Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.



© Kyle W. Morrison 2015

# Factors affecting the population dynamics of Eastern Rockhopper Penguins (*Eudyptes chrysocome filholi*) on Campbell Island, New Zealand

A thesis presented in partial fulfilment of the requirements for the degree of

Doctor of Philosophy in Ecology

Massey University

Palmerston North, New Zealand

**Kyle William Morrison** 

2015

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

### **A**BSTRACT

The population dynamics of seabirds may be influenced by 'top-down' predation effects, or from the 'bottom-up' by environmental limitations on food availability. Southern Rockhopper Penguin (*Eudyptes chrysocome*) populations have declined hugely at multiple sites across their circumpolar, sub-Antarctic range in recent decades, resulting in an extinction risk of 'Vulnerable'. They are a small-bodied penguin, adapted to exploit seasonally abundant, pelagic prey by being migratory and having prolonged fasting periods onshore and foraging offshore during breeding. Mysteriously, like other *Eudyptes* penguins they lay an extremely dimorphic two-egg clutch in which the first-laid egg is smaller and less successful, and rarely fledge two chicks.

The world's largest population (c. 620,000 pairs) of the Eastern sub-species (E. c. filholi) of Rockhopper Penguin formerly bred at Campbell Island, New Zealand. Prior to the current work, the only previous intensive research at this site in the mid-1980s revealed the population had declined by a startling 94% since the early 1940s as local sea-surface temperatures (SSTs) increased. It was hypothesized that climate change had reduced the availability of the penguins' preferred zooplankton prey, so that the Campbell population's decline was caused by its unusual reliance on a fish-based diet which resulted in low body masses and demographic rates. I examined this hypothesis of bottom-up population regulation by estimating the population growth rate from 1984–2012 and assessing links between SST, diet quality, chick-provisioning rates, chick and adult body masses, egg masses, reproductive success, and first-year and adult survival rates. Additionally, I considered whether top-down predation effects were causing the recent, unusually rapid population decline in a relatively small, fragmented colony. I assessed the population growth rate using digital imagery analysis of current and historic colony photographs, dietary trophic level using stable isotope analysis of blood samples, and chick-provisioning and adult survival rates using an automated gateway to record the colony-sea transit times of individual transponder-tagged penguins breeding at closely monitored nest sites.

I estimated the total Campbell Island population size to be 33,239 breeding pairs in 2012, a 21.8% decrease from an adjusted estimate of 42,528 pairs in 1984. However, the recent decline occurred before 1996 with most colonies stable or growing thereafter under cooler SSTs and more abundant prey. My results supported the previous assertion that the overall population size declined during periods of warm SST and that a zooplankton-based diet was a higher quality diet, resulting in heavier adults and chicks. However, the primary

determinant of chick growth was how often they were fed, and the rigid division of labour between parents during early-chick rearing reduced potential chick-provisioning rates, especially from males in a poor-food year. The ongoing, localized decline of my study population was caused by high rates of predation on adults by sea lions, as well as on eggs by skuas. I did not find support for overlap between migration and egg-formation underlying egg-size dimorphism.

This study emphasizes the constraints that a species' genotype and ecological context place on the degree of behavioural plasticity it exhibits when faced with environmental variability. My results highlight the vulnerability of Eastern Rockhopper Penguins, and likely other *Eudyptes* penguins, to the more variable and warmer environment and less predictable food supply in a future under climate change.



Figure i Eastern Rockhopper Penguin, Campbell Island. Photo by Kyle Morrison.

# **DEDICATION**

For Sarah, my island girl who is now my wife, now my son's mother, always my foundation when I'm far out at sea



Figure ii Sarah Jamieson and Finnigan Morrison at 6 months old. Photo by Kyle Morrison.

### **ACKNOWLEDGEMENTS**

I am grateful to my supervisory committee, Phil Battley, Doug Armstrong, and David Thompson, for their many essential contributions to my work. I thank you for having faith in my abilities, as demonstrated in the independence I had in choosing my research questions and designing this study. I could say more, but I know I have already asked them to read a lot of words in the past 4.5 years.

Thank you to the anonymous reviewers of my published research chapters and my Massey University thesis examiner John Cockrem, New Zealand examiner Matt Rayner, and international examiner Norman Ratcliffe for the many improvements you suggested.

I am very grateful for receipt of doctoral scholarships from Massey University, Education New Zealand, and the Natural Sciences and Engineering Research Council of Canada. Additional grant funding for equipment and stable isotope analysis was kindly provided by the J.S. Watson Conservation Trust of the Royal Forest and Bird Protection Society of New Zealand, the Hutton Fund of The Royal Society of New Zealand, and the Penguin Fund of Japan.

Paul Sagar gave generously of his time and knowledge in introducing me to Campbell Island, and later to his career-long passion, The Snares. You are a role model to me of the fit, field-working, publishing, back-yard mist-netting, family man I aspire to be.

My faithful field assistants, my brother Neil Morrison, Ray Buchheit, and Rob Dunn, were better help to me than I could ever have hoped for. You each gave up a big chunk of time out of your lives and much sweat to hang out with me and the birds and seals of Penguin Bay. Thank you for going along with what I thought best, even when you must have known better.

Thank you to the albatross-interested folks I shared adventures on Campbell Island with and many good times back at Beeman Base, including Dave Evans, Amanda Ophof, Caitlin Kroeger, Lisa Sztukowski, and Rachel Orben. Thanks 'gam' for never failing to humour me by looking at a few more penguin photos and for not fussing too much about the food in my beard.

I owe a depth of gratitude to Henk Haazen, skipper of RV 'Tiama' for safe transport to Campbell Island and The Snares over five expeditions. Thank you Henk for being up to the challenge of fitting in as many heavy yellow fish bins as we could throw at you. Frequent first mate Andy Whittacker was a good friend to someone like myself with weak sea-legs. Thank you Andy for cheerfully and adeptly assisting with penguin tracking-tag deployment in April 2013.

I am very grateful to the assistance with accessing unpublished information, logistics, and permitting provided by past and current staff of the Department of Conservation (DOC), especially Graeme Taylor, Stu Cockburn, Peter Moore, Phil Moors, Duncan Cunningham, Pete McClelland, and Jo Hiscock. Thank you Jo for assisting me with fieldwork in my first season. Stu Cockburn kindly provided me with dataloggers and antennae for the automated gateway I used to record the movements of transponder-tagged penguins, without which Chapters 4 and 5 would not have been possible. Graeme Taylor assisted me with accessing DOC's National Archives and trained me in transponder-tagging Little Penguins. My enjoyment of the spectacular biodiveristy of Campbell Island would have been much diminished without the heroic efforts of DOC staff in eradicating all introduced mammals, especially rats.

I had an excellent role model for what a PhD on Rockhopper Penguins could deliver from Nina Dehnhard, whose high quality research on Southern Rockhopper Penguins on New Island, Falkland Islands, is frequently cited in this thesis. Thank you Nina for exchanging so many Rockhopper-related e-mails with me.

A fellow Simon Fraser University alumnus, Will Stein, had me interested in *Eudyptes* penguins before I even left Canada. Thank you Will for our many discussions over the evolution of egg-size dimorphism which helped shape my approach not only to Chapter 6, but elsewhere where I use inter-species comparisons to infer ecological constraints and selective forces.

I would like to acknowledge the foundational *Eudyptes* penguin research of the late John Warham (1919–2010). His detailed studies of the breeding biology of all five of the *Eudyptes* penguins of the New Zealand region are still among the best available to the present day. In this thesis I cite his results and ideas extensively, 40–50 years after their publication. I am sorry I never met John, but feel a connection to him when I observe the penguin behaviours he described and illustrated so accurately, and through his supervision at the University of Canterbury of my co-author Paul Sagar.

Thank you for all the laughs my good friends, fellow PhD students, office mates, and football/badminton/hunting/spearfishing buddies at Massey and NIWA: Juan Carlos Garcia Ramirez, Pablo Escobar, Tim Burrell, and Stefan Jendersie.

My brother Neil, and parents Ken and Betty have shown a huge deal of enthusiasm for my penguin research from back home in Canada. Thank you for all of the love and support you have sent me whether I was in Palmerston North, Wellington, or the Penguin Bay Hilton hut.

Sarah Jamieson and I came to New Zealand for her post-doctoral position at Massey University on North Island Brown Kiwi, but have stayed longer than initially intended because of my penguin PhD. I owe Sarah an ocean of gratitude for her assistance reviewing my work, formatting this thesis, and for supporting me during our long separations during my field work. Sarah and I have married and had a beautiful brown-eyed boy of our own since coming to New Zealand. Not surprisingly, finishing a PhD thesis while living away from family and raising a first child with six teeth before six months old has been a huge challenge that I would not have succeeded in without Sarah's self-less love and understanding. Thank you my wonderful wife and motivational son Finnigan! Finn, as you read this sentence picture your head asleep against my chest as I type it, because that was the peculiar and blessed reality of 15-December 2014.







Figure iii Clockwise from top-left: Neil Morrison, Ray Buchheit, Andy Whittacker and Phil Battley, Leigh Torres and David Thompson and Paul Sagar, Henk Haazen, Rob Dunn. Photos by Kyle Morrison.

# **TABLE OF CONTENTS**

Abstract	4
Dedication	6
Acknowledgements	7
Co-authors	12
CHAPTER 1 GENERAL INTRODUCTION	14
SEABIRD ECOLOGY	15
SEABIRD POPULATION DYNAMICS	16
HUMAN-INDUCED CHANGE IN MARINE ECOSYSTEMS	16
BEHAVIOURAL PLASTICITY, CONSTRAINTS, AND CANALIZATION	18
Penguins	18
EUDYPTES PENGUINS	19
Study species	21
Study site	23
AIMS OF THIS THESIS	24
RESEARCH CHAPTERS	25
CHAPTER 2 POPULATION DYNAMICS OF EASTERN ROCKHOPPER PENGUINS ON CAMPBELL ISLAND	IN
RELATION TO SEA SURFACE TEMPERATURE $1942-2012$ : CURRENT WARMING HIATUS PAUSES A LC	NG-
TERM DECLINE	27
Abstract	28
Introduction	28
Materials and Methods	30
Results	39
Discussion	45
Chapter 3 Higher trophic level prey do not represent a higher quality diet in a threati	ENED
SEABIRD: IMPLICATIONS FOR RELATING POPULATION DYNAMICS TO DIET SHIFTS INFERRED FROM ST	
ISOTOPES	55
Abstract	56
Introduction	
MATERIALS AND METHODS	
RESULTS	
DISCUSSION	
CHAPTER 4 CANALIZED PARENTAL ROLES CONSTRAIN THE ABILITY OF EASTERN ROCKHOPPER PENG	
COPE WITH NUTRITIONAL STRESS	
Abstract	
Introduction	
MATERIALS AND METHODS	82

Results	85
Discussion	95
ACKNOWLEDGEMENTS	102
Chapter 5 New Zealand sea lion and Brown Skua predation is causing the	CONTINUED DECLINE
OF AN EASTERN ROCKHOPPER PENGUIN COLONY ON CAMPBELL ISLAND	103
Introduction	104
Materials and Methods	107
Results	119
Discussion	135
ACKNOWLEDGEMENTS	142
Chapter 6 A carry-over effect of migration does not underlie within-indiv	VIDUAL VARIATION IN
EXTREME EGG-SIZE DIMORPHISM IN EASTERN ROCKHOPPER PENGUINS	145
Abstract	146
Introduction	146
Materials and Methods	148
Results	150
Discussion	161
ACKNOWLEDGEMENTS	165
CHAPTER 7 GENERAL DISCUSSION	167
Key findings	168
BOTTOM-UP CONTROL OF POPULATION DYNAMICS	169
TOP-DOWN CONTROL OF POPULATION DYNAMICS	171
CONSTRAINTS ON BEHAVIOURAL PLASTICITY	173
SHIFTING BASELINES: PERCEPTIONS OF ECOSYSTEM HEALTH AND FUNCTION	175
IMPLICATIONS FOR CONSERVATION MANAGEMENT	176
FUTURE DIRECTIONS	177
References	179

### **CO-AUTHORS**

I wrote all parts of this thesis, designed and led all data collection, and performed all analyses. However, I have recognized the essential contributions of eight collaborators by their inclusion as co-authors in specific research chapters.

## Phil F. Battley (Massey University, Ecology Group)

As my primary supervisor, Phil helped me shape my research questions and methods, supported my scholarship, grant, and Animal Ethics applications, provided financial support for field equipment and for myself in my final months of writing, and reviewed all parts of this thesis. Furthermore Phil joined me on a very enjoyable tag-deployment trip to Campbell and The Snares Islands in April 2013. Phil is a co-author on Chapters 2, 4, and 5.

## Doug P. Armstrong (Massey University, Ecology Group)

As my secondary academic supervisor, Doug made important contributions to my study design and interpretation of results, including making quick and helpful comments on research chapters. Doug gave much statistical advice on Chapter 5 on which he is a co-author.

### David R. Thompson (National Institute of Water & Atmospheric Research (NIWA))

As my third PhD supervisor, David helped shape my research questions and study design. David is the principal investigator of NIWA's 'Conservation of New Zealand's iconic marine megafauna' project, which funded almost all aspects of my costly three seasons of fieldwork on remote Campbell Island. David was primarily responsible for organizing the complex logistics around ensuring our field team left Bluff Harbour with all of the permits, food, and gear we needed. David arranged for me to have a desk at NIWA's Wellington office for the final third of my PhD. David is a co-author on Chapters 2-5.

# Paul M. Sagar (NIWA)

Paul introduced our team to Campbell Island in my first season, and got us off the ground in the second year as well. Paul reviewed Chapter 2 on which he is a co-author.

# Sarah J. Bury (NIWA)

Sarah supervised the stable isotope analysis of blood samples for Chapter 3, which she also revised and is a co-author.

**Sarah E. Jamieson** (formerly of the Museum of New Zealand Te Papa Tongarewa and Massey University, Ecology Group)

Sarah supported me in innumerable ways during my fieldwork and writing. Sarah reviewed all research chapters and provided statistical advice on Chapter 5 on which she is a co-author.

## **Neil C. Morrison**

My brother Neil generously agreed to be my volunteer field assistant in my first season. Neil's hard work was instrumental in the successful start to my fieldwork. All of my assistants made essential contributions to collecting the data I used in all research chapters, but are recognized by co-authorship in Chapter 4.

Raymond M. Buchheit (Department of Ecology, Montana State University)

My Aleutian-island friend Ray took a 100% pay cut to join me at the opposite end of the Pacific in my second season of fieldwork. Ray makes me laugh, a lot. Ray is a co-author on Chapter 4.

#### **Rob Dunn**

Rob built upon his MSc seabird experience by assisting me in my third field season. There was no pack too heavy or sea lion to fierce to intimidate Rob. Rob is a co-author on Chapter 4.