletal growth (flipper, tibiotarsus, and foot). There was no support for a relationship between average daily food delivered and growth of mass or bill length, and only weak evidence of a small negative relationship between average foraging trip duration and flipper, tibiotarsus and foot growth rates. Finally, I found limited support for a correlation between growth rates and parent age, but this weak relationship suggested chicks from younger parents grew at a faster rate than chicks from older parents, contrary to predictions.

The relationships observed between provisioning growth rates and Sex,  $\delta^{15}\text{N}$ , FOOD, and FTD are likely to be relevant to the survival and fitness of Adélie Penguin parents and chicks, at least during some years. A difference in fledging weight of only 117 g was shown to influence the likelihood of recruitment back into the breeding population (Chapman et al. 2011). Differences in skeletal size at fledging may also have implications for individual survival and fitness later in life, but thus far these relationships have only been evaluated for mass at fledging. The differences observed here in estimated daily growth rates of chicks that were provisioned differently (less often or with less food, or with proportionally greater fish) are great enough to achieve such differences in fledging mass. Thus, these results identified a possible mechanism for variation in parent fitness based on parental foraging ability. Additionally, observed differences in growth rates between sexes and years could possibly lead to cohort- or sex-based differences in survival or other measures of fitness, and there is some evidence of higher survival in adult males than females in this population (Dugger et al. 2006). The observed variation in provisioning rate (FTD) and the amount of food delivered (FOOD) is likely to also have important implications for the ecology of breeding Adélie penguins. Previous research at Cape Crozier has shown that the range of values in FOOD and FTD observed here are of a magnitude which can have implications for the maintenance of parent condition throughout the breeding season (i.e. upper values for both variables observed here were shown to be associated with loss of parent mass, while lower were associated with mass gain; Ballard et al. 2010). Additionally, a comparison of observed diet and  $\delta^{15}\text{N}$  values at the colony scale revealed that a 1‰ increase in  $\delta^{15}\text{N}$  corresponded to an approximate 10% increase in the proportion of diet comprised of fish (Ainley et al. 2003). While no data exist to directly compare the relative costs to parents



of provisioning with krill vs. fish, this difference in proportion of fish may be costly to parents, particularly at this very large colony where inter- and intraspecific competition for food is thought to be an important limitation to demographic processes (Ainley et al. 2004, 2006).

Data do not exist to adequately evaluate prey availability in the Southern Ross Sea during the time of this study, but the data collected for this study and other observations suggest there was some challenge to parents' ability to provision their young during the second year of this study. Overall chick growth rates were slower (Jennings 2015; Chapter 2) and there were more single-chick broods during 2013. Additionally during 2013, a colony-wide estimate of the number of chicks crèched per active nest was substantially lower than during 2012, and was also below the average for the previous 7 years (2013=0.85 chicks per nest; 2012= 0.94; 7-year mean=1.05; Ballard and Ainley unpublished data). Finally, while chicks that are weakened by starvation are generally depredated by Skua (*Stercorarius* spp.) before they actually die of starvation (Ainley 2002), in 2013 I observed a large number of chicks dying prior to skua attack- presumably due to starvation or disease. Thus it appears that there was colony-wide food limitation in the second year of this study. There were approximately 8% more occupied nests during incubation in 2013 than in 2012 (Ballard and Ainley, unpublished data), so another possibility is that interspecific competition for food was more severe during the second year. However, during the 2014-15 breeding season, colony size increased another 3% over the 2013 population, but the number of chicks crèched per nest was 1.07, near the average value, thus further supporting some limit to food availability in 2013. The average food delivered during 2013 was actually greater than in 2012, and, while foraging trips were longer during 2013 (average duration: 2012 = 31.3; 2013 = 47.8), they were not substantially longer than is generally thought to be sufficient to maintain chick growth (~1-2 days; Clarke et al. 2002, Ballard et al. 2010). Thus, while 2013 may have been characterized by challenging foraging conditions (either environmental or competition-based), conditions were apparently still within the range of variability to which this species is adapted. It is also interesting to note that there were greater amounts of food delivered to chicks during 2013, despite longer FTD, which is in contrast to the pattern often observed in seabirds (Granadeiro et al. 1998, Ropert-Coudert

2004, Ballard et al. 2010). Thus it seems that the parents in my sample who were able to breed during 2013 compensated for reduced food-availability by making longer foraging trips, a possible reflection of variation in individual quality. Previous research has suggested that during challenging environmental conditions it is higher quality adults, with greater foraging efficiency, that are able to breed successfully (Lescroël et al. 2009, 2010)

I showed that different aspects of growth may be better predicted by different aspects of provisioning, and these relationships may be different for males and females. For the three skeletal measures, average food delivered per day was more important than the proportion of the diet comprised of fish in predicting growth rates, and the proportion of fish was in turn more important than average trip length. In contrast, mass and bill length growth rates were better described by the proportion of diet comprised of fish, while food delivered per day and foraging trip duration were less important. These different relationships may have important consequences to the trade-offs parents make in provisioning male and female chicks under different environmental conditions. Male Adélie Penguin chicks in this study grew, faster than females, and males may have been provisioned with more fish than females (Jennings 2015; Chapter 2). Mass growth in this species is highly-dependent on an increase in the number and size of fat cells (Raccurt et al. 2008), and thus, it is perhaps not surprising that a lipid-rich diet was more important for mass growth only in males during the apparent food-limited year. Average FTD was longer in 2013, and thus, it may be a diet with a greater proportion of fish was required for males to maintain their faster growth rates with this greater time between individual feedings. In contrast, the average slower growth rates for females may have made their growth rates less sensitive to increased time between feedings, and less needy of a higher-lipid diet.

Growth rates have often been considered a measure of individual quality of parents or offspring. However, individual variation in growth rates may represent adaptive responses to environmental conditions, such that individuals with different growth rates may achieve equal fitness (Abrams et al. 1996). Indeed, fast growth may negatively impact a range of factors including immune response, resistance to physical

stressors, and the development of mature function in various organs (reviewed by Mangel and Stamps 2001). Additionally faster-growing individuals may be more susceptible to reductions in feeding rates, because of their greater absolute food requirements. In sexually-dimorphic species such as Adélie Penguins, different selective pressures may be operating on the growth rates of males and females, which could in turn lead to the observed sex-based differences in the relationships between growth rates and explanatory variables investigated here.

I considered relative lipid content as the only factor determining the importance of krill versus fish for chick growth. However, protein (i.e., amino acids), specific lipid types (fatty acids), or other components of chick diet may vary between these 2 prey types, and this is an area that warrants further research to fully understand the importance of diet type to chick growth. An additional factor to consider when interpreting the results presented here is that simple correlations between offspring growth and parent expenditure may be confounded by differences in quality of parents (i.e., the relationship between parental investment and benefits to offspring may vary with individual heterogeneity in parent quality; Clutton-Brock 1991). Finally, I did not directly measure cost to parents in this study, but rather estimated parental investment via variations in provisioning. However, based on previous research we believe that the variables considered here are reasonable indices for variation in parental investment.

This study increases our understanding of the relationships between provisioning and offspring growth in a long-lived seabird species. Variation in parental investment strategies appeared to have a stronger influence on chick growth in times of apparent resource limitation. Additionally, my results suggest that simultaneous optimization of both mass and skeletal growth may not be attainable, and that offspring sex may play a role in the trade-off between these optimizations. This greater understanding of the consequences for offspring growth of the interaction between parental investment and environmental variability can be particularly important for the management and conservation of species living in high latitudes or other areas with increasingly unpredictable climatic variability.

## ACKNOWLEDGMENTS

I would like to thank Libby Porzig, Annie Schmidt, Annie Pollard, Amelie Lescroël, Melanie Massaro, Arvind Varsani, Megan Elrod and Jean Pennycook for their assistance with field work, and additionally Arvind Varsani and Melanie Massaro for contributing funds, expertise and personal time for the molecular sexing. We also thank Donald Lyons and Lorenzo Ciannelli for valuable discussions that helped greatly with this research. The US Antarctic Program provided logistic support; financial support was provided by NSF grants *ANT- 0944411*. S. Jennings received additional support from Oregon State University, Fisheries and Wildlife Department (T.A.'ships, M. A. Ali Graduate Chair Award in Fisheries Biology) and Point Blue Conservation Science. All penguin chick capture, handling, and data collection methods performed during this study were approved under appropriate Antarctic Conservation Act permits from the National Science Foundation Office of Polar Programs and Oregon State University's Institutional Animal Care and Use Committee. This is Point Blue Conservation Science Contribution No. XXXX. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## REFERENCES

- Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *The American Naturalist* 147:381–395.
- Ainley, D. G. 2002. *The Adelie Penguin: bellwether of climate change*. Columbia University Press, New York, New York, USA.
- Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. *The Condor* 105:95–106.
- Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87:2080–93.
- Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adelie Penguin populations: overlap in colony-specific foraging areas. *Ecological Monographs* 74:159–178.
- Ainley, D. G., R. Wilson, and K. J. Barton. 1998. Diet and foraging effort of Adelie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology* 20:311–319.
- Ashmole, N. P. 1971. Sea bird ecology and the marine environment. *Avian Biology* 1:223–286.
- Ballard, G., D. G. Ainley, C. A. Ribic, and K. R. Barton. 2001. Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adelie Penguins. *The Condor* 103:481–490.
- Ballard, G., K. Dugger, N. Nur, and D. Ainley. 2010. Foraging strategies of Adélie Penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405:287–302.
- Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa, and A. Stien. 2011. Plastic reproductive allocation as a buffer against environmental stochasticity - linking life history and population dynamics to climate. *Oikos* 120:245–257.
- Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness. 2010. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and biochemical zoology* : PBZ 75:451–458.
- Berman, C. M. 1988. Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. *The American Naturalist* 29:913–930.

- Bunce, A., S. J. Ward, and F. I. Norman. 2005. Are age-related variations in breeding performance greatest when food availability is limited? *Journal of Zoology* 266:163–169.
- Burnam, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York.
- Burns, J. M., S. J. Trumble, M. A. Castellini, and J. W. Testa. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology* 19:272–282.
- Byers, J., and J. Moodie. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioral Ecology and Sociobiology* 26:157–164.
- Chapman, E., E. Hofmann, D. Patterson, C. Ribic, and W. Fraser. 2011. Marine and terrestrial factors affecting Adélie Penguin (*Pygoscelis adeliae*) chick growth and recruitment off the western Antarctic Peninsula. *Marine Ecology Progress Series* 436:273–289.
- Chapman, E. W., E. E. Hofmann, D. L. Patterson, and W. R. Fraser. 2010. The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie Penguin (*Pygoscelis adeliae*) chick growth: A modeling study. *Deep Sea Research Part II: Topical Studies in Oceanography* 57:543–558.
- Clarke, J., K. Kerry, L. Irvine, and B. Phillips. 2002. Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. *Polar Biology* 25:21–30.
- Clutton-Brock, T. H. 1991. The evolution of parental care. Pages 1–352. Princeton University Press, Princeton, New Jersey.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487–489.
- Daunt, F., P. Monaghan, S. Wanless, M. P. Harris, and R. Griffiths. 2001. Sons and daughters: age-specific differences in parental rearing capacities. *Functional Ecology* 15:211–216.
- Dugger, K. M., G. Ballard, D. A. Ainley, and K. J. Barton. 2006. Effects of flipper bands on foraging behavior and survival of Adélie Penguins (*Pygoscelis adeliae*). *The Auk* 123:858–869.
- Eastman, J. T. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology* 4:155–160.

- Erikstad, K. E., M. Asheim, P. Fauchald, L. Dahlhaug, T. Tveraa, and P. Dahlhaug. 1997. Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. *Behavioral Ecology and Sociobiology* 40:95–100.
- Fuiman, L. A., R. W. Davis, and T. M. Williams. 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology* 140:815–822.
- Le Galliard, J.-F., R. Ferriere, and J. Clobert. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* 111:368–376.
- Granadeiro, P., M. Nunes, N. C. Silva, and R. W. Furness. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Animal Behaviour* 56:1169–1176.
- Griffeths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. *Molecular Ecology* 7:1071–1075.
- Hodum, P. J., and K. A. Hobson. 2000. Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analyses. *Marine Ecology Progress Series* 198:273–281.
- Kitaysky, A. S., G. L. Hunt Jr, E. N. Flint, M. A. Rubega, and M. B. Decker. 2000. Resource allocation in breeding seabirds : responses to fluctuations in their food supply. *Marine Ecology Progress Series* 206:283–296.
- Kohut, J., K. Bernard, W. Fraser, M. J. Oliver, H. Statscewich, P. Winsor, and T. Miles. 2014. Studying the Impacts of Local Oceanographic Processes on Adélie Penguin Foraging Ecology. *Marine Technology Society Journal* 48:25–34.
- Leonard, M. L., K. L. Teather, A. G. Horn, W. D. Koenig, and J. L. Dickinson. 1994. Provisioning in western bluebirds is not related to offspring sex. *Behavioral Ecology* 5:455–459.
- Lewis, S., S. Wanless, D. A. Elston, M. D. Schultz, E. Mackley, M. Du Toit, J. G. Underhill, and M. P. Harris. 2006. Determinants of quality in a long-lived colonial species. *The Journal of Animal Ecology* 75:1304–12.
- Lishman, G. S. 1985. The food and feeding ecology of Adelie Penguins (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antarctica*) at Signey Island, South Orkney Islands. *The Zoological Society of London* 205:245–263.
- Mangel, M., and J. Stamps. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research* 3:583–593.

- O'Brien, D. P. 1987. Description of Escape Responses of Krill (Crustacea: Euphausiacea), with Particular Reference to Swarming Behavior and the Size and Proximity of the Predator. *Journal of Crustacean Biology* 7:449–457.
- Olson, G. S., E. M. Glenn, R. G. Anthony, E. D. Forsman, Janice A. Reid, P. J. Loschl, and W. J. Ripple. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. *The Journal of Wildlife Management* 68:1039–1053.
- Phillips, R. A., and J. P. Croxall. 2003. Control of provisioning in grey-headed albatrosses (*Thalassarche chrysostoma*): do adults respond to chick condition? *Canadian Journal of Zoology* 116:111–116.
- Polito, M., S. D. Emslie, and W. Walker. 2002. A 1000-year record of Adélie Penguin diets in the southern Ross Sea. *Antarctic Science* 14:327–332.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Raccurt, M., F. Baudimont, J. Tirard, B. Rey, E. Moureaux, A. Gélou, and C. Duchamp. 2008. Growing in Antarctica, a challenge for white adipose tissue development in Adélie penguin chicks (*Pygoscelis adeliae*). *American journal of physiology. Regulatory, integrative and comparative physiology* 295:R1671–R1679.
- Robert-Coudert, Y. 2004. Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. *Behavioral Ecology* 15:824–830.
- Smith, W. O., D. G. Ainley, and R. Cattaneo-Vietti. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:95–111.
- Spurr, E. B. 1975. Behavior of the Adélie Penguin chick. *Condor* 77:272–280.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Taylor, R. H. 1962. The Adélie Penguin (*Pygoscelis adeliae*) at Cape Royds. *Ibis* 104:176–204.
- Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences of the United States of America* 108:7625–8.
- Trivers, R. L., and D. E. Willard. 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. *Science* 179:90–92.



- Tveraa, T., B.-E. Saether, R. Aanes, and K. E. Erikstad. 1998a. Body mass and parental decisions in the Antarctic petrel (*Thalassoica antarctica*): how long should the parents guard the chick? *Behavioral Ecology and Sociobiology* 43:73–79.
- Tveraa, T., B.-E. Saether, R. Aanes, K. E. Erikstad, B.-E. Sether, R. Aanes, and K. E. Erikstad. 1998b. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology* 67:699–704.
- Velando, A. 2002. Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. *Behavioral Ecology* 13:443–449.
- Watanuki, Y., A. Kato, K. Sato, Y. Niizuma, C. A. Bost, Y. Le Maho, and Y. Naito. 2002. Parental mass change and food provisioning in Adelie penguins rearing chicks in colonies with contrasting sea-ice conditions. *Polar Biology* 25:672–681.
- Waugh, S. M., H. Weimerskirch, Y. Cherel, and P. A. Prince. 2000. Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. *The Condor* 102:804–813.
- Weimerskirch, H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten, and O. Chastel. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Ecology* 72:500–508.
- Weimerskirch, H., O. Chastel, and L. Ackerman. 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the Thinbilled prion (*Pachyptila beicheri*). *Behavioral Ecology and Sociobiology* 36:11–16.
- Weimerskirch, H., T. Mougey, and X. Hmdermeyer. 1997. Foraging and provisioning strategies of Black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8:635–643.

Table 3.1. Correlation between relative hatch day and all growth rates (added *a posteriori*), and the period of linear growth (days post-hatch) for morphological measurements collected from Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. P-value is for correlation.

	Pearson correlation coefficient	p-value	duration of linear growth
Mass	-0.49	<0.001	10-40
Flipper	-0.35	0.001	10-40
Tibiotarsus	-0.09	0.42	10-35
Foot	0.01	0.9	10-35
Bill	-0.24	0.03	10-55

Table 3.2. Names and brief description of covariates used to model Adélie Penguin chick growth at Cape Crozier, Ross Island, Antarctica.

	Variable name	Description
Fixed effects	$\delta^{15}\text{N}$	Delta $^{15}\text{N}$ Nitrogen; the ratio of $^{15}\text{N}$ to $^{14}\text{N}$ , measured in ‰. An index of proportion of diet comprised of fish.
	FOOD	Average amount of food delivered per chick per day (g); WB data subset
	FTD	Average foraging trip duration (hrs) ; WB data subset
	PA	Parent Age (years); KA data subset
	Sex	Male=1; Female=0
	Year	Austral summer of 2012=0; 2013=1
Random effects	NEST	Nest identification code; chicks from the same nest received the same ID code.
	HO	Hatching order; designates whether chick was hatched 1st or 2nd
	BSz	Brood size; designates whether chick comes from 1- or 2-chick nests

Table 3.3. Number of Adélie Penguin chicks measured for each data subset, sex, and year of the study, at Cape Crozier, Ross Island, Antarctica.

Data subset	WB		KA	
	2012	2013	2012	2013
Year	2012	2013	2012	2013
Male	17	6	na	19
Female	17	2	na	16
Total	42		35	

Table 3.4. Correlation between pairs of continuous covariates measured for Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. See Table 3.2 for covariate descriptions.

Covariate pair	Pearson correlation coefficient	p-value
PA and $\delta^{15}\text{N}$	0.16	0.37
FOOD and FTD	0.10	0.50
FTD and $\delta^{15}\text{N}$	0.26	0.09
FOOD and $\delta^{15}\text{N}$	0.55	<0.001

Table 3.5. Model selection results for growth of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, including all models accounting for 90% of the AICc weight and the intercept-only model. Results include 3 subsets of the data (All, WB, KA) and growth of 5 morphological measurements (Mass, Flipper, Tibiotarsus, Foot, Bill); see text for details. Footnotes for each set of results indicates the random effect structure included in the model set, the AICc value of the best-supported model, and an indication of the % process variance explained by best model (either  $R^2$  value for models with fixed effects only; or result of variance component analysis for mixed models). K is number of model parameters,  $\Delta$  AICc is the difference in corrected AIC values of each model from the best-supported model. AICc Wt. is the relative AICc weight for each model, and  $-2\ln L$  is negative 2 times the log-likelihood.

ALL CHICKS				
Mass growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	$-2\ln L$
Sex*Year* $\delta^{15}\text{N}$	11	0.000	0.679	690.220
Year + $\delta^{15}\text{N}$	6	3.939	0.095	707.021
$\delta^{15}\text{N}$ + Year* Sex	8	4.107	0.087	702.271
Year + $\delta^{15}\text{N}$ * Sex	8	4.710	0.065	702.874
intercept only	4	37.283	0.000	745.010
RE: NEST and HO. Best model AICc=716.282. VCA: 19.3%				
Flipper growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	$-2\ln L$
Sex *Year* $\delta^{15}\text{N}$	10	0.000	0.997	174.512
intercept only	3	20.777	0.000	212.294
RE: NEST. Best model AICc=197.846. VCA: 25.6%				
Tibiotarsus growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	$-2\ln L$
Sex *Year* $\delta^{15}\text{N}$	10	0.000	0.545	119.663
Sex + Year* $\delta^{15}\text{N}$	7	2.776	0.136	130.149
Year	4	3.745	0.084	138.186
intercept only	3	4.233	0.066	140.900
Sex + Year	5	5.174	0.041	137.325
Sex	4	5.877	0.029	140.317
Year + $\delta^{15}\text{N}$	5	6.034	0.027	138.184
RE: NEST. Best model AICc=142.996. VCA: 12.0%				
Foot growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	$-2\ln L$
$\delta^{15}\text{N}$	4	0.000	0.309	97.446
Year + $\delta^{15}\text{N}$	5	0.296	0.267	95.452
Sex + Year* $\delta^{15}\text{N}$	7	1.374	0.156	91.752
Sex + $\delta^{15}\text{N}$	5	2.245	0.101	97.401
Sex + Year + $\delta^{15}\text{N}$	6	2.626	0.083	95.427
intercept only	3	11.957	0.001	111.662
RE: NEST. Best model AICc=106.001. VCA: 5.0%				

Table 3.5. cont.

Bill growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex *Year* $\delta^{15}\text{N}$	9	0.000	0.555	-230.094
$\delta^{15}\text{N}$ + Year*Sex	6	1.601	0.249	-221.006
Year	3	4.185	0.069	-211.551
Sex + Year	4	5.067	0.044	-212.896
intercept only	2	21.913	0.000	-191.656

RE: none. Best model AICc=-209.407.  $R^2=0.39$ 

## WB SUBSET

mass growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex + Year + $\delta^{15}\text{N}$	6	0.000	0.194	374.618
Sex + $\delta^{15}\text{N}$	5	0.549	0.147	377.900
Sex + Year + $\delta^{15}\text{N}$ + FOOD	7	1.242	0.104	372.966
Sex + Year + FOOD	6	1.942	0.073	376.559
Sex + FOOD	5	2.406	0.058	379.757
Sex + Year + $\delta^{15}\text{N}$ + FTD	7	2.467	0.056	374.190
Sex	4	2.472	0.056	382.408
Sex + Year* $\delta^{15}\text{N}$ + FOOD + FTD	9	2.803	0.048	368.195
Sex + $\delta^{15}\text{N}$ + FOOD	6	2.917	0.045	377.534
Sex + $\delta^{15}\text{N}$ + FTD	6	3.231	0.039	377.849
Sex + Year + $\delta^{15}\text{N}$ + FOOD + FTD	8	3.497	0.034	372.150
Sex + Year + FOOD + FTD	7	3.625	0.032	375.348
Sex + Year	5	4.529	0.020	381.880
intercept only	3	15.821	0.000	398.207

RE: NEST. Best model AICc= 389.018. VCA: 26.9%

Flipper growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex + $\delta^{15}\text{N}$ + Year*FOOD + FTD	8	0.000	0.531	74.194
Sex + Year* $\delta^{15}\text{N}$ + FOOD + FTD	8	2.808	0.131	77.002
Sex	3	4.764	0.049	92.690
Sex + FTD	4	4.843	0.047	90.320
Sex + Year	4	5.019	0.043	90.496
Sex + $\delta^{15}\text{N}$	4	6.458	0.021	91.935
Sex*Year* $\delta^{15}\text{N}$ + FOOD + FTD	11	6.462	0.021	70.220
Sex + Year + FTD	5	6.741	0.018	89.632
Sex + FOOD	4	7.082	0.015	92.558
Sex + $\delta^{15}\text{N}$ + FTD	5	7.146	0.015	90.037
Sex + FOOD + FTD	5	7.371	0.013	90.262
intercept only	2	7.747	0.011	97.997

RE: none. Best model AICc = 94.558.  $R^2 = 0.43$

Table 3.5. cont.

Tibiotarsus growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex + $\delta^{15}\text{N}$ + Year*FOOD + FTD	8	0.000	0.449	52.919
Sex + $\delta^{15}\text{N}$	4	2.921	0.104	67.122
intercept only	2	4.737	0.042	73.712
Sex	3	5.009	0.037	71.660
$\delta^{15}\text{N}$	3	5.217	0.033	71.868
Sex + $\delta^{15}\text{N}$ + FTD	5	5.282	0.032	66.898
Sex + $\delta^{15}\text{N}$ + FOOD	5	5.351	0.031	66.966
Sex + Year + $\delta^{15}\text{N}$	5	5.417	0.030	67.032
Sex + FOOD	4	5.471	0.029	69.672
FOOD	3	6.001	0.022	72.652
FTD	3	6.499	0.017	73.150
Sex + FTD	4	6.582	0.017	70.783
Year	3	6.976	0.014	73.627
Sex + Year	4	7.101	0.013	71.302
Sex + FOOD + FTD	5	7.352	0.011	68.968
$\delta^{15}\text{N}$ + FTD	4	7.491	0.011	71.692
Year + $\delta^{15}\text{N}$	4	7.540	0.010	71.741

RE: none. Best model AICc = 73.282.  $R^2 = 0.39$ 

Foot growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex + $\delta^{15}\text{N}$ + Year*FOOD + FTD	8	0.000	0.934	20.325
intercept only	2	9.699	0.007	46.079

RE: none. Best model AICc = 40.688.  $R^2 = 0.46$ 

Bill growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
intercept only	4	0.000	0.332	-122.770
$\delta^{15}\text{N}$	5	2.267	0.107	-123.089
FOOD	5	2.428	0.098	-122.928
FTD	5	2.581	0.091	-122.775
Sex + Year* $\delta^{15}\text{N}$ + FOOD + FTD	3	4.016	0.045	-116.305
Year*Sex + $\delta^{15}\text{N}$ + FOOD + FTD	3	4.521	0.035	-115.800
Sex + $\delta^{15}\text{N}$ + Year*FOOD + FTD	4	4.622	0.033	-118.149
Sex + $\delta^{15}\text{N}$ + Year*FTD + FOOD	6	4.823	0.030	-123.266
Sex*Year* $\delta^{15}\text{N}$ + FOOD + FTD	6	4.970	0.028	-123.119
Year + $\delta^{15}\text{N}$ *Sex + FOOD + FTD	6	5.098	0.026	-122.991
Sex + Year + $\delta^{15}\text{N}$	4	5.392	0.022	-117.379
Sex + Year + $\delta^{15}\text{N}$ + FOOD + FTD	4	5.834	0.018	-116.936
Sex + Year + FOOD	2	5.917	0.017	-112.080
Sex + $\delta^{15}\text{N}$ + FOOD	4	6.673	0.012	-116.098
Year + $\delta^{15}\text{N}$ + FOOD	4	6.733	0.011	-116.038

RE: none. Best model AICc = -113.689

Table 3.5. cont.

## KA SUBSET

Mass growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex* $\delta^{15}\text{N}$	6	0.000	0.706	304.008
Sex* $\delta^{15}\text{N}$ + PA	7	2.596	0.193	303.456
Sex + $\delta^{15}\text{N}$	5	5.517	0.045	312.456
intercept only	3	8.679	0.009	320.912

RE: NEST and HO. Best model AICc= 319.008. VCA: 79.5%

Flipper growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex* $\delta^{15}\text{N}$ + PA	7	0.000	0.906	81.288
intercept only	3	8.518	0.013	101.180

RE: NEST. Best model AICc= 99.436. VCA: 32.5%

Tibiotarsus growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex* $\delta^{15}\text{N}$	6	0.000	0.795	46.304
Sex* $\delta^{15}\text{N}$ + PA	7	2.931	0.184	46.087
intercept only	3	9.272	0.008	63.801

RE: NEST. Best model AICc= 61.304. VCA: 88.5%

Foot growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
intercept only	3	0.000	0.194	49.768
$\delta^{15}\text{N}$ + PA + PA <sup>2</sup>	6	0.462	0.154	42.004
$\delta^{15}\text{N}$	4	0.543	0.148	47.752
PA + PA <sup>2</sup>	5	1.469	0.093	45.942
Sex + $\delta^{15}\text{N}$	5	2.025	0.070	46.498
Sex	4	2.059	0.069	49.268
PA	4	2.532	0.055	49.741
Sex + $\delta^{15}\text{N}$ + PA + PA <sup>2</sup>	7	2.733	0.049	41.127
Sex*PA	7	3.193	0.039	41.587
$\delta^{15}\text{N}$ + PA	5	3.266	0.038	47.739

RE: NEST. Best model AICc= 56.542

Bill growth				
model structure- fixed effects	K	$\Delta$ AICc	AICc Wt	-2lnL
Sex* $\delta^{15}\text{N}$	6	0.000	0.656	-110.129
Sex* $\delta^{15}\text{N}$ + PA	7	3.017	0.145	-110.261
intercept	3	4.989	0.054	-96.915
Sex	4	5.276	0.047	-99.187

RE: NEST. Best model AICc= -95.129. VCA: 42.1%

Table 3.6. Coefficient estimates, standard errors, and 95% CI for the best supported model explaining growth of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Growth rates were modeled for each of 5 morphological measurements and 3 data subsets (see text for details). 95% CI for mixed models (identified by bold text) were obtained by bootstrapping. Spaces are blank for covariates not included in the best-supported model for a particular data subset and morphological measurement.

	Mass				Flipper				Tibiotarsus				Foot				Bill			
	95% CI				95% CI				95% CI				95% CI				95% CI			
	Est.	SE	lwr	upr	Est.	SE	lwr	upr	Est.	SE	lwr	upr	Est.	SE	lwr	upr	Est.	SE	lwr	upr
<b>ALL CHICKS</b>																				
(Intercept)	-188.0	155.5	<b>-460.4</b>	<b>112.0</b>	3.66	5.37	<b>-6.82</b>	<b>15.86</b>	8.45	3.93	<b>0.64</b>	<b>16.07</b>	0.66	1.29	<b>-2.12</b>	<b>3.07</b>	0.34	0.43	-0.52	1.20
$\delta^{15}\text{N}$	24.3	14.7	<b>-4.2</b>	<b>50.0</b>	0.04	0.51	<b>-1.11</b>	<b>1.01</b>	-0.55	0.37	<b>-1.26</b>	<b>0.20</b>	0.05	0.12	<b>-0.18</b>	<b>0.30</b>	-0.01	0.04	-0.09	0.07
Sex	111.2	185.6	<b>-255.4</b>	<b>467.8</b>	9.03	6.38	<b>-5.23</b>	<b>20.55</b>	1.06	4.85	<b>-8.06</b>	<b>10.04</b>					0.05	0.54	-1.02	1.13
Year	321.0	223.1	<b>-99.3</b>	<b>761.6</b>	8.79	7.70	<b>-6.95</b>	<b>26.07</b>	-0.41	5.61	<b>-11.60</b>	<b>10.69</b>					0.46	0.61	-0.77	1.68
Sex:Year	-745.9	264.6	<b>-1284.4</b>	<b>-223.0</b>	-36.00	9.02	<b>-55.02</b>	<b>-15.77</b>	-14.58	6.74	<b>-28.46</b>	<b>-2.76</b>					-1.41	0.75	-2.90	0.08
Sex: $\delta^{15}\text{N}$	-8.5	17.4	<b>-41.2</b>	<b>25.7</b>	-0.79	0.60	<b>-1.88</b>	<b>0.53</b>	-0.06	0.45	<b>-0.91</b>	<b>0.80</b>					0.00	0.05	-0.10	0.10
Year: $\delta^{15}\text{N}$	-32.2	21.0	<b>-73.9</b>	<b>7.3</b>	-0.86	0.73	<b>-2.47</b>	<b>0.63</b>	0.03	0.53	<b>-1.02</b>	<b>1.09</b>					-0.05	0.06	-0.16	0.07
Sex:Year: $\delta^{15}\text{N}$	67.2	24.7	<b>18.5</b>	<b>116.9</b>	3.27	0.84	<b>1.38</b>	<b>5.06</b>	1.32	0.63	<b>0.21</b>	<b>2.62</b>					0.12	0.07	-0.02	0.26
<b>WB SUBSET</b>																				
(Intercept)	-184.7	88.2	<b>-368.9</b>	<b>2.1</b>	5.39	2.84	-0.38	11.16	6.88	2.21	2.40	11.36	2.67	1.50	-0.37	5.71	0.21	0.01	0.18	0.24
Sex	25.1	6.8	<b>11.0</b>	<b>39.3</b>	0.53	0.22	0.09	0.97	0.33	0.17	-0.01	0.67	0.11	0.11	-0.12	0.34	0.05	0.02	0.01	0.09
Year	-18.2	9.8	<b>-37.0</b>	<b>1.3</b>	-2.54	0.67	-3.90	-1.18	-1.39	0.52	-2.44	-0.33	-0.78	0.35	-1.50	-0.07	-0.06	0.02	-0.11	-0.01
$\delta^{15}\text{N}$	23.7	8.3	<b>5.8</b>	<b>40.8</b>	-0.08	0.28	-0.64	0.48	-0.35	0.21	-0.79	0.08	-0.10	0.15	-0.40	0.19				
Food					-0.002	0.001	-0.004	0.001	-0.002	0.001	-0.004	0.000	-0.002	0.001	-0.004	-0.001				
FTD					-0.004	0.009	-0.024	0.015	-0.003	0.007	-0.018	0.012	-0.006	0.005	-0.016	0.004				
Year:Food					0.008	0.002	0.004	0.013	0.006	0.002	0.003	0.009	0.005	0.001	0.002	0.007				
<b>KA SUBSET</b>																				
(Intercept)	-122.8	71.0	<b>-266.6</b>	<b>17.2</b>	-4.14	1.07	<b>-6.29</b>	<b>-2.06</b>	1.76	1.07	<b>-0.31</b>	<b>3.93</b>					1.12	0.37	<b>0.31</b>	<b>1.94</b>
Sex	-340.5	84.8	<b>-514.6</b>	<b>-165.8</b>	-21.65	1.03	<b>-23.69</b>	<b>-19.55</b>	-12.89	1.27	<b>-15.63</b>	<b>-10.39</b>					-1.74	0.45	<b>-2.75</b>	<b>-0.78</b>
$\delta^{15}\text{N}$	16.4	6.7	<b>3.2</b>	<b>29.9</b>	0.76	0.08	<b>0.59</b>	<b>0.93</b>	0.08	0.10	<b>-0.14</b>	<b>0.27</b>					-0.09	0.03	<b>-0.17</b>	<b>-0.01</b>
PA					-0.05	0.07	<b>-0.18</b>	<b>0.08</b>												
Sex: $\delta^{15}\text{N}$	30.6	8.0	<b>14.0</b>	<b>47.3</b>	2.02	0.10	<b>1.82</b>	<b>2.21</b>	1.18	0.12	<b>0.95</b>	<b>1.44</b>					0.16	0.04	<b>0.07</b>	<b>0.25</b>



Figure 3.1. Morphological measurements collected during the austral summers of 2012-13 and 2013-14 on Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Dashed line indicates distal edge of the humeral head which can be palpated on the underside of the flipper.

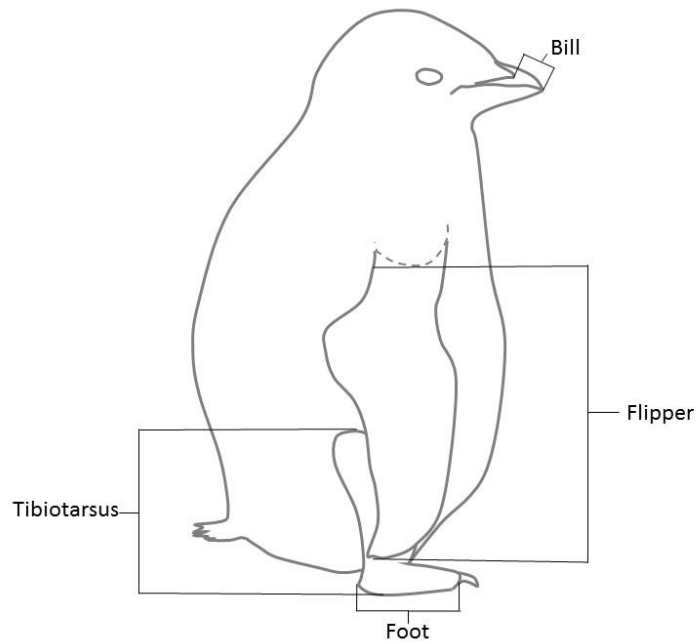


Figure 3.2. Estimated growth rates (mass, bill, flipper and tibiotarsus; and 95% confidence intervals) for measurements of  $\delta^{15}\text{N}$  for Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (“2012”) and 2013-14 (“2013”). Estimates are from the best model, across the range of observed values for  $\delta^{15}\text{N}$  (larger value = greater proportion of diet comprised of fish) calculated separately for females and males during both years of the study. Includes data from all chicks combined (i.e. WB and KA subsets; see text for details). Note different units and scales for y-axes.

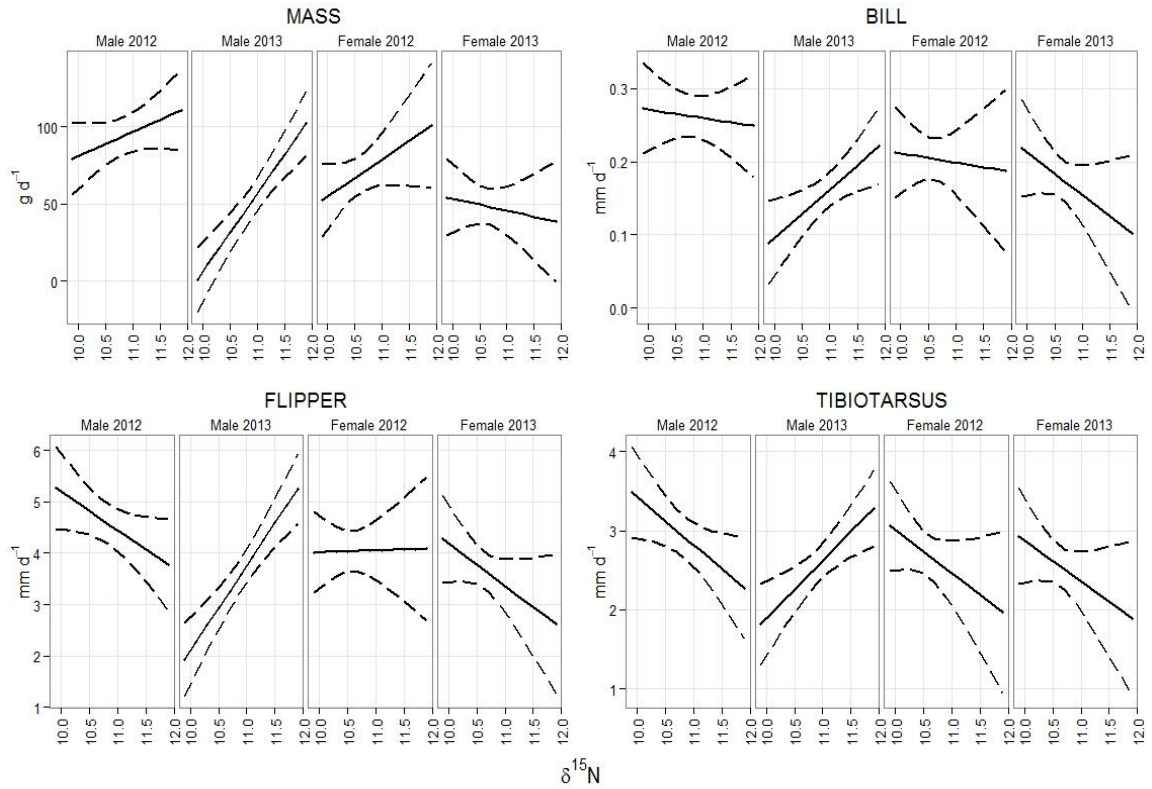


Figure 3.3. Estimated growth rates (flipper, tibiotarsus, foot; and 95% confidence intervals) for measurements of average food delivered per day per chick (FOOD) for Adélie Penguin chicks in the Weighbridge data subset at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (“2012”) and 2013-14 (“2013”). Estimates are from the best model, across the range of observed values for FOOD, calculated for females during the two years of the study, and with mean values for all other continuous variables in the model. Note: the model included an additive sex effect, thus growth rates for males had the same slope but greater intercept than for females.

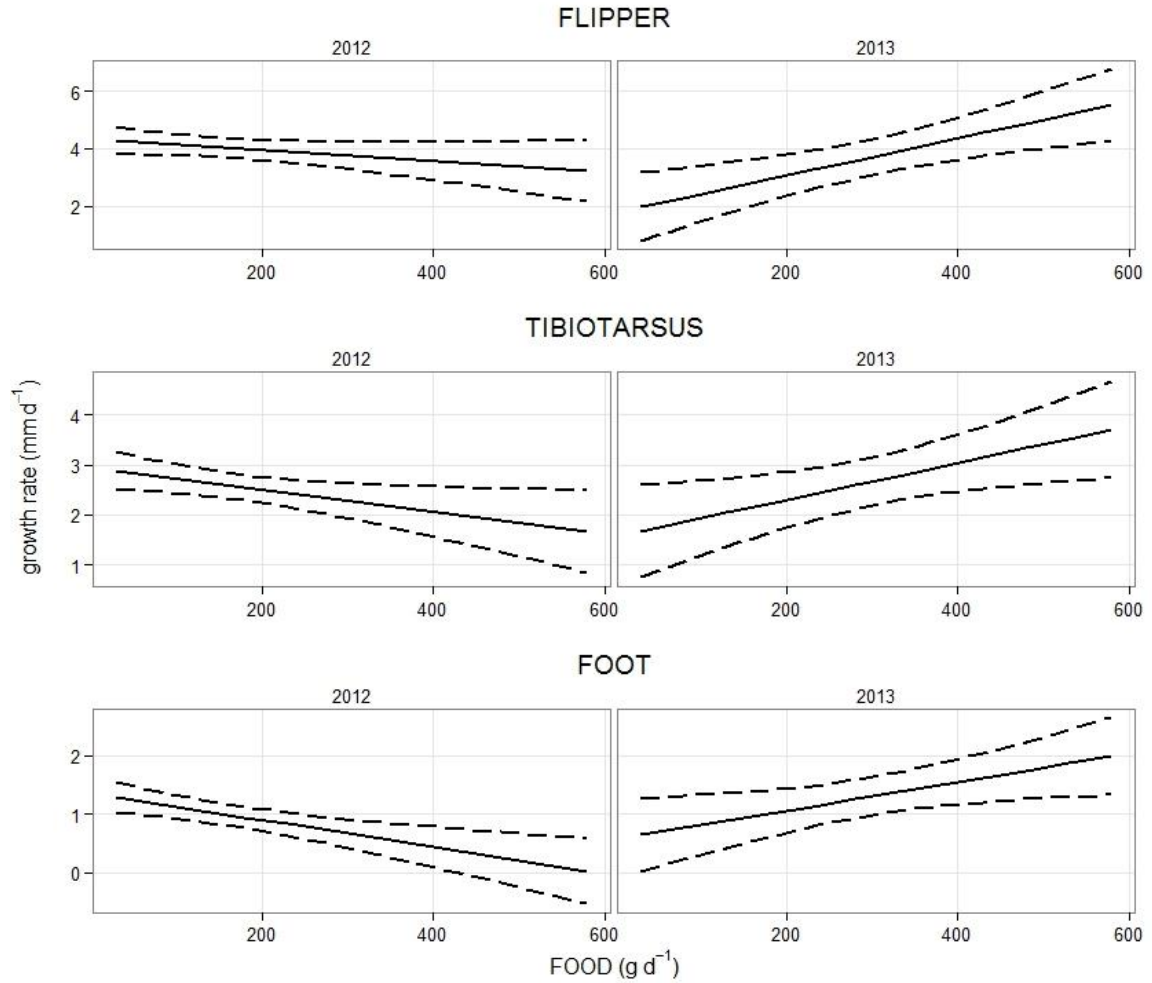
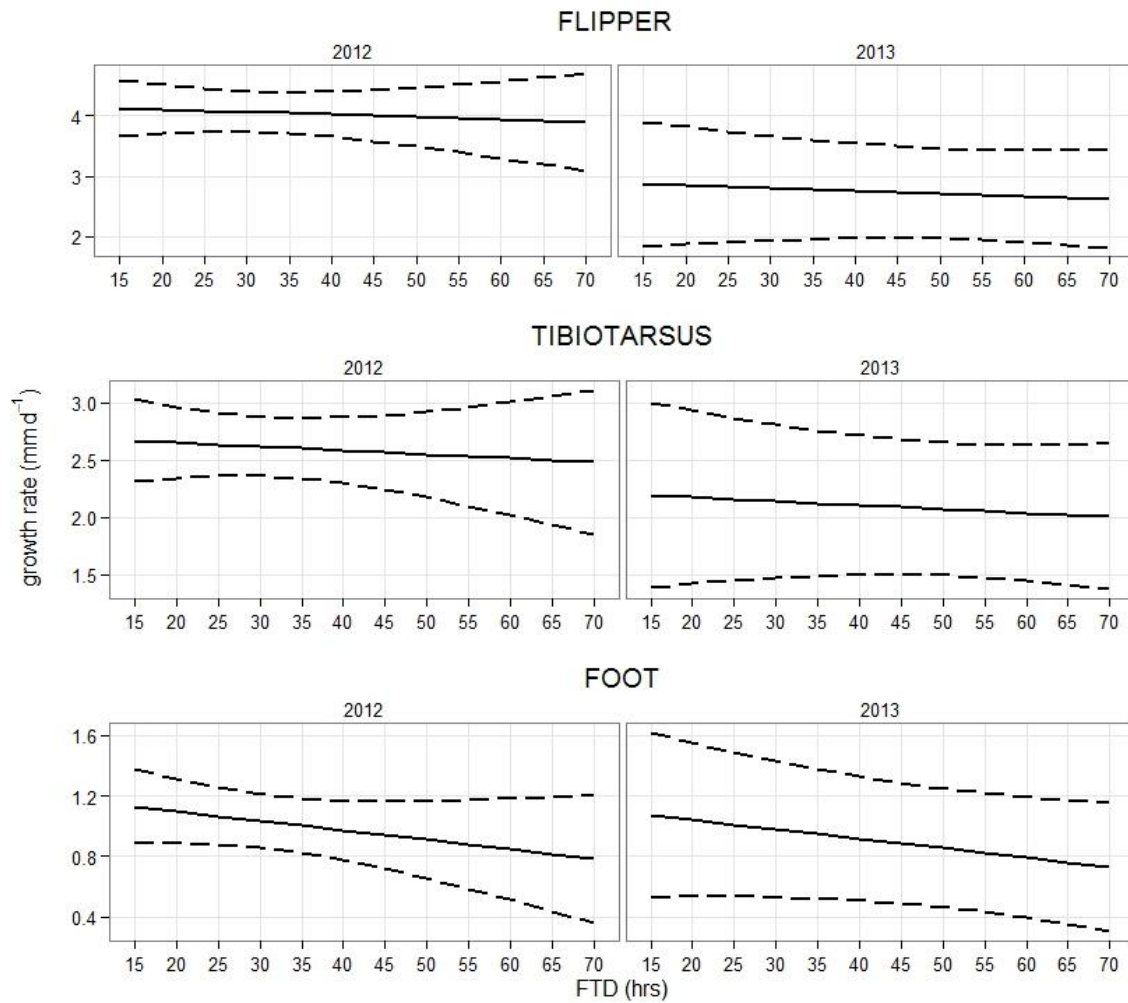


Figure 3.4. Relationship between estimated growth rates (flipper, tibiotarsus, foot) and foraging trip duration (FTD) for Adélie Penguin chicks in the Weighbridge data subset at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (“2012”) and 2013-14 (“2013”). Estimates are from best model, across the range of observed foraging trip duration (FTD) values, calculated for females during the two years of the study, and with mean values for other continuous covariates in the model. Dashed lines are 95% confidence intervals.



## Chapter 4

### TRADE-OFFS IN OFFSPRING-REARING BEHAVIOR: UNDERSTANDING THE RELATIONSHIPS BETWEEN GROWTH, BROOD-GUARDING, AND OFFSPRING SURVIVAL IN THE ADÉLIE PENGUIN

Scott Jennings

## ABSTRACT

Trade-offs in parental investment are a fundamental component shaping individual variation in reproductive success. In long-lived, slow-reproducing species, trade-offs may exist between investment in multiple offspring in the same season, or between current and future offspring. Seabirds are an interesting group of animals to study these trade-offs in because of the unique constraints associated with foraging at sea yet nesting on land. Using data collected across two seasons of apparently contrasting food availability, I investigated the relationships between growth, brood-guarding, and survival of Adélie Penguin chicks. I first examined the relationships between chick growth rate and the timing of a critical transition from parents guarding the chicks, to the crèche stage, when both parents simultaneously forage while chicks remain in the colony without parental protection from predation or weather. I next examined whether there was a relationship between growth rate and chick survival across the entire chick-rearing period. Finally I examined whether survival during the crèche stage could be predicted by the size or age at which chicks entered the crèche. Relative hatching date was the most important predictor of the age at which chicks entered the crèche, with later hatching chicks being guarded a shorter time. In contrast, both growth rates and the duration of the guard period were together the best predictors of chick size when entering the crèche, a result that provides evidence that certain parents can simultaneously maximize chick defense and growth rates. There was no relationship between growth rates and survival probability across the entire chick-rearing period, but there was a positive relationship between the size of chicks (but not their age) when entering the crèche stage and their subsequent survival. These results suggest that early nest initiation provides parents with the *opportunity* to extend the guard period and increase chick survival, however to extend the guard stage they must also be proficient foragers. Thus this study provides an example of a situation where the factors governing trade-offs in parental investment may vary as environmental conditions fluctuate, a result which can aid our ability to understand and predict changes to population processes and levels.

## INTRODUCTION

Trade-offs are a central component of life history theory (Stearns 1989). Extensive empirical and theoretical work has investigated trade-offs between adult survival and reproduction (Ghalambor and Martin 2001; Kim et al 2011), investment in single offspring as clutch/litter size varies (Ydenberg and Bertram 1989, Badyaev and Ghalambor 2001), and how these trade-offs vary under different environmental conditions (Jodice et al. 2002, Bårdsen et al. 2011). Trade-offs in parental behavior can not only alter costs and benefits between parents and offspring, but certain behaviors can also benefit offspring in one way, yet jeopardize offspring in another (i.e., increased food delivery may increase risk of detection by predators). When food is difficult to acquire and a concurrent risk to offspring exists which can be minimized through guarding by the parent (i.e., predation, weather), an important set of such trade-offs is the division of time spent foraging to provision young versus guarding young from threats, and parents likely adjust the division of effort between these activities based on predation risk and parental foraging costs (Markman et al. 1995, Komdeur 1999). Further investigation of the consequences of these trade-offs on chick survival is important to understanding how parents maximize reproductive success under different conditions, and to our understanding of population level responses (i.e., reproductive success and recruitment) to these conditions.

Larger offspring are often less-susceptible to a range of risks. For example, in a system with aggressive territorial defense, faster-growing Glaucous-winged Gull (*Larus glaucescens*) chicks are less-susceptible to intra-specific attack from neighboring conspecifics (Hunt and Hunt 1976). Additionally, post-fledging survival in a number of seabird species has been positively related to growth rates or size at fledging (Maness and Anderson 2013), so where there is a time constraint on the period of parental care there can be additional pressure. However, the relationship between offspring size and risk may not be linear (Ricklefs 1973) and the point at which this relationship diminishes is likely to vary under different circumstances. Many studies of the relationships between seabird parent behavior and chick survival during chick-rearing have focused on extremes in parental behavior, particularly conditions under which parents abandon the nesting

attempt (Vleck et al. 2000, Wanless et al. 2005). Less attention has been given to less-catastrophic effects of variation in parental investment, such as the extent to which growth rates and overall size of nestling might influence survival during the dependent stage. Where studied, results are contradictory, with evidence for a positive relationship between growth and survival in some species (e.g., Roseate Terns [*Sterna dougalli*]; Nisbet et al 1998), and negative or no relationships for other species (e.g., Gentoo penguins [*Pygoscelis papua*]; Williams and Croxall 1991). Further investigation in species with a range of breeding behaviors is required to more clearly understand these patterns.

Several colonial-nesting avian species partially accomplish the requirements of simultaneously provisioning chicks and reducing mortality risk with crèching behavior, in which the chicks from multiple nests gather for protection from predation and inclement weather while parents make foraging bouts (Munro and Bédard 1977, Evans 1984, Wanker et al. 1996). Predation or other environmental risks to young are key factors determining the length of brood-guarding (before initiation of crèching). For example, brood-guarding might be extended in edge versus central nests (Tenaza 1971, Catry et al. 2009), and brood-guarding may be shortened in late-hatched broods to better match the timing of neighbor nests and take advantage of predator-swamping (Catry et al. 2008, Rothenbach and Kelly 2012). Chick age and condition may also influence the length of brood-guarding, but a consistent pattern has yet to emerge. In some cross-fostering experiments, brood-guarding duration depended on time since the foster-parents' chick had hatched (Catry et al. 2006), but in others the end of brood-guarding was more highly correlated with the brooded chick's true age (Moreno et al. 1997, Varpe et al. 2004). Thus the degree to which changes in offspring condition might influence how animals optimize offspring care appears to vary by species, and additional species-specific case studies are required to identify broad patterns in how these types of trade-offs in investment can influence reproductive success and lifetime fitness.

The Adélie Penguin (*Pygoscelis adeliae*) is a crèching species, with chicks generally entering crèches when between 15 and 30 days old (Ainley 2002, Davis 1982b). Research indicates that Adélie Penguins adjust the length of brood-guarding



based on their ability to provision the chick(s) and maintain their own condition, and these relationships may vary with changing environmental conditions (Chappell et al. 1993, Ballard et al. 2010). However, it has also been suggested that the onset of the crèche period may be partially determined by chick ontogeny and behavior, and not just parental ability to provide food (Ainley 2002), but this has yet to be formally investigated. Survival to crèching has often been assumed to be an accurate proxy for survival to fledging, but there is mixed support for this assumption. Evidence ranges from variable mortality (Taylor 1962, Volkman and Trivelpiece 1980) to high survival (essentially no mortality) amongst crèched chicks (Clarke et al. 2002).

The Adélie Penguin colony at Cape Crozier, Ross Island, Antarctica, is one of the largest known colonies for this species, and further increases in colony size are thought to be potentially limited by density dependent competition for food (Lyver et al. 2014). Chick mass is lower at Cape Crozier than at neighboring smaller colonies on Ross Island, further indicating general energetic limitations to reproduction at this large colony (Dugger et al. 2014). Previous research here has provided evidence of individual heterogeneity in parent quality (Lescroël et al. 2009, 2010), and has linked aspects of chick provisioning to changes in parent quality (Ballard et al. 2010). Additionally, field observations at this colony suggest post-crèche mortality may be higher than previously thought, or perhaps a new pattern has emerged in recent years.

The goal of this study was to better understand how trade-offs in parental investment might influence chick survival during the dependent stage in Adélie Penguins. I hypothesized a general pattern in which parents might decrease the length of brood-guarding in order to increase chick growth rate (through an increased provisioning rate achieved via both parents foraging simultaneously). I first investigated the relationships between growth rates and the size and age at which chicks entered the crèche stage (collectively “crèche-timing”) to understand how parental investment in provisioning might influence crèche-timing. I hypothesized that a negative relationship between growth and crèche-timing would indicate trade-offs between provisioning and brood-guarding, while a positive relationship would indicate (at least some) parents can simultaneously maximize both. Next I investigated patterns of chick survival over 2

different time scales: 1) the entire chick provisioning period (guarding and crèche), and 2) the crèche stage. For this part of the study I tested the following predictions: 1) faster growth rates will be associated with higher daily survival probability across the entire provisioning period; 2) daily survival probability will decline as the season progresses (reflecting lower survival during the crèche stage); and 3) older age or larger size when entering the crèche stage will be associated with higher daily survival probability during the crèche period.

## METHODS

### *Field methods*

The data for this study were collected as part of a larger, long-term effort to investigate the reproductive ecology and demographics of Adélie Penguins on Ross Island, Antarctica ([www.penguinscience.com](http://www.penguinscience.com)). This long term project involves monitoring the nesting success of a population of individually-marked, known-age and known breeding history penguins. Data were collected over the Austral summers of 2012-13 and 2013-14 (hereafter referred to as 2012 and 2013). The individual chicks in this study were associated with nests which were selected to represent a range of parent ages, and nest position within a subcolony (clusters of adjacent nests within the larger colony) since nests located on the outside edge of subcolonies have lower chick survival rates than those located on the interior (Davis and McCaffrey 1986).

I monitored each nest every 1-3 days through the incubation and chick-rearing period to determine hatch day and the first day chicks were left unattended (beginning of crèche stage). Morphological measurements to determine chick growth rates commenced on day 10 after hatching for the first-hatched chick, and continued every 5 days thereafter until the end of the chick-rearing period (50-55 days old). Because siblings are on average only 1.4 days apart in age (Taylor 1962), if present, second-hatched chicks were measured on the same day as first-hatched chicks to avoid disturbing the nest on consecutive days. On the first day of measurement, chicks were also individually-marked with a T-bar fish tag (Floy Tags Inc., USA) attached to the loose skin on the back of the

neck. Tags were light grey in color with a unique number, and a unique stripe pattern added with black ink to facilitate individual identification without recapturing chicks.

The size at which chicks entered the crèche stage was determined during the first year of the study by measuring chicks on the first day they were observed unattended. However, this was done only if the first day unattended was two days before or after a scheduled measurement on the 5-day routine (i.e., chicks were not measured on consecutive days). These data revealed that size at crèching could be accurately calculated using the equation of a linear model fit to the growth data collected on the 5-day schedule, so to reduce disturbance during the second year of the study these crèche-day measurements were not collected. Morphological measurements collected included mass (to nearest 25 g), and lengths of flipper (1 mm) and tibiotarsus (1 mm). Full details regarding how these measurements were collected can be found in Jennings (2015, Chapter 3). Growth rates of the morphological features considered in this analysis were previously shown to have a positive relationship with either the overall amount of food delivered or with the proportion of the diet comprised of higher calorie fish (rather than lower quality krill), two aspects of provisioning which represent increased parental investment (Jennings 2015; Chapter 3).

Chick fate was determined during nest monitoring and individually-marked chicks were identified with binoculars from a distance of approximately 5 m (so chicks were only recaptured every 5 days for measurement). Once chicks had entered the crèche stage, I would search a radius of 10-25 m around the nest until I found the chick or for 15 minutes, whichever came first. If a chick was not resighted on a scheduled check day, I returned the following day to conduct the same search. If a chick was not detected by these methods for 4-5 consecutive days, further searches for that chick were not conducted and it was assumed to have died. In the final days before fledging, Adélie Penguin chicks often congregate on the beach away from their natal territory. Thus toward the end of the chick-rearing period I also conducted several systematic searches along beaches and heavily-trafficked routes between subcolonies and beaches.

## *Analysis*

Individual growth rates were calculated by fitting a linear model to each measurement for each chick (Jennings 2015, Chapter 2, 3). For each morphological measurement, the period of linear growth was determined by a combination of the  $R^2$  values and visual inspection of linear model fit to incrementally longer periods of measurement. The growth rates for each morphological measurement were calculated only during the phase of linear growth, a period which varied for each measurement but which did not vary substantially between individual chicks. The slope coefficients of these linear models were taken as the daily growth rates for each morphological measurement for each chick, to be used in subsequent analyses.

I used an information theoretic approach and compared AIC values corrected for small sample size (AICc) or for extra binomial variation (QAICc) to evaluate the relative strength of support for each candidate model (Burnham and Anderson 2002). I considered inclusion of a covariate in the best-supported model to represent some support for that variable in explaining the pattern of interest, while the magnitude of the model coefficients and degree to which 95% CI overlapped 0, were used to further evaluate both the strength of evidence for relationships and the strength of the relationships. Previous analyses had indicated important year- and sex-based variability in chick growth rates (Jennings 2015; Chapters 2, 3), so these factors were also considered in the development of *a priori* models. Except where specified all analysis was conducted in R version 3.1.1 (R Core Team 2014).

### *Growth rates and crèche timing*

I used linear models to examine the relative importance of mass, flipper, and tibiotarsus growth rates in predicting the age at crèching. I also investigated the importance of these growth rates and crèching age in predicting the size of each of these morphological parameters at the time chicks entered the crèche. I included relative hatching day as a fixed effect, and nest ID (identifying chicks from the same nest) as a random effect in these models to account for the lack of independence between siblings. However, for all models of size at crèche, the random effect variances were estimated as

zero or very small relative to the residual variance, and thus for modeling size at crèche I used linear models with fixed components only. For these 4 analyses investigating the effect of growth rates and relative hatch date on age at crèche, plus the size at crèche for the 3 morphological measurements, I limited the total number of models considered by first determining the importance of Year and Sex in predicting the response variables. I then used the best-supported Sex and Year model structure to evaluate the additional importance of growth rates and relative hatch date. Relative hatch date was calculated separately for each year, with negative values representing earlier than average hatch dates. For age at crèche, I evaluated the relative importance of the 3 growth rates and relative hatch date in predicting crèching age. For size at crèching of each morphological measurement, I evaluated relative importance of hatch date, crèching age, and the growth rate of that morphological feature only.

### *Survival*

I used the Cormack-Jolly-Seber (CJS) open population model (Lebreton et al. 1992) implemented in Program MARK via the R package RMark (Laake 2013) to evaluate relationships between daily survival rates of penguin chicks and the predictor variables of interest (Table 4.1). The CJS model allowed me to account for resighting probabilities  $< 1.0$ , which despite the relatively stationary nature of nests and dependent chicks, were likely as the season progressed and chick mobility increased. Since chicks were located on 1 to 3 day intervals and every chick was not searched for every day, I coded those occasions as “missing data” in the MARK input file. Consequently, I couldn’t use the median  $\hat{c}$  approach in Program MARK to evaluate overdispersion and goodness of fit, but instead relied on program RELEASE to estimate  $\hat{c}$  using the most general model with Year\*Sex\*t structure for both apparent survival ( $\phi$ ) and resighting probabilities ( $p$ ).

I constructed candidate model sets to evaluate the relative importance of the variables under consideration on daily survival rates ( $\phi$ ) and resighting ( $p$ ) probabilities of Adélie Penguin chicks (Table 4.1). To limit the total number of models considered, I used a multi-stage process to arrive at the candidate model set, where the best model structure from each stage was retained and parameters were added to it for the next stage

(see Doherty et al 2010). I began with a general model structure for apparent survival [ $\phi$  (Year\*Sex\*t)], and tested various combinations of variables which I hypothesized might be important sources of variability in resighting rates ( $p$ ; Table 4.1).

I then retained the best structure on  $p$ , and proceeded with the first stage of modeling apparent survival by evaluating combinations of Year and Sex structure for  $\phi$ . I then moved forward with the best Year and Sex structure on  $\phi$  and evaluated the importance of the relative hatch date in predicting survival. During the next stage of modeling  $\phi$ , temporal variation was evaluated, including linear, quadratic, and natural log trends within each season, and constraints on time related to two time-varying individual covariates: 1) Age: Chick age on a given day; and 2) InCr: whether or not a chick was in the crèche stage on a given day (binary covariate: 1=in crèche, 0=not in crèche). I then used all models in the candidate model set for this stage to calculate model averaged estimates of daily survival for each sex and year across the entire provisioning period.

Finally I evaluated the 2 primary objectives of the study: 1) I included growth rate covariates to examine the relationships between these covariates and survival across the entire provisioning period; and 2) I included covariates for age and size at crèching to examine the relationships between these variables and survival during the crèche period. The full candidate sets from these two objectives were considered separately. However, the best-supported model from the first objective was included in the candidate set for the second objective to compare whether growth rates or crèche-timing were more important in predicting survival.

## RESULTS

I measured and monitored survival of 88 (35 in 2012, 53 in 2013) Adélie Penguin chicks across the two years of the study. Of these, 16 died before reaching the crèche stage, while an additional 10 chicks were confirmed to have died during the crèche stage (carcass found). In 2012, parents left their chicks alone for the first time (beginning of crèche) between 15-26 days old (mean = 21; 25% quartiles = 19; 75% quartiles = 24). In 2013 chicks entered the crèche between 11-25 days old (mean = 19; 25% quartiles = 17; 75% quartiles = 22). Earlier Hatch date was associated with older crèching age (Pearson

correlation coefficient,  $r = -0.68$ ,  $p\text{-value} < 0.001$ ). In subsets of the data for which information was known, there was a very weak positive correlation between crèching age and parent age ( $r=0.37$ ,  $p = 0.02$ ), and no correlation between crèching age and the amount of food delivered to each chick per day ( $r=0.13$ ,  $p\text{-value}=0.44$ ), or the average length of foraging trips ( $r=0.14$ ,  $p = 0.40$ ; see Jennings 2015, Chapter 3 for details of data subsets and these variables).

### *Growth rate and crèche-timing*

During the initial modeling of age and size at crèching, the Year + Sex structure was determined to be the best-supported model structure predicting crèche-timing. Adding growth rates and relative Hatch date to this base model, hatch date alone had the strongest support as the best predictor of crèching-age (Table 4.2), with later Hatch dates associated with younger crèching ages ( $\beta = -0.44$ ; 95% CI = -0.57 to -0.32). The best-supported model also indicated some weak evidence that male chicks entered the crèche older than females ( $\beta = 0.20$ ; CI: -0.45 to 0.90), and that for both males and females, chicks crèched at younger ages in 2013 ( $\beta = -1.21$ ; CI: -2.61 to 0.17). The 3 models with the additive effect of hatch day and each of the 3 growth covariates received little support, with  $\Delta\text{AICc}$  values ranging between 2.1-2.3, and with the top-ranked model being 2.9-3.3 times more likely than the models including the growth covariates (Table 4.2). In addition, the 95% confidence interval on each of the growth coefficients broadly overlapped zero, indicating little support for a relationship between growth and the age at which chicks crèche (mass growth:  $\beta = 0.003$ ; 95% CI = -0.010 to 0.018; flipper:  $\beta = -0.099$ ; CI = -0.553 to 0.336; tibiotarsus:  $\beta = -0.058$ , CI = -0.721 to 0.625).

Models containing the additive effects of crèching-age and growth rates (including Year + Sex base effects) were best-supported for predicting the mass and flipper length at crèching (Table 2). The best model for mass at crèching suggested that while accounting for the negative effect of hatch date there was a positive relationship with both age at crèching ( $\beta = 55.3$ ; SE = 9.2; 95% CI = 36.2 to 75.5) and mass growth rate ( $\beta = 9.3$ ; SE = 1.2; CI = 7.0 to 11.6). Thus each added day before entering the crèche and each 1 g d<sup>-1</sup> increase in growth rate corresponded to an average increase in mass at crèching of 55.3 g and 9.3 g, respectively. Similarly, chicks that entered the crèche older

had longer flippers when entering the crèche than chicks that crèched younger ( $\beta = 3.7$ ; SE = 0.5; CI: 2.8 to 4.6), and there was also evidence for a positive relationship between flipper length at crèching and flipper growth rates ( $\beta = 6.9$ ; SE = 1.7; CI: 3.4 to 10.4). In this case, for each additional day chicks were guarded by parents, and for each 1 mm d<sup>-1</sup> increase in flipper growth rate, the length of flipper when entering the crèche was 3.7 mm and 6.9 mm greater, respectively.

For both mass and flipper length at crèching, the model that also included the additive effect of Hatch date received some support ( $\Delta AICc < 2$ ). However, due to the correlation between hatch date and crèching age, these models should be used cautiously to evaluate the relative importance of these two variables in combination in predicting mass or flipper length at crèching. Nevertheless, for both models, there was very weak evidence that coefficient for Hatch date was different than zero (mass:  $\beta = 8.9$ ; SE=10.2; CI: -11.3 to 29.2; flipper length:  $\beta = -0.5$ ; SE=0.5; CI: -1.4 to 0.4), and thus most of the variation in mass and flipper length at crèching was attributed to age at crèching and growth rates rather than relative Hatch date.

For tibiotarsus length at crèching, the best supported model only included age at crèching (with Year and Sex), and again there was a positive relationship between age at crèching and tibiotarsus length at crèching ( $\beta = 2.3$ ; SE=0.3; CI: 1.7 to 2.9). Three additional models were also competitive for tibiotarsus length at crèching: the additive effect of Hatch date ( $\Delta AICc = 0.06$ ); tibiotarsus growth rate ( $\Delta AICc = 1.7$ ); and tibiotarsus growth plus relative hatch date ( $\Delta AICc = 1.8$ ). However, in all three of these competitive models there was strong support for the positive effect of crèching age on crèching tibiotarsus length ( $\beta$  values ranging from 1.9 to 2.2; no 95% confidence intervals overlapped zero), but little support for the strength of Hatch date or tibiotarsus growth rates, as covariate coefficients all included 95% confidence intervals that broadly overlapped zero.

### *Survival*

The estimated overdispersion factor ( $\hat{c}$ ) was 1.24. This value was used to adjust variance for estimated model coefficients and calculate Quasi-likelihood AICc (QAICc)



values for use in model comparison. However, because RELEASE may not estimate all parameters when data are sparse (as in this analysis), I also evaluated the sensitivity of results and model selection with some other values for  $\hat{c}$ : 1, 1.5, and 2. The Year effect was most sensitive to increasing the overdispersion factor, with the 95% confidence intervals overlapping zero when  $\hat{c}$  was adjusted upward to 2.0 (but not when  $\hat{c}=1.5$ ). However, the overall results and inferences were not substantially altered under different values of  $\hat{c}$ , so I used 1.24 for the variance inflation factor.

The best supported structure for modeling daily chick resighting probability (“ $p$ ”), was an additive year and general time structure [ $p$  (Year+t)]. This model received 100% of the QAICc model weight. Thus resighting probability differed between years (higher in the second year:  $\beta = 3.15$ ; SE= 0.27; 95% CI = 2.63 to 3.67) but with no discernable temporal pattern within years, and daily estimates of resighting rates ranged from 0.05-0.97 in 2012 and 0.56-0.99 in 2013. The very low estimates in 2012 occurred on days when I only attempted to locate a small number of chicks, and when failing to locate one or two chicks had a large impact on resighting probability. I retained this best  $p$ -structure through the rest of the apparent survival modeling process.

The first stage of apparent survival modeling supported a Year by Sex interaction [ $\phi(\text{Year*Sex})$ ] as the best model, which received 59% of the model weight and was 2 times more likely to be the best model than the second ranked model. Thus, I moved forward into the second survival modeling stage with this best model [ $\phi(\text{Year*Sex})$ ] and found that the addition of relative Hatch Date to the year and sex interaction model from the previous step received the most support. This model [ $\phi(\text{Year*Sex} + \text{Hatch})$ ] had 69% of the QAICc model weight and was approximately 3 times more likely to be the best model than the second ranked model, which contained the quadratic effect of Hatch Date. Thus the first two stages of modeling apparent daily survival indicated that the interaction between Year and Sex, and the additive effect of Hatch date best explained variation in chick survival. The estimated coefficients from this model indicated weak evidence that survival was greater for females during 2012 (male  $\beta = -1.05$ ; SE = 0.68; 95% CI = -2.39 to 0.29). However, this model also indicated survival was lower for both sexes in 2013 compared to 2012 ( $\beta = -1.65$ ; SE = 0.65; CI = -2.92 to -0.37), but that in 2013 male

survival was higher than female (2013: male interaction:  $\beta = 1.54$ ; SE = 0.76; CI = 0.04 to 3.04). Across both years, there was good evidence for a decline in survival with later Hatch Dates ( $\beta = -0.098$ ; SE = 0.03; CI = -0.165 to -0.031).

For the third stage of survival modeling, time constraints were added to the base model developed in the preliminary modeling stages [ $\phi(\text{Year} * \text{Sex} + \text{Hatch})$  p (Year+t)], and the linear time trend (T) was best supported with 48.7% of the QAICc model weight and 95% confidence limits on the trend coefficient did not overlap zero ( $\beta = -0.059$ ; 95% CI = -0.090 to -0.028; Table 4.6). However, there were two competitive models (within 2 QAICc) and the best model was only 1.5 and 2.5 times more likely to be the best model than were the second and third ranked models, respectively. The competitive models all included variations in the time trend within season (lnT and TT), suggesting strong support for some sort of time trend in survival within each season. At this stage I model-averaged to generate my best estimates of daily survival rates for males and females in each year of the study across mean relative hatch date (Figure 4.2). Thus in 2012, my best estimate of the probability that a female chick survived from the time when measurements and resighting began (~10 days old) until fledging, was 0.668. For males, the probability of surviving this period was 0.356 in 2012 and 0.361 in 2013. In contrast, the probability of surviving this period for female survival during 2013 was only 0.168.

The fourth stage of survival modeling included the evaluation of the relationship between the growth rates of morphometric measurements (mass, flipper, tibiotarsus) and survival across the entire provisioning period. The morphometric measurements were added singly, to the best model from the previous modeling stage (stage 3; [ $\phi(\text{Year} * \text{Sex} + \text{Hatch} + \text{T})$  p (Year+t)]; Table 4.7). The model including the covariate for tibiotarsus growth received over 92% of the QAICc model weight and was over 16 times more likely to be the best model than was the second ranked model (Table 4.7). However, a higher tibiotarsus growth rate was associated with lower survival over the entire chick provisioning period ( $\beta = -0.745$ ; SE = 0.225; 95% CI = -1.185 to -0.305), contrary to what was predicted.

In the fifth and final stage of survival modeling, the best-supported model for evaluating the relationship between size or age at crèching and survival during the crèche period contained the effect of flipper length at crèche (Table 4.8). It is important to note that the candidate set at this stage of modeling included the best supported models from both stages 3 and 4. This model at stage 5 received 32.6% of the QAICc model weight, but the models containing the covariates for mass and tibiotarsus size at crèche were competitive and received 22.9% and 18.0% of the model weight, respectively (Table 4.8). The top model was only 1.4 times more likely to be the best model than the second ranked model and 1.8 times more likely than the third ranked model. However, all 3 competitive models suggested strong evidence for a positive relationship between crèche period survival and flipper length (CrFlip:  $\beta = 0.038$ ; SE = 0.01; 95% CI = 0.015 to 0.061), mass (CrMass:  $\beta = 0.0018$ ; SE = 0.0006; 95% CI = 0.0006 to 0.0029), and tibiotarsus length (CrTib:  $\beta = 0.060$ ; SE = 0.019; 95% CI = 0.022 to 0.097) at crèching, as all covariate coefficients were positive (as predicted) and 95% confidence intervals did not overlap zero. Thus, chicks entering the crèche at larger sizes (based on all three morphological measurements) were more likely to survive the crèching period. The highest-ranking model that included the covariate for the age at which chicks entered the crèche (ranked fourth,  $\Delta\text{QAICc}=2.13$ ) received only 11.2% of the QAICc model weight and was 2.9 times less likely to be the best model than the top-ranked model (Table 4.8). In addition, the coefficient for age at crèching in this model strongly overlapped zero ( $\beta = -0.02$ ; SE = 0.08; 95% CI = -0.18 to 0.14), providing no evidence for a relationship between survival during the crèche period and age at crèche.

Using the estimates from this final, best-supported model [ $\phi(\text{Year}*\text{Sex} + \text{Hatch}+\text{T}+ \text{Cr}+\text{CrFlip}) \text{ p } (\text{Year}+\text{t})$ ] (Table 4.8), I calculated the mean daily survival probability for chicks before mean crèche date, and after mean crèche date (mean crèche date was the same both years), with mean values for Hatch and CrFlip. In 2012 mean daily survival probability for females was 0.999 (SD=0.0004) before mean crèche date, and 0.989 (SD=0.010) after mean crèche day, while for males mean daily survival probabilities were 0.996 (SD=0.002) before mean crèche and 0.944 (SD=0.046) after. In 2013, mean daily survival probability for females was 0.996 (SD=0.002) before mean

crèche and 0.947 (SD=0.044) after, while for males it was 0.997 (SD=0.002) before and 0.955 (SD=0.037) after mean crèche date.

## DISCUSSION

The results of my study add to our understanding of seabird population dynamics and the nature of individual heterogeneity in quality of parents. My results also have important implications for our assumptions about what constitutes a successful breeding attempt in crèching species, as I documented decreasing daily survival rates throughout the chick-rearing period for a long-lived seabird population. These results are perhaps most interesting when considered in the context of colony size because this study took place at one of the largest (if not the largest) Adélie Penguin colony in the world, where competition for food resources has been well-documented (Ainley et al. 2003, 2006) and where density-dependent mechanisms are suspected to be underway to limit colony growth and possibly chick size (Lyver et al. 2014, Dugger et al. 2014). Reduced chick survival can be a mechanism for reduced population growth, in agreement with our general understanding of the factors limiting seabird colony size (Ashmole 1963). However, with only 2 years of data, it is unclear if the survival rates I documented are really indicative of a population under density dependent limitation, or if perhaps they represent the typical annual variation in chick survival rates for a large colony. Regardless, my results provide an important benchmark against which results from future studies at very large colonies, as well as the smaller colonies within this Ross Sea metapopulation, can be compared.

Nevertheless, field observations suggest some food limitation during 2013 (see Jennings 2015, Chapter 3), and the large difference in the pattern of decline in female chick survival probability between the 2 years may be related to that food limitation. Sex-based differences in offspring survival related to environmental conditions (generally affecting food availability) have been shown in a range of vertebrate species (Wasser and Norton 1993, Hipkiss et al. 2002, Le Galliard et al. 2005). Often, survival of the sex with greater overall requirements in food or other parental care is most sensitive to environmental fluctuations, but this is not always the case (Råberg et al. 2005). Adélie Penguin parents make shorter (i.e., more costly to parents) foraging trips when

provisioning male chicks (Beaulieu et al. 2009). I was unable to determine if such a pattern existed in this study, but male chicks in this study received diets with a greater proportion of higher lipid fish (versus krill), and had higher growth rates than females (Jennings 2015, Chapter 2). Thus males might be the more expensive sex to raise in this species. However, female survival showed the greatest change between years, possibly in response to food limitation in 2013. In situations where siblings compete for food, the larger, more expensive sex is often at an advantage when resources are more limited (e.g., Hipkiss et al 2002). Sibling competition for food is a distinct component of Adélie Penguin provisioning behavior (Spurr 1975), and thus this may explain the differences in survival between the sexes observed here. It remains unclear if, or to what extent, parents might have preferentially fed or otherwise invested in males over females in 2013.

I found that not only was survival probability lower during the crèche stage than the brood-guarding stage, but also that survival continued to decline until chicks fledged. This is somewhat different than the results from other studies of this species. Several previous studies have reported that Adélie Penguin chick survival is generally high and increases during the crèche period (Taylor 1962; Davis 1982; Davis and McCaffrey 1986). However most of this previous work was conducted at colonies that were much smaller in size, with potentially much less intra-specific competition for food. Previous research at Cape Crozier was conducted when the colony had approximately 175,000 breeding pairs, which is 35% smaller than during this study (c. 1970; Ainley et al 2005). To my knowledge this is the only study to monitor survival of individual chicks at an Adélie Penguin colony with over 250,000 breeding pairs. Despite the fact that Cape Crozier has recently experienced substantial growth and is currently possibly the largest Adélie Penguin colony on earth, it is thought that population size of this colony is now limited by food availability (Lyver et al. 2014). Indeed, the average mass of chicks from 2-chick broods when entering the crèche during the present study was 1356 g, while during the early 1970's it was 1600 g (Ainley and Schlatter 1972), during which time a detailed study documented no loss of crèched chicks from experienced breeders and only minor losses amongst young breeders (Ainley et al. 1983). Based on the best model including mass at crèching from this study, the daily survival probabilities at the end of the provisioning period were estimated to be approximately 0.041 greater for chicks

entering the crèche at 1600 g than at 1300 g. Thus the observed difference in chick survival, resulting from smaller chick sizes, could be a population level response to density-dependent limitation.

This study provided good evidence that an earlier relative hatch date was associated with chicks crèching at older ages (i.e., staying in guard stage longer), but did not necessarily lead to crèching at larger sizes. Relative hatch date serves as a proxy for the effect of changing conditions during the course of the season, but perhaps more importantly, may also reflect a gradient in parent age or quality (older or higher quality parents may initiate nesting earlier in the season; Ainley 2002). There was little correlation between relative hatch date and growth rates (Jennings 2015, Chapter 2), and thus I believe an earlier laying date gives parents the *opportunity* to extend the brood-guarding period, but they must also be proficient foragers to simultaneously increase growth rates, and thus the size at which chicks enter the crèche. A similar study in the closely-related Chinstrap Penguin (*Pygoscelis antarctica*) also found negative relationships between crèching age and hatch date, but no relationship between hatch date and growth or survival (Vinuela et al. 1996, Moreno et al. 1997). I found no correlation between parent age and crèche age, and a previous analysis revealed no relationship between parent age and offspring growth rate (Jennings 2015, Chapter 3). Thus these differences may be due to inherent heterogeneity in individual quality, rather than age-related processes. The results presented here are consistent with previous work at this colony and elsewhere indicating that a relatively small proportion of the population regularly breeds successfully and contributes a disproportionate number of recruits to the population, particularly during years with challenging environmental conditions (Lewis et al. 2006, Lescroël et al. 2009). However, it is important to remember that individual parent quality was not explicitly tested in this study, so these results simply suggest a direction for future research.

I found that when chicks had faster mass and flipper growth rates, and were older when they entered the crèche, they also entered the crèche heavier and with longer flippers. At first glance this is an intuitive result. However, because *both* crèching age and growth rates received strong support in the best model, a closer examination of these

results might indicate that parents can maximize chick growth rates while at the same time retaining one parent at the nest for chick defense. In contrast, if only crèching age or only growth rate were included in the best model predicting size at crèching, it would have indicated that parents were making trade-offs between chick provisioning and chick defense. Because I also found a positive relationship between size when entering the crèche and subsequent survival, these results suggests a direct mechanism for increased fitness in the parents that can maximize chick provisioning and defense.

It is important to acknowledge the potential limitations of my research. For example, the repeated capture or disturbance of chicks and adults may disrupt reproductive behaviors (i.e. courtship, nest-guarding) or have negative physiological impacts (increased heart rate) on penguins, with both distance between humans and penguins and duration of contact determining the degree of disturbance (Woehler et al 1994; Lynch et al 2009; Viblanc et al 2012). However, penguins may also habituate to regular disturbance (Walker et al. 2006, Viblanc et al. 2012), and modification of human behavior and research practices has been shown to minimize disturbance (Giese 1998, Martín et al. 2004). In this study I used a combination of time-limited searches, preliminary searches from a distance, and attention to visual cues of apparent stress in penguin adults and chicks to reduce disturbance. The disturbance associated with capture and measurement generally lasted about 10 minutes per chick, and upon release chicks generally returned to their nest or a crèche within 1 minute (generally within seconds), thus I believe capture did not directly increase risk of predation. Measurement visits were separated by 5 days, and between these visits nests were only observed once or twice from a distance of 5-20 m, thus reducing the acute day to day stress associated with human presence and capture of chicks. I believe that mortality amongst the chicks measured for this study was not systematically or substantially higher than for the colony as a whole. I was also unable to explicitly differentiate between variation in parental investment versus variation in individual heterogeneity in quality of parents in this study. However, about half of the nests for this study (“KA” subset; known-breeding history) were selected to represent individual parents across a range of relative breeding qualities. The relative breeding quality was determined by examining the breeding history of each individual and determining whether they were more or less successful than an “average”

individual; these relative breeding success were aggregated across each year that an individual was detected in the breeding colony (similar to Lescroël et al. 2009). Thus, while I did not quantitatively account for individual heterogeneity in quality, my sample was stratified somewhat across individual parent quality.

It is also important to bear in mind that growth rates for this study were calculated only over the period extending to about 40 days old. Thus, this covariate may not have captured all the complexities of plateauing growth rates between chicks. Fitting sigmoid curves to growth rates could have allowed more subtle evaluation of the growth rate-survival relationships. However, using just the linear period to estimate growth rates provided a measure of growth which was more comparable between chicks that survived versus those that did not, and allowed me to address the primary questions of interest in this study. The lack of relationship between growth rates and survival could have been the result of some chicks dying before I had measured them enough times to calculate growth rate ( $\geq 3$  measurements); it is possible that it was the very slowest-growing chicks that died within the first 10-15 days after hatching, and this would not be reflected in my analysis of growth rates and survival. However, in chicks which lived to be measured at least 3 times, there was no relationship between growth and survival. Finally, although nest position (edge or interior of nest group) has been shown to influence chick survival (Davis and McCaffrey 1986), I did not explicitly account for that here because of sample size limitations. Rather, the nests included in this study were selected from groups of nests in different positions within a subcolony with the intent of avoiding systematic bias due to this factor.

This study identified likely mechanisms between parental investment and offspring survival. Interestingly, I found that there was not a direct relationship between growth rate and survival, but rather an indirect relationship based on the size at which offspring reach a critical transition period during the rearing period. My results quantified the way in which some parents can increase offspring survival by simultaneously maximizing the duration of offspring defense and offspring growth rates. These results provide a valuable contribution to our understanding of the complex ways in which



parental investment and environmental conditions interact in determining individual reproductive success.

## ACKNOWLEDGMENTS

I would like to thank Libby Porzig, Annie Schmidt, Annie Pollard, Amelie Lescroël, Melanie Massaro, Arvind Varsani, Megan Elrod and Jean Pennycook for their assistance with field work, and additionally Arvind Varsani and Melanie Massaro for contributing funds, expertise and personal time for the molecular sexing. I also thank Donald Lyons and Lorenzo Ciannelli for valuable discussions that helped greatly with this research. The US Antarctic Program provided logistic support; financial support was provided by NSF grants *ANT- 0944411*. S. Jennings received additional support from Oregon State University, Fisheries and Wildlife Department (M. A. Ali Graduate Chair Award in Fisheries Biology). All penguin chick capture, handling, and data collection methods performed during this study were approved under appropriate Antarctic Conservation Act permits from the National Science Foundation Office of Polar Programs and Oregon State University's Institutional Animal Care and Use Committee. This is Point Blue Conservation Science Contribution No. XXXX. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

## REFERENCES

- Ainley, D. G. 2002. *The Adelie Penguin: Bellwether of Climate Change*. Columbia University Press, New York, New York, USA.
- Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. *The Condor* 105:95–106.
- Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87:2080–93.
- Ainley, D. G., E. D. Clarke, K. Arrigo, W. R. Fraser, A. Kato, K. J. Barton, and P. R. Wilson. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean , 1950s to the 1990s. *Antarctic Science* 17:171–182.
- Ainley, D. G., R. E. LeResche, and W. J. L. Sladen. 1983. *Breeding Biology of the Adelie Penguin*. Page 240.
- Ainley, D. G., and R. P. Schlatter. 1972. Chick raising ability in Adelie Penguins. *Auk* 89:559–566.
- Ashmole, N. P. 1963. The Regulation of Numbers of Tropical Oceanic Birds. *Ibis* 103:458–473.
- Badyaev, A. V, and C. K. Ghalambor. 2001. Evolution of Life Histories along Elevational Gradients: Trade-Off between Parental Care and Fecundity. *Ecology* 82:2948–2960.
- Ballard, G., K. Dugger, N. Nur, and D. Ainley. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405:287–302.
- Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa, and A. Stien. 2011. Plastic reproductive allocation as a buffer against environmental stochasticity - linking life history and population dynamics to climate. *Oikos* 120:245–257.
- Beaulieu, M., A.-M. Thierry, T. Raclot, Y. Le Maho, Y. Ropert-Coudert, H. Gachot-Neveu, and A. Ancel. 2009. Sex-specific parental strategies according to the sex of offspring in the Adelie penguin. *Behavioral Ecology* 20:878–883.
- Catry, P., R. Matias, L. Vicente, and J. P. Granadeiro. 2009. Brood-guarding behaviour in Cory's Shearwaters (*Calonectris diomedea*). *Journal of Ornithology* 150:103–108.

- Catry, P., R. a. Phillips, J. Forcada, and J. P. Croxall. 2006. Factors affecting the solution of a parental dilemma in albatrosses: at what age should chicks be left unattended? *Animal Behaviour* 72:383–391.
- Chappell, M. A., D. N. Janes, V. H. Shoemaker, T. L. Bucher, and S. K. Maloney. 1993. Reproductive effort in Adelie penguins. *Behavioral Ecology and Sociobiology* 33:173–182.
- Clarke, J., K. Kerry, L. Irvine, and B. Phillips. 2002. Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. *Polar Biology* 25:21–30.
- Davis, L. S. 1982. Creching behaviour of Adelie penguin chicks (*Pygoscelis adeliae*). *New Zealand Journal of Zoology* 9:279–286.
- Davis, L. S., and F. T. Mccaffrey. 1986. Survival Analysis of eggs and chicks of Adelie Penguins (*Pygoscelis adeliae*). *Auk* 103:379–388.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152:317–323.
- Dugger, K. M., G. Ballard, D. G. Ainley, P. O. Lyver, and C. Schine. 2014. Adelie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution* 2:1–12.
- Evans, R. M. 1984. Some causal and functional correlates of creching in young white pelicans. *Canadian Journal of Zoology* 62:814–819.
- Laake, J.L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Le Galliard, J.-F., R. Ferriere, and J. Clobert. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* 111:368–376.
- Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science (New York, N.Y.)* 292:494–7.
- Giese, M. 1998. Guidelines for people approaching breeding groups of Adélie penguins (*Pygoscelis adeliae*). *Polar Record* 34:287–292.
- Hipkiss, T., B. Hornfeldt, U. Eklund, and S. Berlin. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings. *Journal of Animal Ecology* 71:693–699.
- Hunt, G. L. J., and M. W. Hunt. 1976. Gull Chick Survival: The Significance of Growth Rates , Timing of Breeding and Territory Size. *Ecology* 57:62–75.

- Jodice, P. G. R., D. D. Roby, S. A. Hatch, V. A. Gill, R. B. Lanctot, and G. H. Visser. 2002. Does food availability affect energy expenditure rates of nesting seabirds? A supplemental-feeding experiment with Black-legged Kittiwakes (*Rissa tridactyla*). *Canadian Journal of Zoology* 222:214–222.
- Kim, S.-Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. *Oecologia* 166:615–26.
- Komdeur, J. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. *Behavioral Ecology* 10:648–658.
- Lebreton, J.-D., K. P. Burnam, J. Clobert, and D. R. Anderson. 1992. Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies. *Ecological Monographs* 62:67–118.
- Lescroël, A., G. Ballard, V. Toniolo, K. J. Barton, P. R. Wilson, P. O. Lyver, and D. G. Ainley. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology* 91:2044–55.
- Lescroël, A., K. M. Dugger, G. Ballard, and D. G. Ainley. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology* 78:798–806.
- Lewis, S., S. Wanless, D. A. Elston, M. D. Schultz, E. Mackley, M. Du Toit, J. G. Underhill, and M. P. Harris. 2006. Determinants of quality in a long-lived colonial species. *The Journal of Animal Ecology* 75:1304–12.
- Lynch, H. J., W. F. Fagan, and R. Naveen. 2009. Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic Peninsula. *Polar Biology* 33:493–503.
- Lyver, P. O., M. Barron, K. J. Barton, D. G. Ainley, A. Pollard, S. Gordon, S. McNeill, G. Ballard, and P. R. Wilson. 2014. Trends in the breeding population of Adélie penguins in the Ross Sea, 1981–2012: a coincidence of climate and resource extraction effects. *PloS One* 9:e91188.
- Maness, T. J., and D. J. Anderson. 2013. Predictors of Juvenile Survival in Birds. Pages 1–55 *Ornithological Monographs*.
- Markman, S., Y. Yom-Tov, and J. Wright. 1995. Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Animal Behaviour* 50:655–669.
- Martín, J., L. de Neve, J. A. Fargallo, V. Polo, and M. Soler. 2004. Factors affecting the escape behaviour of juvenile chinstrap penguins, *Pygoscelis antarctica*, in response to human disturbance. *Polar Biology* 27:775–781.

- Moreno, J., A. Barbosa, J. Potti, and S. Merino. 1997. The effects of hatching date and parental quality on chick growth and creching age in the Chinstrap Penguin (*Pygoscelis antarctica*): a field experiment. *Auk* 114:47–54.
- Munro, A. J., and J. Bédard. 1977. Crèche Formation in the Common Eider. *The Auk* 94:759–771.
- Nisbet, I. C. T., J. S. Hatfield, W. A. Link, and J. A. Spendelow. 1998. Predicting Chick Survival and Productivity of Roseate Terns from Data on Early Growth. *Waterbirds* 22:90–97.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Råberg, L., M. Stjernman, and J.-A. Å. Nilsson. 2005. Sex and environmental sensitivity in blue tit nestlings. *Oecologia* 145:496–503.
- Rothenbach, C. A., and J. P. Kelly. 2012. The parental dilemma under variable predation pressure: adaptive variation in nest attendance by Great Egrets. *The Condor* 114:90–99.
- Ricklefs, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *The Ibis* 115: 177–201.
- Spurr, E. B. 1975. Behavior of the Adelie Penguin chick. *Condor* 77:272–280.
- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Taylor, R. H. 1962. The Adelie Penguin (*Pygoscelis adeliae*) at Cape Royds. *Ibis* 104:176–204.
- Tenaza, R. 1971. Behavior and nesting success relative to nest location in adelie penguins (*Pygoscelis adeliae*). *The Condor* 73:81–92.
- Varpe, Ø., T. Tveraa, and I. Folstad. 2004. State-dependent parental care in the Antarctic petrel: responses to manipulated chick age during early chick rearing. *Oikos* 106:479–488.
- Viblanc, V. a, A. D. Smith, B. Gineste, and R. Groscolas. 2012. Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC ecology* 12:10.
- Vinuela, J., J. Moreno, L. M. Carrascal, J. J. Sanz, J. A. Amat, M. Ferrer, J. Belliure, and J. J. Cuervo. 1996. The effect of hatching date on parental care, chick growth, and chick mortality in the Chinstrap Penguin (*Pygoscelis antarctica*). *The Zoological Society of London* 240:51–58.

- Vleck, C. M., L. L. Ross, D. Vleck, and T. L. Bucher. 2000. Prolactin and parental behavior in Adélie penguins: effects of absence from nest, incubation length, and nest failure. *Hormones and behavior* 38:149–58.
- Volkman, N. J., and W. Trivelpiece. 1980. Growth in pygoscelid penguin chicks. *Journal of Zoology, London* 191:521–530.
- Walker, B. G., P. Dee Boersma, and J. C. Wingfield. 2006. Habituation of adult magellanic penguins to human visitation as expressed through behavior and corticosterone secretion. *Conservation Biology* 20:146–154.
- Wanker, R., L. C. Bernate, and D. Franck. 1996. Socialization of Spectacled Parrotlets (*Forpus conspicillatus*): the role of parents, crèches and sibling groups in nature. *Journal of Ornithology* 137:447–461.
- Wanless, S., M. P. Harris, P. Redman, and J. R. Speakman. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294:1–8.
- Wasser, S. K., and G. Norton. 1993. Baboons adjust secondary sex ratio in response to predictors of sex-specific offspring survival. *Behavioral Ecology and Sociobiology* 32:273–281.
- Williams, T. D., and J. P. Croxall. 1991. Chick growth and survival in gentoo penguins (*Pygoscelis papua*): effect of hatching asynchrony and variation in food supply. *Polar Biology* 11:197–202.
- Woehler, E. J., R. L. Penney, S. M. Creet, and H. R. Burton. 1994. Impacts of human visitors on breeding success and long-term population trends in Adelie Penguins at Casey, Antarctica. *Polar Biology* 14.
- Ydenberg, R. C., and D. F. Bertram. 1989. Lack's clutch size hypothesis and brood enlargement studies on colonial seabirds. *Colonial Waterbirds* 12:134–137.

Table 4.1. Names and descriptions of covariates considered in models to estimate daily survival of Adélie Penguin chicks at Cape Crozier, Ross Island, Antarctica. Also include whether covariate was used for modeling survival ( $\phi$ ), resighting probability ( $p$ ), or both.

Variable name	Variable description	Model parameters
Year	2012-13 (0) or 2013-14 (1)	$\phi, p$
Sex	Female (0) or Male (1)	$\phi, p$
<u>Time constraints</u>		
t	time- represents full time-dependence	$\phi, p$
T	linear time trend	$\phi, p$
TT	quadratic time effect	$\phi, p$
lnT	logarithmic time trend	$\phi, p$
<u>Growth rates</u>		
MassGrowth	Mass growth rate (g d-1)	$\phi$
FlipGrowth	Flipper length growth rate (mm d-1)	$\phi$
TibGrowth	Tibiotarsus length growth rate (mm d-1)	$\phi$
<u>Crèche size and age</u>		
CrMass	Mass on day when entered crèche stage	$\phi$
CrFlip	Flipper length on day when entered crèche	$\phi$
CrTib	Tibiotarsus length on day when entered crèche	$\phi$
CrAge	Age when entered crèche	$\phi$
<u>Time varying individual covariates</u>		
InCr	Whether or not a chick is in the crèche stage on a given day.	$\phi$
age	Age of a chick on a given day	$\phi$
<u>Other</u>		
Hatch	Relative hatch date- calculated separately for each year. Negative value indicates hatch date earlier than average.	$\phi$
Cr	Dummy variable for chicks that survived to crèche stage. Used to exclude chicks that didn't survive to crèche from being considered in comparison of crèche size and age to subsequent survival.	$\phi$

Table 4.2. Model selection results for determining factors related to the size and age at which Adélie Penguin chicks enter the crèche at Cape Crozier, Ross Island, Antarctica. K is number of model parameters,  $\Delta AICc$  is the difference in corrected AIC values of each model from the best-supported model. AICc Wt. is the relative AICc weight for each model, and  $-2\ln L$  is negative 2 times the log-likelihood.

Crèching age	K	$\Delta AICc$	AICc wt	$-2\ln L$
Hatch + Sex + Year	6	0.000	0.506	343.668
MassGrowth + Hatch + Sex + Year	7	2.151	0.173	343.4026
FlipGrowth+ Hatch + Sex + Year	7	2.210	0.168	343.4608
TibGrowth + Hatch + Sex + Year	7	2.387	0.154	343.6376
MassGrowth + Sex + Year	6	31.475	0.000	375.1426
Sex + Year	5	34.520	0.000	380.5382
FlipGrowth + Sex + Year	6	35.780	0.000	379.4484
TibGrowth + Sex + Year	6	36.389	0.000	380.057
Intercept only	3	41.381	0.000	391.912

Crèching Mass	K	$\Delta AICc$	AICc wt	$-2\ln L$
MassGrowth + Hatch + Sex + Year	6	0.000	0.861	1229.067
MassGrowth + Sex + Year	5	3.649	0.139	1235.038
Hatch + Sex + Year	5	33.044	0.000	1264.433
Sex + Year	4	50.992	0.000	1284.643

Crèching flipper length	K	$\Delta AICc$	AICc wt	$-2\ln L$
FlipGrowth + Hatch + Sex + Year	6	0.000	0.708	772.149
Hatch + Sex + Year	5	1.771	0.292	776.2416
FlipGrowth+ Sex + Year	5	18.691	0.000	793.162
Sex + Year	4	25.543	0.000	802.2764

Crèching tibiotarsus length	K	$\Delta AICc$	AICc wt	$-2\ln L$
Hatch + Sex + Year	5	0.000	0.741	720.4216
TibGrowth + Hatch + Sex + Year	6	2.097	0.260	720.1972
Sex + Year	4	19.473	0.000	742.157
TibGrowth + Sex + Year	5	21.693	0.000	742.1142

Table 4.3. Model selection results for determining the best model structure for estimating resighting probability of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2

Model [includes $\phi$ (Year*Sex*t)]	K	$\Delta QAICc$	QAICc wt	$-2\ln L$
$p$ (Year + t)	241	0.000	1.000	1478.786
$p$ (.)	193	404.356	0.000	2154.317



Table 4.4. Model selection results from the first stage of survival modeling: determining factors related the survival probability of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2

Model [includes $p(\text{Year}+t)$ ]	K	$\Delta\text{QAICc}$	QAICc wt	-2lnL
$\varphi$ (Year * Sex)	53	0.000	0.448	1567.393
$\varphi$ (Year)	51	0.331	0.380	1573.205
$\varphi$ (Year + Sex)	52	2.271	0.144	1572.912
$\varphi$ (.)	50	6.124	0.021	1583.082

Table 4.5. Model selection results from the second stage of survival modeling: determining factors related the survival of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2

Model [includes $p(\text{Year}+t)$ ]	K	$\Delta\text{QAICc}$	QAICc wt	-2lnL
$\varphi$ (Hatch + Year * Sex)	54	0.000	0.674	1558.629
$\varphi$ (Hatch + Hatch <sup>2</sup> + Year * Sex)	55	2.187	0.226	1558.629
$\varphi$ (Year * Sex) <sup>1</sup>	53	4.885	0.059	1567.393
$\varphi$ (Hatch * Year * Sex)	57	5.560	0.042	1557.373

<sup>1</sup>Best-supported model from Table 4.4.

Table 4.6. Model selection results from the third stage of survival modeling: determining the best time constraint for estimates of survival of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2

Model [includes $p(\text{Year}+t)$ ]	K	$\Delta\text{QAICc}$	QAICc wt	-2lnL
$\varphi$ (T + Hatch + Year * Sex)	55	0.000	0.485	1544.405
$\varphi$ (lnT + Hatch + Year * Sex)	55	0.825	0.321	1545.428
$\varphi$ (T + TT + Hatch + Year * Sex)	56	1.891	0.189	1544.034
$\varphi$ (Hatch + Year * Sex) <sup>1</sup>	54	9.284	0.005	1558.629

<sup>1</sup>Best-supported model from Table 4.5.

Table 4.7. Model selection results from the fourth stage of survival modeling: determining relationships between growth rates (mass, flipper, tibiotarsus) and daily survival probability of Adélie Penguin chicks during the entire chick-provisioning period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2

Model [includes $p$ (Year+t)]	K	$\Delta\text{QAICc}$	QAICc wt	-2lnL
$\phi$ (TibGrowth + T + Hatch + Year * Sex)	56	0.000	0.925	1531.263
$\phi$ (MassGrowth + T + Hatch + Year * Sex)	56	5.659	0.055	1538.280
$\phi$ (T + Hatch + Year * Sex) <sup>1</sup>	55	8.408	0.014	1544.405
$\phi$ (FlipGrowth + Time + Hatch + Year * Sex)	56	9.792	0.007	1543.404
$\phi$ (MassGrowth)	51	19.741	0.000	1569.279
$\phi$ (TibGrowth)	51	25.465	0.000	1576.377
$\phi$ (FlipGrowth)	51	26.271	0.000	1577.376

<sup>1</sup>Best-supported model from Table 4.6.

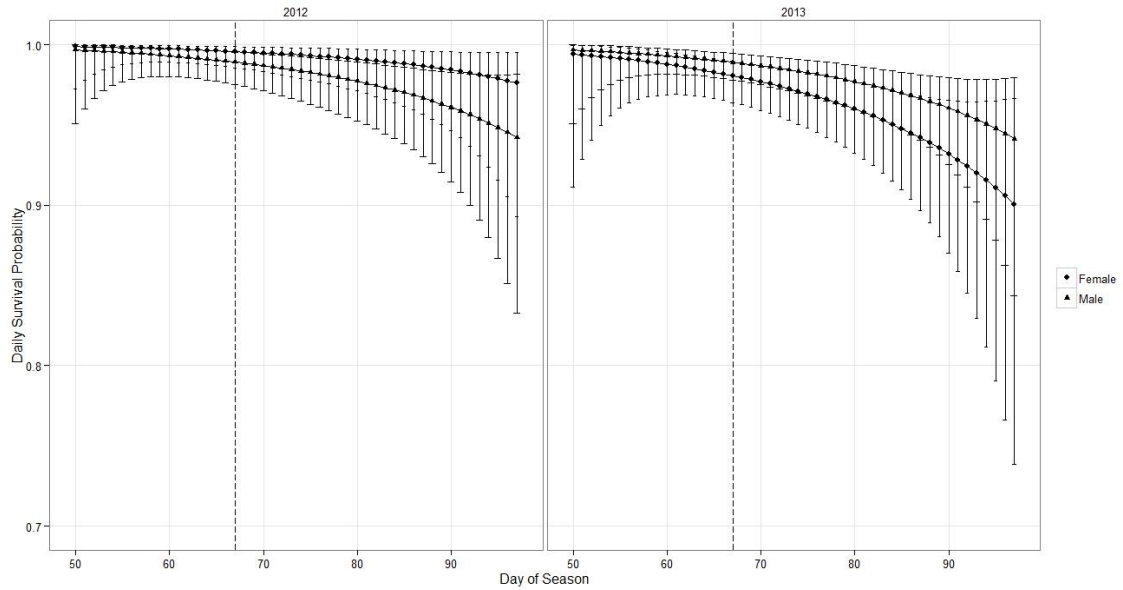
Table 4.8. Model selection results from the fifth stage of survival modeling: determining relationships between size (mass, flipper, tibiotarsus) and age when entering the crèche stage and subsequent daily survival probability of Adélie Penguin chicks during the entire crèche period at Cape Crozier, Ross Island, Antarctica. Overdispersion parameter ( $\hat{c}$ ) = 1.24. Column conventions as in Table 4.2

Model [includes $p$ (Year+t)]	K	$\Delta\text{QAICc}$	QAICc wt	-2lnL
$\phi$ (Cr + CrFlip + T + Hatch + Year * Sex)	57	0.000	0.326	1495.578
$\phi$ (Cr + CrMass + T + Hatch + Year * Sex)	57	0.699	0.230	1496.444
$\phi$ (Cr + CrTib + T + Hatch + Year * Sex)	57	1.180	0.181	1497.041
$\phi$ (Cr + CrAge + Cr:CrFlip + T + Hatch + Year * Sex)	58	2.130	0.112	1495.493
$\phi$ (TibGrowth + T + Hatch + Year * Sex) <sup>1</sup>	56	26.581	0.000	1531.259
$\phi$ (T + Hatch + Year * sex) <sup>2</sup>	55	34.992	0.000	1544.405

<sup>1</sup>Best-supported model from Table 4.7.

<sup>2</sup>Best-supported model from Table 4.6.

Figure 4.1. Model averaged estimates of daily survival probability for male and female Adélie Penguin chick at Cape Crozier, Ross Island, Antarctica, during the Austral summers of 2012-13 (2012) and 2013-14 (2013). Error bar width is greater for males. Dashed line indicates mean crèche date (day 67 in both years; Nov 1= day 1).



## Chapter 5

### GENERAL CONCLUSIONS

Scott Jennings

## PRIMARY FINDINGS

My investigations into the differences in chick growth rates relative to sex (Chapter 2) suggested that male Adélie Penguin chicks grew mass and bill length faster than female chicks, and growth rates of both sexes were faster during the 2012-13 (2012) Austral summer than in 2013-14 (2013). I also found evidence that the diet of male chicks had a greater proportion of fish than females, providing a possible mechanism for the observed differences in growth rates.

In Chapter 3, I observed that mass growth rates of males were most sensitive to proportion of fish in the diet during 2013, when I observed longer foraging trip duration and some evidence of food limitation. In contrast I found little evidence of a relationship between female growth rates and variation in diet composition. I hypothesize that the higher lipid content of a higher-fish diet was required to maintain faster mass growth rates of males when the interval between feedings was greater during 2013. In contrast to mass growth, skeletal growth appeared to be most sensitive to the total amount of food delivered than to diet composition. Growth rates of flipper, tibiotarsus and foot length were all faster when average food delivered per day was greater. However, again this effect was only observed in male chicks, but I found no evidence for year-based differences in this pattern. Finally I found no evidence for a relationship between chick growth rates and foraging trip duration, and no evidence for a relationship between growth rates and parent age.

In Chapter 4 I found that the age at which chicks enter the crèche stage (when both parents forage simultaneously and chicks gather in groups in the colony) was best predicted by hatching date, with earlier-hatching chicks entering the crèche at older ages. In contrast, the mass and flipper length of chicks when they entered the crèche was best predicted by the growth rates of these morphological characteristics, respectively, and also by the age at which they entered the crèche. Chicks that grew faster and were guarded longer also entered the crèche at larger sizes. Because both growth rate and age at crèching were indicated as important in predicting crèching size (rather than just one or the other), these results indicate that Adélie penguin parents can maximize chick growth

through adequate food delivery (see also Chapter 3) and at the same time retain a parent at the nest for chick guarding for a longer period of time.

Daily survival probability for males and females declined through the season during both years of the study, and the pattern of decline was similar for males in both years. In contrast, during the first year female survival probability declined relatively little, while during the second year female survival probability declined more than male survival in either year. Growth rates of mass or skeletal measures had no relationship with chick survival across the entire chick-rearing period. However chick size (mass, and flipper and tibiotarsus length) when entering the crèche was positively-related to subsequent survival during the crèche period. Chicks entering the crèche heavier and with longer flipper and tibiotarsus lengths had higher survival probability during the crèche stage. Interestingly, there was no evidence of a relationship between crèching age and survival during the crèche stage.

Taken together, my results quantify the ways in which reproductive success can be increased when parents invest more in provisioning their offspring, at a presumed greater cost to their own condition. I also document a potential mechanism for increased reproductive success when pairs of parents can simultaneously maximize chick provisioning *and* extend the chick-guarding period. Chick survival was greatest when parents could provide sufficient food for more rapid growth, and at the same time maintain chick-guarding for a longer period, allowing chick(s) to enter the crèche at larger sizes. Survival of male chicks might also be improved in years of challenging environmental conditions if parents can provision their male offspring with a greater proportion of fish.

## CONTRIBUTION AND FINDINGS IN THE CONTEXT OF A CHANGING ROSS SEA

This study provides an important contribution to our understanding of the relationship between offspring sex and patterns of parental investment, and the growth and survival of offspring. These topics have been well studied in terrestrial birds and mammals (e.g., Clutton-Brock et al. 1985) but have received relatively little attention in

seabirds (but see Jones et al. 2009 for a review with some seabird examples). In boobies (*Sula* spp.) and the Great Skua (*Stercorarius skua*), growth of the larger sex (females) was more sensitive to challenging conditions (Velando 2002, Kalmbach 2004), however for the skua, no sex-related differences in chick survival were observed (Kalmbach 2004). In contrast, for the Tengmalm's Owl (*Aegolius funereus*), both growth and survival of the larger sex (female) was less susceptible to fluctuation in food supply (Hipkiss et al. 2002). In partial agreement with these results, for Adélie Penguins I found that growth of the larger sex (males) was more sensitive to variation in type and amount of food delivered, but that survival of the smaller sex showed the biggest response to apparent resource limitation. This study provides evidence that offspring of the two sexes may be provisioned differently, and may have different growth and survival responses, as individuals experience environmental variation.

This study was the first to take resighting probability into account in when examining chick survival of Adélie penguins during the crèche stage. As I observed, daily detection rates could be highly variable; if I had assumed they were 1.0, I would have underestimated daily survival in this study. Despite accounting for imperfect detectability in my estimation of survival estimates I still observed lower chick survival rates after crèche compared to other studies that reported little or no crèche-period chick loss (Taylor 1962, Clarke et al. 2002). It's likely that biological factors were responsible for the differences in my results relative to previous studies, as this is also the first study to examine Adélie Penguin chick survival at such a large colony. Cape Crozier is one of only a few Adélie Penguin colonies with over 100,000 breeding pairs, and it could currently be the largest breeding colony in the world (c. 270,000 pairs; Ainley 2002, Lyver et al. 2014). This colony is likely undergoing density-dependent limitation to colony growth (Lyver et al. 2014) and of particular relevance to this study, there appears to be a consistent negative relationship between colony size and chick mass late in the rearing period amongst the three colonies on Ross Island (Dugger et al. 2014). The fact that the colony continues to grow despite the evidence suggesting density-dependent limitation on reproductive rates may be a consequence of two characteristics of this species: high site fidelity and delayed maturation that results in the majority of birds not recruiting into the breeding population until 5 or 6 years of age (Ainley 2002, Dugger et

al. in prep). Thus there is likely to be a time lag in the response of colony growth to colony size, with the current colony size being the result of environmental conditions 4-10 years in the past.

The results of this study may help us understand or possibly predict Adélie Penguin population responses to two larger scale processes which are currently occurring in the Ross Sea and which may affect penguin prey abundances. The first of these processes is changes in sea ice dynamics. In contrast to areas around the Western Antarctic Peninsula, which have seen marked increases in temperatures and decreases in sea ice in the last decade or so, the Ross Sea region has seen colder temperatures as well as denser sea ice concentration and longer sea ice persistence into the spring (Stammerjohn et al. 2008). Adélie Penguin diet in the Southern Ross Sea can generally be characterized as being comprised of a greater proportion of krill when sea ice concentration (SIC) is high, and a greater proportion of fish when SIC is low (Ainley et al. 1998). Thus the recent increases in SIC might be predicted to result in more krill in penguin diets, which this study suggests may be adequate to maintain chick growth as long as parents are able to capture sufficient quantities of this prey.

A second process with the potential to change the biological community in the Ross Sea is the recent emergence in the Ross Sea of a research-based commercial fishery for Antarctic Toothfish (*Dissostichus mawsoni*) a top predator of this ecosystem. The loss or change in abundance of top predators has profound effects on ecosystem processes in a range of systems (Estes et al. 1989, Fortin et al. 2008). The large scale removal, followed by recovery, of cetaceans from the Southern Ocean has provided evidence that the Ross Sea ecosystem is also sensitive to such changes in predator abundance (Ainley et al. 2007). Food web modeling and empirical observations suggest of this fishery may already be impacting a range of other biota in the Ross Sea (Ainley et al. 2009, Pinkerton et al. 2010). Because Antarctic Silverfish (*Pleurogramma antarcticum*) are a primary prey item of the Toothfish, we may predict an increase in high quality prey items for Adélie Penguin chicks with reduced Toothfish abundance. However, the strength of trophic cascades is highly variable and remains difficult to predict (Borer et al. 2005). Additionally, it is unclear how a potential increase in Silverfish abundance resulting from



Toothfish extraction might interact with the concurrently-occurring increase in SIC concentration described above. Increasing abundance of Silverfish may depress krill populations, potentially resulting in more challenging foraging conditions since in general fish may be more difficult for penguins to capture than krill (O'Brien 1987).

Understanding ecosystem processes and predicting response of organisms to changing conditions is challenging due to the complex nature of ecosystems. Detailed information about the range of demographic and biological response a species can exhibit in relation to varying environmental circumstances is critical to this work. I have shown that as apparent food availability varies, parents may adjust their investment based on offspring sex, likely resulting in sex-based differences in offspring growth and survival under different conditions. These results will allow us to better predict how populations of Adélie Penguins will respond to natural and anthropogenic environmental changes, and will ultimately inform our understanding and management of the Ross Sea Ecosystem.

## BIBLIOGRAPHY

- Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. *The American Naturalist* 147:381–395.
- Ainley, D., G. Ballard, S. Ackley, L. K. Blight, J. T. Eastman, S. D. Emslie, A. Lescroël, S. Olmastroni, S. E. Townsend, C. T. Tynan, P. Wilson, and E. Woehler. 2007. Paradigm lost, or is top-down forcing no longer significant in the Antarctic marine ecosystem? *Antarctic Science* 19:283.
- Ainley, D. G. 2002. *The Adelie Penguin: Bellwether of Climate Change*. Columbia University Press, New York, New York, USA.
- Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and temporal variation of diet within a presumed metapopulation of Adelie Penguins. *The Condor* 105:95–106.
- Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87:2080–93.
- Ainley, D. G., G. Ballard, and S. Olmastroni. 2009. An apparent decrease in the prevalence of “Ross Sea killer whales” in the Southern Ross Sea.
- Ainley, D. G., E. D. Clarke, K. Arrigo, W. R. Fraser, A. Kato, K. J. Barton, and P. R. Wilson. 2005. Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean , 1950s to the 1990s. *Antarctic Science* 17:171–182.
- Ainley, D. G., and W. B. Emison. 1972. Sexual size dimorphism in Adelie Penguins. *Ibis* 114:267–271.
- Ainley, D. G., R. E. LeResche, and W. J. L. Sladen. 1983. *Breeding Biology of the Adelie Penguin*. Page 240.
- Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adelie Penguin populations: overlap in colony-specific foraging areas. *Ecological Monographs* 74:159–178.
- Ainley, D. G., and R. P. Schlatter. 1972. Chick raising ability in Adelie Penguins. *Auk* 89:559–566.
- Ainley, D. G., R. Wilson, and K. J. Barton. 1998. Diet and foraging effort of Adelie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biology* 20:311–319.

- Alonso-Alvares, C., S. Bertrand, B. Faivre, and G. Sorci. 2007. Increased susceptibility to oxidative damage as a cost of accelerated somatic growth in zebra finches. *Functional Ecology* 21:873–879.
- Arendt, J. D. 1997. Adaptive Intrinsic Growth rates: an integration across taxa. *The Quarterly Review of Biology* 72:149–177.
- Arnold, T. W. 2010. Uninformative parameters and model selection using akaike's information criterion. *Journal of Wildlife Management* 74:1175–1178.
- Ashmole, N. P. 1963. The Regulation of Numbers of Tropical Oceanic Birds. *Ibis* 103:458–473.
- Ashmole, N. P. 1971. Sea Bird Ecology and the Marine Environment. *Avian Biology* 1:223–286.
- Badyaev, A. V. 2002. Male and Female Growth in Sexually Dimorphic Species : Harmony , Conflict , or Both ? 11–33.
- Badyaev, A. V, and C. K. Ghalambor. 2001. Evolution of Life Histories along Elevational Gradients: Trade-Off between Parental Care and Fecundity. *Ecology* 82:2948–2960.
- Ballard, G., D. G. Ainley, C. A. Ribic, and K. R. Barton. 2001. Effect of Instrument Attachment and Other Factors on Foraging Trip Duration and Nesting Success of Adelie Penguins. *The Condor* 103:481–490.
- Ballard, G., K. Dugger, N. Nur, and D. Ainley. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405:287–302.
- Bårdsen, B.-J., J.-A. Henden, P. Fauchald, T. Tveraa, and A. Stien. 2011. Plastic reproductive allocation as a buffer against environmental stochasticity - linking life history and population dynamics to climate. *Oikos* 120:245–257.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7, <URL: <http://CRAN.R-project.org/package=lme4>>.
- Bearhop, S., S. Waldron, S. C. Votier, and R. W. Furness. 2010. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and biochemical zoology*: PBZ 75:451–458.
- Beaulieu, M., A.-M. Thierry, T. Raclot, Y. Le Maho, Y. Ropert-Coudert, H. Gachot-Neveu, and A. Ancel. 2009. Sex-specific parental strategies according to the sex of offspring in the Adelie penguin. *Behavioral Ecology* 20:878–883.

- Becker, P. H., and M. Wink. 2003. Influences of sex, sex composition of brood and hatching order on mass growth in common terns *Sterna hirundo*. *Behavioral Ecology and Sociobiology* 54:136–146.
- Berman, C. M. 1988. Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. *The American Naturalist* 29:913–930.
- Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology* 111:977–1017.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–537.
- Bunce, A., S. J. Ward, and F. I. Norman. 2005. Are age-related variations in breeding performance greatest when food availability is limited? *Journal of Zoology* 266:163–169.
- Burnam, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York.
- Burns, J. M., S. J. Trumble, M. A. Castellini, and J. W. Testa. 1998. The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. *Polar Biology* 19:272–282.
- Byers, J., and J. Moodie. 1990. Sex-specific maternal investment in pronghorn, and the question of a limit on differential provisioning in ungulates. *Behavioral Ecology and Sociobiology* 26:157–164.
- Catry, P., R. Matias, L. Vicente, and J. P. Granadeiro. 2009. Brood-guarding behaviour in Cory's Shearwaters (*Calonectris diomedea*). *Journal of Ornithology* 150:103–108.
- Catry, P., R. a. Phillips, J. Forcada, and J. P. Croxall. 2006. Factors affecting the solution of a parental dilemma in albatrosses: at what age should chicks be left unattended? *Animal Behaviour* 72:383–391.
- Chapman, E., E. Hofmann, D. Patterson, C. Ribic, and W. Fraser. 2011. Marine and terrestrial factors affecting Adélie Penguin *Pygoscelis adeliae* chick growth and recruitment off the western Antarctic Peninsula. *Marine Ecology Progress Series* 436:273–289.
- Chapman, E. W., E. E. Hofmann, D. L. Patterson, and W. R. Fraser. 2010. The effects of variability in Antarctic krill (*Euphausia superba*) spawning behavior and sex/maturity stage distribution on Adélie Penguin (*Pygoscelis adeliae*) chick growth: A modeling study. *Deep Sea Research Part II: Topical Studies in Oceanography* 57:543–558.

- Chappell, M. A., D. N. Janes, V. H. Shoemaker, T. L. Bucher, and S. K. Maloney. 1993. Reproductive effort in Adelie penguins. *Behavioral Ecology and Sociobiology* 33:173–182.
- Clarke, J., K. Kerry, L. Irvine, and B. Phillips. 2002. Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. *Polar Biology* 25:21–30.
- Clutton-Brock, T. H. 1991. The evolution of parental care. Pages 1–352. Princeton University Press, Princeton, New Jersey.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1981. Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487–489.
- Clutton-Brock, T. H., S. D. Albon, and F. E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* 313:131–133.
- Daunt, F., P. Monaghan, S. Wanless, M. P. Harris, and R. Griffiths. 2001. Sons and daughters: age-specific differences in parental rearing capacities. *Functional Ecology* 15:211–216.
- Davis, L. S. 1982. Creching behaviour of Adelie penguin chicks (*Pygoscelis adeliae*). *New Zealand Journal of Zoology* 9:279–286.
- Davis, L. S., and F. T. Mc Caffrey. 1986. Survival Analysis of eggs and chicks of Adelie Penguins (*Pygoscelis adeliae*). *Auk* 103:379–388.
- Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? *Biological reviews of the Cambridge Philosophical Society* 86:97–116.
- Doherty, P. F., G. C. White, and K. P. Burnham. 2012. Comparison of model building and selection strategies. *Journal of Ornithology* 152:317–323.
- Dugger, K. M., D. G. Ainley, P. O. Lyver, K. Barton, and G. Ballard. 2010. Survival differences and the effect of environmental instability on breeding dispersal in an Adelie penguin meta-population. *Proceedings of the National Academy of Sciences of the United States of America* 107:12375–80.
- Dugger, K. M., G. Ballard, D. G. Ainley, P. O. Lyver, and C. Schine. 2014. Adelie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution* 2:1–12.
- Dunn, P. O., L. A. Whittingham, T. E. Pitcher, S. Evolution, N. Jan, and P. O. Dunn. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55:161–175.
- Eastman, J. T. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology* 4:155–160.

- Erikstad, K. E., M. Asheim, P. Fauchald, L. Dahlhaug, T. Tveraa, and P. Dahlhaug. 1997. Adjustment of parental effort in the puffin; the roles of adult body condition and chick size. *Behavioral Ecology and Sociobiology* 40:95–100.
- Estes, J. A., D. O. Duggins, and G. B. Rathbun. 1989. The ecology of extinctions in kelp forest communities. *Conservation Biology*. 3: 252–264
- Evans, R. M. 1984. Some causal and functional correlates of creching in young white pelicans. *Canadian Journal of Zoology* 62:814–819.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2008. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Fridolfsson, A.-K., and H. Ellegren. 1999. A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* 20:116–121.
- Fuiman, L. A., R. W. Davis, and T. M. Williams. 2002. Behavior of midwater fishes under the Antarctic ice: observations by a predator. *Marine Biology* 140:815–822.
- Le Galliard, J.-F., R. Ferriere, and J. Clobert. 2005. Juvenile growth and survival under dietary restriction: are males and females equal? *Oikos* 111:368–376.
- Ghalambor, C. K., and T. E. Martin. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science (New York, N.Y.)* 292:494–7.
- Giese, M. 1998. Guidelines for people approaching breeding groups of Adélie penguins (*Pygoscelis adeliae*). *Polar Record* 34:287–292.
- Granadeiro, P., M. Nunes, N. C. Silva, and R. W. Furness. 1998. Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Animal Behaviour* 56:1169–1176.
- Griffeths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. *Molecular Ecology* 7:1071–1075.
- Harris, M. P., M. Frederiksen, and S. Wanless. 2007. Within- and between-year variation in the juvenile survival of Common Guillemots *Uria aalge*. *Ibis* 149:472–481.
- Hipkiss, T., B. Hornfeldt, U. Eklund, and S. Berlin. 2002. Year-dependent sex-biased mortality in supplementary-fed Tengmalm's owl nestlings. *Journal of Animal Ecology* 71:693–699.
- Hodum, P. J., and K. A. Hobson. 2000. Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analyses. *Marine Ecology Progress Series* 198:273–281.

- Hunt, G. L. J., and M. W. Hunt. 1976. Gull Chick Survival: The Significance of Growth Rates , Timing of Breeding and Territory Size. *Ecology* 57:62–75.
- Jodice, P. G. R., D. D. Roby, S. A. Hatch, V. A. Gill, R. B. Lanctot, and G. H. Visser. 2002. Does food availability affect energy expenditure rates of nesting seabirds? A supplemental-feeding experiment with Black-legged Kittiwakes (*Rissa tridactyla*). *Canadian Journal of Zoology* 222:214–222.
- Jones, K. S., S. Nakagawa, and B. C. Sheldon. 2009. Environmental sensitivity in relation to size and sex in birds: meta-regression analysis. *The American naturalist* 174:122–33.
- Kalmbach, E. 2004. Sex-biased environmental sensitivity: natural and experimental evidence from a bird species with larger females. *Behavioral Ecology* 16:442–449.
- Kim, S.-Y., J. C. Noguera, J. Morales, and A. Velando. 2010. Quantitative genetic evidence for trade-off between growth and resistance to oxidative stress in a wild bird. *Evolutionary Ecology* 25:461–472.
- Kim, S.-Y., A. Velando, R. Torres, and H. Drummond. 2011. Effects of recruiting age on senescence, lifespan and lifetime reproductive success in a long-lived seabird. *Oecologia* 166:615–26.
- Kitaysky, A. S., G. L. Hunt. Jr, E. N. Flint, M. A. Rubega, and M. B. Decker. 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Marine Ecology Progress Series* 206:283–296.
- Kohut, J., K. Bernard, W. Fraser, M. J. Oliver, H. Statscewich, P. Winsor, and T. Miles. 2014. Studying the impacts of local oceanographic processes on Adélie Penguin foraging ecology. *Marine Technology Society Journal* 48:25–34.
- Komdeur, J. 1999. Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. *Behavioral Ecology* 10:648–658.
- Kuznetsova, A., P. B. Brockhoff, and R. H. Bojesen. 2014. lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0-11. <http://CRAN.R-project.org/package=lmerTest>.
- Laake, J.L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Western Printing Services, Bristol.
- Lebreton, J.-D., K. P. Burnam, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.

- Leonard, M. L., K. L. Teather, A. G. Horn, W. D. Koenig, and J. L. Dickinson. 1994. Provisioning in western bluebirds is not related to offspring sex. *Behavioral Ecology* 5:455–459.
- Lescroël, A., G. Ballard, V. Toniolo, K. J. Barton, P. R. Wilson, P. O. Lyver, and D. G. Ainley. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology* 91:2044–55.
- Lescroël, A., K. M. Dugger, G. Ballard, and D. G. Ainley. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *Journal of Animal Ecology* 78:798–806.
- Lewis, S., S. Wanless, D. A. Elston, M. D. Schultz, E. Mackley, M. Du Toit, J. G. Underhill, and M. P. Harris. 2006. Determinants of quality in a long-lived colonial species. *The Journal of Animal Ecology* 75:1304–12.
- Lishman, G. S. 1985. The food and feeding ecology of Adelie Penguins (*Pygoscelis adeliae*) and Chinstrap penguins (*P. antarctica*) at Signey Island, South Orkney Islands. *The Zoological Society of London* 205:245–263.
- Lynch, H. J., W. F. Fagan, and R. Naveen. 2009. Population trends and reproductive success at a frequently visited penguin colony on the western Antarctic Peninsula. *Polar Biology* 33:493–503.
- Lyver, P. O., M. Barron, K. J. Barton, D. G. Ainley, A. Pollard, S. Gordon, S. McNeill, G. Ballard, and P. R. Wilson. 2014. Trends in the breeding population of Adélie penguins in the Ross Sea, 1981–2012: a coincidence of climate and resource extraction effects. *PloS One* 9:e91188.
- Maness, T. J., and D. J. Anderson. 2013. Predictors of Juvenile Survival in Birds. Pages 1–55 *Ornithological Monographs*.
- Mangel, M., and J. Stamps. 2001. Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evolutionary Ecology Research* 3:583–593.
- Marchetti, K., and T. Price. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. *Biological Reviews* 64:51–70.
- Markman, S., Y. Yom-Tov, and J. Wright. 1995. Male parental care in the orange-tufted sunbird: behavioural adjustments in provisioning and nest guarding effort. *Animal Behaviour* 50:655–669.
- Martín, J., L. de Neve, J. A. Fargallo, V. Polo, and M. Soler. 2004. Factors affecting the escape behaviour of juvenile chinstrap penguins, *Pygoscelis antarctica*, in response to human disturbance. *Polar Biology* 27:775–781.



- Martins, T. L. F. 2004. Sex-specific growth rates in zebra finch nestlings: a possible mechanism for sex ratio adjustment. *Behavioral Ecology* 15:174–180.
- Moreno, J., A. Barbosa, J. Potti, and S. Merino. 1997. The effects of hatching date and parental quality on chick growth and creching age in the Chinstrap Penguin (*Pygoscelis antarctica*): a field experiment. *Auk* 114:47–54.
- Munro, A. J., and J. Bédard. 1977. Crèche Formation in the Common Eider. *The Auk* 94:759–771.
- Nisbet, I. C. T., J. S. Hatfield, W. A. Link, and J. A. Spendelov. 1998. Predicting Chick Survival and Productivity of Roseate Terns from Data on Early Growth. *Waterbirds* 22:90–97.
- O'Brien, D. P. 1987. Description of escape responses of krill (Crustacea: Eupausiacea), with particular reference to swarming behavior and the size and proximity of the predator. *Journal of Crustacean Biology* 7:449–457.
- Olsen, B. J., R. Greenberg, J. R. Walters, and R. C. Fleischer. 2013. Sexual dimorphism in a feeding apparatus is driven by mate choice and not niche partitioning. *Behavioral Ecology*. 1-12
- Olson, G. S., E. M. Glenn, R. G. Anthony, E. D. Forsman, Janice A. Reid, P. J. Loschl, and W. J. Ripple. 2004. Modeling demographic performance of northern spotted owls relative to forest habitat in Oregon. *The Journal of Wildlife Management* 68:1039–1053.
- Phillips, R. A., and J. P. Croxall. 2003. Control of provisioning in grey-headed albatrosses (*Thalassarche chrysostoma*): do adults respond to chick condition? *Canadian Journal of Zoology* 116:111–116.
- Pinkerton, M. H., J. M. Bradford-Grieve, and S. M. Hanchet. 2010. A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Science* 17:1–31.
- Plavcan, J. M., and C. P. van Schaik. 1997. Intrasexual competition and body weight dimorphism in anthropoid primates. *American journal of physical anthropology* 103:37–68.
- Polito, M., S. D. Emslie, and W. Walker. 2002. A 1000-year record of Adélie Penguin diets in the southern Ross Sea. *Antarctic Science* 14:327–332.
- R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Råberg, L., M. Stjernman, and J.-A. Å. Nilsson. 2005. Sex and environmental sensitivity in blue tit nestlings. *Oecologia* 145:496–503.

- Raccurt, M., F. Baudimont, J. Tirard, B. Rey, E. Moureaux, A. G  lo  n, and C. Duchamp. 2008. Growing in Antarctica, a challenge for white adipose tissue development in Adelie penguin chicks (*Pygoscelis adeliae*). *American journal of physiology. Regulatory, integrative and comparative physiology* 295:R1671–R1679.
- Richter, W. 1983. Balanced Sex Ratios in Dimorphic Altricial Birds: The Contribution of Sex-Specific Growth Dynamics. *The American Naturalist* 121:158–171.
- Ricklefs, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *The Ibis*. 115: 173-201.
- Ricklefs, R. E. 1984. The Optimization of Growth Rate in Altricial Birds. *Ecology* 65:1602–1616.
- Robert-Coudert, Y. 2004. Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. *Behavioral Ecology* 15:824–830.
- Rothenbach, C. A., and J. P. Kelly. 2012. The parental dilemma under variable predation pressure: adaptive variation in nest attendance by Great Egrets. *The Condor* 114:90–99.
- Serrano-Meneses, M.-A., and T. Sz  kely. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113:385–394.
- Shaffer, S. A., H. Weimerskirch, and D. P. Costa. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* 15:203–210.
- Smith, W. O., and K. A. Donaldson. 2014. Photosynthesis–irradiance responses in the Ross Sea, Antarctica: a meta-analysis. *Biogeosciences Discussions* 11:18045–18072.
- Smith, W. O., D. G. Ainley, and R. Cattaneo-Vietti. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences* 362:95–111.
- Smith, W. O., and L. I. Gordon. 1997. Hyperproductivity of the Ross Sea (Antarctica) polynya during austral spring. *Geophysical Research Letters* 24:233-236.
- Spurr, E. B. 1975. Behavior of the Adelie Penguin chick. *Condor* 77:272–280.
- Stammerjohn, S. E., D. G. Martinson, R. C. Smith, and X. Yuan. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Ni  o – Southern Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research* 113:1–20.

- Stearns, S. C. 1989. Trade-offs in life-history evolution. *Functional Ecology* 3:259–268.
- Taylor, R. H. 1962. The Adelie Penguin (*Pygoscelis adeliae*) at Cape Royds. *Ibis* 104:176–204.
- Team, R. C. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Teder, T. 2014. Sexual size dimorphism requires a corresponding sex difference in development time: a meta-analysis in insects. *Functional Ecology* 28:479–486.
- Tenaza, R. 1971. Behavior and Nesting Success Relative to Nest Location in Adelie Penguins (*Pygoscelis adeliae*). *The Condor* 73:81–92.
- Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences of the United States of America* 108:7625–8.
- Trivers, R. L., and D. E. Willard. 1973. Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring. *Science* 179:90–92.
- Tveraa, T., B.-E. Saether, R. Aanes, and K. E. Erikstad. 1998a. Body mass and parental decisions in the Antarctic petrel (*Thalassoica antarctica*): how long should the parents guard the chick? *Behavioral Ecology and Sociobiology* 43:73–79.
- Tveraa, T., B.-E. Saether, R. Aanes, K. E. Erikstad, B.-E. Sether, R. Aanes, and K. E. Erikstad. 1998b. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology* 67:699–704.
- Varpe, Ø., T. Tveraa, and I. Folstad. 2004. State-dependent parental care in the Antarctic petrel: responses to manipulated chick age during early chick rearing. *Oikos* 3.
- Velando, A. 2002. Experimental manipulation of maternal effort produces differential effects in sons and daughters: implications for adaptive sex ratios in the blue-footed booby. *Behavioral Ecology* 13:443–449.
- Viblanc, V. a, A. D. Smith, B. Gineste, and R. Groscolas. 2012. Coping with continuous human disturbance in the wild: insights from penguin heart rate response to various stressors. *BMC ecology* 12:10.
- Vinuela, J., J. Moreno, L. M. Carrascal, J. J. Sanz, J. A. Amat, M. Ferrer, J. Belliure, and J. J. Cuervo. 1996. The effect of hatching date on parental care, chick growth, and chick mortality in the Chinstrap Penguin (*Pygoscelis antarctica*). *The Zoological Society of London* 240:51–58.

- Vleck, C. M., L. L. Ross, D. Vleck, and T. L. Bucher. 2000. Prolactin and parental behavior in Adélie penguins: effects of absence from nest, incubation length, and nest failure. *Hormones and behavior* 38:149–58.
- Volkman, N. J., and W. Trivelpiece. 1980. Growth in pygoscelid penguin chicks. *Journal of Zoology, London* 191:521–530.
- Walker, B. G., P. Dee Boersma, and J. C. Wingfield. 2006. Habituation of Adult Magellanic Penguins to Human Visitation as Expressed through Behavior and Corticosterone Secretion. *Conservation Biology* 20:146–154.
- Wanker, R., L. C. Bernate, and D. Franck. 1996. Socialization of Spectacled Parrotlets *Forpus conspicillatus*: the role of parents, crèches and sibling groups in nature. *Journal of Ornithology* 137:447–461.
- Wanless, S., M. P. Harris, P. Redman, and J. R. Speakman. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294:1–8.
- Warham, J. 1990. *The Petrels: their ecology and breeding systems*. Academic Press, San Diego, CA.
- Wasser, S. K., and G. Norton. 1993. Baboons adjust secondary sex ratio in response to predictors of sex-specific offspring survival. *Behavioral Ecology and Sociobiology* 32:273–281.
- Watanuki, Y., A. Kato, K. Sato, Y. Niizuma, C. A. Bost, Y. Le Maho, and Y. Naito. 2002. Parental mass change and food provisioning in Adélie penguins rearing chicks in colonies with contrasting sea-ice conditions. *Polar Biology* 25:672–681.
- Waugh, S. M., H. Weimerskirch, Y. Cherel, and P. A. Prince. 2000. Contrasting Strategies of Provisioning and Chick Growth in Two Sympatrically Breeding Albatrosses at Campbell Island, New Zealand. *The Condor* 102:804–813.
- Weimerskirch, H., A. Ancel, M. Caloin, A. Zahariev, J. Spagiari, M. Kersten, and O. Chastel. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Ecology* 72:500–508.
- Weimerskirch, H., C. Barbraud, and P. Lys. 2000. Sex differences in parental investment and chick growth in Wandering Albatrosses : Fitness Consequences. *Ecology* 81:309–318.
- Weimerskirch, H., O. Chastel, and L. Ackerman. 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the Thinbilled prion (*Pachyptila beicheri*). *Behavioral Ecology and Sociobiology* 36:11–16.

- Weimerskirch, H., T. Mougey, and X. Hindermeier. 1997. Foraging and provisioning strategies of Black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8:635–643.
- Weimerskirch, H., O. Chastel, L. Ackerman, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeier, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behavior* 47:472–476.
- Whitehead, A. L., P. O. Lyver, G. Ballard, K. Barton, B. J. Karl, K. M. Dugger, S. Jennings, A. Lescroël, P. R. Wilson, and D. G. Ainley. 2015. Factors driving Adélie Penguin chick size, mass and condition at colonies of different sizes in the Southern Ross Sea. *Marine Ecology Progress Series*:199–213.
- Williams, G. C. . 1966. Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. *The American naturalist* 100:687–690.
- Williams, T. D., and J. P. Croxall. 1991. Chick growth and survival in gentoo penguins (*Pygoscelis papua*): effect of hatching asynchrony and variation in food supply. *Polar Biology* 11:197–202.
- Woehler, E. J., R. L. Penney, S. M. Creet, and H. R. Burton. 1994. Impacts of human visitors on breeding success and long-term population trends in Adelie Penguins at Casey, Antarctica. *Polar Biology* 14.
- Ydenberg, R. C., and D. F. Bertram. 1989. Lack's Clutch Size Hypothesis and Brood Enlargement Studies on Colonial Seabirds. *Colonial Waterbirds* 12:134–137.
- Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*.