



<http://researchspace.auckland.ac.nz>

*ResearchSpace@Auckland*

### **Copyright Statement**

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- Any use you make of these documents or images must be for research or private study purposes only, and you may not make them available to any other person.
- Authors control the copyright of their thesis. You will recognise the author's right to be identified as the author of this thesis, and due acknowledgement will be made to the author where appropriate.
- You will obtain the author's permission before publishing any material from their thesis.

To request permissions please use the Feedback form on our webpage.

<http://researchspace.auckland.ac.nz/feedback>

### **General copyright and disclaimer**

In addition to the above conditions, authors give their consent for the digital copy of their work to be used subject to the conditions specified on the [Library Thesis Consent Form](#) and [Deposit Licence](#).

**Biotic and physical forces as determinants of Adélie penguin  
population location and size**

**Grant Ballard**

A thesis submitted in partial fulfillment of the requirements for the degree of  
Doctor of Philosophy in  
Biological Sciences, The University of Auckland, 2009.



## **Abstract**

Adélie penguins (*Pygoscelis adeliae*) are among the most thoroughly studied wild animals, which is remarkable considering they are sea-ice obligates, living only in the Antarctic, one of the most remote regions on Earth. Building on several decades of research on the Ross and Beaufort Island metapopulation, I have focused on understanding the underlying mechanisms related to colony size and growth patterns. I have found that life for a penguin at a large colony is extremely competitive, and that the ultimate size of these colonies is determined by the trade-off between the needs of parents and chicks, with penguins at large colonies approaching an energetic limit not reached at smaller colonies. However, some individuals are consistently able to utilize the available resources within these limits more efficiently than others by diving more deeply and recovering more quickly, especially when environmental conditions are less favorable. It is likely that these individuals thereby exhibit increased fitness in terms of their genetic contribution to the population. At smaller colonies, this kind of advantage does not necessarily translate to increased fitness, since there appear to be ample resources for all, or for none, depending more closely on simple yet extreme physical environmental stochasticity. Finally, in the larger context of Adélie penguin life-history throughout the annual cycle, they are confronting large scale changes in their environment that have been occurring for millennia, but which are currently in an unusual state of flux. Ultimately a lack of sufficient daylight overlapping the region of sea ice that is accessible to them during the inter-breeding period may constrain their populations.

## Acknowledgements

I thank my co-investigators, especially the project leader, David Ainley, for agreeing to take me to Antarctica in the first place, and for showing me the ways of the penguins – there could be no better teacher. Katie Dugger has, with David, played a crucial role in my education as a penguin researcher, guiding me through information theory along the way. I also thank the other penguin project collaborators to date: Peter Wilson (who first taught me how to catch a penguin), Lisa Ballance, Kerry Barton, Phil Lyver, Chris Ribic, Nadav Nur, Kevin Arrigo, Claire Parkinson, Amélie Lescroël, and Viola Toniolo.

Ellie Cohen and John Wiens of PRBO, along with my parents, parents-in-law, and sister all provided enthusiastic support for my rather delayed decision to pursue a Ph.D. And I thank Charly Bost for convincing me to make this decision, with a few fateful comments in Ushuaia. Thank you to Cosimo and Viola, for bringing so many smiles in the home stretch and for being patient and supportive while I spent way too much time in front of the computer instead of playing with blocks and exploring the world outside – that comes next.

My heartfelt thanks to my co-advisor Jacqueline Beggs, and to Hamish and Russell Wilson, who, along with Peter, have been constant supporters and provided much-appreciated housing assistance and hospitality throughout, not to mention spirited ecology discussions and sailing trips. I'm sorry about all the dirty laundry, and for bringing strange Antarctic illnesses back to your house.

Mike Beigel and Nat Polish were crucial in the development of the weighbridges that operated well under challenging conditions. Tony Lewis helped to devise the method for attaching GLS tags to penguins. I. Gaffney, S. Heath, M. Hester, V. Marsaudon, V. Patil, R. Orben, L. Sheffield, S. Webb, J. Blum, B. Saenz, C. McCreedy, T. Dorr, L. Blight, and K. Lindquist provided excellent camaraderie, expert field observations, data vetting, and motivational conversations. A. Archer and staff at U.C. San Diego's Arctic and Antarctic

Research Center assisted with acquiring satellite imagery. G. van Dijken provided assistance with ice data processing. S. Gordon placed reference geolocation sensors at Cape Hallett. M. Herzog, T. de Cornulier, M. Authier and D. Pinaud provided statistical advice. K. Nagy, C. Vleck, T. Reidarson, D. Croll, and T. Bucher provided advice on energetics field methods, and D. Cairns, J. Chardine, D. Croll, J. Croxall, P. Dann, G. Gabrielsen, R. Gales, T. Gaston, I. Jones, F. Mehlum, W. Montevecchi, J. Piatt, D. Roby, and E. Woehler provided unpublished energetics and colony size data. And I thank the University of Auckland Faculty of Science for their steadfast support.

The US Antarctic Program and Antarctica NZ provided logistic support; financial support was provided by NSF grants OPP 9526865, 9814882, 0125608, and 0440643. The prototype weighbridge was funded by N.Z. Foundation for Research, Science, and Technology, grant CO 9527. Thanks to University of Auckland PRESS and SBS research funds for additional financial assistance.

And of course I thank my tireless advisor, Mark Hauber, for his enthusiasm and rigor – always raising the bar one notch higher. Thank you for making this possible.

# Table of Contents

<b>Abstract</b> .....	<b>i</b>
<b>Acknowledgements</b> .....	<b>ii</b>
<b>Table of Contents</b> .....	<b>iv</b>
<b>Chapter I: Understanding coloniality in Adélie penguins</b> .....	<b>1</b>
1.1 Introduction.....	2
1.2 A study to understand coloniality in Adélie penguins.....	3
1.3 Effects of intraspecific trophic competition.....	9
1.4 A “natural experiment” reveals effects of plasticity in philopatry.....	11
1.5 Effects of plasticity in foraging behavior .....	16
1.6 Toward a more complete understanding.....	18
1.7 Overview of thesis structure and contributions.....	20
<b>Chapter II: A species copes with rapid, large-scale environmental change</b> .....	<b>23</b>
<b>Chapter III: Parental foraging and chick provisioning strategies of Adélie penguins in response to body condition and environmental variability</b> .....	<b>28</b>
3.1 Introduction.....	29
3.2 Materials and methods.....	34
Data collection .....	34
Definition of parameters.....	35
Analyses.....	39
3.3 Results.....	45
3.4 Discussion .....	57
Hypothesis one: adults in poor condition invest in self maintenance, which has negative consequences to chicks.....	57
Hypothesis two: lower prey accessibility increases parents’ investment in self-maintenance. ....	59
3.5 Conclusion .....	62
<b>Chapter IV: Working less to gain more: when breeding quality relates to foraging efficiency</b> .....	<b>65</b>
4.1 Introduction.....	66
4.2 Materials and methods.....	68
Species and study sites .....	68
Assessment of foraging behavior .....	69

Dive data analysis.....	70
Assessment of breeding quality .....	73
Foraging conditions.....	76
Re-formulation of predictions.....	77
Statistics.....	77
4.3 Results.....	80
Foraging effort and diving activity.....	80
Foraging success .....	83
Diving parameters .....	86
Foraging efficiency and feeding frequency .....	87
4.4 Discussion.....	87
Better breeders are more efficient foragers .....	88
Quality matters more under difficult conditions .....	89
Limitations of the study.....	90
Proximate mechanisms.....	92
<b>Chapter V: An energetic correlate between colony size and foraging effort in seabirds</b>	
.....	<b>95</b>
5.1 Introduction.....	96
5.2 Materials and methods.....	97
Study Area .....	97
Collection of samples .....	98
Sample analysis.....	98
Statistical analysis .....	99
5.3 Results.....	102
5.4 Discussion.....	105
Intraspecific variation in FMR.....	105
An energetic constraint to colony size?.....	109
<b>Chapter VI: Responding to climate change: Adélie penguins confront astronomical and ocean boundaries.....</b>	<b>115</b>
6.1 Introduction.....	116
6.2 Materials and methods.....	120
Overview.....	120
Details.....	122
6.3 Results.....	128



General migration patterns .....	128
Wintering Areas .....	134
Characteristics of Wintering Area.....	135
6.4 Discussion.....	139
Ocean, ice and biological boundaries.....	139
Astronomical boundaries.....	142
Migration and the millennial scale of sea ice variability.....	143
Migration and the centennial/decadal scale of sea ice variability.....	144
<b>Chapter VII: Conclusion .....</b>	<b>147</b>
7.1 Summary of main findings.....	148
7.2 Limitations of the study .....	151
1. Prey Accessibility.....	152
2. Population size. ....	153
3. Linking chicks to parents.....	153
4. Effects of age and experience .....	154
5. Instrument effects.....	155
6. Non-breeding season .....	156
7. Observational data, experimental design, and statistical approaches.....	157
7.3 Priorities for future research: .....	158
1. Determine the effect of age, experience and physiology on individual foraging efficiency. ....	158
2. Determine the effect of age, experience, and individual quality on breeding success and survival in varying environmental and competitive conditions at the colony level. ....	160
3. Investigate heritability of individual quality, foraging capability, and colony size preference.....	162
4. Develop a comprehensive population model for the Ross-Beaufort Island metapopulation incorporating all the factors investigated previously.....	163
<b>Return to Penguin City .....</b>	<b>165</b>
<b>References.....</b>	<b>167</b>