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

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

Doctor of Philosophy in Ecology
Massey University
Palmerston North, New Zealand

Jesse Ray Conklin

2011

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.

Contents

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.

Acknowledgements

First of all, I'd like to thank 23.5°. If the Earth did not hurtle through space tilted on its axis at this precise angle, there would be no regular seasons and no impetus for birds to migrate. Consequently, I would have to find an honest job.

More recently, my specific research benefited from an array of kind, hard-working individuals spread all over the world. The shorebird world is a close and supportive group, and I am fortunate to have been accepted into their fold on a professional and personal level. Previous decades of godwit work across the flyway created a strong foundation upon which I could build, and I must acknowledge some of the key players (knowing I will also forget some) who contributed both indirectly and very directly to my success. In Alaska: Bob Gill, Brian McCaffery, Dan Mulcahy, Lee Tibbitts, Dan Ruthrauff, and Nils Warnock. In New Zealand: Phil Battley, David Melville, Adrian Riegen, Rob Schuckard, and Keith Woodley. In Australia: Adrian Boyle, Chris Hassell, and Clive Minton.

Many people helped trap and band godwits at Foxton. Long before I reached New Zealand, the seed of my project was sown with some key colour-banding by Phil Battley, David Melville, Ralph Powlesland, Adrian Riegen, Hugh Robertson, Rob Schuckard, and Graeme Taylor, which I continue to benefit from today. I bow to either their skill or luck at mist-netting, because I apparently have neither. During my tenure at Foxton, all of these figures plus legions of Massey Ecology students and others flocked to my aid for trapping attempts (unfortunately, in many cases *attempt* cannot be stressed enough). I am not sure how many make up a legion, but I trust they will understand when I don't even attempt to list them all.

Phil Battley, Jimmy Choi, Paul Gibson, Craig Steed, Brent Stephenson, and Graeme Taylor contributed photographs of Foxton godwits. All photos in this document are my own unless specified otherwise.

The geolocator work central to Chapters 2 and 7 owes its success to many people. In February 2008, Bob Gill tossed me a bag of geolocators, with a casual, 'Here: you might find a use for these.' When they turned out to be the wrong type of units for leg-attachment, James Fox at the British Antarctic Survey replaced them without question and, more importantly, without charge. James also generally guided me through the struggle of retrieval and analysis of the data, and extracted data from troublesome units, with a very quick turn-around time. Several people helped me scatter ground-truthing geolocators around the flyway, to help with interpretation of data: Ty Donnelly, Brian McCaffery, and Dan Ruthrauff in Alaska, Andreas

Kim and Nial Moores in South Korea, and Adrian Riegen in China. It's not Ty's fault (I assume) that the thing got eaten by an Arctic Fox.

Many thanks to the superb team at Massey's Institute of Veterinary, Animal and Biomedical Sciences (particularly Brett Gartrell, Jodi Salinsky, and Janelle Ward), whose tireless work saw me through the undisputed low point of my research.

Other contributions to specific chapters are as follows:

Chapter 2: Thanks to Lee Tibbitts for assistance with the Figure 2.2 map. The manuscript benefited from comments by David Penny on an earlier draft. Comments by Barbara Helm on the final paper helped put these findings into perspective, which greatly benefited my overall thesis.

Chapter 3: I thank Bob Gill, David Melville, and Craig Steed for field assistance in Alaska. Todd Buckley, Randy Hill, Sarah Lovibond, Julie Morse, Adrian Riegen, Rob Schuckard, Craig Steed, Pavel Tomkovich, Keith Woodley, and Steve Zack kindly provided photographs of Alaska godwits. I thank Carla Cicero (Museum of Vertebrate Zoology at the University of California at Berkeley), Bob Gill (U.S. Geological Survey's Alaska Science Center in Anchorage), and Kevin Winker (University of Alaska at Fairbanks) for access to museum specimens. Adrian Riegen provided New Zealand Wader Study Group capture data. Finally, thanks to Brian McCaffery for pumping out an entire paper just so I could cite it.

Chapter 4: I thank Bob Gill, Michael Kemp, and Judy Shamoun-Baranes for thoughts on wind analyses.

Chapters 5 and 8: I thank Theunis Piersma for helpful comments on early drafts of the Chapter 5 manuscript, and for helping flesh out the Black-tailed Godwit section of Table 8.2.

Chapter 7: I thank Yvonne Verkuil for reviewing the manuscript and inspiring the title.

Chapters 2–6 and Appendix 1 greatly benefited from the editorial and review processes at their respective journals.

On a more business-like note, my research was supported by a Massey University Doctoral Scholarship. This project was generally supported by the David and Lucile Packard Foundation through the Pacific Shorebird Migration Project, and by a Marsden Fund grant administered by The Royal Society of New Zealand to Phil Battley. Fieldwork was conducted with Massey University Animal Ethics Committee approval (#07_163). The Ornithological Society of New Zealand provided capture data partly obtained under Department of Conservation Research and Development contracts 3739-01 and 3599.

I was already grateful for the research grant I received from the Manawatu Estuary Trust. Three weeks later, I became even more grateful when my laptop died and had to be quickly replaced during the home stretch of thesis-writing.

On a more personal note, I would not be where I am today (alone and penniless at a computer on a remote South Pacific island) if it weren't for my lucky meeting with a few particular people along the way. I'm not sure why Mark Colwell offered me the job counting shorebirds on Humboldt Bay, a job I almost turned down because I had already decided I wanted to work on any birds *except* the wet and cold ones. I am just glad he did offer it, because I haven't thought about anything but shorebirds since. As my Ornithology TA in my very first semester at Humboldt State, Dan Ruthrauff still claims that he taught me nothing, but in fact he taught me the only thing I really needed to know: go to Alaska. And that led me to Brian McCaffery, who for some reason hired me sight-unseen after I cold-called him and deftly dropped the names of Dan and Mark. Strangely, he insisted on repeating this error, and three years later I was marooned at an Alaskan field camp with David Melville. Somehow, amongst repeatedly fleeing for our lives from Biblical floods, David convinced me that I should endeavour to become the PhD student of a then-unemployed New Zealand biologist who was younger than me. Why wouldn't I do that?

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.

I could not have made it through the last four years without being adopted by a pretty special group of friends in New Zealand. Although some have already dispersed abroad, they have been a wonderful and much appreciated support group: Dorothée Durpoix, Rich Seaton, Jay Gedir, Fleur Maseyk, Robbie Andrew, Pete McGregor, Yvan Richard, Melanie Kiessner, Marco Wenzel, Jay McCartney, and Anne-Marie Emerson, to name a few.

I owe a great deal of the success of this thesis to my supervisors, Phil Battley and Murray Potter, who could hardly have been more supportive and helpful throughout the entire process. I know I am fortunate to have supervisors who are not only so capable and constructively critical, but are also as excited about my research as I am. It has been a great collaboration. However, considering the clear evidence for an inverse relationship between alcohol and the productivity of scientists (Grim 2008), I have to question Phil's deliberate role in my development as an aficionado of single malt whisky. Any shortcomings of this thesis should be considered Phil's sole responsibility.

Chapter 1

Introduction: individuality and long-distance migration

From populations to individuals

Natural selection and I have something in common. We are both focused on individuals. For me, the fascination began when I first put radio-transmitters on Dunlin *Calidris alpina* in 2002 and discovered that each one of these apparently indistinguishable birds had its own way of doing things. As for natural selection, *it* probably became interested as soon as the first unicellular organisms began to develop idiosyncrasies.

Differences among individuals are, of course, the raw material for evolution and therefore the ultimate source of diversity in all higher levels of organisation from population to kingdom. In fact, individuals must differ for natural selection to occur (Darwin 1859). Because not all behavioural or morphological variants are equal in terms of promoting an organism's success, biologists may view individual differences on a continuum from 'adaptive' to 'maladaptive', and expect all examples on the latter end to be removed from the population eventually through a failure to survive and reproduce. Optimal behaviour theory (e.g., Stephens and Krebs 1986) places a similarly low value on individuality, viewing variation as inherently unimodal: for a given scenario, there is a single best solution, and the fringes of variation extending outward from this are increasingly wrong.

A radically different view is that individual differences are not just fodder for natural selection, but also the end product of it (Wilson 1998). There is ample evidence that there can be more than one viable solution to an ecological problem. It is well-established that different priorities and capabilities of individuals based on sex or age can foster multiple strategies in the same population (e.g., Ketterson and Nolan 1983), but more intriguing are differences within a class, such as male mating polymorphisms (e.g., Jukema and Piersma 2006). These show that individual variation need not be discouraged by natural selection, but can be perpetuated when alternative strategies have similar outcomes (Shuster and Wade 1991) or if each is superior in different contexts (Wilson 1998, Dingemanse *et al.* 2004). Examples of stable behavioural or morphological polymorphisms come from taxa as diverse as isopods, fish, lizards, and birds, and are almost certainly more common than has been documented.

A particularly rich and interesting field of study is the fitness consequences of animal personalities (Dingemanse and Réale 2005). Much of this research has focused on the propensity of individuals to exhibit shy or bold behaviour when addressing novel circumstances (Wilson *et al.* 1994, Dingemanse *et al.* 2004), and has shown that such traits can be heritable and linked to entire suites of other behaviours. Recognising study organisms as individuals with distinct personalities and preferences forces biologists to view them as more than automatons seeking optimality or noise around a mean value. Furthermore, population parameters may be seen as merely the downstream manifestations of individual variation.

Science is by nature reductionist: it is fundamental to examine the smallest discernible parts in order to understand larger patterns. Despite this, ecological research was for decades dominated by a focus on populations and species, rather than individual organisms (Łomnicki 1992). One reason for this was philosophical. Proponents of a more holistic approach rejected the application of reductionism to ecology because it seemed to ignore the consequences of evolutionary theory and downplay the importance of interactions among organisms, artificially simplifying what was inherently complicated and hierarchical (Caplan 1988). It was generally believed that evolutionary and ecological processes could best be understood through describing demographic parameters at the population level.

Other obstacles to an individual approach were practical. Intensive study of individuals is difficult and time-consuming, and acquiring large datasets for cryptic, highly mobile, or low-density species can be nearly impossible. Without large samples, an individual approach risks being anecdotal in nature, more naturalistic than empirical. It may bias conclusions by under-representing the range of variation in the population and missing important processes. Another problem is that of analysis; biologists are most accustomed to statistical methods that address average values, and multi-modal (or non-modal) datasets can be difficult to summarise or understand. This is to some extent addressed by the rapidly growing field of individual-based modelling (Judson 1994), but useful models still depend on copious and diverse data that can be very difficult to obtain.

Here, methodological questions find commonality with the ecological problems themselves: there is, of course, no single correct answer. Much can be learned from both ‘bottom-up’ (using individuals to understand how the properties of a larger system emerge) and ‘top-down’ (using higher-level patterns to understand the diversity of individuals) approaches, but neither tells the whole story on its own (Grimm 1999). In fact, these approaches should not be seen as two competing ways to answer the same question. Population-level and individual-level processes must be viewed separately and in conjunction to really see how a system works. The most complete understanding will surely come from a combination of approaches, as I hope this thesis will help demonstrate.

Migration as a research challenge

The field of avian migration research in particular has been historically limited to population-level studies, due to the inherent difficulties of gathering data on individuals that are more mobile than biologists are. Wherever you try to conduct your research, the birds leave. Depending on the nature of your study site, any migratory species will be essentially absent for 5–11 months each year. So, no matter how much information you gather from one location, you are missing a substantial part of the story. More inconveniently, it has long been recognised that events in one season of a migratory bird's annual cycle may be influenced by prior conditions or events on the other side of the globe. These cross-seasonal effects operate at evolutionary scales, shaping long-term patterns within and among populations (Myers 1981), and also at smaller scales, in which environmental conditions in a particular time and place may influence a specific individual's performance later in that year (Harrison *et al.* 2011). Consequently, studies that focus (usually by necessity) on a single season are limited in the spectrum of inferences to be drawn from their data even with regard to *that season*. This is the fundamental challenge of studying migratory species.

Except for species travelling through and to extremely inaccessible regions, it is generally possible to capture more of the annual cycle by observing, for example, breeding birds in one location and non-breeding birds in another, and then drawing reasonable conclusions regarding connections between the two. Historically, most information regarding the annual routines of migratory birds was derived in this manner. This can help describe population parameters, but relies on the central assumption that all variation present in the entire population (or at least equivalent segments of it) exists in the respective study samples. In practice, this assumption is almost always violated to some extent, especially for species that are widely distributed in one or more seasons. It is common for basic attributes of morphology or behaviour to vary geographically across the breeding and/or non-breeding range of a species (Zink and Remsen 1986), and so spurious conclusions may arise when the entire range of variation is not considered. Without evidence of direct connections between studies in different seasons, researchers may unwittingly compare apples to oranges.

Such direct connections are possible only through the tracking of individual birds across seasons, the difficulty of which remains the single biggest hurdle to understanding annual routines of migrants. One of the earliest and most elegant approaches to this problem was the attachment of leg bands (Preuss 2001), which allowed individuals or cohorts captured at one site to be identified when they were observed or captured at another site. Still the most widely-used method to study migration after more than a century, leg bands continue to provide valuable and surprising insights about migratory routes, timing, and distances, as well as survival and longevity. In the last thirty years, rapid technological advances have allowed more precise and thorough tracking of individual movements by radio telemetry, satellite telemetry, and, most recently, geolocation (Fiedler 2009). Each of these technologies experienced exponential increases in both use and effectiveness for bird research as issues regarding price, miniaturisation, attachment, and battery life were resolved.

This ongoing renaissance in the field of bird movements, accompanied by concurrent advancements in physiology and endocrinology, has led inevitably to an increased focus on individuals. Traditionally, researchers used population-level data to infer what specific birds did; this practice tends to obscure individual variation and important links between seasons, and thus hinders understanding of the mechanisms and evolutionary processes underlying the phenomena of interest. New methods and attitudes are allowing us to turn the tables on this approach, by instead viewing populations as the sum of many distinct individuals.

Migration as a lifestyle

To think about how an individual bird manages its migration, it is helpful to first consider what would motivate it to migrate at all. After all, migration is only one of many possible strategies to address the fundamental challenge that faces all organisms, which is to reproduce. In circumstances where resources are consistent and appropriate to support both breeding and year-round survival, there is no need to migrate. But most environments on earth are seasonal, and so a sedentary animal faces peaks of relatively abundant resources alternating with periods of more restricted resources. Mobile animals, on the other hand, can benefit from the fact that seasonal resource peaks occur at different times at different locations by moving among them to essentially create a sustained resource peak. This also means they can go places that are completely inappropriate to their needs at other times of the year. For example, a migrant can use a site that offers prime breeding habitat in the summer but no food during the winter, because it simply leaves before resources disappear.

Thus, migration involves the movement of animals to exploit spatially and temporally variable resources. This is an opportunity, but also a constraint. Because the resources of both breeding and non-breeding locations, and potentially those of locations used in transit between them, operate on different schedules, the migratory lifestyle places considerable time constraints on the annual routines of individuals (Drent *et al.* 2006). If maximising lifetime breeding success is an individual's primary motivation, the breeding season can be considered the focal point of the annual cycle, with all other events theoretically optimised for maximum reproductive output. For this reason, how the timing of arrival on the breeding grounds relates to a migrant's breeding success has received much attention. Successful breeding requires resources (in terms of both habitat and food) for both the production of a clutch of eggs as well as the later development of young through fledging, and therefore should be finely tuned to the phenologies of breeding sites. Early breeding arrival, particularly in species with strong competition among individuals, confers many benefits, including reduced competition for territories and mates, more time for multiple breeding attempts, and appropriate timing of hatch in relation to resources for provisioning young. These benefits are reflected in the seasonal declines in breeding success observed in many species (Daan *et al.* 1990, Wiggins *et al.* 1994, Verhulst *et al.* 1995, Lozano *et al.* 1996, Hasselquist 1998). However, 'early' is not necessarily equivalent to 'optimal'; there is also evidence of the reproductive costs of initiating breeding too early (Prop *et al.* 2003, Bety *et al.* 2004).

In addition to getting the timing right, a migrant must contend with the direct costs of getting to its destination, which can be considerable. Travelling takes time which could be otherwise spent on self-maintenance activities such as rest, moult, or foraging, and can involve survival threats associated with crossing inhospitable geographic barriers (e.g., oceans, mountain ranges) or exposure to inclement weather or predators. Birds must also spend time and energy preparing for the journey; prerequisites include sufficient fuel stores to fly between successive foraging sites along the migratory route, and flight feathers of adequate quality to conduct the trip. For those making protracted non-stop flights of thousands of kilometres, physical preparation includes not only accumulation of sufficient fat stores (in some cases, equal to 50–100% of basal non-breeding mass; Zwarts *et al.* 1990b, Gudmundsson *et al.* 1991, Piersma and Gill 1998, Battley and Piersma 2005), but also increases in mass and capability of flight muscles, and reduction in mass of body organs (e.g., the digestive system) unnecessary for the flight itself (Piersma and Gill 1998, Battley *et al.* 2000, Landys-Ciannelli *et al.* 2003).

Temporal and energetic constraints may be particularly challenging for high-latitude breeders. Seasonal changes are most profound at high latitudes, leading to intense resource peaks of shorter duration than those experienced at temperate latitudes. For example, arctic tundra breeding habitats may be ice-free and available for only 2–4 months per year and the intense annual bloom of insect prey necessary to support fledging of chicks may last just 2–3 weeks (Meltofte *et al.* 2007b, Tulp and Schekkerman 2008). These brief breeding seasons make timing of migration even more critical, because differences of even a week or two may have severe impacts on breeding success or even adult survival. In addition, low food availability and unpredictable conditions at the start of the breeding season may require birds to carry greater nutritional reserves than are needed for the flight itself, to support both survival and immediate investment in breeding after arrival on breeding grounds.

So we see that migration is not just an action, but rather a ‘syndrome’ of behaviours and physiological processes that encompass a bird’s entire annual routine (Piersma *et al.* 2005, Dingle 2006). These traits have deep evolutionary roots that reach far beyond the few specific concerns discussed above, influencing morphology, mating systems, chick development, longevity, and any number of other basic life-history attributes. This fact profoundly influences not just the birds themselves, but how we must view and study them.

Scheduling of moult

The most conspicuous and defining attribute of birds is their feathers. However, because feathers are subject to wear and damage through use, they are not permanent, and most birds replace all of their feathers at least once per year (Howell 2010). Feather replacement involves costs, including both direct costs of feather synthesis and indirect effects of decreased performance in thermoregulation or flight during moult (Payne 1972, Murphy and King 1991, Lindström *et al.* 1993, Swaddle and Witter 1997). How birds schedule their annual moults reflects both these costs and the relative importance of feather quality to performance in different seasons (Holmgren and Hedenström 1995). Scheduling of moult is a particular challenge for migratory species, because activities such as long-distance flights and pre-migratory mass gain may be energetically incompatible with moult. For example, some species initiate mass gain only after the completion or suspension of moult (Thomas and Dartnall 1971, Serra *et al.* 1999), but others may overlap the two processes (Marks 1993, Lindström *et al.* 1994). Compared to breeding and migratory movements, scheduling of moult appears to be much more plastic and open to strategic flexibility at both evolutionary and individual scales (Helm and Gwinner 2006, Flinks *et al.* 2008).

Flight feather moult has obvious functional consequences with regard to migratory performance and is generally completed to the same degree by all migrating individuals. Intra- and inter-specific differences suggest that timing and duration of wing moult is plastic in evolutionary terms (Serra 2001, Summers *et al.* 2004), but there is also evidence that individuals can respond to much more immediate stimuli to alter moult schedule. For example, nutrient deprivation may result in a protracted wing moult (Murphy *et al.* 1988, Marks and Underhill 1994). Also, time-stressed individuals may be able to compensate for a late moult by increasing the growth rate of particular feathers or growing more feathers concurrently (Murphy *et al.* 1988, Dawson 2004, Serra and Underhill 2006). However, this may come at the expense of feather quality, as a hurried moult may produce less durable or more asymmetrical feathers (Serra 2001, Dawson 2004).

Along with flight feathers, all body (or ‘contour’) feathers are typically replaced in the non-breeding season, in what is referred to as the ‘pre-basic’ moult (Humphrey and Parkes 1959). Many species that benefit from different plumages in different seasons have evolved a second annual moult, in which all or most of the contour feathers are replaced again. This ‘pre-alternate’ moult is commonly a transformation into breeding plumage, which, unlike the pre-basic moult, can be a source of substantial individual variation in terms of extent or intensity of colouration. Variation in breeding plumage is traditionally thought to advertise relative individual quality by honestly signalling a bird’s condition (Hill 1991, Fitzpatrick 1998, Jawor and Breitwisch 2003). In addition, young or socially subordinate birds may invest less in breeding plumage, conserving energy and preventing costly agonistic encounters by signalling their low social status (Flood 1984, Lyon and Montgomerie 1986, Chu 1994). Alternatively, plumage may vary geographically with habitat characteristics (Mumme *et al.* 2006), and intra-individual variation may additionally reflect environmental stochasticity (Griffith and Sheldon 2001). Whatever the mechanism, variation in investment in breeding plumage can lead to substantial differences in timing and duration of moult among individuals in the same population.

Individual quality versus individual strategies

The observation that individuals differ in some respect often reveals little regarding why they are different. As discussed earlier, there are clear and demonstrable advantages to performing migration ‘correctly’; if so, why don’t all individuals do exactly the same thing? One possible answer is that they can’t, due to innate differences in quality. To illustrate, let’s assume that for a given population there exists an optimal time to arrive on breeding grounds, an optimal state of breeding plumage, and an optimal body condition with which to begin breeding activity. The highest quality individuals will accomplish all of these optima through proper management of the non-breeding season; perhaps they are highly efficient foragers, or secure the best feeding and roost sites. Other individuals will be forced to trade off some part of the equation, by arriving later, with lesser breeding plumage, or with suboptimal body condition, and thus suffer the likely consequences of reduced breeding success or survival.

Of course, similar disparities can occur without intrinsic differences in quality, if individuals experience very different conditions prior to the breeding season. For example, a bird may arrive late or in poor condition due to unusually low food availability at a particular wintering site, or because it encountered particularly harsh weather during the flight. In this case, individual differences in performance may vary annually, as opposed to quality-based differences that may be persistent.

These scenarios assume that all individuals have the same ‘goal’, a concept that has permeated much of optimal migration theory. Alternatively, birds might differ simply because they had a different plan to begin with. It has long been recognised that different age and sex classes in a population may have different migration patterns (Myers 1981, Cristol *et al.* 1999), but strategic differences within these groups have received much less attention. However, several recent studies have emphasised that temporal and energetic trade-offs related to migration must be evaluated in terms of the individual. This approach recognises that the costs and benefits of early arrival may differ among individuals, perhaps due to factors such as morphology, behaviour, social status, or prior experience (Møller 1994, Forstmeier 2002, Prop *et al.* 2003). In addition, some facets of migratory behaviour such as breeding arrival date appear to be endogenously programmed and to some extent heritable (Rees 1989, Berthold and Pulido 1994, Møller 2001, Pulido *et al.* 2001), and perhaps not strongly influenced by competition and environmental conditions. Individual repeatability of migration timing (Møller 2001, Forstmeier 2002, Bety *et al.* 2004, Battley 2006, Gunnarsson *et al.* 2006) attests to this, but can be difficult to disentangle from differences in individual quality, which may be quite stable over time (Catry *et al.* 1999).

If one optimal migration strategy exists in a population, with only the highest quality individuals achieving optimality, it follows that migration timing should be highly correlated with individual condition. In two recent studies of long-distance migratory waders, timing of departure from non-breeding grounds was unrelated to individual body condition (Battley *et al.* 2004) or extent of breeding plumage (Battley 2006). This suggests that individuals behave according to strategies or constraints that are their own. For example, individuals from a single non-breeding site may breed in different regions, and thus vary their departure dates according to phenologies of their respective breeding areas. In this case, inferring relative quality of individuals based on migration timing would be simplistic and in error. Also, differences in initial departure timing do not necessarily result in corresponding differences in breeding arrival, due to potential variation in migration speed and length of stay at any stopover site *en route* (Bety *et al.* 2004, Warnock *et al.* 2004). Within one population, there may be multiple viable strategies for maximising lifetime reproductive success, and only by viewing each individual’s annual cycle can we begin to understand the significance of individual variation in any one component.

Aims of this thesis

My goal was to study long-distance migration with a combination of fine-resolution focus on individuals and broad annual-cycle perspective never achieved in previous studies. By viewing migration in the context of an individual bird's entire annual routine, I sought to identify the roots and consequences of both persistent and ephemeral individual differences in migration and moult, and to identify constraints and potential bottlenecks in the annual cycle.

Study species

Godwits (Order Charadriiformes, Family Scolopacidae, Genus *Limosa*) are medium-sized, long-legged and long-billed shorebirds that breed on low tundra and grasslands, and spend non-breeding seasons on coastal mudflats and to a lesser extent on pasture and agricultural lands. This circumpolar genus is particularly well-suited for migration studies, because of the diversity of migration systems found both among and within its four species, from relatively short-distance movements within the northern temperate zone to epic journeys linking the far reaches of both hemispheres. The wealth of population-level research previously conducted on godwits has described the broad spatial and temporal patterns of their annual routines, so that new information can be immediately placed in a useful comparative context. In addition, the closely-related and ecologically similar Red Knot *Calidris canutus* is among the most well-studied of migratory birds (see Buehler and Piersma 2008), offering additional scope of comparison and inference.

The Bar-tailed Godwit *Limosa lapponica* (Figure 1.1; hereafter, 'godwit') comprises four recognised subspecies (plus one small population of uncertain taxonomic status) whose arctic and sub-arctic breeding grounds stretch discontinuously from Scandinavia east to Alaska (Engelmoer and Roselaar 1998). The Alaska-breeding subspecies *L. l. baueri* is among the world's most extreme avian migrants. Post-breeding individuals fuel in southwestern Alaska for several weeks, approximately doubling their mass in preparation for the longest non-stop flight reported in the animal world, a trans-Pacific journey of over 11,000 km to non-breeding grounds in New Zealand and eastern Australia (Gill *et al.* 2005). In the austral summer, they moult and refuel once more for a 9,000–10,000 km non-stop flight to the Yellow Sea region of Asia in late March and early April (Battley *et al.* 2012). After a month-long stopover on the productive tidal flats of Korea and China, the godwits embark on a third non-stop flight across the Bering Sea back to their Alaska breeding grounds. This annual routine was spectacularly demonstrated when a female godwit (known as 'E7') captured in New Zealand was tracked by satellite telemetry on her entire round-trip journey, which included three migratory flights

Figure 1.1 Bar-tailed Godwits at the Manawatu River estuary, New Zealand.

encompassing 29,000 km and 21 total days of flying, including the longest single flight ever recorded: 11,690 km non-stop from southwest Alaska to northern New Zealand (Gill *et al.* 2009, Battley *et al.* 2012). Appropriate to these astounding flights, fat content of pre-migratory Bar-tailed Godwits is among the highest recorded in birds: 30–45% of body mass prior to northbound departure (Battley and Piersma 2005) and up to 55% upon southbound departure from Alaska (Piersma and Gill 1998). Adult males in New Zealand increase from non-breeding masses of 230–280 g in October–December to 420–500 g in early March; females increase from 310–360 g to 520–600 g (P. Battley and A. Riegen unpubl. data).

In general, coastal shorebirds greatly simplify research by congregating in great numbers at a limited number of predictable sites in both winter and on migration, as opposed to dispersed, broad-fronted migrations of, for example, continental passerines (Busse 2001). The annual routine of *L. l. baueri* is particularly elegant, in that individual birds essentially use only three or four sites for most of their lifetimes: one wintering site, one staging site in Asia, and one or two areas of Alaska. From a population perspective, the entire subspecies stops only in small areas of the Yellow Sea and Alaska during extended stops on migration, as opposed to species that make numerous shorter stops *en route* (Warnock *et al.* 2004, Eichhorn *et al.* 2006). While this is a potential conservation concern, it greatly simplifies the researcher's job by limiting the sources of potential variation that must be considered.

In addition, Bar-tailed Godwits are ideal subjects for individual-based studies of moult and migration in the non-breeding season. They are long-lived (~10–25 years) and have very high inter- and intra-annual site fidelity, making it possible to monitor individual birds throughout a multi-year study. They are gregarious, use open habitats, and have predictable daily routines according to tidal cycles, allowing relatively easy capture and very profitable resighting efforts of individually marked birds. They undergo conspicuous and dramatic seasonal changes in plumage, which enables visual observation of moult without the need to repeatedly capture birds. Finally, they are large and durable enough for the use of instrumentation such as satellite transmitters and geolocators to track movements far from the capture site, including to remote and relatively inaccessible breeding sites where direct observation is extremely difficult.

Bar-tailed Godwits show delayed maturity; after making the southbound flight from Alaska at 3–4 months of age, most young birds do not return to the breeding grounds or acquire full adult breeding plumage until their third or fourth summer (McCaffery and Gill 2001). However, some individuals apparently migrate in their second year (Battley 2007), and godwits on their first northward migration have less extensive breeding plumage than they do in later years (Battley 2006). The bright red ventral breeding plumage of adult male godwits is assumed to play a role in mate selection by females, although direct evidence for this is scant in this species (McCaffery and Gill 2001). It has been proposed that godwit plumage signals relative individual quality to potential mates and rivals (Piersma and Jukema 1993, Drent *et al.* 2003). However, there is mounting evidence for a geographical cline in male breeding plumage within Alaska, with redder males disproportionally represented in the northern parts of the breeding range (Rynn 1982, McCaffery *et al.* 2010). Also, males and females share incubation of ground nests, so plumage of both sexes has a crypsis function.

Tantalising results from recent studies have shown there is much to learn about how individual godwits optimise their timing of migration. In the Firth of Thames, a major New Zealand non-breeding site, individual godwits had highly repeatable departure dates and extent of pre-migratory breeding plumage (Battley 2006). However, plumage at departure, which was highly variable among individuals, was not related to departure date. Also, there was a trend of larger males departing earlier. These findings contradict the simple prediction that high-quality individuals complete their breeding plumage and depart first, with others departing later upon reaching an optimal breeding plumage. Rather, it suggests that birds operate on individualised schedules, which may result from heritable or derived differences in behaviour, endogenously programmed schedules of moult and migration, variation in breeding area and migration route, or carry-over effects from other parts of the annual cycle.

Body composition analysis on a cohort of fuelling male Bar-tailed Godwits in northern New Zealand (Battley and Piersma 2005) revealed two distinct groups. Fatter birds had longer wings, more developed flight muscles, less developed breeding plumage, and had suspended body moult. Lighter birds, presumably further from readiness for departure, had more developed breeding plumage, but were still in active body moult. This strongly suggests that multiple migration strategies exist in the population, which may include: (1) achieve early New Zealand departure and early Alaska arrival by compromising extent of breeding plumage; (2) achieve early New Zealand departure in order to spend more time in Asia, allowing the completion of the breeding moult; and (3) complete the breeding moult in New Zealand, and thus have a shorter stopover in Asia or later arrival in Alaska. Whether these strategies exist on a continuum in the population, or represent distinct subgroups, perhaps according to breeding area, requires further investigation.

Differential timing of migration to the breeding grounds occurs in many species; specifically, the sex which benefits most by early occupation of breeding territories often migrates earlier (Myers 1981, Cristol *et al.* 1999). This is not apparent in Bar-tailed Godwits; sexes appear to depart New Zealand across the same time period (Battley 2006). This could be because New Zealand departure and Alaska arrival are not closely correlated, once additional variation is introduced by migration speed and length of stay at Asian stopover sites. However, there is some evidence that males and females arrive on breeding grounds approximately simultaneously (McCaffery and Gill 2001), indicating there may simply be no benefit to earlier arrival by one sex.

Even so, sex differences in Bar-tailed Godwits are of particular interest, due to substantial sexual dimorphism in the species. Females are approximately 20–40% larger than males, the sexes have minimal overlap in bill length (McCaffery and Gill 2001), and no other monogamous scolopacid shorebird shows such extreme plumage dimorphism (Figure 1 in Jukema and Piersma 2000). These differences may have significant implications for how the sexes prepare for migration. For example, consequences of larger female body size might include greater energetic costs of maintaining body condition throughout the non-breeding season, greater absolute fuel mass required for migration, and greater mass of flight feathers to be replaced. Also, females may forage (and thus fuel) quite differently from males due to their longer bills, and may invest less energy growing their less extensive breeding plumage. The contribution of sexual dimorphism to patterns of moult and migration has great relevance for understanding individual constraints and strategies within the population.

In summary, the annual routines of New Zealand Bar-tailed Godwits pose some serious challenges for them. Their northerly breeding grounds are profoundly seasonal, with very short breeding seasons and brief but intense blooms of resources. Their migratory flights are extreme and unforgiving, stretching the bounds of physical endurance, while offering little or no opportunity to stop along the way. Their non-breeding season is a busy schedule of physical preparation for the next northbound migration. Thus, Bar-tailed Godwits may be among the most time- and energy-constrained of migratory birds, and therefore represent an excellent model for understanding both the potential extremes of the migratory lifestyle and the basic challenges faced by all migrants. In an annual cycle with so little apparent room for error, we might expect to find the greatest benefits of strict adherence to individually-optimised schedules, and also the most profound consequences of environmental variation and individual condition.

Study site

The Manawatu River estuary (hereafter, ‘Foxton’; 40.47°S, 175.22°E; Figure 1.2) is a small river mouth on the west coast of New Zealand’s North Island. Before emptying into the Tasman Sea at a sandy beach, the Manawatu River is bordered for approximately 3 km by tidal mudflat and saltmarsh, and accommodates moderate human recreational use from the

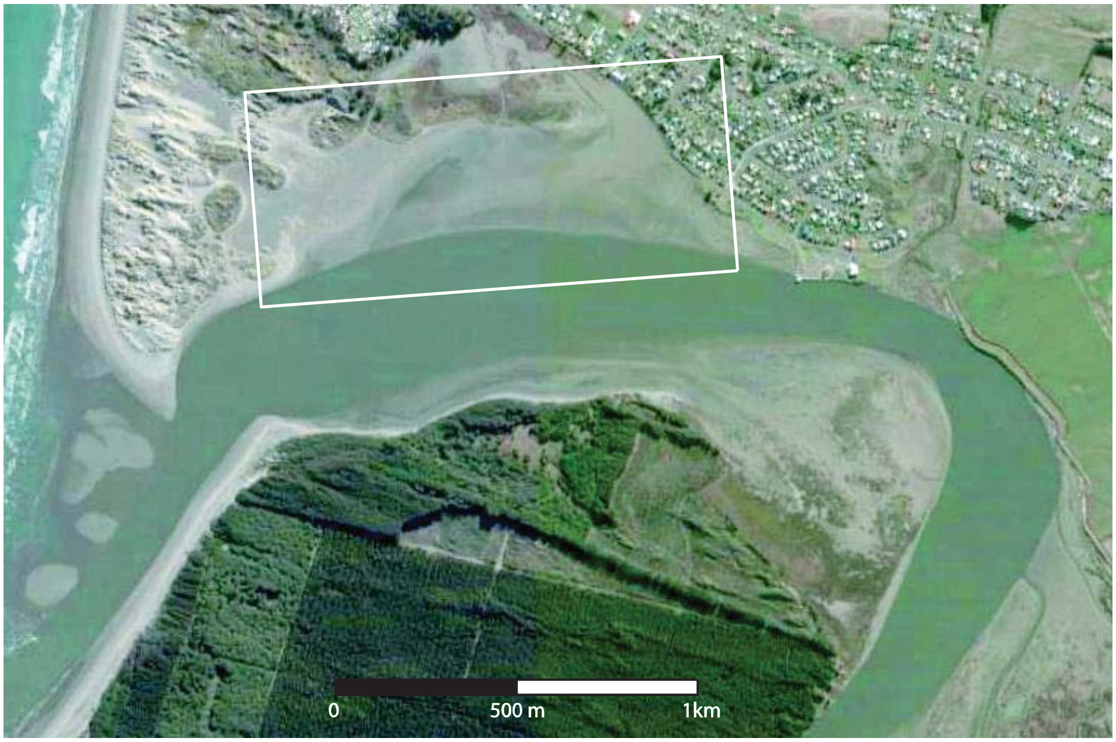

Figure 1.2 The Manawatu River estuary, New Zealand. Box indicates core study area. Image source: Google Earth.

adjacent community of Foxton Beach. One of the more popular bird-watching spots in New Zealand, the estuary hosts small populations of both local- and arctic-breeding shorebirds during the austral summer months.

Although godwits use many sites in New Zealand in larger numbers (Figure 1.3), Foxton is ideal for studies of individual variation for several reasons. First, intra-season movements of individuals to and from the site are rare and negligible; the estuary is isolated by many kilometres from other suitable godwit sites and appears to provide for all of their non-breeding requirements. The site is small and easy to access, allowing observation of the entire godwit population from several single (and dry) vantage points in most circumstances, even when the flock is widely scattered and foraging at low tides. The resident godwit population is less than 300 birds, so it is much easier to locate and follow specific individuals than at other sites where they may be easily lost among thousands of flock-mates. Despite the small population,

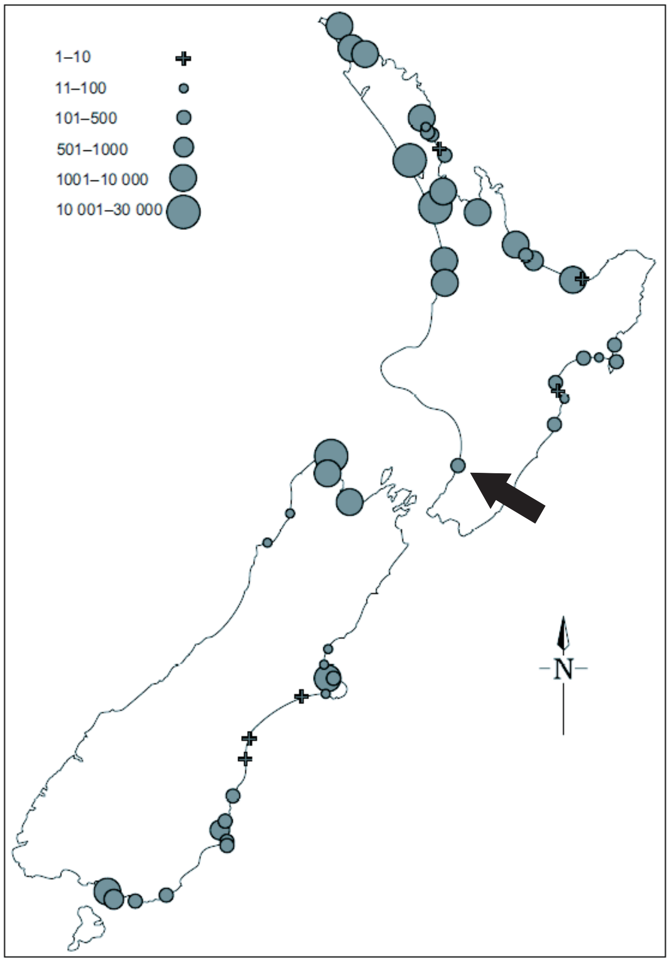

Figure 1.3 Numbers of Bar-tailed Godwits at non-breeding sites in New Zealand (from Southey 2009). Arrow indicates location of Manawatu River estuary study site.

variation in plumage and migration timing is similar to that seen at larger sites and in the population as a whole, and so extrapolation of findings to the larger New Zealand context seems appropriate.

Most important for my specific study are two final points. Due to the prescience of my primary supervisor, more than 60 godwits were individually colour-banded at the estuary in 2006–2007, 45 of which were still using the site when I began research in November 2007. This allowed the immediate collection of observational data without trapping, and the opportunity to observe any effect of new trapping on the phenomena of interest. Lastly and perhaps most crucially, predictable high-tide roost use by a small population of extremely site-faithful birds allowed the repeated captures necessary for the deployment and retrieval of geolocators. This fostered a previously unheard-of recapture rate of non-breeding shorebirds that is presently the envy of shorebird biologists worldwide.

Overview of research chapters

The methodological approach for my research was quite simple. Using direct observation and digital photography, I closely monitored individually marked Bar-tailed Godwits in New Zealand for multiple years, through the major non-breeding events of migratory arrival, contour and flight feather moults, and ultimately northbound departure. I linked this information with events outside of New Zealand by tracking a subset of the same individuals on their complete round-trip migrations, through stopover in Asia, breeding in Alaska, and eventual return to New Zealand. I used these data to address the following key questions:

1. *How are a godwit's moult and migration schedules in New Zealand influenced by its ultimate destination in Alaska?*
2. *Do individual differences in timing of migratory departure from New Zealand persist through the migration and result in differences in timing of arrival at breeding sites?*
3. *What external local factors affect timing of departure from New Zealand?*
4. *How do individuals with varying extents of breeding plumage schedule their moults differently?*
5. *What magnitude of delay in migratory arrival or moult in the non-breeding season will compromise a godwit's breeding plumage or migration schedule the following season?*
6. *How do flexibility in moult and migration schedules differ, and what does this tell us about selective forces operating throughout the annual cycle?*

The heart of this thesis is six research chapters, each written as stand-alone contributions for international peer-reviewed journals. Therefore, there is a certain amount of redundancy among them that was necessary to make each an independent piece, but I have standardised the formats to make the entire thesis more cohesive. Furthermore, the chapters appear in the order in which they were written. This is important because I generally analysed, wrote, and submitted each chapter for publication before I fully understood what would be revealed in subsequent chapters. So, a chronological reading of this thesis is a good representation of the process of discovery that I experienced across a period of nearly two years. In some cases, I propose hypotheses in one chapter that are rejected in the next one. That is one of the exciting parts of science, and so I have left it all in there.

In the following overview, I describe the central challenges of each chapter, with an emphasis on how specific methods addressed my key questions.

Chapter 2. Breeding latitude drives individual schedules in a trans-hemispheric migrant bird

When I started this project, a new technology was revolutionising the study of long-distance migration. Light-level geolocation is an elegant concept: because day length varies with latitude and time of day varies with longitude, a datalogger that records only sunrise and sunset can allow the calculation of an animal's daily position on the globe. By 2008, geolocators had already taken the seabird world by storm (Shaffer *et al.* 2006, González-Solís *et al.* 2007), and had recently been miniaturised sufficiently to enable tracking of birds smaller than 200 grams (e.g., Stutchbury *et al.* 2009). Today, scores of geolocator-equipped studies worldwide are unmasking heretofore-unknown migratory routes and patterns at an astonishing rate (e.g., Egevang *et al.* 2010, Klaassen *et al.* 2011). Geolocators offer some major benefits over satellite transmitters, which have been prohibitively expensive and bulky, have limited battery life, and require attachment methods (implantation or backpack harness) that have potentially significant impacts on bird behaviour and survival. Geolocators are relatively inexpensive, much smaller, and last up to two years. The drawbacks are reduced precision of locations, including an inability to calculate latitude within about two weeks of either equinox, and the requirement to recapture birds to access the data. This last problem had previously limited deployment of geolocators to the breeding season; typically, only site-faithful breeding birds offered much likelihood of recapture. The fortuitous nature of my study site and species allowed the first deployment of geolocators on birds from a non-breeding site, and the first on any shorebird. One challenge was to design an attachment method that would withstand extremes of temperature and salt-water immersion for multiple migrations, and yet be easily removed when the bird was recaptured (see Appendix 1).

Many of the big, fundamental questions regarding Bar-tailed Godwit migration had already been answered with satellite telemetry (Gill *et al.* 2009, Battley *et al.* 2012) and a very successful mark-resight programme (Riegen 1999, Battley *et al.* 2011), and so I generally knew where New Zealand godwits would go, and about when they would go there. My goal was to go beyond just tracking movements, by linking geolocation data with detailed non-breeding information on the same individuals. I sought to describe the entire range of migration strategies in the population, and so it was crucial to deploy geolocators on a fairly representative sample of birds. For the first deployment in March 2008, we captured a small group of godwits whose migratory habits were entirely unknown. Because we made these captures after migration had already begun, we did not sample early-departing birds, and by chance we also captured few late-departing birds. For the second deployment in October 2008, I therefore specifically targeted some individuals that had previously departed very early or late relative to the population, to try to explain what these birds were doing differently. This was probably the most important single decision of my entire project.

With year-round information on individual godwits, I could investigate whether patterns observed in New Zealand were strongly influenced by what godwits were doing elsewhere. Where in the world (literally) should I be looking for the reasons behind a godwit's plumage and migration timing? Also, I could test whether differences in timing of departure from New Zealand persisted through subsequent stages of migration. Did early-departing godwits actually arrive in Alaska and breed earlier, or did variation in the Asia stopover erase initial timing differences?

Chapter 3. Geographic variation in morphology of Alaska-breeding Bar-tailed Godwits is not maintained on their non-breeding grounds in New Zealand

Over several decades, a mostly unpublished body of evidence had accumulated, suggesting that plumage and size of godwits might vary geographically across their breeding range in Alaska (Rynn 1982, McCaffery *et al.* 2010). This was not particularly surprising, as many shorebird species with broad Northern Hemisphere distributions, including Bar-tailed Godwits, demonstrated measurable inter-population differences (Engelmoer and Roselaar 1998). However, these differences generally occurred along a longitudinal axis, between populations that were isolated by discrete breeding ranges and separate migratory flyways. Geographic variation within Alaskan godwits would have to occur along a latitudinal axis and within a population using a single migratory route.

Because such a pattern in the breeding range could significantly affect inferences I would make about godwits in New Zealand, I needed to formally describe it. This required me to assemble and add to all previously collected data on Alaskan godwits. First, I 'simply' (an elegant solution masking great expense, effort, and logistical difficulty) went to two Alaskan breeding areas, on the Seward Peninsula and the north slope of the Brooks Range, and digitally photographed every godwit I could find. Then I visited three museum collections in North America and examined every available Alaskan Bar-tailed Godwit specimen. I supplemented this by compiling all available godwit photographs taken by myself and other biologists during previous work in Alaska, and morphometric data from all previous captures in Alaska and all New Zealand-banded birds that had been tracked to precise breeding locations. Together, these data formed the most comprehensive dataset on Alaskan godwits yet assembled. For comparison, I compiled non-breeding morphometric data from over 20 years of captures across New Zealand (with a span of latitude similar to the breeding range in Alaska).

Chapter 4. Impacts of wind on individual migration schedules of New Zealand Bar-tailed Godwits

Individual Bar-tailed Godwits are very consistent across years in the dates they depart from New Zealand on migration (Battley 2006). However, godwits are not just automatons with accurate calendars, and a non-stop flight of 9,000–10,000 km is not something to enter into lightly. An individual's readiness or willingness to embark on migration on a given day may depend on previous conditions (in terms of its ability to moult and fuel sufficiently for migration) or factors experienced on the day in question. For example, a bird otherwise ready to migrate may not do so if current weather would make the flight more difficult, or if no other birds were willing to serve as travelling companions.

Such day-to-day influences can be very difficult to study, due to the requirement of precise movement data for a large number of individuals simultaneously. Many species migrate at night or from habitats that do not allow direct observation, so that departures can only be detected through remote tracking of individuals, which limits sample size and cannot provide a population context. For gregarious species that migrate conspicuously from open habitats, such as shorebirds, the challenge is to know the individual composition of departing flocks. Once again, my study site was the star and saviour of my project, this time allowing me to collect near-perfect departure data on 50–60 individual godwits each year (to the exact minute in 76% of cases), using only a spotting scope and a digital camera (Figure 1.4). A worrisome question at the start of my project was whether godwits migrating from a very small site would behave similarly to those at sites hosting thousands of birds. At two large sites in New Zealand, godwits departed over a four-week period (Battley 1997, 2006), trickling out in flocks of tens to hundreds. What if my entire flock of 250 departed together, or moved to other sites before their actual departures from New Zealand? I would not have much of a study. Fortunately, that was not the case.

Figure 1.4 Migratory departure of Bar-tailed Godwits from the Manawatu River estuary on 26 March 2010. There are five colour-banded birds in this flock.

Though it required considerable physical and mental endurance, relentless focus, and more patience than I thought I possessed, standing out on a mudflat for hours on end for four weeks straight waiting for individual birds to migrate was (all three years) among the most rewarding wildlife experiences I have ever had. It was particularly during these times that the godwits transcended the data they provided and were clearly individuals. It was truly humbling to watch an individual bird that I had followed intimately for the previous six months lift its wings and disappear to the horizon, for I knew it would next touch earth on a mudflat in China or Korea.

Chapter 5. Contour feather moult of Bar-tailed Godwits in New Zealand and the Northern Hemisphere reveals multiple strategies by sex and breeding region

In Alaska, male godwits have more extensive breeding plumage than females, and plumage within each sex varies substantially. How are these differences accomplished? During the non-breeding season, all godwits undergo a complete feather replacement (including flight feathers) into winter plumage and then replace a portion of their body feathers again to transform into breeding plumage. Godwits with more extensive breeding plumage must either moult faster or spend more time in moult, and this extra investment could occur either before northbound migration in New Zealand or during a month-long stopover in Asia.

Describing moult rate and duration at the individual level has rarely been attempted in wild populations, because it usually requires 'in-hand' assessment involving multiple captures.

Because plumage changes in Bar-tailed Godwits are very conspicuous, and individuals at Foxton could be encountered and photographed reliably throughout the non-breeding season, I decided to try it without captures. Three years and more than 18,000 digital photographs later, I had described the progression of pre-basic and pre-breeding contour feather moult in New Zealand for every marked godwit in my study. However, the problem remained that neither of these moults occurred entirely in New Zealand; pre-basic moult began in Alaska before southbound migration, and pre-breeding moult was completed in Asia after the first leg of the northbound trip. Based on ultimate breeding plumage in Alaska (Chapter 3), I estimated the duration and proportion of moults performed by godwits while they were in the Northern Hemisphere.

Chapter 6. Carry-over effects and compensation: late arrival on non-breeding grounds affects wing moult but not plumage or schedules of departing Bar-tailed Godwits

The idea that long-distance migrants are highly constrained by their demanding annual routines contains the assumption that they are operating near the limits of their capabilities. The logical and testable prediction from this is that unfavourable conditions or events during one part of the year will negatively affect a bird’s performance in subsequent stages, by reducing the time or energy available for later activities. In my study, I had the unique opportunity to test whether timing of arrival after the longest non-stop flight ever recorded affected an individual bird’s ability to prepare for its next migration. During six months in New Zealand, godwits recover from their 8-day flight from Alaska, complete pre-basic contour feather moult, replace their entire set of flight feathers, start moulting back into breeding plumage, and fuel for another 7-day flight to the Yellow Sea. If ever there was a scenario in which to expect carry-over effects, this was it.

The non-breeding season of godwits is largely occupied by their 3–4 month full replacement of flight feathers, and to assess the effects of migration timing on this task, I had to do what had never been done before: describe timing and duration of primary feather moult for individuals in a wild population, for multiple years and without capturing the birds. Fortunately, I possessed 18,000 photographs of individually identifiable godwits, many of which contained birds flying or stretching their wings. From these, I extracted two-year primary moult phenology information for 43 individual godwits. I added corresponding data on migratory arrival, contour feather moult (Chapter 5), and migratory departure (Chapter 4) to make inter-year comparisons across the entire non-breeding season.

Chapter 7. Absolute consistency: individual versus population variation in timing of annual life-history stages of a long-distance migrant bird

Sometimes punctuality is important and at other times it doesn’t matter. Presumably, natural selection has shaped the annual routines of birds such that they schedule life-history stages very precisely when the fitness benefits of correct timing are great, but are more lax when the costs of precise timing outweigh the benefits. Many studies have focused on how migratory birds schedule arrival on their breeding grounds, because it is clear that timing of breeding is important in seasonal habitats. However, the scheduling of this important event is rarely viewed in the context the entire annual cycle, due to the difficulty of following individual birds through successive seasons. This is a significant omission, because the relative precision with which an event is scheduled, as opposed to absolute precision, may tell us more about a bird’s annual priorities.

Using multi-year data on individual godwits observed directly in New Zealand (Chapters 4–6) and remotely via geolocators for the rest of the year (Chapter 2), I constructed the most complete picture of year-round schedules available for long-distance migrant bird. With these data, I tested two key predictions: (1) that both inter- and intra-individual variation in timing would decrease through successive stages leading up to the breeding season, and (2) that migratory movements would be more precisely scheduled than moults.

Chapter 8. Synthesis: an evolving view of long-distance migration

In this chapter, I focus on synthesising the disparate research chapters into a coherent whole, and discuss the significance of the collective findings to our understanding of individuality, constraints, regulation of the annual cycle, and long-distance migration.

Chapter 9. Future directions

In conclusion, I briefly outline some potential avenues of research that logically follow from the findings of this thesis.

Chapter 2

Breeding latitude drives individual schedules in a trans-hemispheric migrant bird

Conklin, J.R., P.F. Battley, M.A. Potter & J.W. Fox
Nature Communications 1: article 67, online (2010)
doi: 10.1038/ncomms1072

Abstract

Despite clear benefits of optimal arrival time on breeding grounds, migration schedules may vary with an individual's innate quality, non-breeding habitat, or breeding destination. Here, we show that for the Bar-tailed Godwit Limosa lapponica baueri*, a shorebird that makes the longest known non-stop migratory flights of any bird, timing of migration for individuals from a non-breeding site in New Zealand was strongly correlated with their specific breeding latitudes in Alaska, USA, a 16,000–18,000 km journey away. Furthermore, this variation carried over even to the southbound return migration, six months later, with birds returning to New Zealand in approximately the same order in which they departed. These tightly scheduled movements on a global scale strongly suggest endogenously-controlled routines, with breeding site as the primary driver of temporal variation throughout the annual cycle.*

Introduction

Some migratory birds 'winter' vast distances from where they nest, yet are under strong selection pressure to arrive on the breeding grounds at the time that best assures successful reproduction. Despite clear links between the timing and success of breeding, substantial variation exists in the migration timing of individuals, which can largely be explained in terms of three primary mechanisms: (1) variation in individual quality; (2) variation in fuelling resources; and (3) geographic variation among breeding destinations. In the first case, which has received the most attention in studies of migration timing, individuals possess heritable or acquired differences in moulting or fuelling efficiency, with only the highest-quality individuals achieving an optimal migration schedule (Møller 1994). In the second, individuals from high-quality non-breeding habitats may migrate earlier than those in low-quality habitats (Marra *et al.* 1998, Gunnarsson *et al.* 2006) and consequently experience increased breeding success (Smith and Moore 2005). The third scenario involves geographic variation in temporal availability of breeding resources, resulting in individuals having different optimal schedules based on their respective breeding sites. This phenomenon is easily illustrated when races of the same species have clear differences in breeding range and migration timing (Wood 1992, Battley *et al.* 2005), but within-population demonstrations are rare. For example, tundra-breeding birds at northerly latitudes generally begin nesting as soon as snow recedes from their breeding sites (Smith *et al.* 2010). Within Alaska, tundra becomes snow-free 2–4 weeks earlier in the southwest than it does in the far north (NOAA 2010b). As a result, optimal arrival dates for individuals in widely-distributed breeding populations may vary substantially (Holmes 1971).

Bar-tailed Godwits *Limosa lapponica baueri* depart New Zealand during March and early April, and fly approximately 10,000 km to sites on the Yellow Sea coast of Korea and China (McCaffery and Gill 2001). After refuelling, godwits depart Asia from late April to late May, and fly approximately 6,000 km to coastal sites in southwestern Alaska. They then disperse to coastal tundra sites across western and northern Alaska (59–71°N) for breeding in May–July. The godwits then congregate in southwestern Alaska to refuel before departing in late August–early October on a non-stop trans-Pacific flight of 11,000–12,000 km to New Zealand, the longest non-stop flight recorded in birds (Gill *et al.* 2009).

The difficulty of tracking small-bodied birds across great distances has hampered our understanding of cross-seasonal interactions between events on opposite sides of the globe. Studies are often limited to methods (e.g., stable isotopes) that require indirect steps to link the breeding and non-breeding grounds of individuals. The advent of small, lightweight geolocators allows these links to be made directly (Stutchbury *et al.* 2009), but the need to retrieve units to access data has limited their use to site-faithful species using accessible, high-density breeding sites (Eichhorn *et al.* 2006, Shaffer *et al.* 2006). Bar-tailed Godwits breed cryptically in low densities across over 1,800 km of remote coastal tundra within Alaska (McCaffery and Gill 2001), making breeding studies extremely difficult. However, high non-breeding site-fidelity of godwits in New Zealand allows the use of geolocators for inferences across the entire breeding range, while controlling for non-breeding habitat quality.

Our study is the first to deploy geolocators on non-breeding birds, and also the first involving shorebirds (suborder Charadrii), a group famous for extreme long-distance migrations. We attached geolocators to non-breeding Bar-tailed Godwits (Figure 2.1) at a small estuary in New Zealand, and recaptured them after their return migration. We show that the timing of each step in a >30,000 km round-trip migration (northbound departure from New Zealand, departure from fuelling sites in Asia, arrival on Alaska breeding grounds, and subsequent southbound departure) is primarily dependent upon the latitude of an individual's breeding site.

Methods

Geolocation data[1]

During two non-breeding seasons (2007–2008 and 2008–2009), we captured godwits from a small (200–280 birds) population at the Manawatu River estuary, New Zealand (40.47°S, 175.22°E) and attached leg-mounted light-sensitive geolocators (British Antarctic Survey

---

[1] See Appendices 1–2 for more detailed methods.

Figure 2.1 Individually colour-banded male Bar-tailed Godwit with tibia-mounted geolocator, prior to departure from New Zealand. Photo by Phil Battley.

model MK14; 1.4g; 2-year life). Return rate of these birds was 95%; we recaptured 80% of those available. Some birds carried geolocators for two migrations, and some units failed during deployment; for each bird, we used the first year with the most complete data. We calculated breeding locations for 16 birds (7 males, 9 females); for three of these, subsequent date of Alaska departure was unavailable due to geolocator failure. One other female was tracked for the entire migration, but did not settle at a breeding site (thus *n* = 14 in Figure 2.5).

The geolocators record sunrise/sunset, allowing calculation of latitude and longitude (±130 km error, based on ground-truthing units and resightings of instrumented godwits), except during ±15 days (d) of the vernal or autumnal equinox, when only longitude is reliable. To derive fuelling sites in Asia and breeding sites in Alaska, we averaged twice-daily locations over periods when birds were relatively stationary, excluding clear outliers caused by weather or bird behaviour. For three birds breeding north of the Arctic Circle (thus providing no sunrise/sunset data during this time), we assumed a breeding latitude of 70.2°N (known breeding range in this region occurs 69.5–70.8°N; McCaffery and Gill 2001). Based on resightings of colour-marked godwits at the Manawatu River estuary, timing of migration was similar between years; mean northbound departure (*n* = 48 birds) and southbound arrival

(n = 45 birds) in 2008 and 2009 differed by 0.48 and 1.0 d, respectively. In addition, snow-free dates for Alaska breeding sites differed by <5 d between the two years (NOAA 2010b), despite annual variation up to 18 d (1998–2009). Therefore, we combined geolocator data from 2008 (11 birds) and 2009 (6 birds) for analysis. Departure from the Manawatu River estuary was similar for colour-banded males and females in both years (2008: t_{61} = 1.42, P = 0.16; 2009: t_{60} = 0.747, P = 0.46), as was post-breeding return to the site (2008: t_{51} = 0.546, P = 0.59; 2009: t_{57} = 0.807, P = 0.42). Among geolocators, there was no apparent difference in migration timing between males and females after controlling for breeding latitude, although sample sizes were quite small. In addition, field observations on the breeding grounds provide no evidence for protandry in breeding arrival (J. Conklin pers. obs.) Therefore, we combined male and female geolocator data for analysis.

Hatching success

Geolocators also allowed estimation of hatching success by indicating periods of nest incubation (Eichhorn *et al.* 2006). During the breeding season, geolocators registered nights as regular, cleanly demarcated periods of 0–4.5 hours (h) of darkness, depending on latitude. Conversely, days appeared as continuous light, irregularly broken by very brief (<1 h) shading events, most likely corresponding to behaviours such as wading or sitting. Within 6–25 d of apparent arrival on breeding grounds, most birds displayed a conspicuous pattern of incubation, in which semi-regular shading events of 4–13 h were overlayed upon the day/night pattern for periods up to 25 d. When data clearly indicated incubation (n = 14), we designated birds as ‘successful’ (21–25 consecutive days of incubation; expected incubation duration 20–21 d; McCaffery and Gill 2001) or ‘failed’ (<18 d).

Breeding plumage

Prior to departure from New Zealand, Bar-tailed Godwits undergo a breeding plumage moult, during which some portion of non-breeding ventral contour feathers are replaced with bold rufous-coloured feathers (McCaffery and Gill 2001). Using field observations and digital photographs, we scored breast and belly plumage on a scale of 1–7 (1 = no red feathers; 7 = completely replaced with red feathers; Piersma and Jukema 1993). Males carrying geolocators departed the study site with plumage scores of 4.5–5.5.

Results

Timing of migration

Godwits from our study site used breeding sites spanning 59.7–70.2°N latitude (Figure 2.2), encompassing most of the known Alaska breeding range for the subspecies. Northerly

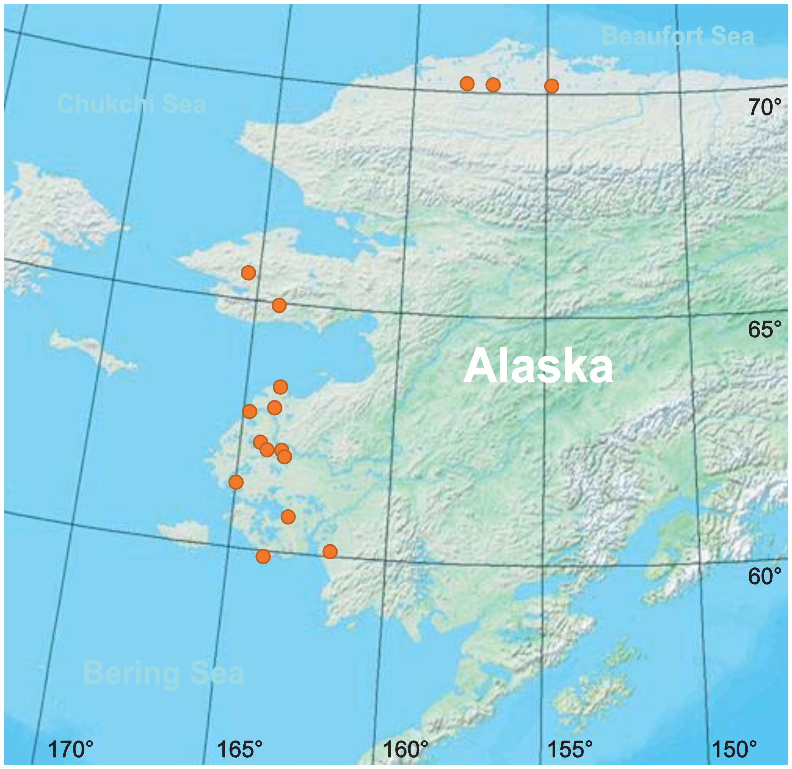

Figure 2.2 Breeding locations derived from geolocators for 16 Bar-tailed Godwits tracked from New Zealand. Alaska image courtesy of NASA.

breeders migrated later than southerly breeders in each phase of the northward journey: departure date from New Zealand was significantly correlated with breeding latitude (Figure 2.3a), as were Yellow Sea departure (Figure 2.3b) and date of arrival at breeding sites (Figure 2.3c). The correlation between New Zealand departure date and the location of a breeding site a 16,000–18,000 km journey away strongly suggests endogenously-controlled schedules, as environmental cues indicating tundra conditions in the opposite hemisphere are improbable. The relationship between migration timing and latitude became stronger with each stage of the northbound migration, implying a tightening of these programmed schedules with proximity to the breeding grounds. For the post-breeding southbound return flight, northerly breeders again migrated later: departure date from Alaska was significantly correlated with breeding latitude (Figure 2.3d).

Duration of stopover in the Yellow Sea was highly variable (30–50 d), which may reflect individual strategies with regard to moult and fuelling, or variation in stopover site quality. Godwits use fuelling sites spanning 600 km of latitude in the Yellow Sea, and these sites vary greatly in size, level of human impacts, and competition with other migrating shorebirds. There was no apparent relationship between choice of fuelling site and timing of migration, stopover duration, or breeding latitude. However, stopover duration for godwits breeding at

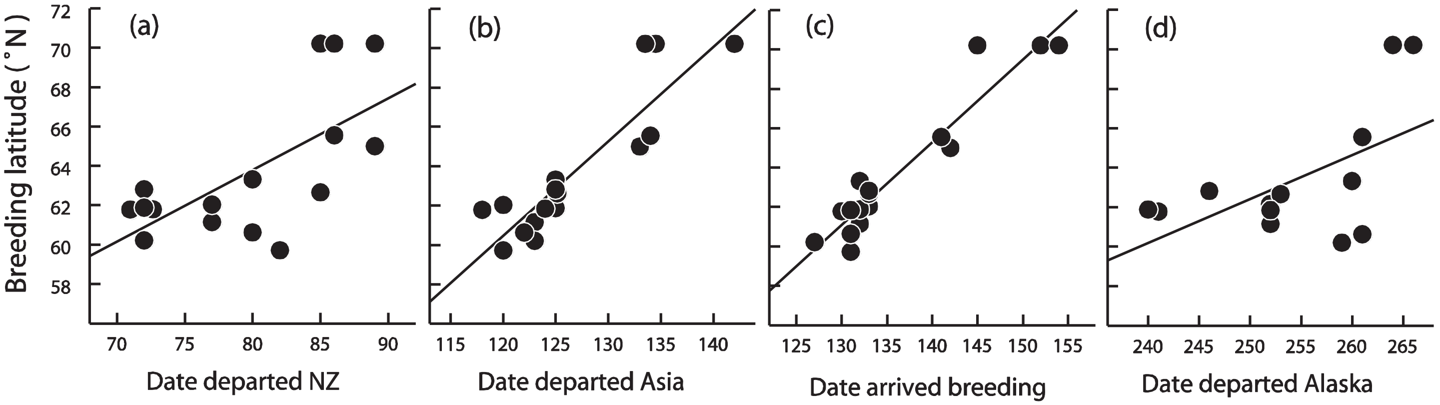

Figure 2.3 Timing of migration of Bar-tailed Godwits was correlated with breeding latitude in Alaska. Some overlapping points have been neutrally offset for clarity. Figure axes have been transposed to aid visualisation of geographical relationships. **(a)** Date (Day 1 = 1 January) of departure from New Zealand in relation to breeding latitude (r^2 = 0.45, slope = 1.22 ± 0.36, n = 16, P = 0.005). **(b)** Date of departure from the Yellow Sea in relation to breeding latitude (r^2 = 0.80, slope = 1.67 ± 0.22, n = 16, P < 0.001). **(c)** Date of arrival on breeding grounds in relation to breeding latitude (r^2 = 0.91, slope = 2.16 ± 0.19, n = 16, P < 0.001). **(d)** Date of departure from Alaska in relation to breeding latitude (r^2 = 0.32, slope = 1.43 ± 0.64, n = 13, P = 0.046).

higher latitudes was greater than those breeding farther south (Figure 2.4). Similarly, after arrival in Alaska, northerly breeders remained at coastal sites slightly longer before moving to breeding sites (range: 0–13 d; duration vs. breeding latitude: $r^2 = 0.32$, $n = 16$, $P = 0.023$). Thus, the variation among individuals increased with each successive segment of the migration (range of New Zealand departure = 20 d; Yellow Sea departure = 23 d; breeding arrival = 28 d), and total travel time from New Zealand to breeding sites increased with breeding latitude (range: 48–67 d; duration vs. breeding latitude: $r^2 = 0.40$, $n = 16$, $P = 0.009$). This is unsurprising, as godwits breeding in northern Alaska must travel 1,000–1,600 km further than southerly breeders, and may require greater reserves to prepare for colder and less predictable conditions on their breeding grounds.

Although breeding arrival has well-understood time constraints, migration to non-breeding grounds is considered to be much less time-selected (Alerstam and Lindström 1990, McNamara *et al.* 1998). However, birds departed Alaska in approximately the same order in which they departed New Zealand (Figure 2.5), and the span of departures from Alaska was 27 d, similar to the northbound migration. Breeding success creates great potential variation in the date an individual may begin fuelling for southbound migration, because birds caring for young through fledging may invest 3–6 weeks more than those that fail during incubation. However, there was no evidence that failed breeders used this ‘advantage’ to achieve earlier southbound departure: total time spent in Alaska was nearly identical for successful (mean = 125.0 d, $n = 4$) and failed (mean = 125.6 d, $n = 7$) breeders. Furthermore, southerly breeders might be expected to migrate south later, because apparently suitable breeding conditions persist later at lower latitudes and offer greater re-nesting opportunity; our findings do not support this. These data suggest rigidity in migration schedule, perhaps evolved to best exploit a predictable peak of fuelling resources or favourable wind conditions (Battley *et al.* 2005) necessary for the southbound flight.

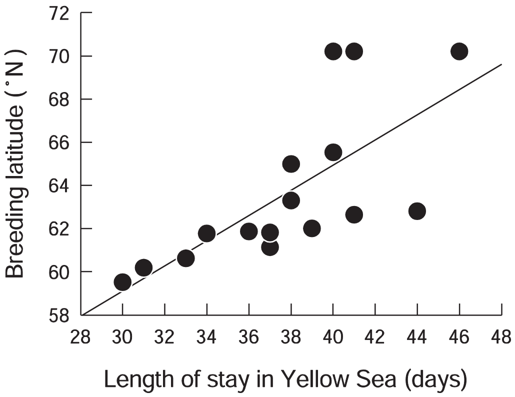

Figure 2.4 Length of stay in the Yellow Sea for Bar-tailed Godwits on northbound migration was positively correlated with breeding latitude in Alaska ($r^2 = 0.51$, $n = 16$, $P = 0.002$).

Breeding plumage

For species in which one sex competes for breeding partners or territories, variation in plumage may communicate relative individual quality to competitors or potential mates (Jawor and Breitwisch 2003). The extremely variable breeding plumage of male godwits has led to the hypothesis that redder males may be higher quality individuals, and therefore may migrate earlier than paler males (Drent *et al.* 2003). In our study, extent of male breeding plumage was unrelated to departure from New Zealand ($r^2 = 0.36$, $n = 9$, $P = 0.87$); this was also true at another non-breeding site in New Zealand (Battley 2006). However, redder males departed from the Yellow Sea later than paler males ($r^2 = 0.46$, $n = 9$, $P = 0.044$) and arrived later on the breeding grounds ($r^2 = 0.79$, $n = 7$, $P = 0.007$), contrary to the prediction, but similar to observations of *L. l. taymyrensis* in Europe (Drent *et al.* 2003).

Although supported in other species, the use of breeding plumage as an index of individual quality in Bar-tailed Godwits is far from straightforward. First, there is no empirical evidence linking breeding plumage with reproductive success in this species, and links with other parameters such as body condition, parasite loads, or survival are equivocal (Piersma and Jukema 1993, Piersma *et al.* 2001, Drent *et al.* 2003, Battley and Piersma 2005, Battley 2007). Second, plumage varies geographically among Alaskan godwits, with redder males breeding at higher latitudes, on average (Chapter 3). Accordingly, redder males in this study bred at higher latitudes ($r^2 = 0.73$, $n = 7$, $P = 0.015$). However, due to continued contour moult during northbound stopover (Piersma and Jukema 1993), the degree of which may vary among individuals, it is unknown how closely variation in plumage upon New Zealand departure reflects that on the breeding grounds.

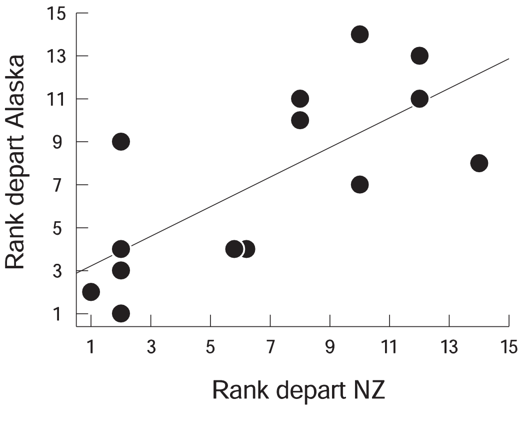

Figure 2.5 Order of migratory departure from New Zealand and Alaska were similar for individual Bar-tailed Godwits (Spearman rank correlation: $r_s = 0.74$, $n = 14$, $P = 0.003$). Some overlapping points have been neutrally offset for clarity.

Discussion

Our findings implicate individually-optimised breeding arrival date as the primary driver of variation in migration schedule of godwits: latitude of an individual's breeding site (and, by extension, the approximate timing of snow melt from that patch of Alaskan tundra) could be traced back to that bird's departure from New Zealand 7–10 weeks earlier and more than half a world away. This strongly suggests endogenous programming of migration, and warns against quality-based inferences regarding any single stage of the migration without knowledge of the entire annual cycle. Nonetheless, competition and individual quality may yet act at a fine scale; i.e., birds at the same latitude vary in quality, arrival date, and breeding success. Our sample is insufficient to evaluate timing differences among birds breeding at the same latitude, but the small amount of variation in breeding arrival left unexplained by latitude itself (10%) suggests such variation is relatively minor. Latitude is a coarse index for earliest availability of a site, and does not account for small-scale geographic variation, which may promote differing optimal arrival dates even for sites at similar latitudes (Smith *et al.* 2010). This makes the extremely tight relationship between breeding arrival and latitude all the more surprising. However, given the brief breeding season at high latitudes, it is nonetheless conceivable that a few days difference in arrival could significantly affect mate acquisition or retention (Gunnarsson *et al.* 2004), or breeding success.

If individual quality or condition were largely driving timing of migration, we would expect early-arriving birds to maximise reproductive potential by occupying the highest-quality breeding sites. Low-latitude breeding sites could be more desirable, due to a shorter migration distance, milder and more predictable conditions, and a longer snow-free season. However, the drawbacks of breeding farther north may be offset by a latitudinal cline in nest predation rates (McKinnon *et al.* 2010). Given the low breeding density of Bar-tailed Godwits and a general lack of evidence of food- or habitat-limitation among tundra-breeding shorebirds, it is improbable that early-arriving birds, through early occupation of low-latitude breeding sites, force later birds to breed at high latitudes. It is more likely that migration timing and breeding site are linked and heritable, and maintained by either genetic structure within the population or environmentally-mediated regulation of gene expression (Jaenisch and Bird 2003). Some Holarctic shorebird species appear to have radiated across vast regions very recently, such that clear population differences in breeding range and migration are only weakly reflected in genetic structure within the population (Buehler *et al.* 2006). In some cases, epigenetics, a field of vast potential for ecologists, may be the key mechanism for persistent intra-specific variation.

Our study sheds light upon tantalising results from prior Bar-tailed Godwit studies. At the Firth of Thames, New Zealand, individual godwits showed high annual repeatability of both departure date and extent of breeding plumage, but did not conform to expectations of 'high-quality' (redder) birds migrating earlier (Battley 2006). Likewise, male godwits whose moult and mass indicated readiness for early departure were paler and larger than males not yet in migratory condition (Battley and Piersma 2005). Both of these results are now explained by the links between breeding site, timing, and plumage. The similar later northbound departure of redder males in the European population (*L. l. taymyrensis*; Drent *et al.* 2003) suggests these patterns may exist across the entire range of the species, but that study found no evidence of geographic variation in plumage within the breeding range. Interestingly, the population structure within Alaska does not appear to persist in the non-breeding season. Other sites in New Zealand show a range of northbound departure dates similar to our study site (Battley 1997, 2006), suggesting that godwits from the entire Alaska breeding range mix freely in the non-breeding season.

For long-distance migrants, selection for the timing of breeding may occur at very different temporal and spatial scales than selection for timing of migration *per se*. In Bar-tailed Godwits, timing of migration appears quite consistent, both at the population and individual (Battley 2006) level, despite substantial annual variation in date of snow melt; this pattern appears common among tundra-breeding, long-distance migrant shorebirds (Niehaus and Ydenberg 2006, Smith *et al.* 2010). Timing of long-distance flights likely evolved in response to long-term global patterns in the timing of fuelling resources and beneficial prevailing winds, while nesting phenology appears very sensitive to local and annual variation in conditions dictating availability of breeding sites (Smith *et al.* 2010). This may explain why timing of southbound migration was unresponsive to apparent duration of breeding investment in our study. Unfortunately, the potentially conflicting pressures of optimal timing of migration and breeding may make long-distance migrants such as godwits particularly vulnerable to effects of climate change (Both *et al.* 2006), if rigid flight schedules contribute to a mismatch between breeding arrival and optimal nest initiation (Both and Visser 2001), or preclude adaptation to temporal shifts in resources or weather during migration.

The departure of individuals from New Zealand and Alaska (two events separated by six months and over 11,000 km) in approximately the same order and span of days is quite surprising, in light of potential intervening variation caused by individual differences in flight speed, stopover duration, migration distance, duration of suitable breeding conditions, breeding success, body size, moult speed, foraging ability, and habitat quality. This relationship between timing of northbound and southbound migration, which lacks a clear theoretical foundation in migration literature (McNamara *et al.* 1998), may reflect constraints operating on the entire annual cycle. Although flexibility in duration and investment in annual activities such as moult (Hall and Fransson 2000, Dawson 2004) and fuelling (Prop *et al.* 2003), and even in migration route (Eichhorn *et al.* 2009), have been demonstrated in other species, the extreme nature of the godwit's migration may naturally ensure reduced variation in these parameters. Accordingly, the specificity with which breeding site dictates migration timing and the rigid repeatability of individual migration schedules (Battley 2006) seem especially high, compared to that found in shorter-distance migrant birds. Every New Zealand Bar-tailed Godwit breeding in Alaska must be capable of a 10,000 km non-stop flight to Asia, followed by a 6,000 km flight across the northern Pacific Ocean; this is surely among the most challenging migrations in birds. Low-quality individuals are unlikely to complete this migration, and those in poor condition may not attempt it at all. It is unlikely that any truly 'low-quality' godwits reach the breeding grounds.

In this model of godwit migration, an individual's breeding site is endogenously controlled, and all other annual events are shifted temporally to optimise arrival on the breeding grounds. Among the consequent predictions is that northerly breeders should exhibit delayed completion of feather moult and pre-migratory mass gain in New Zealand, and the duration of these activities may be relatively constant, regardless of migration schedule. Using migration timing as a reliable index for breeding latitude, these predictions are now testable by godwit studies restricted to non-breeding sites. We might also expect to find similar patterns in other long-distance migrant species in which individuals from one non-breeding site may breed across vast geographic ranges (e.g., Great Knots *Calidris tenuirostris*; Battley *et al.* 2004).

Chapter 3

Geographic variation in morphology of Alaska-breeding Bar-tailed Godwits is not maintained on their non-breeding grounds in New Zealand

Conklin, J.R., P.F. Battley, M.A. Potter & D.R. Ruthrauff
Auk 128: 363–373 (2011)

Abstract

Among scolopacid shorebirds, Bar-tailed Godwits Limosa lapponica *have unusually high intra- and inter-sexual differences in size and breeding plumage. Despite historical evidence for population structure among Alaska-breeding Bar-tailed Godwits* L. l. baueri*, no thorough analysis, or comparison with the population's non-*breeding distribution, has been *undertaken. We used live captures, field photography, museum specimens, and individuals tracked from New Zealand to describe geographic variation in size and plumage within the Alaska breeding range. We found a north–south cline in body size in Alaska, in which the smallest individuals of each sex occurred at the highest latitudes. Extent of male breeding plumage (proportion of non-breeding contour feathers replaced) also increased with latitude, but female breeding plumage was most extensive at mid-latitudes. This population structure was not maintained in the non-breeding season: morphometrics of captured birds and timing of migratory departures indicated that individuals from a wide range of breeding latitudes occur in each region and site in New Zealand. Links among morphology, phenology, and breeding location suggest the possibility of distinct Alaska breeding populations that mix freely in the non-breeding season, and also imply that the strongest selection for size occurs in the breeding season.*

Introduction

Within the breeding range of many species, individuals exhibit geographic variation in morphology, appearance, or behaviour, reflecting either inherited or environmental differences (Zink and Remsen 1986). In migratory species, differential migration patterns within an apparently continuous geographic range (e.g., 'leapfrog' or 'chain' migration systems) may create stable population segregation (Lundberg and Alerstam 1986) and, potentially, breeding isolation, promoting population structure and phenotypic diversification (Mayr 1963). Therefore, spatial distribution of individuals throughout the entire annual cycle may indicate the strength of population structure, and may also reveal where differential selection for phenotypic traits occurs.

The Bar-tailed Godwit *Limosa lapponica* (hereafter, 'godwit'), a long-distance migratory shorebird, breeds in a discontinuous band of arctic and sub-arctic tundra from Scandinavia east to Alaska. There are four recognised subspecies (from west to east: *L. l. lapponica, taymyrensis, menzbieri, and baueri*; Engelmoer and Roselaar 1998) and a small, isolated population in far-eastern Russia of uncertain taxonomic status (purported *L. l. anadyrensis*; Engelmoer and Roselaar 1998, Tomkovich 2010). These populations have distinctive migratory routes, timing of migration, and morphology (Rynn 1982, Engelmoer and Roselaar 1998).

Although the sexes are similar in non-breeding plumage, male godwits grow much more striking breeding plumage than females, resulting in unusually dramatic sexual plumage dimorphism among scolopacid shorebirds (Figure 1 in Jukema and Piersma 2000). Size dimorphism in godwits (larger females) is also remarkably high among monogamous shorebirds that share incubation and parental care (McCaffery and Gill 2001). In addition, significant individual variation in both plumage and size occurs within each sex. In particular, individuals undergo substantially different degrees of pre-supplemental contour feather moult (from very little to >90%), which results in conspicuous variation in breeding plumage (Piersma and Jukema 1993).

The subspecies *L. l. baueri* breeds in western and northern Alaska (Figure 3.1) and migrates >10,000 km to non-breeding grounds in New Zealand and eastern Australia (McCaffery and Gill 2001). Field observations suggest geographic variation within Alaska: males with the greatest extent of breeding plumage were absent from southern breeding sites, but arrived later than local breeders and passed through these areas *en route* to northerly breeding areas (McCaffery *et al.* 2010). This agrees with data from Alaska museum specimens, in which males collected north of 64°N latitude had a greater extent of breeding plumage and were smaller than southern males (Rynn 1982). Distinct strategies in timing of moult and fueling among pre-migratory godwits in New Zealand also support the possibility of multiple breeding populations within *L. l. baueri* (Battley and Piersma 2005).

Recently, godwits tracked on migration with light-sensitive geolocators shed further light on population structure: males departing New Zealand with a greater extent of breeding plumage arrived later in Alaska, and later-arriving birds of both sexes bred farther north (Chapter 2). In fact, breeding latitude was linked with timing of every stage of northbound migration, as well as with post-breeding departure from Alaska. It is thus plausible that breeding latitude may influence the distribution of individuals in the non-breeding season, but this hypothesis has yet to be tested.

Here, we describe population structure within the breeding range of *L. l. baueri* and ask whether this structure persists in the non-breeding season. We examined geographic variation in size and plumage of both sexes within Alaska, using museum specimens in conjunction with capture, photography, and tracking of live birds. For comparison, we examined historical capture data within New Zealand to describe the population structure by morphology across a similar range of latitude in the non-breeding season.

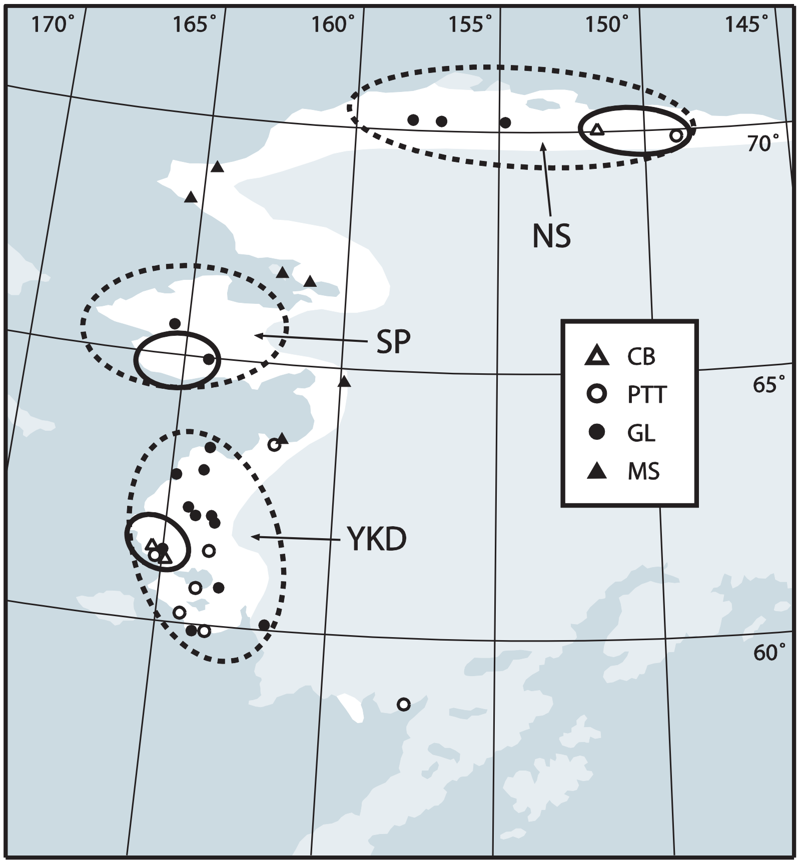

Figure 3.1 Alaska breeding locations of Bar-tailed Godwits in this study. Dashed ellipses indicate three main regions used for geographic comparisons (YKD = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope). Solid ellipses indicate sites of godwit captures and field photography. CB = resights of godwits colour-banded in New Zealand (*n* = 3). PTT = godwits tracked from New Zealand using satellite telemetry (*n* = 8). GL = godwits tracked from New Zealand using geolocators (*n* = 16). MS = sites of museum specimens collected outside the three main regions. Unshaded area indicates known breeding range (McCaffery and Gill 2001).

Methods

Morphometric and plumage data

Morphometrics

For live captures, we report culmen (mm; exposed length), wing chord (mm; maximum flattened), and mass (g); not all measurements were available for all captures. Despite numerous observers, we assume insignificant systematic observer bias. Godwit mass undergoes drastic seasonal changes; for New Zealand captures, we report mass only for captures during October to mid-December, when non-breeding mass is relatively stable (Wilson *et al.* 2007, P. Battley and J. Conklin unpubl. data). For Alaska (AK) captures, we pooled masses taken during incubation and brood rearing, although data are lacking on breeding-season mass changes.

For museum specimens, we measured length of exposed culmen (mm); all measurements were taken by JRC. On the basis of expected post mortem shrinkage of 1.69% (Table 6 in Engelmoer and Roselaar 1998), we corrected culmen lengths of museum specimens for direct comparison with live culmen measurements.

Plumage

Beginning in January, godwits moult from non-breeding ('basic') to breeding plumage, in partially overlapping 'pre-alternate' and 'pre-supplemental' contour feather moults (Jukema and Piersma 2000), the latter of which appears to affect only ventral regions. In general, males undergo much more extensive pre-supplemental moult than females, but there is substantial individual variation in both sexes. Ventral alternate plumage typically features lateral barring on a pale background, whereas supplemental feathers are reddish and lack barring (Jukema and Piersma 2000). Therefore, we characterised ventral breeding plumage as the extent of red supplemental feathers visible against a pale background of basic and/or alternate feathers. We visually estimated proportion (in 5% increments) of red feathers in three ventral regions: 'vent' (posterior ventral plumage from leg to vent); 'breast' (anterior ventral plumage from leg to upper breast); and 'throat' (ventral plumage above breast to chin).

Dorsal plumage appears to undergo only one pre-breeding moult: basic feathers are plain gray with a dark central stripe, whereas alternate feathers are blackish brown with pale or reddish spotting on the edges (McCaffery and Gill 2001). We estimated 'dorsal' (mantle and scapulars, not including wing coverts) breeding plumage as the proportion (in 5% increments) represented by dark, spotted feathers.

The extent of ventral alternate barring varies among individuals, and the amount of barring still evident during the breeding season depends on the extent of pre-supplemental moult that is subsequently completed. We scored barring in the anterior ventral region as follows: 0 = no barring; 1 = barring on flanks only; 2 = barring on flanks and upper breast; 3 = barring on flanks, breast, and belly.

To remove potential observer differences, all plumage was scored from photographs by JRC. Depending on available photographs, not all plumage regions were scored for every individual. To gauge the comparability of different photographic sources (see below), we conducted a blind scoring trial using individuals photographed both free-living and in-hand during the same week ($n = 13$); 92% of scores differed by ≤10%, and there was no consistent directional bias in plumage scores. Therefore, we combined plumage scores from all data sources for analysis.

Bill colour

Bill colour of godwits varies seasonally: non-breeding birds have predominantly pinkish bills that darken to black at the distal end, while bills of breeding birds are mostly black. From photographs of live godwits in Alaska, we scored bill colour as the proportion (in 5% increments) of both mandibles that looked black. We excluded museum specimens because of potential post mortem changes in bill colour.

Sources of data

Museum specimens

From three collections of godwit specimens, we examined breeding individuals (*n* = 70; 40 male, 30 female) collected from 1891 to 2001 in Alaska (60.4–71.3°N). To exclude passage birds, we included only birds collected at known breeding areas from late May to late July or recorded as exhibiting breeding behaviour. We photographed specimens using standardised lighting and multiple angles, to enable scoring of plumage at a later date.

Live captures

We compiled morphometric data from adult godwits captured during incubation or brood rearing at breeding sites in Alaska (61.8–70.0°N; Figure 3.1) during May–July of 2005–2010 (*n* = 57; 30 male, 27 female). We compiled morphometric data from adult godwits captured at non-breeding sites in New Zealand (34.5–46.6°S; Figure 3.2) during late September to early April of 1987–2010 (*n* = 1,807; 932 male, 875 female). Godwits were aged based on plumage (McCaffery and Gill 2001); we excluded birds of unknown age and those aged <3 years. Godwits were sexed by culmen length, plumage, or both. Females are generally larger than males (culmen > 99 mm = female; < 90 mm = male), but intermediate birds (culmen = 90–99 mm) cannot be sexed by size alone. Plumage enables subjective sexing when supplemental plumage is present (January–October): greater extent and richer red colour indicate male. However, we estimate that 1–2% of godwits in the New Zealand sample may be incorrectly sexed (P. Battley and J. Conklin unpubl. data).

Some godwits captured in New Zealand were tracked to Alaska breeding sites using satellite telemetry (*n* = 8; Battley *et al.* 2012), geolocators (*n* = 16; Chapter 2), or colour-band resightings (*n* = 3). Consequently, morphometric data from these individuals occur in both Alaska and New Zealand data sets.

Field photography

To collect plumage data from free-living godwits in Alaska, we visited known breeding areas

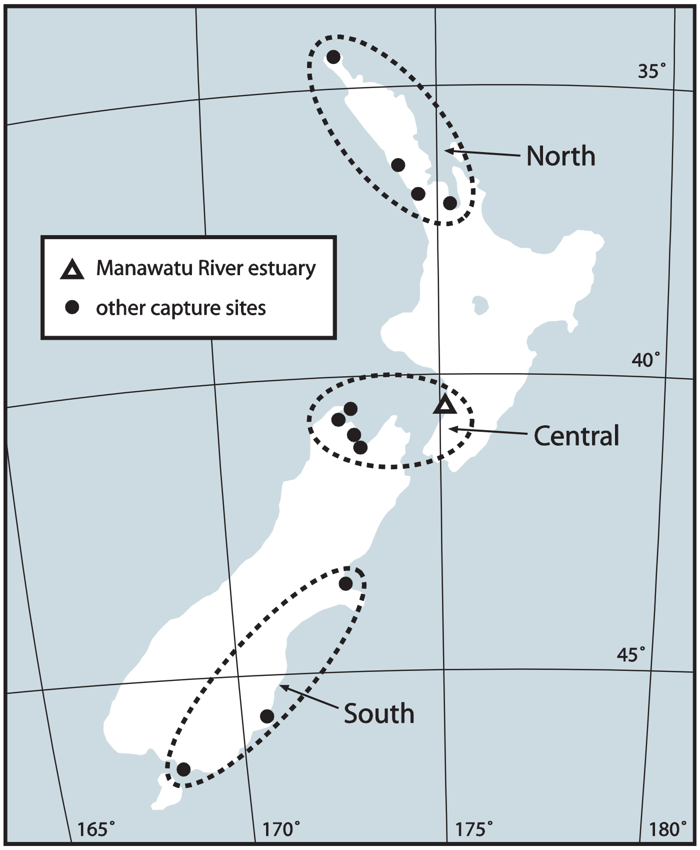

Figure 3.2 New Zealand capture sites of non-breeding Bar-tailed Godwits. Dashed ellipses indicate three main regions used for geographic comparisons.

near Nome, on the Seward Peninsula (64.5–65.2°N, 164.8–166.7°W), and south of Deadhorse, on the north slope of the Brooks Range (69.7–70.1°N, 148.7–151.5°W; Figure 3.1) during June to early July 2009. We conducted walking surveys, digitally photographing all breeding individuals encountered. We used geographic positioning system (GPS) locations, times, and individual characteristics (e.g., bill length, unique plumage traits) to avoid pseudoreplication of individuals.

Biologists involved in prior field work (2003–2009) provided photographs of free-living godwits from numerous Alaska breeding sites (58.8–70.5°N), plus in-hand photos of eight godwits captured at three sites on the Yukon-Kuskokwim Delta National Wildlife Refuge (61.1–61.4°N, 165.4–165.6°W; Figure 3.1). The final data set of live photographs included 123 Alaska godwits (72 male, 51 female; median = 11 photos/bird, range = 1–135).

Migratory departures from New Zealand

At the Manawatu River estuary, New Zealand (40.47°S, 175.22°E; Figure 3.2), we monitored departures in a small population of godwits (200–280 individuals; ~25% were individually colour-banded). Using direct observation and digital photography, we recorded exact time and individual membership of departing flocks during three migration periods (4 March–5 April, 2008–2010). We conducted daily high-tide surveys to confirm remaining flock size and presence of marked godwits; daily resighting probability of marked birds was >95%. As a result, departures of marked birds were known to the day in 84% of cases, and for the remaining 16% we are confident of accuracy within ±1 day. Geolocator data (Chapter 2) confirmed that observed departures from the estuary matched departure from New Zealand. We determined departure dates for 76 marked godwits (36 male, 40 female); for individuals monitored in multiple years, we averaged departure dates across available years.

Analysis

Although godwits breed in a nearly continuous band of coastal tundra in Alaska from near the Canadian border in the northeast to Bristol Bay in the southwest (McCaffery and Gill 2001; Figure 3.1), for logistical reasons most field work (including all live captures and photographs in this study and most historical collection) has been conducted in three discrete regions (Figure 3.1): Yukon-Kuskokwim Delta (‘YKD’; 59.7–63.3°N, 161.8–166.2°W), Seward Peninsula (‘SP’; 64.4–65.8°N, 162.3–166.7°W), and North Slope (‘NS’; 69.6–71.3°N, 148.4–160.1°W). For comparison, we divided godwit captures in New Zealand into three regions separated by >200 km (Figure 3.2): ‘North’ (34.5–37.2°S), ‘Central’ (40.4–41.3°S), and ‘South’ (43.5–46.6°S).

Because of differences in size and plumage, we considered the sexes separately in our analyses. For each morphometric variable, we examined geographic variation using single-factor analysis of variance (ANOVA), and Tukey’s post-hoc test for between-region differences. For plumage variables and bill colour, we used Kruskal-Wallis non-parametric ANOVA, and Tamhane’s post-hoc test.

Museum specimens offered a more continuous representation of the breeding range than capture and field photography (Figure 3.1). In addition, two New Zealand-captured females were tracked to breeding areas outside the three Alaska regions. For these reasons, Alaska totals and sample sizes for some tests exceed the sums for the three regions. We examined the association between breeding latitude and culmen length (pooled live and corrected museum culmen lengths) using linear regression, and compared male and female regression coefficients using Student’s *t* (Zar 1999). For male plumage variables, we pooled the three regions with specimens collected elsewhere in Alaska (n = 13), and examined associations with breeding latitude using linear regression.

Results

Morphometrics

Female godwits are much larger than males, on average (Tables 3.1 and 3.2), despite overlap in bill length, wing chord, and body mass (*t*-tests, all measures for both AK and NZ: $P < 0.0001$). Body proportions also differed by sex: females had longer bills compared with wing chord (wing/culmen) than males (*t*-tests, both AK and NZ: $P < 0.0001$).

Alaska

Within AK, we found geographic variation in size for both sexes. On average, birds were largest on YKD, smallest on NS, and intermediate on SP (Table 3.1). Body proportions also varied geographically, and for both sexes, wing/culmen length was greatest for NS, least for YKD, and intermediate for SP. Geographic variation was strongest in culmen length: the three regions were statistically distinguishable for both sexes. SP could not consistently be distinguished from YKD and NS, but the trend of decreasing size with increasing latitude was consistent across nearly all measures.

Considering the full range of sizes present in AK, the smallest birds of each sex by culmen, wing, and mass were absent on the YKD, whereas the largest birds were absent on the NS (Figure 3.3). The single exception was a conspicuously long-winged male captured on the NS; however, his other measurements were consistent with other NS males. The pattern was similar for relative wing/culmen length, as birds with extremely long wings in relation to bill did not appear on the YKD, and vice versa.

Including samples outside the three main AK regions, culmen lengths demonstrated a continuous north–south cline in both males ($r^2 = 0.390$, $F = 45.35$, $P < 0.001$, $n = 73$) and females ($r^2 = 0.474$, $F = 64.03$, $P < 0.001$, $n = 73$; Figure 3.4). In addition, the slope of the line describing the cline was lower in males (slope = $-0.949 \pm$ SE 0.141) than in females (slope = -1.523 ± 0.190; $t = 11.88$, df = 142, $P < 0.001$), which resulted in a progressive south-to-north reduction in sexual dimorphism of culmen length: females had 30% longer bills than males on YKD, 28% longer on SP, and 24% longer on NS. Dimorphism in wing and mass showed no latitudinal clines.

New Zealand

In contrast to AK, we detected minimal population structure among regions in NZ, despite much larger samples (Table 3.2). Although southern birds of both sexes were slightly larger in mean culmen and wing, there was no consistent evidence for a north–south cline in size. Mean differences among regions were much smaller than similar comparisons within AK, with large sample sizes conferring statistical significance to differences of much lower magnitude and

Table 3.1 Geographic variation in morphometrics of breeding adult Bar-tailed Godwits in Alaska. Data from live captures only, including New Zealand godwits tracked to Alaska breeding sites. Significant results in among-region ANOVA are indicated in bold. Asterisk indicates significant result in between-region post-hoc test (*P* < 0.05). Abbreviations: YK = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope.

		All Alaska			**YK Delta**			**Seward Peninsula**			**North Slope**			**ANOVA**			**Tukey post-hoc**		
		n	**mean**	**range**	***n***	**mean**	**SE**	***n***	**mean**	**SE**	***n***	**mean**	**SE**	***F***	**df**	***P***	**YK–SP**	**YK–NS**	**SP–NS**
Male	**Culmen** (mm)	38	84.6	71.3–94.0	21	88.0	0.94	7	83.6	0.96	10	78.4	1.32	19.65	2,35	**< 0.001**	*	*	*
	Wing (mm)	37	232.3	218–243	20	235.2	1.30	7	231.7	1.21	10	227.0	2.29	6.56	2,34	**0.004**		*	
	Wing/Culmen	37	2.76	2.45–3.20	20	2.68	0.03	7	2.77	0.03	10	2.91	0.06	7.45	2,34	**0.002**		*	
	Mass (g)	29	255.7	205–326	16	269.9	5.07	5	238.8	9.90	8	237.9	5.43	9.55	2,26	**0.001**	*	*	
Female	**Culmen** (mm)	46	108.0	88.5–125.5	25	114.2	1.10	4	106.8	1.25	15	97.5	1.58	42.84	2,41	**< 0.001**	*	*	*
	Wing (mm)	44	244.7	228–261	25	249.0	1.14	4	241.5	1.89	14	237.3	1.69	19.06	2,40	**< 0.001**		*	
	Wing/Culmen	44	2.28	2.02–2.73	25	2.18	0.02	4	2.26	0.03	14	2.47	0.03	28.73	2,40	**< 0.001**		*	*
	Mass (g)	28	319.4	265–384	12	339.7	6.63	4	294.5	9.98	12	307.3	7.96	7.48	2,40	**0.003**	*	*	

Table 3.2 Geographic variation in morphometrics of non-breeding adult Bar-tailed Godwits in New Zealand. Significant results in among-region ANOVA are indicated in bold. Asterisk indicates significant result in between-region post-hoc test ($P < 0.05$). Abbreviations: N = North, S = South, and C = Central.

		All New Zealand			**North**			**Central**			**South**			**ANOVA**			**Tukey post-hoc**		
		n	**mean**	**range**	***n***	**mean**	**SE**	***n***	**mean**	**SE**	***n***	**mean**	**SE**	***F***	**df**	***P***	**N–C**	**N–S**	**C–S**
Male	**Culmen** (mm)	920	83.8	69.0–98.6	593	83.5	0.24	238	84.1	0.39	89	84.8	0.66	2.28	2,917	0.10			
	Wing (mm)	472	230.5	210–256	264	229.8	0.39	156	231.8	0.53	52	230.2	0.94	4.73	2,469	**0.009**	*		
	Wing/Culmen	461	2.73	2.31–3.32	253	2.71	0.01	156	2.77	0.01	52	2.74	0.03	5.60	2,458	**0.004**	*		
	Mass (g)	353	277.4	194–384	197	279.5	1.55	121	276.4	2.11	35	269.3	3.96	3.24	2,350	**0.040**		*	
Female	**Culmen** (mm)	862	108.9	90.0–129.0	641	108.5	0.30	168	109.8	0.58	53	111.1	1.03	4.30	2,859	**0.014**		*	
	Wing (mm)	549	243.7	216–264	388	243.2	0.37	117	244.3	0.65	44	247.0	1.08	5.90	2,546	**0.003**		*	
	Wing/Culmen	538	2.23	1.85–2.66	377	2.23	0.01	117	2.24	0.01	44	2.21	0.02	0.57	2,535	0.57			
	Mass (g)	343	333.2	245–400	234	333.4	1.40	81	330.3	2.41	28	339.8	5.58	1.92	2,340	0.15			

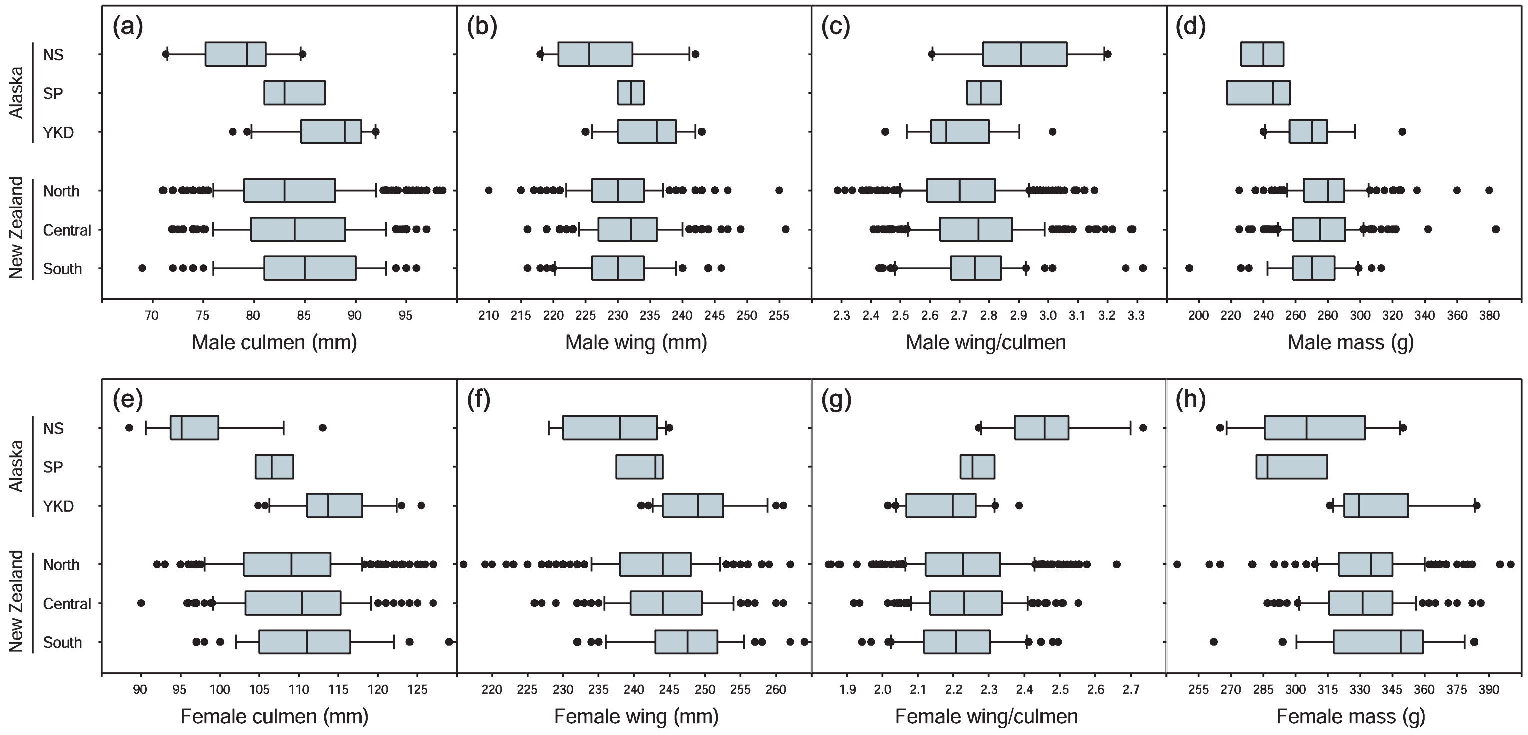

Figure 3.3 Morphometrics of adult Bar-tailed Godwits by region in Alaska (YKD = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope) and New Zealand. **(a)** Male culmen; **(b)** male wing chord; **(c)** male wing/culmen; **(d)** male mass; **(e)** female culmen; **(f)** female wing chord; **(g)** female wing/culmen; and **(h)** female mass. See Tables 3.1 and 3.2 for sample sizes. Boxes indicate median and 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles, and dots indicate more extreme values.

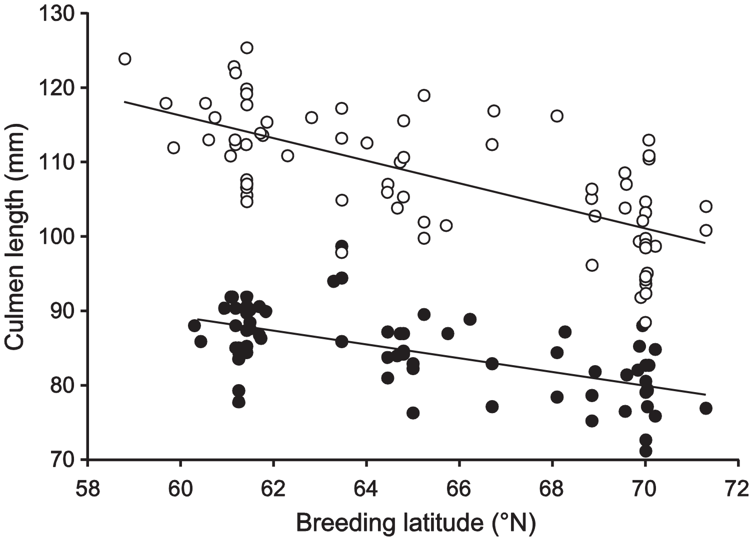

Figure 3.4 Culmen length was negatively related to breeding latitude of Bar-tailed Godwits in Alaska. Includes live captures and corrected culmen lengths of museum specimens. Filled circles = males; open circles = females.

presumably less biological significance. Each NZ region contained the full range of variation in culmen and wing found in AK (Figure 3.3).

Alaska vs. New Zealand

The grand means for culmen length and wing chord in AK and NZ (Tables 3.1 and 3.2) were similar for both males (culmen: $t = 0.86$, df = 956, $P = 0.39$; wing: $t = 1.64$, df = 507, $P = 0.10$) and females (culmen: $t = 0.82$, df = 906, $P = 0.41$; wing: $t = 0.87$, df = 591, $P = 0.38$). Hence, no morphological segment of the AK population appeared to be missing from NZ. For most variables, NZ data contained extremes of distribution not found in AK, as expected given the much larger NZ samples. One exception was a northern AK female with a culmen length of 88.5 mm, smaller than the currently recognised minimum for females in NZ (90 mm). This suggests that overlap in male and female size, and consequently the number of NZ-captured godwits that are missexed, is greater than previously recognised.

Migratory departures from New Zealand

At the Manawatu River estuary, northbound migratory departures occurred from 4 March to 5 April (2008–2010). Among colour-banded individuals of both sexes, larger birds departed earlier than smaller birds (mean departure date vs. culmen length; males: $r = 0.562$, $F = 15.26$, $P < 0.001$, $n = 35$; females: $r = 0.651$, $F = 28.76$, $P < 0.001$, $n = 41$; Figure 3.5).

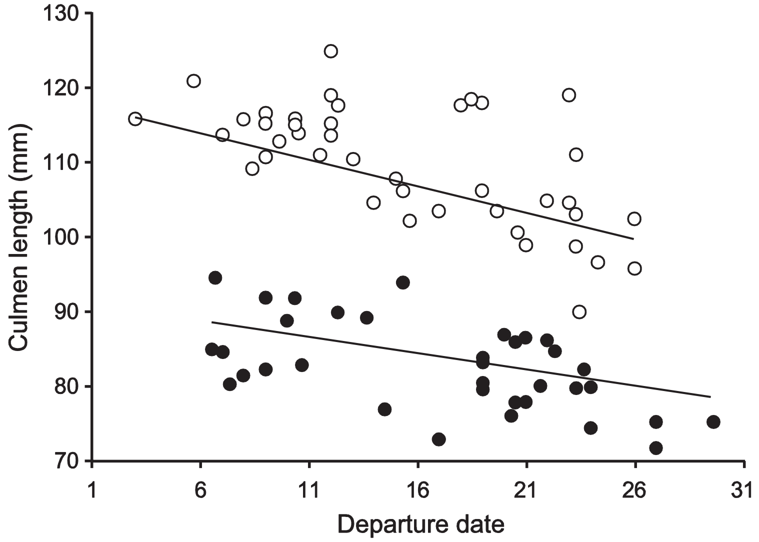

Figure 3.5 Culmen length was negatively correlated with migration departure date (day 1 = 6 March) of colour-banded Bar-tailed Godwits from the Manawatu River estuary, New Zealand (2008–2010). Filled circles = males; open circles = females.

Plumage and bill colour in Alaska

Plumage

On average, male godwits in AK had a greater extent of breeding plumage than females in all body regions (Mann-Whitney tests, all measures: $P < 0.0001$; Table 3.3). For both sexes, an individual's breast plumage score was positively correlated with vent (male: $r = 0.794$, $n = 109$; female: $r = 0.810$, $n = 78$), throat (male: $r = 0.837$, $n = 108$; female: $r = 0.758$, $n = 75$), and dorsal plumage (male: $r = 0.615$, $n = 95$; female: $r = 0.587$, $n = 69$; for all tests, $P < 0.001$).

Patterns of geographic variation in plumage differed by sex. For males, extent of breeding plumage was greatest for NS and least for YKD (Table 3.3). For all plumage variables, SP males were more similar to NS than to YKD; with the exception of vent plumage, the two northern regions were statistically indistinguishable.

Among the reddest males, the great majority were found north of 64°N (Figure 3.6). For example, 53% of males from SP and NS had breast scores >90%, compared with only 3% of YKD males. Conversely, only one male (1.5%) from SP–NS had a breast score <70%, whereas 22% of YKD males were in that category. A similar pattern occurred in vent scores, although far fewer males attain extensive red vent plumage; only one male (from SP) reached

Table 3.3 Geographic variation in plumage and bill colour of breeding adult Bar-tailed Godwits in Alaska, including both live birds and museum specimens. Significant results in among-region Kruskal-Wallis test are indicated in bold. Asterisk indicates significant result in between-region post-hoc test (*P* < 0.05). Abbreviations: YK = Yukon Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope. Dorsal, vent, breast, and throat values indicate proportion of breeding plumage in each body region. Barring values indicate amount of barring in anterior ventral region. Bill values indicate proportion of black colour.

		All Alaska			**YK Delta**			**Seward Peninsula**			**North Slope**			**Kruskal-Wallis**			**Tamhane post-hoc**		
		n	**mean**	**range**	***n***	**mean**	**SE**	***n***	**mean**	**SE**	***n***	**mean**	**SE**	**$\chi 2$**	**df**	***P***	**YK–SP**	**YK–NS**	**SP–NS**
Male	**Dorsal** (%)	95	92.3	65–100	25	88.2	1.78	31	93.7	0.93	26	94.8	0.76	11.44	2	**0.003**	*	*	
	Vent (%)	109	64.5	5–100	30	49.2	4.17	33	68.2	3.05	33	77.0	1.79	28.49	2	**< 0.001**	*	*	*
	Breast (%)	111	85.7	35–100	32	74.8	2.57	33	89.9	1.76	33	92.4	1.36	34.40	2	**< 0.001**	*	*	
	Throat (%)	108	92.8	60–100	31	88.5	1.56	33	95.2	0.99	31	95.8	1.07	17.81	2	**< 0.001**	*	*	
	Barring (0–3)	99	1.00	0–3	26	1.19	0.12	32	0.69	0.12	28	0.93	0.15	7.16	2	**0.028**	*		
	Bill (%)	60	93.1	75–100	19	92.6	1.85	22	93.6	1.62	19	92.9	1.23	0.89	2	0.64			
Female	**Dorsal** (%)	70	78.8	20–95	14	72.5	3.51	28	86.4	0.96	17	72.7	6.13	10.97	2	**0.004**	*		
	Vent (%)	78	19.5	0–50	17	14.7	2.37	29	26.9	2.08	21	12.9	2.82	18.37	2	**< 0.001**	*		*
	Breast (%)	80	35.4	0–80	17	24.1	2.85	30	47.5	2.96	22	26.6	4.47	21.13	2	**< 0.001**	*		*
	Throat (%)	76	55.4	0–90	17	48.5	4.94	28	62.3	2.99	20	50.5	4.64	6.03	2	**0.049**			
	Barring (0–3)	74	1.74	1–3	16	1.31	0.15	28	1.68	0.14	19	2.11	0.15	11.38	2	**0.003**		*	
	Bill (%)	46	83.2	40–100	16	80.0	2.81	19	85.8	3.32	10	87.7	2.61	4.09	2	0.13			

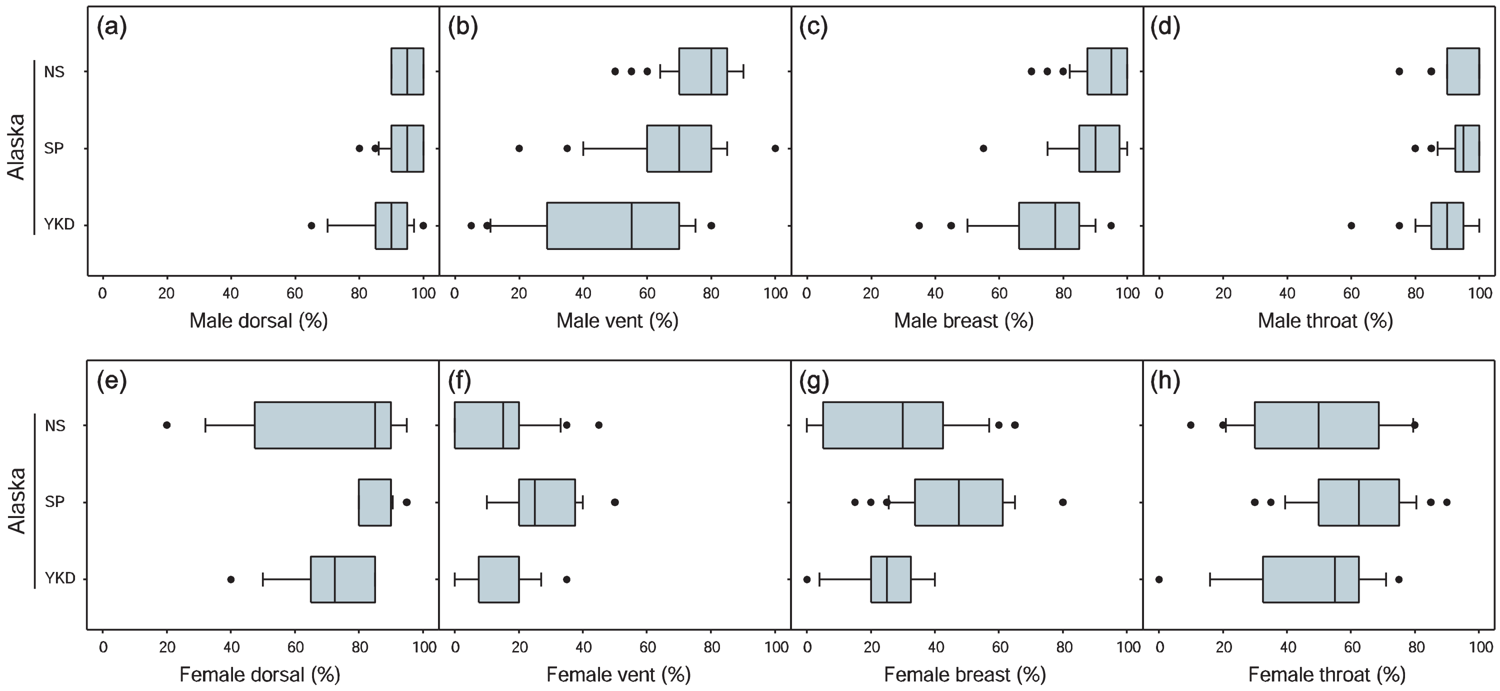

Figure 3.6 Plumage of breeding adult Bar-tailed Godwits by region in Alaska (YKD = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope). Values indicate extent (%) of breeding plumage in each body region: **(a)** male dorsal; **(b)** male vent; **(c)** male breast; **(d)** male throat; **(e)** female dorsal; **(f)** female vent; **(g)** female breast; and **(h)** female throat. See Table 3.3 for sample sizes. Boxes indicate median and 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles, and dots indicate more extreme values.

100%, and 50% of YKD males scored ≤50%. Patterns in throat and dorsal plumage were less dramatic because those plumage scores showed relatively little variation; all males reached ≥60% in both throat and dorsal scores. Variation in male plumage was consistent with a north–south cline: all measures of breeding plumage demonstrated significant linear increases with latitude (vent: $r^2 = 0.258$, $n = 109$; breast: $r^2 = 0.246$, $n = 111$; throat: $r^2 = 0.116$, $n = 108$; dorsal: $r^2 = 0.128$, $n = 95$; for all tests, $P < 0.001$).

By contrast, female plumage did not conform to a north–south cline. For all breeding-plumage variables, female scores were greatest for SP, whereas YKD and NS were statistically indistinguishable (Table 3.3). Differences in breast plumage were most conspicuous; 43% of SP females scored >50%, compared with 9% for NS and 0% for YKD. We also found no SP females with dorsal scores <80%, whereas 35% of NS and 57% of YKD females fell in this category.

On average, females had more heavily barred underparts than males in each AK region (Table 3.3). For females, ventral barring increased with latitude. For males, barring was greatest for YKD and least for SP, although neither was statistically distinguishable from NS.

Bill colour

In AK, males had darker bills than females, on average (Table 3.3), and all birds with bills <75% black were female. Bill colour did not vary significantly by geographic region for either sex. Blackness of bill was positively correlated with breast score for males ($r = 0.321$, $P = 0.013$, $n = 59$), but not for females ($r = 0.135$, $P = 0.37$, $n = 46$).

Discussion

Our study confirms and clarifies geographic variation within the breeding range of *L. l. baueri*, indications of which date back more than a century (McCaffery *et al.* 2010). In the only previous quantitative analysis, Rynn (1982) arbitrarily divided Alaska into two regions (at 64°N) and found regional differences in size and plumage among museum specimens of both sexes. By treating the Seward Peninsula and North Slope separately and examining linear relationships with latitude, we have demonstrated that variation in size of both sexes and in breeding plumage of males are consistent with north–south clines. However, we found no evidence that the Alaska population maintains its structure in the non-breeding season, despite occupying a similar range of latitude in New Zealand.

Where does selection for body size occur?

No geographic variation in size was evident among New Zealand godwits. By contrast, directional selection appears to occur in the breeding season in Alaska; godwits were smaller at higher latitudes. In >70% of bird species, colder climates are associated with larger body size, but this pattern appears to be least applicable to migratory species, whose annual routines are an adaptation to avoid environmental extremes (Meiri and Dayan 2003). However, the hypothesis that migration distance limits body size is not supported by our data. The additional 1,000–1,200 km traveled to northern Alaska represents <8% of the total migration distance from New Zealand, and because northern breeders stop in southwest Alaska on both northbound and southbound migration (Chapter 2), they do not actually perform longer non-stop flights than southerly breeders.

On the breeding grounds, male godwits perform spectacular, aerobatic displays in their efforts to secure mates and territories (McCaffery and Gill 2001). These aerial displays may select for smaller males, whose greater maneuverability allows them to outperform larger males (Jehl and Murray 1986, Székely *et al.* 2000). In turn, if mate competition (and, thus, selection for these displays) is stronger at higher latitudes, it could foster the observed size cline in males. However, there is no evidence for geographic variation in mate competition in godwits, and this scenario fails to explain the equivalent size cline in females.

Because bill morphology is related to foraging method in probing shorebirds (Barbosa and Moreno 1999), both intra- and inter-specific variation in bill length is often attributed to partitioning of prey resources (Nebel *et al.* 2005). Non-breeding godwits forage primarily on mudflats, where their long bills are suited to probing for subsurface prey. By contrast, they spend the breeding season primarily on tundra, often far from mudflats, and forage primarily near or above the surface (McCaffery and Gill 2001). We therefore expect stronger selection for bill length in the non-breeding season. However, although culmen length did not vary geographically in New Zealand, there was a cline within Alaska beyond that found in wing chord and mass; northern birds were not just shorter-billed but were proportionally shorter-billed for their size. In addition, sexual dimorphism in culmen length varied geographically, with male and female bills most similar in the north.

These findings suggest selection against long bills at high latitudes, consistent with Allen's Rule (for a given body volume, surface area will be minimised in colder climates; Allen 1877). Bird bills can be a significant source of heat loss (Symonds and Tattersall 2010), and the very long bill of godwits may be a thermoregulation liability during the breeding season, particular at the highest latitudes. Alternatively, habitat differences may also contribute to geographic variation in bill length.

Why does breeding plumage vary geographically?

Broad geographic patterns within Alaska weaken the hypothesis that variation in godwit breeding plumage is primarily driven by relative individual quality and its honest signaling to rivals and mates (Piersma and Jukema 1993, Piersma *et al.* 2001, Drent *et al.* 2003). The distinct geographic patterns in male and female plumage indicate nonparallel selection acting upon the sexes, which is consistent with the assumption that male plumage plays a greater role in pair formation. However, godwit plumage has yet to be linked to basic fitness components such as reproductive success or quality of territories or mates.

One clear function of godwit plumage is nest crypsis, because both sexes incubate eggs in open ground nests (McCaffery and Gill 2001), relying on the disruptive pattern of mantle and scapular feathers to blend with the surrounding tundra. Accordingly, dorsal scores of the sexes differed by much less than ventral scores. Furthermore, dorsal plumage was the least variable plumage region within each sex, indicating similar selection across the breeding range. However, dorsal and ventral plumage covaried in both sexes, which suggests that geographic variation in dorsal plumage is not driven exclusively by adaptation to local habitats.

The patchy red and white ventral plumage of females and southern males, roughly matching tundra backgrounds (J. Conklin pers. obs.), may provide crypsis for non-incubating godwits. However, the striking full-red breasts of northern males are very conspicuous, drawing attention to themselves and often away from their more cryptic mates. This suggests trade-offs between crypsis and mate acquisition that vary geographically, which could occur if competition for mates were more intense in the north, or if the brevity of the northern breeding season increased the importance of rapid mate acquisition.

Bill colour may be a component of the breeding 'plumage' of godwits, and thus subject to sexual selection itself, as in some passerines (e.g., Jawor *et al.* 2003). Alternatively, the seasonal increase in bill blackness may be an adaptation to mediate heat loss at high latitudes (Symonds and Tattersall 2010), given that black pigmentation confers greater absorption of heat. However, we found no geographic variation in bill colour, despite a correlation with breast plumage in males.

Because barred feathers are a component of alternate plumage rather than the subsequent supplemental plumage, interpretation of ventral barring in Alaska is complicated, particularly for males. However, it is intriguing that ventral barring of females was consistent with a north–south cline, whereas their vent, breast, and throat scores were highest at mid-latitudes. This suggests that alternate plumage is, or was, subject to different selection than supplemental plumage. If alternate plumage represents the ancestral 'breeding' plumage, subsequently replaced (in evolutionary terms) by the supplemental plumage (Jukema and

Piersma 2000), the conflicting patterns may reflect selection at different points in evolutionary history. The temporal overlap of pre-alternate and pre-supplemental moults (Piersma and Jukema 1993) warrants further investigation, but geographic variation suggests that the extent of barring apparent on the non-breeding grounds prior to most pre-supplemental moult (i.e., January–February) may roughly indicate a godwit's breeding region.

Population structure in the breeding season

Geographic variation in size and plumage among Alaskan godwits is similar in magnitude to differences among recognised godwit subspecies that occupy separate migratory flyways (Rynn 1982, Engelmoer and Roselaar 1998). Within *L. l. baueri*, links between breeding latitude and migration timing (Chapter 2) indicate that morphology is linked with phenology and behaviour as well. In New Zealand, godwits are extraordinarily site-faithful (P. Battley and J. Conklin unpubl. data) and have highly repeatable individual migration schedules (Battley 2006). If such behavioural rigidity extends to natal philopatry and breeding-site fidelity, segments of the Alaskan population could be reproductively isolated despite having completely overlapping non-breeding ranges. However, latitudinal clines in size and plumage, with substantial overlap among regions, suggest no distinct geographic limits to breeding populations. Genetic analyses may elucidate the age and degree of any division within *L. l. baueri* in relation to recognised godwit subspecies.

Geographic variation within Alaska has direct relevance to the diagnosis of godwits breeding in the Anadyr region of Russia as a separate subspecies (*L. l. anadyrensis*; Engelmoer and Roselaar 1998). Tomkovich (2010) found *L. l. anadyrensis* specimens to be intermediate between *menzbieri* and *baueri* specimens in both size and plumage, and concluded that *anadyrensis* was a valid subspecies. However, his Alaska sample ($n = 5$) was entirely from the Yukon-Kuskokwim Delta, where *baueri* godwits are largest. Considering all of Alaska, the measurements of Anadyr specimens fall largely within the range of values we have presented. Geographic variation in plumage of *baueri* suggests that the separation of *anadyrensis* on the basis of plumage also warrants further investigation. Therefore, it remains plausible that Anadyr godwits represent a geographically isolated segment of *baueri*.

Is latitudinal variation within Alaska consistent with patterns in other godwit populations? Among the four recognised subspecies, extent of male breeding plumage is greater in northerly breeding races (*L. l. taymyrensis* and *menzbieri*; 63–75°N) than in southerly races (*lapponica* and *baueri*; 58–70°N), and the southernmost male *baueri* are the palest in the species (Rynn 1982). In body size, the most northerly race (*taymyrensis*) is the smallest and the most southerly (*baueri*) is the largest, but latitudinal trends are obscured by a longitudinal pattern, in which western races are smaller than eastern races (Rynn 1982, Engelmoer and

Roselaar 1998). Thus, variation within Alaska may reflect more general processes, but because latitude is only an index for a suite of environmental factors (e.g., temperature, habitat type, duration of breeding season), identifying sources of selection will require detailed analysis. A comparison of *L. l. baueri* and *taymyrensis* may be instructive, for they breed across similar spans of latitude (~12°) and may contain comparable variation (but see Drent *et al.* 2003).

In the ecologically similar Red Knot *Calidris canutus*, northerly populations also had redder plumage than southerly populations (Buehler and Piersma 2008). In addition, there was a negative relationship between extent of breeding plumage and migration distance, implying energetic and temporal trade-offs between moult and migration. This latter relationship is not apparent in godwits, because the shortest distance migrant (*L. l. lapponica*) is among the paler races, and redder males in Alaska migrate farther.

Reports of intra-population variation such as we have described are rare among arctic-breeding shorebirds. Engelmoer and Roselaar (1998) identified latitudinal variation for only 1 of 14 shorebird species, the Grey Plover *Pluvialis squatarola*. Among Alaska-breeding shorebirds, we are aware of only one other example: northern-breeding Dunlin *Calidris alpina arcticola* are smaller than southern breeders (*C. a. pacifica*), but these populations follow very different migration patterns (Warnock and Gill 1996).

Population structure in the non-breeding season

The lack of population structure in New Zealand shows that *L. l. baueri* lacks the differential migration patterns (e.g., leap-frog migration) often found to accompany structure in breeding populations (e.g., Swarth 1920, Kelly *et al.* 2002). Because a significant portion of the Alaska population winters in eastern Australia (McCaffery and Gill 2001), some structure may yet occur across the entire non-breeding range. However, the morphological diversity in each New Zealand region suggests that godwits from across Alaska mix freely at non-breeding sites.

This is consistent with geolocator data showing that individuals from the Manawatu River estuary used breeding sites spanning most of the known Alaska breeding range (59.7–70.2°N; Chapter 2). Links between migratory timing and breeding location in that study are further supported by morphological data presented here: early-departing (presumably southerly-breeding) godwits were larger (Figure 3.5), in accordance with the size cline that we found within Alaska. This pattern appears general to New Zealand sites, because larger males also departed earlier at the Firth of Thames (although this was reported in error as the opposite relationship; Battley 2006), and the 4-week span of departures implies individuals from a wide range of breeding latitudes.

We did not examine geographic variation in plumage in New Zealand, because the correlation between plumage at departure and ‘ultimate’ breeding plumage is unclear, as a result of the resumed pre-supplemental moult during a stopover of 4–7 weeks[1] in Asia (Chapter 5). Also, plumage at departure has been studied at only two New Zealand sites (Battley 2006, this study). However, male plumage was highly variable at both sites (range of breast scores: 20–100%), which is consistent with individuals from a wide range of breeding latitudes occurring at each site.

The factors that govern non-breeding distribution of godwits remain mysterious. Although many aspects of godwit life history, such as breeding site and migration timing, appear to be ‘hard-wired’ and presumably heritable, non-breeding site does not. After their first migration from Alaska, young godwits (<2 years) appear to freely roam New Zealand and eastern Australia before settling on specific sites, to which they are extraordinarily faithful as adults (P. Battley and J. Conklin unpubl. data). Identifying the social and ecological factors that govern this site ‘choice’ may reveal patterns in an apparently random non-breeding distribution of individuals.

---

[1] This was reported in error as ‘3–5 weeks’ in the published version.

Chapter 4

Impacts of wind on individual migration schedules of New Zealand Bar-tailed Godwits

Conklin, J.R. & P.F. Battley
Behavioral Ecology 22: 854–861 (2011)

Abstract

Despite clear links between wind conditions and timing of migration at the population level, no study has examined the contribution of winds to annual variation in the migration timing of individual birds. At a single non-breeding site in New Zealand, we closely monitored three years of departures of Bar-tailed Godwits Limosa lapponica baueri, *a long-distance migrant with remarkable annual consistency in individual migration schedules. Although individual godwits showed very little variation in departure date and generally experienced favourable departure conditions, most off-schedule departures were explained by maximising initial wind assistance for the non-stop flight to Asia. Surprisingly, early departures attributable to wind were more common and of greater magnitude than wind-related departure delays, and prolonged weather-related departure lulls did not always result in late-departing individuals. Thus, our results show that knowledge of individual departure decisions with regard to wind can strongly influence interpretation of population patterns. Early departures associated with winds, previously only demonstrated theoretically, may reflect conservative timing and extent of pre-migratory fuelling, a possible adaptation for extreme long-distance migration in variable conditions.*

Introduction

Favourable winds confer significant time- and energy-minimisation benefits for migrating birds (Alerstam and Lindström 1990, Liechti and Bruderer 1998), promoting timely arriving at breeding sites in appropriate physiological condition (Drent *et al.* 2003). Accordingly, birds respond to wind conditions with flexibility in departure timing, flight altitude, and migratory route (Liechti 2006). Specifically, headwinds or crosswinds may discourage migratory departure, but, in theory, trade-offs between optimal timing and flight costs may lead to departure in unfavourable winds if such conditions persist for extended periods (Weber *et al.* 1998a). Numerous studies have demonstrated the influence of wind on intensity and timing of migration at the population level, but such data do not directly address departure decisions of individual birds. No multi-year study has examined how individuals reconcile migration schedules with annual variation in weather.

Optimisation models typically view departure date as flexible, varying with individual differences in body condition and fuelling rate, and with temporal variation in fuelling resources and weather (Hedenström 2008). This view is most appropriate for species with multiple stopovers *en route* to breeding grounds (Weber *et al.* 1998b, Clark and Butler 1999), a strategy allowing potential compensation for 'errors' in initial departure timing or unanticipated conditions encountered after departure (Shamoun-Baranes *et al.* 2010). By contrast, departure of migrants making extreme long-distance flights (now known to reach >11,000 km; Gill *et al.* 2009) may require a more rigid concept of 'optimal' departure date. These birds typically cross vast inhospitable barriers offering no refuelling sites (Gill *et al.* 2005) and little opportunity to correct errors in timing or fuel load. In addition, they initiate these journeys effectively blind to conditions at the destination, as environmental cues are unlikely to correlate at such great distances (but see Järvinen 1989). Therefore, departure date in long-jump migrants (Piersma 1987) is likely to be conservative and 'hard-wired' by adaptation to long-term and large-scale environmental trends, showing less annual variation than in short-hop migrants.

Such rigid migration schedules are exemplified by New Zealand Bar-tailed Godwits *Limosa lapponica baueri*. Their round-trip migration to Alaska breeding grounds covers approximately 30,000 km in three trans-oceanic flights, including the longest non-stop flight recorded in birds (Gill *et al.* 2009, Battley *et al.* 2012). Accordingly, godwits in New Zealand and Alaska accumulate among the highest pre-migratory fuel loads yet reported (Piersma and Gill 1998, Battley and Piersma 2005). Despite these apparent hardships, godwits demonstrate extraordinary inter-annual rigidity in migration timing: individuals' departure dates from New Zealand generally varied by less than one week, amid inter-individual variation of nearly a month (Battley 2006). This latter variation is strongly linked with phenology of Alaska breeding sites across a wide range of latitude, with southern breeders departing New Zealand earliest (Chapter 2). These findings imply that migration timing in godwits reflects endogenous, individually-optimised schedules, rather than putative annual or individual differences in fuelling rate.

Weather may therefore be the primary source of intra-individual variation in migration timing in this system, offering the opportunity to examine the effects of wind with few confounding factors. In this study, we monitored godwits departing from a single site in New Zealand for three consecutive years, to examine the association between wind conditions and repeatability of individual departure date, and how individual departure decisions were reflected in migration patterns at the population level.

Methods

Migratory departures

We monitored northbound migratory departures (4 March–5 April, 2008–2010) of Bar-tailed Godwits from the Manawatu River estuary, New Zealand (40.47°S, 175.22°E). At this small estuary (~1 x 2 km), the small godwit population (200–280 birds; ~25% are individually colour-banded) is highly approachable, and can usually be observed entirely from one of several vantage points. We monitored expected peak departure hours (13:00–21:00 local time) on 72 of 99 days (d); migratory departures of shorebirds generally occur 1–6 hours (h) before civil twilight (Piersma *et al.* 1990b, Battley 1997). During surveys, a single observer watched and listened for migratory behaviour, which included distinct vocalisations and low, circling flights expressing intent to depart (Piersma *et al.* 1990b, Battley 1997). Typically, flocks engaged in very active calling, preening, and short exploratory flights, for 0.5–4 h before actual departure. During this time, the observer recorded all marked individuals involved, using a spotting scope and digital camera. All flying flocks were watched and/or photographed until resettling or disappearing from sight. Departures were easily distinguished from local movements by both altitude and direction (always NW/NNW and slowly disappearing to the horizon). After a departure, the observer quickly surveyed the estuary for all remaining marked godwits. In addition, we conducted daily high-tide surveys to confirm size and composition of the remaining flock; daily resighting probability of marked godwits was >95%.

The final dataset included 45 individuals (25 female, 20 male) with known departure dates in all three years; we excluded birds with <3 years of data from analyses. For 102 (75.5%) cases, individuals were directly observed preparing and/or actually departing with an observed flock. The remaining individuals were assigned a departure date based on the last day they were recorded at the estuary. For 16 (11.9%) cases, this coincided with an observed departing flock of partially or completely unknown individual composition; therefore, we considered time and flock size to be known. For 17 (12.6%) cases, this coincided with a decrease in local flock size unexplained by observed departures; we considered these departures ‘unobserved’ and calculated flock size based on successive high-tide counts. Observed departures occurred 13:30–20:55, and unobserved departures likely occurred outside survey times (Leyrer *et al.* 2009). By including unobserved departures, annual totals represent a virtually complete accounting of individuals migrating.

We are confident that movements out of the estuary represented migratory departure from New Zealand. Site-fidelity of marked godwits was extremely high for the entire non-breeding season (September–March), and non-migratory movements in and out of the estuary were extremely rare (J. Conklin and P. Battley unpubl. data). Furthermore, some marked godwits carried geolocators (Chapter 2), and subsequently provided independent support for departures in 2008–2009. In all cases, longitude data from geolocators indicated birds were clearly west of New Zealand on the day subsequent to observed (n = 23) or assigned (n = 6) departure date, and all continued directly to Asia (J. Conklin and P. Battley unpubl. data).

We calculated repeatability (intra-class correlation coefficient) of individual departure date according to Lessells and Boag (1987). We used the median of an individual's three departures to represent its preferred departure date, and considered departures within ±3 d of this median date to be 'on schedule'.

Weather data

During surveys, we estimated local surface wind direction (in 16 categories; e.g., NNW) and velocity (in 5-km/h increments) hourly and whenever departing flocks were observed. Concurrently, we recorded precipitation in three subjective categories: 'heavy' = steady or heavy rain; 'light' = drizzle or intermittent light rain; or 'none'. For days with observed departures, we used winds at the exact time of departure to represent conditions. For days with multiple departures (n = 7 d), we used the mean wind direction and velocity among all departures that day; in all cases, winds were similar among same-day departures. For days without departures and for two days in which departures were apparently missed despite a survey, we used winds at 18:00 local time to represent conditions (median observed departure time = 17:38). For days without surveys, we used local predicted winds and precipitation (MetVUW 2010), when available (n = 7), to represent surface conditions.

To represent wind conditions at likely migration altitude (Landys *et al.* 2000, Green 2004), we obtained data from the NCEP/NCAR Reanalysis Project (NOAA 2010a) for 40°S, 175°E (50 km NW of the study site) at 850 mb geopotential height (~1,500 m altitude) at 18:00 local time. From these data, we calculated wind direction and velocity.

Calculation of wind effect

Because wind effect calculation method may affect conclusions, we compared two commonly-used formulae[1]. The first (Tailwind, hereafter 'TW'; see formula in Åkesson and Hedenström 2000) derives relative wind profit ('WP', in which positive values indicate assisting winds) considering only the magnitude of tailwind or headwind along the preferred migratory direction. The second (Crosswind, hereafter 'CW'; see formula in Piersma and Jukema 1990) additionally accounts for drift from the intended flight path caused by crosswinds; thus, this method always produces an equal or less favourable assessment of winds. We assumed a migratory direction of NNW (337.5°), consistent with observed migratory departures from the site (315–350°) and tracks of satellite-tagged godwits after New Zealand departure (Battley *et al.* 2012). CW requires an assumption of preferred air speed; we used 65 km/h, consistent with northbound tracks of satellite-tagged godwits (Battley *et al.* 2012). For days when both local surface and 850 mb wind data were available (n = 87 d), we calculated maximum wind profit ('MWP') as the greater of the two WP values.

---

[1] See Appendix 3 for formula details.

We considered MWP values −5 to +5 km/h to represent calm conditions; lesser or greater values indicated headwinds or tailwinds, respectively.

Results

Migratory departures – population level

We observed 39 departing flocks on 29 days (1–4 flocks/d) across three years. Surveys indicated unobserved departures on seven additional days (Figure 4.1). Observed departing flocks contained 3–34 godwits each (mean = 14.1, $n = 39$ flocks); 3–70 godwits departed on each departure day (mean = 18.1, $n = 36$ d). In 2008, a total of 251 godwits departed on 13 days (6–48 birds/d) from 10 March–2 April (Figure 4.1a). In 2009, 212 godwits departed on 13 days (3–38 birds/d) from 4 March–3 April (Figure 4.1b). In 2010, 189 godwits departed on 10 days (5–70 birds/d) from 6 March–5 April (Figure 4.1c).

Wind profit calculated by Tailwind and Crosswind were nearly identical for local surface winds ($r^2 = 0.99$, $n = 87$ d, $F = 9966.4$, $P < 0.001$), indicating that significant low-altitude crosswinds were rare. At 850 mb, the two measures were less similar ($r^2 = 0.78$, $n = 99$ d, $F = 344.7$, $P < 0.001$), indicating more frequent crosswinds at higher altitudes. However, crosswinds did not appear to deter departures, as four flocks departed when MWP calculated by CW (including crosswinds) was −7.6 to −32.4 km/h. When crosswinds were not considered (TW), no flocks departed when MWP was <−5.0 km/h. Therefore, we conclude that TW better reflects conditions relevant to godwit departure decisions, and consider CW no further (all WP values in Figures 4.1–2 and hereafter are calculated by TW).

Local surface winds were highly variable: WP = −37.0 to +32.4 km/h, mean = −3.3, $n = 87$ d. On departure days, mean surface WP = +5.0 km/h (range: −32.4 to +32.4, $n = 35$ d), and 29 departure days (83%) featured tailwinds or calm conditions. On days without departures, mean surface WP = −9.1 km/h (range: −37.0 to +27.8, $n = 52$ d). We have no local surface wind data for an additional 12 days (including 1 departure day).

Greater extremes of velocity occurred at 850 mb: WP = −61.1 to +41.3 km/h, mean = −2.6, $n = 99$ d. On departure days, mean WP at 850 mb = +3.9 km/h (range = −47.4 to +40.6, $n = 36$ d), and 26 departure days (72%) featured tailwinds or calm conditions. For non-departure days, mean WP at 850 mb = −6.1 km/h (range = −61.1 to +41.3, $n = 63$ d).

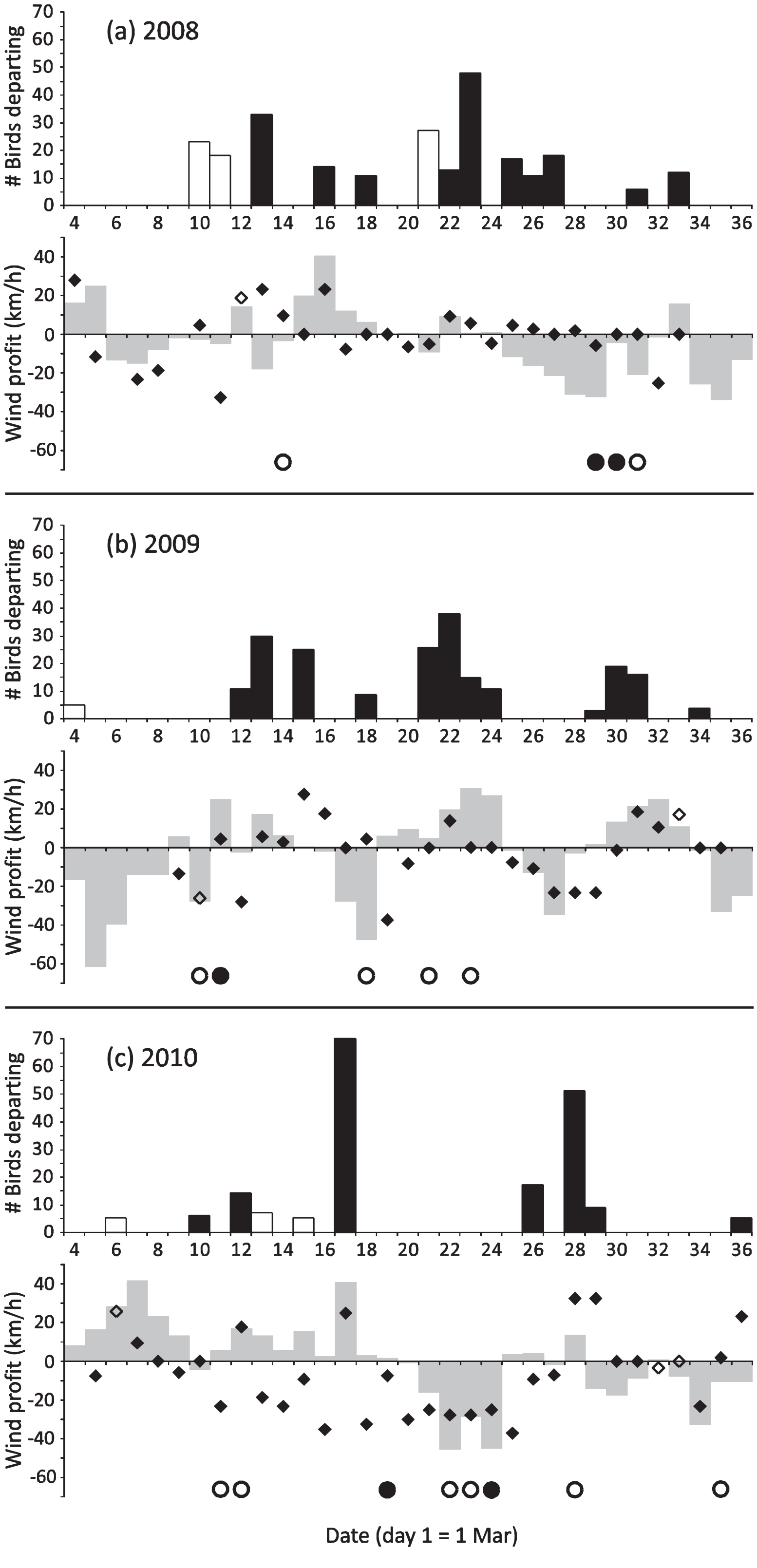

Figure 4.1 Godwit departures in relation to wind and rain (2008–2010). Departures: black bar = observed, open bar = unobserved. Wind profit: filled diamond = observed local surface wind, open diamond = predicted local surface wind, missing diamond = surface wind data unavailable, grey bar = 850 mb wind. Precipitation: open circles = light rain, black circles = heavy rain.

Surface and 850 mb wind profit were only weakly correlated (r^2 = 0.11, *n* = 87, *F* = 10.5, *P* = 0.002), with headwinds at one altitude often accompanied by tailwinds at the other (Figure 4.2). Consequently, 76 of 87 days (87%) featured tailwinds or calm conditions at one or both altitudes, and every flock that departed amid headwinds at one altitude (*n* = 15) met tailwinds or calm conditions at the other. Mean MWP on departure days was +13.5 km/h (range = −5.0 to +40.6, *n* = 35), compared with +2.6 km/h on non-departure days (range = −27.8 to +41.3, *n* = 52). Among observed departures, the lowest MWP value was −2.0 km/h. Departing flocks preferred days with MWP tailwinds (21 used of 41 d; expected = 16.5 based on availability), used calm days equal to availability (14 of 35 d; expected = 14.1), and completely avoided headwinds (0 of 11 d; expected = 4.4; χ^2 incalculable due to zero value).

Among departure days, MWP was positively correlated with number of birds departing (proportion of that year's total migrants, range = 0.01–0.37; r^2 = 0.15, *n* = 35 d, *F* = 5.97, *P* = 0.020). MWP was greater on days with multiple flocks departing (mean = +21.1 km/h,

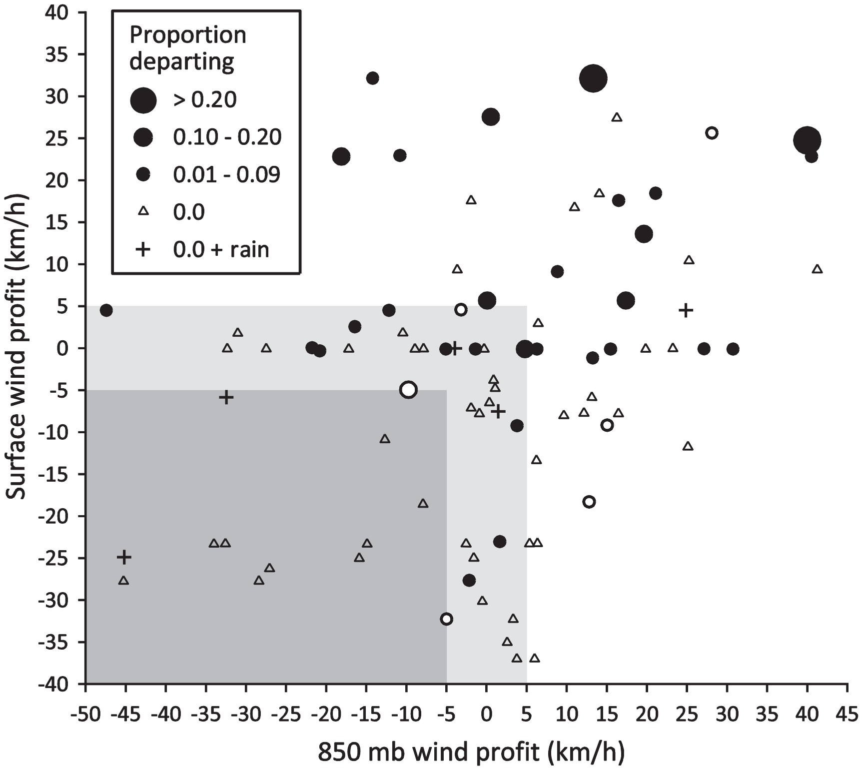

Figure 4.2 Daily wind profit at two altitudes vs. proportion of godwit population departing (2008–2010). Open circles = unobserved departures. Pale shading indicates calm conditions (maximum wind profit = −5 to +5 km/h). Dark shading indicates headwinds (maximum wind profit <−5 km/h).

range = +5.0 to +40.4, n = 7 d, 2–4 flocks/d) than on days with a single flock departing (mean = +12.6 km/h, range = −2.0 to +40.6, n = 22 d), but this was not statistically significant (t = 1.70, df = 27, P = 0.066).

No departures occurred on days with heavy rain (n = 5; Figure 4.1). Light rain occurred on six departure days and six non-departure days.

Migratory departures – individual level

Across three years, mean departure date of 45 marked godwits was 20 March, 21 March, and 19 March, respectively. Individual departure dates were very consistent across years: repeatability = 0.836 ($F_{44,90}$ = 16.34, $P < 0.001$). Despite a 33-day window of departures in the population, the median individual span of departures was 5 days (range = 1–15 d), and 35 individuals (78%) departed within a 7-day period in all three years (Figure 4.3). Out of 135 departures, 117 (87%) were 'on-schedule' (±3 d of the individual's median departure date, or 'MDD'; Figure 4.3). The remaining 18 departures occurred at MDD ±4–10 d; nine were 'late' and nine were 'early'. Among days with departures of marked godwits, 25 of 33 (76%) contained only on-schedule birds.

Recent capture appeared to affect some departures; on 12 March 2008, we captured 15 birds by cannon-net (Figure 4.3). Among birds captured 0–5 d before MDD (n = 7), two departed late (MDD +4 and +9 d) and two departed on MDD +3 d. All individuals whose MDD were 9–16 d subsequent to capture (n = 7) departed on schedule (MDD ±2 d). One other bird was captured six days *after* her MDD. Capture did not affect all individuals equally: three godwits departed the day after capture.

Ten off-schedule departures (56%) achieved improved wind assistance. For six early departures in 2010 (Figure 4.3), MWP was greater (by 8.0–37.0 km/h) than on any day in the individual's 7-day expected departure window. For four late departures (1 in 2008 and 3 in 2009), MWP was greater than the previous 4–6 days; these birds departed on the best day immediately subsequent to MDD. Only six off-schedule departures (33%; 3 early, 3 late) were unexplained by capture or weather; for these birds, more favourable conditions and departures occurred during their expected departure windows.

Although they avoided headwinds, individuals did not always choose the most favourable winds available to them. Among on-schedule departures (n = 117), only 42% occurred on the day with the greatest MWP in the individual's 7-day expected departure window (10 of 38 in 2008, 11 of 40 in 2009, 28 of 39 in 2010).

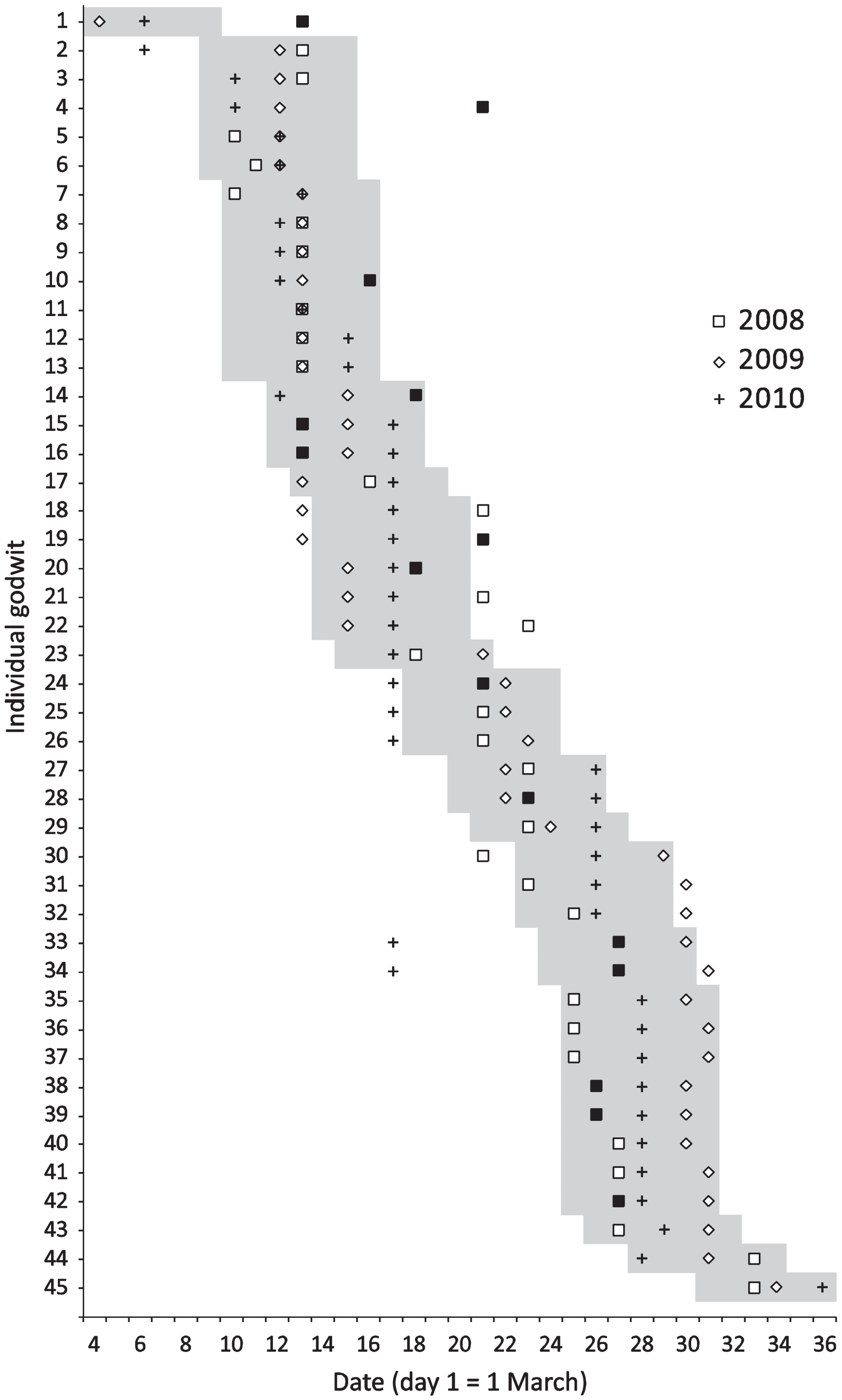

Figure 4.3 Departure schedules of 45 marked godwits (2008–2010). Shaded area indicates 'on-schedule' departures (±3 days of individual's median departure date). Filled squares indicate departures of birds captured on 12 March 2008.

Combining population and individual data

We can use the 7-day expected departure windows of individuals to understand how many godwits were 'available' for departure each day. Throughout the departure period, the pool of birds likely to depart did not gradually drop as the population declined, but rather continually fluctuated (accumulating until depleted by departures, then increasing again as new birds approached MDD) until the entire pool of individuals was spent (Figure 4.4).

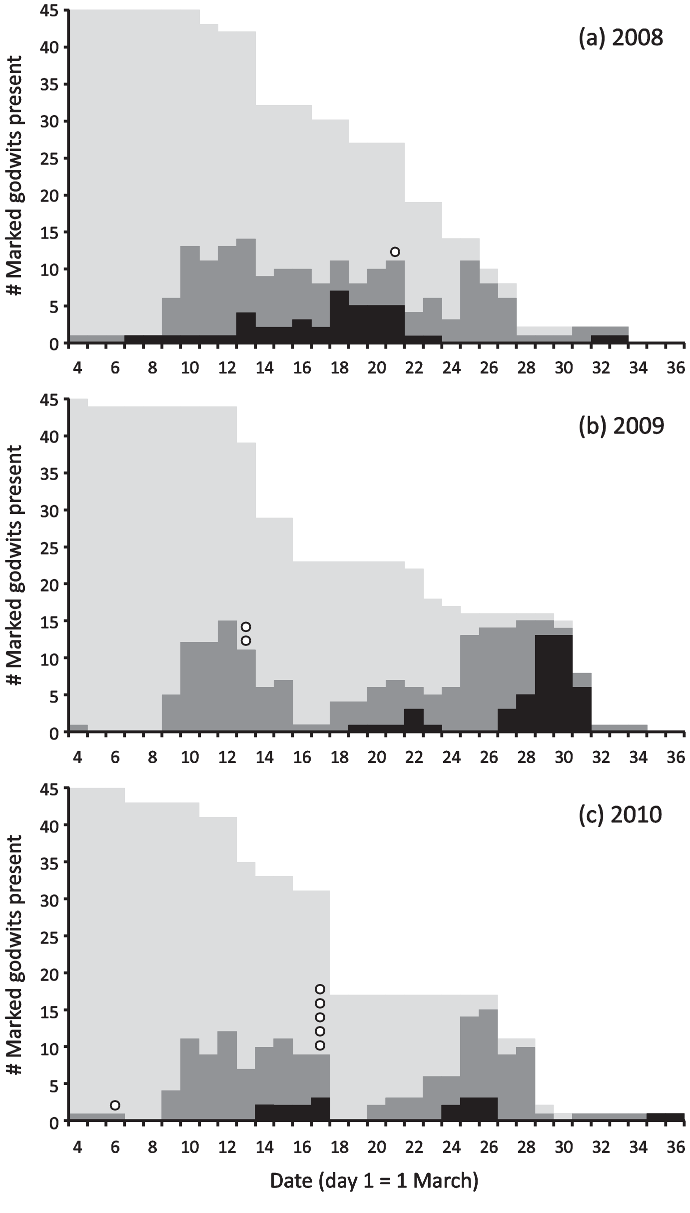

Figure 4.4 Daily number of marked godwits available for departure (2008–2010). Pale grey bars indicate all marked birds present. Black bars indicate individuals at ≥median departure date ('MDD'). Dark grey bars indicate individuals at ≥MDD −3 d. Circles indicate departure of individuals prior to MDD −3 d.

Each year, the first major peak in departures occurred 10–15 March (Figure 4.1), which featured favourable winds as well as ≥10 individuals approaching MDD in all three years (Figure 4.4). If good conditions promote on-schedule departure, birds experiencing favourable winds near MDD every year should vary least in departure date. We found evidence of this: all seven individuals with departure spans of 1–3 days had MDD of 12–13 March (Figure 4.3). This fell within a period (12–18 March) during which no headwinds or heavy rain occurred during the entire study (Figure 4.1).

In 2008 and 2009, a second peak occurred 21–24 March, when approximately 40% of the population departed (Figure 4.1a–b). In 2010, this period featured sustained headwinds and rain and eight consecutive days without departures (Figure 4.1c). Consequently, all marked birds with MDD of 21–24 March either departed early on 17 March (n = 3), or waited for improved conditions on 26 March (n = 3; Figure 4.3). Surprisingly, this 8-day departure lull caused not a single late departure: 17 March had completely depleted the pool of available birds, and no remaining birds passed MDD until 24 March (Figure 4.4c), just as conditions began to improve.

Briefer late-season lulls in unfavourable conditions occurred at different times in 2008 (28–30 March 2008) and 2009 (25–28 March), making departure of the final 20% of the population inconsistent among years (Figure 4.1a–c). However, the effect of these lulls was quite consistent across individuals: all marked godwits with MDD of 28–29 March (n = 9) departed on MDD −3 to −1 d in 2008, and MDD +2–3 d in 2009, resulting in a 4–7 day departure span for all of them (Figure 4.3).

No flocks departed despite good conditions (>+3 MWP and no heavy rain) on 19 days (6 in 2008, 7 in 2009, and 6 in 2010; Figure 4.2), suggesting that no individuals were waiting to depart on these days. On 12 of 19 days (63%), no remaining marked godwits were past MDD; 7 of these days were before 10 March, when very few godwits (and only 2 marked birds) ever departed. On four days in 2008, 1–2 individuals had reached MDD +1–6 d, but all had been captured in the previous five days. On three other days, 1–2 birds had reached MDD +1–2 d, but waited one more day to depart, still on schedule.

Three departing flocks (6, 9, and 13 godwits) contained no marked birds. MDD helps explain why all remaining marked birds skipped two of these departures: on 31 March 2008 and 18 March 2009, none had passed MDD yet (Figure 4.4a–b). In the third case (22 March 2008), one late-running bird had passed MDD (having skipped three departures within his 7-day departure window), and departed the following day (MDD +6 d).

Discussion

Variation in individual departure date

Several striking results derive from our study, which is the first to examine the effect of winds on intra-individual variation in migration timing. First, individual departure date was extremely consistent across years, leaving very little variation to explain. Second, unfavourable departure conditions occurred infrequently, so godwits apparently had little difficulty reconciling preferred departure date with weather. Third, most off-schedule departures were attributable to either recent capture or the avoidance of unfavourable winds. Most surprisingly, cases of individuals departing earlier than expected due to wind conditions were more numerous than wind-related departure delays.

Repeatability of individual departure date ($r = 0.836$) was nearly identical to that found among godwits at another New Zealand site ($r = 0.83$; Battley 2006). To our knowledge, these are by far the highest figures for repeatable migration timing in birds (see Bety *et al.* 2004 and references in Battley 2006); the nearest comparable finding was breeding arrival in Barn Swallows *Hirundo rustica* ($r = 0.51$; Møller 2001). In both godwit studies, most individuals departed within a one-week period each year, but the rate was higher in the current study (87% vs. 73% of departures). This difference is probably methodological, as a smaller population and greater intensity of effort at the Manawatu River estuary led to greater precision in departure dates. Regardless, we confirm that the bird making the longest known non-stop flights may also have the most rigid migration schedules.

This rigidity may be enabled by the generally favourable conditions experienced by godwits: only 14 of 87 days (16%) featured headwinds and/or heavy rain. A visible setting sun has been proposed as a vital navigational cue for departing shorebirds, explaining their tendency to depart in late afternoon (Moore 1987, Piersma *et al.* 1990b). However, New Zealand godwits have been shown to depart without a visible sun (Battley 1997), and this was true during the current study, although we did not specifically measure cloud cover. Therefore, weather rarely presented an obstacle to departure. Furthermore, godwits often departed in calm conditions and did not always choose the most favourable day close to MDD, suggesting that significant wind assistance, at least at the time of departure, was not a requirement for migration. However, most off-schedule departures (10 of 18) appeared directly attributable to wind: these birds achieved greater wind assistance by departing 1–7 days outside their expected windows.

Weather-related departure delays are easily understood in terms of optimal migration: a bird reaches migratory condition, and then should depart on the first occasion of favourable winds after its optimal departure date (Weber *et al.* 1998a). This principle may explain four late departures in our study, in which birds experienced poor winds at MDD, but departed as soon as conditions improved. Wind conditions causing early departure is less intuitive, and we believe has never before been demonstrated. Weber and Hedenström (2000) showed theoretically that birds may benefit from early departure in favourable conditions, provided that sustained unfavourable winds can be expected to follow. Thus, a bird below its optimal fuel load for migration may be ‘promoted’ to readiness by favourable winds, because wind assistance effectively decreases the fuel required for the flight (Alerstam and Lindström 1990).

On 17 March 2010, the greatest single departure day of the study, four flocks comprising 37% of the migratory population departed. Joining many on-schedule birds, five godwits departed 4–10 days prior to MDD, avoiding delay by a subsequent 8-day departure lull and experiencing better conditions than any during their expected departure windows. This is consistent with two different scenarios, both intriguing. In the first, birds anticipated sustained poor conditions, and avoided those by departing on the last favourable day before the change in weather. The second scenario requires no foresight, but only recognition of extremely good current conditions: winds that day were among the most favourable in our study (MWP +40.4 km/h), and unusual conditions north of New Zealand suggested significant wind assistance for perhaps 2–3 days along the migratory route. The benefits of an unusually easy flight may have outweighed any costs of early departure or early arrival in the Yellow Sea. Godwits may respond to weather at larger temporal and spatial scales than those addressed here, and we don’t know how well local conditions reflect those encountered later in the 7–8 day flight to Asia.

Migration schedules may also be disrupted by trauma or stress. Four godwits captured near MDD in 2008 appeared to delay departure by 3–9 days, only to resume their normal schedules in following years. Delays may have resulted from capture-related stress or mass loss (Warnock *et al.* 1997), which has been linked with extended stopover duration (Warnock and Bishop 1998). However, any capture effect was brief and did not affect individuals equally: other godwits captured near MDD and all of those captured more than eight days prior to MDD departed on schedule.

Only six off-schedule departures (33%) were unexplained by wind or recent capture, implying that little variation in departure can be attributed to annual variation in fuelling rate or body condition, or to carry-over effects from previously disrupted moult schedules or delayed arrival on non-breeding grounds. In addition, we used an admittedly coarse measure of an individual’s preferred departure date (median departure among three years). Although most birds had two or three temporally clumped departure dates during our study, others left more uncertainty regarding their ‘intended’ departure dates. With additional years of data, and the inclusion of weather variables at greater spatial and temporal scales, even these few unexplained departures may become scrutable.

Understanding population patterns with individual data

The tendency of individual godwits to depart in a 7-day period each year (Battley 2006, this study) allows inferences regarding the proportion of a population available to migrate at a given time (Figure 4.4). For example, after a prolonged departure lull, it is reasonable to expect that subsequently departing flocks will largely comprise late individuals (e.g., Battley 1997). Indeed, there is a clear case of this in 2009: after a 4-day lull during 25–28 March, approximately 20% of the population departed over a 3-day period (Figure 4.1b). Figure 4.4b reveals a conspicuous accumulation of individuals past MDD during this time, and 3 of 4 wind-related late departures in our study occurred 30–31 March (Figure 4.3).

By contrast, individual data provided an unexpected view of the departure lulls in 2010. After an 8-day lull amid sustained prohibitive conditions, there was an intense migration peak 26–29 March once conditions improved (Figure 4.1c). In this case, however, the prolonged lull caused no accumulation of late individuals: by 26 March, only three godwits had passed MDD (Figure 4.4c), and no late departures resulted (Figure 4.3). In fact, although 2010 featured two significant departure lulls and the most extreme weather conditions in the study, not a single late departure occurred that year. These insights are impossible from population data alone.

Individual data also allow conclusions regarding apparently favourable departure days that were unused by the population. Using our expected departure windows, it was clear that these days were unused primarily due to a lack of ready and/or late individuals in the population. Likewise, some departures contained no marked birds, due to a lack of individuals approaching MDD.

Shorebirds typically migrate in flocks, which may confer navigational, energetic and/or safety benefits to individuals (Alerstam 1990). Departing flock sizes in our study were quite small compared to departing Bar-tailed Godwit flocks observed elsewhere (mean flock sizes 40–235, and up to 700; Piersma *et al.* 1990b, Tulp *et al.* 1994, Battley 1997), but these studies involved larger populations (1,500–8,000 birds). In small populations, individuals may encounter few others willing to migrate on a given day, and the smallest departing flocks we observed (3–6 birds) may attest to the prioritisation of individual departure date over flock size. But there are apparently limits. In 2009, one female (bird #30 in Figure 4.3) attempted to depart during the departure lull of 25–28 March (Figure 4.1b). For four days, she conspicuously called and flew about, but could not rally others for a successful departure. On 29 March, her vocalisations were more vehement, and she attempted to depart alone, circling high above the estuary and several hundred metres NW before turning back in a significant surface headwind. Finally, two godwits joined her in preparation for departure, and this tiny flock departed late on 29 March. The next day, in much improved wind conditions (Figure 4.1b), 19 godwits departed, including several individuals at MDD +3–4 d (Figure 4.3). For those three earlier birds, departure date appeared more important than flock size or wind assistance. The costs of such apparently suboptimal departures are unknown, but departing flock size did not appear to influence likelihood of returning the following autumn in this study.

Interpretation of wind data

Migrating birds may experience very different winds at low and high altitudes (e.g., Piersma and Jukema 1990, Piersma *et al.* 1990a, Schaub *et al.* 2004), and have been shown to adjust flight altitude to encounter favourable winds (Gauthreaux 1991, Bruderer *et al.* 1995). Studies evaluating departure conditions using winds at a single altitude have typically indicated some proportion of flocks departing in suboptimal winds (e.g., Battley 1997, Åkesson and Hedenström 2000), suggesting that not all birds can achieve favourable departure conditions. Consistent with this, birds in our study often departed when either surface winds or 850 mb appeared quite unfavourable. However, when both altitudes were considered, it was clear that godwits only avoided departing when *both* were unfavourable (Figure 4.2). Viewed this way, winds were rarely an important obstacle, and birds were not obligated to depart in unfavourable conditions. Flocks often made several aborted flights before ultimate departure, and occasionally circled slowly upward before leaving the site, possibly testing different altitudes for favourable winds. On a 7–8 day flight to Asia, it is likely that godwit flocks change altitude frequently to achieve the course of least resistance.

Conclusions regarding the influence of wind on departure decisions can depend upon the method of calculating wind profit. When we included the displacement effect of crosswinds, several flocks appeared to depart in very poor conditions. However, this was not the case when we ignored crosswinds and calculated only the tailwind component. This may suggest the energetic cost of compensation for crosswinds is negligible for godwits departing this site, or that they simply allow themselves to drift without compensation, expecting that winds encountered later may compensate for drift from the shortest-distance path. With variable winds, theoretically optimal behaviour of migrants with a distant destination is to allow lateral drift without compensation initially, but to increase compensation upon approaching the destination (Alerstam 1979, Green *et al.* 2004). This is consistent with tracks of satellite-tagged godwits, which deviated laterally from the shortest-distance route by as much as 500–

600 km in the first days after departure from New Zealand, only converging upon approaching the Yellow Sea (Battley *et al.* 2012). Deviations of this magnitude add very little distance or time to a flight of approximately 10,000 km. Therefore, we believe crosswinds do not significantly influence departure decisions of New Zealand godwits.

Implications for understanding long-distance migration

Results of the current study support our view of departure timing in Bar-tailed Godwits as a fundamental, ostensibly fixed window, primarily governed by overall migration speed and appropriate timing of arrival on distant breeding grounds (Chapter 2). At the population level, mean departure date varied by only two days, suggesting a negligible effect of annual variation in non-breeding resources, at least during the period we studied. Individual godwits demonstrated astoundingly repeatable departure when presented with consistently favourable weather, but easily tolerated ±3 days of variation around a preferred date, and responded to more extreme conditions with greater deviations in departure. This implies strong selection for individually-optimised departure date, but also flexibility to respond to unpredictable circumstances. In this study, no bird failed to return the next year after off-schedule departures up to MDD ±9–10 days; however, we do not know what magnitude of error in departure will reduce survival or reproductive success. Northbound godwits have an extended stopover (30–50 d) in Asia, perhaps allowing compensation for suboptimal timing of New Zealand departure before the flight to Alaska, which appears much more rigorously scheduled with regard to breeding-site phenology (Chapter 2).

The early departure of individuals in response to wind has intriguing implications for optimal migration. Achieving optimal fuel loads well before departure is considered disadvantageous, because an associated decrease in maneuverability may increase mortality risk from predation (Alerstam and Lindström 1990, Dietz *et al.* 2007). It is unclear whether wind benefits could compensate for 10 days of lost fuelling time, as required by the most extreme cases we observed. However, New Zealand godwits face minimal danger from avian predators, currently or historically, and so the cost of carrying full fuel loads prior to departure may be negligible. In addition, we have no evidence that departure of godwits is limited by fuel deposition rates in New Zealand; they fuel quite slowly, starting up to three months before departure (J. Conklin and P. Battley unpubl. data). Thus, godwits may regularly reach migratory condition well in advance of departure and may be prone to overloading (Gudmundsson *et al.* 1991), allowing flexibility to address unusual weather patterns.

The extraordinary migratory flights and high-latitude breeding areas of Bar-tailed Godwits imply extreme time and energy constraints. However, the maintenance of rigid schedules and high survival rate (>90% individual return rate in this study) do not suggest a bird near the limit of its capabilities. In evolutionary terms, such an unforgiving annual routine may foster a conservative approach to fuelling and migration timing, as opposed to the strategies of short-hop migrants, which may precariously balance crucial trade-offs in time-, energy-, and predation-minimisation (Alerstam and Lindström 1990) with lesser consequences. Thus, safe and predictable fuelling conditions and generally favourable wind patterns may be prerequisites for the evolution and persistence of such extreme migration systems.

Chapter 5

Contour feather moult of Bar-tailed Godwits in New Zealand and the Northern Hemisphere reveals multiple strategies by sex and breeding region

Conklin, J.R. & P.F. Battley
Emu 111: 330–340 (2011)

Abstract

The extreme long-distance migration of Alaskan breeding Bar-tailed Godwits Limosa lapponica baueri *may present severe constraints on annual moult, and high individual variation in plumage and migration timing suggests that multiple strategies by sex and breeding region may exist. We used digital photography of free-living Bar-tailed Godwits to describe the timing and extent of pre-basic and pre-breeding contour feather moults in New Zealand, and used plumage of breeding birds in Alaska to infer the proportion of moults occurring in Alaska and Asia. These data demonstrated that: (1) godwits conducted overlapping pre-alternate and pre-supplemental moults; (2) pre-basic and pre-breeding moults were scheduled differently in relation to southbound and northbound migration respectively; (3) northern and southern Alaskan breeding godwits of each sex were distinguishable by plumage differences throughout the non-breeding season; and (4) males and northern breeders achieved more extensive breeding plumage by spending longer in pre-breeding moult in New Zealand, rather than through faster moult rates or greater investment in moult during migratory stopover in Asia. The existence of a ventral pre-supplemental moult implies that contemporary selection for red breeding plumage overrides older selection for barred alternate plumage. Our use of individual-based data revealed a continuum of annual moult strategies within the population, which may reflect individual differences in any combination of sex, size, migration distance, or breeding location. Even within the highly constrained annual cycle of extreme long-distance migrants, differential selection influences how individuals manage trade-offs among non-breeding activities such as moult, fuelling, and migration.*

Introduction

The scheduling of moult is finely tuned by the balancing of direct and indirect costs of feather replacement, the availability of resources, and competing energetic requirements of other annual activities (Payne 1972, Murphy and King 1991, 1993). Migratory birds face the particular challenge of conducting moult amidst the demands of pre-migratory fuelling, time-critical reproductive efforts on seasonal breeding grounds, and migration itself (Alerstam and Lindström 1990), any of which may be to some extent incompatible with moult. Thus, moult schedules in relation to migration may indicate the relative fitness consequences of feather quality and the strength of selection in different segments of the annual cycle (Holmgren and Hedenström 1995, Barta *et al.* 2008).

Bar-tailed Godwits *Limosa lapponica* achieve extraordinarily high pre-migratory fuel loads (Piersma and Gill 1998, Battley and Piersma 2005), undertake the most extreme non-stop migratory flights yet recorded (9,000–12,000 km; Gill *et al.* 2009, Battley *et al.* 2012), and breed during brief high-latitude summers. Consequently, godwits may face severe time and energy constraints. In addition, their dramatic seasonal changes in plumage (Figure 1 in Jukema and Piersma 2000) present potentially significant conflicts between investment in moult and other mandatory annual tasks.

Bar-tailed Godwits moult from non-breeding to breeding plumage in what appear to be overlapping pre-alternate and pre-supplemental contour feather moults (Piersma and Jukema 1993, Jukema and Piersma 2000). European Bar-tailed Godwits *L. l. taymyrensis* appeared to have three generations of ventral plumage: at the population level, plain (basic) feathers were replaced by barred (alternate) feathers, the extent of which then decreased, particularly in males, as the extent of red (supplemental) feathers increased (Piersma and Jukema 1993). Data from individuals are required to confirm that specific feathers are actually replaced twice in the pre-breeding moult(s). However, it has been proposed that barred feathers constitute the ancestral breeding plumage, whereas red feathers reflect more current selection processes (Jukema and Piersma 2000). If true, this presents a conundrum: if moult is costly, why would godwits retain a redundant and seemingly wasteful moult?

Recently, geographical variation in the Alaskan breeding population of Bar-tailed Godwits *L. l. baueri* has been demonstrated: northern breeders of both sexes were smaller, had more extensive breeding plumage, and migrated later on both northbound and southbound migrations (Chapters 2–3, McCaffery *et al.* 2010). It is not yet clear whether the observed variation constitutes discrete evolutionary units or a latitudinal cline within Alaska. However, coupled with dramatic sexual dimorphism in size and breeding plumage (Chapter 3), this population structure suggests multiple strategies for scheduling of moult in relation to migratory flights. For example, how do males manage a more extensive moult in the non-breeding season, when both sexes must accomplish full flight feather replacement and prepare for equivalent migratory flights? How do northern breeders reconcile a more extensive moult with a longer migration (~1,200 km longer each way) between New Zealand and Alaska? If high-quality breeding plumage increases reproductive success, birds should schedule moult as late as possible before breeding (Holmgren and Hedenström 1995). This predicts a significant portion of moult may occur during the godwits' 4–7 week stopover in Asia before arrival in Alaska (Chapter 2), consistent with observations of continued moult on migration in *L. l. taymyrensis* (Piersma and Jukema 1993). In addition, we expect that moults (both pre-basic and pre-breeding) should be temporally shifted according to breeding phenology, as is migration itself (Chapter 2). However, scheduling of moult in the Alaskan breeding godwit population has never been described at the individual level (but see McCaffery and Gill 2001).

In this study, we use detailed observations of colour-banded Bar-tailed Godwits to describe plumage and moults throughout the non-breeding season in New Zealand, and compare these with plumage of breeding godwits in Alaska (Chapter 3) to estimate the duration and proportion of moults occurring outside New Zealand. We use the resulting data to: (1) present the first individual-based evidence for three feather generations in godwits, and describe the temporal overlap of pre-alternate and pre-supplemental moults; (2) assess whether the timing of moults matches intra-population differences in timing of migration; (3) demonstrate the extent to which geographical patterns in Alaskan breeding plumage correspond to differences upon migratory arrival and departure in New Zealand, and in basic plumage; and (4) determine whether differences in the extent of breeding plumage by sex and breeding region are achieved through strategic differences in timing, rate, or duration of moult. We then discuss the implications of multiple moult strategies within the population for differential selection for plumage and potential trade-offs with other non-breeding activities.

Methods

Fieldwork in New Zealand

We studied plumage and migration timing in a small population of Bar-tailed Godwits (200–280 individuals, ~25% of which were colour-banded) at the Manawatu River estuary, New Zealand (40.47°S, 175.22°E). During two migratory arrival periods (1 September–20 October 2008–2009) we conducted high-tide surveys every 3–4 days (d) to record initial arrival and plumage of marked individuals. During three migratory departure periods (4 March–5 April 2008–2010) we conducted daily surveys to record departure date (details in Chapter 4) and plumage of marked birds. In the intervening summer months (1 January–3 March 2008, 20 October 2008–3 March 2009, 20 October 2009–3 March 2010) we conducted surveys every 4–8 d. During surveys, we digitally photographed marked godwits to enable detailed scoring of plumage later. This resulted in ~18,000 identifiable photographs of 78 birds[1].

Ageing and sexing

Bar-tailed Godwits <2–3 years old were excluded from the study by considering only migratory individuals (young birds do not migrate). Although plumage at departure from New Zealand may be age-dependent (Battley 2006), we included individuals on their first northbound migration (3 males, 1 female).

---

[1] See Figure 6.2 for more details. The number of days per season each individual was photographed was incorrectly reported here in the published version.

Godwits were sexed by culmen length and plumage. Females are larger and have longer bills than males (culmen length >99 mm for females and <90 mm for males), but intermediate birds cannot be sexed by size alone. However, obvious plumage differences at departure (Table 5.1) allowed unambiguous sexing of all individuals of intermediate size (5 males, 3 females).

Moults and plumage scoring

Bar-tailed Godwits have three types of ventral feathers (Piersma and Jukema 1993, Jukema and Piersma 2000): 'basic' (plain whitish), 'alternate' (dark barring on a pale background), and 'supplemental' (plain pale to rusty red). They have two types of dorsal feathers: non-breeding feathers are plain grey with a dark central stripe, whereas breeding feathers are blackish brown with pale or reddish spotting on the edges (McCaffery and Gill 2001). Following the suggestion by Jukema and Piersma (2000) that barred ventral feathers represent a distinct moult, we include red ventral and spotted dorsal feathers in all references to 'breeding plumage' (BP) or 'pre-breeding moult', and consider the barred, alternate plumage separately.

The non-flight feather component of pre-basic moult begins July–August in Alaska, after breeding, and continues on the non-breeding grounds (McCaffery and Gill 2001). The flight feather component of pre-basic moult begins after southbound migration, and is not addressed in this study. Hereafter, all references to 'pre-basic moult' consider only non-flight feathers.

Table 5.1 Evidence for Bar-tailed Godwit contour feather moult outside New Zealand. Breeding data represent godwits in Alaska (Chapter 3). Non-breeding data represent marked godwits at the Manawatu River estuary, New Zealand (arrival = 2008–2009; departure = 2008–2010). Barring scores indicate amount of barring in anterior ventral region. BP scores indicate extent (%) of breeding plumage.

		NZ departure			**Breeding**			**NZ arrival**		
		mean	**range**	***n***	**mean**	**range**	***n***	**mean**	**range**	***n***
Male	**Barring** (0–3)	1.30	0–3	37	1.00	0–3	99			
	Dorsal BP (%)	71.8	30–95	37	92.3	65–100	95	24.3	0–55	30
	Ventral BP (%)	56.9	23–96	37	81.0	33–100	105	19.6	0–43	30
Female	**Barring** (0–3)	1.59	0–3	41	1.74	1–3	74			
	Dorsal BP (%)	20.9	0–80	41	78.8	20–95	70	18.6	0–50	32
	Ventral BP (%)	2.5	0–33	41	37.1	0–68	75	5.3	0–27	32

Using the digital photographs (all scoring done by JRC), we characterised plumage as follows. Barring on the anterior ventral region (belly, flanks, and breast): 0 = no barring visible; 1 = barring on flanks only; 2 = barring on flanks and upper breast; 3 = barring on flanks, breast, and belly. Ventral supplemental plumage: the proportion (5% increments) of red feathers visible against a pale background of basic or alternate feathers on the vent (posterior ventral plumage from leg to vent), breast (anterior ventral, as above) and throat (ventral plumage above breast to chin) regions. We averaged these to create a summary 'ventral' BP score. 'Dorsal' (mantle and scapulars, not including wing coverts) BP: the proportion represented by dark, spotted feathers (5% increments).

Alaskan data

For comparison with plumage in New Zealand, we summarised population-wide data from Alaskan breeding grounds (60–71°N; details in Chapter 3). These data include breeding godwits captured or photographed in the field during May–July 2003–2009 or collected from breeding sites from 1891–2001 and preserved as museum specimens.

Marked birds at the New Zealand site contained similar variation in size (culmen length: males 71–95 mm, females 90–125 mm) evident in the entire population (Chapter 3), and used breeding sites encompassing most of the known Alaskan breeding range (Chapter 2). Therefore, we assumed that New Zealand and Alaskan godwits in this study represent comparable samples.

Analysis

When a marked bird was first observed after arrival, we assigned the midpoint of the period after the previous survey as its arrival date. Consequently, we are confident of individual arrival dates within 2–6 d, and recorded initial BP scores ≤10 d after arrival for nearly all birds; other individuals were omitted from analyses of arrival BP. We are confident of individual departure dates within ±1 d (see Chapter 4) and photographed every individual within 1–5 d of departure.

We defined the completion of pre-basic moult as the latest calendar day on which any worn, unmoulted contour feathers were visible; as the pre-breeding moult is partial, these were not necessarily BP. We defined the initiation of pre-breeding moult as the first day on which dorsal or ventral BP was visible. For birds departing New Zealand with no BP, we used departure date + 8 d (the earliest possible day after arrival in Asia) to represent initiation date of pre-breeding moult. We considered pre-breeding moult suspended when an individual's plumage was first equal to its score at departure. We excluded individuals with >10 d of uncertainty in completion, initiation, or suspension of moult from relevant analyses.

Breeding latitude of New Zealand Bar-tailed Godwits has been strongly linked with migration timing (Chapter 2) and body size (Chapter 3). We assigned the likely Alaskan breeding region (‘north’ or ‘south’ of 64°N) to marked godwits at the Manawatu River estuary (*n* = 78) by the following process. Sixteen godwits were tracked to breeding sites using geolocators (Chapter 2); among these, all birds departing New Zealand by 24 March bred south of 64°N, and five of six that departed after 24 March bred north of 64°N. We therefore divided the remaining 62 godwits into ‘early’ and ‘late’ by average departure date (cutoff: 24 March). Also, northern breeders of both sexes are smaller than southern breeders (Chapter 3), so we divided the birds into ‘small’ and ‘large’ classes using culmen length (cutoffs: males 82 mm, females 108 mm). For 46 birds (74%), the two criteria suggested the same breeding region (small and late departure or large and early departure). When the criteria disagreed, we used the criterion more divergent from the cutoff to assign breeding region (e.g., very large + slightly late = ‘south’). This method may misclassify a small number of individuals.

To test whether data on the phenology of moult and migration were comparable across years, we first ran analyses of variance (ANOVA) for each parameter (sexes separate), using Alaskan region and year as fixed factors (results not shown); there were no significant region × year interactions. Therefore, we averaged values for each individual across available years (1–3 years, depending upon bird and parameter).

Results

Contour feather moult in New Zealand

Upon arrival at the Manawatu River estuary (September–early November), all marked godwits had both worn and new contour feathers (e.g., Figure 5.1a). Most individuals (95–98%) arrived with visible dorsal or ventral BP, the extent of which then decreased after moult resumed within 1–2 weeks of arrival. The last trace of BP was seen 23 September–22 December (sexes similar). Worn dorsal feathers (basic type, or unknown type owing to extreme wear) were often visible 10–35 d after an individual’s last BP disappeared. All birds completed pre-basic moult by late December (Figure 5.2).

Basic plumages (Figure 5.1b) of males and females were similar. All birds were strongly barred on the vent and completely lacked barring on the throat, central breast, and belly. All males and most females had some barring on the flanks (score 1); 29% of females had none (score 0).

Figure 5.1 Plumage of one northern breeding male Bar-tailed Godwit through the non-breeding season in New Zealand. **(a)** 6 October, showing incomplete pre-basic moult; **(b)** 5 January, in basic plumage; **(c)** 29 January, showing increases in ventral barring, dorsal spotted feathers, and red ventral feathers; and **(d)** 1 March, showing further increases in dorsal and ventral breeding plumage, and a decrease in barring.

First increases in ventral barring occurred on all males between 5 January and 9 February (Figure 5.3a). Most females showed increased barring between 9 January and 4 March; 18% showed no increase before leaving New Zealand.

For males, the first increases in ventral barring, dorsal spotting, and red ventral feathers were approximately simultaneous (generally within 1–2 weeks; see Figure 5.1c); first dorsal BP appeared 12 January–28 February (Figure 5.3b) and ventral BP appeared 7 January–17 February (Figure 5.3c). After initial increases, 74% of male barring scores subsequently dropped as ventral BP scores increased (e.g., Figure 5.1c–d). All males appeared to suspend moult before migration: breast plumage scores stopped increasing 5–40 d (mean = 18.5 d) before departure.

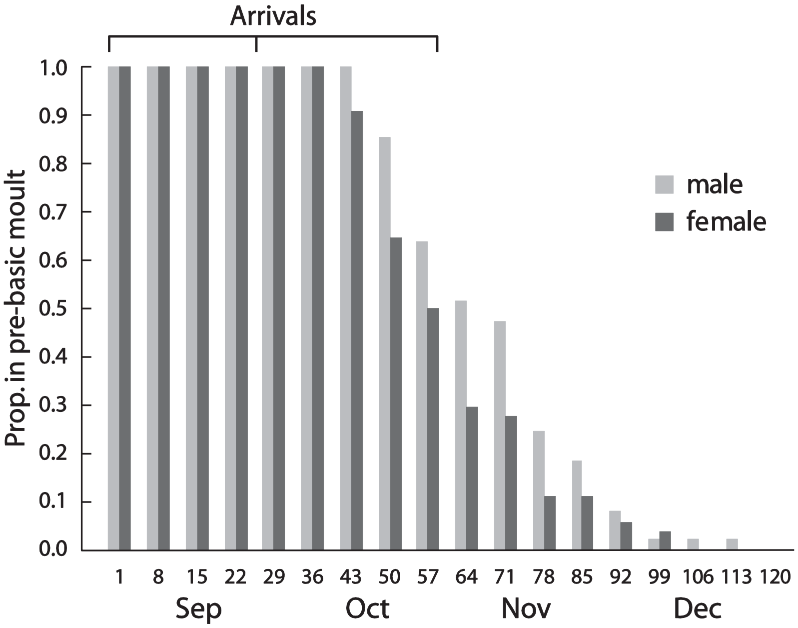

Figure 5.2 Timing of pre-basic contour feather moult of male and female Bar-tailed Godwits in New Zealand, 2008–2009; Day 1 = 1 September, Day 120 = 29 December. Values represent mean proportion of individuals with visible, unmoulted feathers. For migratory arrivals, median and span of dates are indicated.

By contrast, female BP appeared later and not universally. A total of 79% of females gained dorsal BP, which first appeared 30 January–23 March (Figure 5.3b); 41% gained ventral BP, which appeared 23 January–23 March (Figure 5.3c). No female barring scores dropped after a pre-departure peak. Among moulting females, suspension was not uniformly evident: some appeared to add BP as late as 1–5 d before departure.

Evidence for moult beyond New Zealand

Dorsal and ventral BP scores of both sexes were higher in Alaska than at arrival or departure in New Zealand (Table 5.1; Mann–Whitney tests, all $P < 0.001$), indicating that portions of both pre-basic and pre-breeding moult occurred outside of New Zealand. Males had lost 75% of total Alaskan BP before southbound migration, and females had lost 81% of BP. Upon departure from New Zealand, total BP scores of males and females were 74% and 17%, respectively, of Alaskan scores. Barring scores of males were lower in Alaska than at departure from New Zealand ($U_{99,37} = 2271.5$, $Z = 2.34$, $P = 0.02$), but female scores did not differ ($U_{74,41} = 1379.0$, $Z = -0.87$, $P = 0.39$).

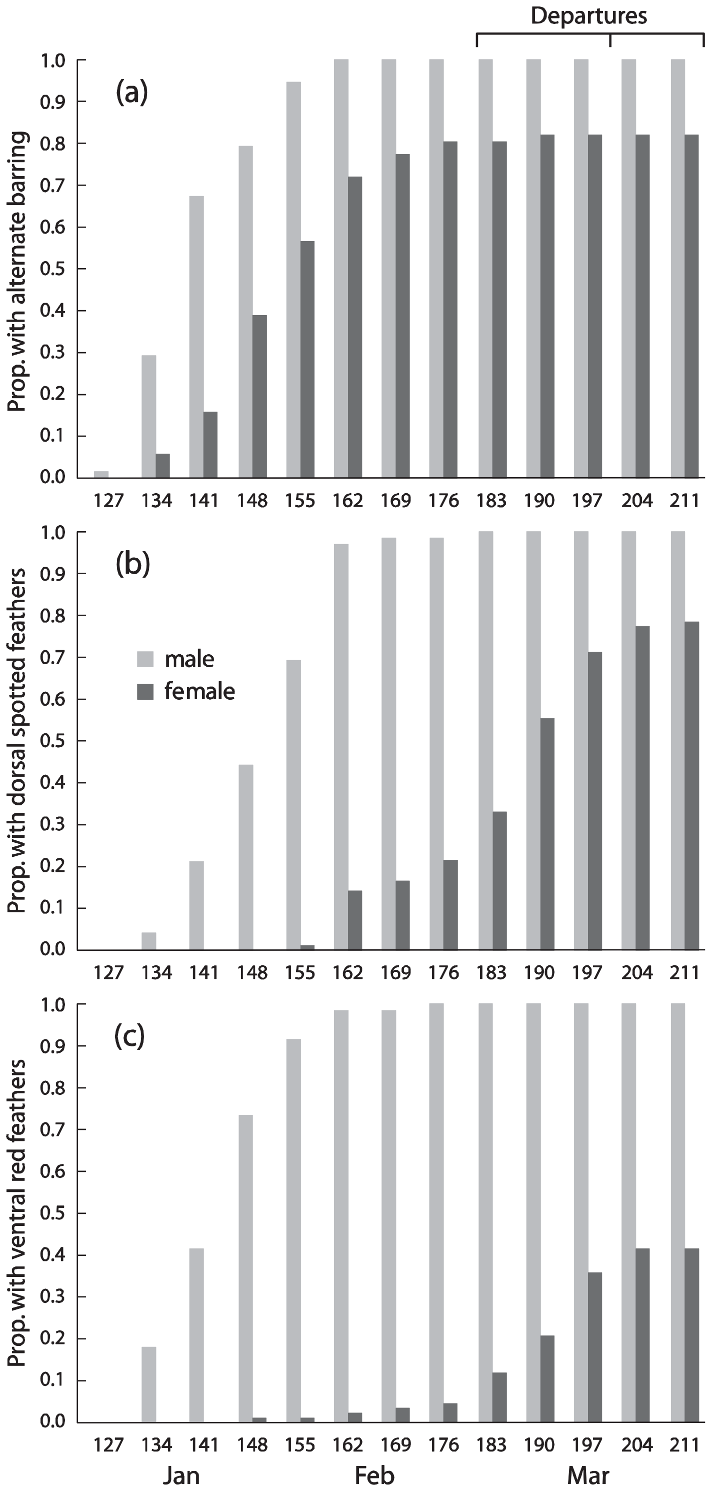

Figure 5.3 Timing of pre-alternate and pre-supplemental contour feather moults of male and female Bar-tailed Godwits in New Zealand, 2008–2010; Day 127 = 5 January, Day 211 = 30 March. Values represent mean proportion of individuals with: **(a)** alternate ventral barring; **(b)** dorsal spotted feathers; and **(c)** ventral red feathers. For migratory departures, median and span of dates are indicated.

Plumage differences by breeding region

Ventral barring scores of northern and southern breeding males were indistinguishable throughout the non-breeding season in New Zealand (Figure 5.4a; all tests $P > 0.20$). For both groups, the peak barring score in New Zealand was greater than the score at departure (Wilcoxon paired tests, north: $W_{19} = 0.0$, $Z = -3.35$, $P = 0.001$; south: $W_{16} = 0.0$, $Z = -3.30$, $P = 0.001$). In Alaska, northern breeding males had less barring than southern breeding males ($U_{68,31} = 1344.5$, $Z = 2.38$, $P = 0.017$).

Northern breeding females had more barring than southern breeding females at every stage in New Zealand and Alaska (Figure 5.4b; Basic: $U_{11,23} = 71.5$, $Z = -2.56$, $P = 0.010$; NZ peak and departure: $U_{15,26} = 56.0$, $Z = -4.00$, $P < 0.001$; Breed: $U_{54,20} = 324.0$, $Z = -2.85$, $P = 0.004$). All godwits with barring scores of 0 in basic plumage were southern breeding females.

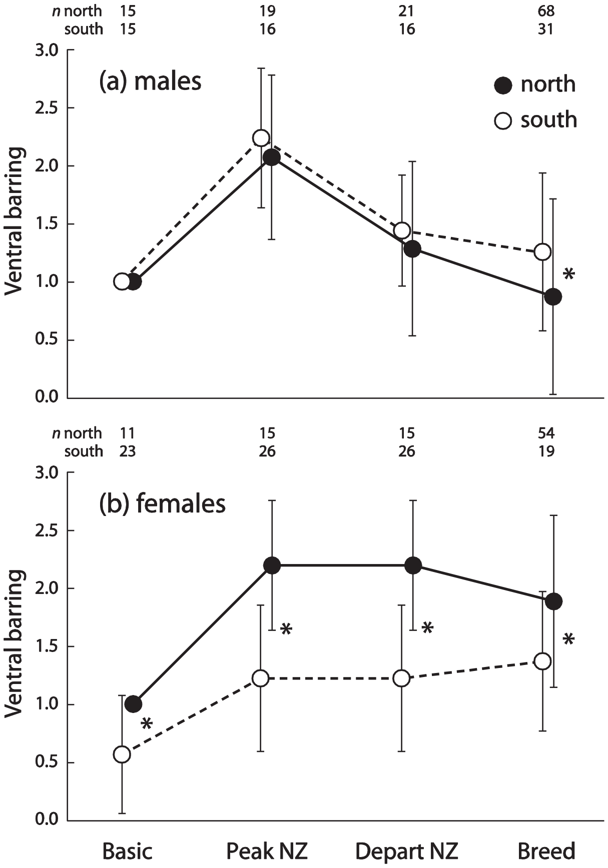

Figure 5.4 Change in ventral barring (score 0–3; data are mean score ± 1 SD) of **(a)** male and **(b)** female Bar-tailed Godwits from northern and southern Alaskan breeding regions (north or south of 64°N). On *x*-axis, Basic indicates full basic plumage in mid-December, Peak NZ indicates highest score achieved before departure from New Zealand, Depart NZ indicates plumage at departure, and Breed indicates full breeding plumage in Alaska. Cohorts are offset horizontally for clarity. Asterisks indicate significant north–south differences.

Northern breeders of both sexes always had more extensive BP than southern breeders (Figure 5.5). On departure from New Zealand, northern and southern breeding males differed in ventral BP ($U_{21,16} = 87.0$, $Z = -2.48$, $P = 0.012$) but not dorsal BP ($U_{21,16} = 113.5$, $Z = -1.67$, $P = 0.10$). In Alaska, male cohorts differed in both dorsal BP ($U_{65,30} = 566.5$, $Z = -3.42$, $P = 0.001$) and ventral BP ($U_{71,34} = 388.5$, $Z = -5.61$, $P < 0.001$). On arrival in New Zealand, males differed in dorsal BP ($U_{16,14} = 64.5$, $Z = -1.99$, $P = 0.047$) but not ventral BP ($U_{16,14} = 85.0$, $Z = -1.13$, $P = 0.28$).

Northern and southern breeding females were always distinguishable by both dorsal BP (NZ departure: $U_{15,26} = 93.0$, $Z = -2.77$, $P = 0.006$; breeding: $U_{52,18} = 306.5$, $Z = -2.21$, $P = 0.027$; NZ arrival: $U_{10,22} = 47.0$, $Z = -2.57$, $P = 0.010$) and ventral BP (NZ departure: $U_{15,26} = 90.0$, $Z = -3.17$, $P = 0.002$; breeding: $U_{54,21} = 319.5$, $Z = -2.92$, $P = 0.003$; NZ arrival: $U_{10,22} = 18.0$, $Z = -3.78$, $P < 0.001$).

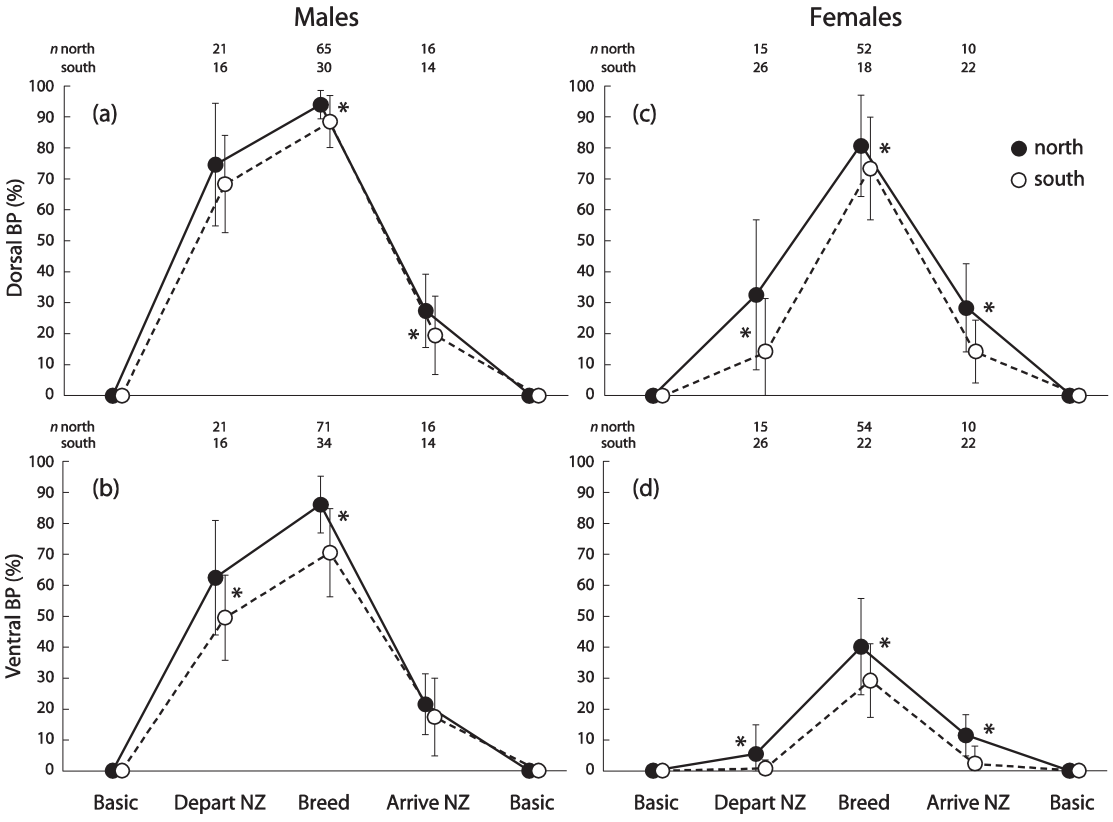

Figure 5.5 Change in breeding plumage (BP): **(a)** male dorsal; **(b)** male ventral; **(c)** female dorsal; and **(d)** female ventral breeding plumage of Bar-tailed Godwits from northern and southern Alaskan breeding regions (north or south of 64°N). Data are mean % ± 1 SD. See Figure 5.4 for explanation of *x*-axis categories. Cohorts are offset horizontally for clarity. Asterisks indicate significant north–south differences.

Moult schedules by breeding region

Northern breeding godwits of both sexes arrived in New Zealand later than southern breeders (Table 5.2). On average, northern breeding females and all males completed pre-basic moult 40–45 d after arrival, compared with 33.5 d for southern breeding females.

Both male cohorts initiated pre-breeding moult ca. 21 January and suspended moult ~18 d before departure; thus, northern breeding males spent longer in moult owing to their later departure (Table 5.2). Northern breeding males moulted 68.6% of their contour feathers (dorsal and ventral BP combined; Figure 5.5a–b) in 45.9 d, for a mean moult rate of 1.49% per day. Southern breeding males moulted 58.9% of their contour feathers in 36.1 d, a rate of 1.63% per day. These moult rates did not differ ($t_{18,16} = 1.52$, df = 32, $P = 0.07$); the overall mean rate for males was 1.57 ± SD 0.42% per day.

Southern breeding females initiated pre-breeding moult ca. 8 March, just 9 d before departure (Table 5.2). Northern breeding females began moult ca. 2 March, 25 d before departure. For females, the brief time in moult and uncertainty regarding suspension of moult precluded the calculation of useful moult rates. Assuming the moult rate observed in males (1.6% per day), northern breeding females spent on average 12 d in moult to reach departure BP, and southern breeding females spent just 5 d (Table 5.2).

Projected pre-breeding moult in Asia

During staging in Asia, northern breeding males must increase BP from 69% (New Zealand departure) to 90% (breeding; Figure 5.5). At the observed New Zealand moult rate (1.6% per day), this would require ~13 d. Southern breeding males similarly require 13 d to increase from 59 to 79%. Assuming the male moult rate, northern breeding females require 26 d (from 19 to 61%), compared with 27 d for southern breeding females (from 8 to 51%). Thus, total investment in pre-breeding moult is 59 d for northern breeding males, 49 d for southern breeding males, 38 d for northern breeding females, and 32 d for southern breeding females (Figure 5.6).

Table 5.2 Moult and migration schedules of godwits during non-breeding season in New Zealand. Arrival/pre-basic moult = 2008–2009; pre-breeding moult/departure = 2008–2010. For dates, day 1 = 1 Sep; day 211 = 30 Mar. North = presumed Alaska breeding region >64°N; south = <64°N. Asterisks indicate significant north–south differences.

			South			North						
		unit	**mean**	**SD**	***n***	**mean**	**SD**	***n***	***t***	**df**	***P***	
Male	**NZ arrival**	date	22.6	4.2	15	29.9	4.4	17	4.80	30	< 0.001	*
	End pre-basic moult	date	67.4	14.6	14	70.8	13.8	16	0.64	26	0.53	
	NZ pre-basic moult	days	44.8	15.2	14	41.6	13.1	14	0.59	26	0.56	
	Start pre-breeding moult	date	141.8	7.9	16	144.1	7.3	18	0.88	32	0.39	
	Suspend pre-breeding moult	date	178.1	7.9	16	190.4	8.0	19	4.56	33	< 0.001	*
	NZ departure	date	197.1	4.1	16	208.3	3.1	19	9.07	33	< 0.001	*
	NZ pre-breeding moult	days	36.1	8.1	16	45.9	7.9	18	3.56	32	0.001	*
Female	**NZ arrival**	date	21.0	11.2	22	33.4	12.2	10	2.81	30	0.009	*
	End pre-basic moult	date	52.6	9.5	20	73.4	16.3	9	4.35	27	< 0.001	*
	NZ pre-basic moult	days	33.5	8.2	20	40.1	6.5	9	2.12	27	0.043	*
	Start pre-breeding moult	date	188.5	15.8	26	182.1	12.5	12	1.24	36	0.22	
	NZ departure	date	197.8	4.4	26	207.9	2.9	15	8.03	39	< 0.001	*
	NZ pre-breeding moult [A]	days	4.7	5.9	26	11.9	9.2	15	3.07	39	0.004	*

[A] Calculated using male moult rate 1.6%/d

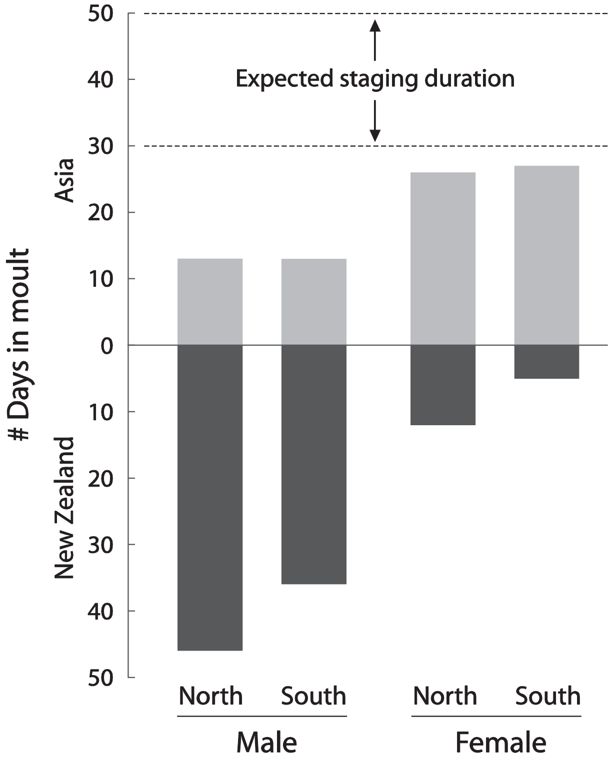

Figure 5.6 Estimated average duration of Bar-tailed Godwit pre-breeding moult occurring in New Zealand and Asia by sex and Alaskan breeding region (north or south of 64°N). For reference, expected staging duration in Asia (30–50 days; Chapter 2) is indicated.

Discussion

Evidence for pre-supplemental moult

Our study provides the first direct evidence that individual godwits replace some ventral feathers twice during pre-breeding moult, confirming that the barred and plain-red feathers represent distinct plumages (alternate and supplemental, respectively; Humphrey and Parkes 1959). This was strongly suggested by a population-level decline of (recently grown) barred feathers of male European Bar-tailed Godwits *L. l. taymyrensis* during northbound stopover in the Netherlands (Piersma and Jukema 1993), but population turnover during the study precluded strong inferences regarding individual moult. Furthermore, hormonal changes during moult potentially produce colour differences between feathers grown at different stages of the same moult (Howell 2010). Our photographic monitoring of individuals throughout moult provided many specific examples of red feathers replacing barred feathers that were just 3–5 weeks old (e.g., Figure 5.1b–d).

This rapid replacement of alternate feathers resulted in pre-departure decreases in barring of most males, and lower scores in Alaska testify to additional loss of alternate feathers in Asia. In females, the extent of pre-supplemental moult was insufficient to cause significant decreases in barring before departure from New Zealand or arrival in Alaska. However, some females may conduct additional pre-alternate moult in Asia: 7% of females departed New Zealand with a barring score of 0, whereas all females in Alaska had some degree of barring.

The red ventral feathers of males are generally darker than those of females (Piersma and Jukema 1993, J. Conklin pers. obs.), and males perform an earlier and more extensive pre-supplemental moult than females. By contrast, the barred feathers of males and females are indistinguishable, and the extent and timing of pre-alternate moult were also similar. This supports the view that historical selection for alternate plumage was similar for the sexes (promoting equivalent crypsis during shared parental duties), whereas pre-supplemental plumage reflects current sexual selection acting more strongly upon males, as in Ruffs *Philomachus pugnax* (Jukema and Piersma 2000). Because the ventral breeding 'aspect' of female Bar-tailed Godwits contains significant contributions from two moults, both may be under current selection. However, breeding males retain little alternate barring, and so this moult may be an evolutionary artefact which is insufficiently costly to be maladaptive. If barred feathers represent the ancestral breeding plumage within Scolopacidae, other species with both barred and red ventral feathers (e.g., Curlew Sandpiper *Calidris ferruginea*, dowitchers *Limnodromus* spp.) may undergo pre-supplemental moults that have yet to be described.

It is intriguing that increases in the extent of ventral barred, dorsal spotted, and ventral red feathers occurred approximately synchronously in males, whereas the three types were staggered in females (Figure 5.3). This means that initiation of dorsal and ventral pre-alternate moults are temporally decoupled, by ~3–5 weeks, in females but not in males. Another consequence is that temporal overlap of pre-alternate and pre-supplemental moults differs substantially between the sexes. Because most male godwits begin the two moults simultaneously, it appears that ventral pre-supplemental moult replaces some basic feathers and some alternate feathers. Presumably, selection for early timing of pre-supplemental moult in males has led to the effective loss of pre-alternate moult in some follicles, which 'skip' directly from plain to red feathers without an intervening barred feather. As discussed by Battley *et al*. (2006) with regard to dorsal pre-supplemental moult in Great Knots *Calidris tenuirostris*, this creates an inconsistency within the Humphrey and Parkes (1959) nomenclature, in which follicles undergoing just two moults in the definitive cycle can only produce 'basic' and 'alternate' plumage. Because pre-alternate moult appears partial in both sexes, certain follicles may skip directly from basic to supplemental plumage in females as well, but we have no conclusive evidence of this. Regardless, it seems sensible to refer to the red ventral feathering of godwits as supplemental plumage, irrespective of the number of moults undertaken by individual follicles. Thus far, there is no evidence that godwits perform a dorsal pre-supplemental moult.

Are timing of moult and migration linked?

Because the timing of both northbound and southbound migration were 2–4 weeks later in northern breeding Bar-tailed Godwits tracked with geolocators (Chapter 2), we hypothesised that other annual events may be shifted temporally to accommodate individually optimised migration schedules (e.g., Buehler and Piersma 2008). This predicts that northern breeders should complete pre-basic moult and initiate pre-breeding moult later than southern breeders. However, evidence here does not uniformly support this. On average, northern breeding males completed pre-basic moult and initiated pre-breeding moult later than southern breeding males by ~3 d, which was less than differences in migration timing and not statistically significant. For females, the prediction was upheld for completion of pre-basic moult, but not for initiation of pre-breeding moult.

Achieving breeding plumage has an effective deadline (arrival on breeding grounds) and, therefore, timing of pre-breeding moult should be closely linked to migration timing (Holmgren and Hedenström 1995). However, geographical breeding cohorts of godwits differed substantially in extent of BP and, consequently, in the duration of pre-breeding moult, obscuring any simple relationship between moult initiation and migratory departure.

Because pre-basic is a complete moult for all godwits, we do not expect systematic differences in moult duration by sex or breeding region. Therefore, variation in completion of pre-basic moult is likely to mirror variation in onset of moult, which may be triggered by hormonal changes associated with cessation of breeding activity (Hahn *et al.* 1992, Dawson 2006). Accordingly, we found no evidence of active moult on the breeding grounds in Alaska (May–early August; n = 77 captures or specimens); godwits appear to initiate pre-basic moult on post-breeding staging grounds (McCaffery and Gill 2001). Earlier thawing of southern Alaskan breeding sites allows clutch initiation 2–4 weeks earlier than northern breeding sites (Chapter 2), and godwits caring for young through fledging may spend 3–6 weeks longer on breeding sites than those that fail during incubation. Thus, the timing of pre-basic moult reflects both breeding-site phenology, which may vary little annually, and duration of breeding investment, which should vary substantially among individuals and years. This explains why completion of pre-basic moult varied by 10–11 weeks between individuals in our study.

Bar-tailed Godwits tracked with geolocators moved from breeding sites to staging sites 40–88 days before departing Alaska (J. Conklin and P. Battley unpubl. data). Birds in this study had completed ~50–90% of pre-basic moult upon arrival in New Zealand, and finished moulting 33–45 days after arrival. Godwits suspend moult for several days before migratory flights, perhaps to prioritise fuel accumulation and preparation of flight muscles and internal organs for migratory condition (Piersma *et al.* 1999, Landys-Ciannelli *et al.* 2003). Upon arrival, they may invest primarily in recovery from long-distance flights before resuming moult (Piersma and Jukema 1993). Accounting for these periods of suspension, the estimated total duration of pre-basic moult is ~70–90 days.

Are breeding cohorts distinguishable in New Zealand?

The plumage of Bar-tailed Godwits varies across the latitude of the Alaskan breeding range (59–71°N): the extent of male breeding plumage increases with latitude, whereas the reddest females occur ~66°N (Chapter 3). This population structure is not maintained in the non-breeding season, as godwits from all Alaskan regions mix freely at New Zealand sites. By assigning individuals to probable breeding region based on size and migration timing (which also vary geographically), we asked whether cohorts were distinguishable by plumage in the non-breeding season. In New Zealand, northern breeders of both sexes had more dorsal and ventral breeding plumage than southern breeders at both arrival and departure. Because investment in moult in Asia was similar for cohorts within each sex, plumage differences upon departure from New Zealand were similar to those found in Alaska.

In Alaska, alternate barring of females increases with latitude (Chapter 3). Males, however, do not show this pattern, probably owing to their more extensive replacement of barred feathers during pre-supplemental moult. We hypothesised that the ancestral alternate plumage occurred in a north–south cline, before the evolution of the pre-supplemental moult. Thus, the extent of barring at the onset of pre-supplemental moult in present-day godwits may indicate breeding region. This could not be adequately tested for males, because pre-alternate and pre-supplemental moults were nearly simultaneous rather than sequential. However, the prediction held for females: north–south differences in barring were greatest in New Zealand, before substantial pre-supplemental moult in Asia.

We were surprised to find differences among females in *basic* plumage: all birds with barring scores of 0 were southern females. The drab basic plumage of godwits may provide crypsis in tidal estuaries (Ferns 2003), with barring on the flanks and vent serving to enhance countershading (Rowland 2009). However, because the population is not geographically structured year-round, plumage differences among breeding cohorts are unlikely to have functional significance in New Zealand. It is possible that variation in basic plumage barring simply represents a non-adaptive carry-over from alternate plumage.

Moult strategies by sex and breeding region

The more extensive BP of northern breeders was not the result of faster moult rates in New Zealand or greater investment in moult in Asia. Rather, northern birds of both sexes achieved greater BP than southern birds by spending ~7–10 days longer in pre-breeding moult in New Zealand. All cohorts required moult in Asia to reach expected Alaskan plumage, but the extent of this additional moult was nearly identical for cohorts within each sex, despite evidence that the duration of stopovers in Asia increases with breeding latitude (Chapter 2).

Our findings confirm previous indications of distinct strategies of moult and migration in New Zealand godwits (Battley and Piersma 2005). In early March, non-moulting males were larger and fatter, and had lower BP scores and larger testes than those in active moult. Godwits were collected between the average dates of moult suspension for southern (25 February) and northern (9 March) breeding males in our study. Thus, the inference by Battley and Piersma (2005) that non-moulting birds were preparing for earlier migration was correct: these were clearly southern males, which are larger (Chapter 3) and migrate earlier and with less BP than northern males.

Because we calculated moult in Asia from cohort means, the proportion of individuals conducting additional moult after New Zealand departure is unclear. In the Netherlands, moulting male godwits were redder and heavier than non-moulting males, suggesting that only ‘high-quality’ birds could afford to invest in moult during migration (Piersma and Jukema 1993). This predicts greater plumage variation in Alaska than at New Zealand departure, because differential moult in Asia should magnify individual differences. Our data contradict this: variation at departure from New Zealand was generally greater than in Alaska. The lowest BP scores in Alaska were greater than the lowest scores at New Zealand departure, indicating that the palest birds moulted in Asia. Conversely, some males departed New Zealand with BP scores very close to the greatest observed in Alaska, and thus could add little to their plumage in Asia.

If plumage quality influences reproductive success, godwits should complete pre-breeding moult at the latest opportunity (Asia) to ensure that not all breeding feathers must endure flights of 16,000–18,000 km and two months of migration wear before serving their ultimate function (Holmgren and Hedenström 1995). Consistent with this, 75% of female pre-breeding moult occurred in Asia, and some southern females did not moult in New Zealand at all. Godwits spend 30–50 days staging in Asia (mean = 40 d, sexes similar; Chapter 2), and presumably suspend moult at both ends of their stay. Thus, 26–27 days of moult in Asia, as we have projected, may approach the maximum achievable by females, without adopting faster moult rates than observed in New Zealand.

Time spent in Asia is insufficient for a male's entire pre-breeding moult (Figure 5.3), which explains why all males initiated moult in New Zealand. However, males performed only half as much moult in Asia as females, and so apparently did not moult as late as possible. This may suggest that females are better suited to moult during migration, owing to greater flight or fuelling efficiency. Alternatively, if moulting conditions were more reliable in New Zealand than in Asia, males may simply follow a more conservative moult strategy; that is, males are unwilling to 'risk' leaving a large proportion of moult until the latest opportunity, whereas females face lower costs of this risk. This assumes that godwits respond to poor conditions during the northbound flight or at staging sites by increasing investment in thermoregulation and fuelling at the expense of moult. A consequence would be annual variation in plumage in Alaska, potentially population-wide and more extreme in females; there are currently no data to address this.

The existence of a pre-supplemental moult strongly implies contemporary sexual or natural selection for plumage in Alaska. Presumably, sexual differences in plumage reflect the greater role of males in competition for mates and territories (McCaffery and Gill 2001), and north–south differences result from geographical variation in habitat or competition for mates. It is significant that females invested disproportionately in dorsal BP over ventral BP in both New Zealand and Asia; shared incubation requires both sexes to be cryptic, and so selection for male and female plumage should be more similar for dorsal than ventral plumage. Hypothetically, relaxed selection for ventral BP may 'free' females and southern breeders to conduct slower, higher quality flight feather moults (Dawson *et al.* 2000, Serra 2001) or migrate with greater fuel stores, at the expense of pre-breeding moult. Conversely, prioritisation of ventral BP by males and northern breeders may constrain their investment in wing moult or fuelling.

An alternative view is that plumage differences among godwits arise from energetic constraints on moult imposed by body size (Hedenström 2006). This simple, but not mutually exclusive, hypothesis requires no differential selection for plumage in Alaska. Ranked smallest to largest (northern males, southern males, northern females, southern females), the cohorts showed decreases in both duration and proportion of pre-breeding moult in New Zealand. Because pre-migratory fuel stores scale proportionally with body size (Battley and Piersma 2005), larger birds must accumulate a greater absolute fuel mass, while maintaining a greater non-breeding mass. In addition, they must grow a greater mass of both contour and flight feathers (Hedenström 2006, Rohwer *et al.* 2009). If larger birds were consequently limited in time or energy available for pre-breeding moult in New Zealand, it would predict the relative departure plumages that we observed. This hypothesis may be tested by comparing rates of pre-migratory mass gain or duration of primary feather moults by sex and body size, and by examining the extent of overlap in the timing of moults and fuelling.

Most current knowledge of moult strategies derives from population-level studies, in which individuals contribute but one data point, owing to the difficulty of capturing or otherwise sampling free-living birds multiple times during a season. Although adequate to describe general patterns of moult, this approach can mask considerable variation of ecological interest. Our use of repeatedly sampled individuals revealed a continuum of annual moult strategies within the New Zealand population of Bar-tailed Godwits, which may reflect individual differences in sex, size, migration distance, or breeding location, or some combination of these. Because successive life-history stages of long-distance migrants may be inextricably linked, and differential selection may occur at any stage of the annual cycle, true understanding of how individuals manage trade-offs between moult and other non-breeding activities may require a year-round individual approach.

Chapter 6

Carry-over effects and compensation: late arrival on non-breeding grounds affects wing moult but not plumage or schedules of departing Bar-tailed Godwits

Conklin, J.R. & P.F. Battley
Journal of Avian Biology in press (2012)
Published online May 2012, doi: 10.1111/j.1600-048X.2012.05606.x

Abstract

In the annual cycle of migratory birds, temporal and energetic constraints can lead to carry-over effects, in which performance in one life-history stage affects later stages. Bar-tailed Godwits Limosa lapponica baueri, *which achieve remarkably high pre-migratory fuel loads, undertake the longest non-stop migratory flights yet recorded, and breed during brief high-latitude summers, may be particularly vulnerable to persistent effects of disruptions to their rigidly-timed annual routines. Using three years of non-breeding data in New Zealand, we asked how arrival timing after a non-stop flight from Alaska (>11,000 km) affected an individual godwit's performance in subsequent flight feather moult, contour feather moults, and migratory departure. Late arrival led to later wing moult, but godwits partially compensated for delayed moult initiation by increasing moult rate and decreasing the total duration of moult. Delays in arrival and wing moult up to 34–37 days had no apparent effect on an individual's migratory departure or extent of breeding plumage at departure, both of which were extraordinarily consistent between years. Thus, 'errors' in timing early in the non-breeding season were essentially corrected in New Zealand prior to spring migration. Variation in migration timing also had no apparent effect on an individual's likelihood of returning the following season. The Bar-tailed Godwits' rigid maintenance of plumage and spring migration schedules, coupled with high annual survival, imply a surprising degree of flexibility to address unforeseen circumstances in the annual cycle.*

Introduction

The annual cycles of birds are organised into distinct, sequential life-history stages, adapted to promote reproduction and survival in the context of likely environmental conditions (McNamara and Houston 2008). With greater environmental variation, the number of adaptive life-history stages (e.g., migration, distinct breeding and non-breeding plumages) increases, but flexibility in the scheduling of each stage necessarily decreases (Wingfield 2008). Some successive stages may be temporally distinct, due to energetic or logistical incompatibility (e.g., reproduction and migration) or because they are under related endocrine control (Jacobs and Wingfield 2000). For example, hormonal changes associated with the cessation of breeding appear to have a role in triggering the initiation of pre-basic moult (Dawson 2006). Other stages may show some extent of regular or facultative overlap (e.g., pre-basic moult and pre-migratory fat deposition; Lindström *et al.* 1994). With greater time and energy constraints, there is increasing potential for circumstances experienced in one life-history stage to affect performance in subsequent stages (Harrison *et al.* 2011). These carry-over effects can occur within (Earnst 1992) or across seasons (Marra *et al.* 1998), and may profoundly influence individual fitness and consequently population dynamics (Norris 2005).

The non-breeding season of a migratory bird is composed of a series of stages scheduled to facilitate travel to and from its wintering quarters and preparation for the following breeding season. These stages include: (1) replacement of breeding plumage with non-breeding plumage; (2) replacement of flight feathers; (3) fuelling and conducting post-breeding (autumn) migration; (4) replacement of non-breeding plumage with breeding plumage; and (5) fuelling and conducting pre-breeding (spring) migration. Within and among species, there exist many strategies for the scheduling of moults relative to migrations, depending on resource availability, costs of moult, and benefits of feather quality, any of which may vary seasonally (Holmgren and Hedenström 1995, Barta *et al.* 2008). Long-distance migrants face the two-fold challenge of scheduling annual events according to highly seasonal temperate or arctic environments, while meeting the considerable demands of travel itself, such as large fuel stores and high-quality flight feathers (Alerstam and Lindström 1990). These constraints may lead to energetic or temporal bottlenecks in the annual cycle (Buehler and Piersma 2008), making long-distance migrants particularly susceptible to carry-over effects among successive life-history stages. For example, if the non-breeding season is very tightly scheduled, a delay early in the season (e.g., a weather-related delay in arrival on wintering grounds) may cascade through later stages to affect performance during the return migration to breeding grounds.

The annual routine of New Zealand Bar-tailed Godwits *Limosa lapponica baueri* features the longest and second-longest non-stop migratory flights yet recorded (>11,000 km from Alaska to New Zealand in autumn and 9,000–10,000 km from New Zealand to staging sites in the Yellow Sea in spring (Gill *et al.* 2009, Battley *et al.* 2012). At post-breeding fuelling sites in southwestern Alaska (July–September), Bar-tailed Godwits (hereafter, ‘godwits’) initiate the contour feather component of pre-basic moult, performing ~50–90% of the transition to winter plumage before suspending moult for the southward migration (Chapter 5). After arrival on non-breeding grounds (September–October), godwits resume the pre-basic contour moult and initiate flight feather moult, which occupies more than half of the approximately six months godwits spend in New Zealand (McCaffery and Gill 2001). During January–March, godwits fuel for spring migration and initiate the moult into breeding plumage (Chapter 5). This moult is also suspended for migration, and is completed on staging grounds in the Yellow Sea.

Despite the challenges presented by their extraordinary flights and the fuel stores required to conduct them (Piersma and Gill 1998, Battley and Piersma 2005), individual godwits departing New Zealand on spring migration show remarkable annual consistency in both date of departure and extent of breeding plumage (Battley 2006, Chapter 4). This suggests that 'errors' in the timing of prior events that may affect spring departure are either inconsequential or corrected prior to migration. Godwits could compensate for delays through faster moult rates, greater temporal overlap among moults and fuelling, or decreased body condition at departure.

In this study, we assess the consequences of timing of arrival in New Zealand for Bar-tailed Godwits throughout the non-breeding season. To do this, we make the first description of timing and duration of primary feather moult at the individual level for a long-distance migrant, using detailed photographic documentation of free-living colour-banded godwits across three non-breeding seasons. Combining these data with migration and contour feather moult schedules of the same individuals (Chapters 4–5), we ask whether annual variation in an individual's arrival in New Zealand affects its subsequent timing of contour or flight feather moults, extent of breeding plumage on departure, or timing of departure on spring migration. In addition, we ask whether delays in migration in one season are related to an individual's likelihood of survival to the following non-breeding season.

Methods

Data collection

During three non-breeding seasons (Year 1 = January–April 2008, Year 2 = September 2008–April 2009, and Year 3 = September 2009–April 2010), we studied plumage and migration timing in a small, site-faithful population of Bar-tailed Godwits (200–280 birds) at the Manawatu River estuary, New Zealand (40.47°S, 175.22°E). Data presented in this study are derived from 77 individually colour-banded godwits (42 female, 35 male); 63 of these were present in Year 1, 62 in Year 2, and 58 in Year 3. We conducted high-tide surveys every 3–4 days (d) during migratory arrival (1 September–20 October), daily during migratory departure (4 March–5 April), and every 4–8 d during the intervening summer months (21 October–3 March). During surveys, we digitally photographed marked godwits, where possible depicting the state of primary feather moult (i.e., flying and wing stretching; Figure 6.1) and extent of breeding plumage; this resulted in 17,535 photographs in which one of 77 individuals was identifiable (Figure 6.2). For purposes of geolocator deployment and retrieval, we conducted three cannon-net captures during the study; for all captured godwits, we scored primary moult in the hand (19 individuals in March 2008, 44 in October 2008, and 39 in November 2009). From a combination of photographs and direct observation, we determined timing of migratory arrival, completion of pre-basic non-flight feather moult (in this paper, 'pre-basic

Figure 6.1 Examples of photographs used to evaluate state of primary feather moult. **(a)** Moult score 2; **(b)** score 34; and **(c)** score 47; see text for scoring method.

moult' refers to contour feathers only; flight feather moult is considered separately), initiation of 'pre-breeding moult' (which occurs in overlapping pre-alternate and pre-supplemental contour feather moults; Chapter 5), and migratory departure, as well as extent of breeding plumage at departure, for each individual (not all data were available for every bird each year). Migratory departures were observed directly or estimated to within 1 d (Chapter 4), and other timing parameters were estimated to within approximately 1–6 d (Chapter 5). Extent of breeding plumage ('BP') was scored as the proportion (%) of ventral and dorsal basic

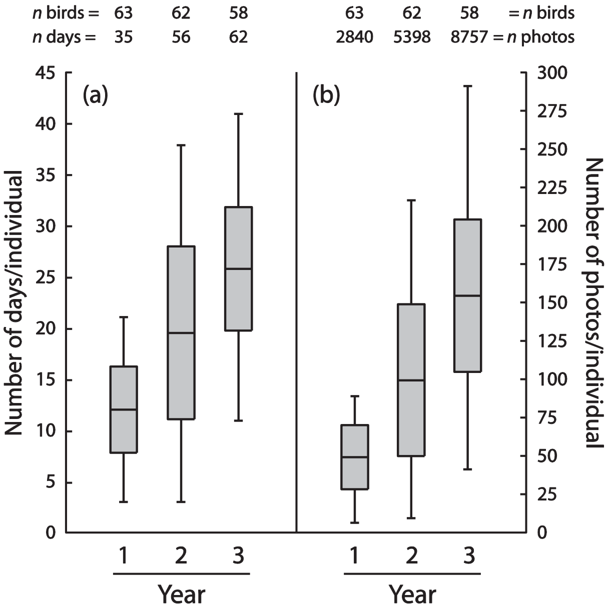

Figure 6.2 Photographic data used for assessment of primary and contour feather moult. **(a)** Number of days each individual was photographed per season. **(b)** Total number of photographs of each individual per season. Box plots indicate mean ±1 standard deviation; whiskers indicate entire range of values.

plumage feathers that had been replaced by breeding plumage; this was scored 1–5 d before departure for all individuals (details in Chapter 5). During the following non-breeding season (Year 4 = September 2010–April 2011), we monitored the site regularly to determine the presence/absence of marked individuals, but moult was not studied.

Ageing and sexing

For all marked godwits, we measured exposed culmen (mm) and maximum flattened wing chord (mm) at the time of initial capture (*n* = 26 in 2006, 21 in 2007, 28 in 2008, and 2 in 2009). Most godwits (*n* = 68) were sexed by culmen length (>99 mm = female; <90 mm = male), but intermediate birds (90–99 mm) cannot be sexed by this measure. However, strong sexual dimorphism in plumage before departure from New Zealand (Chapter 5) allowed unambiguous sexing of the remaining individuals (*n* = 4 females, 5 males). Non-migrating individuals (aged <2–3 yrs) and those known to be making their first northbound migration were excluded from the study.

Scoring of primary feather moult

We collected 1069 in-moult records (83 in-hand, 986 from photographs) of 74 individual godwits across three seasons (44 in Year 1, 64 in Year 2, and 58 in Year 3; Figure 6.3). We scored primary moult according to the method of Newton (1966; illustrated in Ginn and Melville 1983): each of 10 primaries (denoted P1 through P10, from innermost to outermost) was assigned a score 0–5 (0 = old, unmoulted feather; 5 = fully grown new feather), for a total moult score of 0–50. Godwits moult their primaries successively from P1 outward to P10. In mid-moult, there are typically three feathers growing simultaneously, in predictable relative stages of growth, whereas only 1–2 feathers are growing near the beginning and end of moult. In 439 of 488 (90%) cases where both of an individual's wings could be evaluated, state of wing moult appeared symmetrical. Therefore, we assumed symmetrical moult when only one wing was scored. In cases of observed asymmetry, we scored each wing separately (mean score difference = 1.94, range = 1–6) and averaged these for the individual's moult score.

For approximately 67% of in-moult records, 1–3 growing feathers were obstructed, out of focus, or not visible beyond the length of adjacent coverts in the photographs, and thus could not be scored directly. In these cases, we reconstructed scores for the unviewed feathers based on the godwits' very predictable progression of moult, using in-hand scores from historical captures of adult godwits in New Zealand (1983–2008, *n* = 1,434; P. Battley and A. Riegen unpubl. data) as reference[1]. For example, the bird in Figure 6.1a was scored ??00000000 (P1–10, respectively) from the photograph. Godwits typically initiate primary moult by

---

[1] See Appendix 4 for details.

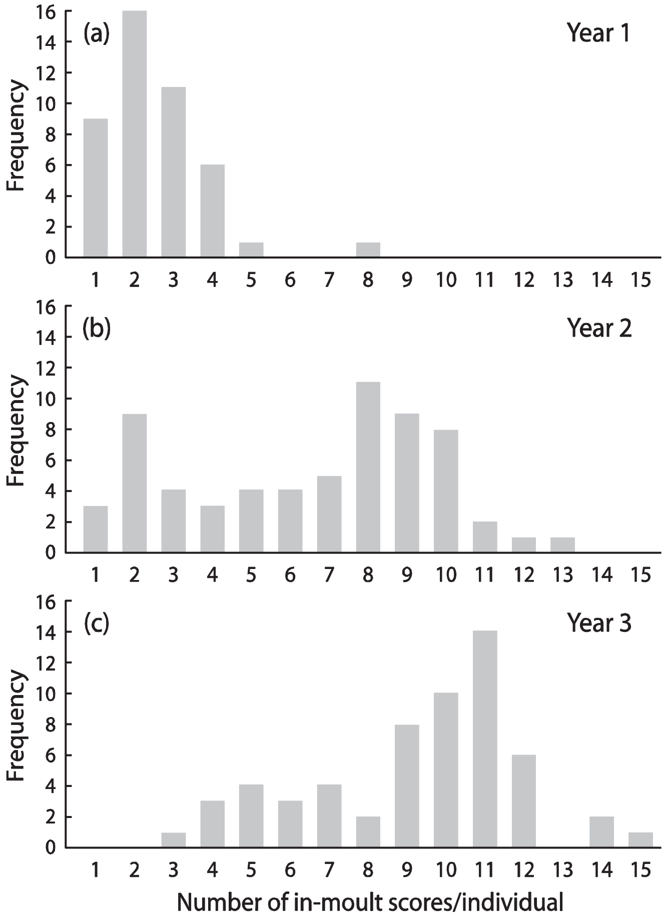

Figure 6.3 Number of in-moult records available per individual per season for the assessment of primary moult. **(a)** Year 1, *n* = 44 individuals; **(b)** Year 2, *n* = 64; **(c)** Year 3, *n* = 58.

dropping P1 and P2 nearly simultaneously, and in every historical case when only P1 and P2 were growing (*n* = 11), both feathers were scored as 1. Therefore, this bird's final score was 2. Usually, however, both growing and unmoulted feathers were visible. In Figure 6.1b, for example, nine primaries are visible (scored 5555543?00). In this case, the hidden P7 was assigned score 2, for a final score of 34. When reconstruction of feather scores introduced more than minimal potential scoring error, we excluded the record.

When fully grown, the distal tip of P10 generally extends slightly beyond that of P9, in both extended and folded wing positions. Consequently, photographs of birds roosting with wings folded were useful to evaluate state of moult after score 49 was reached (Figure 6.4). However, the final length of P10 relative to P9 varied among individuals; we considered moult completed when the length of P10 matched its apparent length in photographs of that individual just prior to migratory departure.

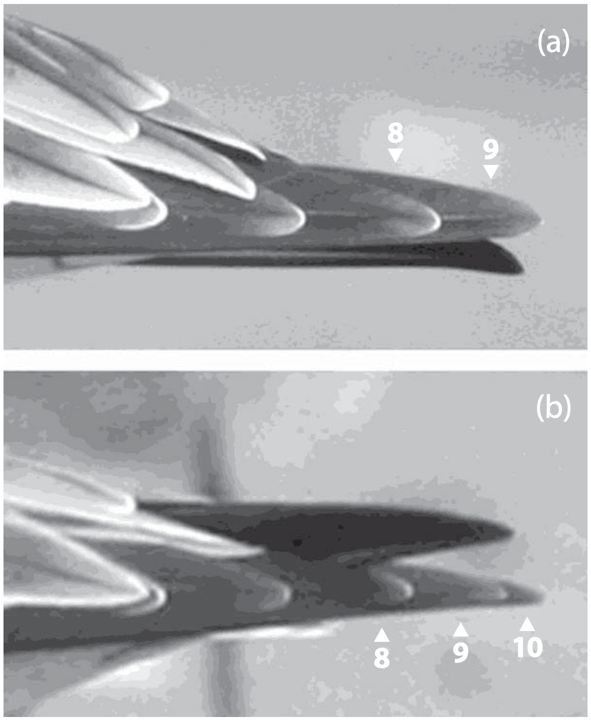

Figure 6.4 Two photographs of one male godwit taken on **(a)** 16 January and **(b)** 26 January of the same year. On the left wing, note that P10 is not yet visible beyond the tip of P9 in **(a)**, but has grown to its full length in **(b)**. Thus, the bird completed primary moult between these two observations.

Conversion of primary moult scores to feather mass

Because moult scores are not linearly related to the proportion of new feather mass grown, we converted individual feather scores to proportional mass values (Summers *et al*. 1983). Using three godwit specimens (with short, medium, and long wing chords relative to the population) from New Zealand, we derived population-specific mean proportional feather masses (methods in Underhill and Summers 1993)[2]. Also, feather mass is not distributed evenly along the length of a primary feather. Therefore, we derived proportional masses for each of 12 equal-length segments along each feather (methods in Dawson 2003), and used mean values among all primaries to calculate population-specific conversions for moult score to proportional feather mass. Thus, a feather at score 1 has grown on average 0.10 of its ultimate mass, score 2 = 0.25, score 3 = 0.50, and score 4 = 0.80; these values vary substantially from those recommended by Underhill & Zucchini (1988), which did not account for variable mass along feather length. By summing the proportional masses of all 10 primaries, we converted moult scores to total Percentage Feather Mass Grown (hereafter, 'PFMG'; Underhill and Summers 1993).

---

[2] See Appendix 4 for details.

Compared with inner primaries, outer primaries take longer to grow, have greater mass, and are more visible in photographs, making it both appropriate and feasible to score their growth with greater precision than the 0–5 scoring system allows. For all moult scores ≥46, we estimated the length of P9 and P10 in 12 equal-length increments (effectively splitting score 3 and 4 into four sub-scores each), and calculated proportional mass accordingly. In Figure 6.1c, for example, P9 is approximately 11/12 grown and P10 is 8/12 grown, resulting in total PFMG of 0.90 (compared with 0.88 if score 47 were simply converted to PFMG).

Individual primary moult regressions

We analysed primary moult duration individually for each godwit with ≥4 in-moult scores spanning ≥50% of total moult (mean = 7.4 scores, range = 4–15). This sample included 1 godwit in Year 1, 46 in Year 2, and 49 in Year 3 (56 total individuals); Year 1 fieldwork began late in moult, and so only one very late-moulting female fit the criteria (Figure 6.3a).

Dawson (2003) demonstrated that feather mass accumulates at a linear rate over most of primary moult, but slower near the beginning and end, when fewer feathers are growing simultaneously. This was true in our study: in all 96 cases, PFMG increased across moult scores 4–47 (accounting for 86% of total feather mass) at a linear rate (linear regressions; mean $r^2 = 0.987$, range = 0.908–1.00, all $P < 0.001$), but the rate was generally slower outside that range. Consequently, using observed moult rate (PFMG/day) derived from scores 4–47 to calculate total moult duration will produce an underestimate (illustrated in Figure 6.5a). Unfortunately, high variation in moult rates late in moult indicated that rates derived from scores 4–47 could not simply be scaled proportionally to produce reliable estimates of total moult duration (see below). Therefore, we derived two primary moult parameters for analysis: moult rate across scores 4–47 (PFMG/d; hereafter, ‘primary moult rate’ or ‘PMR’) and total estimated moult duration from scores 0–50 (d; hereafter, ‘primary moult duration’ or ‘PMD’).

For estimation of rates early and late in moult, we examined cases in which birds were scored twice within scores 1–4 or 47–49. On average, moult rates during scores 1–4 were 0.47 ± SD 0.29 ($n = 21$) of an individual’s PMR. Late in moult, mean rates slowed from 0.75 ± SD 0.25 ($n = 43$) of the PMR during scores 47–48 to 0.54 ± SD 0.24 ($n = 39$) within score 49. From these data, we constructed an idealised moult progression for the early and late segments of moult. For each bird, we used the individual’s PMR regression equation to calculate dates of scores 4 and 47, and then applied the idealised early-moult segment to calculate the date of moult initiation (last day of score 0) backward from score 4. All godwits in our study appeared to progress from score 0 to 4 in a 5–7 d period; therefore, this method introduced only minor potential errors (<2 d) in date of moult initiation. However, duration of moult after score 47 was extremely variable (~10–30 d). When scores of 48–49 were available (85 of 96

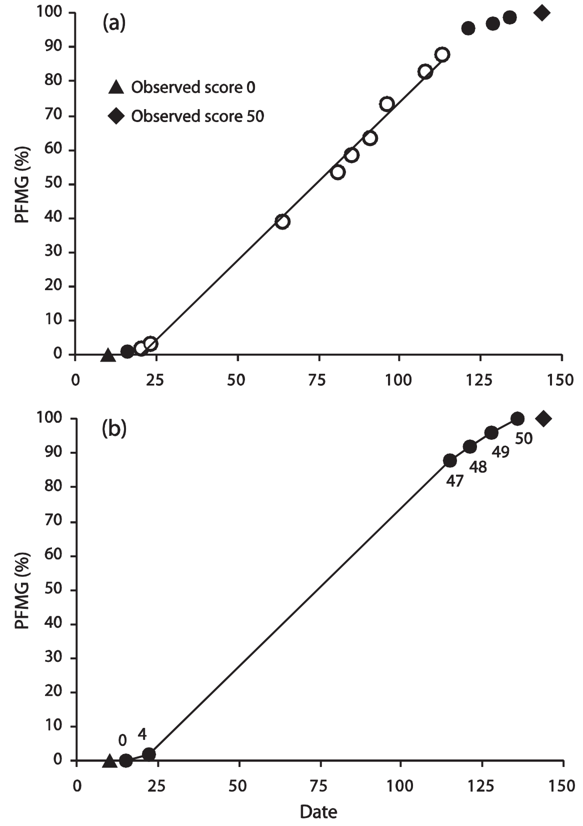

Figure 6.5 Illustration of individual primary moult progression analysis. Day 1 = 1 September 2009; 150 = 28 January 2010. 'PFMG' = Percentage Feather Mass Grown. **(a)** Raw data. Open circles = observed moult scores 4–47, with linear trendline (r^2 = 0.995, n = 9, P < 0.0001). Filled circles = moult scores outside 4–47. This female godwit was observed in moult on days 16–134, and was not in moult on day 10 (score 0) and day 144 (score 50); thus, moult duration must be between 119 and 134 d. The daily moult rate calculated from scores 4–47 (0.922 PFMG/day) predicts a total moult duration of 108 d, a demonstrable underestimate. **(b)** Idealised moult progression, using observed linear rate to predict dates of scores 4 and 47, and modified rates (see text) to predict scores 0, 48, 49, and 50. The resulting estimate of moult duration is 121 d.

cases), we proportionally scaled the idealised late-moult progression to fit observed data, and calculated the days from score 47 to score 50 to derive the date of moult completion; Figure 6.5b illustrates the application of this method to the data in Figure 6.5a. For the remaining cases (n = 11), we could not confidently estimate date of moult completion, and so these are excluded from analyses of moult completion and PMD, but are included in those of moult initiation and PMR.

For some godwits with insufficient data for a full moult regression analysis, there was sufficient information to estimate date of moult completion. For birds scored once at 47 and at least once during score 48–49, we scaled the idealised late-moult progression to observed data (as above) to estimate the first date of score 50 (n = 15 in Year 1, 1 in Year 2, and 4 in Year 3).

In addition, some birds were photographed at score 49 and then score 50 in a period of just 3–8 d (*n* = 18 in Year 1 and 3 in Year 3); for these birds, we used the midpoint between the two dates to represent the date of moult completion.

Analysis

For analysis, we limited our sample to individuals observed in 2–3 seasons (*n* = 58; 31 females, 27 males); each individual contributed 0–3 observations per parameter. To illustrate the degree of individual variation in each migration and moult parameter, we calculated the difference between the greatest and least values for each individual and summarised these across all birds of each sex (Table 6.1). To examine differences by sex and year in each parameter, we used mixed-model regression (PASW Statistics 18.0, SPSS Inc.) with sex and year as fixed effects and individual as a random effect.

To examine within-season carry-over effects of the timing of non-breeding events, we looked for within-individual correlations between each predictor and subsequent parameter using within-subject centering (van de Pol and Wright 2009) and mixed-model regression. Predictor variables included dates of migratory arrival, completion of pre-basic moult, initiation and completion of primary moult, and initiation of pre-breeding moult; within- and between-individual variation in the predictor variable were included separately as fixed effects.

Table 6.1 Within-individual between-year variation in non-breeding Bar-tailed Godwits in New Zealand. Values represent the difference between the greatest and least values for each individual across 2–3 years, summarised for all birds of each sex.

	Within-individual variation							
	Males				**Females**			
	n	**mean**	**SD**	**range**	***n***	**mean**	**SD**	**range**
Arrive (date)	19	5.8	4.3	1–15	25	7.1	7.3	0–34
End pre-basic moult (date)	20	15.8	11.6	2–43	25	12.1	9.0	1–31
Start primary moult (date)	16	5.4	2.9	0–11	24	10.0	8.7	0–37
End primary moult (date)	18	7.8	5.8	0–28	25	10.8	7.9	1–27
Primary moult rate (PFMG/d)	16	0.07	0.05	0.0–0.2	24	0.09	0.07	0.0–0.3
Primary moult duration (d)	12	4.3	3.7	0–11	19	6.4	4.7	0–17
Start pre-breeding moult (date)	24	12.5	5.7	1–28	27	8.5	7.1	1–25
Departure BP (%)	25	2.4	2.0	0.0–7.5	29	2.3	2.5	0.0–7.5
Depart (date)	27	4.8	3.3	0–14	31	4.6	3.2	0–13

Dependent variables included completion of pre-basic moult, initiation of primary and pre-breeding moults, PMR, PMD, extent of BP at departure, and departure date. Thus, significant within-subject correlations represent between-year differences (carry-over effects) in an individual's moult or behaviour, after controlling for persistent between-subject variation.

To explore the effect of non-breeding schedules on subsequent survival outside of New Zealand, we examined return probability after earlier and later migratory arrival and departure the previous year. For each godwit with two or more years of migration data in Years 1–3, we classified each year as 'early' or 'late' based on the extreme values of arrival or departure for that individual; we excluded birds when migration timing was identical between years and discarded the intermediate year for birds with three values. We then calculated the return probability of early- and late-migrating godwits based on their presence/absence at the site in the subsequent year (Years 2–4).

Results

Non-breeding schedule differences by sex

Male and female godwits both spent an average of 177 d (range = 140–195 d) in New Zealand per non-breeding season (Figure 6.6); timing of migratory arrival and departure were similar for the sexes (Table 6.2), although the earliest and latest arrivals were typically females. On average, females completed pre-basic contour moult 9 d earlier than males and initiated pre-breeding moult 43 d later than males; 19% of females did not initiate pre-breeding moult until after departing New Zealand. Accordingly, males departed New Zealand with much greater mean BP scores (females 11%, males 64%) and were more likely to overlap primary and pre-breeding moults: 5% of females and 88% of males overlapped these moults (mean overlap; females = –30.9 d ± SD 20.0 d, range = –66 to +30 d; males = 5.9 d ± SD 11.1 d, range = –10 to +33 d). Overlap of pre-basic and primary moults was also greater for males (females = 19.5 d ± SD 20.0 d, range = 0–38 d; males = 27.1 d ± SD 15.3 d, range = 2–77 d).

All godwits initiated primary moult 3–29 d (mean = 15.7 d) after arrival in New Zealand (Figure 6.6); date of initiation did not differ by sex (Table 6.2). Females completed primary moult 6 d later than males, reflecting their greater moult duration (females = 114.7 ± SD 7.5 d, range = 97–128 d; males = 107.4 ± SD 5.8 d, range = 96–120 d). Males had a slightly greater primary moult rate than females (females = 1.008 ± SD 0.094 PFMG/d; males = 1.044 ± SD 0.080 PFMG/d); this non-significant difference equates to about 4 d across scores 4–47. Because females are larger than males (mean wing chord; females = 246.9 mm, range = 236–261 mm; males = 231.5 mm, range = 216–243 mm), differences in primary moult rate or

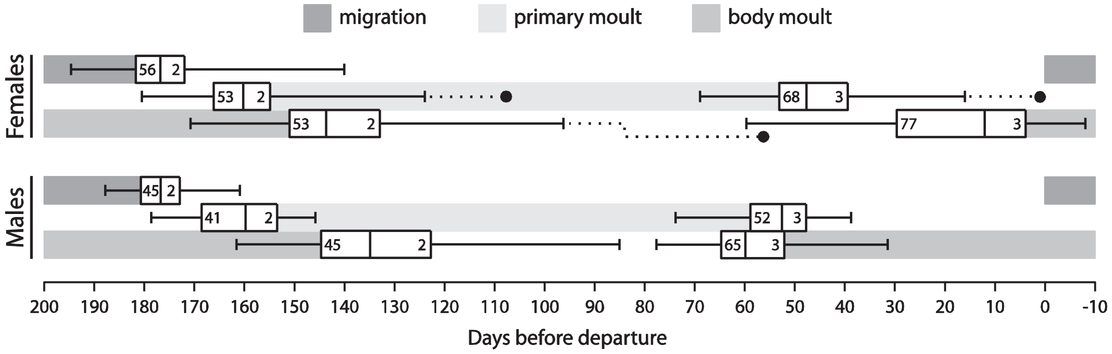

Figure 6.6 Timing of migratory arrival and moults in relation to departure from New Zealand. For illustration, dates are standardised against an individual's timing of departure to control for known migration timing differences based on breeding location. For each sex, upper bar = arrival and departure (Day 0; mean = 20 March, range = 4 March–5 April); middle bar = start and finish of primary moult; lower bar = finish pre-basic contour moult and start pre-breeding moult. Numbers indicate total observations (left) and years (right) of combined data; individual godwits (*n* = 58) contributed 0–3 values in each parameter. Boxplots indicate median and 25th and 75th percentiles; whiskers indicate total range of values. Filled circles represent one late-moulting female in Year 1 (see text; start of pre-breeding moult and departure were within population norms).

duration could result from size or sex differences (Figure 6.7). In mixed-model regression (wing chord as a fixed effect and individual as a random effect), wing chord was strongly positively associated with primary moult duration ($F_{1,45} = 13.67$, $n = 83$, $P = 0.001$) but not with primary moult rate ($F_{1,51} = 3.22$, $n = 94$, $P = 0.078$). However, with sex as an additional fixed effect, neither sex nor wing chord was significant in either test (all $P > 0.07$); therefore, we cannot distinguish the effects of wing chord and sex *per se* on primary moult.

Within-individual variation in timing of migratory arrival was greater for females than males (Table 6.1); variation in departure was generally less and similar for the sexes. Variation in timing of contour feather moults (both pre-basic and pre-breeding) was generally greater for males than for females, but females showed greater intra-individual variation in timing and duration of primary moult. Extent of BP at departure was extremely consistent for individuals of both sexes, varying by only 0–7.5% between years.

Non-breeding schedule differences by year

At the population level, timing of migratory arrival did not vary among years (Table 6.2), but average migratory departure was slightly earlier (<2 d) in Year 3 than in Years 1–2. Completion of pre-basic moult did not vary by year, but initiation of pre-breeding moult was earliest (by 2–6 d) in Year 3. Average initiation of primary moult was 4 d later in Year 2 than

Table 6.2 Results of mixed-model regression analysis of the effect of sex and year on non-breeding parameters for Bar-tailed Godwits in New Zealand. For significant results (in bold), estimates represent mean effect of sex (female shown relative to male) or year (Year 1 or 2 shown relative to Year 3) on *y* (±SE).

			Sex					Year				
***y*-variable**	***n* years**	***n* obs**	**df**	***F***	***P***	**Estimate**	**SE**	**df**	***F***	***P***	**Estimate**	**SE**
Arrive (date)	2	101	1,54	0.04	0.850			1,46	0.68	0.415		
End pre-basic moult (date)	2	98	**1,53**	**4.86**	**0.032**	**–9.00**	**4.08**	1,49	3.04	0.087		
Start primary moult (date)	2	94	1,52	0.04	0.844			**1,45**	**5.15**	**0.028**	**3.59 (Y2)**	**1.58**
End primary moult (date)	3	120	**1,55**	**6.83**	**0.012**	**6.03**	**2.31**	2,72	1.35	0.266		
Primary moult rate (PFMG/d)	2	94	1,51	3.30	0.075			1,47	0.60	0.442		
Primary moult duration (d)	2	83	**1,46**	**16.55**	**0.000**	**7.29**	**1.79**	1,37	0.86	0.359		
Start pre-breeding moult (date)	3	142	**1,55**	**189.05**	**0.000**	**42.87**	**3.12**	**2,85**	**9.68**	**0.000**	**2.06 (Y1)** **5.66 (Y2)**	**1.47** **1.30**
Departure BP (%)	3	146	**1,56**	**239.14**	**0.000**	**–53.60**	**3.47**	**2,86**	**3.41**	**0.038**	**0.63 (Y1)** **–0.38 (Y2)**	**0.39** **0.38**
Depart (date)	3	161	1,56	0.75	0.391			**2,102**	**4.53**	**0.013**	**1.76 (Y1)** **1.24 (Y2)**	**0.62** **0.57**

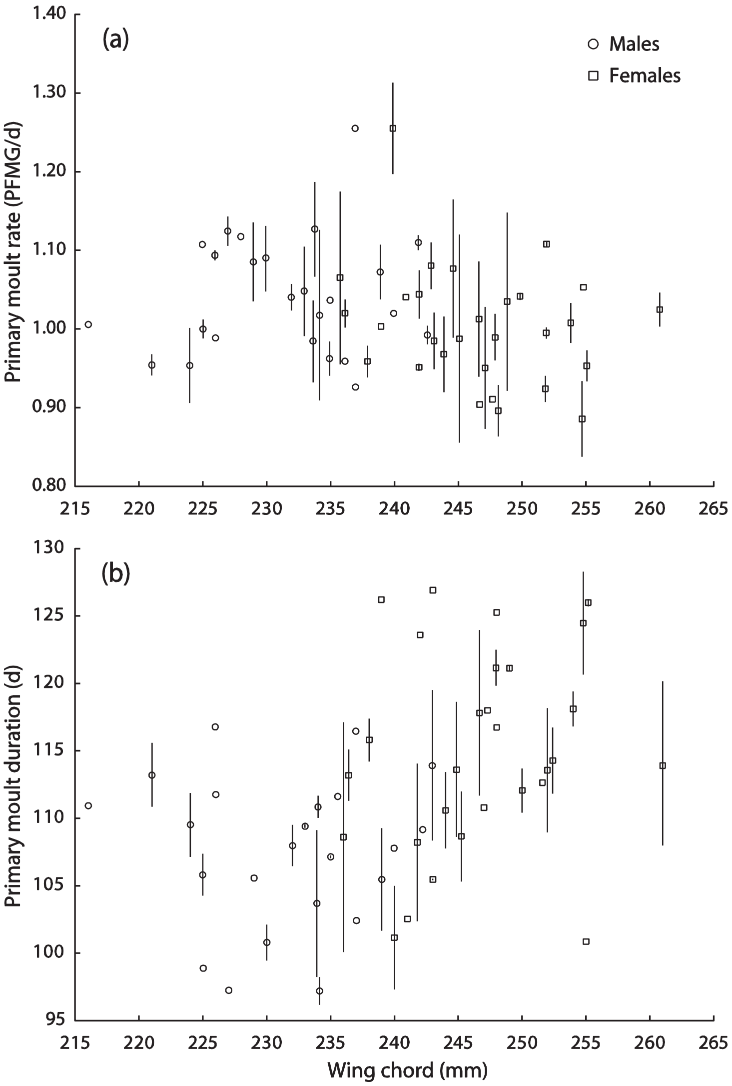

Figure 6.7 (a) Primary moult rate (daily percentage of total feather mass gained across moult scores 4–47) and **(b)** estimated total primary moult duration (scores 0–50) of individual Bar-tailed Godwits in relation to maximum flattened wing chord. Values are individual means (*n* = 54) across 1–2 years. Lines indicate range of values for individuals with two years of data.

in Year 3, but rate, duration, and completion of primary moult did not differ among years. Because variation in plumage at departure was minimal, annual differences of <1% were statistically significant; such differences are unlikely to have biological significance, and are within expected measurement error.

Within-season individual carry-over effects

The timing of arrival in New Zealand is more variable than timing of departure: at the population level, marked godwits arrived across 54–55 d each year (Year 2–3), compared to departure spans of 23–30 d (Years 1–3). Within individuals, later arrival had no influence on dates of departure, pre-basic moult completion, or pre-breeding moult initiation (Table 6.3). However, later arrival led to later initiation of primary moult; this effect was exactly 1:1 d, on average.

Although timing of arrival and pre-basic moult were unrelated, later completion of pre-basic moult was associated with slightly later primary moult initiation (Table 6.3). Later pre-basic moult completion had no effect on primary moult rate or duration, or on timing of pre-breeding moult initiation.

Individuals performed a faster wing moult in years when they started moult later: timing of primary moult initiation was significantly associated with both primary moult rate and total duration (Table 6.3). However, the degree of the effect on moult duration (–0.32 d) indicates that the decrease in moult duration did not fully compensate for the late start, and so moult was completed later as well. Later completion of primary moult had no effect on timing of pre-breeding moult initiation or departure.

Although pre-breeding moult appeared unaffected by any previous parameters, within-individual variation in initiation of pre-breeding moult was surprisingly high (up to 28 d; Table 6.1). However, variation in initiation date had no influence on extent of BP at departure (Table 6.3).

For all significant within-season carry-over effects (Table 6.3), there was great variation in the degree and uniformity of response by individuals (Figure 6.8). The effect of arrival date on primary moult initiation was relatively strong and uniform (Figure 6.8a). For other carry-over effects involving primary moult, the significant results indicate general trends, but some individuals demonstrated no effect or even the opposite pattern (Figure 6.8b–d).

Cross-seasonal carry-over effects

Non-breeding delays had no apparent effect on an individual's likelihood of undertaking spring migration: in all three years, every marked adult godwit departed the site on migration during March–early April. Return rates of marked godwits in Years 2–4 (after departures in Years 1–3) were 0.85 (53 of 62), 0.93 (56 of 60), and 0.90 (52 of 58), respectively. Among individuals with two years of New Zealand arrival data (*n* = 44), return rate was 0.93 in the year following 'early' arrivals and 0.95 after 'late' arrivals. For departures from New Zealand (*n* = 58), return rate was 0.96 after 'early' departures and 0.95 after 'late' departures. When we limited data to the most extreme delays (≥10 d intra-individual difference between years), there was still no discernible effect: 8 of 9 late-arriving godwits and 5 of 5 late-departing godwits returned the following year.

Table 6.3 Carry-over effects within the non-breeding season of Bar-tailed Godwits in New Zealand, as shown by mixed-model regression analysis using within-subject centering. Units are dates except for primary moult rate (PFMG/d), primary moult duration (d) and departure BP (% breeding feathers). Significant within-subject results (in bold) indicate a correlation between individual timing of the predictor variable (*x*) and subsequent performance in the dependent variable (*y*). For significant results, estimates represent mean effect on *y* per unit *x* (±SE).

			Between-subject					**Within-subject**				
***x*-variable**	***y*-variable**	***n* obs**	**df**	***F***	***P***	**Estimate**	**SE**	**df**	***F***	***P***	**Estimate**	**SE**
Arrive	End pre-basic	96	1,49	28.95	0.000	0.98	0.18	1,45	2.61	0.113		
	Start primary	91	1,50	166.70	0.000	0.84	0.06	**1,39**	**92.91**	**0.000**	**1.00**	**0.10**
	Start pre-breeding	100	1,55	0.22	0.641			1,42	0.004	0.948		
	Depart	101	1,56	18.70	0.000	0.36	0.08	1,44	0.37	0.544		
End pre-basic	Start primary	92	1,48	52.68	0.000	0.44	0.06	**1,45**	**5.70**	**0.021**	**0.23**	**0.10**
	Primary rate	92	1,47	1.71	0.198			1,44	2.13	0.152		
	Primary duration	81	1,43	6.91	0.012	–0.16	0.06	1,35	0.13	0.711		
	Start pre-breeding	97	1,50	3.20	0.079			1,43	1.95	0.170		
Start primary	Primary rate	94	1,50	3.59	0.064			**1,38**	**37.21**	**0.000**	**0.007**	**0.001**
	Primary duration	83	1,43	11.02	0.002	–0.30	0.09	**1,31**	**9.11**	**0.005**	**–0.32**	**0.10**
End primary	Start pre-breeding	119	1,56	4.31	0.042	0.71	0.34	1,60	0.92	0.341		
	Depart	120	1,58	4.40	0.040	0.20	0.09	1,61	1.82	0.182		
Start BP	Departure BP	130	1,55	281.01	0.000	–1.12	0.07	1,72	0.072	0.790		

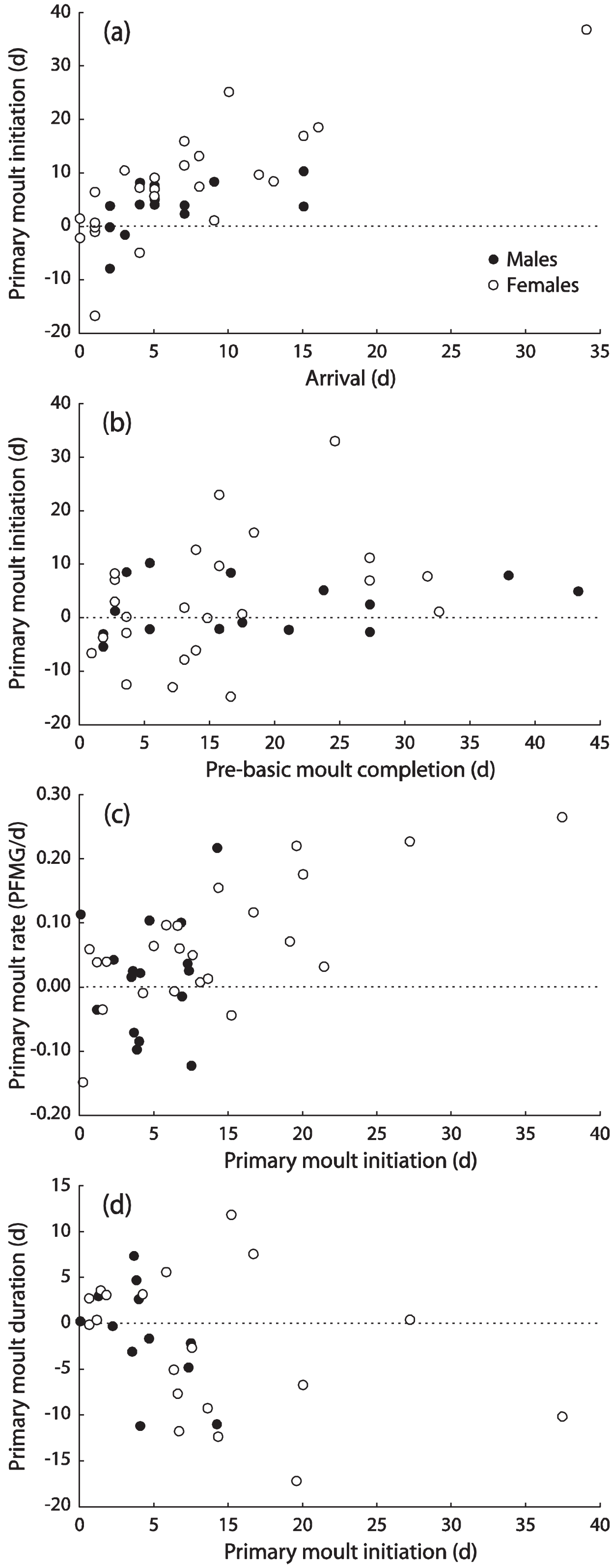

Figure 6.8 Significant within-individual carry-over effects indicated in Table 3. For individuals with two years of data, difference (absolute value in days) between dates of the predictor variable in Year 2 and 3 is indicated on *x*-axis. *Y*-axis indicates degree and direction of change in the dependent variable during the year of later *x*. For reference, the dotted line represents no effect of *x* on *y*.

Discussion

This study presents the most detailed examination of within-individual carry-over effects of the timing of post-breeding migration on the subsequent non-breeding schedules of a long-distance migratory bird. Surprisingly, annual variation (up to 34 d) in arrival in New Zealand after the longest known non-stop migratory flight had no apparent effect on an individual Bar-tailed Godwit's extent of breeding plumage or timing of departure from New Zealand on the following spring migration. In general, godwits compensated for later autumn arrival by conducting a faster wing moult and through a greater overlap of wing and pre-breeding moults. Thus, 'errors' in timing at the start of the non-breeding season were essentially corrected in New Zealand prior to spring migration.

Seasonal carry-over effects can arise from many causes and take countless forms (Harrison *et al.* 2011). In migratory birds, the most commonly examined carry-over effect is that of spring migration timing on breeding success (e.g., Bety *et al.* 2004). Also, the relationship between breeding investment and timing of pre-basic moult has been evaluated for species that breed and initiate moult at the same site (e.g., Earnst 1992). Carry-over effects in the non-breeding season have received less attention, largely due to the difficulties of tracking moult, fuelling, and migration of individual birds. Our study, the first to examine intra-individual variation in duration of primary moult in a wild migratory population, represents a significant advance in understanding how individuals manage potential carry-over effects to maintain time-critical migration schedules.

Individuality in primary moult

Very little is known about inter- or intra-individual variation in flight feather moult in wild populations, because most information comprises average values from population-level studies (e.g., Summers *et al.* 1983, Underhill 2003) or is derived from controlled experiments (e.g., Dawson 2004). Estimating wing moult parameters for individuals typically requires multiple captures (but see Bensch and Grahn 1993), which generally provides small samples, except for colonial species that moult during breeding (e.g., Emslie *et al.* 1990). Although wing moult can be conspicuous in the field (Howell 2010), we know of only one previous study using repeated photographs of free-living individuals to measure primary moult progression (California Condor *Gymnogyps californianus*; Snyder *et al.* 1987). Our study was possible because godwits in New Zealand have high non-breeding site-fidelity, make predictable daily movements to open-habitat high-tide roosts, are relatively approachable, and are large enough for discernment of both colour-bands and state of moult even in photographs of relatively low quality. Such an approach remains impractical for most systems, and our labourious methods probably cannot be transferred to other studies without a similar investment of time and effort.

We found substantial between-individual variation in moult duration (Figure 6.7b): the longest duration we observed (128 d) exceeded the shortest (96 d) by 33%. This illustrates the magnitude of individual variation that may be masked by average values calculated from traditional population-level methods (e.g., Underhill *et al.* 1990). Across species, duration of primary feather moult generally increases allometrically with wing length and body size (Rohwer *et al.* 2009); therefore, some of the variation we observed may result from individual differences in size. In Bar-tailed Godwits, wing chord varies substantially between sexes (on average, females 15 mm greater than males) and within each sex (variation up to 25–27 mm). However, our analysis lacked the power to separate confounding effects of size and sex, and so the greater moult duration of females may be an effect of sex *per se*. As we observed no sex differences in timing of migration or initiation of primary moult (Table 6.2), it is probably unrelated to systematic differences in reproductive effort or parental care in Alaska. However, males conduct a much more extensive pre-breeding moult than do females (Chapter 5), which could result in a more time-constrained flight feather moult for males.

It is intriguing that the rate of new feather mass gain throughout 86% of moult (PMR), though clearly linear, was not a reliable predictor of total moult duration. On average, moult durations (PMD) were 13% longer than a straight regression based on scores 4–47 would predict (Figure 6.5), similar to the findings of Dawson (2003), but there was substantial individual variation in the degree to which mass gain slowed when only P9 and 10 were growing (scores 47–49). This variation constituted another sex disparity: although PMR was statistically similar for males and females, PMD was significantly longer for females (Table 6.2). For the average male, PMD was 9% longer than PMR would predict, compared to 16% for females, indicating that the final phase of primary moult was generally more protracted in females. Again, this may indicate that completion of primary moult is more time-constrained for males than females in this system. The lack of a direct correlation between PMR and PMD also raises the question of whether total duration is the variable of greatest interest for studies of flight feather moult. Arguably, variation at the fringes of primary moult may be of less biological significance than the linear rate across the great majority of total feather mass gain.

We know of only one previous study that examined intra-individual variation in timing of primary moult. For Barnacle Geese *Branta leucopsis*, date of initiation of primary moult appeared quite consistent annually and to some extent heritable (Larsson 1996); however, initiation dates were generally estimated from single captures during moult and did not account for potential individual variation in moult rates. In our study, timing of primary moult was largely dependent upon date of arrival in New Zealand, with intra-individual variation up to 37 d in date of moult initiation and up to 17 d in moult duration. Such flexibility does not exclude a heritable component to moult schedules, but does demonstrate short-term ability to respond to conditions that vary annually. According to population-level studies, initiation of primary moult on wintering grounds may vary with breeding success (Barshep *et al.* 2011b) and later-moulting individuals appear to compensate by moulting faster (Johnson and Minton 1980, Barter 1989). Starlings *Sturnus vulgaris* responded to experimentally delayed moult by decreasing moult duration as much as 20–30% (Dawson 2004). Our study, in which an individual's primary moult duration varied up to 17% annually, explicitly demonstrates this in a wild population.

Influence of conditions prior to arrival in New Zealand

In this population, between-individual variation in migration timing, and to a certain extent scheduling of the entire annual cycle, is linked with breeding latitude in Alaska (Chapters 2 and 5); in general, southern breeders migrate earlier in both spring and autumn. Additional intra-individual variation in timing and condition upon arrival in New Zealand may result from fuelling conditions in Alaska, timing of weather systems conducive to southbound departure, and conditions experienced *en route* (Gill *et al.* 2009). Although breeding success (i.e., duration of parental investment) has been linked with autumn migration timing in other studies (e.g., Kjellén *et al.* 2001), it does not appear to affect timing of southward departure from Alaska by Bar-tailed Godwits (Chapter 2). However, cessation of breeding activity very likely affects the timing of pre-basic moult (Hahn *et al.* 1992, Dawson 2006); godwits initiate this moult at post-breeding staging areas (McCaffery and Gill 2001, Chapter 5). This probably explains why intra-individual variation in timing of arrival in New Zealand and pre-basic moult completion were not strongly correlated (Table 6.3).

The direct flight from Alaska to New Zealand takes 8–9 d in favourable conditions, but godwits may make opportunistic stops or detours in adverse weather (Gill *et al.* 2009). Variable trans-Pacific conditions therefore likely result in some birds arriving in New Zealand in good condition with unused fuel accumulated in Alaska, some arriving in poor condition with completely depleted fuel stores, and some arriving later after recuperating and refuelling in locations such as New Caledonia and southeast Australia. Godwits reaching New Zealand in poor condition may be unable to initiate moult and replenish body stores simultaneously; this may explain why some birds initiated primary moult just 3–6 d after arrival, while others delayed up to 29 d.

Population-wide patterns of moult initiation after arrival may therefore indicate whether godwits experienced a relatively easy or difficult autumn migration that year. For example, average timing of arrival was similar in Years 2–3, but mean primary moult initiation was 3.6 d later in Year 2 (Table 6.2). In Year 2, the first four females to arrive (3–14 September) delayed the start of primary moult for 19–29 d after arrival, on average 10 d longer than they did after similar arrivals in Year 3. Geolocator data from one of these birds revealed a dramatic detour to the vicinity of New Caledonia (800–900 km west of her prior course toward New Zealand), resulting in a 3-day delay in arrival (J. Conklin and P. Battley unpubl. data). Other possible indications of a difficult autumn migration in Year 2 included a lower return rate (85% vs. 90–93% in Years 3–4) and a greater number of birds stopping elsewhere in New Zealand rather than flying directly to our study site (3 of 10 geolocators in Year 2, and 0 of 9 in Year 3; J. Conklin and P. Battley unpubl. data).

Within-season trade-offs and carry-over effects

Pre-basic moult is typically viewed as a single stage, comprising both flight feather replacement and the transition into non-breeding plumage (Humphrey and Parkes 1959). However, these two components are to some extent modular (Piersma *et al.* 2008); many long-distance migrants initiate pre-basic contour moult prior to autumn migration but delay flight feather moult until arrival on wintering grounds (e.g., Thomas and Dartnall 1971, this study). This strategy avoids potential flight performance costs of migrating with incompletely moulted wings (Swaddle and Witter 1997), and also raises the question of energetic trade-offs between the two components of pre-basic moult, which only partially overlap in the non-breeding season. We found that intra-individual variation in date of pre-basic contour moult completion had a small but significant effect on the initiation of primary moult, beyond the greater effect of arrival (Table 6.3). This suggests that the state of contour moult (which could reflect annual variation in breeding success or conditions during fuelling or migration) presents some limitation on the timing of primary moult. However, timing of pre-basic moult completion did not affect rate or duration of primary moult, so we have no evidence that overlap of the two moults (0–38 d) affected moult performance.

Adaptive responses to experimentally delayed primary moult have varied among studies. In Bluethroats *Luscinia svecica*, neither timing nor duration of primary moult changed in response to a photoperiod-simulated delay of one month (Lindström *et al.* 1994). By contrast, starlings responded to a 3-week testosterone-induced delay in primary moult by decreasing moult duration by about 12 days (from 104 to 94 d) and the response to a photoperiod-induced delay was even more dramatic (from 119 to 92 d; Dawson 2004). In our study, godwits responded to later primary moult initiation by moulting faster, but decreases in moult duration compensated for only 32% of the delay in initiation, on average (Table 6.3). This could indicate that flexibility in moult rate has an absolute limit, or perhaps that only individuals in the best condition have the option of accelerating moult. Also, godwits may face a trade-off between the costs and benefits of timely moult completion. It has been demonstrated that faster moult rates can lead to reduced feather quality, in terms of strength, mass, and durability (Dawson *et al.* 2000, Serra 2001), and that condition of primary feathers can significantly affect flight performance (Swaddle *et al.* 1996). New Zealand godwits travel more than 30,000 km between flight feather replacements; this annual routine may tolerate minimal compromise in flight feather quality without jeopardising survival or breeding success.

If flight feather quality is a top priority for long-distance migrants, we may expect primary moult to temporally preclude other potentially costly activities, such as pre-migratory fuelling and pre-breeding moult. For example, Grey Plovers *Pluvialis squatarola* in South Africa gained mass only after completing or suspending wing moult (Serra *et al.* 1999). However, it is clear that fuelling and moult are not mutually exclusive in New Zealand godwits. Godwits appear to fuel quite slowly, starting up to three months before departure (J. Conklin and P. Battley unpubl. data), a period encompassing a significant portion of primary moult and all pre-breeding moult conducted in New Zealand. In fact, due to two closely-timed ventral feather generations (Chapter 5), some godwits in late January/early February are fuelling while conducting portions of three moults (pre-basic flight feathers, pre-alternate and pre-supplemental body feathers) simultaneously. Most males and some females overlapped the primary and pre-breeding moults, and annual variation in the former did not influence timing of the latter (Table 6.3). Overlap of the moults almost always (49 of 51 cases) occurred when only the last two primaries were growing (score 45–49, >80% total moult completed); two late-running females initiated pre-breeding moult while still growing P8. However, some females finished primary moult >50 d before their first breeding feathers appeared; therefore, there is no evidence that completion of wing moult frees birds to start pre-breeding moult. Accordingly, differences in duration or timing of wing moult do not appear to drive individual or sex differences in breeding plumage in Alaska (as hypothesised in Chapter 5).

It is intriguing that variation in an individual’s initiation of pre-breeding moult had no effect on its extent of breeding plumage at departure (Table 6.3). Males conduct 12–58 d of pre-breeding moult while in New Zealand (Chapter 5), which corresponds to variation in plumage at departure. However, moult rates varied substantially among individuals, as did the timing of moult suspension prior to departure. This suggests that individuals may respond to variation in moult initiation by adjusting moult rate and/or date of pre-departure suspension. However, there was no evidence that birds ahead of schedule seized the opportunity to improve breeding plumage. Most godwits resume pre-breeding moult during northbound stopover in Asia (Chapter 5); it may be beneficial to complete moult at the last possible opportunity (Holmgren and Hedenström 1995), even if earlier opportunities present themselves.

In a concurrent study of the same individual godwits, we showed that most unexpectedly early or late spring departures (67%) were attributable to avoidance of departure in headwinds or delay due to recent capture (Chapter 4); none of the unexplained off-schedule departures are attributable to variation in arrival or moult shown in this paper. Still, there must be a point at which a poorly scheduled non-breeding season affects when or whether an individual migrates. Each breeding season, a small number of adult godwits do not migrate from New Zealand in spring (P. Battley unpubl. data), presumably due to poor condition or advanced age. In our study, every bird known to be >3 years old migrated each year, so we could not evaluate circumstances leading to a failure to migrate.

Potential downstream carry-over effects

The demanding annual routines of long-distance migratory birds suggest lives spent precariously pressed against time and energy constraints. With their extreme migrations and tight annual schedules, New Zealand Bar-tailed Godwits may seem particularly vulnerable to ‘errors’ in timing that may cascade through subsequent life-history stages. Despite this, we found no evidence that delays in the non-breeding season carried over to the timing of spring migration, suggesting that flexibility exists to compensate for unforeseen circumstances. Even the most late-moulting individual in our study (Figure 6.6) departed New Zealand within a normal time frame, despite completing primary moult just one day earlier. This bird also did not return the next season, which raises the question: do Bar-tailed Godwits prioritise rigid migration schedules over all other concerns? In this paper, we used timing of non-breeding events and extent of breeding plumage at departure to evaluate carry-over effects. We did not measure other potential qualitative indicators such as feather condition or extent of pre-migratory fuelling, either of which could be reduced by delays in the non-breeding season and lead to downstream effects on breeding success or survival. Migration timing in New Zealand had no apparent effect on survival, as return rates were similar after early and late arrivals and departures. However, it is plausible that a godwit with reduced feather quality or fuel stores could complete migration but fail to breed after arriving in Alaska late or in poor condition. As Bar-tailed Godwits are long-lived and may have 10–20 breeding opportunities in a lifetime, we should expect them to prioritise survival over breeding success in any particular year. Therefore, the ultimate carry-over effects of non-breeding schedules may be subtle, and cannot be truly assessed without measures of individual fitness.

Chapter 7

Absolute consistency: individual versus population variation in timing of annual life-history stages of a long-distance migrant bird

Conklin, J.R., P.F. Battley & M.A. Potter
Submitted manuscript

Abstract

Flexibility in scheduling varies throughout an organism's annual cycle, reflecting relative constraints and fitness consequences among specific life-history stages. Using light-level geolocators and direct observation, we tracked individual Bar-tailed Godwits Limosa lapponica baueri *for two full years (including non-breeding seasons in New Zealand and round-trip migrations to Alaska) to present the most complete annual-cycle view of moult, breeding, and migration schedules yet available for a long-distance migratory bird. At both population and individual scales, our data support two hypotheses: schedules tightened with proximity to the breeding season, and migratory movements were more precisely scheduled than moults. In general, individual godwits were remarkably consistent in timing of events throughout the year, and individual repeatability (*r*) of pre-breeding movements in particular was extraordinarily high (0.82–0.92). However, we demonstrate that* r *values misrepresent* absolute *consistency by confounding two parameters (inter- and intra-individual variation) containing very different information; the biological significance of* r *values can only be understood when these are considered separately. To evaluate potential flexibility to address stochastic or directional environmental change, temporal variation in any single season must be viewed with an annual-cycle perspective and recognition of the different mechanisms and implications of individual and population variation.*

Introduction

The typical vertebrate annual routine is composed of distinct, sequential life-history stages (e.g., breeding, moult) shaped by natural selection to maximise fitness (McNamara and Houston 2008). Performance in any particular stage depends on both the costs of sub-optimal performance (selection pressure) and the individual's ability to behave optimally, which may vary with control mechanisms, resource availability, and individual quality. Species generally respond to substantial and predictable environmental variation by expressing additional life-history stages (e.g., migration), but increasing annual-cycle complexity results in greater temporal or energetic constraints on specific stages (Wingfield 2008) and potential trade-offs among stages. It follows that individuals should prioritise optimal performance in events most critical to fitness (survival or reproductive output) and display more variation in stages with lesser impacts on fitness.

For any life-history parameter, the total range of values observed in a population contains two primary components: (1) inter-individual variation resulting from persistent differences in strategy or performance; and (2) intra-individual variation resulting from annual differences in performance. These two components (which we will refer to as ‘population variation’ and ‘individual variation’, respectively) may reveal very different things about constraints on a population, and the relative contribution of each can only be evaluated in multi-year individual-level studies. For example, migratory departures occurring across an extended period of time could result from all individuals having a similar strategy but being inconsistent in performance, or from individuals performing a range of strategies with very high precision; these scenarios lead to very different conclusions regarding constraints and flexibility in the system. There may be only one ‘correct’ way to accomplish certain annual tasks, whereas other stages tolerate a number of strategies or a range of individual performance with equivalent fitness consequences.

For migratory birds, arrival on breeding grounds is generally thought to impose the greatest temporal constraint in the annual routine (McNamara *et al.* 1998), due to clear associations between the timing and success of breeding (Verhulst and Tinbergen 1991, Bety *et al.* 2004). At high latitudes, extreme seasonality and short breeding seasons make timing of arrival especially important (Meltofte *et al.* 2007b). Thus, annual cycles of long-distance migrants may be expected to have one primary time-critical focal point (breeding arrival), with other stages subjected to increasing time-selection as birds conduct the moults, pre-migratory fuelling, and movements that facilitate timely breeding arrival. We may then expect both population and individual variation in timing to decrease with proximity to the breeding season. This idea is supported by observations of tighter temporal windows for pre-breeding (spring) than post-breeding (autumn) migration (Alerstam *et al.* 2006, Egevang *et al.* 2010), and increasingly precise migration timing in successive stages of spring migration (Farmer and Wiens 1999, Chapter 2).

Long-distance migratory movements are primarily governed by endogenous programmes (Gwinner 1996) that are largely unaffected by annually variable social and environmental cues, and may be more rigidly scheduled than breeding itself (Both and Visser 2001, Smith *et al.* 2010). By contrast, scheduling of moult appears more flexible at both evolutionary (Holmgren and Hedenström 1995, Helm and Gwinner 2006) and annual (Dawson 2004, Chapter 6) time scales, presumably due to lesser fitness consequences of timing of moult. Therefore, we may expect greater population and individual variation in timing of moults than in migratory movements, but this has never been explicitly examined in a wild migratory population.

The annual routine of New Zealand Bar-tailed Godwits *Limosa lapponica baueri* (Figure 7.1) includes a short, high-latitude breeding season, a complex moult (Chapters 5–6), and the two longest non-stop migratory flights yet recorded (Gill *et al.* 2009, Battley *et al.* 2012), and thus may feature considerable time constraints and trade-offs among life-history stages. In this study, we combine two years of detailed observations of colour-banded Bar-tailed Godwits in New Zealand with geolocator-tracking of a subset of the same individuals to present the most complete picture of temporal variation throughout the annual cycle yet available for a long-distance migratory bird. We describe population-level variation and individual-level consistency in moults, movements, and initiation of breeding to test two non-mutually exclusive hypotheses: (1) that variation in timing of key annual events decreases with increasing proximity to breeding; and (2) that timing of migratory movements is more rigidly maintained than that of moults.

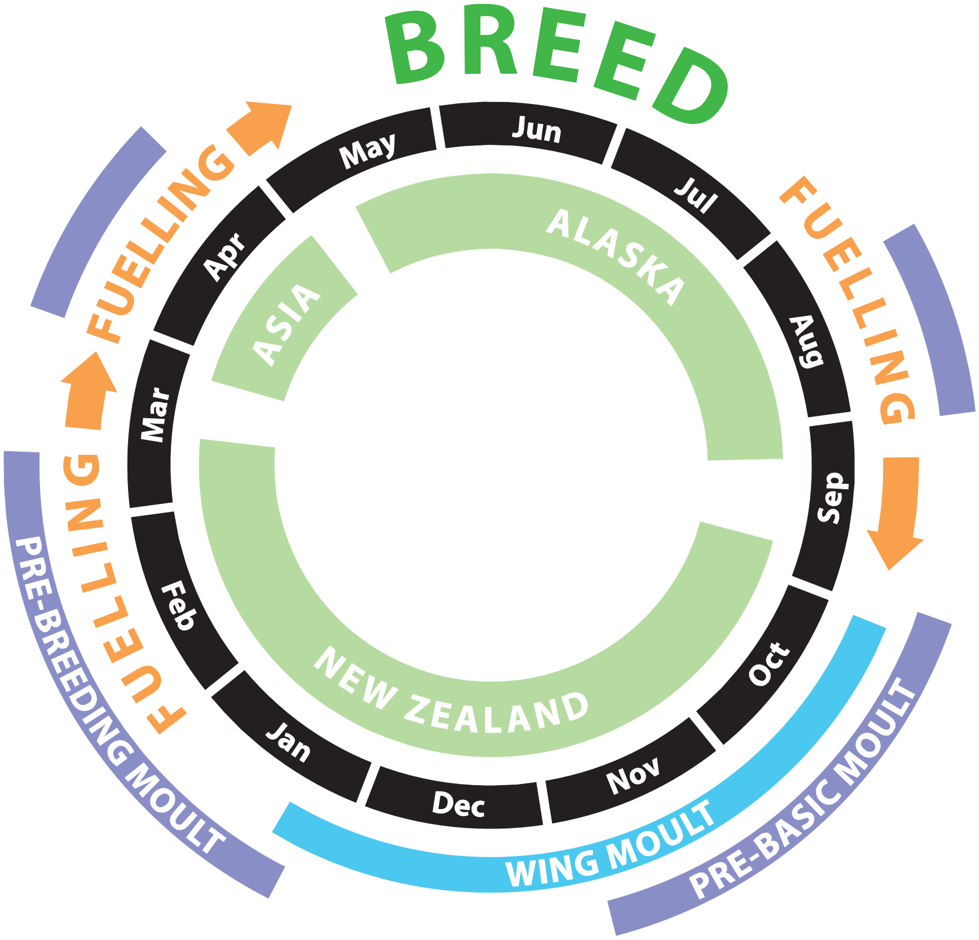

Figure 7.1 Generalised cycle of annual life-history stages of New Zealand Bar-tailed Godwits (typical adult male). Arrows indicate major migratory flights.

Methods

Individually marked birds

During three non-breeding seasons (January–April 2008, September 2008–April 2009, and September 2009–April 2010), we studied moult and migration timing in a small population of Bar-tailed Godwits (200–280 godwits; approximately 25% were individually colour-banded) at the Manawatu River estuary, New Zealand (40.47°S, 175.22°E). We conducted high-tide surveys every 3–4 days (d) during migratory arrival (1 September–20 October), daily during migratory departure (4 March–5 April), and every 4–8 d during the intervening summer months (21 October–3 March). During surveys, we used direct observation and digital photography to monitor primary feather moult, contour feather moult, and presence/absence of all marked individuals (77 total; 35 male, 42 female; n = 58–63 per season). With these data, we determined for each individual the timing of migratory arrival, completion of pre-basic contour feather moult, initiation and completion of primary feather moult, initiation of pre-breeding contour feather moult, and migratory departure. Departures were generally observed directly, and other parameters were estimated to within approximately 1–6 d. We have described details of data collection and analysis specific to each parameter elsewhere: arrival and contour moult (Chapter 5), primary moult (Chapter 6), and departure (Chapter 4).

Light-level geolocators[1]

A subset of colour-banded godwits at the site were additionally equipped with leg-mounted light-level geolocators (British Antarctic Survey model MK14; 1.4 g; 2-year life) to track movements outside of New Zealand. Twenty instrumented individuals (9 male, 11 female) provided data for this study; eight of these were tracked for two entire annual cycles. Derived breeding locations of these godwits spanned most of the known breeding range in Alaska (59–70°N (Chapter 2), indicating that most variation in migration schedules present in the greater New Zealand population was encompassed by our sample.

The geolocators recorded sunrise and sunset, allowing daily calculation of latitude and longitude (±130 km error, based on ground-truthing units and resightings of instrumented godwits), except during ±15 d of the vernal or autumnal equinox, when only longitude is reliable (Fox 2010). To derive fuelling and breeding sites outside New Zealand, we averaged twice-daily locations over periods when birds were relatively stationary, excluding clear outliers likely resulting from weather- or behaviour-related shading events near dawn or dusk. Clear shifts in latitude or longitude indicated the initiation of major migratory movements, which we considered concluded when a bird's location once again stabilised. Sample sizes decreased throughout May–September due to unit failures. Additionally, we could not

---

[1] See Appendices 1–2 for more detailed methods.

determine timing of departure from the breeding area for two birds, because their breeding and post-breeding staging locations differed by less than the location error of the geolocators.

Geolocators also indicated periods of nest incubation (Eichhorn *et al.* 2006, Chapter 2). During the breeding season, geolocators registered nights as regular, clearly demarcated periods of darkness <4.5 hours in length; these did not appear at all if birds bred north of 64°N. Days appeared as continuous light, irregularly broken by very brief (<1 hour) shading events, most likely corresponding to behaviours such as wading or sitting. Within 6–25 d of apparent arrival on breeding grounds, most birds (14 of 16 cases) displayed a conspicuous pattern of incubation, in which semi-regular shading events of 4–13 hours were overlaid on the day/night pattern for periods up to 25 d. We considered the first day of this period to be the start of incubation.

Analysis

We present data for two complete annual cycles, from New Zealand departure in 2008 through the initiation of pre-breeding contour moult in 2010 (the period for which geolocator data are available); this includes geolocator data for events outside New Zealand, and direct observations of colour-banded godwits (including the geolocator-tagged birds) for events within New Zealand. To describe population variation in timing of each stage, we pooled all observed dates across two annual cycles (1–2 observations per bird); population spans are the difference between the earliest and latest individuals. To describe individual variation in timing for each stage, we calculated the difference (d) between the two values for each individual observed in both years. To ask whether population (spans across all birds) or individual (geolocators only) variation decreased with proximity to the breeding season, we ranked data across all stages and tested for differences from hypothesised ranks (stages ranked chronologically from post-breeding dispersal to first incubation) using Spearman-rank correlation.

To see how well our geolocator sample represented variation in the larger population, we tested for statistical differences from colour-banded samples when both types of data were available (six stages within New Zealand). The larger colour-banded samples naturally contained more extreme values (Figure 7.2b), but medians and distributions of values in every stage were similar to geolocator samples for both population (Mann-Whitney tests, all P = 0.25–0.88) and individual data (all tests P = 0.18–0.96). Therefore, we combined the two data sources for the best representation of population variation throughout the year. However, we limited analyses of individual variation to geolocator birds tracked for two entire annual cycles (n = 8), to ensure that samples for all stages were as comparable as possible.

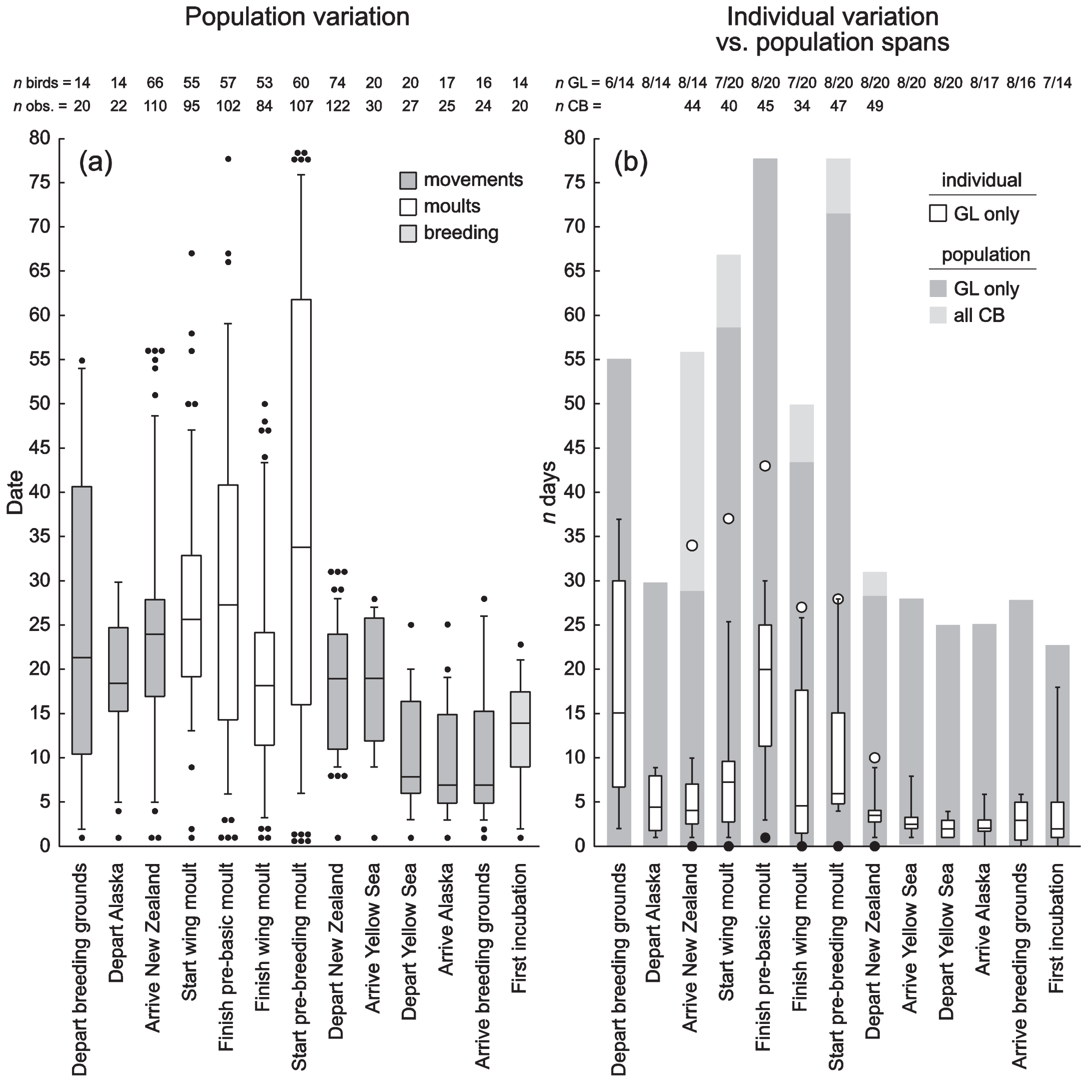

Figure 7.2 Population and individual variation in timing of events throughout the annual cycle of Bar-tailed Godwits. Stages (*x*-axis) are in chronological order, starting with dispersal from breeding grounds (see Figure 7.1). **(a)** Distribution of all observations during March 2008–March 2010, standardised by date (day 1 = earliest observation for each stage). Data are derived from colour-banded (New Zealand only) or geolocator-tracked (outside New Zealand) godwits. Boxplots indicate median and 25th and 75th percentiles; whiskers indicate 5th and 95th percentiles; filled circles indicate more extreme values; overlapping points are offset for clarity. **(b)** Individual consistency in timing (boxplots; difference between dates in successive years) for geolocator-tracked godwits, compared to total population spans (bars) shown in **(a)**. Boxplots indicate median and 25th and 75th percentiles; whiskers indicate entire range of values. Circles indicate greatest (open) and least (filled) within-individual differences in the larger sample of colour-banded (CB) birds (New Zealand only; sample sizes shown). For stages in New Zealand, light grey bars indicate the proportion of variation observed among colour-banded birds that was not present in the smaller geolocator sample (dark grey bars). Geolocator (GL) sample sizes = individuals observed in two successive years (boxplots)/total individuals (dark grey bars).

For each stage, we calculated repeatability (intra-class correlation coefficient, r; Lessells and Boag 1987) ± SE (Becker 1984) of individual timing for all godwits with two years of data. For comparison, we calculated r separately for all colour-banded godwits and the subset of geolocator-tagged birds.

Results

Variation with proximity to breeding

Population variation was least in events leading up to the breeding season (Figure 7.2a): during stages from spring departure from New Zealand through the onset of breeding, the earliest and latest individuals differed by only 23–31 d, compared to spans of 30–78 d for other post-breeding events in Alaska and New Zealand. Population spans decreased chronologically from post-breeding departure to start of incubation (Spearman-rank correlation, one-tailed: $r_s = 0.71$, $n = 13$, $P = 0.003$). When considered separately, movement spans decreased chronologically ($r_s = 0.77$, $n = 8$, $P = 0.013$) but moult spans did not ($r_s = -0.45$, $n = 4$, $P = 0.28$).

In general, individual godwits were extremely consistent in timing (Figure 7.2b): in every stage, some individuals differed by only 0–2 d between years. Individual variation was least for movements toward the breeding grounds, with median differences of only 2.0–3.5 d between years. The greatest individual differences were only 4–10 d in pre-breeding movements, compared to 9–43 d in post-breeding events in Alaska and New Zealand; accordingly, variances differed significantly among annual events (Brown-Forsythe test: $F_{12,29} = 4.44$, $P = 0.001$). Individual variation (mean, standard deviation [SD], and maximum values) decreased chronologically from post-breeding departure to start of incubation (Spearman-rank correlations, all tests $P \leq 0.016$); considered separately, this was true for movements (all tests $P \leq 0.005$) but not for moults (all tests $P \geq 0.20$).

Moults versus movements

Among stages, population and individual variation were strongly correlated ($r = 0.778$, $n = 13$, $F = 16.92$, $P = 0.002$) and were greater for moults than for movements (Figure 7.3). Mean population spans were 68.3 d for moult parameters and 34.8 d for movements (Mann-Whitney test: $U = 2.39$, $n = 12$, $P = 0.017$). Individual variation was also greater for moults than for movements (Mann-Whitney tests of mean, SD, and max; all $P = 0.033$–0.041); these differences were more profound when post-breeding departure was excluded (all tests $P = 0.006$).

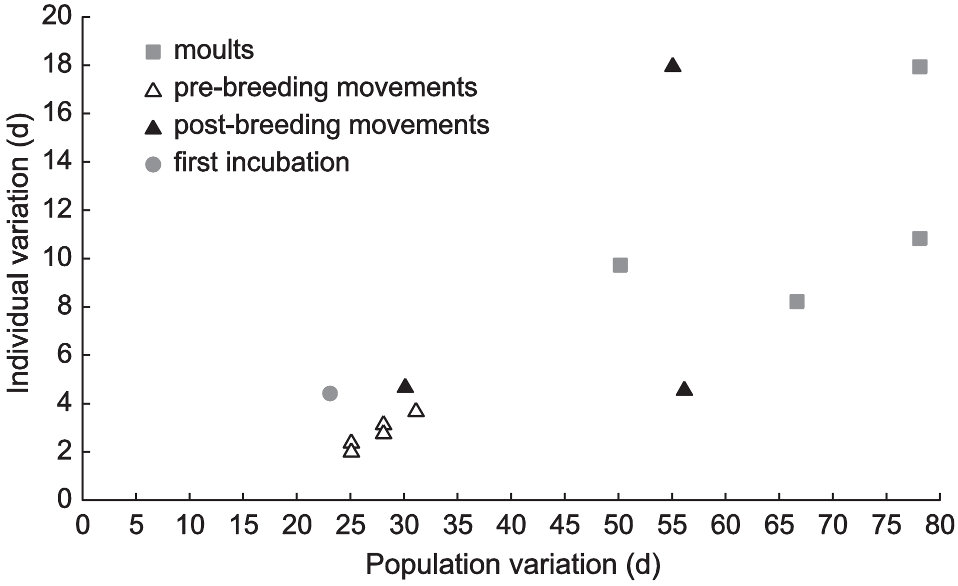

Figure 7.3 Moults were more loosely scheduled than movements at both the population and individual levels. For each stage, population variation represents the difference (in days) between the earliest and latest individuals (from Figure 7.2b). Individual variation indicates the mean difference between years for all individuals (2-year geolocators only; n = 6–8; see Figure 7.2b).

Individual repeatability

Among geolocator-tagged godwits with two years of data, individual repeatability was uniformly very high for timing of spring movements and somewhat lower for autumn migration and initiation of pre-breeding moult (Table 7.1); repeatability was not significant for other moult parameters, incubation, or departure from breeding sites. The larger sample of colour-banded godwits demonstrated significant repeatability in all stages in New Zealand (Table 7.1), and again this was higher for spring departure than for autumn arrival. Repeatability of pre-breeding moult initiation was very high, and substantially higher than other moult parameters.

Discussion

Despite the importance of considering specific stages in the context of the entire annual cycle (McNamara and Houston 2008), few migration studies have empirically addressed the timing of movements in more than one season, and none has additionally included scheduling of

Table 7.1 Individual repeatability of timing of key events throughout the annual cycle of Bar-tailed Godwits. Significant results are indicated in bold.

	Geolocator-tagged only					All colour-banded				
	n	*r*	SE	*F*	*P*	*n*	*r*	SE	*F*	*P*
Depart breeding grounds	6	0.47	0.26	2.8	0.12					
Depart Alaska	8	**0.77**	**0.11**	**7.8**	**0.005**					
Arrive New Zealand	8	**0.77**	**0.11**	**7.7**	**0.005**	44	**0.66**	**0.06**	**4.9**	**<0.001**
Start wing moult	7	0.44	0.25	2.6	0.12	40	**0.53**	**0.08**	**3.3**	**<0.001**
Finish pre-basic moult	8	0.37	0.25	2.2	0.15	45	**0.53**	**0.08**	**3.3**	**<0.001**
Finish wing moult	7	–0.23	0.52	0.6	0.71	34	**0.55**	**0.09**	**3.5**	**<0.001**
Start pre-breeding moult	8	**0.76**	**0.11**	**7.3**	**0.006**	47	**0.91**	**0.02**	**20.3**	**<0.001**
Depart New Zealand	8	**0.86**	**0.07**	**13.2**	**0.001**	49	**0.82**	**0.03**	**10.3**	**<0.001**
Arrive Yellow Sea	8	**0.90**	**0.05**	**19.3**	**<0.001**					
Depart Yellow Sea	8	**0.92**	**0.04**	**24.7**	**<0.001**					
Arrive Alaska	8	**0.89**	**0.05**	**17.4**	**<0.001**					
Arrive breeding grounds	8	**0.91**	**0.05**	**21.4**	**<0.001**					
First incubation	7	0.35	0.28	2.1	0.18					

moults and breeding for a comprehensive view of temporal variation throughout the year. Using a combination of direct observation and geolocator data, we present a unique view of year-round temporal variation for a set of migratory individuals, placed within the context of population-level patterns. In our study, Bar-tailed Godwits were remarkably consistent in timing of spring movements toward the breeding grounds, but showed greater flexibility in timing of post-breeding movements and moults. These results supported two hypotheses: at both population and individual levels, schedules generally tightened as the breeding season approached, and migratory movements were more precisely scheduled than moults.

Variation with proximity to breeding

The idea that time constraints for migratory birds increase with proximity to the breeding season has a wealth of theoretical support (Alerstam and Lindström 1990, McNamara *et al.* 1998), but surprisingly little empirical evidence derived from year-round data from a single population. Previous studies have shown that individual timing is more consistent for spring migration than autumn migration (Rees 1989, Alerstam *et al.* 2006, Egevang *et al.* 2010, Vardanis *et al.* 2011), and that timing becomes increasingly precise in successive stages of spring migration, at either the individual (Bety *et al.* 2004) or population level (Warnock and Bishop 1998, Farmer and Wiens 1999, Battley *et al.* 2004, Warnock *et al.* 2004). Our data confirm that stages of spring migration are the most tightly scheduled of the entire year, viewed at both the individual and population scales. We have previously reported extraordinarily high individual consistency of departure from New Zealand for this population (Battley 2006, Chapter 4), but schedules became even more finely tuned later: all eight geolocator-tracked godwits departed the Yellow Sea in windows of only 1–4 days across two years (Figure 7.2b). Population spans also decreased across stages of spring migration, from 28–31 days for the initial flight from New Zealand to just 25 days for the second flight to Alaska. It is interesting that individual variation was least for Yellow Sea departure, rather than for breeding arrival or incubation. This supports the view of long-distance flights as 'hard-wired' and endogenously programmed according to long-term environmental patterns (Piersma *et al.* 1990a), as opposed to breeding phenologies, which are more dependent on annually variable local conditions (Meltofte *et al.* 2007a, Smith *et al.* 2010). Remarkably, start of incubation differed between years by just 0–2 days for five of seven godwits; differences of 8–18 days for two others may represent delays in mate acquisition or loss of a clutch prior to incubation.

Moults and post-breeding movements generally had population spans 2–3 times those observed for spring migration (Figure 7.2). Differences in individual variation between autumn and spring migration were perhaps not as great as expected, given the unclear fitness benefits of arrival timing on wintering grounds. Each year of our study, 92–96% of colour-banded godwits arrived in a 32-day span ending by 4 October, and the remainder trickled in over the subsequent four weeks. Because our relatively small geolocator sample failed to capture this tail of variation represented by late-arriving birds (Figure 7.2b), we do not know how much variation in New Zealand arrival is explained by late departures from Alaska, as opposed to delays or detours *en route* (Gill *et al.* 2009).

Moults versus movements

Temporal variation in moults was generally greater than in movements at both the population and individual levels (Figure 7.2); this presumably reflects differences in both regulatory mechanisms and selection consequences of moults and movements. Migration timing has theoretical and demonstrated consequences for subsequent activities such as breeding (Alerstam and Lindström 1990, Møller 1994) and moults (Holmgren and Hedenström 1995, Barshep *et al.* 2011b), and timing of protracted trans-oceanic flights (9,000–12,000 km non-stop for New Zealand Bar-tailed Godwits; Gill *et al.* 2009, Battley *et al.* 2012) may have direct survival consequences, particularly if wind assistance is necessary for successful migration (Liechti 2006). Fitness consequences of moult timing are less clear (but see Dawson *et al.* 2000); moult is typically seen as flexible, with birds adjusting both timing and duration to keep to their annual schedules (Noskov *et al.* 1999, Helm and Gwinner 2006).

In this godwit population specifically, within-individual variation in timing of autumn migration carried over to moult schedules in New Zealand, but timing of spring migration was unresponsive to variation in preceding life-history stages (Chapter 6).

It is surprising that timing of moults in New Zealand did not tighten with proximity to the breeding season. High individual variation in completion of pre-basic moult was as expected; like departure from the breeding grounds (by far the most flexible annual movement in our study), initiation of this moult is strongly associated with cessation of breeding activity (Hahn *et al.* 1992, Dawson 2006, Mitchell *et al.* 2012), which may vary by more than eight weeks in this population, due to differences in laying date and breeding success (Chapter 2). However, individual variation in pre-breeding moult initiation was greater than expected, given its presumably strict photoperiod control (Noskov *et al.* 1999) and proximity to the very tightly scheduled spring migration. The cause of this variation is unclear, but it had no apparent effect on subsequent plumage or migration (Chapter 6).

Geolocator data included all major annual movements, but we could not evaluate two moult stages that occur in the Northern Hemisphere: initiation of pre-basic moult in Alaska and completion of pre-breeding moult in Asia (Chapter 5). If these are respectively the most and least variable moult parameters of the year (which is plausible), moult schedules could show significant tightening toward the breeding season with their inclusion.

Problems with repeatability

With increasing interest in how flexible individuals are in variable circumstances (e.g., climate change), there is a growing desire to describe the consistency with which individuals perform certain annual tasks, and to make direct comparisons within and among studies. In bird migration literature, repeatability (intra-class correlation coefficient, r; Nakagawa and Schielzeth 2010) is becoming standard for representing the consistency with which individuals perform, but it is not precisely a measure of that; rather, it indicates how consistently individuals differ from each other. This is the variable of interest in some studies (for instance, as an indication of the upper bound of heritability; Nakagawa and Schielzeth 2010), but it unfortunately tells us little about *absolute* consistency, which may be of greater interest to many migration studies. The problem is that r combines population and individual variation to arrive at one value, and thus obscures two parameters that may signify fundamentally different things about the constraints and selection forces in play. This renders r values essentially incomparable, even among parameters within a single study.

In our data, the problem is exemplified by the repeatability of pre-breeding moult initiation among all colour-banded godwits (Table 7.1). The very high r (0.91) implies extraordinary individual consistency in timing, but in fact the individual variation in this parameter is higher than in migratory arrival and departure, which counter-intuitively show lower repeatability values. This apparent paradox results from the relatively high population variation in pre-breeding moult initiation; due to a wide range of moult strategies in the population (Chapter 5), individuals are more consistently different from each other while being less consistent individually than in other parameters. For this reason, we propose that authors should not report repeatability values without presenting accompanying descriptions of absolute variation at the population and individual levels, as we have in Figure 7.2. This will be a step toward understanding the biological significance of within- and between-study differences in repeatability.

Our data also demonstrate the problem of comparing *r* values derived from different sample sizes. Both our geolocator-only and larger colour-banded samples indicate that moults in New Zealand are generally less repeatable than movements (Table 7.1), but three parameters that had strongly non-significant *r* values in the former dataset appeared highly repeatable in the latter dataset. Beyond the obviously greater statistical power afforded by larger samples even when effect sizes are identical, *r* values also naturally increase as more of the total population variation is described in the sample (because *r* is driven by the ratio of population to individual variation). This is a particular problem for comparing *r* values currently available in migration literature, because multi-year individual studies made possible by recent advances in geolocation and satellite-telemetry typically contain small samples (Alerstam *et al.* 2006, Vardanis *et al.* 2011) that cannot describe total population variation as completely as studies based on large samples of marked individuals (Rees 1989, Battley 2006).

Individual versus population variation

The greatest understanding of variation, and the selection forces implied by it, comes from considering the two components of repeatability (population and individual variation) separately. Because the fitness of migratory animals can be particularly sensitive to fine-scale timing of certain life-history stages, migration research has been especially focused on describing ‘optimal’ timing and assessing the propensity of individuals to achieve it. Variation in an individual’s performance results from the interaction of a number of factors, including: (1) environmental variation; (2) fitness consequences of this variation; (3) availability of relevant cues; and (4) the degree of flexibility afforded by control mechanisms and available resources. Thus, individual variation comprises both what an individual *should* do and what it *can* do. Concluding that individual consistency implies strong selection for that trait is somewhat simplistic, as consistency may also result from failing to change when circumstances call for it; this may persist unless it is strongly maladaptive. For example, despite annual variation in breeding phenologies, spring movements of long-distance migrants may be very consistent largely because relevant cues are not available from their non-breeding grounds. Thus, rigidity, although not precisely optimal, is the best long-term strategy available to them.

As we have defined it, population variation necessarily contains all within-individual variation, but additionally includes between-individual differences. Thus, the difference between population and individual variation essentially represents the system's tolerance for persistent differences in performance (e.g., due to available resources or intrinsic 'quality') and strategy (e.g., by sex, age, or geographic region). For New Zealand Bar-tailed Godwits, timing differences among individuals contain 3–4 weeks of variation related to breeding site phenology: due to relative timing of spring thaws, godwits breeding in northern Alaska migrate later than southern breeders in both spring and autumn (Chapter 2), and timing of moults show roughly corresponding differences (Chapters 5–6). Accordingly, minimum population spans of nearly a month are expected for all stages, even before additional variation based on individual performance is considered. For spring movements to the breeding grounds, population spans of 25–31 days approached this minimum expected window, reflecting very precise scheduling at the individual level. By contrast, some population spans found in moults (up to 78 d) are greater than accounted for by breeding latitude and individual variation combined, and thus suggest greater tolerance for strategic differences within the population. For godwits, profound sexual dimorphism and within-sex variation in size and plumage (Chapter 3) give rise to a wide range of moult schedules in terms of duration and extent (Chapters 5–6), whereas no significant sex differences in migration timing have been observed in this population (Battley 2006, Chapters 4–5).

Future directions

Although we expect that progressively tightening schedules leading up to breeding are general to migratory birds, some of the patterns we demonstrate may be peculiar to extreme long-distance migrants, or to this particular godwit population. For instance, the autumn migration of Alaskan Bar-tailed Godwits is unique in that it typically covers 11,000–12,000 km in a single non-stop flight of 8–10 days (Gill *et al.* 2009, Battley *et al.* 2012), the timing of which depends primarily on breeding latitude (Chapter 2) and the occurrence of favourable weather systems (Gill *et al.* 2009). These factors contribute to a surprisingly rigid autumn migration: the median individual between-year difference was just 4 days and most of the population arrived in New Zealand in a span similar to that of spring departure (Figure 7.2b). We expect differences between spring and autumn to be much more profound in systems in which timing or duration of autumn migration is strongly influenced by extent of prior breeding investment (Barshep *et al.* 2011a) or annual variation in conditions at staging or stopover sites (Weber *et al.* 1998b). In terms of moults, birds wintering in the northern temperate zone may be more time-constrained than godwits in New Zealand, because mid-winter periods of inclement weather and low prey availability may be incompatible with moult (Holmgren and Hedenström 1995). Year-round comparative studies among species along a continuum of time and energy constraints will greatly enhance our understanding of both evolutionary adaptations to the migratory lifestyle at the species level and smaller-scale variation that may result from differences in individual personality and experience.

The aim of most contemporary studies of temporal variation is to ascertain levels of flexibility to address stochastic or directional environmental change. Cross-seasonal and cross-species comparisons of temporal variation are certainly a step toward understanding flexibility inherent in systems and identifying specific stages prone to critical time-constraints and seasonal carry-over effects. For migratory birds, however, there has been a general lack of relevant long-term studies; due to the logistical difficulties of tracking individual migrants, few studies have contained individual data spanning more than 2–3 years. Unfortunately, because both individual behaviour and environmental conditions are more likely to be consistent in consecutive years than over longer periods (Catry *et al.* 1999), short-term studies may misrepresent the flexibility of a system. For our study, individual and population spans of variation would necessarily increase with additional years of data, but the extent of increase should vary among stages. For instance, we would predict start of incubation, which varies directly with local conditions on the breeding grounds, should show a greater long-term increase in overall variation than long-distance movements, which vary little with annual conditions. In a long-term study, temporal variation in certain annual events will respond to persistent environmental change while others may not, and this will help identify the life-history stages most prone to critical timing mismatches.

Chapter 8

Synthesis: an evolving view of long-distance migration

Key findings of this thesis

The aims of this research were to determine the factors leading to both persistent and ephemeral differences in plumage and migration timing among individual Bar-tailed Godwits, and to identify possible constraints or bottlenecks in the annual cycle. Each of six research chapters addressed different key questions arising from these central goals.

In ***Chapter 2***, I found that an individual's migration schedule was linked to the location of its breeding site in Alaska, with northern breeders migrating later than southern breeders on each stage of both northbound and southbound migrations. In addition to explaining the 4–5 weeks of variation in timing of migratory departure, this showed that schedule differences observed in New Zealand persist throughout the six months that godwits spend in the Northern Hemisphere.

Adopting an Alaskan perspective for ***Chapter 3***, I found that the population was structured geographically in body size and plumage during the breeding season. With increasing breeding-site latitude, godwits of both sexes were smaller, and extent of male breeding plumage increased; however, female plumage was most extensive at mid-latitudes. Interestingly, this population structure did not carry over to the non-breeding season, as individuals from all regions of Alaska appear to mix at New Zealand sites.

In ***Chapter 4***, I showed that godwits have extraordinarily consistent individual schedules when departing New Zealand on migration and that most of the exceptions to this pattern can be explained by birds avoiding unfavourable winds at the start of the northbound journey. A surprising finding was that some godwits departed several days earlier than expected when particularly favourable winds occurred, implying that they were physically ready for migration well before their customary departure dates.

Chapter 5 revealed that individuals with more extensive breeding plumage achieved it by spending more time moulting in New Zealand prior to northbound migration, rather than through faster moult rates or greater investment in moult during their stopover in the Yellow Sea. However, males and females had very different strategies: despite their more extensive breeding plumage, males performed a much higher proportion of their moult in New Zealand, so that females were required to perform twice as much additional moult in Asia as males.

Perhaps the most surprising revelation in my study derived from ***Chapter 6***: variation in timing of arrival after the epic flight from Alaska had no apparent influence on an individual's ability to prepare for the following northbound migration. Late-arriving birds (by 7–34 days) partially compensated for this by moulting their wing feathers faster, but the delays had no effect on an individual's timing of pre-breeding moult, extent of breeding plumage at departure, or timing of departure from New Zealand.

In ***Chapter 7***, I showed that temporal variation at both the individual and population levels generally decreased through successive life-history stages leading up to arrival on the breeding grounds. Scheduling of migratory movements was increasingly rigid from post-breeding events in Alaska through arrival on breeding grounds the following year, but this was not true among successive moults, which were much more loosely scheduled. Northbound migration was even more precisely timed than breeding, consistent with the former's presumed greater reliance on endogenous programming.

Overall, these findings show that Bar-tailed Godwits are very much individuals, and their behaviour, morphology, and schedules cannot be viewed simply as deviation from optimum values. Most of the inter-individual variation observed in New Zealand had its roots in the Alaskan breeding season, indicating that a full annual-cycle perspective is required to understand patterns in any particular season. Furthermore, the precision with which godwits conduct their annual routines, while still demonstrating flexibility to address unpredictable circumstances, challenges us to reconsider the view of extreme long-distance migrants as severely constrained organisms operating at the limits of their capabilities.

Regulation of the migrant annual cycle

My methodological approach to this research was decidedly observational: I sought to understand long-distance migration by simply viewing individual behaviour and moult with a resolution that had never previously been achieved. This approach yielded many surprising and important revelations, but my data cannot directly address the mechanisms underlying the observed patterns. To understand the significance of the godwit's extraordinary annual routine, we must consider how birds in general manage their schedules.

This rich subject is replete with mysteries, but it is clear that regulation of annual cycles involves cooperation between internal programmes and external information gleaned from the environment. Virtually every animal with a lifespan longer than a year displays a cyclical pattern of annual activities (such as breeding and moult) occurring repeatedly in a certain order (Jacobs and Wingfield 2000). Unexpectedly, an individual's innate circannual rhythm does not automatically occur in a regular 365-day cycle, but must be constantly corrected to stay in line with external seasonal patterns (Gwinner 1990). Conveniently, day length, or 'photoperiod', is an entirely reliable external cue, providing a perfect calendar with which to synchronise endogenous rhythms with the natural year. Photoperiodic control of the annual cycle of birds has been firmly established through experimentally demonstrated links with gonadal development, moult, and migratory behaviour (reviewed in Dawson 2008), but it remains unclear whether absolute day length or change in day length is the more important cue. Photoperiod regulates physiological processes through an intricate relationship between photoreceptors in the avian brain (which have yet to be described) and the endocrine system (Dawson *et al.* 2001).

Of course, resources and environmental conditions are not completely predictable, and so an absolutely rigid annual schedule is not always beneficial. For example, if spring arrives earlier or later than expected, a bird should adjust its breeding schedule to best exploit the peak of resources necessary for brood development and survival. In this case, photoperiod information can be supplemented with locally relevant short-term cues, such as temperature, rainfall, or food abundance (Dawson 2008), to refine the timing of specific events. In general, it appears that such fine-tuning must still occur in a framework ultimately controlled by photoperiod (Gwinner 1996); i.e., endogenous programming provides a window in which the event can occur, and other cues influence the exact timing within that window.

Plasticity in timing varies among annual events and within and among species in ways dictated by natural selection. This will influence the extent to which rigid photoperiodic control is tempered by other information. For example, a short-distance migrant may be able to roughly predict the phenology of its breeding site while still at its winter site, due to a correlation between climatic conditions at the two locations (e.g., Järvinen 1989). This bird should accept local information to inform its decision about when to migrate, and we may expect significant annual differences in timing of both pre-migratory fuelling and migratory departure. By contrast, a bird that winters in the opposite hemisphere from its breeding site cannot expect reliable cues about upcoming breeding phenology from its non-breeding site. This bird should ignore local environmental information and prepare for migration according to long-term patterns in breeding-site phenology, and thus may rely entirely on photoperiod (Gwinner 1996) and show less flexibility in schedules (Both and Visser 2001). In both cases, the exact timing of migratory departure may respond to cues at yet another temporal scale, which is daily or hourly conditions. For example, initiating migration in a severe headwind is a poor tactic (Liechti 2006), and so even the rigidly-prescribed departure plan of the long-distance migrant should show small-scale plasticity in this regard.

Because each life-history stage has its own set of available cues, mechanistic constraints, and selection processes, flexibility in timing varies dramatically throughout the year (Chapter 7). Most of our knowledge regarding regulation of specific stages in birds comes from passerines

(Dawson 2008), which perform well in captive experiments, but some relevant work has been conducted with shorebirds (Cadee *et al.* 1996, Piersma 2002, Piersma *et al.* 2008). There has been no formal study of how specific stages are regulated in Bar-tailed Godwits. Based on general knowledge of regulation in birds generally and biology of Bar-tailed Godwits specifically, Table 8.1 summarises, in broad terms, the factors potentially involved in the timing of key events throughout the year. Post-breeding events (movement to staging grounds and initiation of pre-basic moult) are expected to be the most temporally variable, as they are associated with the cessation of breeding, which contains substantial variation based on breeding success. However, there may be very different regulatory mechanisms at work, as post-breeding dispersal is a behavioural 'decision' based on the lack of young to care for, and pre-basic moult is a physiological response related to the endocrinology of gonadal regression (Dawson 2006). Although wing moult is generally considered an integral part of pre-basic moult (Humphrey and Parkes 1959, Howell 2010), godwits and other long-distance migrants illustrate that the two are somewhat modular in both timing and control mechanisms (Piersma *et al.* 2008). Initiation of wing moult appeared to be primarily governed by timing of arrival on non-breeding grounds (Chapter 6), and so may be related to hormonal changes associated with the cessation of migratory flight. Arguably, initiation of migratory flights should be the least flexible, as they are under more strict photoperiodic control and may vary primarily with daily weather conditions. We saw in Chapter 4, however, that even the most rigidly-scheduled

Table 8.1 Factors thought to influence the timing of key events throughout the year for New Zealand Bar-tailed Godwits. Seasonal local cues include weekly or monthly weather, food availability, etc. Daily local cues include hourly or daily weather, behaviour of conspecifics, etc.

	Regulation of start		**Regulation of end**
	Primary cue	**Secondary cue**	**Primary cue**
Depart breeding	end breeding	—	—
Pre-basic moult	end breeding	—	photoperiod
Flight Alaska–New Zealand	photoperiod	daily local	weather *en route*
Wing moult	arrive NZ	—	photoperiod
Pre-breeding moult	photoperiod	—	photoperiod
Flight New Zealand–Yellow Sea	photoperiod	daily local	weather *en route*
Flight Yellow Sea–Alaska	photoperiod	daily local	weather *en route*
Arrive breeding	seasonal local	—	—
Breeding	seasonal local	daily local	breeding success

movements may show surprising flexibility in extreme weather. On northbound migration, final movements to breeding sites after brief stopovers in southwestern Alaska should vary more than the major migratory flights, because godwits may receive local cues to breeding-site phenology, which may vary annually by days or even weeks (Meltofte *et al.* 2007a, Tulp and Schekkerman 2008). The initiation of a clutch of eggs may vary still more, due to the additional influence of unpredictable social factors such as acquiring a mate and performance of pre-copulatory rituals.

Photoperiod also has a role in the way some stages are performed after their initiation, and thus influences the timing of termination as well. Experimental changes in photoperiod have been linked changes in moult rate (Hall and Fransson 2000, Dawson 2004); it appears that photoperiod is the cue late-moulting birds use to adjust moult rate to make up time (as godwits did in Chapter 6). In some species, individuals that are running late on migration are similarly urged by photoperiod to 'hurry up' during later stages of migration (e.g., Fransson 1995). Increasing the speed of migration may be possible for short-hop migrants that incorporate several staging episodes into their journey, but appears unfeasible for those, like godwits, that migrate in only one or two major flights. Once a godwit embarks across the Pacific from Alaska, it may have little control of its own speed. After initiation of such flights, weather encountered during the flight is probably the greatest source of additional variation before arrival (Gill *et al.* 2009, Shamoun-Baranes *et al.* 2010).

Most of this generally agrees with the patterns of temporal variation I found across the annual cycle of godwits (Chapter 7). One stage is puzzling, however: pre-breeding moult. Presumably, initiation of this moult is associated with gonadal maturation in advance of the breeding season (Peters *et al.* 2000). In some passerines, non-photoperiodic cues have been implicated in gonadal maturation (Dawson 2008), suggesting that not just the act of breeding but the readiness to breed can be influenced by environmental variation. However, I have suggested that relevant phenological cues are unavailable to non-breeding godwits, and have shown that pre-breeding moult is unresponsive to timing of both migratory arrival and wing moult (Chapter 6). Despite this, intra-individual variation in initiation of pre-breeding moult was much greater than that of northbound migration or breeding itself (Chapter 7). Furthermore, this temporal variation (up to 28 days) had no apparent consequence, as it did not affect extent of breeding plumage at departure from New Zealand (Chapter 6). The mechanisms and functional significance of this await explanation. It is possible that the first evidence of pre-breeding moult (visible emergence of new breeding feathers) is not a perfect indicator of the initiation of the moult process.

How are individually-optimised schedules maintained?

A separate question from how annual routines are generally regulated is how distinct routines within a population are maintained. External cues may provide a perfect calendar and roughly predict future resource phenologies, but an individual must still determine how this information applies to its own specific strategies. For simplicity, let's assume that photoperiod alone informs migration timing and that all godwits breeding at a given latitude in Alaska migrate at precisely the same time. Obviously, all the birds at the same New Zealand site are exposed to the same external information (e.g., 'It is March 13'), but respond differently; those intending to migrate on March 13 do so, while later migrants remain and await their turn. In this example, all birds receive the same cue, but somehow either perceive the cue differently or employ different thresholds for translating the information into action. Now imagine the thousands of 'March 13' godwits that are scattered at different New Zealand sites across 12° of latitude. Birds at different sites experience different day lengths, but are able to judge date correctly by somehow accounting for their own geographic position. That they do this is supported by the very similar population-level departure windows observed at different sites across New Zealand (Battley 1997, 2006, Chapter 4). These same issues occur in Alaska as well: during the breeding season, birds are scattered across a range of latitudes with different breeding phenologies and experience very different day lengths (including 24-hour daylight in the northern half of the range). After breeding, the entire population congregates in a small geographical area before southbound migration, but retains individual departure schedules despite receiving similar photoperiod cues.

Setting aside how a bird knows its own position on the globe, how are godwits 'programmed' with their individual schedules? Certainly we expect there to be a genetic component. Heritability of migratory traits such as timing and direction has been demonstrated in a number of bird species (Pulido 2007), although the genetic basis for individual variation in migration remains somewhat poorly studied (van Noordwijk *et al.* 2006). In Bar-tailed Godwits, migration timing, body size, and plumage all varied geographically within Alaska, and this suite of potentially co-evolved traits could be inherited together, or each could result from independent underlying mechanisms. Geographic variation in genotype can be maintained by 'isolation-by-distance' in highly structured populations or by geographic clines in polymorphic allele frequencies even when gene flow is high (Endler 1977). Particularly intriguing is the discovery of 'clock genes', providing a molecular basis for the timing of annual events (Tauber and Kyriacou 2005). Polymorphism in clock genes has been preliminarily identified in Bar-tailed Godwits (A. Fidler pers. comm.) and could hold the key to understanding individual schedules in this population. Latitudinal clines in clock gene polymorphisms have been demonstrated in birds (Johnsen *et al.* 2007), fish (O'Malley and Banks 2008), and flies (Costa *et al.* 1992), and there is evidence that stable clines can be maintained by selection for local adaptation, as opposed to genetic drift (O'Malley *et al.* 2010).

Alternatively, persistent individual differences need not be inherited in the traditional sense. The expression of a single genotype may be altered by epigenetic factors during cellular development (Jaenisch and Bird 2003) or by later facultative phenotypic responses to the environment (Piersma and Drent 2003). Thus, a godwit's early environment may permanently imprint upon it certain behavioural or physiological routines and the sensory mechanisms required to maintain them. Experiments with mice have shown that photoperiods experienced perinatally can permanently entrain an individual's responses to seasonal photoperiod changes (Ciarleglio *et al.* 2011). This provides a potential mechanism for godwits hatched at a given latitude to return there at the appropriate time every year.

It is also possible that some aspects of migration are learned. Particularly in the case of specific migration routes and stopover sites, a bird may engage in some level of experimentation and generally repeat what has worked in the past. However, stable social associations did not appear to influence timing of Bar-tailed Godwit migration, despite the gregarious nature of the birds. Scolopacid family groups do not persist in the non-breeding season; members of breeding pairs may winter hundreds or thousands of kilometres from each other (Nebel *et al.* 2002, Gunnarsson *et al.* 2004), and godwit adults migrate separately from juveniles (McCaffery and Gill 2001). Subgroups in non-breeding sandpiper populations generally appear to represent ephemeral and fluid daily associations, rather than a persistent social organisation (Myers 1983, Conklin and Colwell 2008). Accordingly, godwits in my study did not migrate consistently with the same other birds each year, despite each being very consistent in departure date (Chapter 4). The decision to depart on migration was very much an individual action.

How 'close to the edge' are long-distance migrants?

One of the key tenets of ecology is that organisms are constrained. Existence is full of trade-offs, and there is always an array of obstacles standing between an individual and its optimal performance. Constraints, which may be temporal, environmental, physiological, or social, have been the cornerstone of wildlife research and conservation because of their central role in natural selection and the success of both individuals and populations. Migratory birds are often portrayed as models of constrained organisms, because their lifestyle of travelling to exploit seasonal resources naturally imposes substantial temporal and energetic demands

(Alerstam and Lindström 1990) that require a finely-tuned suite of behavioural and physiological adaptations to overcome (Hedenström 2008). These demands only become more profound as migration distance increases. Long-distance migrants typically breed at high latitudes, where brief, intense resource blooms make timing of migration and breeding even more critical (Tulp 2007). To make their epic flights, they accumulate large fuel stores and undergo other physiological changes to optimise flight performance (Piersma and Gill 1998, Battley *et al.* 2000, Landys-Ciannelli *et al.* 2003). They often cross vast, inhospitable barriers such as oceans, deserts, or mountain ranges without the option of resting or refuelling along the way (Henningsson and Alerstam 2005), and may enter circumstances of unknown predation danger and resource availability. These factors combine to create an annual routine with seemingly little room for error.

At the extreme end of this continuum, New Zealand Bar-tailed Godwits seem to approach the limits of physical performance (Hedenström 2010). But just how constrained are they? By considering their behaviour and performance in certain stages throughout the year, we can ask if and when godwits conform to expectations for birds operating close to their limitations.

Annual survival

First of all, they have very high annual survival. Mark-recapture studies have recorded individuals of the Alaska-breeding Bar-tailed Godwit population at minimum ages of 21 years in New Zealand (A. Riegen pers. comm.) and 20–24 years in southeastern Australia (C. Minton pers. comm.). There is no reason to think this approaches the limit. Bar-tailed Godwits in the United Kingdom, where banding has occurred for a much longer period, have reached 33 years of age (WWRG 2011), although this population (*L. l. lapponica*) has a much shorter migration. At my study site, the average annual return rate of individually marked godwits was 90% (86% in 2008, 93% in 2009, and 90% in 2010). When you consider that this figure includes all possible causes of disappearance, such as accidents, hunting, depredation, and simply choosing another non-breeding site, it is clear that very little mortality results from godwits being physically overcome by their migrations. Three times per year, these birds fling themselves over vast spans of open water, with only their wings and fuel stores to fend off whatever meteorological challenges the Pacific Ocean can throw at them. And yet they seem to do just fine.

Flight distance

The longest non-stop avian flight ever recorded was that of the famous ‘E7’, a satellite-tagged female godwit from the Firth of Thames that flew 11,690 km on a reasonably direct course from southwestern Alaska back to the site of her capture in New Zealand (Gill *et al.* 2009, Battley *et al.* 2012). This is impressive, but actually is fairly close to the minimum necessary to travel from Alaska to New Zealand in a single flight. There is plenty of indirect evidence that tens of thousands of godwits make longer flights than this every year, and in fact fly farther than they have to. Most geolocator-tracked godwits in my study (7 of 10 in 2008, 9 of 9 in 2009) appeared to fly directly to Foxton from Alaska, a trip approximately 400 km longer than E7's flight. Even godwits that stop somewhere else *en route* do not always do so in order to shorten the trip: one bird in my study routinely travels hundreds of kilometres *past* the North Island on southbound migration and spends a month or more at the Avon-Heathcote estuary near Christchurch, before returning to Foxton. If the southbound flight approached the maximum capabilities of godwits, we would expect many or all South Island birds to stop for rest and recovery at North Island sites before continuing south. However, despite enthusiastic colour-band resighting efforts every year at major northern sites (e.g., Manukau Harbour and the Firth of Thames) during migratory arrival, only a handful of godwits colour-banded on the South Island are ever encountered at these sites (Battley *et al.* 2011). I have never seen one at my study site in four years. It is also worth noting the location of the start of the southbound flight. As most of the population does every year, E7 departed Alaska from the southwestern coast of the Yukon-Kuskokwim Delta, rather than from apparently suitable sites farther south on the Alaska Peninsula, approximately 400 km along her flight path. None of this suggests that godwits are attempting to minimise the length of this extraordinary flight.

Carry-over effects

Surprisingly, godwits also rarely choose to not to migrate. When I first conceived my study, I thought that close monitoring of godwits throughout the non-breeding season would help me explain why certain individuals did not migrate each year, thus identifying the system's effective limits. For example, I might be able to trace a departure 'failure' back to a very late arrival or moult, and this would suggest a bird had insufficient time or energy to prepare for migration. Four migrations later, not a single adult godwit ever failed to depart my study site. As detailed in Chapter 6, even godwits arriving or moulting 30–45 days later than expected still made timely departures the following season without any compromise to their breeding plumage. Surely, there must be limits. Every year, small numbers of apparently adult godwits remain in New Zealand during the northern summer (P. Battley unpubl. data), and these are presumably birds whose health or advanced age has caused them to forego breeding. But these are clearly in a small minority—most godwits simply get the job done every year. The precision with which they perform it (Chapters 4 and 7) additionally suggests that they have little trouble doing it well.

Fuelling

Other signs that the performance of godwits may not be tightly constrained are more subtle, but perhaps no less instructive. A substantial body of literature has focused on the idea that birds accumulating fuel for migration must balance this task with the costs of carrying the extra weight (Hedenström and Alerstam 1992, Witter and Cuthill 1993, Weber *et al.* 1998b), which include reductions in flight performance and ability to escape avian predators. This predicts that birds should fuel as quickly and as late as possible, to reduce the amount of time spent in heightened danger. An even larger body of literature has focused on the difficulties of attaining optimal mass for migration, due to ephemeral peaks of fuelling resources (Atkinson *et al.* 2007), direct competition with conspecifics or other species (Schneider and Harrington 1981, Moore and Yong 1991), and physiological constraints such as digestive bottlenecks (McWilliams and Karasov 2005). These seem like particularly serious concerns for birds fuelling for a 9,000–10,000 km non-stop flight. However, none of them appeared to seriously trouble godwits in my study. New Zealand lacks any important avian predators for shorebirds, and so there may be little cost to carrying extra mass well before migration. Perhaps as a result, godwits fuel very slowly, starting as early as late December (Anderson 2003), which is approximately three months before northbound migration. I did not specifically measure foraging effort in my study, but increases in foraging leading up to migration (Zwarts *et al.* 1990a) were not conspicuous at the estuary. Throughout March, many godwits routinely stayed at high-tide roosts even as the mudflat was exposed by the falling tide, and could often be found roosting even at low tide, suggesting they were not under great pressure to maximise their foraging opportunities just before migration. Consistent with this, some godwits appeared to depart 1–2 weeks earlier than usual to take advantage of unusually strong tailwinds (Chapter 4); this implies they were sufficiently fat well before their expected departure dates. At this estuary, a one-year study of the godwits' main polychaete prey *Nicon aestuariensis* revealed a moderate decline in biomass from January–March (Powell 2011), but natural fluctuations or reduction by foraging shorebirds did not appear sufficient to threaten a godwit's ability to fuel for migration.

The situation may be different during fuelling for southbound migration, as southwestern Alaska features many avian predators, such as falcons *Falco* spp. and jaegers *Stercorarius* spp., which routinely attack shorebirds conspicuously assembled at coastal mudflats. Regardless, godwits may fuel quite slowly in Alaska as well, as geolocator-tracked birds moved to post-breeding staging grounds as early as 88 days before they departed Alaska. However, those that appeared to incubate eggs until hatching moved to staging grounds only 40–65 days before departure. Successful breeders may begin fuelling later and be required to fuel at faster rates than failed breeders, or they may begin gaining mass while still attending broods on their breeding grounds. In any case, breeding success did not appear to significantly influence a godwit's ability to fuel sufficiently, as departure timing was unaffected (Chapter 2). Furthermore, the demands of fuelling for the >11,000 km southbound flight do not preclude a concurrent moult, as all godwits arriving in New Zealand had already finished 50–90% of their pre-basic contour feather moult (Chapter 5). These observations may testify to very high productivity of the mudflats they use for fuelling; it appears that nearly all Alaska-breeding Bar-tailed Godwits (this study and Battley *et al.* 2012) congregate before migration near Kuskokwim Shoals (59.83ºN, 164.13ºW) along a stretch of coastline <200 km long.

Migratory birds routinely perform feats previously thought beyond their capabilities (Hedenström 2010), and force theoretical models to change to fit empirical observations they couldn't otherwise explain (e.g., Pennycuick and Battley 2003). We may never find a more extreme example of endurance flight than New Zealand Bar-tailed Godwits, simply because the geography of the earth doesn't present many scenarios in which such a flight is required (Hedenström 2010). This does not necessarily suggest that birds are demonstrating the greatest performance that physics and physiology will allow. Viewing their annual routines as I have in this study, I failed to identify a point at which godwits were clearly pushed to the limits of their capabilities. Of course, it would require long-term data on survival and reproductive success to honestly evaluate how their performances translate to overall fitness. But I believe Bar-tailed Godwits encourage us to revisit the traditional view of long-distance migrants as severely constrained creatures perpetually operating at maximum capacity.

By monitoring changes in any of the life-history parameters discussed above, we might be alerted if changing circumstances actually push godwits to their limits. Unfortunately, we may have many future opportunities to assess how close migratory birds are to critical tipping points, as we witness their responses to continuing climate change (Crick 2004) and human-induced modification of habitats. Bar-tailed Godwits may be particularly vulnerable to negative effects of climate change if rigid, endogenously programmed migration schedules preclude their ability to adapt to changing phenologies at breeding or fuelling sites (e.g., Both and Visser 2001). Also, predictable long-term weather conditions may have contributed to the evolution and persistence of certain migratory strategies (Liechti 2006). If changes in prevailing wind patterns reduce the tailwind assistance available to godwits during their flights, they may require more fuel for migration or suffer reductions in flight range. Although the remote and largely inaccessible breeding range of this godwit population is relatively free from direct human impacts, critical staging areas in the Yellow Sea are under great threat of development and habitat loss (van de Kam *et al.* 2010), which could severely constrain the migrations of many shorebird species in the East Asian-Australasian flyway.

The role of individual quality

The relative ‘quality’ of individuals is a topic closely associated with constraints on optimal performance. An individual’s condition, whether this is an innate or acquired state, will naturally influence its ability to survive and reproduce in whatever circumstances befall it. In birds, two relevant phenomena are so commonly observed that they have become axiomatic: higher-quality individuals have better breeding plumage, and they also migrate earlier.

In mate competition, individuals of the competing sex typically display behavioural or physical attributes that signal their quality to potential mates and rivals. In birds, the size and intensity of plumage ornaments have been demonstrated to honestly signal individual quality, through demonstrated correlations with immunocompetence (Folstad and Karter 1992, Dufva and Allander 1995), parasite loads (Figuerola *et al.* 2003), parental investment (Keyser and Hill 2000), social status (Lyon and Montgomerie 1986), and foraging ability (Hill and Montgomerie 1994, Senar and Escobar 2002, McGraw *et al.* 2005). In migratory birds, these ornaments may advertise that an individual is sufficiently fit to invest in energetically expensive plumage even after the considerable costs of migration itself. Such individuals will presumably be desirable reproductive partners, either by passing on good genes to the young, or by excelling at defense of territories, nests, or broods. Another way birds demonstrate their quality is by breeding at the right time. High-quality individuals (variously defined in terms of age, breeding plumage, parasite loads, or immunocompetence) typically arrive earlier on the breeding grounds (Flood 1984, Francis and Cooke 1986, Hill 1988, Møller 1994, Potti 1998).

Plumage and migration timing have been correlated explicitly with breeding success or survival frequently enough that they are often considered reliable indices of relative individual quality or condition. This may be appropriate when such relationships are empirically established for the particular study system, and can allow powerful inferences across seasons (see next section for one such example). By contrast, my study illustrates that inferring individual quality from plumage or migration timing on non-breeding grounds can be completely spurious. In New Zealand, Bar-tailed Godwits of each sex varied substantially in departure date (Chapter 4) and plumage at departure (Chapter 5), but both of these attributes were strongly correlated with latitude of their individual breeding sites in Alaska (Chapters 2–3). There is no reason to believe that quality or condition of individuals varies systematically across more than 12° of latitude in Alaska, particularly when this pattern cannot be linked to differences in non-breeding habitat quality (e.g., Gunnarsson *et al.* 2005, Studds and Marra 2007). Furthermore, quality-based predictions based on plumage and migration timing would be contradictory, as southern breeding birds migrate earlier whereas northern breeding birds have more extensive breeding plumage. It seems that plumage and migration timing in New Zealand tell us very little about the relative quality or condition of individual godwits.

An intensive study of individuals in Alaska should be more instructive. At particular breeding locations, individuals vary in both arrival time (McCaffery *et al.* 2010) and plumage (Chapter 3), and this may translate to differences in breeding success. However, these presumed relationships await verification in this species. In particular, the function of ventral breeding plumage of Bar-tailed Godwits is unclear. It seems intuitively obvious that the striking red ventral plumage of most male godwits must function to advertise status to mates and rivals, and the evolution of a pre-supplemental moult (Chapter 5) implies strong selection for this trait. To date, however, there is no direct evidence that females use plumage to choose mates, or that plumage in either sex is related to social status, quality of breeding site, or reproductive success. Furthermore, attempts to link Bar-tailed Godwit plumage to other fitness measures such as body condition, parasite loads, or survival have been largely inconclusive or contradictory (Piersma and Jukema 1993, Piersma *et al.* 2001, Drent *et al.* 2003, Battley and Piersma 2005, Battley 2007). Understanding the significance of godwit plumage is complicated by geographic variation in Alaska (Chapter 3), the reasons for which remain obscure, but which presumably results from a gradient in habitat or sexual selection, or both. It is intriguing that in Black-tailed Godwits *L. limosa* in the Netherlands, males with less plumage ornamentation appeared to have *higher* fitness than more colourful males (Schroeder *et al.* 2009). This illustrates that relationships between plumage and fitness can be more complicated than, or even opposite to, our expectations.

One argument against plumage as a reliable indicator of quality in godwits is the extraordinary consistency of individual plumage on departure from New Zealand (Figure 8.1; Chapter 6, Battley 2006). In fact, individual godwits were not just consistent in their plumage scores, but in the specific feathers that were moulted each year; many birds could be identified by distinct patterns of both ventral and dorsal pre-breeding moult prior to departure (Figure 8.2). If individuals were competing to display the most impressive plumage, they should take every opportunity to perform more extensive pre-breeding moult. Surprisingly, annual variation in moult initiation (up to 28 days) did not result in differences in plumage on departure; each bird appeared to have a prescribed extent of moult to perform in New Zealand, regardless of the precise scheduling of it. Since godwits resume moult at staging sites in the Yellow Sea, it is possible that the extent of additional moult conducted there is condition-dependent, and thus reflects an individual's migratory quality (Piersma and Jukema 1993). Currently, there are no data from Alaskan breeding grounds to address annual variation in the ultimate breeding plumage of individuals.

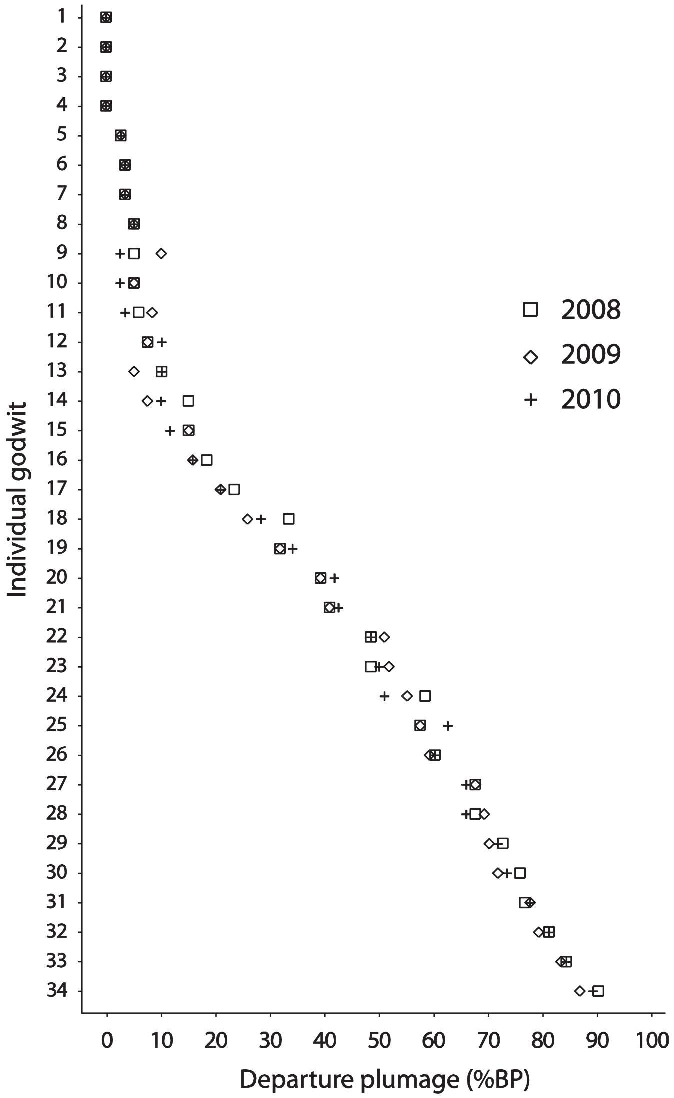

Figure 8.1 Plumage (% breeding plumage in all body regions; see Chapter 5 for scoring details) at departure from New Zealand for 34 godwits with 3 years of data. Individual repeatability (Lessells and Boag 1987) of plumage score = 0.98. Birds 1–18, 21, and 22 are females, and the rest are males.

One might expect the impacts of variation in individual quality or condition to be particularly profound in long-distance migrants, due to the unforgiving nature of their annual routines. I did not attempt to directly assess condition in this study, but I found that most inter-individual variation appeared attributable to individually optimised strategies based on sex, size, and breeding location. Furthermore, my data alone do not support any condition-dependence hypotheses to explain godwit behaviour or moult. Why would this be true? Are Bar-tailed Godwits a race of unstoppable super-migrants? Where are all the low-quality godwits?

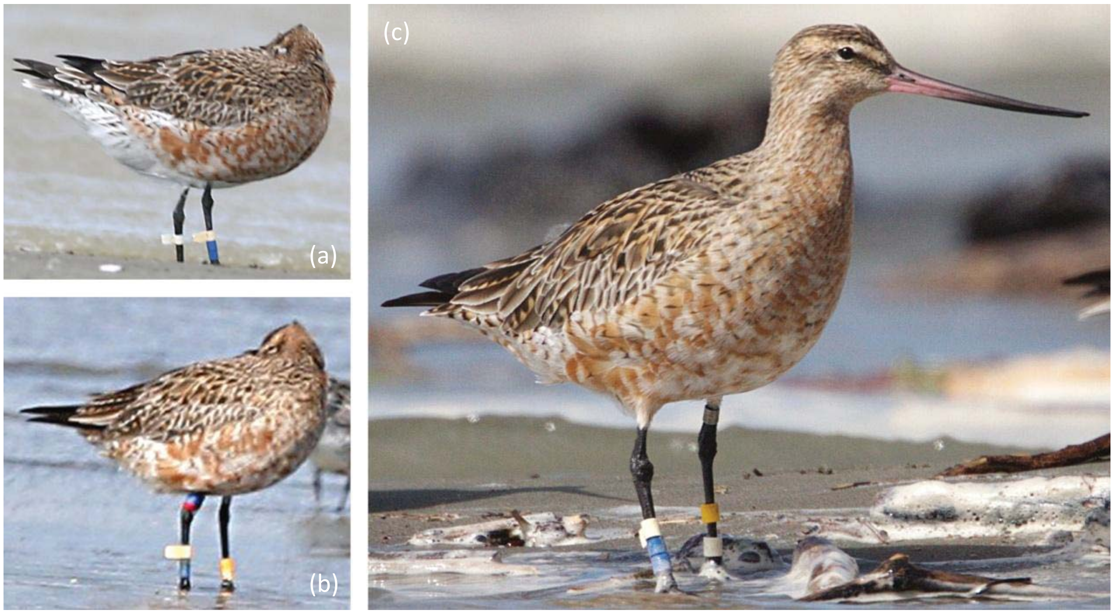

Fig 8.2 Plumage of one male Bar-tailed Godwit (bird #26 in Figure 8.1) before migratory departure in three successive years: **(a)** 11 March 2008; **(b)** 13 March 2009; **(c)** 1 March 2010. The bird’s median departure date was 15 March. Photo in **(c)** by Phil Battley.

My hypothesis is that the system simply does not tolerate low-quality individuals, which are weeded from the population very quickly. This first occurred to me when I realised that the juvenile godwits arriving in New Zealand around early October (Figure 8.3), having just accomplished an epic trans-Pacific flight with no experience or safety net, had all still been folded up inside their eggs, 12,000–14,000 km away, just three and half months previously. Consider what had to occur in that short period. First, they hatched and began foraging for themselves within hours. Within about 30 days, they grew to near adult size (an increase in mass of ~1,000%) while manufacturing a complete set of flight feathers capable of travelling non-stop to Australasia. Next, they found their way to staging grounds in southwestern Alaska, up to ~1,200 km away, without any help from the parents who had already abandoned them. Once there, they nearly doubled their weight in about two months, approximately the same time it takes for an adult with an already fully-grown bill and at least two years of foraging experience. Finally, they set off from Alaska, and flew 7–9 days straight before touching the earth again.

A more efficient method for immediately removing low-quality individuals from a population could hardly be conceived. For most migratory birds, the greatest mortality rate is certainly in the first few months of life (Sullivan 1989, Anders *et al.* 1997, Thomson *et al.* 1999), but most

Figure 8.3 Bar-tailed Godwits at the Manawatu River estuary on 2 October 2008. The juvenile on the left had arrived on southbound migration from Alaska within the previous 3 days.

systems allow some flexibility in the way young birds perform their first migration (Woodrey and Moore 1997, Hake *et al.* 2003). So, low-quality individuals have the chance to remain in the population and subsequently be out-performed by high-quality individuals in someone's research project. In the case of godwits, the low-quality individuals probably never make it to New Zealand.

Model system or evolutionary outlier?

I have discussed how godwits in my study appear to defy expectations derived from traditional migration theory and sometimes common sense. In general, Alaskan Bar-tailed Godwits occupy an extreme position along a well-understood continuum, and in some respects the evolutionary context of godwit migration may be quite singular. It is fair to ask what such an unusual system can teach us about, for example, the short-distance migration of a temperate-breeding songbird. For discussion, I have chosen two well-studied birds with migrations and life-histories that offer instructive contrasts to Bar-tailed Godwits: the American Redstart *Setophaga ruticilla* and the Black-tailed Godwit *L. limosa limosa* (see Table 8.2 for key characteristics and information sources for each species).

Table 8.2 Life-history characteristics influencing northbound migration strategies of three species.

		American Redstart *Setophaga ruticilla*	**Black-tailed Godwit** *L. limosa limosa*	**Bar-tailed Godwit** *L. lapponica baueri*
Non-breeding season	Latitude	5°S–25°N	5°S–30°N	46–15°S
	Territoriality	yes	no	no
	Fuelling resources	unpredictable	unpredictable	predictable
Northbound migration	Migration distance (km)	2,000–4,000	3,000–5,000	15,000–18,000
	Maximum single flight distance (km)	1,200	1,800	10,000
	Flexibility in stopover location	high	moderate	low
	Number of stopovers	multiple	few	one
	Migration bout duration (d)	≤1	1–3	4–8
Breeding phenology cues	Available at non-breeding site	no?	no	no
	Available at stopover site	yes	yes	no
Breeding season	Latitude	20–60°N	45–62°N	58–71°N
	Arrival window, 1 site (wk)	2–4	6–7	1–2
	Clutch initiation window, 1 site (wk)	6–7	6–7	3–4
	Incubation period (d)	10–13	22–24	20–23
	Duration to chick independence (d)	≤30	25–30	28–30
	Annual breeding attempts	1–4	1–2	1–2
Individual repeatability	Northbound departure timing	0.38	0.30–0.42	0.84

Sources of information presented here and in text: American Redstart: Sherry and Holmes 1997, Marra 2000, Norris *et al.* 2004, Studds and Marra 2007, Reudink *et al.* 2009, Angelier *et al.* 2011, Studds and Marra 2011; Black-tailed Godwit: Groen and Hemerik 2002, Gill *et al.* 2008, Lourenço and Piersma 2008, Lourenço *et al.* 2010, 2011, Masero *et al.* 2011, T. Piersma pers. comm.; Bar-tailed Godwit: McCaffery and Gill 2001, Hussell 2004, Gill *et al.* 2009, McCaffery *et al.* 2010, Battley *et al.* 2012, this study.

American Redstarts are small (6–10 g), insectivorous wood-warblers (Family Parulidae) that winter in the Neotropics and breed in the northern temperate zone. Like many woodland passerines, their migration is broad-fronted, with individuals breeding roughly north of their non-breeding sites and using multiple stopover sites in between. Migration bouts are generally a few hundred kilometres and occur within a single night, but some birds probably cross the Gulf of Mexico in one flight; for most, crossing such extensive barriers is unnecessary. For redstarts, annually variable environmental conditions and habitat quality in the non-breeding season have demonstrable effects on individual condition, migration timing, the quality of sexually-selected plumage ornaments, and ultimately breeding success.

Let's consider the aspects of redstart life history that might foster migratory strategies so different from those of Bar-tailed Godwits. I group these fundamental drivers into four main categories (Table 8.2): non-breeding resources, the geography of the journey itself, availability of cues for breeding phenology, and factors specific to the breeding season. For redstarts, non-breeding food resources are unpredictable, both annually and among individuals via territorial defense. The largely overland migratory route is relatively short, contains no especially daunting barriers, and birds may be quite flexible in stopover locations, number of stops, and overall migration speed. Their tropical non-breeding grounds may offer few cues for phenology of the upcoming breeding season, but such cues are available when birds reach stopover sites in North America, still hundreds or thousands of kilometres from breeding sites. Their breeding season is relatively long and chick development is rapid, allowing multiple attempts should earlier nests fail. Another possible source of differences between the species is longevity: redstarts are short-lived (~3–10 years; Sherry and Holmes 1997) and thus should place a higher priority on breeding success in any one year, as opposed to godwits, which may have 10–20 breeding opportunities in a lifetime and therefore should prioritise annual survival.

All of these characteristics of redstarts predict a plastic migration system, in which flexibility in response to seasonal and daily conditions takes precedence over rigid endogenous programming (Studds and Marra 2011). Not only do unpredictable circumstances make rigid timing unfeasible for redstarts, but opportunities exist to correct 'errors' in timing or pre-migratory fuelling during the northbound journey (Marra *et al.* 2005, Calvert *et al.* 2012). Furthermore, timing of arrival on the breeding grounds might be somewhat forgiving, with birds arriving even 2–3 weeks later than normal having some chance to breed successfully. Little of this is true for Bar-tailed Godwits. For these birds, vast barriers between successive stops mean that cues for future resource phenologies are unavailable, and departing with insufficient fuel stores can result in a complete loss of breeding opportunity or perhaps death. The short arctic summer means that even brief delays in arrival can severely decrease a godwit's chances of breeding. These factors have resulted in a relatively structured, yet conservative, migration strategy. Stable and predictable non-breeding resources enable unhurried fuelling and moults that allow room for flexibility in timing but are reliable enough to ensure the performance of rigid, endogenously programmed movements. For both redstarts and godwits, natural selection has provided the tools and the flexibility to succeed in their respective circumstances.

How are the various influences on the schedules of these populations reflected in the migration behaviour of individual birds? Repeatability (or intra-class correlation coefficient; Nakagawa and Schielzeth 2010) is a measure of how consistently different individuals are through time, on a scale of 0 (not at all) to 1 (each individual is completely distinguishable from all others). In the case of Bar-tailed Godwits, repeatability of timing of northbound departure from New Zealand was 0.84 (Chapter 4; Table 8.2), which is among the highest values yet reported for migration timing in any species. For comparison, repeatability of departure by American Redstarts from Jamaica was 0.38 (Studds and Marra 2011), showing that birds were less faithful to individualised schedules. It should be kept in mind that repeatability reflects the 'individuality' of a parameter in the context of population variation, rather than absolute individual consistency (Chapter 7). However, these relative values strongly suggest that individual Bar-tailed Godwits place a high value on consistency, whereas redstarts keep their options open.

It is quite possible that stable and safe non-breeding conditions are necessary for a migration such as the Bar-tailed Godwits' to evolve in the first place. It is also possible that the same behaviours and physiological processes that equip them for this lifestyle will render them unable to adapt to future circumstances dictated by climate change and habitat loss. Are birds as different as redstarts and godwits trapped by their evolutionary pasts, no longer able to converge near the centre of the flexible–rigid spectrum? One only has to look at the Genus *Limosa* to find striking examples to the contrary. This group includes several members strongly in the camp of New Zealand Bar-tailed Godwits, breeding at sub-arctic or higher latitudes and migrating in two or three jumps to the southernmost regions available to them (Hudsonian Godwit *L. haemastica* and two other Bar-tailed Godwit subspecies, *L. l. taymyrensis* and *L. l. menzbieri*). However, godwits also include relatively short-distance migrants (*L. l. lapponica* and Marbled Godwit *L. fedoa*) and another congener, the western European Black-tailed Godwit (Table 8.2), whose annual routine contrasts about as sharply as imaginable from the Bar-tailed Godwits in my study. This race of Black-tailed Godwits is primarily terrestrial rather than estuarine throughout the year, using mostly human-altered agricultural and freshwater habitats for breeding and foraging. They winter in tropical sub-Saharan Africa, but depart as early as late December on a long, direct flight to the Iberian

Peninsula, where the population is highly concentrated while staging for several weeks on rice fields. Subsequently, they move to breeding sites in one or a few shorter continental flights. They nest in grasslands of temperate Europe in a very loosely-scheduled breeding season: variation in arrival is extensive and some do not start breeding until 3–5 weeks after arrival.

As may be expected from these patterns, individual repeatability of northbound migration timing in this Black-tailed Godwit population more closely resembles that of redstarts than of the godwits in my study (Table 8.2). This is clearly a bird with a different concept of time constraints than the Bar-tailed Godwit has. In fact, the lack of correlation between timing of arrival on the breeding grounds and the start of breeding (Lourenço *et al.* 2011) goes against everything we know about migrating to exploit resources at just the right time. The unusual schedule of the Black-tailed Godwit is generally explained by the conversion of wetlands throughout its range (Gill *et al.* 2008); the human-altered habitats it now uses throughout the year are no longer on natural schedules, and the birds' schedules have changed accordingly. Godwits begin to depart winter sites in Africa when the rice fields they use for foraging are drained and harvested (Gill *et al.* 2008). On the European breeding grounds, warmer spring temperatures over the last century have led to earlier mowing schedules on commercial grasslands, making early breeding by Black-tailed Godwits increasingly advantageous (Schroeder *et al.* 2012). In response, the godwits advanced their egg-laying dates by about 2 weeks during 1930–1976, but then stopped advancing breeding despite continuing change in climate and agricultural practices.

These patterns may tell us quite a bit about regulation mechanisms and the potential in godwits to respond to change. Under natural conditions, we would expect the northbound flight from tropical Africa to be under primarily endogenous control and perhaps very consistent, as it is unlikely to be informed by temporal cues regarding resources in Europe and involves a non-stop crossing of the Sahara Desert and Mediterranean Sea. Yet, departure from Africa (in December and January, unusually early for a long-distance migrant) appears to have shifted earlier in response to regular annual declines in local food availability. Apparently, rice fields are profitable enough to support fuelling for this flight in an abbreviated season. It would be interesting to know whether this population has altered its wing moult schedule to accommodate this earlier migration, and how quickly any such adaptation occurred.

There is growing concern that long-distance migrants may be unable to keep pace with earlier breeding phenologies resulting from climate change, because their regulation mechanisms or fuelling resources may not accommodate appropriate timing of arrival at breeding sites (Both and Visser 2001, Ahola *et al.* 2004, but see Jonzén *et al.* 2006). The Black-tailed Godwit is an intriguing case of arrival advancing in response to earlier conditions but breeding not responding appropriately. It is possible that further advancement of breeding is constrained by conditions for nesting itself becoming temporally decoupled with food resources required to raise chicks to fledging (Schroeder *et al.* 2012). Another possibility is that endogenous programmes regulating the timing of breeding have limits to their flexibility.

How do these patterns influence the view of New Zealand Bar-tailed Godwits as inflexible and trapped by the endogenous programmes necessary for their extreme migration? The Black-tailed Godwit, a congeneric long-distance migrant, has shown startling shifts in timing of annual events in response to extrinsic factors. Why shouldn't Bar-tailed Godwits be capable of similar flexibility? It is important to remember that what animals do is not always an indication of their capabilities in other circumstances. We don't know the evolutionary history or age of the New Zealand godwit population, and therefore whether it has withstood great challenges posed by habitat and climate changes in the past. Perhaps this system is an evolutionary blip, a noble experiment that will not stand the test of time due to the perfect suite of circumstances that must collude for it to persist. Alternatively, perhaps conditions have not yet persuaded it to display its inherent flexibility and perseverance.

Perhaps Bar-tailed Godwits migrate this way simply because *they can*.

Chapter 9

Future directions

What now?

As with any ecological research that is worth doing, my project answered far fewer questions than it raised or left unresolved. Some of these latter mysteries are general to migratory birds, but have never been satisfactorily answered in any system. These include: How does a bird 'know' when it is fat enough to start or continue a migration? How exactly does a bird assess the weather conditions prior to departure?

Particularly fascinating to me is the formation of departure flocks. In my study, I had departing flocks as small as three birds. Did this tiny flock really fly all the way to the Yellow Sea by itself, or do flocks somehow join up with others after initial departure? Departure flock size had no apparent impact on an individual's likelihood of returning to Foxton the following season. Godwits from my study site used many staging areas in China and Korea, and appear to have at least regional fidelity between years. Do departing godwits flock together based on *when* or *where* they are going? Is it a 'carpool' paradigm, in which all birds going to a particular destination about the same time depart and arrive together? Or is it a 'city bus' paradigm, in which all birds leaving on a particular day travel most of the way together, but then drop out one by one as the flock passes their intended destinations?

Other big questions specifically raised by my findings are central to understanding the evolution and maintenance of this particular system, and provide a foundation for some rich and rewarding future research. I conclude with a brief overview of just three of these.

How did this migration evolve?

'Why do they go so far?' Regarding Bar-tailed Godwits, this is the question I hear most often, from both scientists and non-scientists. Of course, the answer to every evolutionary 'why?' question is: 'because it worked.' The question we really want to ask is: '*how* did this evolve?' Although evolution can sometimes work in unexpectedly brief time scales, it is hard to envision epic trans-oceanic flights suddenly resulting from the actions of naïve but lucky birds, because many associated behaviours and physiological processes must have pre-existed to enable such flights (Alerstam *et al.* 2003). It seems safe to conclude that the migration developed somewhat incrementally. As described by Hedenström (2010), the two most plausible scenarios are: (1) a Siberian-breeding population gradually shifted both its summer and winter quarters eastward until Alaska breeders were flying directly to New Zealand and Australia without an overland Asia route; and (2) an Alaskan-breeding population wintering in Asia gradually shifted its wintering quarters to the southeast toward New Zealand. In fact, the original population from the first scenario may still exist today in the form of *L. l. menzbieri*, which migrates between Siberia and Australia (Battley *et al.* 2012). There is also the possibility that *menzbieri* is a later offshoot from an Alaska-breeding population that persisted in ice-free refugia during the last Pleistocene glacial extreme (25,000–10,000 years ago) and then spread its breeding range westward when glaciers retreated.

Because no extensive genetic analysis of Bar-tailed Godwits has yet been conducted, we know very little about the evolutionary relationships among the four or five extant subspecies. Tundra-breeding shorebirds are thought to have radiated across vast areas of the arctic and sub-arctic during the most recent inter-glacial period (Kraaijeveld and Nieboer 2000); consistent with this, genetic analyses have failed to uphold some recognised taxonomic divisions based on clear differences in morphology and/or migration routes (e.g., Dunlin *Calidris alpina*: Wenink *et al.* 1993, Red Knot *C. canutus*: Buehler *et al.* 2006). If diversification of godwits is similarly recent, genetic analysis may raise as many questions as it answers. But it is clearly the best first step.

What is the adaptive significance of geographic variation in Alaska?

More relevant for elucidating the specific results of my study is identifying any genetic structure *within* the Alaska population. For instance, how does the scale of genetic variation in Alaska compare to that found within and among the other subspecies? The present, continuous breeding range in Alaska was at one time interrupted (between the Seward Peninsula and the North Slope) by glaciers, so any historical Alaskan godwits could have persisted in one or both of these refugia. Thus, Bar-tailed Godwits may have expanded either north or south of the Brooks Range relatively recently, or two historical populations may have united (or reunited) to form the present distribution. This is relevant for understanding the selective forces maintaining size and plumage clines within Alaska, particularly if they are shown to be correlated with genetic structure in the population. What did the ancestral Alaskan godwits look like? Small, red godwits in northern Alaska could have spread south and met with relaxed selection for those traits, or vice versa.

Of course, a more direct way of understanding plumage and size in Alaska is through intensive breeding studies, which have yet to be conducted in any Bar-tailed Godwit population. Is there assortative mating by plumage or size within a particular breeding site? Do members of either sex honestly advertise their quality as reproductive partners with these traits? Do latitudinal clines in breeding plumage reflect subtle habitat differences or variation in intensity of sexual selection?

How do young godwits ‘learn’ their routines?

Endogenous programming, social behaviour, and learning may all play roles in the development and maintenance of individual routines in Bar-tailed Godwits. Adult godwits are extremely habitual, with unwavering non-breeding site-fidelity and remarkably consistent migration schedules, but young birds spend some time growing into their roles. It seems from recoveries of godwits banded in eastern Australia as juveniles (Minton *et al.* 2011) that many birds on their first southbound migration end up in Australia, only to later become faithful New Zealand residents. Whether this reflects unskilled navigation or a different strategy on the first migration is an intriguing subject by itself. After arrival from their first southbound migration, young godwits typically skip two breeding seasons before they begin migrating annually to Alaska. They spend the first year or more freely roaming New Zealand and eastern Australia with other young birds, before settling at their permanent non-breeding sites. Also, scheduling of departure on the first northbound migration appears to be less precise than in subsequent years (Battley 2006). These patterns suggest that experience and ‘choice’ play some role in the development of repeatable adult routines, as opposed to strict and complete control by endogenous programming. As yet, no juvenile from a known Alaska breeding site has been tracked to adulthood, and there is no information on natal-site fidelity, but presumably this must exist at least at a regional scale for geographic variation in the population to be maintained. If breeding location and migration timing are found to have a genetic component, it would suggest that programming for adult routines essentially lies dormant until somehow being ‘switched on’ at about three years of age. Combined with genetic studies, trace element and stable isotope analyses have potential for identifying the natal regions of young godwits in New Zealand. If these birds can then be followed until they recruit into the migratory population (a difficult proposition), it may elucidate how young godwits choose their ultimate non-breeding sites and the roles of endogenous programmes and experience in shaping their first northward migrations.

Appendix 1

Attachment of geolocators to Bar-tailed Godwits: a tibia-mounted method with no survival effects or loss of units

Conklin, J.R. & P.F. Battley
Wader Study Group Bulletin 117: 56–58 (2010)

Abstract

We describe a method for tibia-mounted geolocator attachment successfully used on Bar-tailed Godwits Limosa lapponica baueri *in New Zealand. The return rate of 95% for instrumented godwits was higher than for other colour-banded individuals in the same study, and we observed no negative physical or behavioural effects of attachment. There was no loss of units, even after 24 months and two return migrations to Alaska. We believe this method is appropriate for a wide variety of migratory waders.*

Introduction

With recent advancements in radio telemetry and datalogger technology, the need for long-term instrument attachment to medium- and small-sized birds is increasing. Glue applied to the skin and/or feathers is appropriate only for short-term deployment (Warnock and Warnock 1993, Mong and Sandercock 2009), with the expectation of natural shedding after instrument batteries are expended. Harness attachment, whether backpack or leg-loop design (e.g., Rappole and Tipton 1991), offers longer retention, but can negatively affect behaviour (Sykes *et al.* 1990), breeding success (Rotella *et al.* 1993), flight speed (Irvine *et al.* 2009), or survival (Mong and Sandercock 2009). Long-distance migrants may be particularly ill-suited to back-mounted instrumentation, because drastic body mass changes make a proper harness fit problematic (Gill *et al.* 2009), and increased wind drag may significantly decrease flight range (Obrecht *et al.* 1988).

Instrument attachment to the tibia is a viable option for sufficiently large birds, and is made practical by the availability of leg bands and flags used for individual identification. Instruments have typically been attached to metal or plastic leg bands with epoxy (e.g., Morris and Burness 1992, Haig *et al.* 2002) or cable ties (e.g., Phillips *et al.* 2009). With the advent of small-sized dataloggers that require recapture for data retrieval, and also have sufficient longevity to warrant redeployment of units, there is a growing need for durable attachment that is simple to both apply and remove. Here, we describe a leg-mounted attachment method successfully used on the Bar-tailed Godwit *Limosa lapponica baueri*, which performs the longest known non-stop flight (>11,000 km) of any migratory bird (Gill *et al.* 2009).

Methods

We captured Bar-tailed Godwits at the Manawatu River estuary, New Zealand (40.47°S, 175.22°E), from a local non-breeding population of 200–280 individuals. Approximately 25% of the godwits in this highly site-faithful population are individually colour-marked as part of an ongoing non-breeding study. We attached geolocators (British Antarctic Survey model MK14; 9 mm x 21 mm; 1.4 g; 2-year life) to double-wraparound Darvic leg bands (external diameter 9 mm; height 8 mm) by the following procedure:

Step 1: Using a flame-heated large sewing needle, we pierced two holes approximately 5 mm apart on an axis perpendicular to the length of the band, equidistant from either end, and opposite the band opening. Only holes through the outer layer were required, but it was easiest to pierce through both layers. We then filed off excess plastic so that the inner and outer band surfaces were smooth again.

Step 2: Using a small sewing needle, we passed a length of mist-net repair thread through both holes of the outer layer of the band three times, so that a double loop was formed, plus two ends free.

Step 3: After roughening the back surface of the geolocator slightly with sandpaper, we used a drop of cyanoacrylate glue to attach the geolocator to the band, within the loops of thread and parallel to the length of the band. The MK14 units were designed with a ‘waist’ to accommodate cable-tie attachment, and we centred this waist on the length of the band (and thus with the holes), with the light sensor below the waist.

Step 4: We tightened the double loop around the unit and tied a simple knot with the loose ends, so that the unit was encircled three times. We snipped off excess thread and placed a single drop of cyanoacrylate glue to secure the knot.

Step 5: We spread a thin layer of Araldite® two-part epoxy over the centre of the unit, just covering the thread to where it reached the band on either side of the unit (carefully avoiding the light sensor) and filling the crevice between the edges of the unit and the band. We removed excess epoxy and let the assembly dry. Some epoxy flowed through the holes and glued the two layers of the band together; after drying, we gently snapped this bond by sending a small knife between the band layers, and filed off the excess epoxy so the band layers sat closely together again.

Step 6: Because some of the natural curvature of the band is held fast by the mounting, care must be taken to open the band as little as possible to avoid breaking the band or the epoxy bond during application to the tibia. With the MK14, we positioned the unit with the light-sensor end toward the ground, to ensure maximum exposure of the sensor. Because the units were longer than our colour-bands, we placed an additional half-length colour-band below the geolocator assembly, to stop the downward-pointing contact pins from irritating the bird's leg joint (Figure A.1a).

Step 7: Upon recapture, we removed the assembly from the bird by simply cutting the band with small scissors. Removal of the unit from the band was simple: with two pairs of pliers, we twisted the band and unit in opposite directions, breaking the epoxy bond with the band. By pulling the length of thread, the epoxy then peeled off easily without damaging the geolocator sheath. Very little additional cleaning of epoxy was required, as it generally came off in a single strip. After data retrieval and testing, the unit could then be remounted to another band for redeployment.

In our study, the mounted units weighed approximately 1.8 g. The additional half-band weighed 0.14 g. Godwits in our study carry an individual metal band, a region-specific plastic flag, and an individual combination of four colour-bands. Thus, a normal bird carried 2.1 g of markings, while an instrumented bird carried a total of 4.1 g. Due to extreme temporal changes and substantial individual variation, mass of Bar-tailed Godwits varies from 210–570 g for males, and 240–660 g for females (J. Conklin and P. Battley unpubl. data); the combined bands and geolocator represented 0.6–1.9% of body mass.

Results

We deployed 17 geolocators on godwits (7 males, 10 females) on 12 March 2008, when birds were very fat and preparing for northbound departure from New Zealand. Despite the disruption of capture by cannon-net and geolocator attachment, all instrumented birds departed on migration within 16 days of capture, during the same period as local birds that were not recently captured. In fact, three instrumented females departed New Zealand on 13 March, just one day after capture.

The following non-breeding season, 15 of 17 (88%) instrumented birds returned to the site, compared with 38 of 45 (84%) other individually-marked godwits. One of two females that did not return was last resighted on 23 April 2008 at Yalu Jiang National Nature Reserve in China (J. Conklin pers. obs.), and so successfully completed at least the first leg of migration (approximately 10,300 km) after departing New Zealand.

On 30 October 2008, we captured godwits to retrieve geolocators and make a second deployment. We retrieved 11 of 15 units, and deployed 19 new units (11 on the original

Figure A.1 Geolocators attached to Bar-tailed Godwits: **(a)** 12 March 2008; newly-attached geolocator on female godwit; **(b)** 22 March 2010; male godwit with geolocator, 17 months after deployment Photos by Phil Battley.

cohort, and 8 on new birds). On 1 March 2009, we redeployed one of the original units on a new bird, captured by mist-net. All 24 instrumented birds (20 newly-deployed and 4 not recaptured since original deployment in March 2008; 12 males, 12 females) departed on migration 4–31 March 2009, within the departure period of non-instrumented birds.

The following non-breeding season, all 24 (100%) instrumented godwits returned to the site, compared with 32 of 36 (89%) other individually-marked godwits. On 3 November 2009, we captured godwits by cannon-net, retrieving 17 of 24 geolocators. Seven instrumented godwits were not recaptured, and departed on northbound migration in March 2010.

We retrieved 26 units after one return migration (minimum 30,000 km travelled), 7–12 months after deployment. We retrieved two units after two return migrations (minimum 60,000 km travelled), 19 months after deployment. All units remained firmly attached to the band upon retrieval, and the attachment showed no signs of significant deterioration. With birds in the hand, we observed no physical effects of the attachment method. We also observed no behavioural effects of the geolocators, during detailed observations of individuals at the deployment site from September through March in both non-breeding seasons (Figure A.1b).

In addition, instrumentation did not appear to preclude normal breeding activity. Because tibia-mounted units are shaded during incubation of nests, periods of nest attendance were roughly indicated by light-sensor data. In 2008, all 11 birds with available breeding data apparently incubated nests. In 2009, 12 of 15 birds apparently incubated nests. The longest periods of nest attendance (24–25 days) were sufficient to indicate probable hatching.

Discussion

Direct effects of instrument attachment are often difficult to ascertain in migratory species, due to confounding natural influences on return rates. However, high annual survival and site-fidelity of Bar-tailed Godwits allowed an opportunity to test both attachment retention and effects on the birds themselves. We observed no behavioural or survival effects in instrumented godwits, and no loss of units even after two return migrations to Alaska. The Bar-tailed Godwit performs one of the most extreme long-distance migrations of any bird, and the attached units were exposed to regular salt water immersion, as well as extreme UV-radiation and low temperatures. Therefore, we conclude that this attachment method is appropriate for a wide range of long-distance migratory wading birds, and probably for other species as well.

Body size of smaller species naturally represents a limit to the use of any attachment method, depending upon the size of the units in question. Our attachment, including other individual markings, represented <2% of godwit mass. The generally accepted limit of appropriate tag weight for birds is 3–5% of body mass, but this should be evaluated with regard to the species in question (Caccamise and Hedin 1985). Also, appropriate limits have not been fully investigated specifically for leg-attachment, which is naturally asymmetrical, unlike other methods; this could have specific importance for perambulatory species. As the size of available geolocators decreases, researchers will target increasingly smaller species; we are aware of current projects involving Pacific Golden-Plovers *Pluvialis fulva*, Ruddy Turnstones

Arenaria interpres, Dunlin *Calidris alpina*, Red Knots *C. canutus*, and Hudsonian Godwits *L. haemastica*. It is critical for researchers to document the short- and long-term effects of leg-attachment. Many waders display strong size dimorphism, and thus may show greater negative effects of instrumentation in the smaller sex. However, in our study, instrumented birds of both sexes returned at slightly *higher* rates than colour-banded individuals at the same site.

In various large-bodied seabird species, geolocators have been attached using cable-ties, requiring little pre-deployment preparation. However, for godwits, which are smaller and spend a significant amount of their time walking, we sought to reduce the additional mass and bulk, and minimise uneven surfaces that might cause irritation to the legs. Some researchers have attached similar units to the flanges of plastic leg-flags, rather than to the leg-band itself. However, placement of the unit away from the axis of the leg creates torque that may irritate the bird, and we recommend avoiding this when possible.

Most studies reporting the use of epoxy alone to attach leg-mounted radio transmitters have done so on permanent aluminium bands, resulting in indefinite retention far exceeding the life of the units (Warnock and Takekawa 2003). Our aim was to create a secure yet easily-removed attachment to aid both retrieval and redeployment of units. The combination of thread and epoxy was well-suited to this: after the initial time investment in mounting the units, deployment or removal of the attachment in the field required less than one minute per bird, hardly more than a conventional colour-band. The assembly showed no significant weakening after 19 months, and two units remained attached after 24 months, and so this method may be appropriate for considerably longer deployments.

Appendix 2

Analysis of geolocator data

Geolocation basics

The geolocator I used (British Antarctic Survey model MK14; Fox 2010) is essentially a light-sensor attached to a memory chip. The unit is not a transmitter, and therefore access to the data requires manual download after recapture of the bird. For periods up to two years, the unit measures light every minute, and then records the maximum light level for each 10-minute period. When this information is compared to a known time and location of deployment, it allows the rough calculation of latitude and longitude twice per day; the former is derived from the length of day or night, and the latter from absolute time of local noon or midnight. The exceptions to this are periods close to the vernal and autumnal equinoxes (approximately ±15 d), during which day lengths are roughly equal at all locations, and so only longitude is reliable.

Processing light-level data

In general, I followed data processing instructions provided by British Antarctic Survey (Fox 2010). Communication with geolocators was conducted through a custom USB interface box provided by BAS and the program Hyperterminal in Microsoft Windows. For each retrieved unit, I copied raw downloaded geolocator data from Hyperterminal and saved it as a .txt file in the program Notepad. I opened each .txt file through the BASTrak data decompression software, and entered the time the unit was originally activated. With this information, BASTrak compensated for any clock drift that occurred since activation, and automatically created a .lig file compatible with the program TransEdit.

Using TransEdit, I applied a linear interpolation to smooth the light-level data, and identified sunrises and sunsets based on transitions through a user-prescribed light threshold level of 32 (on a scale of 0–64). I then visually inspected all derived transitions for quality, removing false and indistinct transitions that clearly resulted from shading events or other interference. At this point, I applied an arbitrary 10-minute retardation of sunset transitions; this corrects for the way the geolocators record light levels (as the maximum value across a 10-minute period). TransEdit then created a transition file (.trn) for the next stage of analysis.

I opened each .trn file in the program BirdTracker and specified a sun angle corresponding to sunrise/sunset (see below for derivation of these sun angles). BirdTracker then calculated a geographical location for each noon and midnight bracketed by valid sunrise and sunset transitions, thus producing two locations per day in the best of circumstances.

Determination of sun angles

For calculation of locations, BirdTracker requires a user-prescribed sun angle, which represents the sun's position below the horizon at the time the sunrise/sunset threshold light level prescribed in TransEdit is reached. Because the sun angle is applied to sunrise and sunset equally, it profoundly affects derivation of latitude, but has no influence on longitude. The appropriate sun angle must be determined for each unit individually, because the light-sensitivity of the units is not entirely uniform at the time of manufacture. BAS recommends a pre-deployment calibration period, in which the units are placed outdoors to collect light-level data for a period of days or weeks at a known location. Upon retrieval, this information can be used to determine the sun angle appropriate to identify the known location, and then this sun angle can be applied to the data of interest. In my case, I knew that my birds were at my study site for weeks or months after geolocator deployment and prior to retrieval. Therefore, I used these periods as my calibration data. In every case, BirdTracker correctly identified the longitude of the study site within 0.23–1.15° (mean = 0.49°), representing mean linear-distance errors of 20–98 km. Calibration-derived sun angles for correctly identifying the latitude of the study site ranged from –2.8° to –4.0°.

Outside of the breeding season, Bar-tailed Godwits are restricted to coastlines, and this fact greatly improved my ability to assess the plausibility of derived locations during migratory stopovers in the Yellow Sea and Alaska. During northbound migration, approximately 70% of New Zealand godwits use an east-west coastline in northwest China (the vicinity of the Yalu Jiang Nature Reserve). When staging for southbound migration, nearly all of this population uses a roughly east-west coastline in southwest Alaska (the vicinity of Kuskokwim Shoals). These two locations allowed me to fine-tune my calibration-derived sun angles for the greatest confidence in the latitude of locations during the breeding season. In some cases, derived locations were clearly implausible, because they were either too far inland (northward error) or off the coast in open sea (southward error). For each bird, I adjusted the sun angle until the locations for both northward and southward migrations were plausible. I then used the final adjusted sun angle for the entire tracking period. In every case, locations during the breeding season appeared to fall within the known breeding range, giving me confidence in this technique. The corrected sun angles ranged 3.0–3.8° and differed from the initial Foxton-derived sun angles by 0.0–0.6°. The reason for these discrepancies is unknown, but they demonstrate that use of calibration-derived sun angles without year-round knowledge of the biology of the study species can lead to unrecognised errors.

Estimation of location error

To help assess the reliability of geolocator-derived locations outside of Foxton, I deployed ground-truthing units to various locations along the godwits' migratory route in 2009, during the times of year the birds would be using these regions. I deployed two units to staging sites in the Yellow Sea, and five to staging and breeding areas in Alaska (Table A2.1). In each case,

Table A2.1 Ground-truthing geolocators deployed in 2009 at locations along the Bar-tailed Godwits' migratory route, to aid interpretation of data provided by instrumented birds. Mean errors show difference between true and derived locations, using sun angle of –3.5°.

					Deployment period		Mean error (°)	
Region	**Location**	**Deployment site**	**Latitude**	**Longitude**	**Start**	**End**	**Latitude**	**Longitude**
Yellow Sea	Korea	Mokpo	34.81°N	126.42°E	14 Apr	25 May	–0.35	–0.16
Yellow Sea	China	Yalu Jiang Nature Reserve	39.82°N	124.06°E	4 Apr	17 Apr	-	-
Alaska	Alaska Peninsula	Cold Bay	55.20°N	162.72°W	3 Aug	3 Oct	-	-
Alaska	Yukon-Kuskokwim Delta	Bethel	60.79°N	161.76°W	3 May	8 Sep	–0.31	–0.25
Alaska	Yukon-Kuskokwim Delta	Punoarat Point	61.31°N	165.81°W	21 Aug	13 Sep	+0.64	–0.22
Alaska	Seward Peninsula	Nome	64.50°N	165.41°W	12 Jun	28 Jun	-	-
Alaska	North Slope	Galbraith Lake	68.48°N	149.49°W	1 Jul	7 Jul	-	-

the unit was placed for 1–17 weeks in an open location free from obstructions along the sun's daily path.

Two ground-truthing units failed to provide data: the Yalu Jiang unit failed for unknown reasons, and the Cold Bay unit was rendered useless after apparently being chewed by an Arctic Fox *Vulpes lagopus*. As expected from their high latitudes, the North Slope and Seward Peninsula units failed to record nights at all during the summer. In the latter case, which is south of the Arctic Circle, there were technically sunsets during the deployment period, but the sun did not quite reach the requisite angle below the horizon for the light sensor to register darkness; the latitude threshold for registering nights during late June is approximately 64°N. For the other three units, the average error from the true location was 0.31–0.64° in latitude (at sun angle –3.5°) and 0.16–0.25° in longitude (Table A2.1); these represent location errors of approximately 50–130 km.

In two fortuitous cases, I could compare geolocator-derived bird locations outside New Zealand to actual locations obtained through direct observation of the instrumented godwits. Colleagues working along the flyway observed female godwit 6YBBY at the Geum River estuary in South Korea (36.01°N, 126.74°E) on 5 April 2008 (G. Stiles pers. comm.) and female 6YBYY at Cape Avinof, Alaska (59.83°N, 164.08°W) on 5 September 2008 (D. Ruthrauff pers. comm.). My independent geolocator-derived locations for these birds differed from the true locations by 91 km and 55 km, respectively.

Breeding locations

After departing the Yellow Sea, godwits typically (23 of 25 cases) arrived in coastal southwestern Alaska, and then clearly moved 2–13 d later to a different Alaska location, in most cases further north. This was consistent with birds arriving at coastal staging sites, and then dispersing to breeding sites after a brief period of refuelling and assessment of likely breeding conditions. In one other case, there was no discernible movement after initial arrival in Alaska; this bird presumably either flew straight to its breeding site, or bred <130 km from the spot of its initial arrival. All individuals were apparently stationary (within location error) for 32–85 d after arrival at breeding sites. For birds breeding south of 64°N (n = 16), I determined breeding location by calculating mean latitude and longitude among twice-daily locations (from the BirdTracker program) during this stationary period, after removal of clear outliers.

North of 64°N, determining breeding location is problematic, because geolocators do not register regular nights during most of the breeding season. On the Seward Peninsula (~65–66°N), nights were discernible in the geolocator data until about 24–26 May, and then were absent until 4–15 July. For two birds, the last reliable information in May and the first reliable information in July indicated the same approximate location on the Seward Peninsula. Therefore, I used the final available locations in May to represent these birds' breeding sites.

In five cases, birds were apparently still moving north when the final discernible night occurred 24 May–2 June, suggesting that they continued to the North Slope of Alaska. In three of these cases, the bird was still stationary above the Arctic Circle when discernible nights returned 28–30 July. The derived longitudes for these locations spanned 154.9–158.1°W, also indicating the North Slope segment of the breeding range. Latitude for locations derived from such brief nights (<1 hour) is not very reliable, but in each case was clearly >68°N. In two other cases, the bird was never stationary above the Arctic Circle during a period of discernible night, but the trajectories of northbound (May) and southbound (July) tracks were consistent with North Slope locations 151.9–158.5°W. At such easterly longitudes, the known breeding range is a narrow east-west band spanning just 69.5–70.8°N (McCaffery and Gill 2001). Therefore, I assumed a breeding latitude of 70.2°N (the midpoint of this range) for all apparent North Slope breeders. Longitudes for these breeding locations must also be viewed as approximate, as I cannot rule out eastward or westward movements after arrival on the North Slope.

In every case in which I had two years of breeding data for an individual (*n* = 8), the between-year differences in derived breeding locations were within the expected location error (24–124 km), and so were consistent with breeding site-fidelity.

Nest incubation

As previously demonstrated with Barnacle Geese *Branta leucopsis* (Eichhorn *et al.* 2006), light-level geolocators have an additional benefit of indicating periods of nest incubation. In my study, geolocators recorded nights during the breeding season as regular, clearly demarcated periods of darkness <4.5 hours in length; these did not appear at all if birds bred north of 64°N. Days appeared as continuous light, irregularly broken by very brief (<1 hour) shading events, most likely corresponding to behaviours such as wading or sitting. Within 6–25 d of apparent arrival on breeding grounds, most birds (21 of 23 cases) displayed a conspicuous pattern of incubation, in which semi-regular shading events of 4–13 hours were overlaid on the day/night pattern for 4–25 d. Three birds that showed no such pattern (including one that never appeared to settle at a breeding site) were considered non-breeders, but this could have resulted from either failure to find a mate or loss of a clutch prior to incubation. The full-time incubation period for Bar-tailed Godwits is thought to be 20–23 d (McCaffery and Gill 2001, Hussell 2004), and godwits typically begin part-time incubation when clutches are not yet complete (J. Conklin pers. obs.). Therefore, periods of 21–25 consecutive days of incubation indicated a high likelihood of hatching success, and I considered these cases to be successful breeding attempts. Periods of 4–18 consecutive days of incubation were clearly insufficient for eggs to have hatched (either by loss of a clutch or nest abandonment), and I considered these attempts unsuccessful. In four cases, two periods of incubation were separated by several days without shading events; these appeared to indicate renesting attempts after initial clutch losses. Of five apparent renesting attempts, one was successful and four were unsuccessful.

Appendix 3

Calculation of wind effect

Wind profit equations

In Chapter 4, I used two different methods to calculate how a bird gained or lost speed as a result of winds experienced at the time of migratory departure from my study site. The first (Tailwind, or ‘TW’) simply represents the magnitude of tailwind (positive values) or headwind (negative values) along the axis of the bird’s chosen flight path (as described in Åkesson and Hedenström 2000) and ignores the effect of crosswinds. TW is calculated as:

$$\mathrm{WP} = \mathrm{V_W} \cos(\mathrm{D_B} - \mathrm{D_W})$$

where:
WP = wind profit experienced by the bird (km/h)
$\mathrm{V_W}$ = wind velocity (km/h)
$\mathrm{D_B}$ = bird flight direction (radians)
$\mathrm{D_W}$ = wind direction (radians)

The second formula (Crosswind, or ‘CW’) additionally accounts for the work required by the bird to stay on its preferred flight path in the presence of crosswinds (as described in Piersma and Jukema 1990). In this method, wind profit is incalculable when the velocity of crosswinds exceeds the bird’s preferred flight speed. CW is calculated as:

$$\mathrm{WP} = \mathrm{G_B} - \mathrm{A_B}$$

where:
$\mathrm{G_B}$ = bird ground speed (km/h)
$\mathrm{A_B}$ = bird air speed (km/h)

For $\mathrm{A_B}$, I assumed a preferred flight speed of 65 km/h. $\mathrm{G_B}$ is calculated as:

$$\mathrm{G_B} = (\mathrm{V_W}\ \cos x) + \sqrt{\mathrm{A_B}^2 - (\mathrm{V_W}\ \sin x)^2}$$

where:
$x = |D_B - D_W|$ (the difference between bird direction and wind direction)

Appendix 4

Supplementary information on primary moult

Table A4.1 Use of historical New Zealand godwit capture data to assign moult scores when only the number of unmoulted primary feathers was known. Source data includes 1,434 captures of adult godwits in New Zealand during 1983–2008 (P. Battley and A. Riegen unpubl. data). 'Moult' represents primaries 1–10, left to right; 0 = old, unmoulted feather.

Moult	Mean score	Range	*n*	Assigned score
?000000000	1	1	3	1
??00000000	2	2	11	2
???0000000	4.2	3–7	36	4
????000000	8.1	4–16	62	8
?????00000	15.4	9–21	81	15
??????0000	22.6	14–26	61	23
???????000	29.8	28–33	36	30
????????00	35.1	27–39	39	35
?????????0	40.1	36–44	45	40

Table A4.2 Masses of individual godwit primary feathers (*n* = 3 individuals), as a proportion of total mass of primaries 1–10.

Feather	Mean length (mm)	Mean mass (g)	Mean prop. mass
P01	92.0	0.044	0.035
P02	100.7	0.055	0.044
P03	110.7	0.071	0.056
P04	124.3	0.090	0.072
P05	136.3	0.110	0.087
P06	148.7	0.132	0.105
P07	160.3	0.154	0.122
P08	173.0	0.178	0.141
P09	181.3	0.201	0.160
P10	179.7	0.220	0.176

References

Ahola, M., T. Laaksonen, K. Sippola, T. Eeva, K. Rainio & E. Lehikoinen. 2004. Variation in climate warming along the migration route uncouples arrival and breeding dates. *Global Change Biology* 10: 1610–1617.

Åkesson, S. & A. Hedenström. 2000. Wind selectivity of migratory flight departures in birds. *Behavioral Ecology and Sociobiology* 47: 140–144.

Alerstam, T. 1979. Wind as selective agent in bird migration. *Ornis Scandinavica* 10: 76–93.

Alerstam, T. 1990. *Bird Migration*. Cambridge University Press, Cambridge.

Alerstam, T., M. Hake & N. Kjellén. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. *Animal Behaviour* 71: 555–566.

Alerstam, T., A. Hedenström & S. Åkesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103: 247–260.

Alerstam, T. & Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy and safety. Pages 331–351 in *Bird Migration: Physiology and Ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin.

Allen, J.A. 1877. The influence of physical conditions in the genesis of species. *Radical review* 1: 108–140.

Anders, A.D., D.C. Dearborn, J. Faaborg & F.R. Thompson. 1997. Juvenile survival in a population of neotropical migrant birds. *Conservation Biology* 11: 698–707.

Anderson, M.G. 2003. Investigations into shorebird community ecology: interrelations between morphology, behaviour, habitat and abiotic factors. MSc thesis, University of Auckland.

Angelier, F., C.M. Tonra, R.L. Holberton & P.P. Marra. 2011. Short-term changes in body condition in relation to habitat and rainfall abundance in American redstarts *Setophaga ruticilla* during the non-breeding season. *Journal of Avian Biology* 42: 335–341.

Atkinson, P.W., A.J. Baker, K.A. Bennett, N.A. Clark, J.A. Clark, K.B. Cole, A. Dekinga, A. Dey, S. Gillings, P.M. González, K. Kalasz, C.D.T. Minton, J. Newton, L.J. Niles, T. Piersma, R.A. Robinson & H.P. Sitters. 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. *Journal of Applied Ecology* 44: 885–895.

Barbosa, A. & E. Moreno. 1999. Evolution of foraging strategies in shorebirds: an ecomorphological approach. *Auk* 116: 712–725.

Barshep, Y., A. Hedenström & L.G. Underhill. 2011a. Impact of climate and predation on autumn migration of the Curlew Sandpiper. *Waterbirds* 34: 1–9.

Barshep, Y., C. Minton, L.G. Underhill & M. Remisiewicz. 2011b. The primary moult of Curlew Sandpipers *Calidris ferruginea* in north-western Australia shifts according to breeding success. *Ardea* 99: 43–51.

Barta, Z., J.M. McNamara, A.I. Houston, T.P. Weber, A. Hedenström & O. Feró. 2008. Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society of London, Series B* 363: 211–229.

Barter, M. 1989. Bar-tailed Godwit *Limosa lapponica* in Australia, Part 2: weight, moult and breeding success. *Stilt* 14: 49–53.

Battley, P.F. 1997. The northward migration of arctic waders in New Zealand: departure behaviour, timing and possible migration routes of red knots and bar-tailed godwits from Farewell Spit, north-west Nelson. *Emu* 97: 108–120.

Battley, P.F. 2006. Consistent annual schedules in a migratory shorebird. *Biology Letters* 2: 517–520.

Battley, P.F. 2007. Plumage and timing of migration in bar-tailed godwits: a comment on Drent *et al*. (2003). *Oikos* 116: 349–352.

Battley, P.F. & T. Piersma. 2005. Body composition and flight ranges of bar-tailed godwits (*Limosa lapponica baueri*) from New Zealand. *Auk* 122: 922–937.

Battley, P.F., T. Piersma, M.W. Dietz, S.X. Tang, A. Dekinga & K. Hulsman. 2000. Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proceedings of the Royal Society of London, Series B* 267: 191–195.

Battley, P.F., T. Piersma, D.I. Rogers, A. Dekinga, B. Spaans & J.A. van Gils. 2004. Do body condition and plumage during fuelling predict northwards departure dates of great knots *Calidris tenuirostris* from north-west Australia? *Ibis* 146: 46–60.

Battley, P.F., D.I. Rogers & C.J. Hassell. 2006. Prebreeding moult, plumage and evidence for a presupplemental moult in the great knot *Calidris tenuirostris*. *Ibis* 148: 27–38.

Battley, P.F., D.I. Rogers, J.A. van Gils, T. Piersma, C.J. Hassell, A. Boyle & Y. Hong-Yan. 2005. How do red knots *Calidris canutus* leave Northwest Australia in May and reach the breeding grounds in June? Predictions of stopover times, fuelling rates and prey quality in the Yellow Sea. *Journal of Avian Biology* 36: 494–500.

Battley, P.F., R. Schuckard & D.S. Melville. 2011. Movements of bar-tailed godwits and red knots within New Zealand. In *Science for Conservation 315*, 56 pp. New Zealand Department of Conservation.

Battley, P.F., N. Warnock, T.L. Tibbitts, R.E. Gill, Jr., T. Piersma, C.J. Hassell, D.C. Douglas, D.M. Mulcahy, B.D. Gartrell, R. Schuckard, D. Melville & A. Riegen. 2012. Contrasting extreme long-distance migration patterns in bar-tailed godwits *Limosa lapponica*. *Journal of Avian Biology* 43: 21–32.

Becker, W.A. 1984. *A Manual of Quantitative Genetics*. Academic Enterprises, Pullman, Washington.

Bensch, S. & M. Grahn. 1993. A new method for estimating individual speed of molt. *Condor* 95: 305–315.

Berthold, P. & F. Pulido. 1994. Heritability of migratory activity in a natural bird population. *Proceedings of the Royal Society of London, Series B* 257: 311–315.

Bety, J., J.F. Giroux & G. Gauthier. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). *Behavioral Ecology and Sociobiology* 57: 1–8.

Both, C., S. Bouwhuis, C.M. Lessells & M.E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441: 81–83.

Both, C. & M.E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296–298.

Bruderer, B., L.G. Underhill & F. Liechti. 1995. Altitude choice by night migrants in a desert area predicted by meteorological factors. *Ibis* 137: 44–55.

Buehler, D.M., A.J. Baker & T. Piersma. 2006. Reconstructing palaeoflyways of the late Pleistocene and early Holocene red knot *Calidris canutus*. *Ardea* 94: 485–498.

Buehler, D.M. & T. Piersma. 2008. Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society of London, Series B* 363: 247–266.

Busse, P. 2001. European passerine migration system – what is known and what is lacking. *The Ring* 23: 3–36.

Caccamise, D.F. & R.S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 97: 306–318.

Cadee, N., T. Piersma & S. Daan. 1996. Endogenous circannual rhythmicity in a non-passerine migrant, the knot *Calidris canutus*. *Ardea* 84: 75–84.

Calvert, A.M., S.A. Mackenzie, J.M. Flemming, P.D. Taylor & S.J. Walde. 2012. Variation in songbird migratory behavior offers clues about adaptability to environmental change. *Oecologia* 168: 849–861.

Caplan, A.L. 1988. Rehabilitating reductionism. *American Zoologist* 28: 193–203.

Catry, P., G.D. Ruxton, N. Ratcliffe, K.C. Hamer & R.W. Furness. 1999. Short-lived repeatabilities in long-lived great skuas: implications for the study of individual quality. *Oikos* 84: 473–479.

Chu, P.C. 1994. Historical examination of delayed plumage maturation in the shorebirds (Aves, Charadriiformes). *Evolution* 48: 327–350.

Ciarleglio, C.M., J.C. Axley, B.R. Strauss, K.L. Gamble & D.G. McMahon. 2011. Perinatal photoperiod imprints the circadian clock. *Nature Neuroscience* 14: 25–27.

Clark, C.W. & R.W. Butler. 1999. Fitness components of avian migration: a dynamic model of Western Sandpiper migration. *Evolutionary Ecology Research* 1: 443–457.

Conklin, J.R. & M.A. Colwell. 2008. Individual associations in a wintering shorebird population: do dunlin have friends? *Journal of Field Ornithology* 79: 32–40.

Costa, R., A.A. Peixoto, G. Barbujani & C.P. Kyriacou. 1992. A latitudinal cline in a *Drosophila* clock gene. *Proceedings of the Royal Society of London, Series B* 250: 43–49.

Crick, H.Q.P. 2004. The impact of climate change on birds. *Ibis* 146: 48–56.

Cristol, D.A., M.B. Baker & C. Carbone. 1999. Differential migration revisited: latitudinal segregation by age and sex class. *Current Ornithology* 15: 33–88.

Daan, S., C. Dijkstra & J.M. Tinbergen. 1990. Family-planning in the kestrel (*Falco tinnunculus*) – the ultimate control of covariation of laying date and clutch size. *Behaviour* 114: 83–116.

Darwin, C. 1859. *On the Origin of the Species by Natural Selection*. Murray, London.

Dawson, A. 2003. A detailed analysis of primary feather moult in the Common Starling *Sturnus vulgaris* – new feather mass increases at a constant rate. *Ibis* 145 (online): E69–E76.

Dawson, A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in common starlings *Sturnus vulgaris*. *Ibis* 146: 493–500.

Dawson, A. 2006. Control of molt in birds: association with prolactin and gonadal regression in starlings. *General and Comparative Endocrinology* 147: 314–322.

Dawson, A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society of London, Series B* 363: 1621–1633.

Dawson, A., S.A. Hinsley, P.N. Ferns, R.H.C. Bonser & L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London, Series B* 267: 2093–2098.

Dawson, A., V.M. King, G.E. Bentley & G.F. Ball. 2001. Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* 16: 365–380.

Dietz, M.W., T. Piersma, A. Hedenström & M. Brugge. 2007. Intraspecific variation in avian pectoral muscle mass: constraints on maintaining manoeuvrability with increasing body mass. *Functional Ecology* 21: 317–326.

Dingemanse, N.J., C. Both, P.J. Drent & J.M. Tinbergen. 2004. Fitness consequences of avian personalities in a fluctuating environment. *Proceedings of the Royal Society of London, Series B* 271: 847–852.

Dingemanse, N.J. & D. Réale. 2005. Natural selection and animal personality. *Behaviour* 142: 1165–1190.

Dingle, H. 2006. Animal migration: is there a common migratory syndrome? *Journal of Ornithology* 147: 212–220.

Drent, R., C. Both, M. Green, J. Madsen & T. Piersma. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* 103: 274–292.

Drent, R.J., A.D. Fox & J. Stahl. 2006. Travelling to breed. *Journal of Ornithology* 147: 122–134.

Dufva, R. & K. Allander. 1995. Intraspecific variation in plumage coloration reflects immune-response in great tit (*Parus major*) males. *Functional Ecology* 9: 785–789.

Earnst, S.L. 1992. The timing of wing molt in Tundra Swans: energetic and non-energetic constraints. *Condor* 94: 847–856.

Egevang, C., I.J. Stenhouse, R.A. Phillips, A. Petersen, J.W. Fox & J.R.D. Silk. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences* 107: 2078–2081.

Eichhorn, G., V. Afanasyev, R.H. Drent & H.P. van der Jeugd. 2006. Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation. *Ardea* 94: 667–678.

Eichhorn, G., R.H. Drent, J. Stahl, A. Leito & T. Alerstam. 2009. Skipping the Baltic: the emergence of a dichotomy of alternative spring migration strategies in Russian barnacle geese. *Journal of Animal Ecology* 78: 63–72.

Emslie, S.D., R.P. Henderson & D.G. Ainley. 1990. Annual variation of primary molt with age and sex in Cassin's auklet. *Auk* 107: 689–695.

Endler, J.A. 1977. *Geographic Variation, Speciation, and Clines*. Princeton University Press, Princeton, New Jersey.

Engelmoer, M. & C.S. Roselaar. 1998. *Geographic Variation in Waders*. Kluwer Academic Publishers, Dordrecht.

Farmer, A.H. & J.A. Wiens. 1999. Models and reality: time-energy trade-offs in pectoral sandpiper (*Calidris melanotos*) migration. *Ecology* 80: 2566–2580.

Ferns, P.N. 2003. Plumage colour and pattern in waders. *Wader Study Group Bulletin* 100: 122–129.

Fiedler, W. 2009. New technologies for monitoring bird migration and behaviour. *Ringing & Migration* 24: 175–179.

Figuerola, J., J. Domenech & J.C. Senar. 2003. Plumage colour is related to ectosymbiont load during moult in the serin, *Serinus serinus*: an experimental study. *Animal Behaviour* 65: 551–557.

Fitzpatrick, S. 1998. Colour schemes for birds: structural coloration and signals of quality in feathers. *Annales Zoologici Fennici* 35: 67–77.

Flinks, H., B. Helm & P. Rothery. 2008. Plasticity of moult and breeding schedules in migratory European Stonechats *Saxicola rubicola*. *Ibis* 150: 687–697.

Flood, N.J. 1984. Adaptive significance of delayed plumage maturation in male northern orioles. *Evolution* 38: 267–279.

Folstad, I. & A.J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139: 603–622.

Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology* 71: 1–9.

Fox, J.W. 2010. *Geolocator Manual*, version 8. British Antarctic Survey.

Francis, C.M. & F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103: 548–556.

Fransson, T. 1995. Timing and speed of migration in North and West European populations of *Sylvia* warblers. *Journal of Avian Biology* 26: 39–48.

Gauthreaux, S.A., Jr. 1991. The flight behavior of migrating birds in changing wind fields: radar and visual analyses. *American Zoologist* 31: 187–204.

Gill, J.A., R.H.W. Langston, J.A. Alves, P.W. Atkinson, P. Bocher, N.C. Vieira, N.J. Crockford, G. Gélinaud, N. Groen, T. Gunnarsson, B. Hayhow, J. Hooijmeijer, R. Kentie, D. Kleijn, P.M. Lourenço, J.A. Masero, F. Meunier, P.M. Potts, S.P. Roodbergen, H. Schekkerman, J. Schröder, E. Wymenga & T. Piersma. 2008. Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. *Wader Study Group Bulletin* 114: 43–50.

Gill, R.E., Jr., T. Piersma, G. Hufford, R. Servranckx & A. Riegen. 2005. Crossing the ultimate ecological barrier: evidence for an 11000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by bar-tailed godwits. *Condor* 107: 1–20.

Gill, R.E., Jr., T.L. Tibbitts, D.C. Douglas, C.M. Handel, D.M. Mulcahy, J.C. Gottschalck, N. Warnock, B.J. McCaffery, P.F. Battley & T. Piersma. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society of London, Series B* 276: 447–457.

Ginn, H.B. & D.S. Melville. 1983. *Moult in Birds – BTO Guide 19*. British Trust for Ornithology, Hertfordshire.

González-Solís, J., J.P. Croxall, D. Oro & X. Ruiz. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* 5: 297–301.

Green, M. 2004. Flying with the wind – spring migration of arctic-breeding waders and geese over south Sweden. *Ardea* 92: 145–160.

Green, M., T. Alerstam, G.A. Gudmundsson, A. Hedenström & T. Piersma. 2004. Do Arctic waders use adaptive wind drift? *Journal of Avian Biology* 35: 305–315.

Griffith, S.C. & B.C. Sheldon. 2001. Phenotypic plasticity in the expression of sexually selected traits: neglected components of variation. *Animal Behaviour* 61: 987–993.

Grim, T. 2008. A possible role of social activity to explain differences in publication output among ecologists. *Oikos* 117: 484–487.

Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? *Ecological Modelling* 115: 129–148.

Groen, N.M. & L. Hemerik. 2002. Reproductive success and survival of black-tailed godwits *Limosa limosa* in a declining local population in The Netherlands. *Ardea* 90: 239–248.

Gudmundsson, G.A., Å. Lindström & T. Alerstam. 1991. Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres*. *Ibis* 133: 140–152.

Gunnarsson, T.G., J.A. Gill, P.W. Atkinson, G. Gelinaud, P.M. Potts, R.E. Croger, G.A. Gudmundsson, G.F. Appleton & W.J. Sutherland. 2006. Population-scale drivers of individual arrival times in migratory birds. *Journal of Animal Ecology* 75: 1119–1127.

Gunnarsson, T.G., J.A. Gill, J. Newton, P.M. Potts & W.J. Sutherland. 2005. Seasonal matching of habitat quality and fitness in a migratory bird. *Proceedings of the Royal Society of London, Series B* 272: 2319–2323.

Gunnarsson, T.G., J.A. Gill, T. Sigurbjornsson & W.J. Sutherland. 2004. Arrival synchrony in migratory birds. *Nature* 431: 646–646.

Gwinner, E. 1990. Circannual rhythms in bird migration: control of temporal patterns and interactions with photoperiod. Pages 257–268 in *Bird migration: Physiology and Ecophysiology* (E. Gwinner, Ed.). Springer-Verlag, Berlin.

Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* 138: 47–63.

Hahn, T.P., J. Swingle, J.C. Wingfield & M. Ramenofsky. 1992. Adjustments of the prebasic molt schedule in birds. *Ornis Scandinavica* 23: 314–321.

Haig, S.M., L.W. Oring, P.M. Sanzenbacher & O.W. Taft. 2002. Space use, migratory connectivity, and population segregation among willets breeding in the western Great Basin. *Condor* 104: 620–630.

Hake, M., N. Kjellén & T. Alerstam. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103: 385–396.

Hall, K.S.S. & T. Fransson. 2000. Lesser whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. *Journal of Avian Biology* 31: 583–587.

Harrison, X.A., J.D. Blount, R. Inger, D.R. Norris & S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80: 4–18.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology* 79: 2376–2390.

Hedenström, A. 2006. Scaling of migration and the annual cycle of birds. *Ardea* 94: 399–408.

Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society of London, Series B* 363: 287–299.

Hedenström, A. 2010. Extreme endurance migration: What is the limit to non-stop flight? *PLoS Biology* 8: 1–6.

Hedenström, A. & T. Alerstam. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *Journal of Experimental Biology* 164: 19–38.

Helm, B. & E. Gwinner. 2006. Timing of molt as a buffer in the avian annual cycle. *Acta Zoologica Sinica* 52 (suppl.): 703–706.

Henningsson, S.S. & T. Alerstam. 2005. Barriers and distances as determinants for the evolution of bird migration links: the arctic shorebird system. *Proceedings of the Royal Society of London, Series B* 272: 2251–2258.

Hill, G.E. 1988. The function of delayed plumage maturation in male black-headed grosbeaks. *Auk* 105: 1–10.

Hill, G.E. 1991. Plumage coloration is a sexually selected indicator of male quality. *Nature* 350: 337–339.

Hill, G.E. & R. Montgomerie. 1994. Plumage color signals nutritional condition in the house finch. *Proceedings of the Royal Society of London, Series B* 258: 47–52.

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan red-backed sandpipers (*Calidris alpina*). *Condor* 73: 93–99.

Holmgren, N. & A. Hedenström. 1995. The scheduling of molt in migratory birds. *Evolutionary Ecology* 9: 354–368.

Howell, S.N.G. 2010. *Molt in North American Birds*. Houghton Mifflin Harcourt, New York.

Humphrey, P.S. & K.C. Parkes. 1959. An approach to the study of molts and plumages. *Auk* 76: 1–31.

Hussell, D.J.T. 2004. Incubation period and behavior at a bar-tailed godwit nest. *Wilson Bulletin* 116: 177–178.

Irvine, R.J., F. Leckie & S.M. Redpath. 2009. Cost of carrying radio transmitters: a test with racing pigeons *Columba livia*. *Wildlife Biology* 13: 238–243.

Jacobs, J.D. & J.C. Wingfield. 2000. Endocrine control of life-cycle stages: a constraint on response to the environment? *Condor* 102: 35–51.

Jaenisch, R. & A. Bird. 2003. Epigenetic regulation of gene expression: how the genome integrates intrinsic and environmental signals. *Nature Genetics* 33 (suppl.): 245–254.

Järvinen, A. 1989. Geographical variation in temperature variability and predictability and their implications for the breeding strategy of the pied flycatcher *Ficedula hypoleuca*. *Oikos* 54: 331–336.

Jawor, J.M. & R. Breitwisch. 2003. Melanin ornaments, honesty, and sexual selection. *Auk* 120: 249–265.

Jawor, J.M., S.U. Linville, S.M. Beall & R. Breitwisch. 2003. Assortative mating by multiple ornaments in northern cardinals (*Cardinalis cardinalis*). *Behavioral Ecology* 14: 515–520.

Jehl, J.R., Jr. & B.G. Murray, Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Current Ornithology* 3: 1–86.

Johnsen, A., A.E. Fidler, S. Kuhn, K.L. Carter, A. Hoffmann, I.R. Barr, C. Biard, A. Charmantier, M. Eens, P. Korsten, H. Siitari, J. Tomiuk & B. Kempenaers. 2007. Avian clock gene polymorphism: evidence for a latitudinal cline in allele frequencies. *Molecular Ecology* 16: 4867–4880.

Johnson, C. & C.D.T. Minton. 1980. The primary moult of the Dunlin *Calidris alpina* at the Wash. *Ornis Scandinavica* 11: 190–195.

Jonzén, N., A. Lindén, T. Ergon, E. Knudsen, J.O. Vik, D. Rubolini, D. Piacentini, C. Brinch, F. Spina, L. Karlsson, M. Stervander, A. Andersson, J. Waldenström, A. Lehikoinen, E. Edvardsen, R. Solvang & N.C. Stenseth. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. *Science* 312: 1959–1961.

Judson, O.P. 1994. The rise of the individual-based model in ecology. *Trends in Ecology and Evolution* 9: 9–14.

Jukema, J. & T. Piersma. 2000. Contour feather moult of ruffs *Philomachus pugnax* during northward migration, with notes on homology of nuptial plumages in scolopacid waders. *Ibis* 142: 289–296.

Jukema, J. & T. Piersma. 2006. Permanent female mimics in a lekking shorebird. *Biology Letters* 2: 161–164.

Kelly, J., V. Atudorei, Z. Sharp & D. Finch. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130: 216–221.

Ketterson, E.D. & V. Nolan, Jr. 1983. The evolution of differential bird migration. Pages 357–402 in *Current Ornithology*, vol. 1 (R.F. Johnston, Ed.). Plenum Press, New York.

Keyser, A.J. & G.E. Hill. 2000. Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology* 11: 202–209.

Kjellén, N., M. Hake & T. Alerstam. 2001. Timing and speed of migration in male, female and juvenile Ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *Journal of Avian Biology* 32: 57–67.

Klaassen, R.H.G., T. Alerstam, P. Carlsson, J.W. Fox & Å. Lindström. 2011. Great flights by great snipes: long and fast non-stop migration over benign habitats. *Biology Letters* 7: 833–835.

Kraaijeveld, K. & E.N. Nieboer. 2000. Late Quaternary paleogeography and evolution of arctic breeding waders. *Ardea* 88: 193–205.

Landys-Ciannelli, M.M., T. Piersma & J. Jukema. 2003. Strategic size changes of internal organs and muscle tissue in the bar-tailed godwit during fat storage on a spring stopover site. *Functional Ecology* 17: 151–159.

Landys, M.M., T. Piersma, G.H. Visser, J. Jukema & A. Wijker. 2000. Water balance during real and simulated long-distance migratory flight in the bar-tailed godwit. *Condor* 102: 645–652.

Larsson, K. 1996. Genetic and environmental effects on the timing of wing moult in the barnacle goose. *Heredity* 76: 100–107.

Lessells, C.M. & P.T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116–121.

Leyrer, J., S. Pruiksma & T. Piersma. 2009. On 4 June 2008 Siberian Red Knots at Elbe Mouth kissed the canonical evening migration departure rule goodbye. *Ardea* 97: 71–79.

Liechti, F. 2006. Birds: blowin' by the wind? *Journal of Ornithology* 147: 202–211.

Liechti, F. & B. Bruderer. 1998. The relevance of wind for optimal migration theory. *Journal of Avian Biology* 29: 561–568.

Lindström, Å., S. Daan & G.H. Visser. 1994. The conflict between molt and migratory fat deposition: a photoperiodic experiment with bluethroats. *Animal Behaviour* 48: 1173–1181.

Lindström, Å., G.H. Visser & S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology* 66: 490–510.

Łomnicki, A. 1992. Population ecology from the individual perspective. Pages 3–17 in *Individual-based Models and Approaches in Ecology: Populations, Communities, and Ecosystems.* (D.L. DeAngelis & L.J. Gross, Eds.). Chapman and Hall, New York.

Lourenço, P.M., R. Kentie, J. Schroeder, J.A. Alves, N.M. Groen, J.C.E.W. Hooijmeijer & T. Piersma. 2010. Phenology, stopover dynamics and population size of migrating Black-tailed Godwits *Limosa limosa limosa* in Portuguese rice plantations. *Ardea* 98: 35–42.

Lourenço, P.M., R. Kentie, J. Schroeder, N.M. Groen, J.C.E.W. Hooijmeijer & T. Piersma. 2011. Repeatable timing of northward departure, arrival and breeding in Black-tailed Godwits *Limosa l. limosa*, but no domino effects. *Journal of Ornithology* 152: 1023–1032.

Lourenço, P.M. & T. Piersma. 2008. Changes in the non-breeding distribution of continental black-tailed godwits *Limosa limosa limosa* over 50 years: a synthesis of surveys. *Wader Study Group Bulletin* 115: 91–97.

Lozano, G.A., S. Perreault & R.E. Lemon. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. *Journal of Avian Biology* 27: 164–170.

Lundberg, S. & T. Alerstam. 1986. Bird migration patterns: conditions for stable geographical population segregation. *Journal of Theoretical Biology* 123: 403–414.

Lyon, B.E. & R.D. Montgomerie. 1986. Delayed plumage maturation in passerine birds – reliable signaling by subordinate males. *Evolution* 40: 605–615.

Marks, J.S. 1993. Molt of bristle-thighed curlews in the northwestern Hawaiian Islands. *Auk* 110: 573–587.

Marks, J.S. & L.G. Underhill. 1994. Molt, migration and mass of a handicapped bristle-thighed curlew *Numenius tahitiensis*. *Ardea* 82: 153–155.

Marra, P.P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11: 299–308.

Marra, P.P., C.M. Francis, R.S. Mulvihill & F.R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142: 307–315.

Marra, P.P., K.A. Hobson & R.T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282: 1884–1886.

Masero, J.A., F. Santiago-Quesada, J.M. Sánchez-Guzmán, A. Villegas, J. Abad-Gómez, R.J. Lopes, V. Encarnação, C. Corbacho & R. Morán. 2011. Long lengths of stay, large numbers, and trends of the Black-tailed Godwit *Limosa limosa* in rice fields during spring migration. *Bird Conservation International* 21: 12–24.

Mayr, E. 1963. *Animal Species and Evolution*. Oxford University Press, London.

McCaffery, B.J. & R.E. Gill, Jr. 2001. Bar-tailed Godwit (*Limosa lapponica*). In *The Birds of North America*, vol. 581 (A. Poole & F. Gill, Eds.). The Birds of North America, Inc., Philadelphia.

McCaffery, B.J., R.E. Gill, Jr., D. Melville, A. Riegen, P. Tomkovich, M. Dementyev, M. Sexson, R. Schuckard & S. Lovibond. 2010. Variation in timing, behavior, and plumage of spring migrant Bar-tailed Godwits on the Yukon-Kuskokwim Delta, Alaska. *Wader Study Group Bulletin* 117: 179–185.

McGraw, K.J., G.E. Hill & R.S. Parker. 2005. The physiological costs of being colourful: nutritional control of carotenoid utilization in the American goldfinch, *Carduelis tristis*. *Animal Behaviour* 69: 653–660.

McKinnon, L., P.A. Smith, E. Nol, J.L. Martin, F.I. Doyle, K.F. Abraham, H.G. Gilchrist, R.I.G. Morrison & J. Bety. 2010. Lower predation risk for migratory birds at high latitudes. *Science* 327: 326–327.

McNamara, J.M. & A.I. Houston. 2008. Optimal annual routines: behaviour in the context of physiology and ecology. *Philosophical Transactions of the Royal Society of London, Series B* 363: 301–319.

McNamara, J.M., R.K. Welham & A.I. Houston. 1998. The timing of migration within the context of an annual routine. *Journal of Avian Biology* 29: 416–423.

McWilliams, S.R. & W.H. Karasov. 2005. Migration takes guts: digestive physiology of migratory birds and its ecological significance. Pages 67–78 in *Birds of Two Worlds* (R. Greenberg & P.P. Marra, Eds.). Smithsonian Institution Press, Washington, D.C.

Meiri, S. & T. Dayan. 2003. On the validity of Bergmann's rule. *Journal of Biogeography* 30: 331–351.

Meltofte, H., T. Høye, N. Schmidt & M. Forchhammer. 2007a. Differences in food abundance cause inter-annual variation in the breeding phenology of High Arctic waders. *Polar Biology* 30: 601–606.

Meltofte, H., T. Piersma, H. Boyd, B. McCaffery, B. Ganter, V.V. Golovnyuk, K. Graham, C.L. Gratto-Trevor, R.I.G. Morrison, E. Nol, H. Rösner, D. Schamel, H. Schekkerman, M.Y. Soloviev, P.S. Tomkovich, D.M. Tracy, I. Tulp & L. Wennerberg. 2007b. Effects of climate variation on the breeding ecology of Arctic shorebirds. *Bioscience* 59: 1–48.

MetVUW Weather and Climate Service. 2010. Available at: http://www.metvuw.com/forecast/

Minton, C., J. Wahl, H. Gibbs, R. Jessop, C. Hassell & A. Boyle. 2011. Recoveries and flag sightings of waders which spend the non-breeding season in Australia. *Stilt* 59: 17–43.

Mitchell, G.W., N.T. Wheelwright, C.G. Guglielmo & D.R. Norris. 2012. Short- and long-term costs of reproduction in a migratory songbird. *Ibis* 154: 325–337.

Møller, A.P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* 35: 115–122.

Møller, A.P. 2001. Heritability of arrival date in a migratory bird. *Proceedings of the Royal Society of London, Series B* 268: 203–206.

Mong, T.W. & B.K. Sandercock. 2009. Optimizing radio retention and minimizing radio impacts in a field study of upland sandpipers. *Journal of Wildlife Management* 71: 971–980.

Moore, F.R. 1987. Sunset and the orientation behaviour of migrating birds. *Biological Reviews* 62: 65–86.

Moore, F.R. & W. Yong. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28: 85–90.

Morris, R.D. & G.P. Burness. 1992. A new procedure for transmitter attachment: effects on brood attendance and chick feeding rates by male common terns. *Condor* 94: 239–243.

Mumme, R.L., M.L. Galatowitsch, P.G. Jabloński, T.M. Stawarczyk & J.P. Cygan. 2006. Evolutionary significance of geographic variation in a plumage-based foraging adaptation: an experimental test in the slate-throated redstart (*Myioborus miniatus*). *Evolution* 60: 1086–1097.

Murphy, M.E. & J.R. King. 1991. Nutritional aspects of avian molt. Pages 2186–2193 in *Acta XX Congressus Internationalis Ornithologici* (B.D. Bell, Ed.). New Zealand Ornithological Congress Trust Board, Wellington.

Murphy, M.E., J.R. King & J. Lu. 1988. Malnutrition during the postnuptial molt of white-crowned sparrows – feather growth and quality. *Canadian Journal of Zoology* 66: 1403–1413.

Myers, J.P. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behavioral Ecology and Sociobiology* 8: 195–202.

Myers, J.P. 1983. Space, time and the pattern of individual associations in a group-living species – sanderlings have no friends. *Behavioral Ecology and Sociobiology* 12: 129–134.

National Oceanic and Atmospheric Administration (NOAA), Earth System Research Laboratory. 2010a. Available at: http://www.esrl.noaa.gov/psd/data/gridded/data.ncep.reanalysis2.html

National Oceanic and Atmospheric Administration (NOAA), National Climatic Data Center. 2010b. Available at: http://lwf.ncdc.noaa.gov/snow-and-ice/snow-cover.php

Nakagawa, S. & H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* 85: 935–956.

Nebel, S., D.L. Jackson & R.W. Elner. 2005. Functional association of bill morphology and foraging behaviour in calidrid sandpipers. *Animal Biology* 55: 235–243.

Nebel, S., D.B. Lank, P.D. O’Hara, G. Fernandez, B. Haase, F. Delgado, F.A. Estela, L.J.E. Ogden, B. Harrington, B.E. Kus, J.E. Lyons, F. Mercier, B. Ortego, J.Y. Takekawa, N. Warnock & S.E. Warnock. 2002. Western sandpipers (*Calidris mauri*) during the nonbreeding season: spatial segregation on a hemispheric scale. *Auk* 119: 922–928.

Newton, I. 1966. The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41–67.

Niehaus, A. & R. Ydenberg. 2006. Ecological factors associated with the breeding and migratory phenology of high-latitude breeding western sandpipers. *Polar Biology* 30: 11–17.

Norris, D.R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* 109: 178–186.

Norris, D.R., P.P. Marra, T.K. Kyser, T.W. Sherry & L.M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London, Series B* 271: 59–64.

Noskov, G., T. Rymkevich & N. Iovchenko. 1999. Intraspecific variation of moult: adaptive significance and ways of realisation. Pages 544–563 in *Proceedings of the 22nd International Ornithological Congress, Durban* (N. Adams & R. Slotow, Eds.). BirdLife South Africa, Johannesburg.

O’Malley, K.G. & M.A. Banks. 2008. A latitudinal cline in the Chinook salmon (*Oncorhynchus tshawytscha*) clock gene: evidence for selection on PolyQ length variants. *Proceedings of the Royal Society of London, Series B* 275: 2813–2821.

O’Malley, K.G., M.J. Ford & J.J. Hard. 2010. Clock polymorphism in Pacific salmon: evidence for variable selection along a latitudinal gradient. *Proceedings of the Royal Society of London, Series B* 277: 3703–3714.

Obrecht, H.H., C.J. Pennycuick & M.R. Fuller. 1988. Wind-tunnel experiments to assess the effect of back-mounted radio transmitters on bird body drag. *Journal of Experimental Biology* 135: 265–273.

Payne, R.B. 1972. Mechanisms and control of molt. Pages 103–155 in *Avian Biology*, vol. 2 (D.S. Farner & J.R. King, Eds.). Academic Press, New York.

Pennycuick, C.J. & P.F. Battley. 2003. Burning the engine: a time-marching computation of fat and protein consumption in a 5420-km non-stop flight by great knots, *Calidris tenuirostris*. *Oikos* 103: 323–332.

Peters, A., L.B. Astheimer, C.R.J. Boland & A. Cockburn. 2000. Testosterone is involved in acquisition and maintenance of sexually selected male plumage in superb fairy-wrens, *Malurus cyaneus*. *Behavioral Ecology and Sociobiology* 47: 438–445.

Phillips, R.A., J.C. Xavier, J.P. Croxall & A.E. Burger. 2009. Effects of satellite transmitters on albatrosses and petrels. *Auk* 120: 1082–1090.

Piersma, T. 1987. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. *Limosa* 60: 185–194.

Piersma, T. 2002. When a year takes 18 months: evidence for a strong circannual clock in a shorebird. *Naturwissenschaften* 89: 278–279.

Piersma, T., M. Brugge, B. Spaans & P.F. Battley. 2008. Endogenous circannual rhythmicity in body mass, molt, and plumage of great knots (*Calidris tenuirostris*). *Auk* 125: 140–148.

Piersma, T. & J. Drent. 2003. Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution* 18: 228–233.

Piersma, T. & R.E. Gill, Jr. 1998. Guts don't fly: small digestive organs in obese bar-tailed godwits. *Auk* 115: 196–203.

Piersma, T., G.A. Gudmundsson & K. Lilliendahl. 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiological and Biochemical Zoology* 72: 405–415.

Piersma, T. & J. Jukema. 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of bar-tailed godwits at successive spring staging sites. *Ardea* 78: 315–337.

Piersma, T. & J. Jukema. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the bar-tailed godwit. *Condor* 95: 163–177.

Piersma, T., M. Klaassen, J.H. Bruggemann, A.M. Blomert, A. Gueye, Y. Ntiamoa-Baidu & N.E. van Brederode. 1990a. Seasonal timing of the spring departure of waders from the Banc d'Arguin, Mauritania. *Ardea* 78: 123–134.

Piersma, T., L. Mendes, J. Hennekens, S. Ratiarison, S. Groenewold & J. Jukema. 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. *Zoology* 104: 41–48.

Piersma, T., J. Pérez-Tris, H. Mouritsen, U. Bauchinger & F. Bairlein. 2005. Is there a "migratory syndrome" common to all migrant birds? *Annals of the New York Academy of Sciences* 1046: 282–293.

Piersma, T., L. Zwarts & J.H. Bruggemann. 1990b. Behavioral aspects of the departure of waders before long-distance flights – flocking, vocalizations, flight paths and diurnal timing. *Ardea* 78: 157–184.

Potti, J. 1998. Arrival time from spring migration in male pied flycatchers: individual consistency and familial resemblance. *Condor* 100: 702–708.

Powell, M. 2011. Seasonal and spatial variation of *Nicon aestuariensis* (Polychaeta: Nereididae) at the Manawatu Estuary, New Zealand. Honours thesis, Massey University.

Preuss, N.O. 2001. Hans Christian Cornelius Mortensen: aspects of his life and of the history of bird ringing. *Ardea* 89: 1–6.

Prop, J., J.M. Black & P. Shimmings. 2003. Travel schedules to the high arctic: barnacle geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103: 403–414.

Pulido, F. 2007. The genetics and evolution of avian migration. *Bioscience* 57: 165–174.

Pulido, F., P. Berthold, G. Mohr & U. Querner. 2001. Heritability of the timing of autumn migration in a natural bird population. *Proceedings of the Royal Society of London, Series B* 268: 953–959.

Rappole, J.H. & A.R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62: 335–337.

Rees, E.C. 1989. Consistency in the timing of migration for individual Bewick's swans. *Animal Behaviour* 38: 384–393.

Reudink, M.W., C.E. Studds, P.P. Marra, T. Kurt Kyser & L.M. Ratcliffe. 2009. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American redstart *Setophaga ruticilla*. *Journal of Avian Biology* 40: 34–41.

Riegen, A.C. 1999. Movements of banded Arctic waders to and from New Zealand. *Notornis* 46: 123–142.

Rohwer, S., R.E. Ricklefs, V.G. Rohwer & M.M. Copple. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biology* 7: e1000132.

Rotella, J.J., D.W. Howerter, T.P. Sankowski & J.H. Devries. 1993. Nesting effort by wild mallards with 3 types of radio transmitters. *Wildlife Society Bulletin* 57: 690–695.

Rowland, H.M. 2009. From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philosophical Transactions of the Royal Society of London, Series B* 364: 519–527.

Rynn, S. 1982. A revision of the taxonomy of the genus *Limosa.* PhD thesis, Liverpool Polytechnic.

Schaub, M., F. Liechti & L. Jenni. 2004. Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal Behaviour* 67: 229–237.

Schneider, D.C. & B. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98: 801–811.

Schroeder, J., P.M. Lourenço, J.C.E.W. Hooijmeijer, C. Both & T. Piersma. 2009. A possible case of contemporary selection leading to a decrease in sexual plumage dimorphism in a grassland-breeding shorebird. *Behavioral Ecology* 20: 797–807.

Schroeder, J., T. Piersma, N. Groen, J. Hooijmeijer, R. Kentie, P. Lourenço, H. Schekkerman & C. Both. 2012. Reproductive timing and investment in relation to spring warming and advancing agricultural schedules. *Journal of Ornithology* 153: 327–336.

Senar, J.C. & D. Escobar. 2002. Carotenoid derived plumage coloration in the siskin *Carduelis spinus* is related to foraging ability. *Avian Science* 2: 19–24.

Serra, L. 2001. Duration of primary moult affects primary quality in grey plovers *Pluvialis squatarola*. *Journal of Avian Biology* 32: 377–380.

Serra, L. & L.G. Underhill. 2006. The regulation of primary molt speed in the grey plover, *Pluvialis squatarola*. *Acta Zoologica Sinica* 52: 451–455.

Serra, L., D.A. Whitelaw, A.J. Tree & L.G. Underhill. 1999. Moult, mass and migration of grey plovers *Pluvialis squatarola* wintering in South Africa. *Ardea* 87: 71–81.

Shaffer, S.A., Y. Tremblay, H. Weimerskirch, D. Scott, D.R. Thompson, P.M. Sagar, H. Moller, G.A. Taylor, D.G. Foley, B.A. Block & D.P. Costa. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences* 103: 12799–12802.

Shamoun-Baranes, J., J. Leyrer, E. van Loon, P. Bocher, F. Robin, F. Meunier & T. Piersma. 2010. Stochastic atmospheric assistance and the use of emergency staging sites by migrants. *Proceedings of the Royal Society of London, Series B* 277: 1505–1511.

Sherry, T.W. & R.T. Holmes. 1997. American Redstart (*Setophaga ruticilla*). In *The Birds of North America*, vol. 277 (A. Poole & F. Gill, Eds.). The Birds of North America, Inc., Philadelphia.

Shuster, S.M. & M.J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350: 608–610.

Smith, P.A., H.G. Gilchrist, M.R. Forbes, J. Martin & K. Allard. 2010. Inter-annual variation in the breeding chronology of arctic shorebirds: effects of weather, snow melt and predators. *Journal of Avian Biology* 41: 292–304.

Smith, R.J. & F.R. Moore. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology* 57: 231–239.

Snyder, N.F.R., E.V. Johnson & D.A. Clendenen. 1987. Primary molt of California condors. *Condor* 89: 468–485.

Southey, I. 2009. Numbers of waders in New Zealand 1994–2003. In *Research & Development Series 308*, 70 pp. New Zealand Department of Conservation.

Stephens, D.W. & J.R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton.

Studds, C.E. & P.P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Climate Research* 35: 115–122.

Studds, C.E. & P.P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. *Proceedings of the Royal Society of London, Series B* 278: 3437–3443.

Stutchbury, B.J.M., S.A. Tarof, T. Done, E. Gow, P.M. Kramer, J. Tautin, J.W. Fox & V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323: 896.

Sullivan, K.A. 1989. Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). *Journal of Animal Ecology* 58: 275–286.

Summers, R.W., R.W. Swann & M. Nicoll. 1983. The effects of methods on estimates of primary moult duration in the Redshank *Tringa totanus*. *Bird Study* 30: 149–156.

Summers, R.W., L.G. Underhill, M. Nicoll, K.-B. Strann & S.Ø. Nilsen. 2004. Timing and duration of moult in three populations of Purple Sandpipers *Calidris maritima* with different moult/migration patterns. *Ibis* 146: 394–403.

Swaddle, J.P. & M.S. Witter. 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): an experimental approach. *Canadian Journal of Zoology* 75: 1135–1146.

Swaddle, J.P., M.S. Witter, I.C. Cuthill, A. Budden & P. McCowen. 1996. Plumage condition affects flight performance in Common Starlings: implications for developmental homeostasis, abrasion and moult. *Journal of Avian Biology* 27: 103–111.

Swarth, H.S. 1920. Revision of the avian genus *Passerella* with special reference to the distribution and migration of the races in California. *University of California Publications in Zoology* 21: 75–224.

Sykes, P.W., Jr., J.W. Carpenter, S. Holzman & P.H. Geissler. 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wildlife Society Bulletin* 18: 41–48.

Symonds, M.R.E. & G.J. Tattersall. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. *American Naturalist* 176: 188–197.

Székely, T., J.D. Reynolds & J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* 54: 1404–1413.

Tauber, E. & C.P. Kyriacou. 2005. Molecular evolution and population genetics of circadian clock genes. *Methods in Enzymology* 393: 797–817.

Thomas, D.G. & A.J. Dartnall. 1971. Moult of the curlew sandpiper in relation to its annual cycle. *Emu* 71: 153–158.

Thomson, D.L., S.R. Baillie & W.J. Peach. 1999. A method for studying post-fledging survival rates using data from ringing recoveries. *Bird Study* 46 (suppl.): 104–111.

Tomkovich, P.S. 2010. Assessment of the Anadyr Lowland subspecies of bar-tailed godwit *Limosa lapponica anadyrensis*. *Bulletin of the British Ornithologists Club* 130: 88–95.

Tulp, I. 2007. The arctic pulse: timing of breeding in long-distance migrant shorebirds. PhD thesis, University of Groningen.

Tulp, I., S. McChesney & P. De Goeij. 1994. Migratory departures of waders from north-western Australia – behavior, timing and possible migration routes. *Ardea* 82: 201–221.

Tulp, I. & H. Schekkerman. 2008. Has prey availability for Arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic* 61: 48–60.

Underhill, L.G. 2003. Within ten feathers: primary moult strategies of migratory waders (Charadrii). Pages 187–197 in *Avian Migration* (P. Berthold, E. Gwinner & E. Sonnenschein, Eds.). Springer-Verlag, Berlin.

Underhill, L.G. & R.W. Summers. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bulletin* 71: 29–31.

Underhill, L.G. & W. Zucchini. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Underhill, L.G., W. Zucchini & R.W. Summers. 1990. A model for avian primary moult-data types based on migration strategies and an example using the Redshank *Tringa totanus*. *Ibis* 132: 118–123.

van de Kam, J., P.F. Battley, B.J. McCaffery, D. Rogers, J.-S. Hong, N. Moores, J. Yung-Ki, J. Lewis & T. Piersma. 2010. *Invisible Connections: Why Migrating Shorebirds Need the Yellow Sea*. CSIRO Publishing, Collingwood, Australia.

van de Pol, M. & J. Wright. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour* 77: 753–758.

van Noordwijk, A.J., F. Pulido, B. Helm, T. Coppack, J. Delingat, H. Dingle, A. Hedenström, H. van der Jeugd, C. Marchetti, A. Nilsson & J. Pérez-Tris. 2006. A framework for the study of genetic variation in migratory behaviour. *Journal of Ornithology* 147: 221–233.

Vardanis, Y., R.H.G. Klaassen, R. Strandberg & T. Alerstam. 2011. Individuality in bird migration: routes and timing. *Biology Letters* 7: 502–505.

Verhulst, S. & J.M. Tinbergen. 1991. Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. *Journal of Animal Ecology* 60: 269–282.

Verhulst, S., J.H. van Balen & J.M. Tinbergen. 1995. Seasonal decline in reproductive success of the great tit – variation in time or quality? *Ecology* 76: 2392–2403.

Warnock, N. & M.A. Bishop. 1998. Spring stopover ecology of migrant western sandpipers. *Condor* 100: 456–467.

Warnock, N. & R.E. Gill, Jr. 1996. Dunlin (*Calidris alpina*). In *The Birds of North America*, vol. 203 (A. Poole & F. Gill, Eds.). The Birds of North America, Inc., Philadelphia.

Warnock, N., G.W. Page & B.K. Sandercock. 1997. Local survival of dunlin wintering in California. *Condor* 99: 906–915.

Warnock, N. & J.Y. Takekawa. 2003. Use of radio telemetry in studies of shorebirds: past contributions and future directions. *Wader Study Group Bulletin* 100: 138–150.

Warnock, N., J.Y. Takekawa & M.A. Bishop. 2004. Migration and stopover strategies of individual dunlin along the Pacific coast of North America. *Canadian Journal of Zoology* 82: 1687–1697.

Warnock, N. & S. Warnock. 1993. Attachment of radio-transmitters to sandpipers: review and methods. *Wader Study Group Bulletin* 70: 28–30.

Wash Wader Ringing Group (WWRG). 2011. Available at: http://freespace.virgin.net/holme.vale/WaderLongevity.htm

Weber, T.P., T. Alerstam & A. Hedenström. 1998a. Stopover decisions under wind influence. *Journal of Avian Biology* 29: 552–560.

Weber, T.P., B.J. Ens & A.I. Houston. 1998b. Optimal avian migration: a dynamic model of fuel stores and site use. *Evolutionary Ecology* 12: 377–401.

Weber, T.P. & A. Hedenström. 2000. Optimal stopover decisions under wind influence: the effects of correlated winds. *Journal of Theoretical Biology* 205: 95–104.

Wenink, P.W., A.J. Baker & M.G. Tilanus. 1993. Hypervariable-control-region sequences reveal global population structuring in a long-distance migrant shorebird, the Dunlin (*Calidris alpina*). *Proceedings of the National Academy of Sciences* 90: 94–98.

Wiggins, D.A., T. Part & L. Gustafsson. 1994. Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. *Oikos* 70: 359–364.

Wilson, D.S. 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society of London, Series B* 353: 199–205.

Wilson, D.S., A.B. Clark, K. Coleman & T. Dearstyne. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution* 9: 442–446.

Wilson, J.R., S. Nebel & C.D.T. Minton. 2007. Migration ecology and morphometrics of two bar-tailed godwit populations in Australia. *Emu* 107: 262–274.

Wingfield, J.C. 2008. Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society of London, Series B* 363: 425–441.

Witter, M.S. & I.C. Cuthill. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London, Series B* 340: 73–92.

Wood, B. 1992. Yellow Wagtail *Motacilla flava* migration from West Africa to Europe: pointers towards a conservation strategy for migrants on passage. *Ibis* 134: 66–76.

Woodrey, M.S. & F.R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114: 695–707.

Zar, J.H. 1999. *Biostatistical Analysis*, 4th ed. Prentice Hall, Englewood Cliffs, New Jersey.

Zink, R.M. & J.V. Remsen, Jr. 1986. Evolutionary processes and patterns of geographic variation in birds. *Current Ornithology* 4: 1–69.

Zwarts, L., A.M. Blomert & R. Hupkes. 1990a. Increase of feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* 78: 237–256.

Zwarts, L., B.J. Ens, M. Kersten & T. Piersma. 1990b. Molt, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* 78: 339–364.