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**Extreme migration and the annual cycle:
individual strategies in
New Zealand Bar-tailed Godwits**

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Synopsis

Long-distance migration places severe constraints on the annual cycles of birds, as they balance the energetic and scheduling requirements of breeding, moult, pre-migratory fuelling, and the journey itself. The most extreme migrations, traversing vast, inhospitable areas of the globe in protracted non-stop flights, may push birds to the limits of their capabilities, and would be expected to tolerate little variation in performance. Despite this, Bar-tailed Godwits *Limosa lapponia baueri*, which are among the world's greatest endurance migrants, embark on northward migration from New Zealand across a month-long period, and individuals are quite faithful to their particular schedules. Godwits are highly sexually dimorphic in plumage and body size, and there is additionally substantial individual variation within each sex in both traits. These patterns demonstrate a surprising diversity of strategies within a system that should contain little room for error.

In this thesis, I sought to identify the roots and consequences of both persistent and ephemeral individual differences in migration and moult of New Zealand Bar-tailed Godwits, and to identify constraints and potential bottlenecks in their annual cycle. To do this, I combined a fine-resolution multi-year focus on individuals and an entire annual-cycle perspective, both of which have generally been impossible in studies of long-distance migratory birds. At a single non-breeding site, I closely monitored moult and migration of individual Bar-tailed Godwits for three non-breeding seasons, and linked these with events outside of New Zealand by tracking a subset of the same individuals on their complete migrations to Alaska breeding grounds and back. I supplemented this by travelling to Alaska myself and describing how godwits are distributed by size and plumage across their vast breeding range.

I found that most of the variation among individual Bar-tailed Godwits was linked to where they nested in Alaska: within each sex, northerly breeders were smaller, had more extensive breeding plumage, and migrated later on both northbound and southbound migrations. The differences in migration timing can be explained by variation in when tundra breeding sites become snow-free and available across a latitudinal gradient, but reasons for geographic differences in plumage and size are less clear. Variation in breeding plumage was associated with different strategies for scheduling moult, both in New Zealand and during northbound migratory stopover in the Yellow Sea. Individual godwits were extraordinarily consistent between years in their timing of departure from New Zealand, and most 'off-schedule' departures were attributable to birds avoiding unfavourable winds for migration. Surprisingly,

timing of arrival in New Zealand after the longest recorded non-stop flight did not appear to influence a godwit's ability to prepare for its next migration, as timing of subsequent migratory departure and extent of breeding plumage on departure were both unaffected and very consistent. Across the entire year, scheduling of events became more precisely timed as the breeding season approached, but movements were generally much more tightly scheduled than moults.

These findings show that Bar-tailed Godwits adopt and enact an array of individualised strategies within an apparently constrained system. The inter-relationships among events in different parts of the globe show that an individual-based, full annual-cycle perspective is required to understand patterns in any particular season. The consistent manner in which godwits conduct their annual routines, while still demonstrating flexibility to address unforeseen circumstances, challenges us to reconsider the view of extreme long-distance migrants as organisms operating at the limits of their capabilities.

Preface

'I'm sorry—they do *what*?'

The above quotation is only a dramatisation. I can't honestly remember how I reacted upon first hearing the idea that an otherwise unremarkable shorebird might spread its wings in Alaska and fly the length of the Pacific Ocean without stopping, only to next touch ground on some mudflat in New Zealand. But over the last seven years, I have explained this concept to a sufficient number of people to see the entire range of possible reactions. Some people can't get past the simple fact of it, and stand bewildered or move straight to denial—they must have misunderstood what I was saying. Others roll with it, their minds moving quickly to the pertinent questions: Why? How? After years of intimate involvement with those exact problems, it sometimes requires the reactions of others to remind me that what I now take for granted is by no means commonplace. Although difficult to maintain on a daily basis, awe is in fact the proper response. Whatever my immediate reaction was years ago, my ultimate response was profound: I was going to study Bar-tailed Godwits.

Since 2005, through the wonders of satellite telemetry, hypothesis became reality: it was in fact possible for a godwit to sustain powered flight for eight or nine consecutive days without stopping once to eat, drink, or rest, crossing more than 11,000 kilometres of open ocean. Furthermore, there were tens of thousands of godwits performing this astounding migration every year without drawing much attention to themselves, only to head back north six months later on a non-stop flight to Asia that was only slightly shorter than the southward trip. However, each does not go about these flights in precisely the same way. Godwits depart New Zealand across a month-long period from early March to early April, and they don't all look the same when they leave; some are as dull and gray as mid-winter birds, while others sport the full regalia of summer breeding plumage found in Alaska. It became apparent that individual godwits were remarkably consistent in these qualities across years: certain birds always migrated earlier than others, and the reddest birds were always the reddest. But *why* was this true? What makes a particular godwit an early bird, or a red bird? I had found my research topic, and what follows will describe my four years of attempts to address this ostensibly simple question.

For Brian McCaffery,
who never ceases to inspire.

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Co-authors

I wrote all portions of this thesis, collected nearly all of the data, and performed all analyses. However, four of my collaborators made essential contributions warranting co-authorship of specific sections.

Phil F. Battley (Massey University, Ecology Group)

As my primary supervisor, Phil collaborated with me to conceive and design every part of this research, and is consequently a co-author on Chapters 2–7 and Appendix 1. He provided logistical and financial support for all trapping, tracking, and travel enterprises, and assisted in the field for local captures and geolocator deployments. He reviewed all manuscripts and helped proof the final publications.

Murray A. Potter (Massey University, Ecology Group)

As my secondary supervisor, Murray contributed to many aspects of study design and interpretation of results, and reviewed most chapters. His inclusion as co-author on Chapters 2, 3, and 7 reflects his greater role in developing the results and ideas of those chapters for publication. He additionally contributed to Chapter 3 by accompanying me to Alaska, helping with nest-searching and trapping, and providing many in-field photographs of godwits.

James W. Fox (formerly of British Antarctic Survey, UK)

For the geolocator portion of this study, James provided the units and analysis software, advised on matters of data analysis and interpretation, and provided technical assistance. He reviewed and is a co-author on Chapter 2.

Dan R. Ruthrauff (U.S. Geological Survey, Alaska Science Center, USA)

Dan contributed to Chapter 3 by providing equipment and logistical support for all fieldwork in Alaska, and leading the expedition to the North Slope. He additionally provided data on historic captures and tracking data for godwits in Alaska (property of USGS), contributed in-field photographs, and reviewed the manuscript.

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I'd like to thank my parents, Barbara and Les, who never seem to question the wisdom of the many strange things I have considered good ideas in my supposed adulthood. Their trust (as well as the knowledge that I am not completely reliant on these exploits for financial support!) has given me the confidence to go where I needed to go.

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