



Global Flyway Network: the first progress report – for 2006



Individually ringed Ruff *Philomachus pugnax*, photographed on Texel, The Netherlands, on 18 November 2006 by Paul Cools.

Compiled by Theunis Piersma, for *Global Flyway Network*, a foundation based on Texel, The Netherlands, February 2007

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Appendices:

A0. Cover of *Public Library of Science – Biology* (*PLoS-Biology*, the current runner-up to *Nature* and *Science* in terms of academic prestige!) placing the ‘endangerment of red knots’ next to new studies on neurons and HIV.

A1. published paper by J.A. van Gils *et al.* in *Public Library of Science – Biology* (the current runner-up to *Nature* and *Science* in terms of academic prestige!) in 2006 in which it was established that the Dutch shellfish dredging practices in the protected Wadden Sea could account for West-European declines in Red Knots *Calidris canutus islandica*.

A2. Editorial in *PLoS-Biology* about this paper.

A3. Coverage in *New Scientist* of this paper.

A4. Summary in *New Scientist*, putting the message of this *PLoS-Biology* paper in a review of the most important and disturbing scientific facts of 2006.

B. accepted manuscript for the *Journal of Applied Ecology* by P.W. Atkinson *et al.* on the role of horseshoe crab bait fisheries to the ongoing decline of Red Knots *Calidris canutus rufa*.

C. published paper by D.I. Rogers *et al.* in *Biological Conservation* in 2006 providing an analysis of the importance of human disturbance in the use of critical shorebird high tide roosts around a tropical bay in Northwest Australia.

D. manuscript (2006) by R.E. Gill Jr *et al.* in which it is established, based on the latest generation satellite technology, that Bar-tailed Godwits *Limosa lapponica baueri* indeed make transPacific flights from Alaska to New-Zealand in relation to synoptic wind systems.

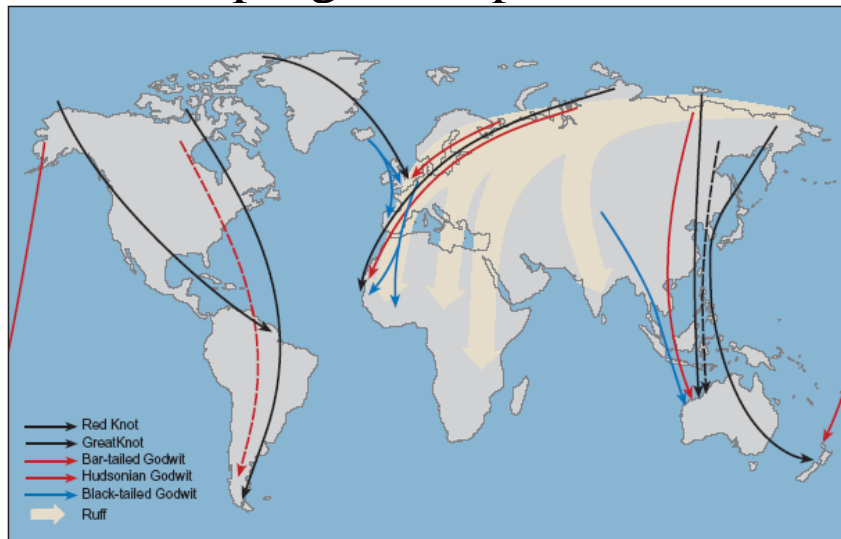
E1. paper by P.F. Battley in *Biology Letters* in 2006 on the repeatability of individual breeding plumage scores in Bar-tailed Godwits, helping such measures to be used to assess individual body condition in relation to environmental change.

E2. paper by P.F. Battley in *Oikos* on the age-dependence of plumage score of Bar-tailed Godwits.

F1. accepted manuscript by P.M. González *et al.* for *El Hornero* on the stopover ecology of Red Knots *Calidris canutus rufa* in Argentina

F2. nearly published book chapter by P.M. González on the wetland and coastal resources in Patagonia, and the threats to these systems.

Global Flyway Network: the first progress report – for 2006



The shorebird ecological demographics and conservation initiative:
a sentinel system for our longest-distance migrant birds

Executive summary

1. Following intense discussions among science partners and BirdLife Netherlands, in 2006 the outlines of a long-term *Global Flyway Network* were established and endorsed by BirdLife. Briefly, the Global Flyway Network is a partnership between researchers worldwide devoted to long-term — usually demographic — work on long-distance migrating shorebirds. The partnership aims to build on the strengths of comparative demographic shorebird studies worldwide, with the aim to understand and analyse the factors determining shorebird numbers in a rapidly changing world. In practice it also tries to fill major gaps in coverage of fieldwork of the world's most threatened shorebird flyways.
2. In late 2006 a foundation by Dutch law was established, and from December 2006 we started to support two long-established key-workers along the West-Atlantic Flyway (Patricia M. González, San Antonio Oeste, Argentina) and the East Asian-Australasian Flyway (Chris Hassell, Broome, Australia) for a period of at least three years.
3. Here we report on the fieldwork carried out by González and Hassell and their volunteer co-workers, and summarize some of the newly published conservation-relevant work that was contributed to by core-members of the Global Flyway Network. Briefly, important contributions were made to (1) elucidating the role of horsehoe crab bait fisheries to the ongoing decline of Red Knots *Calidris canutus rufa*, (2) establishing the involvement of Dutch shellfish dredging practices in protected nature reserves in accounting for West-European declines in *Calidris canutus islandica*, (3) providing an analysis of the importance of human disturbance in the use of critical shorebird high tide roosts around a tropical bay in Northwest Australia, (4) establish the existence of transPacific flights by Bar-tailed Godwits *Limosa lapponica baueri* from Alaska to New-Zealand in relation to synoptic wind systems, based on the latest generation satellite technology, and (5) for the first time establishing repeatability measures for individual breeding plumage scores in Bar-tailed Godwits, to validate their use to assess individual body condition in relation to environmental change.

Introduction

Shorebirds or *waders* are unique among the truly long-distance migrant birds by virtue of the way that they connect continents and hemispheres with their intercontinental movements. Shorebirds depend on rare and remote open habitats for their breeding (mainly in the far North). For their survival over the nonbreeding season they rely on the coastal fringes of continents and ephemeral freshwater habitats of continental basins. By their very nature, shorebirds are particularly susceptible to the effects of human encroachment on coastal habitats, overexploitation of marine resources, loss of scarce freshwater resources and global climate change. A survey by the international Wader Study Group in 2003 showed that of 207 shorebird populations with known population trajectories (out of a total of 511 populations), almost half (48 %) are now known to be in decline whereas only 16% are increasing. With three times as many populations in decline rather than growth, shorebirds must be considered as the most globally endangered segment of the long-distance migrants of the world.

Using the *Global Flyway Network*, established in association with BirdLife Netherlands and BirdLife International, as an umbrella, we propose the amalgamation of a series of existing demographic research initiatives into a truly *worldwide observatory* of the changing fates of the world's shorebird populations and the habitats upon which they depend for their existence. This program intends to combine and coordinate the efforts of a worldwide consortium of well-established shorebird scientists that over the past decade have demonstrated productive collaborations at many different levels. Covering all major flyways and incorporating representatives of several different scientific specializations, it is our aim to encompass the changing world with a system of continuous critical observations on the demography, body condition, health status and relevant genetic variability in sixteen (or more) distinct populations of long-distance migrant shorebirds.

Application of science

The objectives of the Global Flyway Network are to make important contributions of three different kinds:

- (1) To provide an instantaneous **sentinel service** for the global conservation community: an early warning system of flyway populations under threat, the early identification of populations in decline and in need of recovery action, as well as monitoring the fates of populations known to be in dire straits.
- (2) To help generate the **stories** that need to be told to fuel the imagination and the good will of people that can make a difference to the fate of the habitats and populations under threat.
- (3) To further the **science**, including the understanding of the historical background and the current demographic processes and ecological, genetic and immunological constraints that determine whether populations flourish or flounder. The ongoing demographic work will represent cases of integrated monitoring (Reneerkens *et al.* 2005) for each of the proposed study populations.

We believe that we can make exceptional contributions with respect to all three objectives. Never before has a sentinel system for population change been considered on this worldwide scale, especially one that has already been shown to work in

individual flyways. The worldwide scope, the comparative approach between different populations or subspecies within species and between different species, and the increasing ability to follow marked individuals around the globe will enable us to tell the stories of migrant birds and the importance of the habitats they use in new and surprising ways, ensuring high impact publicity. With regard to the science, this program is believed to be unrivalled with respect to the geographic scope and the coordinated approach. We aim to provide a tight integration of the ecological basis of demographic variation within and among populations, focussing on the fitness of individuals with respect to genotype (regions of the genome associated with survival of individuals can now be screened), phenotype (body size, condition, moult, plumage, immunity, etc.) and health status (using the latest generation of field-based assays for a variety of pathogens and parasites). All of these are critical to conservation and restoration of threatened populations (Baker 2006, see Appendix F1). In fact, we want our science to be uncompromised, of the highest international standards.

Deliverables

With respect to each of the three services to the international conservation and science communities, the Global Flyway Network aims to deliver as follows:

(1) **Sentinel services.** (A) Annual reports on the latest results of our work in each of the flyways submitted to the relevant BirdLife partners – the present report for 2006, the year that the network was established, being the first. (B) After the initial three years, we aim to compile a detailed assessment of population trends, demographic developments and annual cycle bottlenecks for each of the studied populations, an assessment for which some of the groundwork will be done during a workshop to be organised in March 2008 in Argentina in conjunction with the BirdLife International triennial conference.

(2) **Stories.** After introductory overviews for popular bird conservation outlets (*Vogels* in The Netherlands, *World Birdwatch* for BirdLife International, *Wingspan* for Birds Australia, etc.), the Global Flyway Network will continue to provide popular accounts of the latest findings for the popular press. We aim to develop this further with our BirdLife partners.

(3) **Science.** We aim to continue to produce scientific papers of the highest possible standards for peer-reviewed journals. For example, a series of publications are in the pipeline on population structure, annual cycle events and demographic parameters of the *rufa*, *islandica*, *canutus* and *rogersi* populations of Red Knots as well as the *baueri* and *taymyrensis* populations of Bar-tailed Godwits. T.G. Gunnarsson and colleagues are presently publishing a whole body of work on habitat use and demographic developments of Icelandic Black-tailed Godwits. PhD projects are well underway on the Black-tailed Godwits and Ruffs in The Netherlands, projects closely interlinked with the Global Flyway Network. All this work should underpin our sentinel services and story-telling contributions.

For the present report, we have selected six (groups of) publications that involves core-workers within the Global FlywayNetwork, these Appendices showing the extent to which this informal network of shorebird scientists already makes critical contributions to shorebird-related conservation science.

What happened in 2006?

Following intense discussions among science partners and BirdLife Netherlands, in 2006 the outlines of a long-term *Global Flyway Network* were established and endorsed by BirdLife. The Global Flyway Network is directed by Prof. Allan J. Baker of the Royal Ontario Museum/University of Toronto and Prof. Dr Theunis Piersma of the Royal Netherlands Institute for Sea Research (NIOZ)/Univ. of Groningen, with managerial help from Dr Petra de Goeij (NIOZ/Univ. of Groningen) and financial assistance from Bob Loos (Texel), who also acts as treasurer. In late 2006 the Global Flyway Network was established as a foundation by Dutch law. The people just listed act as the executive board of GFN.

By late December 2006 it became clear that BirdLife Netherlands would come forward with the financial support for two long-established key-workers along the West-Atlantic Flyway (Patricia M. González, San Antonio Oeste, Argentina) and the East Asian-Australasian Flyway (Chris Hassell, Broome, Australia), support that we expect to continue for a period of at least three years. Both González and Hassell have more than a decade of intense involvement with international shorebird banding and population studies, and they both find themselves in a unique position with respect to urgent shorebird demographic work, i.e. in places where (academic or conservation) support for these kind of work is very hard or impossible to find and where the shorebird populations are under severe ongoing pressures from encroaching humans?? Use development or population pressures?. We are most fortunate in being able to support these people, having the resources to financially support them!

Travel in 2006 was not financially supported by GFN, but helped establish the network started. Theunis Piersma and Petra de Goeij travelled to Argentina in March, Northwest Australia in June-July and Mauritania in December, contributing to the development and activities of the Global Flyway Network. Allan Baker travelled to Argentina in March, and Argentina and Brasil in October-November for GFN-related fieldwork. Patricia M. González and Chris Hassell both travelled to Delaware Bay, USA, in May 2006 to study the Red Knots during their migration stopover.

Apart from many communications among involved scientists and conservationists, the Global Flyway Network was announced in a plenary lecture by Theunis Piersma at the International Ornithological Congress in Hamburg, Germany, August 2006, a lecture witnessed by more than 1200 attendees. The concept of a Global Flyway Network was also developed in a lecture by Theunis Piersma at a symposium in September 2006 in Wageningen, The Netherlands, celebrating the winner of the 2006 Dutch Heineken Prize for Conservation, Prof. Stuart Pimm. Finally, in his 2006 Witherby Lecture at the annual conference of the British Trust for Ornithology in Swanwick, UK, Theunis Piersma briefly mentioned the Global Flyway Network and the involvement of BirdLife. In 2006 Allan Baker received the prestigious Doris Speirs Award for contributions to the field of Canadian Ornithology, in the citation of which it is mentioned that "a vital component of Baker's work is his involvement with the founding of a Global Flyway Network, a network of collaborative researchers, an organization that provides a warning service for identification of migratory shorebirds at risk."

Finally, in 2006 our collaborators Robert E. Gill Jr of the USGS Alaska Science Center and Dr Nils Warnock of the Point Reyes Bird Observatory, received a large grant from the David and Lucile Packard Foundation for their Pacific Shorebird Migration Project, funds that will be used especially for satellite tagging projects in association with Dr Phil F. Battley, New Zealand, and others, to establish the flight routes of endangered shorebirds around and across the Pacific Basin. This independent project will greatly augment the research efforts of the Global Flyway Network, especially in northwest Australia and New Zealand.

Summary of 2006 activities Patricia M. González

CATCHES

Number of red knots caught in Argentina during 2006 and origin of recaptures. All new birds were individually marked with inscribed flags and/or color bands.

Place	Date	New	Recaptures	N recapt. from			Catch Total
				Argentina	Chile	USA	
San Antonio Oeste	28-March	208	31	18	2	10	239
Río Grande	10-Nov	394	117	101	0	16	511
Total		602	148	119	2	26	750

RESIGHTINGS

San Antonio Oeste

Resighting number and origin of individually color banded red knots observed at San Antonio Oeste (SAO), Río Negro, Argentina, during 2006.

	N resighting from:				Total
	Argentina	Chile	Brazil	USA	
February 2006	38	9	0	12	59
March 2006	380	56	0	209	645
April 2006	239	24	1	49	313
Total SAO	657	89	1	270	1017

Delaware Bay

Resighting number and origin of individually color banded red knots observed at Delaware Bay, USA, during 2006.

	N resighting from:				Total
	Argentina	Chile	Brazil	USA	
May 2006	196	21	3	855	1075

Total resightings of Argentinian banded knots obtained by all of the Delaware Bay team (including the previous table), was **383** (without debugging, as yet). Chris Hassell was one of the observers here.

PUBLICATIONS

#1

González, P.M. (Catalog date November 2005- publication April 2006). *Las aves migratorias. Las preguntas de la ida y vuelta de los chorlos y playeros entre los Hemisferios Sur y Norte. Su estadía temporaria en el Área Natural Protegida "Bahía de San Antonio" y su reconocimiento como "Sitio Internacional". Estudio de su potencial ecoturístico. La declinación.*

Chapter in "Las Mesetas Patagónicas que caen al Mar" . Eds Ricardo Freddy Masera et al. Secretaría de Estado de Acción Social, Gobierno de Río Negro.

This chapter is already used by biologists in South America who don't have access to international literature about shorebirds or are not familiar with the English language. It is the basis of knowledge for the professionals (educators, graphic designer and a psychologist) who are developing the exhibition in the future shorebird interpretation center at San Antonio Oeste. Besides, it is the key reading advised to rangers and tourist guides at San Antonio Oeste who are now working in the area during the summer holiday time. This is the first Spanish publication in South America of this kind.

#2

González, P.M., A.J. Baker and M.E. Echave (in press). *Annual survival of red knots (Calidris canutus rufa) using the San Antonio Oeste stopover site is reduced by domino effects involving late arrival and food depletion in Delaware Bay.*

This paper will be published in the Special Section about Migratory Shorebirds in the next issue of *El Hornero*, Vol. 21 Number 2, December 2006. At this moment the authors are waiting for the proofs.

THESIS MANUSCRIPT

Patricia M. González

Thesis of Licenciatura en Ciencias Biológicas, Univ. of Buenos Aires, Argentina.

Declinación poblacional del playero rojizo (Calidris canutus rufa) (Scolopacidae): rol de la supervivencia específica por sexo y estrategias migratorias de larga distancia.

Director: Dr. Allan Baker, Royal Ontario Museum y Universidad de Toronto.

Co-Director: Dr. Juan Carlos Reboreda, Universidad de Buenos Aires.

The actual version is being reviewed by Prof. J.C. Reboreda.

TRAINING

In San Antonio Oeste there are rangers to protect the mean roosting and feeding places for shorebirds, especially Red Knots, during their northern migration. Increasing tourism and development put pressure on the conservation of their habitats. Luckily, every year the Río Negro Government is improving the conservation work under advice from our NGO, Fundación Inalafquen and other institutions. Rangers work from January to April. In November 2006 two of them went with us on the Río Grande

expedition for training. In December a training course for new rangers and community was run in SAO. Patricia González gave the first lecture about shorebird conservation and all participants had to take a test which was marked by selected rangers. At this moment (February 2007), rangers are already working on the beaches during this austral summer, once Red Knots will begin to arrive she will keep training them in conservation issues and data collection to help monitoring of populations during the migration season.

LINKAGES WITH OTHER PROJECTS

For 2007 our work will be related with the monitoring of Red Knots in four places of Patagonia funded by Western Hemisphere Site and Reserve Network-WHSRN (where GFN can be a match and Patricia González is the coordinator); and the Interpretation Center project at SAO, partially funded by Neotropical Migratory Bird Conservation Act (USA),

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Preparatory discussions by the shorebird students and rangers at Patricia's home at San Antonio Oeste in March 2006. Patricia sits on the right.



Juan Pablo, a shorebird ranger, addressing people attending a shorebird conservation course organised by Fundación Inalafquen in March 2006. Speeches were followed by visits to the intertidal 'restinga' in the background. The chemical plant of Solvay, a possible threat to the ecosystem, is noticeable in far back.



Patricia, in foreground, checking the colour-band combination of a red knot caught with 205 others at San Antonio Oeste on 28 March 2006.

Summary of 2006 activities Chris Hassell

With financial support of an early grant of BirdLife Netherlands administered by the Australian Wader Study Group of Birds Australia (the Australian BirdLife partner), much work could be done in 2006. Volunteer participation was high with both experienced people contributing heavily and novices being introduced to the wonders of shorebird conservation and research, mostly via the Broome Bird Observatory's guests.

300 birds had individual colour bands placed on them and this produced over a 1,100 re-sightings (see tables for details).

One Great Knot was seen at Ogku Salt Works, near Saemungum, South Korea on 16 April 2006. This individual was banded at Stilt Viewing, Roebuck Bay, Broome on 15 January 2006. Even more exciting for the start of the project was a male Bar-tailed Godwit caught at Chongming Dongtan Nature Reserve (CDNR), Chongming Dao, Shanghai on 7 April 2006. The bird was banded during the same catch as the Great Knot. The researcher in China was Zhang Kejia who Chris Hassell has worked with at CDNR and who has been to Roebuck Bay to work with the team.

Shorebirds colour-banded by date and species (BTG is Bar-tailed Godwit *Limosa lapponica menzbieri*, GK is Great Knot *Calidris tenuirostris* and RK is Red Knot *Calidris canutus piersmai*)

DATE	BTG BANDED	GK BANDED	RK BANDED	TOTAL
30/12/2005	18	0	0	18
15/01/2006	4	13	0	17
19/02/2006	13	13	1	27
1/07/2006	20	25	10	55
9/07/2006	29	0	0	29
30/07/2006	1	21	22	44
27/08/2006	24	20	13	57
19/12/2006	46	7	0	53
TOTAL	155	99	46	300

Shorebirds resighted by date and species (BTG is Bar-tailed Godwit *Limosa lapponica menzbieri*, GK is Great Knot *Calidris tenuirostris* and RK is Red Knot *Calidris canutus piersmai*)

	BTG	GK	RK	TOTAL
Jan-06	4	0	0	4
Feb-06	13	8	0	21
Mar-06	93	46	1	140
Apr-06	13	1	0	14
May-06	0	0	0	0
Jun-06	6	2	0	8
Jul-06	192	75	24	291
Aug-06	20	16	22	58
Sep-06	87	101	21	209
Oct-06	148	122	37	307
Nov-06	6	13	2	21
Dec-06	37	30	2	69
TOTAL	619	414	109	1142

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Chris Hassell, in foreground, counting and checking for colour-band combinations in flocks of shorebirds at Bush Point, Roebuck Bay, in early July 2006.



Chris, in foreground, demonstrating the working of a cannon-net to a group of local and visiting volunteers at Broome Bird Observatory, in the hours before the actual catching attempt, in early July 2006.



Chris attaching an individual colour-band combination to a Great Knot on one of the northern beaches of Roebuck Bay after a successful cannon-net catch in early July 2006.

List of contributing scientists and institutions

	Affiliation(s)	Specialization (flyway, species or trade)	% funded by program(06-10)
Program co-leaders			
Prof. Dr Theunis Piersma	Univ. Groningen/NIOZ, Netherlands	East Atlantic, general ecology	p.m.
Prof. Dr Allan J. Baker	ROM/Univ. Toronto, Canada	West Atlantic, population genetics	p.m.
Flyway co-ordinators			
Dr Phil F. Battley	Massey Univ., New Zealand	Australasian, ecology/demography	p.m.
B.Sc. Patricia M. González	GFN/Fundacion Inalafquen, Argentina	W. Atlantic, ecology/demography	100
Prof. Dr Yaa Ntiama-Baidu	WWF/Univ. Ghana, Ghana	East Atlantic, ecology/conservation	50*
Field technician			
Chris Hassell	NIOZ/GFN, Australia	Australasian, migration studies	100
Managing co-ordinator			
Dr Petra de Goeij	Univ. Groningen/NIOZ, Netherlands	general ecology	p.m.
Treasurer			
Bob Loos	Texel	shorebird ringing studies	p.m.
Associated program participants			
Robert E. Gill, Jr	USGS, Alaska, USA	Pacific, Bar-tailed Godwit	
Dr Nils Warnock	Point Reyes Bird Obs., CA, USA	Pacific/American, radiotracking	
Dr Pavel S. Tomkovich	Zool. Museum Moscow, Russia	Population biology, sandpipers	
Dr R.I. Guy Morrison	Canadian Wildlife Service, Canada	West Atlantic, Red Knot	
Grant B. Pearson	WA Dept. Env. Conserv., Australia	Australasian, migration & resource studies	
Dr Danny I. Rogers	Charles Sturt Univ., Australia	Australasian, Red & Great Knots	
Dr Clive D.T. Minton	for Australasian Wader Studies Group	Australasian, sandpipers	
Dr Tomas Gunnarsson	Univ. of Iceland	East Atlantic, shorebirds	
Pete Potts	UK	Black-tailed Godwits	
Dr Jenny Gill	Univ. of East Anglia	Black-tailed Godwits	
Dr Phil W. Atkinson	BTO, UK	Red Knots	
Dr Nigel A. Clark	BTO, UK	Red Knots	
Dr Pierrick Bocher	Univ. La Rochelle, France	Red Knots, Black-tailed Godwits	
Drs Bernard Spaans	NIOZ, Netherlands	East Atlantic, demography, sandpipers	
Drs Jutta Leyrer	NIOZ, Netherlands	Red Knots	
Dr Jeroen Reneerkens	Univ. of Groningen, Netherlands	Sanderling	
Drs Jos Hooijmeijer	Univ. of Groningen, Netherlands	Demography, Ruff, Black-t. Godwits	
Associated research advisors			
Prof. Dr Brett Sandercock	Univ. of Kansas, USA	Demography	
Prof. Dr David W. Winkler	Cornell University, USA	Smart tag development, population biology	
Dr B. Irene Tieleman	Univ. of Groningen, Netherlands	Field immunology	
Dr Christaan Both	Univ. of Groningen, Netherlands	Population biology & migration	
Dr Javier Perez-Tris	Univ. of Madrid, Spain	Avian blood parasites	
Prof. Dr Ron Fouchier	Erasmus MC, Netherlands	Avian virology	
International policy advisors			
Dr Nick C. Davidson	Ramsar Convention, Switzerland	Shorebird flyway biology & conservation	
Dr David Stroud	JNCC, UK	Waterbird conservation biology	

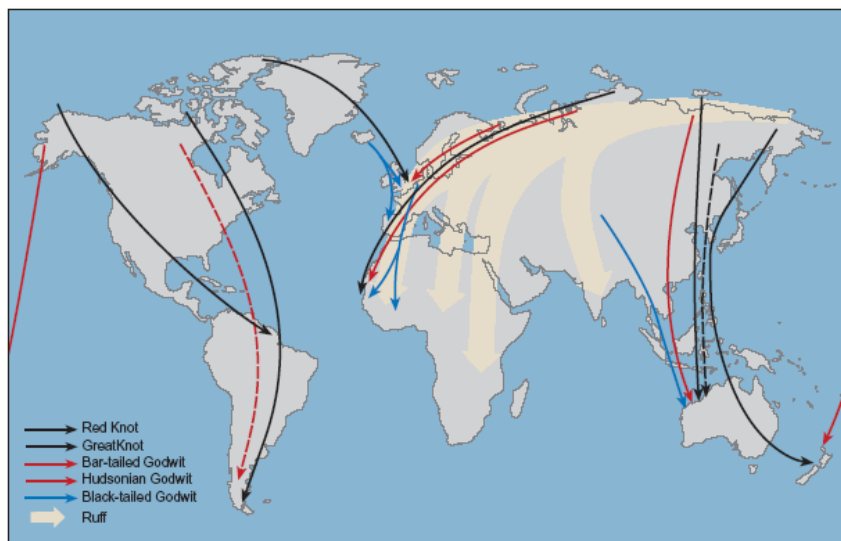
* It is hoped that funds for Prof. Ntiama-Baidu would be provided through WWF-Netherlands

** It is hoped that funds for general coordination would be sourced from different allocations within BirdLife Netherlands

List of focal species and flyways

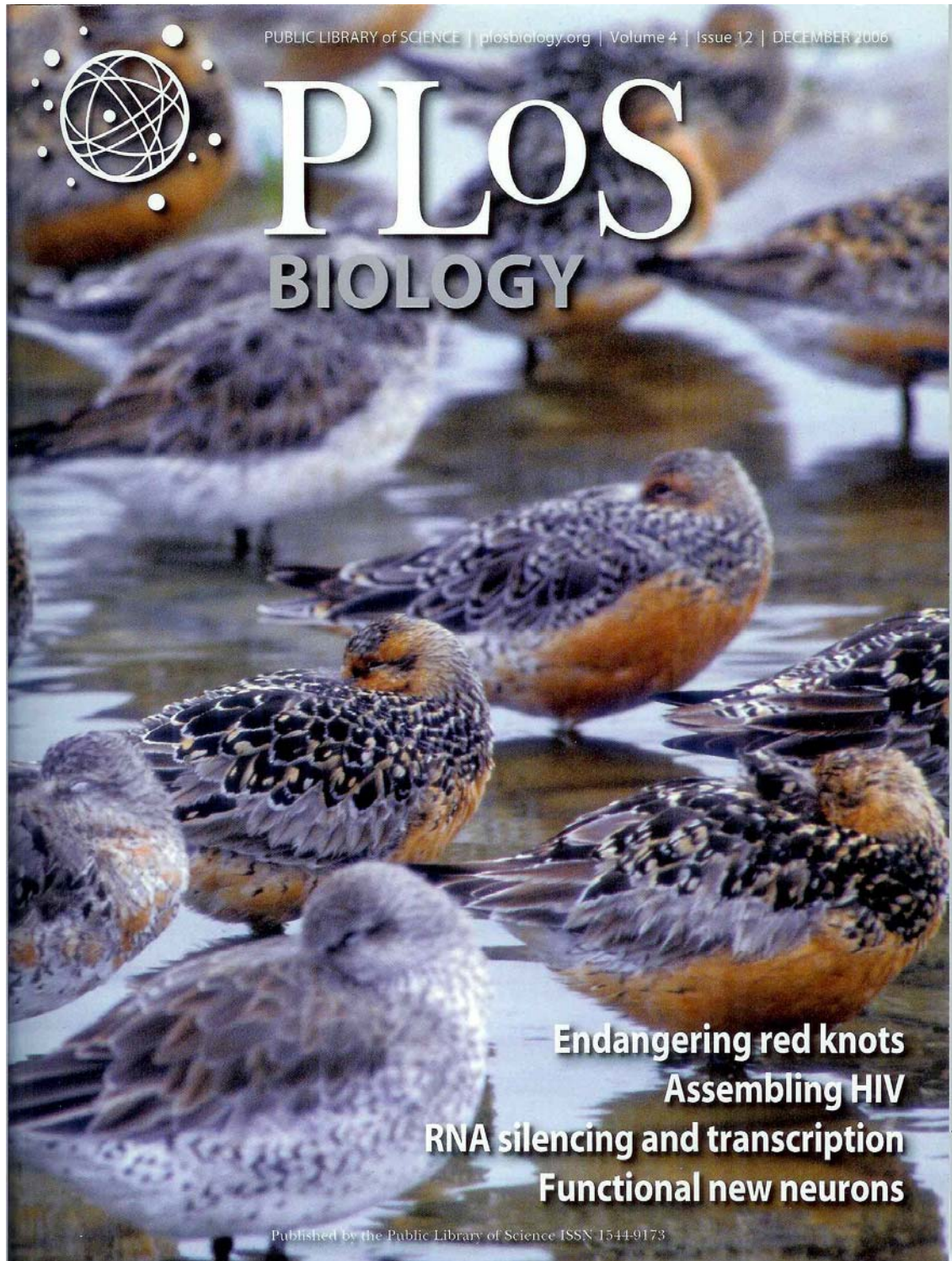
List of species and subspecies, the sites where they are presently studied most intensively (e.g. where marking and resighting efforts are concentrated), two ecological characteristics and an indication of whether the populations are on a trajectory of increase or decline.

Nr	Species	Subspecies	Core study site(s)	Habitat	Diet	Population change
1	Red Knot <i>Calidris canutus</i>	<i>canutus</i>	Mauritania	Coastal	molluscs	negative
2	Red Knot	<i>piersmai</i>	NW Australia	Coastal	molluscs	negative
3	Red Knot	<i>rogersi</i>	New Zealand	Coastal	molluscs	negative
4	Red Knot	<i>roselaari?</i>	NW Brasil	Coastal	molluscs	negative
5	Red Knot	<i>rufa</i>	Argentina & USA	Coastal	molluscs	negative
6	Red Knot	<i>islandica</i>	Netherlands	Coastal	molluscs	negative
7	Great Knot <i>Calidris tenuirostris</i>		NW Australia	Coastal	molluscs	negative
8	Bar-tailed Godwit <i>Limosa lapponica</i>	<i>lapponica</i>	Netherlands	Coastal	worms	positive?
9	Bar-tailed Godwit	<i>taymyrensis</i>	Netherlands & Mauritania	Coastal	worms	negative
10	Bar-tailed Godwit	<i>menzbieri</i>	NW Australia	Coastal	worms	negative
11	Bar-tailed Godwit	<i>baueri</i>	New Zealand	Coastal	worms	negative
12	Hudsonian Godwit <i>Limosa haemastica</i>		Argentina	Coastal	worms	stable?
13	Black-tailed Godwit <i>Limosa limosa</i>	<i>limosa</i>	Netherlands	Inland	worms	negative
14	Black-tailed Godwit	<i>islandica</i>	Iceland, UK, France	Coastal	worms & molluscs	now stable
15	Ruff <i>Philomachus pugnax</i>		Netherlands	Inland	arthropods	negative
16	Sanderling <i>Calidris alba</i>		Ghana, Mauritania, Netherlands, Iceland	Coastal	worms & arthropods	variously stable and negative



Appendices

Appendix A0



Shellfish Dredging Pushes a Flexible Avian Top Predator out of a Marine Protected Area

Jan A. van Gils^{1,2*}, Theunis Piersma^{1,2}, Anne Dekinga¹, Bernard Spaans¹, Casper Kraan¹

1 Department of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands, **2** Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, Haren, The Netherlands

There is a widespread concern about the direct and indirect effects of industrial fisheries; this concern is particularly pertinent for so-called “marine protected areas” (MPAs), which should be safeguarded by national and international law. The intertidal flats of the Dutch Wadden Sea are a State Nature Monument and are protected under the Ramsar convention and the European Union’s Habitat and Birds Directives. Until 2004, the Dutch government granted permission for ~75% of the intertidal flats to be exploited by mechanical dredgers for edible cockles (*Cerastoderma edule*). Here we show that dredged areas belonged to the limited area of intertidal flats that were of sufficient quality for red knots (*Calidris canutus islandica*), a long-distance migrant molluscivore specialist, to feed. Dredging led to relatively lower settlement rates of cockles and also reduced their quality (ratio of flesh to shell). From 1998 to 2002, red knots increased gizzard mass to compensate for a gradual loss in shellfish quality, but this compensation was not sufficient and led to decreases in local survival. Therefore, the gradual destruction of the necessary intertidal resources explains both the loss of red knots from the Dutch Wadden Sea and the decline of the European wintering population. This study shows that MPAs that do not provide adequate protection from fishing may fail in their conservation objectives.

Citation: van Gils JA, Piersma T, Dekinga A, Spaans B, Kraan C (2006) Shellfish dredging pushes a flexible avian top predator out of a marine protected area. PLoS Biol 4(12): e376. DOI: 10.1371/journal.pbio.0040376

Introduction

Worldwide benthic communities of intertidal soft sediments are seriously threatened by bottom-touching fisheries such as dredging [1]. Not only do target species directly decline in numbers because of removal, but target and non-target species are also indirectly affected [2,3]. In turn, predators such as migrant shorebirds, which make a living from benthic invertebrates, are declining in many parts of the world, and a link with commercial fishing activities seems evident [4–6]. Until 2004, three-quarters of the intertidal flats of the Dutch Wadden Sea were open to mechanical dredging for edible cockles, despite the high-level conservation status, despite the concerns about the damaging effects of cockle dredging to intertidal ecosystems, and despite the limited economic value of cockle dredging (a total of only 11 license holders maintained a fleet of just 22 fishing boats [7]).

A direct, immediate effect of dredging is the complete removal of all organisms larger than 19 mm in the 5-cm top layer. Because the sites dredged are usually the most biodiverse (C Kraan, T Piersma, A Dekinga, A Koolhaas, J Van der Meer, unpublished data), dredging may also affect smaller cockles; other bivalves such as blue mussels (*Mytilus edulis*), Baltic tellins (*Macoma balthica*), and sandgapers (*Mya arenaria*); polychaetes; and crustaceans such as shorecrabs (*Carcinus maenas*). More indirectly and over longer time scales, sediments become coarser after dredging events, leading to reduced settlement success in both cockles and Baltic tellins [3]. Because grain size affects the feeding performance of bivalve mollusks [8], one expects prey condition or quality (defined as flesh-to-shell ratio [9]) to be negatively affected by dredging activities. We may thus expect mechanical dredging to lead to both short- and long-term declines in quantity and quality of a variety of macrobenthic organisms.

Shellfish-eating shorebirds can cope with reductions in both prey density and in prey quality, as long as the reductions are not too large and do not occur simultaneously (Figure 1). Red knots have been shown to flexibly adjust their digestive capacity to food quality so that food processing rates are just sufficient to obtain the daily amount of energy (i.e., flesh) required to maintain energy balance [9,10]. Maintaining a larger digestive system would be costly in terms of maintenance and transport costs [11]. Therefore, a knot’s intake rate is often constrained by a digestive bottleneck [9,12]. This implies that a decline in prey density, although it may hamper maximum rates of prey collection (dictated by so-called “short-term functional responses” such as Holling’s type II disk equation), will often only marginally affect the digestively constrained intake rate over the full low-tide period (Figure 1). Likewise, as the digestive system is flexible and can be adjusted rapidly [13], a decline in food quality can be compensated for by an increase in digestive capacity (Figure 1). By contrast, once both density and quality

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Abbreviations: GLM, general linear model; MPA, marine protected area; SE, standard error

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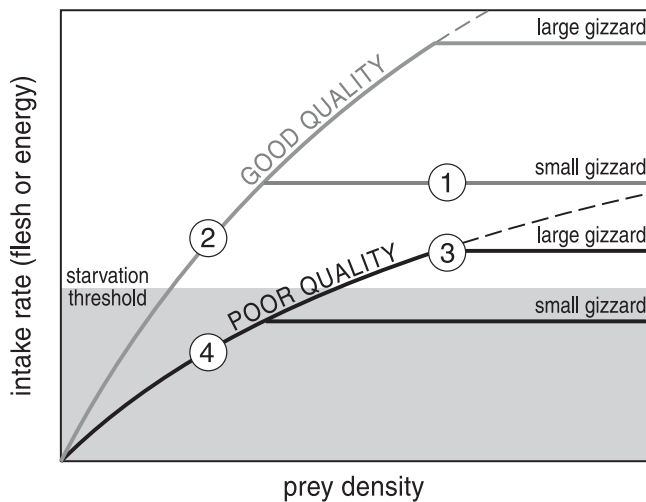


Figure 1. Conceptualization of Why a Simultaneous Reduction in Density and Quality of the Prey is Detrimental

Holling's Type II functional response describes intake rate (be it flesh or energy) as a function of the density of either poor-quality (black lines) or good-quality (gray lines) prey. Digestive constraint limits shell-mass processing rate and is given for two gizzard sizes for each prey quality (horizontal cut-offs in functional response; digestively unconstrained intake rates continue as dashed lines). By knowing the threshold intake rate needed to avoid starvation (border between gray and white background), one can predict a bird's starvation chances on the basis of gizzard size and prey quality and density. (1) A small gizzard is sufficient to stay alive when prey is of good quality and occurs in high densities. Going from (1) to (2), prey density is reduced, which does not affect survival as intake rate remains above the critical threshold. Going from (1) to (3), prey quality (flesh-to-shell ratio) is reduced. To maintain a sufficient intake rate, the knot needs to increase its shell-mass processing rate, which requires a gizzard enlargement. Going from (1) to (4), the combined reduction in density and quality makes a gizzard enlargement no longer sufficient (as intake rate is now constrained by prey density), and the bird is bound to starve.

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decline simultaneously, the situation may become critical. In such cases, intake rate may become too low to maintain daily energy balance (Figure 1).

We studied dredging-induced changes in food quantity and quality and their effects on digestive physiology and survival in red knots (henceforth called knots) in the western Dutch Wadden Sea (53°14' N, 5°10' E). This site is of major importance for wintering *islandica* knots, and it is estimated that about 1/3–1/2 of the population stays or at least passes through the area each winter [14,15]. In an area of roughly 250 km², we annually (1998–2002) sampled densities and qualities of knot food in great detail (Figure 2A). Each year, mechanical dredging took place from early September into December, immediately after the completion of our sampling program. We used the exact locations of dredging to categorize 1-km² sample blocks as dredged or undredged (bearing in mind that this is not an ideal randomized block design, because blocks were selected by the fishermen). Because knots during our study period mostly consumed first-year cockles (mean percentage in diet \pm standard error [SE] = 57.9 \pm 2.8% of ingested flesh; n = 174 dropping samples), quantity and quality effects of dredging were studied with respect to newly settled cockles (≤ 16 mm) only.

We will make the point that shell fishing and shorebird conservation are incompatible. Marine Protected Areas (MPAs) are increasingly seen as a tool to manage sustainable

fisheries in coastal ecosystems [16], which gives policy makers the feeling that they can achieve a win-win for both conservation and commercial exploitation. However, in practice, because nature conservation objectives are often fitted around the ongoing fisheries, conservation and commerce are not compatible [17] as exemplified here in the case of knots and shell fishing in the Dutch Wadden Sea.

Results/Discussion

Densities of small cockles remained stable in areas mechanically dredged, whereas they increased by 2.6% per year in undredged areas (general linear model [GLM] with n = 271 blocks: R^2 = 0.02, p = 0.04) (Figure 2B). Moreover, quality of small cockles declined by 11.3% per year in dredged areas and remained stable in undredged areas (GLM with n = 59 blocks: R^2 = 0.07, p = 0.04) (Figure 2B). These results are consistent with a previous assessment [3] that showed dredged areas to become unattractive areas for cockles to settle, a finding that was explained by dredged sediments losing silt and becoming coarser. In deposit-feeding bivalves such as freshly settled cockles [18,19], coarser sediments may lead to worse feeding conditions [8] and therefore to reduced body condition, which, from the predator's point of view, equals reduced prey quality [20].

To express changes in carrying capacity in relation to dredging activity, we calculated for each year the percentage of blocks that would yield insufficient intake rates for knots to maintain a positive energy balance (taking 4.8 W as the critical metabolizable energy intake rate [21]). During our study period, the percentage of km² blocks that were too poor for knots to feed increased from 66% in 1998 to 87% in 2002 (GLM with n = 5 y: R^2 = 0.80, p = 0.04) (Figure 3A). This was entirely due to an increase in previously suitable blocks that were dredged (GLM with n = 5 y: R^2 = 0.96, p = 0.003) (Figure 3A, dark gray bars). We calculated that of this 21% increase in unsuitability, 8% was due to a decline in prey densities alone, whereas the remaining 13% was due to the simultaneous decline in density and quality (note that these calculations include all potential prey species, not only cockles). In contrast, the percentage of unsuitable blocks that were never dredged before did not change (GLM with n = 5 y: R^2 = 0.02, p = 0.80) (Figure 3A, light gray bars). As a consequence of the widespread dredging in the best areas, diet quality declined by 11.7% per year (GLM with n = 174 dropping samples: R^2 = 0.05, p = 0.003) (Figure 3B), a similar rate of decline (11.3%) as shown by the quality of cockles, the knots' main prey, in dredged areas. To compensate for reductions in diet quality, knots should increase gizzard mass [9,13]. Indeed, in the course of the study period, gizzard mass increased by 3.4% per year (GLM with n = 644 birds: R^2 = 0.02, p = 0.0001) (Figure 3C). This increase in gizzard mass exactly matches our quantitative expectations, because experimental results on shell mass processing rates [9] imply that gizzard mass should vary inversely with the square root of prey quality (i.e., square root of the annual 11.7% decline in prey quality = 3.4%). More specifically, gizzard masses do not deviate from the predicted gizzard masses required to balance the energy budget (predicted from yearly average prey quality values [9,10], p > 0.1, n = 484).

Nevertheless, resightings of individually color-banded birds, whose gizzards were measured before release, suggest

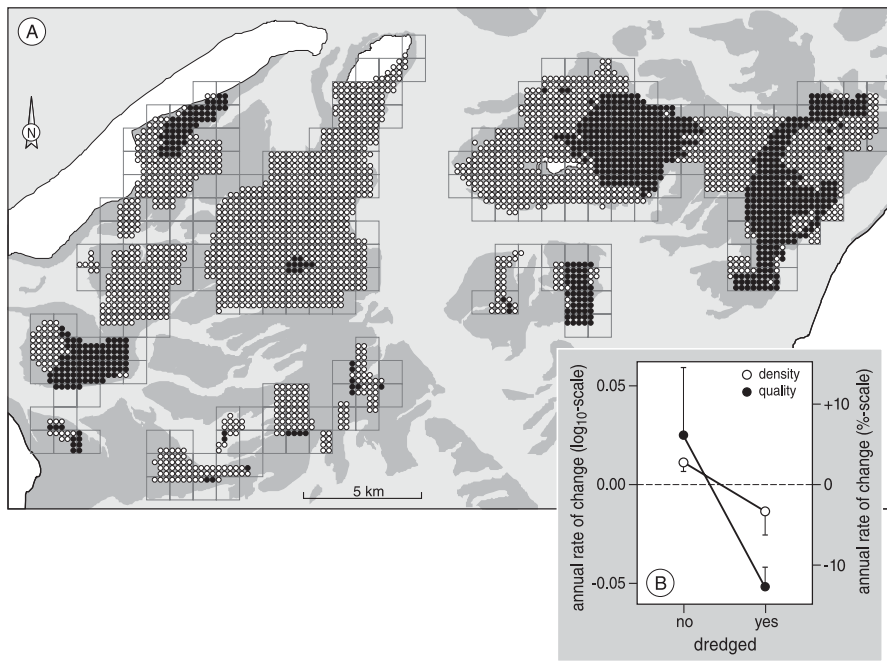


Figure 2. Study Area and Effects of Dredging

(A) Map of the study area with 2,846 sampling stations (dots) categorized into 272 square kilometer blocks (squares containing 16 stations at most). A dot is filled when a station has been dredged at least once in 1998–2002 and is open when the station was never dredged during that period. (B) Densities of available cockles remained stable in dredged blocks, but they increased ($+3\% \text{ y}^{-1}$) in undredged blocks (open dots \pm SE bars). Quality of available cockles declined in dredged areas ($-11\% \text{ y}^{-1}$), whereas it remained stable in undredged areas (filled dots \pm SE bars).

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that on average, birds not seen in our study area within the year after release had undersized gizzards ($p < 0.01$, $n = 362$), whereas individuals that we did see again had gizzards that enabled them to achieve a balanced daily energy budget ($p > 0.4$, $n = 122$) (Figure 4A). That birds returning from the high-arctic breeding grounds with undersized gizzards [22] do not simply enlarge their gizzard may be explained by time and energy constraints [13,23]. Birds arriving with too small a gizzard may need more time to adjust their gizzard than their fat stores allow them, and therefore they face starvation unless they leave the area (indeed we found that birds with a smaller gizzard had a lower body mass; $R^2 = 0.06$, $p < 0.00001$, $n = 483$). This implies that the proportion of birds arriving with a gizzard large enough to survive increases as a function of food quality at the arrival destination (Figure 4A and 4B). Indeed, local annual survival rate (calculated from resighting rates of color-banded birds) increased with food quality in the expected direction (Figure 4C). When we estimated the distribution of gizzard masses upon arrival (by selecting only those birds caught in the Wadden Sea during late July) and calculated, for various degrees of gizzard flexibility, the proportion of birds that would survive the critical gizzard-enlargement phase (Figure 4B and 4C), the best fit with the actual survival data was obtained if knots had time to increase their gizzard by 1 g only (Figure 4C).

Color-banded knots that disappeared from our study area may have died or, perhaps more likely for a wide-ranging migrant, emigrated to other areas such as the estuaries in the United Kingdom, where they probably paid a mortality cost due to the extra travel and/or due to uncertainties in the food supply at their new destination (where they also fed on hard-shelled prey, in the past [24,25] and more recently [26,27], and

thus faced gizzard-related mortality; note that knots are “forced” to feed on hard-shelled prey as their pressure-sensitive bill tip can only detect hard objects buried in soft sediments [28]). In any case, the declining numbers of knots wintering in the Dutch Wadden Sea [29] can be explained as a response to declining food conditions. Moreover, the 25% decline of the entire northwestern European wintering population between 1997–1998 and 2002–2003 (from $\sim 330,000$ to $\sim 250,000$) (G Austin, M Van Roomen, B Koks, T Piersma, unpublished data) can be explained by measured decreases in local survival of the Wadden Sea segment of the population during the study period (using the observed local survival rates, we estimated an extra mortality of 58,000 birds over the 5-y period). This study concludes that industrial forms of commercial exploitation of protected marine nature reserves in The Netherlands, by indirectly reducing food resource quality to such extents that changes can no longer be accommodated by adjustments of the digestive system, are directly responsible for the overall population decline of a fully protected shorebird species. This paper thereby adds to growing list of studies [17,30] stressing the uselessness of declaring a marine area as protected whenever the species living in it are seriously affected by the ongoing but regulated human activities.

Materials and Methods

Sampling prey density and quality. From late July to early September 1998–2002, we sampled macrozoobenthos throughout the western Dutch Wadden Sea in a regular grid (250-m grid intersections; Figure 2A). In total, we visited 2,846 stations, of which the majority (75%) were sampled each year (89% in 4 out of 5 y). Stations were located using handheld global positioning system (GPS) receivers (Garmin 45 and 12; Garmin Corporation, Lenexa, Kansas,

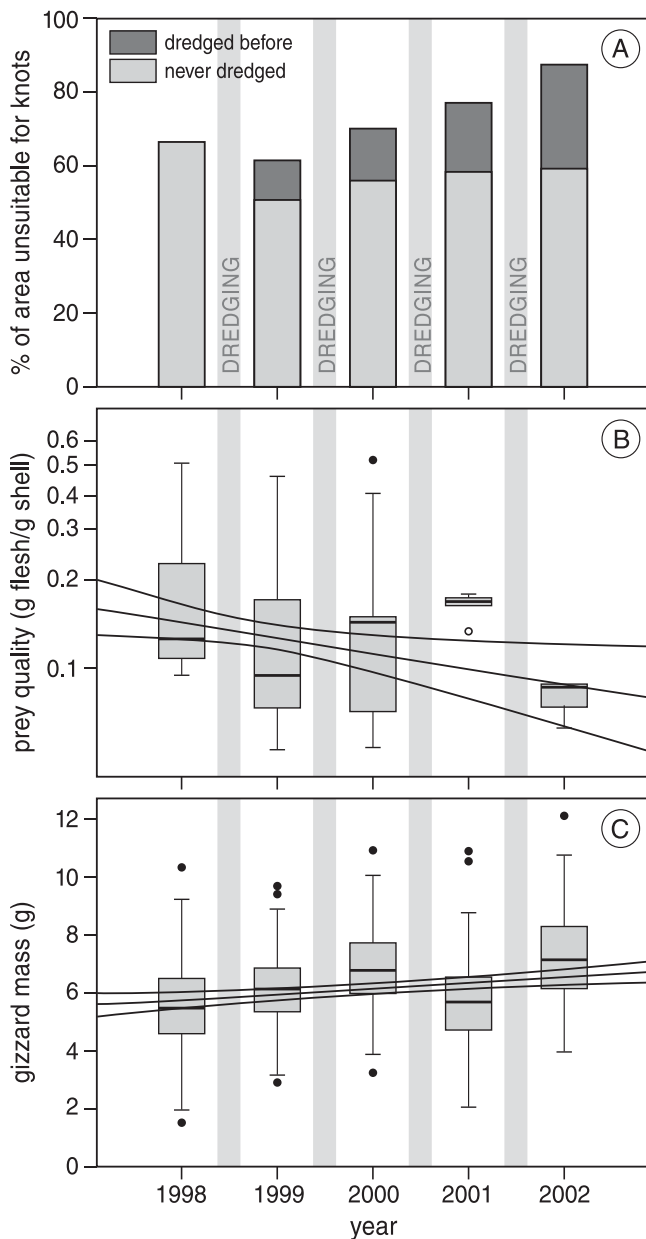


Figure 3. Changes in Suitability, Prey Quality, and Gizzard Mass

(A) The percentage of blocks that yielded insufficient intake rates (<4.8 W) increased over time due to an increase in unsuitable blocks being dredged in previous years (dark gray bars; as opposed to light gray bars indicating unsuitable blocks that were never dredged). (B) Quality of prey included in the diet has declined over time (box-and-whisker plot, line gives GLM \pm 95% confidence intervals). (C) In response, gizzard mass has increased over time (boxes and lines as in (B)).

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United States) and were either visited during low tide (on foot) or during high tide (by rubber boat). At each station, a sediment core was taken (15-cm diameter; 20-cm deep) that was sieved over a 1-mm mesh. To distinguish accessible prey from prey living beyond the reach of a knot's bill (4 cm), we sieved the top layer (upper 4 cm) separately from the bottom layer (only the "low-tide samples"). Mudsnailed (*Hydrobia ulvae*) were sampled using a smaller core (7-cm diameter) and a finer mesh (0.5 mm). All potential prey items retained on the sieve were frozen (-20°C) for later analyses. In the laboratory, items were identified with respect to species and size (to nearest mm; or, in the case of *H. ulvae*, to nearest 0.5 mm). Size classes were determined to distinguish ingestible prey from prey too large to be

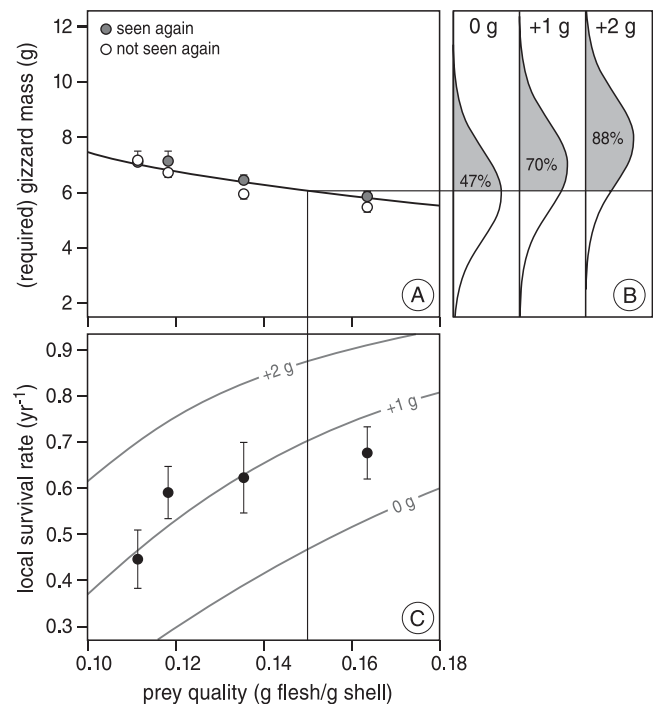


Figure 4. Quantitative Relations between Prey Quality, Gizzard Mass, and Local Survival Rate

(A) Gizzard mass required to maintain energy balance declines as a function of prey quality (solid line). Gizzards of birds seen again after catching fit this relationship (gray dots; mean \pm SE), whereas gizzards of birds not seen again are significantly smaller (open dots; note that both groups almost entirely overlap in the poorest-quality year).

(B) Observed gizzard masses upon arrival are distributed according to the left-most normal distribution. If there were no room for flexibly adjusting gizzard mass (0 g), only 47% of the arriving knots would be able to avoid starvation (shaded area) at an example prey quality of 0.15 g flesh per g shell (dashed line). If there were room for flexibility (+1 and +2 g in this example), a much larger proportion would be able to survive (respectively 70% and 88%).

(C) Observed local survival rate (yr^{-1} ; \pm SE) increased as a function of prey quality and best matched with predicted survival in a +1-g flexibility scenario.

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swallowed [12]. Methods to determine flesh and shell mass are explained elsewhere [3, 31].

Mechanical dredging and its effects on cockle density and quality. During each of the 5 y studied, mechanical dredging took place after our sampling program; i.e., from early September into December. Exact locations of dredging were known, because for reasons of internal control, every vessel had a GPS-logger onboard [7]. Cumulative seasonal data on dredging locations were available in the form of fine-scaled maps (resolution of 0.1 min latitude by 0.5 min longitude).

We analyzed the effects of mechanical dredging on cockles that were actually available to knots (i.e., ≤ 16 mm, because larger ones cannot be swallowed [32]). We pooled sampling stations in 272 blocks measuring 1 km by 1 km each (Figure 2A; many sampling stations did not have cockles available during multiple years making it impossible to study changes in quality at the spatial scale of stations). A block was considered dredged when at least one station was dredged in at least 1 y. Per block, we applied the following GLMs: $\log_{10}(\text{DENSITY} + 1) = \text{CONSTANT} + \text{YEAR}$ and $\log_{10}(\text{QUALITY}) = \text{CONSTANT} + \text{YEAR}$. Subsequently, we tested whether significant variation in the coefficients for YEAR could be explained by whether a block was ever dredged or not during 1998–2001 (again using GLM).

Suitability for knots. The measurements on (available) prey densities and qualities allowed us to predict for each station an intake rate for a knot with an average-sized gizzard (6-g fresh mass). We did so by applying the so-called "digestive rate model," a multi-species functional response that takes rates of digestion into account

[33], which accurately predicted diet choice, patch choice, and intake rate in both free-ranging and captive knots [12,31]. Subsequently, after averaging these intake rates per block, we determined a block's suitability. A block was considered suitable when it yielded an intake rate sufficient to maintain energy balance when feeding for 10 h per day (corresponding to an intake rate of at least 0.3 mg dry flesh mass s^{-1} , which equals a metabolizable energy intake rate of at least 4.8 W; note that the energy contents of 1 g of flesh is more or less constant in mollusks [34]). This approach is widely used [35,36] and adequately predicted the distribution of knots in an earlier study [21].

Diets, gizzard sizes, and observed and predicted survival rates. Diet quality was reconstructed by fecal analyses, following the procedures outlined by Dekinga and Piersma [37]. Dropping samples were collected during low tide at sites where flocks of knots had just fed. Across the 5 y of study, we analyzed 174 dropping samples, comprising 1–100 dropping(s) each (15 on average).

In order to estimate gizzard sizes and survival rates, we annually mistnetted knots from late July to late November, mostly near their main roost at Richel (an island located midnorth of our study area; Figure 2A), but occasionally near the isle of Schiermonnikoog (± 75 km ENE of Richel). Based on the presence or absence of active wing molt [15], we determined subspecific identity and selected for the current analyses *islandica* individuals only (population numbers and survival rates are best known in this subspecies). Gizzard masses were estimated using ultrasonography (Pie 200 ultrasound, Pie Medical Benelux BV, Maastricht, The Netherlands; applied to 644 out of the 1,069 individuals selected). This method has been extensively calibrated [38] and has been successfully applied in earlier studies [9,12,13, 31]. Furthermore, to estimate survival rates, each bird was given a unique combination of color bands. We used the Cormack-Jolly-Seber model of the MARK software package [39] to estimate “local survival,” i.e., the actual survival during the first year after capture minus the (unknown) fraction of birds that emigrated permanently from our study area. In the model, annual survival rate was allowed to differ in the first year after capture and was assumed constant thereafter. This can be biologically interpreted as a variable proportion of birds becoming site faithful in each year. In case permanent emigration leads to death, the extra mortality equals the difference between first-year-after-capture global survival rate (mean = 0.73; SE = 0.03; calculated over all resightings, both inside and outside the Wadden Sea) and first-year-after-capture local survival rate. Assuming that each autumn, 100,000 individuals “try out” the Wadden Sea, this extra mortality in the NW-European wintering population as the result of emigration can thus be estimated. Note that we had 4 rather than 5 y of data, because our color-banding program started in 1998, yielding the first survival estimate for 1998–1999.

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According to the following procedure, we predicted local survival rate for various degrees of gizzard flexibility (0–2 g) upon arrival in our study area (lines in Figure 4C). Based on experimental results on shell mass processing rates as a function of gizzard size [9], we calculated the minimal gizzard size required to avoid starvation as a function of prey quality (line in Figure 4A). Using the observed distribution of gizzard masses upon arrival (the 0-g distribution in Figure 4B, representing knots caught during late July only; $n = 218$; mean = 5.92; variance = 2.61), we then calculated the proportion of birds having a gizzard of at least this critical size, which would be the proportion of birds able to survive in our study area (47% at the example prey quality of 0.15 g flesh per g shell in Figure 4). Assuming that knots upon arrival have the flexibility to increase their gizzard slightly (e.g., by +1 g), we calculated an updated “effective” gizzard mass distribution upon arrival (i.e., a distribution that shifted by, e.g., +1 g; Figure 4B), yielding an updated proportion of birds with a large enough gizzard, i.e., able to survive (70% for the +1-g example). We refer to Van Gils et al. [9,10,20] for more details on modeling gizzard masses.

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Mixing Exploitation and Conservation: A Recipe for Disaster

Liza Gross | DOI: 10.1371/journal.pbio.0040418

Most governments around the world set conservation policy based on the assumption that resource exploitation and species protection can co-exist in the same place. These policies have led to Orwellian “marine protected areas” that host commercial fishing operations, leading one to wonder who’s protecting whom. A new study reveals the danger of this approach and shows that it’s time to let protection mean protection.

For decades, the Dutch government sanctioned mechanical cockle dredging in three-fourths of the intertidal flats of the Wadden Sea—a natural monument protected under two intergovernmental treaties. Before suction dredging began in the 1960s, an estimated 2,000 tons of cockles were hand-harvested from the reserve each year. In 1989, the high-pressure, motor-driven water pumps used in suction dredging sucked up close to 80,000 tons of cockles. By 2004, the Dutch government decided the environmental costs were too great and stopped the practice.

Jan van Gils and colleagues investigated the ecological impacts of commercial cockle dredging on intertidal ecosystems by studying a long-distance migrant shorebird that dines principally on cockles, the red knot (*Calidris canutus islandica*). Up to 50% of the global red knot population uses the Dutch Wadden Sea at some point during their annual cycle.

Red knots are exquisitely adapted to their lifestyle. They have a pressure-sensitive bill that senses hard objects buried in the sand and a shell-crushing gizzard to accommodate the birds’ penchant for swallowing their catch whole. They even have a flexible digestive system that minimizes the energy costs of flying up to 16,000 kilometers between their arctic breeding grounds and winter homes in Europe and the tropics—their gizzard expands and contracts to balance daily food intake and energy needs.

To determine the effects of dredging on the birds, the authors sampled prey quality and density over 2,800 Wadden Sea sites during the late summer months (late July to early September) for five years starting in 1998. Dredging occurred each year from September to December, immediately after their sample collections. In undredged areas, cockle densities increased by 2.6% each year, and the quality remained stable. In dredged areas, cockle densities remained stable, and their quality (flesh-to-shell ratio) declined by 11.3% each year—paralleling the decline in the quality of the birds’ diet (as measured by droppings). This finding falls in line with evidence that dredging disturbs the silt cockles like to settle in, as well as their feeding conditions—which in turn reduces their quality as a food resource.

Based on prey quality and densities, Van Gils et al. predicted the energy intake rate for knots with an average-size gizzard at each site (all sites were pooled into 272 blocks, each with an area of 1 square kilometer), then calculated the percentage of blocks that would not yield sufficient intake rates for knots to avoid starvation. From 1998 to 2002, the percentage of blocks that couldn’t sustain knots increased from 66% to 87%—all attributable to dredging in previously suitable sites. Reduced prey density caused some of this degradation, but most stemmed from declines in both cockle density and quality.



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Commercial shellfish dredging in the Dutch Wadden Sea led to declines in both the quality and amount of the red knot’s food resources, causing the population to crash. (Photo: Jan van de Kam)

The authors caught and color-banded the birds so they could estimate survival rates the following year, and they measured gizzard mass with ultrasonography. As expected, when prey quality declined, birds needed larger gizzards to process the relatively higher proportion of shells in their diet. Their chances of surviving conditions at the Wadden Sea increased as a function of prey quality and gizzard flexibility. Birds that did not return had much smaller gizzards than those that did. Survival rate calculations based on gizzard size and prey quality revealed that if birds could not expand their gizzard and prey quality was low (0.15 grams of flesh per gram of shell), only 47% of arriving birds would avoid starvation. A much greater proportion would survive if their gizzard could expand by at least 1 gram (70% for 1 gram, 88% for 2 grams).

These degraded food conditions, the authors conclude, explains why red knot populations have declined by 80% in the Wadden Sea. And increased mortality in the Wadden Sea—which the authors estimate at 58,000 birds over five years—accounts for the 25% decline of red knots across their entire northwest European wintering grounds. Dredging reduced the quality of red knots’ primary food source so drastically that even the birds’ extraordinarily adaptable digestive system could not save them. The authors point out that dredging doesn’t even provide significant economic benefits—only 11 outfits manage 22 fishing boats—yet is “directly responsible” for the widespread decline of a

protected shorebird. These findings put the lie to the notion that commercial exploitation is consistent with conservation and underscore the risks of disturbing critical habitat for threatened or endangered species.

van Gils JA, Piersma T, Dekinga A, Spaans B, Kraan C (2006) Shellfish dredging pushes a flexible avian top predator out of a marine protected area. DOI: [10.1371/journal.pbio.0040376](https://doi.org/10.1371/journal.pbio.0040376)



up the separation between the ISS and the object, and shorten the time the object remains in orbit before burning up.

The proposal comes as Russian cosmonaut Mikhail Tyurin prepares for a space walk on 22 November during which he will drive a golf ball from the ISS in a stunt for a golf company – probably achieving the longest drive in history. NASA found that there was no threat of the 3-gram golf ball hitting the station either at the time of the swing or on a later orbit – it will quickly hit the atmosphere and burn up.

WHO's boss

IF THE best lessons are learned the hard way, Margaret Chan, who was confirmed as the WHO's new director general on 9 November, should be a star pupil. As director of health for Hong Kong, she was heavily criticised for her slow response to the 2003 outbreak of severe acute respiratory syndrome (SARS) in the region.

To her credit, her record on bird flu is more positive: in 1997 she recommended the slaughter of all poultry in Hong Kong to stop the spread of the H5N1 virus and presided over the successful exclusion of the virus in poultry.

Supporters note that her experience with SARS might make her less likely to soft-pedal any similar information emerging from China, the potential epicentre of flu evolution. As a Chinese citizen she may also be

"Chan's experience with SARS might make her less likely to soft-pedal on bird flu"

more likely to establish good relations with China.

Chan replaces South Korea's Jong-wook Lee, who died suddenly in May. Besides flu, Chan will have to deal with AIDS, tuberculosis, malaria, the tricky endgame of polio eradication and perennial questions on how to promote healthcare and distribute medicines in poor countries.

Abortion ban out

SOUTH Dakotans last week voted to overturn a law banning almost all abortions in the state – but the issue is unlikely to go away.

The South Dakota law would have banned all abortions except when a woman's life was in danger, and was to take effect in July, until a pro-choice campaign forced the issue to a public ballot on 7 November.

The result, in which 56 per cent of people voted to repeal the law, may make other states think twice about introducing such draconian restrictions, says Jan Nicolay, of the South Dakota Campaign for Healthy Families in Sioux Falls.

PROTECTION THAT ISN'T

In an example of doublethink worthy of George Orwell, many so-called "marine protected areas" permit some exploitation of their marine resources. Their food webs are so complex, however, that even a little exploitation may be too much.

A quarter of Europe's red knots have died since 1998 because one of Europe's supposedly protected coasts, in a word, wasn't. The migrant seabirds stop off at intertidal mudflats, including the Wadden Sea off the Netherlands, to refuel on shellfish. The problem is that until 2004 two dozen cockle boats were allowed to dredge the Wadden too.

The boats didn't make much money. They did, however, make the mud coarser and so worse for cockles, whose meat-to-shell ratio fell 11 per cent per

"The law would have banned all abortions except when a woman's life was in danger"

"We felt a responsibility to deter other states," she says.

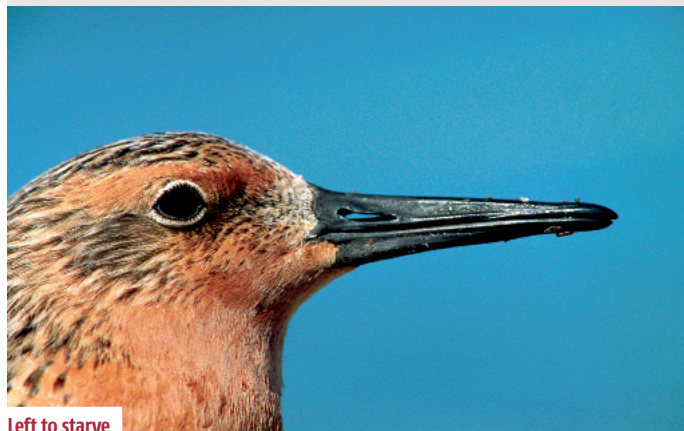
Anti-abortion campaigners have not given up, however. Some believe that voters may accept a law that allows abortion in special circumstances only: in cases of rape or incest, for instance.

Such abortions would have been illegal under the rejected law. Others are talking about introducing laws that would require pregnant women to look at ultrasound scans of their fetuses before aborting them.

year for five years, says Jan van Gils of the Royal Netherlands Institute for Sea Research in Texel. The scrawny cockles did not supply enough food for the red knots, whose numbers fell by 80 per cent, enough to account for the decline of knots across Europe (*Public Library of Science Biology*, vol 4(12), e376).

Many similar seas may suffer too, says van Gils, as "protection" often means nothing more than simplistic regulation of fisheries. "The idea is to exploit resources in a sustainable way. We have shown that does not exist for the Dutch Wadden Sea."

The cockles have failed to recover since dredging ended, van Gils says, as the intertidal mud remains coarse. "Dredging didn't even provide significant economic benefits," he adds.



Left to starve

60 SECONDS

Storm the size of a planet

NASA's Cassini spacecraft has spotted a gigantic storm two-thirds the size of Earth. Fortunately, the 8000-kilometre-wide storm is raging on Saturn's south pole. It is the first storm seen in the solar system, other than on Earth, that has a well-defined wall of towering clouds ringing a dark eye.

Mars probe calls time

Maybe it decided enough was enough. Sent on a two-year mission 10 years ago, the Mars Global Surveyor worked valiantly overtime, sending back more information about Mars than all earlier missions combined. NASA lost contact with the probe on 5 November. Its last signal indicated that it had entered a "safe" mode and was awaiting instructions from Earth.

Fatbuster failure

An anti-obesity vaccine has been abandoned following disappointing results in humans. The vaccine, developed by Cytos Biotechnology of Zurich, Switzerland, was meant to stimulate production of antibodies that would mop up ghrelin, a gut hormone thought to stimulate appetite (see *New Scientist*, 21 May 2005, p 9).

Red meat warning

Daily consumption of red meat may double the risk of certain breast cancers, a study of 90,000 women aged 26 to 46 suggests. Researchers speculate that growth hormones given to cattle or chemicals added during meat processing could fuel hormone-responsive cancers, which account for two-thirds of breast cancers (*Archives of Internal Medicine*, vol 166, p 2253).

Flying towards extinction

Birds around the world are heading for extinction because of global warming. A WWF report released last week says that birds most at risk are migratory, mountain, island, wetland, Arctic, Antarctic and seabirds. A 2 °C warming over pre-industrial levels could render extinct 38 per cent of European species and 72 per cent in north-east Australia.

2006

THE inexorable plunge of the world's fish stocks continued apace this year. It was underlined by an unprecedented collaboration of a dozen research institutions, which briefly grabbed headlines with the warning that the world's commercial fisheries could vanish by 2050.

The scientists behind the report might have preferred it if more emphasis had been given to their finding that we could make things better – often surprisingly quickly – by protecting and restoring the entire marine food web. Every species, however humble, has a part to play in this, and the report advocated setting up marine protected areas to help the whole range of sea creatures recover.

What is possible and what actually happens are two different things, and most of the year's fish stories charted not recovery but rampant destruction of marine biodiversity: Iceland's resumption of whaling; Canada's record seal hunt; Europe's continuing rejection of scientific advice to stop catching North Sea cod and endangered eels; and the discovery that we were catching four times as many sharks as anyone had thought. As a final insult, it emerged

that those crucial marine reserves often aren't protected. In one of them, a few Dutch boats dredging for cockles decimated the population of a local seabird, the red knot.

There were a few bright spots in the gloom. Europe held off, slightly, on making its rapacious boats even more powerful. Thai and Japanese fishermen agreed to go easier on catfish and tuna, respectively. Australians learned how to artificially incubate endangered baby nurse sharks. And the UN debated a ban on destructive bottom trawling on the high seas, despite opposition from Spain, Canada and Russia.

Meanwhile scientists were planning a global census of marine life. They'd better hurry up and do it while there is still something left to count.

DEBORA MACKENZIE



**SO LONG
AND THANKS...**

Appendix B

Rates of mass gain and energy deposition in red knot on their final spring staging site is both time - and condition dependent

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Running title: Mass gain in red knot

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Summary

1. Millions of shorebirds migrate each year through a small number of staging areas to and from their Arctic breeding areas. These birds time their spring migration to take advantage of seasonally abundant food resources and often come into conflict with fisheries interests. Delaware Bay, USA, is the final spring stopover site for the red knot *Calidris canutus* which winter in areas from south-east USA to Tierra del Fuego. In Delaware Bay, red knot undergo rapid mass gain by feeding on the eggs of spawning horseshoe crabs *Limulus polyphemus* before departing for breeding areas.
2. Environmental factors may constrain migration and cause deviations from the best migration schedule. We used within-year mass gain data from red knot caught in Delaware Bay between 1998 and 2005 to determine the degree of flexibility of individuals to vary the speed of migration.
3. Mass gain by birds below 133 g was shown to comprise 15.3% fat (39 kJ g^{-1}), the remainder being lean mass (6 kJ g^{-1}). Above this critical level, fat comprised 83.9% of mass deposition. The rates of energy deposition (kJ d^{-1}) were therefore fundamentally different between the two states but were amongst the highest ever recorded amongst vertebrates, the equivalent long-term energy intake rates routinely reaching equivalents of 5-7 x Basic Metabolic Rate. [THIS IS MORE INTERESTING THAN THE FEW OUTLIERS!]
4. 36-62% of the variation in observed rates of energy deposition (52-71% of the rate of mass gain) between 1998 and 2002 could be explained by a year factor, date and mass at initial capture and interaction terms, such that light weight birds at the end of May had rates of mass gain or energy deposition 2-3 times higher than birds of similar mass at the beginning of May. These results indicate that birds are attempting to achieve a certain mass by a certain date. In 2003 and 2005, this relationship broke down as a result of weather effects, as well as lower densities of eggs caused by weather effects and the over-harvesting of crabs by fishermen & the biomedical industry for bait.
5. *Synthesis and application.* The high rates of mass gain in red knot observed in this study require high densities of crab eggs to be available in the latter half of May. The maintenance of high rates of mass gains requires severe cuts in, or the complete cessation of, the crab harvest, coupled with reduced human and raptor-related disturbance and management of beaches to provide sufficient crab spawning habitat. These findings are widely applicable to other systems where harvesting activities come into conflict with migrating animals and show that certain sections of the population, in this case the long-distance migrants from South America, will be impacted more than short-distance migrants whose physiology may give them access to alternative food resources.

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71 Key words: phenotypic flexibility, migration strategy, spare capacity, time-minimisation

72

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Introduction

Some shorebirds, such as red knot *Calidris canutus* (L.), regularly undertake exceptional migrations to exploit global seasonality by travelling many thousands of kilometres between Arctic breeding areas and wintering areas in the northern and southern hemispheres. For these extreme long-distance migrants, the migration process comprises a series of movement phases and staging phases, in which the necessary resources to complete the next leg of the migration are attained. Therefore, they have to time their migration to take advantage of food resources that vary in space and time, and make decisions about when to leave the wintering grounds, how long to stop-over and gain mass on intermediate sites, and when to arrive in the breeding grounds (Hedenström & Ålerstam 1997). Various models of shorebird migration strategy have been put forward. Building on earlier work, Farmer & Wiens (1999) identified three strategies, which included time-minimisers that aim to arrive at the breeding grounds as fast as possible, energy maximisers that arrive at breeding grounds with excess fuel stores, or birds that followed no strategy, termed random. Ålerstam & Lindström (1990) predicted that time-minimisers should show a positive relationship between fuel deposition rate and departure mass. Across northward migrating red knot populations worldwide, there is indeed a positive relationship (Piersma *et al.* 2005) and a comparison of five subspecies of red knot showed that they time-minimised by selecting stopover sites with high quality prey (van Gils *et al.* 2005a).

In spring, Arctic-breeding shorebirds are on a strict timetable to arrive in their breeding areas in time to breed successfully during the short summer (Drent *et al.* 2003). En route, factors such as adverse weather conditions, predation risk and the predictability, availability and quality of food resources could cause deviations from the optimal arrival times, rates of mass gain and departure times from stop-over sites. Therefore individuals must possess a degree of flexibility to speed up or slow down their migration (Farmer & Wiens 1999; Ydenberg *et al.* 2002, 2004; Lank *et al.* 2003).

If birds are behind the optimal schedule, they can leave a stopover site at a sub-optimum mass, depart at the optimum mass but past the optimum time, spend more time per day feeding or alter the rate at which they put on stores at stopover sites so that stopover duration is reduced (Piersma 1987). The latter can be achieved in one of two ways. First, migrants can exhibit phenotypic flexibility in terms of altering

digestive organ sizes and/or enzyme activities in relation to digestive/energetic bottlenecks (Piersma 1998, 2002; Guglielmo & Williams 2003). This is widespread across migrant shorebirds (van Gils *et al.* 2005b; Stein *et al.* 2005; Piersma *et al.* 1999; Selman & Evans 2005) but may incur a time cost, as it typically takes several days to a week to fully implement these changes, which may need to be reversed before the bird continues its migration (McWilliams & Karasov 2005; Dekinga *et al.* 2001; Piersma *et al.* 1999). Alternatively, birds can exhibit varying degrees of immediate spare volumetric or biochemical capacity (Diamond & Hammond 1992) to ingest and process extra food. For example, in an experiment where fuelling white-throated sparrows *Zonotrichia albicollis* (Gmelin) were rapidly switched from an environment of +21°C to -20°C, birds were able to increase their intake rate by 45% in response to the sudden increase in thermo-regulatory costs (McWilliams & Karasov 2005). If migrants are behind schedule, then this 'spare capacity' may be the only option to increase fattening rates and leave the stopover site on time.

To determine the degree to which individual birds have the spare capacity to 'catch up' due to late arrival in a stopover site, we use data from an ongoing monitoring programme of red knot passing through Delaware Bay on the northeast coast of the United States on spring migration. For these birds, Delaware Bay is the last stopover site on the West Atlantic flyway from wintering areas in Patagonia/Tierra del Fuego (TDF), north-western Brazil and the south-eastern USA (Florida and Georgia), before birds reach their Arctic breeding areas. Individuals make stopovers in the bay of 12-14 days (Gillings *et al.* unpublished data) and rapidly fatten on an abundance of the eggs of horseshoe crabs *Limulus polyphemus* (L.), deposited in the beaches by spawning females between May and August (Castro & Myers 1993; Haramis *et al.* in press). It is predicted that the knots need to depart at between 180-220 g at the end of May, or beginning of June, if they are to reach the Arctic with sufficient nutrient stores to breed successfully (Baker *et al.* 2004; Morrison *et al.* 2005). There are likely to be fitness consequences associated with leaving Delaware Bay with insufficient mass. Indeed, individuals captured at low mass at the end of May were less likely to be seen subsequently in the flyway, thus implying lower survival (Baker *et al.* 2004).

The rate of mass gain in birds is currently used in Delaware Bay as a management tool to assess the 'health' of the shorebird/crab system but this may not be the ideal way of assessing energy deposition. The breakpoint model of van der

Meer & Piersma (1994) hypothesised that body mass should be divided into the 'structural' part and 'stores'. The structural part consisted mostly of water and fat-free lean mass (bone, muscle etc), whereas the stores consisted mostly of fat, the fuel needed for migration. As a bird migrates, it first uses up the fat stores and, if further energy is required, it then enters a phase of protein catabolism. This switch is known as the breakpoint. When the bird refuels at a staging site, this model is reversed and birds first replace the lean mass before depositing fat. As the energy content of protein (6 kJ g^{-1}) is much lower than fat (39 kJ g^{-1}), these different periods of mass gain may have very different energy requirements; consequently, it is more appropriate to deal with the common currency of energy deposition (Klaassen *et al.* 1990; Jenni & Jenni-Eiermann 1998). Mass gain is, however, easily measured as it is used as a tool in the management of the shorebird population that passes through Delaware Bay. We therefore combine the two approaches.

We used red knots caught between 1998 and 2005, and retrapped within the same season to determine the degree of flexibility in the rate of energy deposition and mass gain in relation to the time within the migration period, and the mass at which it was initially caught. From the hypothesis that red knots have spare capacity and/or can exhibit phenotypic flexibility, we predict that rates of energy deposition and mass gain should not be constant throughout the migration season. We expect a significant relationship between the rate of energy deposition and mass gain, and the date and mass when the bird was originally caught, such that the rate of energy deposition or mass gain should be higher for individuals that have a low mass at the end of May.

Methods

Capture of birds and measurement of mass

As part of an ongoing monitoring program, red knots were trapped in Delaware Bay, USA, using cannon nets throughout the spring staging period spanning from the first week in May to the end of the first week in June each year between 1998 and 2005. On capture, birds were banded with an individually numbered metal band and mass was measured using an electronic balance accurate to 0.1g. Although no special efforts were taken to recapture birds again during the same season, 167 birds in their second year or older were recaptured and their mass recorded for a second time.

176

177 *Determining the composition of body stores*

178 A total of 61 red knot were collected from catches over three years (1998: 24 birds;
179 1999; 24 birds; 2000 13 birds). These birds were taken at random from cannon net
180 catches on dates spread out through the spring migration season. Birds were humanely
181 killed using cervical dislocation and, after weighing to the nearest gram, placed in
182 airtight plastic bags and frozen at -20 °C.

183 As the red knot that pass through Delaware Bay come from a mix of wintering
184 populations, we identified their wintering location based on the stable isotopes of
185 carbon and nitrogen in their flight feathers. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained from
186 the sixth primary covert, measured ascendantly, using CF-IRMS (Continuous Flow
187 Isotope Ratio Mass Spectrometry). Atkinson *et al.* (2005) showed that there was a
188 clear division in the values of $\delta^{15}\text{N}$ between birds wintering in Patagonia and Tierra
189 del Fuego ($\delta^{15}\text{N} > 13.5\text{‰}$, termed 'southern' birds) and elsewhere ($\delta^{15}\text{N} < 13.5\text{‰}$,
190 termed 'northern' birds). Northern birds comprise two geographically distinct
191 populations from the south-eastern USA and Brazil but the isotope signatures of birds
192 from each overlap. $\delta^{13}\text{C}$ values were checked to ensure that no sub-adult birds were
193 included. These birds, hatched the previous year would have a carbon isotope
194 signature typical of the freshwater systems ($\delta^{13}\text{C} < -19.5\text{‰}$) where their feathers were
195 grown. None were found amongst the specimens.

196 After thawing, the total fat mass of each specimen was determined by drying
197 the tissues, weighing them and then extracting the fat in a Soxhlet apparatus using
198 petroleum-ether (boiling point range 40-60 °C) as the solvent. The body parts were
199 then dried to constant mass and reweighed, the total fat mass being the difference.

200 To determine the point at which birds deposit fat stores, the total fat mass of
201 each specimen was plotted against the total mass and a 2 phase (broken stick)
202 regression model applied using the inbuilt function of Sigmaplot v10. The slopes of
203 the two regression lines reflect the proportion of fat being stored as total mass
204 increases and the breakpoint indicates the point at which that relationship changes.

205 The energy deposition of fat and protein was calculated as follows. The mass
206 change between captures above and below the breakpoint was multiplied by the
207 appropriate fraction of fat or protein (based on the slopes of the two regression lines)

and its calorific value (6 kJ g^{-1} for protein and 39 kJ g^{-1} for fat, following Klaassen *et al.* 1990). Total energy deposition was the sum of these two values.

Does initial mass or date influence rates of energy deposition?

Generalised Linear Models (GLM) with normal errors and an identity link function were used to determine the factors associated with the rates of mass gain or energy deposition per day. The factors considered were their mass at initial capture (M), the number of days after 1 May of the first capture (D), the year (Y) and their interaction terms. Permutations of these variables were entered sequentially into GLMs and the Akaike Information Criterion corrected for small sample size (cAIC) was calculated in each case ($-2 \times \log \text{likelihood} + 2k + (2k(k+1))/(n-k-1)$), where n is the sample size and k the number of estimable parameters. [I ADDED ITALICS!] cAIC operates on the basis of parsimony by selecting the best fitting model whilst minimising the number of parameters in the final model (Burnham & Anderson 1998). The models were ranked by cAIC and the model with the lowest value was chosen as the final model. It was accepted as more parsimonious than other lower ranking models if the difference in cAIC was greater than two (Burnham & Anderson 1998). To determine the amount of variation in the mass gain data between years explained by the best model, we took the model with the lowest cAIC and tested its performance (using R^2 values) on each year's data in isolation by performing a series of linear regressions for each year between the predicted and observed values, using the PROC REG procedure in SAS.

The rate of mass gain is a function of final mass, initial mass and duration between recaptures. As initial mass was also included as a dependent variable, any significantly large measurement error would result in an automatic negative relationship between rate of mass gain and initial mass. However, as the final result was a significant positive relationship, and AS measurement error was thought to be low because most birds were weighed using a digital balance one hour or more after capture (when most changes in mass take place), we do not consider this to be a major issue.

Using only retrapped birds to measure mass gain is open to bias for two reasons, owing to capture effect (e.g. Warnock *et al.* 2004): first, mass gain after release may show a short-term decline; additionally, departure date may be negatively correlated with rate of mass gain, so that birds with rapid mass gain may not be

available for subsequent recapture (Winker *et al.* 1992). Our estimates of mass gain would therefore be an underestimate. We dealt with this in two ways. With the exception of the day after initial capture (-1.42 g d^{-1}), mean mass gain per day was positive and approximately constant thereafter averaging 4.3 g d^{-1} up to 14 days after first capture (Fig. 1). This lower initial rate was likely to be a capture effect and we therefore have excluded birds with retrap intervals of 1 day from the analysis, thus leaving 167 same-year retraps remaining for analysis. Overcoming the second issue of birds leaving the bay, requires a more subjective judgement. We selected the best models without further data exclusion but performed an additional analysis, in which we calculated whether a bird caught on a particular date would have reached a target mass exceeding 190 g by the time of the second capture and was therefore likely to have left the Bay. The expected mass was calculated assuming a rate of gain of 4.05 g d^{-1} , the mean mass gain from the 167 retraps. If a bird's predicted mass exceeded 190 g it was excluded from this analysis. This removed a further 26 birds, leaving 141. Where means are given these are quoted $\pm 1 \text{ SE}$.

Results

Composition of body stores in relation to total body mass.

The proportion of fat in the body mass laid down changed from 0.153 ± 0.119 to 0.839 ± 0.046 at a breakpoint of $133.01 \pm 5.19 \text{ g}$ (Fig. 2). The overall fit of the broken stick model was good ($F_{3,57} = 320.2$, $P < 0.0001$, adjusted $R^2 = 0.94$). Below the breakpoint, the slope of the regression line was not significantly different from zero ($t=1.29$, $P=0.2$) indicating that very little, if any, of the mass gain at this point was deposited as fat.

Rate of energy deposition & mass gain in relation to date, initial mass and year

The average rate of energy deposition of all 167 retrapped birds was 119.1 kJ d^{-1} (95% CIs: -193.7 to 322.9 kJ d^{-1}). In terms of mass gain, this represented an average rate of $4.05 \pm 0.32 \text{ g d}^{-1}$ and ranged between -14.4 to 18.8 g d^{-1} . The most rapid mass gain of 18.8 g d^{-1} (xx kJ d^{-1}) was exhibited by a bird caught in 2003 at 117 g on 25 May and retrapped three days later on 28 May at a mass of 173.6 g.

Both the rates of energy deposition and mass gain were mass- and time-dependent, and varied between years (Table 1, Fig. 3). Although the form of the model with the lowest cAIC was slightly different in each case, the pattern of the rates of energy deposition and mass gain were similar in that they were both inversely related to the mass at which a bird was caught at (i.e. lighter individuals deposited energy or gained mass at a faster rate). With the exception of the year 2000, light weight birds caught later in May were estimated to have a higher rate of energy deposition than light weight birds caught early in May, thus enabling late-arriving birds to 'catch up' with early arriving birds. The amount of variation explained by the best fit models (Model 1 for energy deposition and Model 4 for mass gain) was generally good and overall explained over half the variation in the dependent variable (R^2 values of 0.54 and 0.55, Table 1). When the birds which were predicted to be >190 g at 31 May were removed, the order of models altered slightly but the two models selected previously still had the lowest cAIC indicating that departure of birds from the bay was not a confounding factor.

The selection of the interaction terms $Y*D$ and $Y*M$ indicated that energy deposition rates varied between years in relation to the time a bird was caught and its initial mass (Table 2). The average pattern of energy deposition and mass gain (Fig. 4) did not hold in every year and was not always reliable. "These parameters" [IT IS NOT ENTIRELY CLEAR WHAT THIS REFERS TO; NOT TO ME, ANYWAY] were most important in 2000 and also 2003 when mass deposition commenced 7 days later compared with other years (Fig. 3). When applied to each year separately, there has been a tendency for the fit of these relatively simple relationships to decline over time. The years 2003 and 2005 exhibited the lowest R^2 values observed (Table 3).

Discussion

Migration strategy and rates of fuelling by red knots

If birds arrive late and conditions are good, red knot passing through Delaware Bay have the flexibility to increase their rate of energy deposition to ensure a departure at the end of May or beginning of June. The tight fit of the broken stick model when applied to the carcass data indicates that red knot below 133 g first replace their structural stores with protein before laying down fat. They then cease depositing

energy at the end of May at a mass of approximately 180 g, thus carrying *c* 50 g of fat to fuel the final part of their journey to the breeding areas.

The rates of energy deposition are amongst the highest observed in the animal kingdom. With maintenance and activity requirements of a minimum of 200-250 kJ d⁻¹ (Piersma 2002), which includes a Basal Metabolic Rate (BMR) component of *c.* 80 kJ d⁻¹ (Wiersma & Piersma 1994), birds were assimilating energy at an average equivalent to 5-5.6x BMR. At the upper confidence limit this was raised to 6.5-7.2x BMR and two individuals with energy deposition rates greater than 500 kJ d⁻¹ probably exceeded 9x BMR.

These rates reflect those observed in captive shorebirds, where soft-shelled food (mealworm larvae) was provided *ad libitum* and available 24 hours a day (Kvist & Lindström 2003). The authors acknowledged that the high energy assimilation rates (10.4 x BMR for red knot) were unlikely to be replicated in the field but did suggest situations where high quality food may be super abundant (including Delaware Bay), would enable birds to fuel so rapidly. Note that the value of 10.4 x BMR was the average of the highest daily (i.e. 24 h) rate observed within individuals. The rates described in the present study are observed under field conditions and are averaged over the course of a number of days.

Why do birds need these stores? First, they are needed for migration, but red knot also arrive in the Arctic with high lipid and muscle stores (Morrison *et al.* 2005). These stores are generally used up in the two weeks after arrival and prior to egg production[!] (Klaassen *et al.* 2001) and are associated with the transformation from a physiological state needed for migration to one needed for successful breeding (Morrison *et al.* 2005). These stores are important also for survival. Birds that were estimated to be of low mass towards the end of May were less likely to be seen in the flyway in subsequent years (Baker *et al.* 2004), indicating negative fitness consequences associated with departing late and light from Delaware Bay.

Are red knots time-minimisers?

The results from this study have indicated that the migration strategy is more complex than previously assumed. Fuelling rates amongst red knot in Delaware Bay are state and time-dependent and, thus, birds are attempting to achieve a certain mass by a certain date. Mean mass gain rates for birds arriving in the Bay at 110 g on 10 May were 4 g day⁻¹ but individuals can increase this by a factor of 2-3 times later on in

May. This raises the question, why do birds arriving earlier not deposit fuel at the high rates observed towards the end of May? The question remains to be answered but several possibilities exist. First, as egg loads in beaches increase in May due to successive spawnings of crabs, there may be insufficient food available early on in May to achieve the rates necessary to fuel at high rates, or a digestive bottleneck such that birds were not able to gain mass faster without increasing the size of their digestive organs. This may be so, but in mid May, when presumably similar food densities are available to all birds, heavier birds fuelled at a lower rate and therefore both the food limitation and digestive bottleneck hypotheses seem insufficient to fully explain the patterns. Alternatively, there may be other costs associated with fuelling at a high rate, such as increased energetic costs and reduced vigilance leading to increased predation risk (Brodin 2001; McLeod *et al.* 2005a,b), or reduced manoeuvrability of high mass birds leading to increased predation (Weber *et al.* 1998; Dietz *et al.* 2007). Indeed, predation risk from raptors may have increased due to the local provision of artificial nest sites for peregrine falcons *Falco peregrinus* (Tunstall) within Delaware Bay. There may also be costs associated with departing the bay early. For example, early departing birds may arrive in the Arctic breeding areas before snow melt and experience a poor feeding environment. Thus, birds appear to be aiming to leave Delaware Bay within a relatively short time window.

Several other studies have shown that individuals behind schedule can respond by reducing stopover time and migrating faster, which is analogous to the results found here, but without information on rates of energy deposition or mass gain it is not possible to determine which type of strategy birds were following. For example, stopover time of dunlin *Calidris alpina* (L.) and male western sandpipers *Calidris mauri* (Cabanis) at their last stopover before reaching the Arctic breeding area (the Copper River Delta in Alaska, USA), was inversely related to arrival date (i.e. late in the migration season migration timing became more compressed) (Warnock *et al.* 2004, Warnock & Bishop 1998, Bishop *et al.* 2005); individual dunlin caught at staging sites further south migrated faster to the Delta, the later they left the capture site. These stopover patterns could be explained either by birds leaving at sub-optimal masses, or leaving at optimum masses achieved by a greater rate of mass gain. Although these studies do not specifically address whether birds are aiming to leave by a certain date, the flexible stopover durations suggest that birds may be using a

similar strategy to the red knots, in that they aim to depart the last staging area by a certain date.

Population-specific consequences of a reduction in horseshoe crab egg densities

That date of initial capture, initial mass and interaction terms explained such a high proportion of the variance in rate of mass gain between 1998 and 2002 demonstrates that, when sufficient resources are available, the relationship is robust between years. In 2003, the late-spawning of crabs due to cold sea temperatures (refs. that document this and other mentioned weather effects?) severely reduced the numbers of eggs available to birds early in the season and, even allowing the day parameter to vary between years (and, thus, allowing for mass gain to commence later in the month), the final model was a relatively poor fit compared with other years. In 2004, a warm spring allowed for early spawning of crabs and high densities of eggs in beaches compared with 2003. In 2005, however, the fit was exceptionally poor. Fuelling rates were generally low, averaging 2.7 g d^{-1} and these did not fit in with the simple relationship observed in previous years. Although sample size was lower in the latter years due to an intentional reduction in catching effort, there is no reason to expect these to be non-random samples, and the coefficient of variation in rates of mass gain were not significantly different in the latter years.

That the relatively simple model of mass gain seemed to have broken down in two of the past three years is extremely worrying in conservation terms, especially given the link between departure mass and the likelihood of an individual being seen again in the flyway (Baker *et al.* 2004). Conditions in Delaware Bay have changed over the past 10 years. The harvesting of horseshoe crabs for bait and the biomedical industry has undergone an order of magnitude increase since the mid 1990s (Walls *et al.* 2002) and has recently been restricted due to concerns that the reduction in the number of adult spawning crabs has reduced the number of eggs available to shorebirds, impinging on their ability to fatten successfully. A reduction in adult red knot survival has been attributed to late arrival into, and reduction in departure masses from, Delaware Bay (Baker *et al.* 2004). This study has shown that in 2000, 2003 and 2005, at least, fuelling did not proceed as normal and was caused by poor foraging and weather conditions within the bay. However, the increase in the number of light weight birds late in May in the preceding period (between 1997 and 2002, Baker *et al.* 2004) could well be attributable to an increase in the number of later arriving birds

into Delaware Bay as our analysis indicated that fuelling proceeded as normal. Although late arrivals may represent individual adjustments to local fuelling difficulties encountered in previous years, we also need to know about conditions at wintering and staging sites elsewhere in the flyway to better understand the increase in later arrivals.

Peak numbers of red knot have declined in Delaware Bay (Niles *et al.* in prep) similar to severe declines that have occurred in the wintering areas in Patagonia and Tierra del Fuego, where numbers declined from 67,000 birds in 1982–85 to 17,650 in February 2005 (Morrison *et al.* 2004; R.I.G. Morrison pers. comm.). Birds from wintering areas in northern Brazil and also the south-eastern USA (both populations in the order of 7,500 – 10,000 birds) also pass through Delaware Bay (Atkinson *et al.* 2005) and there has been no evidence of similar declines in these groups of birds (Niles *et al.* in prep.).

The abundance of crab eggs in Delaware Bay underpins the exceptional rates of mass and energy gain shown here. Using stable isotopes as above, the wintering area of birds passing through the Bay in 2004 and 2005 was determined (Atkinson *et al.* 2005; Atkinson *et al.* in press). In these years, there was a non-random distribution of birds within the Bay. In 2005, at least, those birds feeding on hard-shelled mussels *Mytilus* sp. on the Atlantic side of Delaware Bay were mostly short-distance migrants from wintering areas in the south-eastern USA, although some were from Tierra del Fuego. Mussel feeders were generally heavier than longer-distance migrants from Tierra del Fuego and northern Brazil. Although we were not able to measure gizzard size, fattening on mussels would not be an option for newly arrived long-distance migrants due to the atrophy of their digestive organs prior to and during the long-distance flight (Piersma 1998; Piersma *et al.* 1999). The situation is similar to the Dutch Wadden Sea where there is evidence that recently arrived birds (i.e. those having small gizzards) feed on soft food (crabs and shrimps), while those that have been there for longer (i.e. those having bigger gizzards) feed on hard-shelled bivalves (van Gils *et al.* 2005c). The mussel feeders in Delaware Bay were therefore assumed to have either arrived earlier, or to be short-distance migrants whose short-hop strategy did not require them to reduce the size of their digestive apparatus.

Therefore, for later arrivals to achieve high rates of mass gain and catch up with earlier arriving birds requires a sufficient density of crab eggs to be available because fuelling rate on soft-shelled prey is independent of gizzard size (van Gils *et*

444 *al.* 2003, 2005b). The harvest of spawning crabs over the past decade will have
445 reduced egg loads within beaches. It is likely that the bulk of shorter-distance
446 migrants feeding on mussels (which does not enable such high fuelling rates, van Gils
447 *et al.* 2005a) would, through earlier arrival compared with longer distance migrants,
448 still be able to fatten successfully. Reducing egg densities would have a
449 disproportionately higher impact on longer-distance migrants. Indeed, when staging in
450 the Wadden Sea in spring, knots with the smallest gizzard size, which may be those
451 that have travelled the longest distance, were found to suffer the highest mortality
452 rate. This increased mortality rate was due to the large-scale harvesting of the knots'
453 food resources by the commercial fishing industry (van Gils *et al.* 2006)

454 455 **Conclusion**

456 The red knot passing through Delaware Bay in spring are on a schedule to depart at a
457 certain mass by a certain time. When sufficient crab eggs are available, late arriving
458 birds have the flexibility to increase the rates of mass gain to over three times the
459 mean rate to 'catch up' with earlier arriving birds. Based on the model using data
460 from all years, a bird arriving at 110 g on 21 May could expect to depart by 31 May at
461 a mass of greater than 180 g. Between 1997-2004, the proportion of light weight birds
462 has increased (Baker *et al.* 2004). The simple model of mass gain has showed signs of
463 breaking down in the latter part of the 9 year study period and it is likely that a
464 reduction in the availability of crab eggs in the bay and late arrival are responsible for
465 these poorly-conditioned birds. Further reductions in the availability of crab eggs are
466 predicted to have a greater impact on the longer-distance migrants that
467 physiologically do not have access to alternative food supplies, such as mussel spat. A
468 reduction in the number of crabs harvested or closure of the fishery together with
469 management of beaches to provide optimum crab spawning habitat and reduction in
470 disturbance (both human and from raptors) will maximise the numbers of eggs
471 available to the birds.

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Table 1. Predicting the rate of mass gain and energy deposition of red knot *Calidris canutus* in Delaware Bay. The model selection table is based on a dataset using all birds. Model structure: *Y* = year (1998-2005, 8 level factor), *M* = mass (linear variable), *D* = number of days after 1 May (linear variable). *k* = number of estimable parameters, * = interaction term.

Model number	Model structure	k	Energy deposition			Mass Gain		
			cAIC	ΔcAIC	R ²	AIC	ΔcAIC	R ²
1	Y M D D*M Y*M Y*D	25	1995.74	0	0.54	856.06	3.87	0.59
2	M D M*M	4	2001.36	5.63	0.35	865.95	13.76	0.4
3	M D D*D M*M	5	2001.38	5.65	0.35	866.06	13.87	0.41
4	Y M D D*M Y*D	18	2006.73	10.99	0.54	852.19	0	0.59
5	Y M D D*M Y*M	18	2007.52	11.78	0.44	864.31	12.12	0.51
6	Y M D D*Y	17	2016.78	21.05	0.2	861.75	9.56	0.51
7	Y M D Y*D	17	2016.78	21.05	0.4	861.75	9.56	0.51
8	M D D*M	4	2025.82	30.08	0.35	865.37	13.17	0.41
9	Y M Y*M D	17	2025.86	30.13	0.37	879.73	27.54	0.46
10	Y M M*Y	16	2031.41	35.68	0.34	894.99	42.79	0.35
11	Y D Y*D	16	2033.13	37.39	0.4	914.09	61.89	0.32
12	Y M D D*M	11	2034.51	38.78	0.44	874.13	21.93	0.51
13	M D	3	2037.39	41.66	0.18	875.78	23.59	0.35
14	M D D*D	4	2039.5	43.77	0.18	877.45	25.25	0.36
15	M	2	2041.68	45.95	0.14	890.62	38.43	0.28
16	Y M D	10	2043.92	48.19	0.22	883.82	31.62	0.38
17	Y M	9	2044.76	49.02	0.2	892.89	40.7	0.34
18	Y	8	2061.05	65.32	0.11	935.19	82.99	0.14
19	Y D	9	2062.32	66.58	0.12	936.11	83.92	0.14
20	Intercept only	1	2065.25	69.52	0.00	944.56	92.37	0.00
21	D	2	2067.2	71.46	<0.001	946.29	94.09	<0.001

Table 2. Parameter estimates for the models with the lowest cAIC values. Model number refers to the model numbers in Table 1. *Y* = year (1998-2005, 8 level factor), *M* = mass (linear variable), *D* = number of days after 1 May (linear variable), * = interaction term.

Parameter	Factor level	Rate of energy deposition (Model 1)		Rate of mass gain (Model 4)	
		Estimate	SE	Estimate	SE
Intercept		-611.25	319.25	-7.71	9.13
Y	1998	158.62	268.06	2.48	7.24
Y	1999	302.68	252.66	6.31	7.01
Y	2000	205.39	330.47	9.71	8.02
Y	2001	195.66	266.97	1.59	7.30
Y	2002	-108.94	278.95	-2.38	7.21
Y	2003	-960.69	295.92	-18.57	8.44
Y	2004	824.40	360.04	5.03	7.96
Y	2005	0	0	0.00	0.00
M		5.54	2.99	0.05	0.04
D		37.13	18.34	1.12	0.45
M*D		-0.29	0.07	-0.007	0.002
M*Y	1998	-1.45	2.83	-	-
M*Y	1999	-1.80	2.67	-	-
M*Y	2000	0.37	3.47	-	-
M*Y	2001	-2.67	2.85	-	-
M*Y	2002	-0.69	2.77	-	-
M*Y	2003	3.32	2.84	-	-
M*Y	2004	-7.31	3.40	-	-
M*Y	2005	0	0	-	-
D*Y	1998	2.71	16.20	-0.03	0.36
D*Y	1999	-2.06	15.54	-0.26	0.35
D*Y	2000	-16.88	18.82	-0.56	0.43
D*Y	2001	11.98	16.43	0.04	0.37
D*Y	2002	14.69	15.73	0.29	0.36
D*Y	2003	24.15	16.66	0.79	0.39
D*Y	2004	16.15	17.25	-0.18	0.39
D*Y	2005	0	0	0	0

Table 3. The amount of variation explained (expressed as R^2 values) for the energy deposition and mass gain models with the lowest cAIC. Model number refers to the model number in Table 1.

Year	Energy deposition (Model 1)	Mass gain (Model 4)
1998	0.36	0.59
1999	0.58	0.63
2000	0.62	0.63
2001	0.50	0.52
2002	0.63	0.71
2003	0.31	0.19
2004	0.54	0.33
2005	0.00	0.13

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Fig. 1. Rate of mass gain \pm 1 SE of red knot retrapped during the same season in Delaware Bay in relation to the number of days after capture. Sample size appears at the top of the graph.

Fig. 2. The relationship between the total mass of individual birds and the amount that is fat. A 2 phase regression line is shown. Northern birds are those that winter in northern Brazil and the south-eastern United States; southern refers to those wintering in Patagonia and Tierra del Fuego.

Fig. 3. Contour plots of the rate of energy deposition (kJ d^{-1}) of red knot based on retrapped birds in relation to the date at initial capture and their initial mass. Dots represent individual birds and refer to date and mass at initial capture. To avoid predicting outside of the available data, contours are not shown if there were no data points occurring within the space between it and the next contour line.

Fig. 4. Contour plots of the average rate of (a) energy deposition (kJ d^{-1}) from Model 1 and (b) mass gain (g d^{-1}) from Model 4 in relation to the date a bird was initially caught and its mass at initial capture, excluding any year effects. Model number refers to Table 1.

Fig. 1.

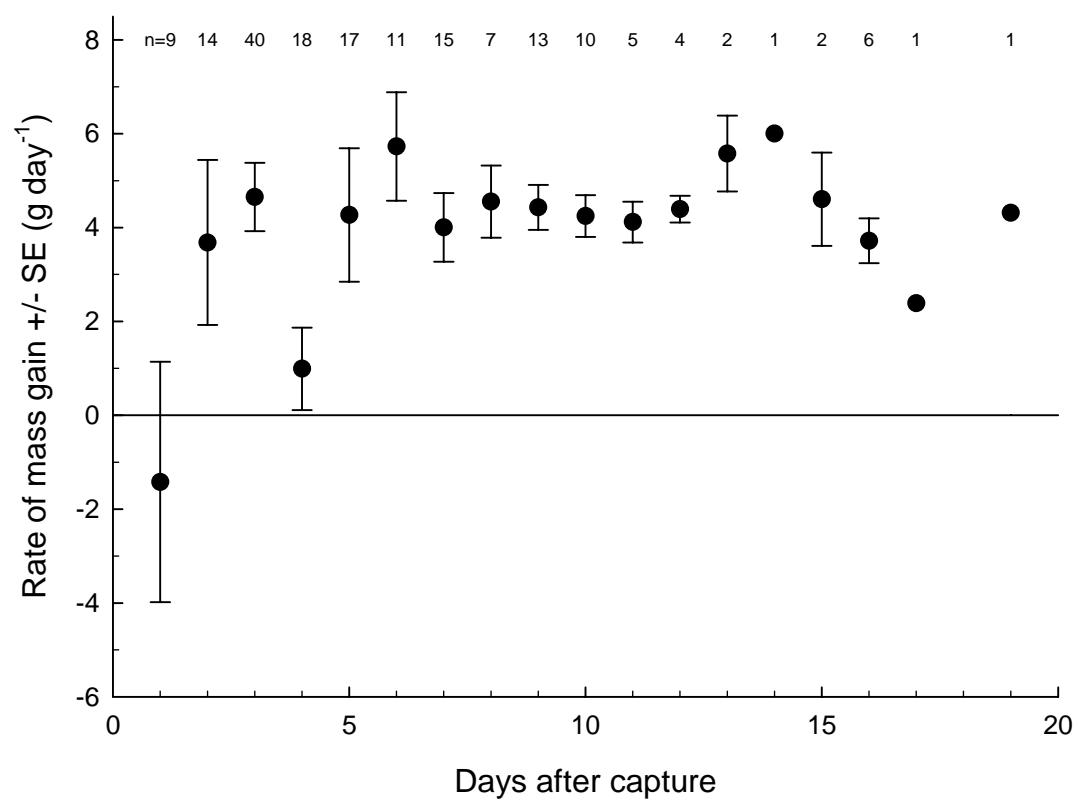


Fig. 2.

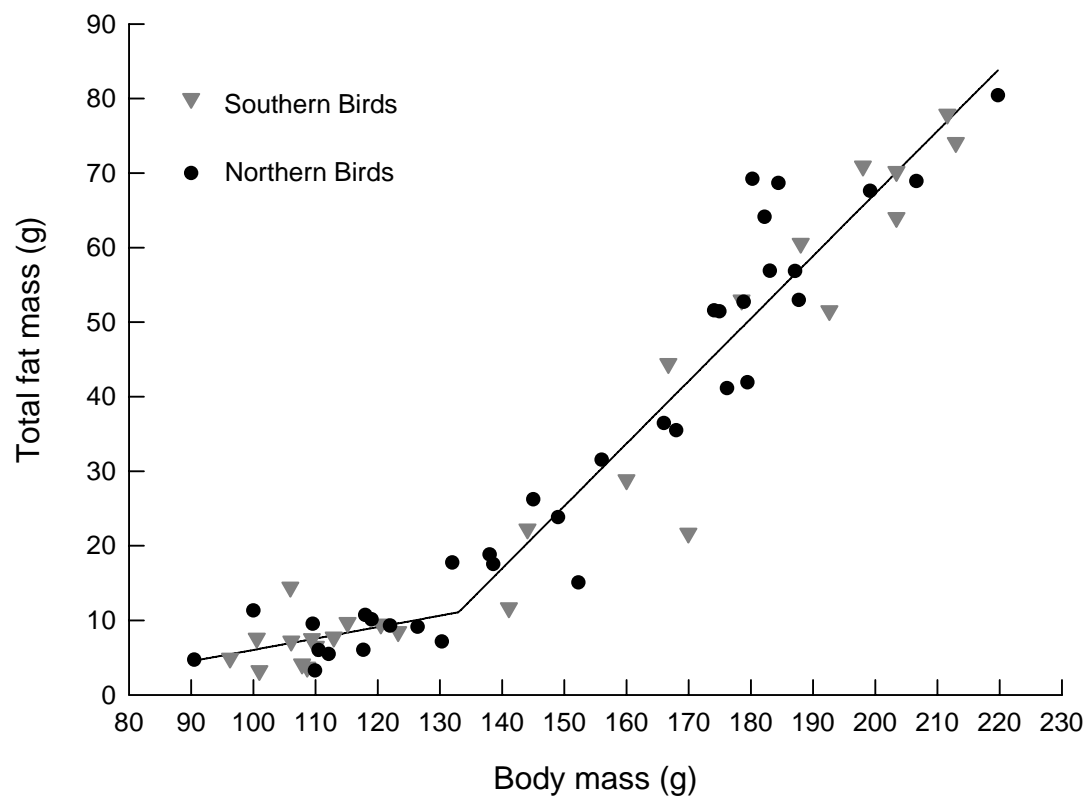


Fig. 3

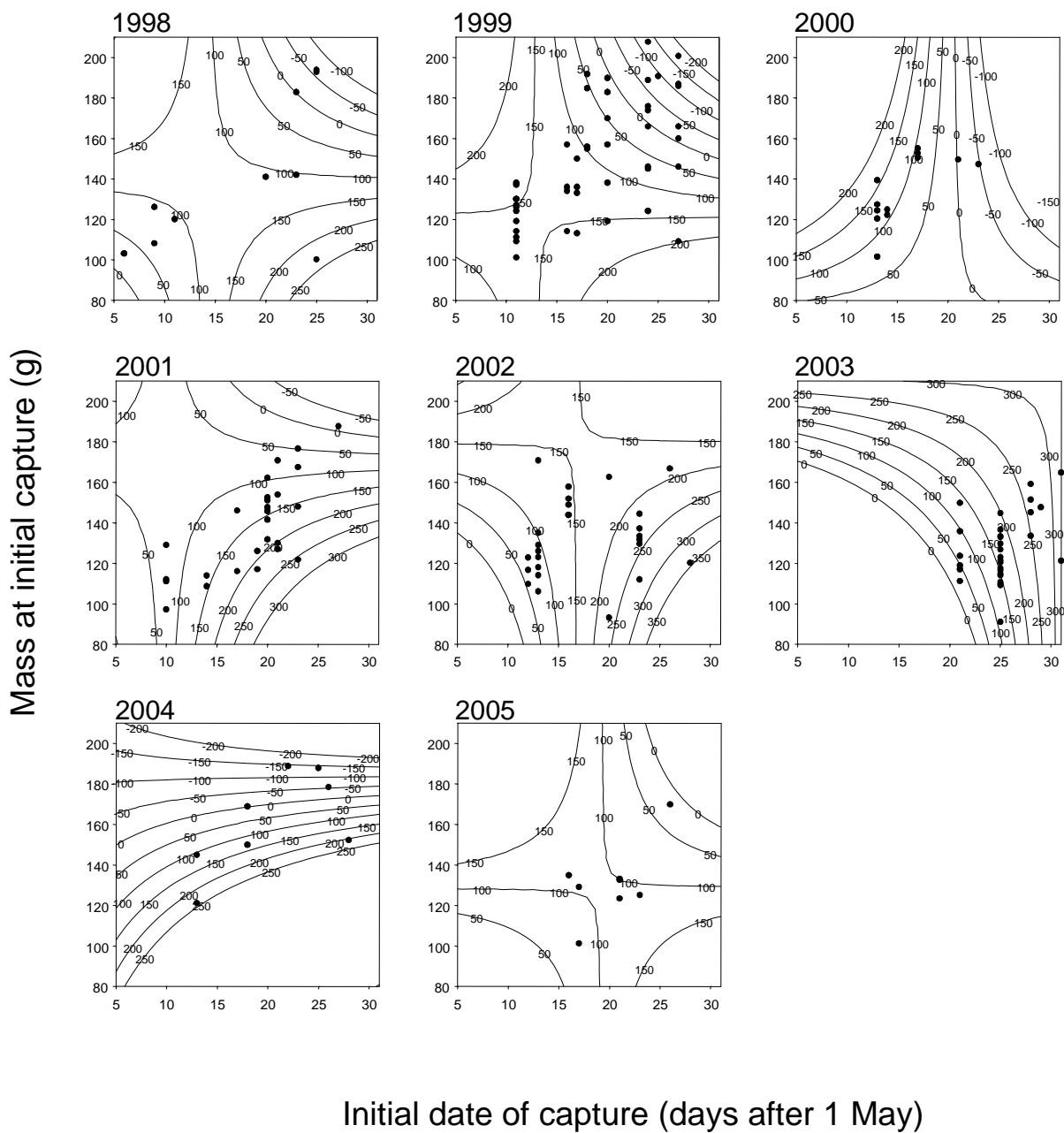
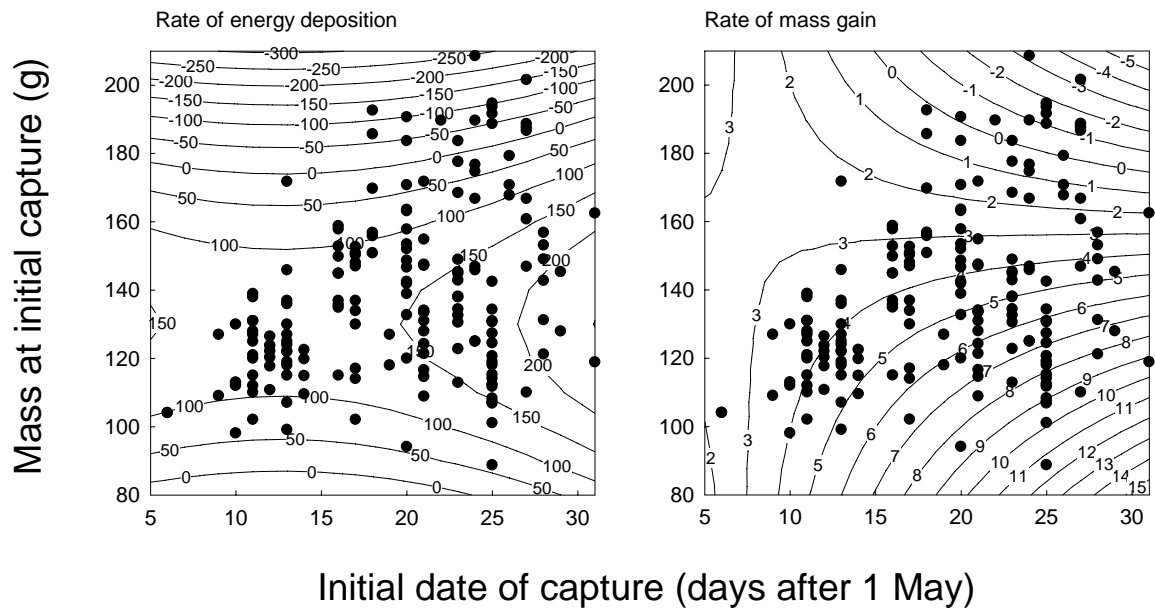


Fig. 4



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Roost availability may constrain shorebird distribution: Exploring the energetic costs of roosting and disturbance around a tropical bay

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ABSTRACT

High tides force shorebirds from their intertidal feeding areas to refuges known as roosts. This paper explores the energetic costs of roost disturbance of great knot (*Calidris tenuirostris*) and red knot (*C. canutus*) at Roebuck Bay, North-western Australia, assessing disturbance levels at different roost sites through direct observation and automatic radio-telemetry, and applying physiological equations and predictive roost choice models to estimate energetic costs of disturbance through a complete tidal cycle. The study area had a variety of roosts, but use of each was constrained by conditions of tide and time. The roost most suitable for shorebirds on daytime high tides of intermediate height experienced high levels of disturbance from both natural sources (birds of prey) and humans. Flight costs caused by disturbance at this site exceeded the costs of flying to and roosting at the nearest alternative roost, 25 km away. However, shorebirds did not roost at the alternate site, possibly because of the risk of heat stress in a prolonged flight in tropical conditions. Increases in disturbance levels at just one of the roost sites of Roebuck Bay would increase energetic costs substantially, and could easily reach the point at which feeding areas accessed from this roost cannot be used without incurring a net energy deficit. Roost availability can therefore limit access to feeding areas and hence limit population size. Adequate provision and management of roost sites is accordingly an important consideration in conservation of sites used by coastal shorebirds.

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1. Introduction

The distribution of animals is usually thought to be restricted by the occurrence of good feeding areas, with predators and disease organisms determining the quality of such areas in

addition to resource abundance (Newton, 1998). However, many animals use feeding areas for only part of the day and at other times rely on alternative areas to roost and loaf. In tidal areas shorebirds have to leave their intertidal feeding areas for high tide roosts. Shorebirds are particular in their

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choice of such roosts (Piersma et al., 1993; Luís et al., 2001; Rogers, 2003), preferring accessible sites where birds are safe and not thermally stressed. Accessibility is a function of the distance from the feeding grounds. Safety is a function of the risk of predator attack, perhaps in combination with human disturbance (Rosa et al., 2006). Thermal stress, either because of wind and cold induced rises in maintenance costs (Wiersma and Piersma, 1994) or excessive heat load (Battley et al., 2003), is a function of the geomorphological features of a place, and may also be influenced by human disturbance.

This study examines the importance of having a range of roosting options available for differing conditions of tide, time of day and season. Using a tropical system, Roebuck Bay in north-western Australia, we build on an analysis of the choices made by two species of shorebird (Rogers et al., in press). Our interest in these roosting options is twofold. First, we would like to examine whether the options available to shorebirds in this particular setting are secure in the face of increasing levels of human disturbance. Secondly, we would like to know if roost availability can limit access to feeding grounds, an issue that has received little attention in shorebirds despite the finding that foraging itineraries of red knot *Calidris canutus* and dunlin *C. alpina* are influenced by the proximity of roosts (Van Gils et al., 2006; Dias et al., 2006).

Several studies have shown that foraging success, and hence potentially the survival, of shorebirds can be limited by interference (Triplet et al., 1999; Van Gils and Piersma, 2004) or excessive depletion of their prey (O'Connor and Brown, 1977; Van Gils et al., 2003; Zharikov and Skilleter, 2003). Roost-constrained access to feeding grounds could therefore interact with density-dependent limits on food availability to regulate shorebird numbers even if the food supply is widespread, a mechanism termed “focal point regulation” by Newton (1998).

The two study species, red knot and great knot *Calidris tenuirostris*, are large migratory sandpipers that breed in Arctic tundra. In the non-breeding season both species occur in large flocks, and are restricted to coastal habitats, where they specialise in hunting buried molluscs in intertidal mud- and sandflats (Tulp and De Goeij, 1994; Van Gils et al., 2003). At high tide they characteristically roost in flocks on the ground in open habitats, taking to the air if threatened by potential predators. Both species are lean for most of their non-breeding period in Australia, but mass increases to about 150% in Feb.–Apr as they accumulate the stores required to fuel northwards migration (Battley et al., 2004; Piersma et al., 2005).

Roebuck Bay (18° S, 122° E; Fig. 1), on the north-west coast of Australia, has large intertidal flats that provide feeding

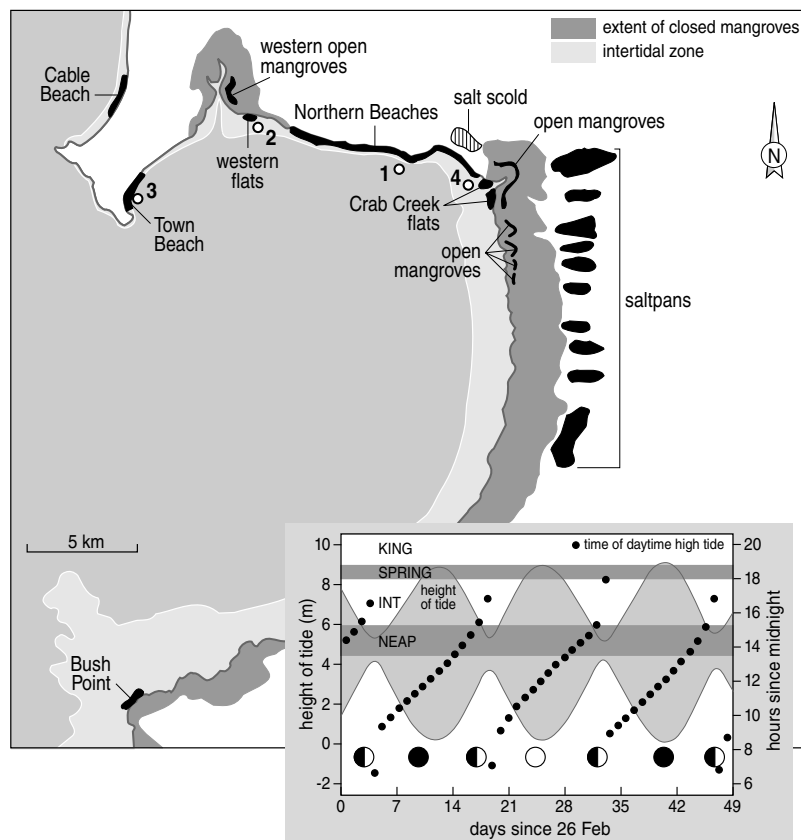


Fig. 1 – Map of the Roebuck Bay study site, adapted from aerial photographs. Feeding sites considered in this study are denoted with white-centred dots and numbered; from left to right: Town Beach, Dampier Flats, Fall Point and Crab Creek. Roosting habitats are marked in black and labeled. Inset: Amplitude of tides in the bay (plotted against the left-hand y-axis) through the study period, 26 Feb. to 15 April. Times of the peak daytime high tides are plotted against the right-hand y-axis. Grey shading depicts high tides classified as springs (8.3–8.95 m) and neaps (>6.0 m); intermediate and king tides are also shown. Lunar phases are shown at the bottom of the graph.

areas for internationally significant numbers of 20 migratory shorebird species (Rogers et al., 2003). It has a hot tropical climate, and extensive mangroves surround much of the bay (Fig. 1). Mangroves are usually too densely vegetated to be suitable roosts for coastal shorebirds (Zwarts, 1988). As a result, shorebird roosts of Roebuck Bay are restricted to a few discrete sites (Fig. 1): small mangrove clearings about 100 m in diameter (Open Mangroves and Western Open Mangroves); supratidal claypans east of the bay (Salt pans); raised mudflats only exposed on high tides during neaps (Western Flats, Crab Creek Flats); and beaches (Bush Point, Cable Beach and the Northern Beaches). Sparsely vegetated white dunes back Cable Beach and Bush Point. The Northern Beaches are narrower, are backed by vegetated dunes and low laterite cliffs and have a few small adjacent sea-stacks sometimes used by roosting shorebirds; they are internationally renowned as a shorebird-viewing site (Rogers et al., 2003). The adjacent town of Broome has a thriving tourist industry and is growing rapidly, increasing the risk of shorebird disturbance on the Northern Beaches.

2. Methods

2.1. Temporal variation in the roosting option set

Rogers et al. (in press) used a radio-telemetry study at Roebuck Bay to calibrate simple bounds-based models of local roost choice in great and red knots. These models were applied in this paper to assess whether roosts were potentially suitable. The models assume that knots roost at the closest site to their low-tide feeding area, provided that at these roosts, threshold values for certain environmental attributes (Table 1) are met. By day, environmental thresholds were: (1) a wet substrate, as sites with dry substrates had too warm a microclimate for roosting shorebirds; (2) nearest tall cover that should be at least 10–59 m from the roost (predictive success of models on non-neap tides, 63.5% for Great Knot, 70.0% for Red Knot; predictive success of models on neap tides, 90.6% for Great Knot, 80.3% for Red Knot). At night, microclimate did not affect the bounds models (it was cool at all sites in the absence of direct solar radiation); thresholds were that the nearest tall cover should be at least 10–59 m from the

roost and that the background colour at the roost should not be dark (predictive success of models on non-neap tides, 59.9% for great knot, 64.6% for red knot; predictive success of models on neap tides, 92.3% for great knot, 80.1% for red knot).

2.2. Disturbance

The frequency of disturbance was measured directly at five sites (final column of Table 2) in October 1997, March and August 1998, and October 2000, by watching roosting flocks from concealed positions. Each time a flock or part of flock took to the air, the time and number of flying shorebirds was noted. Flights were classified as alarm flights if birds towered and gave alarm calls. The cause of observed disturbances was recorded if identified. The percentage of shorebirds that were airborne was recorded at regular 5-min or 10-min intervals throughout the observation periods, and pooled data from these observations were used to estimate the percentage of the high tide period that was spent airborne due to disturbance. At the Northern Beaches a multiple linear regression showed the proportion of shorebirds in alarm flights per half-hour of observation to be significantly related to both tide height ($P = 0.0028$) and a categorical variable describing whether the tide was rising or falling ($P = 0.0029$; $R^2 = 0.641$, $n = 17$), with birds being more likely to be disturbed on a rising tide. In estimating the number of disturbances and amount of time spent in flight due to disturbance throughout a high tide period at this site, it was therefore necessary to account for the number of observations made on rising and falling tides. At other roost sites estimates of the number of alarm flights per hour were based on study days in which disturbance was recorded systematically throughout a high tide period; the number of observations made on rising and falling tides was therefore equal and no correction was needed.

These quantified observations were not made at all roost sites in Roebuck Bay, many of which were not readily accessible to human observers or were otherwise unsuitable for systematic disturbance observations. An ordinal *a priori* assessment of disturbance levels at other sites (Table 2) was made for all Roebuck Bay roosts on the basis of unquantified observations made while birdwatching regularly in the region

Table 1 – Attributes of roost sites of Roebuck Bay

Tide height (m)	Back-ground colour	Distance to tall cover; daytime substrate temperature			
		Neap (<6 m)	Intermediate (6.0–8.2 m)	Low Spring (8.3–8.9 m)	King (≥ 9 m)
Northern beaches	Int.	60–199 m; cool	10–59 m; cool	1–10 m; cool	1–10 m; int.
Crab creek flats	Pale	>200 m; cool	<1 m; flooded	<1 m; flooded	<1 m; flooded
Cable beach	Pale	>200 m; cool	60–199 m; cool	10–59 m; cool	10–59 m; cool
Bush point	Pale	>200 m; cool	>200 m; cool	60–199 m; cool	60–199 m; cool
Western flats	Int.	1–10 m; cool	<1 m; flooded	<1 m; flooded	<1 m; flooded
Western open mangroves	Dark	10–59 m; hot	10–59 m; hot	10–59 m; int.	10–59 m; cool
Open mangroves	Dark	10–59 m; hot	10–59 m; hot	10–59 m; cool	1–10 m; int.
Salt pans	Pale	>200 m; hot	>200 m; hot	>200 m; cool	>200 m; cool
Town beach	Int.	60–199 m; cool	10–59 m; cool	10–59 m; cool	10–59 m; cool

Background colour was scored as pale, intermediate (Int.) or dark. Substrate temperature was scored as wet, intermediate (in situations where it was drying out or the wet area was small) or dry; sites scored as flooded were too deeply immersed for shorebirds to roost.

Table 2 – Parameters and formulae used in models

Site	Disturbance level (a priori classification)	% of radio-signals interrupted	No. of radio records	Alarm flights per hour, time spent in alarm flights per tide
Cable beach – day	Very high		0	
Town beach – day	High	89.5%	143	
Northern beaches – day	High	81.2%	617	3.36 (29 h obs.), 30.1 mins
Open mangroves – night	Moderate	66.7%	9	
Northern beaches – night	Moderate	63.6%	165	
Open mangroves – day	Moderate	58.3%	115	0.90 (10 h obs.), 7.8 mins
Town beach- night	Moderate		0	
Western flats -day	Moderate	50%	2	
Western flats -night	Moderate	50%	2	
Western open mangroves – night	Moderate	50.0%	4	
Western open mangroves – day	Moderate	46.4%	69	
Bush Point – day	Low	43.5%	23	0 (9 h obs.)
Bush Point – night	Low	30.0%	70	
Crab Creek Flats – day	Low	29.7%	118	
Crab Creek Flats – night	Low	25.9%	139	
Saltpans – day	Low	9.0%	89	0 (5 h obs.)
Cable Beach – night	Low	5.2%	677	0 (10 h obs.)
Saltpans – night	Low	3.1%	159	

over several years (DIR, CJH, unpubl. data). These classifications were compared with data obtained in a radio-telemetry study carried out from Feb. to Apr. 2000, reported in detail by Battley et al. (2004) and Rogers et al. (in press). The study involved 25 great and 23 red knots with a 1.8 g Holohil BD2 radio-transmitter superglued to their rumps. Their local movements were monitored with an array of 14 continuously operating automatic radio-tracking stations sited at the key roost sites of Roebuck Bay. The stations had a short radio-reception range (0.7–1.0 km) and individuals were treated as being present at a station if the signal strength was ≥ 1.4 times the background noise. In constructing disturbance indices for this paper, a bird at a specific roost was considered to have been disturbed if its radio-signal was interrupted during within an hour of high water (i.e. if it moved to another roost during high tide, or if its signal stopped and later resumed at the same site). Sites with the highest percentage of interrupted radio-signals were assumed to be the most heavily disturbed.

2.3. Disturbance costs

Roost choice costs were simulated for great and red knots from four feeding sites in northern Roebuck Bay (Fig. 1), all of which are regularly used by one or both knot species (Rogers, 1999, unpubl. data). In theory a roost site would be unsuitable if the energetic costs of roosting there exceeded energy intake minus maintenance requirements. However, energy deficits incurred while roosting on a specific tide might be offset by surpluses made on other tides. The roost choice models (summarised above) were therefore used to predict where great and red knots from the four selected feeding sites would roost on high tide, through a complete cycle of 28 low and 28 high tides. It was assumed that during non-neap tides, individuals would be faithful to only one feeding area, and that on neap tides they would move to the Crab Creek Flats in the east of the bay (Fig. 1); this movement pattern was followed regularly by the knots radio-tracked by Rogers et al. (in press). The average number of neap (<6 m), intermediate

(6–8.2 m), spring (8.3–9 m) and king (>9 m) high tides per cycle was calculated from a year (2000) of tide-height data (National Tidal Centre, Australian Bureau of Meteorology). The landward edge of the intertidal flats of Roebuck Bay corresponds well with mean sea level (pers. obs.), so low and high tide periods were treated as being of equal duration, 370.1 min. Suitability of some roost sites in Roebuck Bay is influenced by heavy rainfall; for the simulations herein it was assumed the tidal cycle occurred in a rainless period (typical of Roebuck Bay, except in the wet season from about December to April).

Parameters and formulae used to calculate costs of maintenance and roost flights are summarised in Table 3. Body mass and Basal Metabolic Rate have been measured in great knot in Roebuck Bay, as has body mass of red knot; Basal Metabolic Rate of red knot in the bay was calculated by scaling down from the great knot estimates using an interspecific mass exponent of 0.71. Remaining parameters and formulae were obtained from published studies in laboratories or extra-limital sites. Thermoneutrality was assumed at all times, as operative temperatures of knots in the study area are typically in the thermoneutral zone (Wiersma and Piersma, 1994; Piersma et al., 1995), except in hot conditions when knots avoid overheating by seeking roosts with cool microclimates (Rogers et al., in press), a preference accounted for by the roost choice models. However, a correction was included for heat loss to ingested cold water during foraging, modifying the equation of Piersma et al. (2003a). The original equation included heat loss of 0.58 W in water of 15 °C, and this was corrected by a factor of 0.792, acting on the assumptions that all such heat loss was conductive, and that average surface- and pore water temperature in Roebuck Bay mudflats was 28 °C (unpubl. data). As the birds in the study site were living under thermoneutral conditions, we additionally assumed that all cost factors were additive (Van Gils et al., 2006).

Durations of commuting flights from the four selected feeding sites to the different roosts of Roebuck Bay were calculated assuming direct flights that were regarded as occur-

Table 3 – Site-specific likelihood of disturbance at the roosts of Roebuck Bay, ordered approximately from most to least highly disturbed, with night roosts shaded grey

Parameter	Assumptions and calculations	Source
Mass (M_b)	Great knot lean mass = 147.7 g Great knot departure mass = 240 g Red knot lean mass = 105 g Red knot departure mass = 165 g	Higgins and Davies (1996) Higgins and Davies (1996) Piersma et al. (2005) Piersma et al. (2005)
Flight speed	54 km h ⁻¹	Kvist et al. (2001)
Power input (P_{in}) in flight	Long flights: $P_{in} = 0.38 + 0.35 \log_{10} M_b$ Short flights: $P_{in} = 250.05 M_b^{0.8741}$	Kvist et al. (2001) Nudds and Bryant (2000)
Basal metabolic rate (BMR, in W)	$-2.57 + 1.24(\log_{10} M_b)$	Battley et al. (2001)
Cost of sleeping (KJ)	BMR \times time spent sleeping (in seconds)	Piersma et al. (2003a)
Cost of active rest (KJ)	BMR \times 1.659	Piersma et al. (2003a)
Cost of foraging (KJ)	$[(BMR \times 1.659) + (BMR \times 0.613)] \times$ time spent foraging (in seconds)	Piersma et al. (2003a)
Cost of digestion (KJ)	$(BMR \times 1.105) \times$ time spent foraging (in seconds) \times 0.792	Piersma et al. (2003a)

ring during the high tide period. Alarm flights, in which both species of knot take off rapidly and climb to considerable height (often >100 m, pers. obs.) were assumed to be more costly than steady flight (Hambly et al., 2004). Their costs were calculated using the allometric equation for short flights of Nudds and Bryant (2000), which predicted the short-flight costs of our study species to be 3.03 times greater than steady-state flight in lean red knots, 3.58 times greater than steady-state flight in lean great knots. This equation has not been calibrated on birds >150 g, so may not be perfectly suitable for red and great knots approaching departure mass. The alarm flights of knots include bursts of high speed, rapid changes in direction and substantial height gain, so our suspicion is that their costs are more likely to exceed than to fall short of the costs predicted by the equation. In another respect; disturbance may cause increased heartbeat rate and metabolic costs without actually forcing birds to take flight (Giese,

1998), and our models did not attempt any correction for this effect.

The amount of time spent sleeping, in active rest (e.g. standing, walking or preening) or foraging was estimated through activity scans made at feeding and roosting habitats in Roebuck Bay.

3. Results

3.1. Temporal variation in the roosting option set

The suitability of individual roost sites used by the great and red knots of northern Roebuck Bay (Fig. 1) varied according to whether it was day or night, and with tide and climate conditions (Rogers et al., in press). In general usage of roosts corresponded well with that predicted by the bounds models (Table 4). The Northern Beaches were used more than expected on spring and king tides because some knots roosted on a few

Table 4 – Suitability of roost sites, Feb.–Apr. 2000, in different conditions of tide, climate and time

Conditions and no. of records	Crab creek flats	Western flats	Northern beaches	Town beach	Cable beach	Bush point	Western open mangroves	Open mangroves	Salt pans
Day (dry)									
Neap (112)	90.2%	1.8%	7.1%	0.9%	0%	0%	0%	0%	0%
Intermediate (254)	0%	0%	85.0%	5.1%	0%	0%	0.4%	4.3%	5.1%
Spring (193)	0%	0%	65.3%	5.2%	0%	0%	11.9%	16.1%	1.6%
King (0)	–	–	–	–	–	–	–	–	–
Day (wet)									
Neap (75)	81.3%	2.7%	16.0%	0%	0%	0%	0%	0%	0%
Intermediate (225)	0%	0%	45.3%	7.1%	0%	0%	11.6%	3.1%	32.9%
Spring (118)	0%	0%	40.7%	5.9%	0%	0%	16.1%	18.6%	18.6%
King (111)	0%	0%	33.3%	20.7%	0%	0%	27.9%	0%	18.0%
Night									
Neap (153)	86.3%	0.7%	3.9%	0%	8.5%	0.7%	0%	0%	0%
Intermediate (464)	0%	0%	11.0%	0.2%	58.6%	1.1%	1.3%	0%	27.8%
Spring (88)	0%	0%	27.3%	0%	26.1%	4.5%	2.3%	0%	39.8%
King (0)	–	–	–	–	–	–	–	–	–

Unshaded cells depict potentially suitable roost sites. Cells shaded dark grey depict flooded sites where roosting was impossible. Cells shaded light grey depict other cases where climate, distance from tall cover or background colour were outside the thresholds of bounds models (Rogers et al., in press). Percentages of radio-tagged birds found at specific roosts in different tide conditions are shown, with the number of total cases given in parentheses in the first column.

small adjacent sea-stacks; only a small proportion of the knots present could fit onto these sites, so their habitat attributes were not included in the roost choice models. Roosts on mudbanks on the intertidal flats of Roebuck Bay were frequently used during neaps, but were submerged and never used by shorebirds on tides >6 m. At night, knots avoided sites that had nearby tall cover or had a dark background colour, one or both of these considerations making them avoid roosts in mangrove clearings, Town Beach and the Northern Beaches. As a result, distances flown from feeding areas to roosts were significantly greater at night than by day, on both non-neaps (at night 6.69 ± 4.61 km, $n = 655$; by day 1.72 km ± 1.59 , $n = 734$, $z = 26.313$, Dunn-Sidak adjusted $P < 0.01$) and on neaps (at night 2.66 ± 3.46 km, $n = 136$; by day 1.89 km ± 2.87 , $n = 175$, $z = 2.095$, Dunn-Sidak adjusted $P < 0.05$).

Microclimate was similar at all sites at night. By day when exposed to direct solar radiation, shorebirds were at risk of heat stress, and only used roost sites with wet substrates or shallow water, where counter-current exchange mechanisms could be used to lower body temperature (Battley et al., 2003). Suitably cool microclimates could be found along the wave-washed sand of beaches in all tide conditions by day. However, Cable Beach is next to a tourist resort and is often unsuitable by day because of continuous human disturbance; the Northern Beaches became unsuitable on the highest tides, when the water-edge was too close to tall cover. In such tide conditions, however, roosting options became available in habitats that were otherwise too hot. Spring tides extended far into the mangroves to form shallow lakes within some large mangrove clearings. King tides flooded these clearings so deeply that they became unsuitable for shorebirds, but in these conditions the tide extended completely through the mangroves to flood extensive lakes on the claypan systems beyond. The claypans and mangrove clearings are also suitable for shorebirds when flooded by heavy rain.

3.2. Disturbance

Classifications of roost disturbance levels made through opportunistic observations corresponded well with more rigorous data obtained through radio-telemetry or systematic observation (Table 2), suggesting our assessment of relative disturbance levels of the roosts is adequate. The most heavily disturbed daytime roosts were beaches that are also the roosts most easily and often visited by humans (pers. obs.). In particular, Cable Beach (the most frequently used roost at night) is a popular tourist resort and the lack of radio-records from the site by day may have been due to near-continuous human disturbance.

Of 105 cases of disturbance observed along the Northern Beaches by day, most (24.8%) were caused by birds of prey: Brahminy kite (*Haliastur indus*), whistling kite (*H. spheurnus*), black kite (*Milvus migrans*), white-bellied sea-eagle (*Haliaeetus leucogaster*), spotted harrier (*Circus assimilis*), nankeen kestrel (*Falco cenchroides*) and Australian hobby (*Falco longipennis*). Raptors used a concealed approach when attacking shorebird roosts, flying towards them behind the cover of dunes, cliffs or trees. Attacks were abandoned if a shorebird flock became airborne before any birds could be taken from the ground.

Roosting shorebirds were wary on the Northern Beaches and often (21.9% of cases) took off in response to false alarms, such as ospreys (*Pandion haliaeetus*), Caspian terns (*Sterna caspia*) or silver gulls (*Larus novaehollandiae*) flying low over roosts. Ospreys were never seen attacking shorebirds and were generally ignored by them, so instances in which they flushed waders were treated as false alarms. Many disturbances (20.9%) were caused by humans, their dogs or their vehicles. This measure probably underestimated the effect of human disturbance, for unlike birds of prey, humans often remained on beaches for some time after disturbing shorebirds, potentially preventing them from resettling. In 32.6% of cases we could not identify the cause of disturbance.

3.3. Disturbance costs

Total flight costs during a high tide for different roost sites were plotted against the time spent in alarm flights. Results for great knot from Fall Point (Fig. 2) were conceptually similar to those for red knots, and for both species at other feeding sites of northern Roebuck Bay (not presented here). Heavy birds at departure mass incurred higher flight costs than lean

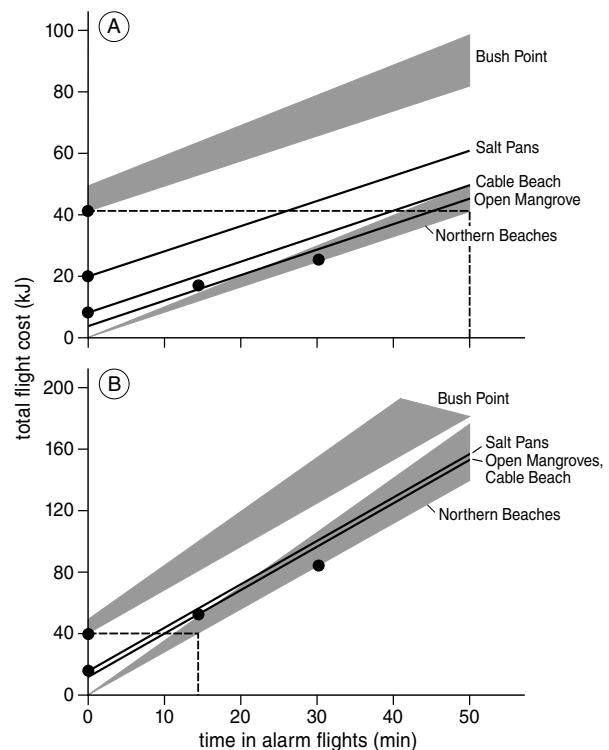


Fig. 2 – Flight costs (kJ) per high tide of lean great knots flying to different roosts from a feeding area at Fall Point, assuming equal costs s^{-1} for commuting and alarm flights (Panel A) or that alarm flights are 3.58 times more costly (Panel B). Grey-shaded areas indicate variation in flight costs related to variation in body mass at Bush Point and the Northern Beaches (upper boundary = costs for birds at departure mass). Observed levels of disturbance at each roost are indicated by black dots. Dotted lines indicate the level of disturbance at the Northern Beaches above which flying to Bush Point becomes a more economical option.

birds, but the difference was relatively small, considerably lower than the difference in costs between roosting at the closest potential roost site or the most distant (Fig. 2). If short alarm flights were assumed to be no more costly per time unit than commuting flights, the Northern Beaches turned out to be the most economical roost, provided the time spent in alarm flights per high tide did not exceed 50 minutes (Fig. 2A). However, the allometric equation of Nudds and Bryant (2000) predicts that costs of short flights in lean great knot will be 3.58 times those of commuting flights, and following this assumption, Bush Point (when undisturbed) turns out to be a more economical roosting option than the Northern Beaches if disturbance levels at the latter exceed 15.79 minutes (Fig. 2B). On average 30.17 ± 6.63 minutes ($n = 233$ scans) were spent in alarm flights per high tide at the Northern Beaches, making that site a more expensive roost option than an undisturbed Bush Point if short flights were 2.18 or more times more costly than steady-state flight; this threshold factor was 1.84 for red knots at the same feeding site.

The relative amounts of energy allocated to different activities at current levels of disturbance over a complete tidal cycle did not appear to differ greatly between species or between feeding sites within northern Roebuck Bay (Table 5). Foraging and digestion consumed more energy than other activities. However, the additional costs of roosting were also considerable. The combined costs of flying to roosts, and disturbance flights at roosts, ranged from 17.3% to 25.4% of the total energy expenditure of great knot at different feeding sites in northern Roebuck Bay (Table 5), and from 19.4% to 28.7% of the expenditure of the smaller red knot. In both species the cost of roost flights exceeded the amount of energy expended when sleeping or when at active rest (i.e. awake, but carrying out minimal activities such as vigilance or preening), although much more time was invested in these activities.

Estimates of total energy expenditure during a complete high tidal cycle increased with body mass. Energetic costs of great knots at departure mass (of c. 240 g) were almost twice

Table 5 – Energy budgets of great knots (white background) and red knots (shaded grey) from four different feeding sites (Fig. 1): (1) Fall Point; (2) Dampier Flats; (3) Town Beach; (4) Crab Creek Flats

	Site 1	Site 2	Site 3	Site 4	Site 1	Site 2	Site 3	Site 4
Relative cost of activity								
Sleeping	10.3%	8.7%	8.6%	10.7%	9.9%	8.2%	8.2%	10.4%
Active rest	11.6%	11.8%	12.4%	12.0%	10.6%	10.7%	11.3%	11.1%
Foraging	35.7%	33.2%	33.5%	36.8%	34.9%	32.1%	32.7%	32.7%
Digesting	22.6%	21.0%	21.2%	23.3%	22.1%	20.3%	20.7%	22.9%
Commuting	5.2%	6.6%	4.5%	2.3%	6.8%	8.5%	5.8%	2.9%
Alarm flights	14.6%	18.7%	19.7%	15.0%	15.8%	20.2%	20.3%	16.4%
Total roost flights	19.8%	25.4%	24.2%	17.3%	22.6%	28.7%	27.1%	19.4%
Average daily energy budget								
Expenditure (kJ day^{-1})	336.2	362.3	358.0	326.7	230.4	250.6	246.2	221.8
Expenditure/BMR	4.53	4.88	4.83	4.40	4.36	4.75	4.66	4.20
Daily requirement for pre-migratory mass gain (kJ day^{-1})	386.2	412.3	408.0	376.7	271.3	291.6	287.2	262.7
Required intake rate to balance expenditure and fuelling								
Intake (mg AFDM s^{-1})	0.58	0.62	0.61	0.56	0.40	0.43	0.42	0.38

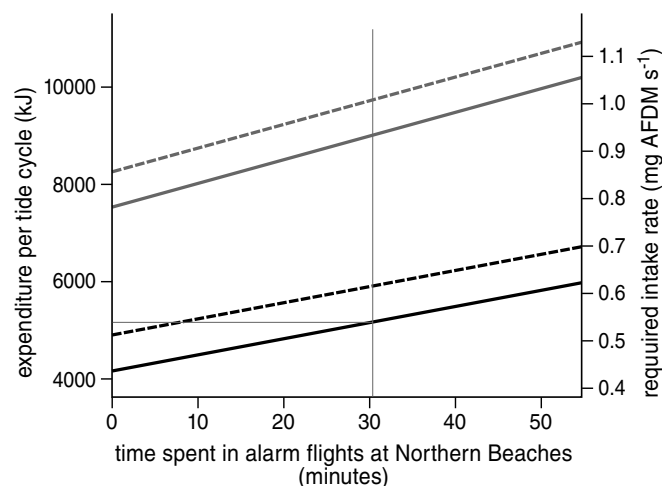


Fig. 3 – Energy expenditure (solid lines) and extra requirement for mass gain (dashed lines) of 1.1 g day^{-1} in great knot from Fall Point over a full tidal cycle, plotted against the average duration of disturbance per high tide when roosting on the northern beaches. Models for a lean great knot (147.5 g) are shown in black, for a fat great knot (240 g) in grey. The vertical line indicates the disturbance levels found at the Northern Beaches in this study.

as high as those at the usual non-breeding mass of 147.5 g (Fig. 3). Costs were still higher in periods of pre-migratory mass gain (Fig. 3), assuming mass-gain rates of 1.1 g day^{-1} in great knots (linearly scaled up from red knot estimate of 0.9 g day^{-1} at Roebuck Bay, Piersma et al., 2005). Energy expenditure per tidal cycle was also sensitive to the amount of disturbance on the Northern Beaches, although this roost was only used on 25.9% of high tides. For example, the half-hour of alarm flight per high tide observed at the Northern Beaches consumes almost as much energy per day as does undertake pre-migratory mass gain at a typical rate (Fig. 3).

4. Discussion

4.1. Roosting options at night

At night on non-neap tides birds were prepared to pay a high commuting price to roost in ideal conditions, most flying to Cable Beach or the saltpans. Both sites were considerably more distant than the roosts used on corresponding daytime high tides. Use of different roost sites by day and night appears to be common in coastal shorebirds (Hockey, 1985; Handel and Gill, 1992; Smit and Visser, 1993; Sitters et al., 2001), though it is by no means universal (Warnock and Takekawa, 1996; Van Gils and Piersma, 1999; Leyrer et al., 2006).

The roost choice models correctly predicted the observed preferences for Cable Beach and the saltpans on night-time neap high tides because the sites had pale backgrounds and were distant from tall cover (the same applied to Bush Point, but this site was rejected by the models as it was considerably further away). Both attributes would increase the ease of detecting approaching predators. In addition Cable Beach and the saltpans happened to have the lowest levels of disturbance of the night-time roost sites (Table 3), suggesting they were particularly “safe” roosts.

Although this reasoning is plausible, it is not entirely consistent with field observations. Shorebirds at Cable Beach at night spent 87% of the high tide period asleep, and did not appear vigilant enough to detect predators; human observers could walk to within 10 m of them as they slept, provided that they moved quietly without using torchlight (pers. obs.). In addition, Cable Beach is not free of predators; barking owls (*Ninox connivens*) and house cats (*Felis catus*) have been observed hunting shorebirds there at night (pers. obs.).

Sleeping is the most energy-efficient activity possible for shorebirds (Piersma et al., 2003a) and probably a physiological necessity (Rattenborg et al., 1999); recent studies indicate that birds are most predisposed to sleep in darkness (Rattenborg et al., 2005). If there is a physiological requirement to spend much of the night asleep, shorebirds may therefore select night-time roosts perceived to have low levels of “danger” (i.e. the inherent probability of becoming a prey item if no anti-predator measures are taken, Lank and Ydenburg, 2003). This consideration has received little consideration in the disturbance literature (e.g. Davidson and Rothwell, 1993), but may be critical in urban shorebird habitats. Our repeated field experience at Roebuck Bay is that shorebirds avoid roosting at sites where they are exposed to artificial lighting such as streetlights or traffic. Possibly such lighting makes roosting shorebirds too easily detected by predators,

or otherwise makes them perceive night-roosts to be too dangerous for sleeping.

At Roebuck Bay the lack of vehicle access to the remote saltpans should protect night roosts in this habitat for the foreseeable future. Cable Beach is potentially more sensitive, being close to the town of Broome; the roost there has serendipitously been protected from intrusion or illumination at night because the dunes behind it are part of the Minyirr Coastal Park, maintained for its cultural importance to Aboriginal people.

4.2. Roosting options by day

Shorebirds at Roebuck Bay are more tolerant of disturbance by day than at night, and on daytime high tides the most commonly used roosts, Northern and Town Beaches, were also among the most heavily disturbed. Much of this disturbance is natural, caused by birds of prey. However, it is now augmented by human activity, and the combined disturbance effects could reach the point at which the roosts become unsuitable. This point may not be far away, given that alternative roosts in mangrove clearings and saltpans are preferred when they become suitable on spring tides, or if flooded by rains. In 2003, unseasonal rainfalls in May flooded large salt-scoolds on Roebuck Plains (Fig. 1) and before they dried out in August, they were used in preference to the Northern Beaches in all tide conditions.

Despite the high levels of disturbance at the Northern Beaches, they were the preferred roost on daytime high tides of intermediate height (6.0–8.2 m). Our models indicate that this is because knots roost on wet substrates with a relatively cool microclimate; on tides of intermediate height the only alternative roosts for knots using feeding areas in the North of Roebuck Bay are Cable Beach (frequently unsuitable due to near-continuous human disturbance by day) and Bush Point (about 25 km away). The combined commuting and alarm flight costs of roosting on the frequently-used Northern Beaches exceed the costs of commuting to roost at the undisturbed Bush Point. Surprisingly though, Bush Point was not used by day by any radio-tracked birds from feeding grounds in northern Roebuck Bay (Rogers et al., in press). We suspect this is because an uninterrupted flight of about 25 km in the middle of the day could cause heat stress problems. Captive studies indicate that the water efflux rate of flying knots increases rapidly with temperature, starting to exceed water influx rates somewhere between 15 and 23 °C (Kvist, 2001). Evidence that this critical water efflux rate is readily exceeded in the tropical conditions of Roebuck Bay is provided by observations of panting in great and red knots; this heat loss behaviour occurs regularly for a minute or so after short flights (Battley et al., 2003). In cool climates where the costs of flight are offset by the thermoregulatory advantages of obtaining metabolic heat through locomotion (Bruinzeel and Piersma, 1998), shorebirds can probably undertake longer flights at high tide, an extreme example being a few sites where intertidal shorebirds will spend an entire high tide on the wing (Dekker, 1998; Hötker, 2000).

On present knowledge it is not possible to predict how high disturbance levels can get on the Northern Beaches of Roebuck Bay before shorebirds are forced to roost elsewhere

in all tide conditions. The present abundance of shorebirds there suggests that they can cope with the current levels of disturbance. In future management of the site, it would be prudent to ensure that disturbance levels do not increase further.

4.3. Energetic consequences of Roost choice

Our attempt to assess the energetic costs of roosting in Roebuck Bay is the first to use effective roost choice models to predict local movements throughout a tidal cycle, taking into account that shorebirds roost in different places according to tide height and whether it is day or night. The overall energy expenditure of knots in Roebuck Bay over a tidal cycle was estimated to be 4.2–4.9 times as high as basal metabolism. This is a high level of sustained expenditure, approaching the inferred ‘metabolic ceiling’ of 4–5 times Basal Metabolic Rate that was once considered to be found only in hard-working parent birds and growing animals (Weiner, 1992). However, high levels of energy expenditure appear to be typical of shorebirds (Piersma, 2002; Piersma et al., 2003b). Our estimate is similar to the only direct measurements available of field metabolic costs of non-breeding shorebirds (sanderling *Calidris alba*), which ranged from 2.1 to 4.2 times Basal Metabolic Rate according to non-breeding area (Castro et al., 1992). Field metabolic costs of shorebirds are higher in colder climates (Castro et al., 1992; Wiersma and Piersma, 1994), and it has been suggested that an advantage of migrating to warm non-breeding grounds is the energetic saving of spending several months in sites where insulation costs are low (Wiersma and Piersma, 1994). The estimates of energy costs in Roebuck Bay suggest that the tropics are not necessarily “cheaper” non-breeding sites when the costs of activity (including roost movements) are also considered.

The combined costs of flying to roosts, and at roosts because of disturbance, ranged from 17.3% to 28.7% of the total energy budget of red and great knots in Roebuck Bay, a level of expenditure that does not appear to be unusual. Commuting flights accounted for 2.3–8.5% of the total tidal energy expenditure. In studies of red knot elsewhere, estimates of costs of routinely made roost-flights (as a proportion of daily expenditure) were of similar scale: 12.2% at the Dee Estuary (Mitchell et al., 1988) and 5.6% in the Dutch Wadden Sea (Piersma et al., 1993; Rehfsch et al., 1996). The distances between feeding sites and roosts in Roebuck Bay are also consistent with those observed in previous studies, which range from 2.2 km in western sandpipers *Calidris mauri* in San Francisco Bay (Warneck and Takekawa, 1996), to about 20 km or more for red knots at estuaries in western Europe (Mitchell et al., 1988; Van Gils et al., 2006). Comparison of disturbance levels with other shorebird studies is difficult because different workers have used different indices of disturbance. Disturbance levels at the Northern Beaches were high, but the observed frequency of 3.36 alarm flights per hour is not unique. Similar frequencies of disturbance incidents have been recorded on the Dee Estuary (Kirby et al., 1993) and Tagus Estuary (Rosa et al., 2006).

Energy expenditure over a tidal cycle was sensitive to the amount of disturbance. For example, an average 30-min increase per tide in the amount of time spent in alarm flights

at the Northern Beaches (a site used on only 25% of high tides) would increase the total energy expenditure by 13.3% in a lean great knot (Fig. 3). Shorebirds may be able to compensate for these costs to some extent by extending their food intake but the extent to which they can do this will be finite; it will be limited ultimately by digestive capacity or the prey available at a site (Van Gils et al., 2005). Energy expenditure and required intake rates over a tidal cycle increase with body mass (Fig. 3), and would therefore be expected to be highest in the final stages of pre-migratory mass gain. The higher energy demands of heavier birds might be helpful in identifying situations where shorebirds are experiencing difficulty in meeting the energetic costs of roosting, as such individuals may be obliged to select roosts with lower energy costs but presumably higher risk levels. Such scenarios appear to have been observed by Handel and Gill (1992) and by Van Gils and Piersma (1999), who described changes in roosting behaviour of dunlin (*Calidris alpina*) and red knots, respectively, as they approached departure mass.

In one of the few detailed investigations of roost choice in intertidal shorebirds, Rehfsch et al. (2003) remarked that “... any change in roosting conditions is likely to be less detrimental than loss of feeding areas”. While we agree that feeding areas are vital, we do not agree that loss of roosts should not be considered a separate concept; feeding areas are only of use to shorebirds if they are associated with acceptable roosts (Dias et al., 2006). If the energetic costs of roosting should increase expenditure to the point where shorebirds cannot meet their energy requirements for maintenance, moult and pre-migratory fuelling, then diminished survival (Durell et al., 2005) and a loss of feeding areas are inevitable. Our models demonstrate that within the scale of a naturally occurring shorebird site, a relatively small increase in disturbance levels can result in a substantial increase in energy expenditure. The capacity of shorebirds to compensate for such increases will vary according to the feeding and roosting options available at a site, but it is very likely that circumstances can develop where roost costs could drive the energy budget into deficit. The adequacy of roost habitats should therefore be considered carefully in management of coastal shorebird sites.

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Appendix D

Extreme endurance flights by birds crossing the Pacific

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Birds captivate us with their ability to fly, especially when crossing vast expanses of land and sea. That even non-soaring landbirds may engage in nonstop flights of several 1000 km is widely recognized (1), but details about such flights are scarce (2). Herein we document two shorebird species approaching 10 days of nonstop flight over 10,000 km of open ocean. These feats of endurance double the previously established maximums (3) and summon a review of our thinking about adaptations for avian migration and the limits to vertebrate performance.

Using satellite telemetry, we examined the southward migrations of two large shorebirds, bristle-thighed curlew (*Numenius tahitiensis*) and bar-tailed godwit (*Limosa lapponica*). Both species nest in Alaska, USA, and were hypothesized to migrate directly to nonbreeding areas in Oceania, New Zealand, and Australia (4). During nesting (June 2006), we fitted 10 adult curlews and 7 adult godwits with miniaturized Argos satellite transmitters (platform transmitting terminals or PTTs) (3). After nesting, all birds spent 8 to 12 weeks in western Alaska building fat reserves for southward migration. Nine

curlews and at least 5 godwits migrated. One curlew was probably killed by a predator and 2 PTTs failed before godwits departed. Individuals began their migrations on different days (curlews: 6–25 August; godwits: 31 August–22 September). Seven of 9 curlews were tracked entirely over open ocean until they made landfall in French Polynesia; 2 were flying near French Polynesia when their transmitters stopped reporting (Fig. 1). Total tracking distance for curlews ($n = 9$) from their last reported location in Alaska to their first landfall in the South Pacific (or last reported location) ranged from 7050–9725 km (8800 ± 900), and their flight duration ranged from 5.7–8.3 days (7.2 ± 1.2). Godwits followed more direct routes to nonbreeding areas than curlews (Fig. 1); however, due to PTT failure, no godwit was observed to reach its predicted final destination in New Zealand or Australia (Fig. 1). Before signal loss, godwits ($n = 5$) were tracked in nonstop flights for 7000–10,800 km (8600 ± 1600) and 5.5–9.6 days (7.0 ± 1.6). Unlike curlews, godwits passed islands en route to their final destination but their tracking velocity remained constant, indicating they did not stop.

Both species left Alaska when large-scale meteorological conditions provided tail winds (3) over the first 500–1500 km (Fig. 1, Fig. S1). Departing in August, curlews initially flew southeast then turned south aided by prevailing winds along the eastern flank of the summertime Eastern Pacific High (3). During September, this high pressure cell weakened and bifurcated, creating a more direct southward migratory corridor for godwits to exploit (3, 4).

These extraordinary nonstop flights not only require an adaptive interpretation but also have profound implications for understanding avian migration and physiological processes of vertebrates in general. Such long flights require ‘hubs’ of excellent quality in terms of food and safety at both departure and arrival locations (4). They also enable birds to use travel corridors relatively free of both predators and pathogens. That some birds go ≥ 9 days without drinking demands reevaluation of the water budget in long-distance migrants, particularly catabolism of protein as a source of water (5, 6). Additional questions are raised about how birds meet their requirement for sleep (7) and how current models of flight mechanics should be adjusted (e.g., drag coefficients [8]) to accommodate such long

flights. Finally, the migration trajectories themselves challenge current paradigms about avian orientation and navigation, including the sensory systems involved (3, 9).

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Supporting Online Material

www.sciencemag.org/content/full

Materials and Methods

SOM Text

Fig. S1

Table S1, S2

References

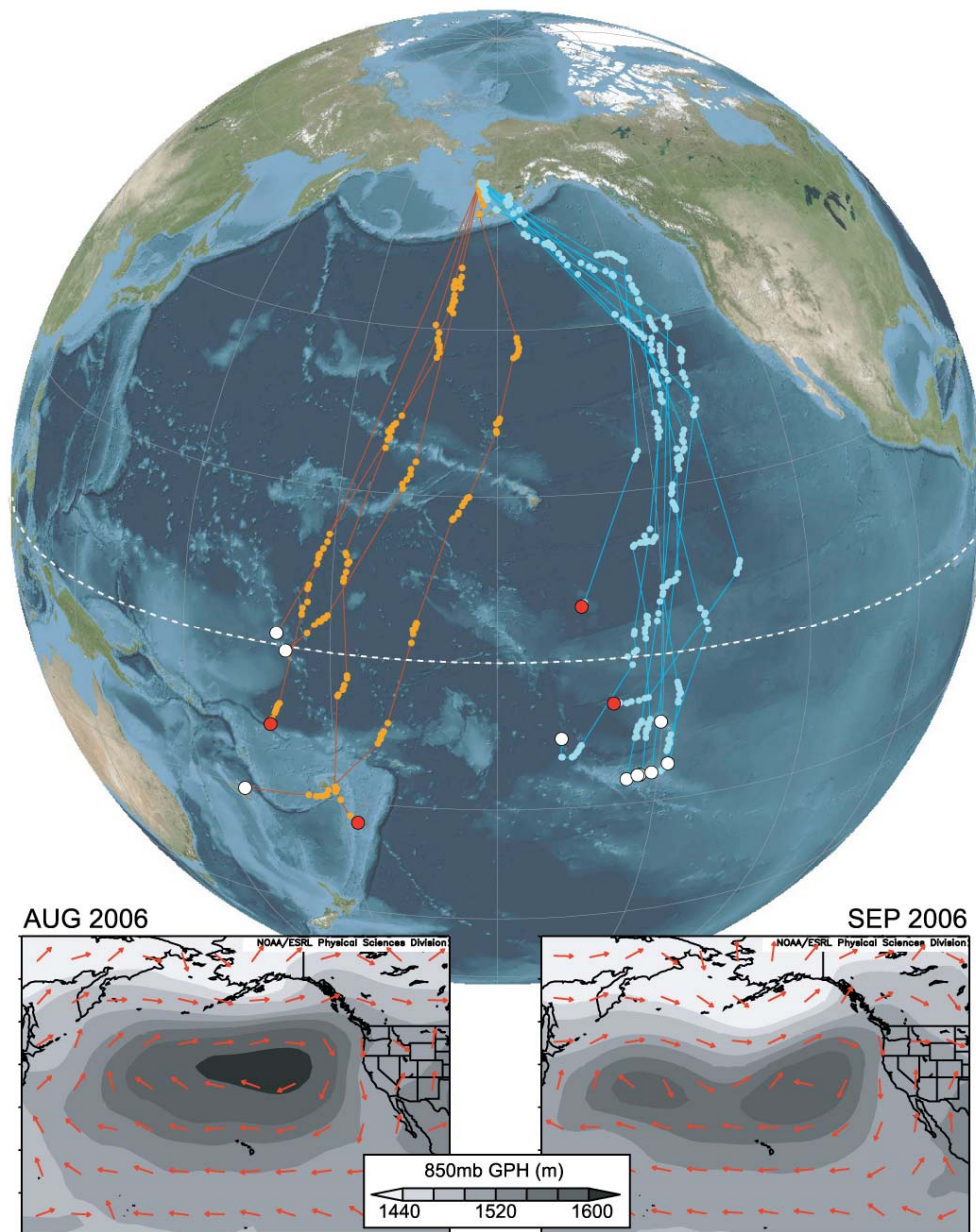


Fig. 1. Nonstop trans-Pacific flights of 9 bristle-thighed curlews (light blue) and 5 bar-tailed godwits (orange) during August and September 2006, respectively. White symbols at the end of tracks denote locations of first landfall, red symbols denote last location before signal was lost. Insets show average 850 mb geopotential heights and wind direction vectors north of the equator for August (curlew migration) and September (godwit migration). Tracks are depicted on orthographic projection centered at 20°N, 160°W. Wind/pressure is on a Mercator projection.

Supporting Online Material.

Material and Methods

We tracked movements of adult bristle-thighed curlews (*Numenius tahitiensis*) and bar-tailed godwits (*Limosa lapponica*) using 2 models of satellite transmitter (PTT) built by Microwave Telemetry (Columbia Maryland; USA). A 24-g battery-powered model was surgically implanted in the coelomic cavity (S1, 2) of 5 female godwits and 4 male and 4 female curlews. A 10.5-g solar-powered model was attached using a Teflon leg-loop harness to the backs of 3 male godwits and to 1 male and 1 female curlew. To reduce wind drag, we contoured antennas of both PTT models to the birds' in-flight horizontal plane. When attached to the birds during the nesting season, implantable PTTs ranged between 6.4 and 7.5% of the current body mass for godwits and 5.5 and 6.2% for curlews. Body mass of both species at the onset of migration is likely double that during the nesting period (S3–6). Transmissions by the implantable PTTs were initially constrained by pre-programmed duty cycles to conserve battery life. During the likely migration periods for curlews (August) and godwits (September–October) the implanted PTTs transmitted for 8 h and then rested for 24 h. The solar PTTs were permanently scheduled to transmit for 10 h separated by 48-h recharging intervals.

Argos Data Collection System receivers aboard NOAA polar-orbiting satellites collected the PTT transmissions and CLS America, Inc. (<http://www.clsamerica.com/>) derived location estimates based on satellite overpass geometry and Doppler-shifts in the PTT uplink frequency (401.5 MHz). Locations were disseminated by CLS with an index (LC) of location accuracy. Standard location classes (LC 1, 2, or 3) have an approximate 1σ error radius of <1500 m, while accuracy of the auxiliary classes (LC 0, A, B, or Z) is poorer and highly variable (http://www.cls.fr/html/argos/general/faq_en.html). We used a systematic filtering algorithm (<http://alaska.usgs.gov/science/biology/spatial/douglas.html>) to remove improbable auxiliary locations. Auxiliary locations within 10 km of a preceding or subsequent location were retained by virtue of spatial redundancy, and the remaining auxiliary locations were retained only if resultant movement rates were <100 km h⁻¹ and the internal angles (α , in degrees) formed by preceding and subsequent vectors (of lengths

d1 and d2 km) were not suspiciously acute ($\alpha < -25 + 25 \cdot \ln[\text{minimum}(d1, d2)]$). Of the 543 total Argos locations recovered during migration, 121 were standard locations that were always retained, whereas 27% of 422 auxiliary locations were filtered leaving a total of 430 locations for analysis (Fig. 1). Given the spatial scales considered herein, this filtering approach is suitable for establishing and analyzing long-distance movement paths.

We calculated tracking distances using the standard orthodrome (great circle) formula. Values represent mean \pm SD. Onset and termination points of the migratory flights were assumed to be the last and first terrestrial (or last open ocean) locations recorded in Alaska and the South Pacific, respectively. Since tracking relocations were intermittent due to PTT duty cycles and satellite overpass frequency, we estimated departure times by extrapolating the net tracking velocity during the first in-flight duty cycle from the first in-flight location back to the departure location. Arrival times were analogously estimated using velocity data from the last in-flight duty cycle extrapolated from the last in-flight location forward to the arrival location.

Our use of trade, product, or company names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

Supplementary Text

Winds and migration

That many species of migratory birds regularly initiate flights under favorable wind conditions is well documented (S7). This is particularly true in the Bering Sea in autumn (S8–10), so it was not unexpected that godwits and curlews would be added to the growing list of birds from this region using wind-selected migration. What was surprising was that curlews, unlike godwits, did not follow a more direct route to their nonbreeding grounds (Fig. 1). Curlews instead initially migrated southeastward towards the California coast before turning directly south towards the sites where they eventually made landfall. Not only was their initial track aided by winds but it also carried them to an area where their

flights were further aided by another source of winds, the eastern Pacific high pressure ridge. This seasonally persistent feature off the Pacific coast of the United States provides southerly and southwesterly flow back into the central Pacific Ocean (S11, 12), the area where curlews eventually made landfall. The mean departure vector followed by the 9 curlews ($140^{\circ} \pm 8$; $128\text{--}155^{\circ}$) (Fig. S1) took them just north of the center of the eastern Pacific high pressure ridge where they then altered their course southward to capitalize on the southerly wind flow (Fig. 1, Fig. S1). To our knowledge this is the first empirical evidence of long-distance migratory landbirds using multiple meteorological systems to aid migratory flight. This raises questions about if and how birds can detect weather conditions that are far-distant (2300 km in this case) and to what extent birds can map pressure gradients and use them to their advantage.

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Table S1. Histories of birds fitted with PTTs and followed on southward migration from Alaska, August–September 2006.

Species/sex [*]	Bird ID	PTT type [†]	Departure date	Departure location	Arrival location ^{††}	Flight duration (d)	Track distance (km)
Curlew/M	DØ	I	6 Aug	Alaska Peninsula	Iles Tuamotu	6.7	8850
Curlew/F	A7	S	15 Aug	Alaska Peninsula	Unknown	7.2	8100
Curlew/F	C3	I	17 Aug	S. Yukon-Kuskokwim Delta	Iles Tuamotu	6.9	9725
Curlew/F	D2	I	17 Aug	S. Yukon-Kuskokwim Delta	S. Line Isl.	7.3	9550
Curlew/M	C5	S	18 Aug	S. Yukon-Kuskokwim Delta	Unknown	5.7	7050
Curlew/F	B5	I	19 Aug	S. Yukon-Kuskokwim Delta	Iles Marquises	6.0	7910
Curlew/M	D3	I	19 Aug	S. Yukon-Kuskokwim Delta	Iles Tuamotu	6.5	9230
Curlew/M	D4	I	20 Aug	S. Yukon-Kuskokwim Delta	Iles Tuamotu	6.8	9180
Curlew/M	E3	I	25 Aug	S. Yukon-Kuskokwim Delta	Iles Tuamotu	8.3	9500
Godwit/F	Z7	I	31 Aug	S. Yukon-Kuskokwim Delta	Unknown	6.8	9600
Godwit/F	BØ	I	31 Aug	S. Yukon-Kuskokwim Delta	Unknown	5.9	8110
Godwit/F	H4	I	10 Sep	S. Yukon-Kuskokwim Delta	New Caledonia	9.6	10,800
Godwit/M	Z3	S	21 Sep	S. Yukon-Kuskokwim Delta	Tungaru Isl.	7.0	7343
Godwit/M	H6	S	22 Sep	S. Yukon-Kuskokwim Delta	Tungaru Isl.	5.5	6955

^{*} Bristle-thighed curlew (*Numenius tahitiensis*) or bar-tailed godwit (*Limosa lapponica*); Male or Female. [†]I = battery-powered implant. S = solar-powered external attachment. ^{††}Unknown = PTT stopped transmitting while the bird was flying. PTTs on curlews A7 and C5 stopped transmitting 24–25 August with their last locations 600 km and 1000 km, respectively, from the nearest land. These birds likely either perished at sea or made landfall but shed their transmitters in the ensuing 48-h-period before the PTTs were scheduled to report again. PTTs on godwits Z7 and BØ lost power and stopped reporting while birds were flying. At the time Z7 was 1500 km north of New Zealand and tracking towards New Zealand at 25 m s⁻¹; BØ was 2700 km west of Queensland, Australia, and tracking SSW at 14 m s⁻¹.

Table S2. Previous maximum estimates of long-distance nonstop flight by landbirds using forward flapping flight.

Species	Flight	Barrier	Distance	Evidence	SOM reference
Bar-tailed godwit <i>Limosa lapponica</i>	New Zealand to China	Ocean	6000–8000	Indirect: flight range model; absence of sightings of marked birds en route	S6
Red knot <i>Calidris canutus</i>	NE Australia to Yellow Sea	Ocean	6900	Indirect: flight range model; absence of sightings of marked birds en route	S13
Bristle-thighed curlew <i>Numenius tahitiensis</i>	Alaska to NW Hawaiian Islands	Ocean	4000–6000+	Indirect: flight range model, open ocean crossing without land	S3
Eastern curlew <i>N. madagascariensis</i>	E. Australia to Taiwan	Ocean	3400–5500	Direct: satellite tracking over open ocean	S14
Great knot <i>C. tenuirostris</i>	NW Australia to China	Ocean	5420	Indirect: flight range model; absence of sightings of marked birds en route	S15
Pacific golden-plover <i>Pluvialis fulva</i>	Hawaii to Alaska	Ocean	4500	Direct: open ocean crossing without land, VHF radio-telemetry	S16
Bar-tailed godwit <i>L. lapponica</i>	Africa to Wadden Sea	Ocean	4300	Indirect: flight range model; absence of sightings of marked birds en route	S17

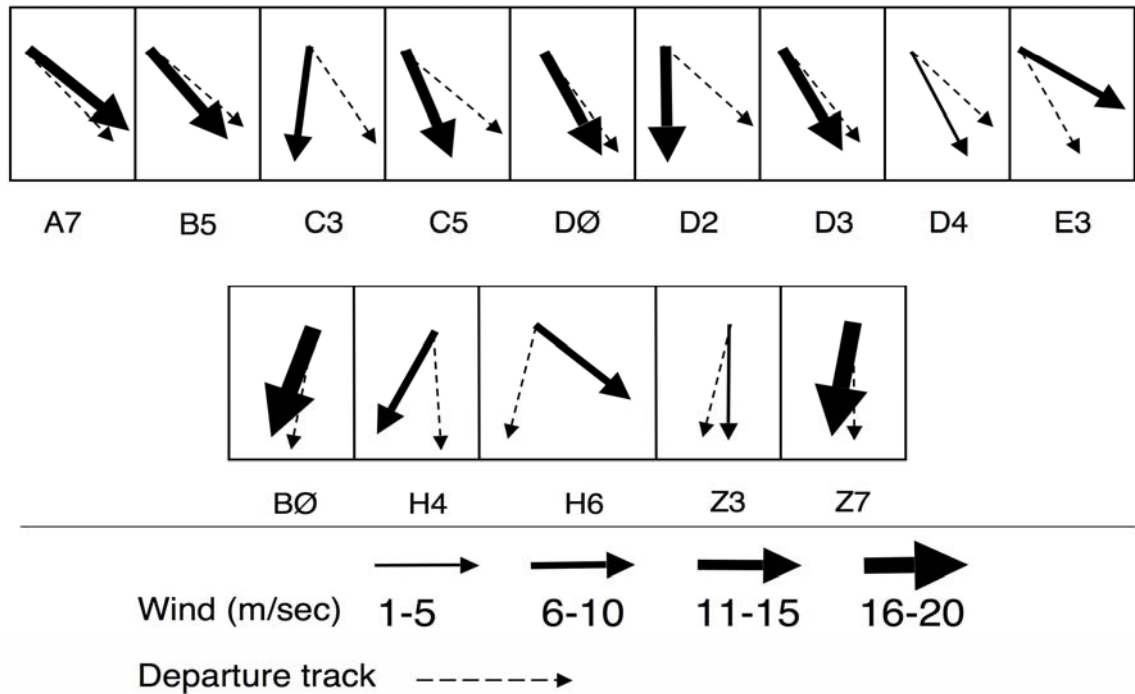


Fig. S1. Concordance between winds at departure and the departure tracks of bristle-thighed curlews (top) and bar-tailed godwits (bottom) on southward migration from Alaska (see Fig. 1). Direction and magnitude of 850 mb winds from the NASA GEOS-5 model at 100 km distance from the departure location along the departure track. Vector paths of winds and birds were extracted from merged overlays on orthographic projections. See Table S1 for departure dates.

Consistent annual schedules in a migratory shorebird

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Many migratory birds start prebreeding moult and premigratory fuelling some months before the breeding season and face severe time constraints, while travelling up to 15 000 km between non-breeding and breeding grounds. Shorebirds typically leave Southern Hemisphere non-breeding areas over a 3–4 week period, but whether they benefit from interannually consistent timing of departure is unknown. Here, I show that individual bar-tailed godwits (*Limosa limosa baueri*) from New Zealand are highly consistent in their migratory scheduling. Most birds left within the same week each year (between-year repeatability, r , of 0.83) and adult males, which moult into a bright breeding plumage, were also highly repeatable in the extent of their prebreeding moult ($r=0.86$). This is consistent with the hypothesis that birds have individually optimized migration schedules. Within adult males, but not females, smaller birds tended to migrate earlier than large birds. Whether this reflects differences in size-related migration speed, optimal breeding time at different sites or size-related natural or sexual selection pressures, remains unknown.

Keywords: migration; timing; repeatability; plumage; shorebird; age differences

1. INTRODUCTION

The timing of arrival on the breeding grounds can be a critical element in the fitness of migratory birds (Both & Visser 2001), and migration is often portrayed as being a period of severe time constraints; but while there are ample examples of the benefits of early nesting (such as increased reproductive output and subsequent recruitment of young, e.g. Møller 1994a), little is known about how individuals schedule their entire migrations (Drent *et al.* 2003).

It is clear that there can be both extrinsic and intrinsic influences on the timing of migration. Habitat quality, for instance, can affect fuelling rates and consequently when individuals depart from non-breeding grounds (Marra *et al.* 1998) and arrive on the breeding grounds (Gill *et al.* 2001; Norris *et al.* 2004). Individual variation also exists, with early arrival on the breeding grounds being related to the quality in barn swallows (*Hirundo rustica*; Møller 1994b), but to body size in dusky warblers (*Phylloscopus fuscatus*; Forstmeier 2002). Whether individuals show interannually consistent

migratory schedules is less known, though repeatabilities of arrival date on the breeding grounds of 0.18–0.51 have been reported for barn swallows (Møller 2001), dusky warblers (Forstmeier 2002) and black-tailed godwits (*Limosa limosa islandica*; Gunnarsson *et al.* 2006). These suggest that individual timetables may exist.

Here, I assess whether individual bar-tailed godwits (*Limosa lapponica baueri*) show year-to-year consistency in the timing of migration from a Southern Hemisphere non-breeding site and in the extent of their prebreeding moult (which is often interpreted as a signal of quality; Piersma & Jukema 1993), as is expected if birds migrate according to regular individual schedules. By studying birds at a single non-breeding site, confounding factors such as different habitat qualities and environmental conditions experienced by birds could be avoided. I tested whether individuals: (i) departed on a 15 000 km northward migration from New Zealand at the same time in different years, having (ii) undergone the same amount of prebreeding moult, as is expected if migration is internally rather than externally controlled.

2. MATERIAL AND METHODS

Bar-tailed godwits of the subspecies *baueri* breed in Alaska and 'winter' in Australia and New Zealand, making the longest migrations of any bar-tailed godwit population and possibly the longest single migratory flight of any bird (Gill *et al.* 2005). Returning to the breeding grounds, birds depart New Zealand from the second week of March to the first week of April (Battley 1997; P. F. Battley 2003–2006, unpublished data) and make a long flight towards eastern Asia (Battley & Piersma 2005). After refuelling in the Yellow Sea region of China and the Korean Peninsula, birds fly another 5000 km from late April/early May to the breeding grounds (McCaffery & Gill 2001).

Godwits were caught from 2004 to 2006 in the western Firth of Thames, North Island, New Zealand (37°11'S, 175°19'E), measured and individually colour banded. Birds were sexed on bill length (Battley & Piersma 2005) and aged on wing moult and contour feather appearance and wear. Intensive (near daily) resighting efforts were made at roosts in the western Firth of Thames in March 2004–2006 to determine when individual birds left on migration and what stage of prebreeding moult they were in. Whenever possible, banded birds were sexed visually on the basis of body size, bill length and breeding plumage (only males moult into an extensively red plumage; Higgins & Davies 1996). Breeding plumage was scored on a 1–7 scale (including half scores where necessary) for males (from non-breeding to complete breeding plumage; Piersma & Jukema 1993) and on a 1–4 scale for females (which do not develop much red plumage). Plumage scores assigned in the field proved to be highly consistent. The repeatability (discussed later) of plumage score based on 671 consecutive resightings not more than 7 days apart in March (so that differences in plumage score probably arose from scoring differences rather than from moult) involving 106 birds was 0.96 ($F_{670,671}=43.851$, $p<0.001$). Frequent resightings of site-faithful birds allowed estimation of the date of departure for some individuals (the date of the last sighting). Dates of last sighting are given as 'March days', starting on March 1. They were standardized to account for 2004 being a leap year and are referred to as 'apparent departure dates'. Late-departing birds tend to be resighted more often than early-departing birds (number of records in March was positively correlated with date; Pearson's $r=0.55$) as they were 'available' for longer, and the declining number of birds present through the departure period probably also caused detection rates to be higher late in the season. The number of resightings per bird was positively correlated between years (Pearson's $r=0.68$), so the relative accuracy of last dates should not systematically differ between years. As dates of last sightings and plumage do not score exact measures, reduced major axis (RMA) regressions are used to explore their consistency among years. Individual apparent departure dates were treated as independent in each year. Birds aged as immature (2 or 3 years old) and adult are separated in analyses. Repeatabilities (the intraclass correlation coefficient) of

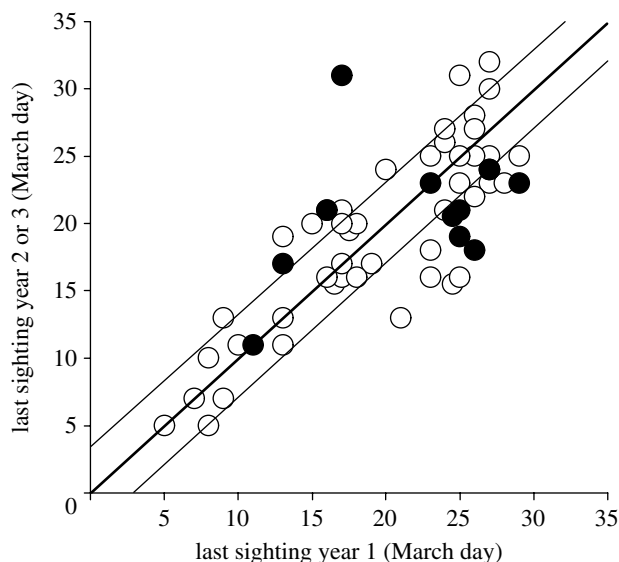


Figure 1. Apparent departure dates of bar-tailed godwits from the Firth of Thames, New Zealand, in successive years from 2004 to 2006. Adults are shown by hollow symbols, immatures by filled ones. The bold reference line shows a 1 : 1 relationship; thin reference lines demarcate the period of 3 days on either side of that. Some overlapping points have been offset for clarity.

departure date and plumage score were calculated according to Lessells & Boag (1987).

3. RESULTS

Departure dates were estimated for 41 birds in 2 years and eight birds in 3 years, giving a total of 57 comparisons. The date of the last sighting in 1 year was strongly correlated with the last date in the previous year (figure 1). The slope of the RMA relationship between departure dates in different years was $1.02 (\pm \text{s.e. } 0.08, 95\% \text{ CI}=0.85\text{--}1.19, R^2=0.60)$, which was not significantly different from a 1 : 1 relationship. However, variation was present, with some birds differing by up to 14 days. Some of this variation appears to be age-related; of the birds whose last records varied by more than 3 days between years (reference lines in figure 1), immatures were disproportionately represented. Of 11 immatures, 8 (73%) were recorded outside the ± 3 day window, compared with 17 of 46 adults (37%; Fisher's exact test, $p < 0.05$). Generally, the majority of birds (32 of 57 comparisons) left in the same week each year, despite migration occurring over a four-week period in total.

Some individuals were remarkably consistent in their timing. For 23 comparisons, birds were recorded last within 2 days of their previous last record, and five birds were consistent to within 3 days over all 3 years. Overall repeatability (r) of the apparent departure date was $0.77 (F_{48,57}=8.144, p < 0.001)$, but if immatures (which had poorer repeatability; $r=0.38, F_{10,11}=2.233, p > 0.1$) are excluded, repeatability becomes $0.83 (F_{37,46}=1.958, p < 0.001)$.

The extent of prebreeding moult done before departure was also highly consistent among years for adults (figure 2; RMA slope of $1.05 \pm 0.04, 95\%$

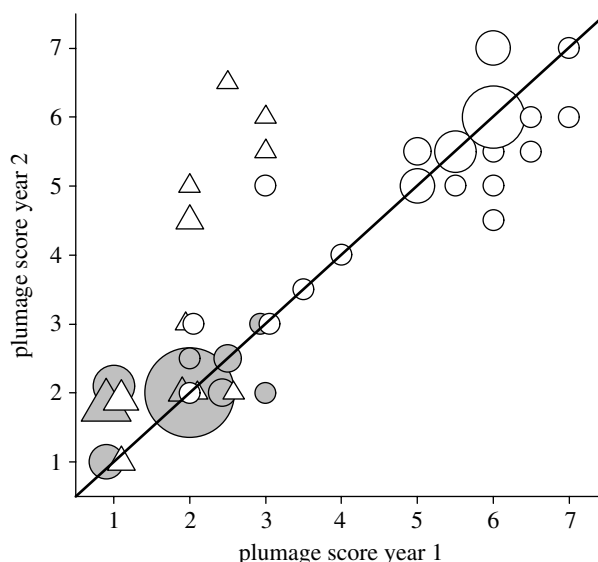


Figure 2. Plumage scores of bar-tailed godwits in different years before migration from the Firth of Thames, New Zealand, in 2004–2006. Circles, adults; triangles, immatures; filled symbols, females. Symbols are scaled relative to the number of records of birds in those plumages. The reference line shows a 1 : 1 relationship. Some overlapping points have been offset for clarity.

$\text{CI}=0.98\text{--}1.12, R^2=0.91$, did not differ from one). Between-year repeatability of plumages for adult males was $0.86 (F_{26,33}=14.773, p < 0.001)$. As breeding plumage is age related in young birds and some birds increased their breeding plumage scores across years, repeatability for immature males was much lower, ($r=0.21, F_{13,15}=1.551, p > 0.2$). Repeatability of adult female breeding plumage scores was lower than for males ($r=0.61, F_{22,25}=4.279, p > 0.001$).

For adult males, apparent departure date was unaffected by breeding plumage score (multiple regression using mean plumages and departure dates for 20 males recorded in more than 1 year and seven males recorded in 1 year; plumage standard coefficient = $-0.060, t = -0.345, p = 0.7$), but it was by body size: smaller males left earlier than larger males (total head length standard coefficient = $-0.576, t = -3.296, p = 0.003$; overall $R^2=0.313$; the same relationship held for other morphological measures). Neither plumage score nor total head length influenced departure date in females ($n=28, p > 0.6$ for both variables).

4. DISCUSSION

Adult bar-tailed godwits migrating north from New Zealand are highly consistent, in when they leave on migration and in what plumage they depart in. Even allowing for year-to-year variation in weather conditions that doubtlessly affected whether birds departed on a given day (Battley 1997; Green 2004), the repeatabilities of apparent departure date (0.83) and the extent of breeding plumage of adults (0.86) imply that birds have quite strict individual 'schedules' for physical appearance and timing of migration. The repeatabilities of migration timing for godwits are considerably higher than those for male

barn swallows (arrival date $r=0.51$; Møller 2001), dusky warblers (arrival date $r=0.34$; Forstmeier 2002), black-tailed godwits (arrival date $r=0.18$; Gunnarsson *et al.* 2006) and Bewick's swans (*Cygnus columbianus bewickii*; r_{approx} of Lessells & Boag (1987) is 0.15 for arrival at and 0.06 for departure from the non-breeding grounds, calculated from Rees 1989). This suggests that the individual optimization of departure schedules in bar-tailed godwits is especially strong.

While the control of migration is at least partially genetic (Berthold 1996), the greater variation in migration timing of immatures than adults implies that behavioural refinement with experience may be involved in determining the optimal departure date. For plumage, the consistent appearance of adult males suggests that differences between individuals have a genetic basis. Photographs of males in different years reveal them to be qualitatively identical in terms of where on the body retained non-breeding plumage is (unpublished data), indicating a high level of control of the moulting process. The lower repeatability of plumage score for females probably reflects the limited number of categories used and the small differences between them.

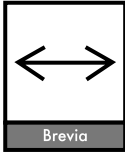
The breeding plumage of godwits has been suggested to be a reliable indicator of individual quality (Piersma & Jukema 1993), yet in my study, it had no influence on the timing of migration. Instead, there was a size gradient in departure dates, with smaller males migrating before larger ones. This gradient is unlikely to be a function of absolute size *per se*, because females are larger than all males yet overlapped completely with them in the timing of migration. Whether it reflects natural or sexual selection pressures is not clear: small males could migrate slower, breed earlier (e.g. in lower latitudes or altitudes) or need to arrive earlier for competitive reasons than large males, but there is no direct evidence on any of these possibilities. Predicted flight ranges of New Zealand godwits do not vary with body size (Battley & Piersma 2005), suggesting that a systematic size-related difference in flight length and number of stopovers is unlikely. However, there are no data on actual departure masses of birds in this study.

Gunnarsson *et al.* (2004) found that black-tailed godwits breeding in Iceland showed remarkable synchrony in the arrival of mates despite birds having wintered up to 1900 km apart. One suggestion for how such synchrony was maintained is that pairs independently synchronize their arrival to the optimal time for each specific breeding location. If, as I suggest here, birds do have strong individual time-tables for migration, then synchronous arrival on the breeding grounds is a likely consequence. In fact, given how short the window of opportunity for pair formation seems to be in black-tailed godwits (the two divorces in 10 pairs were both in pairs where mates arrived 8 days or more apart; Gunnarsson *et al.* 2004), it could be argued that mate retention is simply a by-product of strong individual migration schedules that happened to coincide and allow pair formation in the first place.

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Plumage and timing of migration in bar-tailed godwits: a comment on Drent et al. (2003)

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Rudi Drent and co-workers presented data on the plumage and apparent quality of bar-tailed godwits (*Limosa lapponica*) migrating northwards through the Netherlands en route from Africa to Siberia (Drent et al. 2003). They identified two groups of males in their samples based on the extent of the prebreeding moult – birds with extensive red breeding plumage ('dark' birds) and birds with little red plumage ('pale' birds). The pale birds were considered to be low quality individuals, which showed a higher incidence of cestode infestation (32.4% of individuals c.f. 12.2%) and, while the dataset was very small, lower subsequent survival (no pale birds were recaptured in later years whereas 11 red males were). They radio-tracked birds to determine the migration date of pale and dark birds towards the breeding grounds and were surprised to find that, contrary to expectation, the pale birds left on migration earlier than the dark birds. Noting that there was no evidence for any age-related changes in the breeding plumage score of male godwits (though their Fig. 7 indicates they never recaptured any pale birds so could not test this), Drent et al. erected a hypothesis to explain the unexpected finding. The pale birds were suggested to be 'desperates', birds of low quality whose only chance of successful breeding was to arrive early on the breeding grounds and achieve the benefits of prior occupancy on good territories. Given that it is generally high-quality individuals that can afford the risks of early arrival on the breeding grounds (Møller 1994), the lower apparent survival of these pale godwits reflected the costs associated with this strategy.

Appealing as this idea may be, data collected on the non-breeding grounds of a more accessible population of godwits show that most pale birds in Drent et al.'s study are almost certainly immature birds, potentially on their first migration. Together with colleagues from

the Ornithological Society of New Zealand, I have individually colour-banded godwits (subspecies *baueri*) in New Zealand since 2004 and aged these birds at capture. Godwits show delayed maturity and young birds remain on the non-breeding grounds for up to 3–4 years before migrating northward (McCaffery and Gill 2001). Where possible birds were aged as 1 (in the 1st year of life), 2 or 3+, though at some times of year birds could simply be designated as immature (age 2/3). Ageing was by plumage (juveniles have distinctive upperpart contour feathers that are retained until birds reach the non-breeding grounds), timing of wing moult (adults start wing moult only after arrival on the non-breeding grounds in September–October, whereas immatures that did not migrate to the breeding grounds start earlier; juveniles may undergo partial wing moult in the southern autumn) and feather condition (juvenile primaries become highly abraded by the time of the southern winter; adult breeding plumage contour feathers and tertials become very worn during the breeding season). Checks were then made at high-tide roosts to determine the presence of colour-banded birds and, when practical, the breeding plumage of males was scored on the same scale as used by Drent et al. (where 1 = complete non-breeding plumage, 2 = a trace of breeding plumage, 3 = 25% breeding plumage, 4 = 50% breeding plumage, 5 = 75% breeding plumage, 6 = only a trace of non-breeding plumage remains, and 7 = complete breeding plumage).

Resightings of marked birds in New Zealand show that the breeding plumage grown by male godwits is strongly age-related (Fig. 1). Across all birds, most age 1 and 2 godwits had very little breeding plumage, whereas many 3rd-year and most 'adult' godwits had substantial breeding plumage scores (Fig. 1, upper). The pattern of

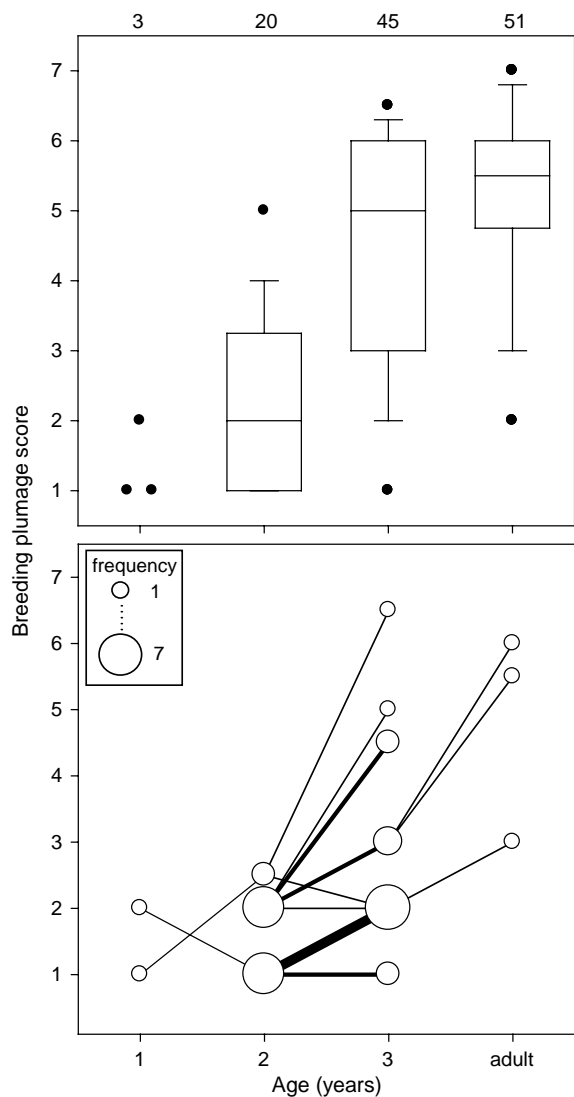


Fig. 1. Plumage scores of male bar-tailed godwits in the Firth of Thames, New Zealand. Scores represent the maximum plumage score recorded for birds before migration (which occurs in March) or, in the case of non-migrating immatures, over the northern summer period when adults are on the breeding grounds. Upper plot: plumages of males of different ages. Boxes enclose the 25th, 50th and 75th percentiles, whiskers the 5th and 95th, and outliers are shown as dots. Sample sizes are shown above the plot. Lower plot: changes in breeding plumage of individuals over time. Point areas are proportional to sample size. Lines join plumages of individuals seen in different years (thin line = 1 individual with that plumage change, medium line = 2 individuals, thick line = 4 individuals).

increasing breeding plumage with age is confirmed by resightings of individuals in consecutive years (Fig. 1, lower): scores increased for most birds as they got older, and the only birds that did not were recorded as having

a trace of breeding in one year and not the next and score 2–3 in one year and 2 the next. While there is variation between individuals of the same age, most pale birds are young birds.

Once adult, however, plumage scores of adults are highly repeatable between years ($r = 0.86$, $F_{26,33} = 14.773$, $p < 0.001$; Battley 2006; repeatabilities calculated according to Lessells and Boag 1987). In contrast, repeatability of plumage scores of birds aged as immatures (age 2 or 3) when banded is much lower ($r = 0.21$, $F_{13,15} = 1.551$, $p > 0.2$), as young birds increased their breeding plumage scores as they got older.

The age of first migration of godwits is difficult to ascertain fully, as the figures in the literature (not until nearly 4 years old in *baueri*; McCaffery and Gill 2001) are based on the presence of birds of these ages on the nonbreeding grounds during the breeding season. This can only determine the age that some birds do not migrate until – it does not prove that no younger birds have migrated. Five sightings of colour-banded birds from New Zealand on migration have confirmed that not all godwits delay migration until they are what would be considered adult. Two birds banded as juveniles in December 2004 were seen on migration in South Korea and China in 2006, making them 2nd-years when migrating (the official birth-day for northern hemisphere breeding shorebirds is 1 August; these birds would have been around 21 months old when they started their first northward migration). Three birds banded as probable 2nd-years have been seen on migration, one while still two years old, two while probably three years old. The probable 2nd-year was photographed in Japan in April 2005 (Fig. 2) and in appearance is virtually identical to the pale birds shown in Drent et al. (2003, their Fig. 6). A further bird was banded as a juvenile on the staging grounds in Alaska in September 2004 and resighted there in September 2006, also having migrated as a 2nd-year (R.E. Gill and M. Green, pers. comm.).

Together, these data from colour-banded birds in New Zealand establish (a) that immature godwits have low breeding plumage scores that tally with the pale birds recorded on migration by Drent et al., (b) adult godwits mostly have the higher breeding plumage scores taken to represent the 'good quality' Dutch birds, (c) once adult there is little if any plumage change between years, and (d) young pale birds can migrate towards the breeding grounds earlier than hitherto recognised. Because there would be little difference between immatures and true adults on migration apart from the extent of breeding plumage (primary feather wear would only be subtly different), it is not surprising that Drent et al. treated all their pale and dark birds as adults.



Fig. 2. Immature male bar-tailed godwit on migration in Japan, April 2005. This bird was banded in New Zealand on 31 October 2004 as a probable 2-year old, seen leaving its non-breeding site in a flock on migration on 17 March 2005 and photographed in Japan on 2 April 2005. Photo: Kouji Takenaka.

So what do these findings mean for the hypothesis of risky deserters of Drent et al. (2003)? Instead of representing a state-dependent behavioural strategy adopted by low-quality or poor condition birds, these birds should probably be considered naïve first-time migrants with no prior experience of final flight duration, spring conditions and the optimal arrival date on the breeding grounds. Young migrants can only have a basic genetic program of where and when to migrate (though they might travel in flocks with adults), whereas adults have the benefit of fine-tuning their migrations based on experience. Suboptimal decisions on when to migrate are therefore expected in immatures more than adults. Supporting this idea, immature godwits in New Zealand changed their departure dates in subsequent years more than adults did (Battley 2006). The tendency for these birds, however, was to advance their departure date, as they left on average slightly later than adults did (but not significantly; mean of 23 March for nine probable first-time migrants versus 20 March for average departure dates of 41 adults recorded in 2 or 3 years; T-test assuming unequal variances, $T_{12,7} = 1.434$, $p > 0.1$; note that the departure span for adults completely encompassed the dates for immatures).

With the small sample size of pale godwits radio-tracked by Drent et al. it is difficult to know how real the earlier departures of pale (young) birds are. If they are real, the question becomes why immatures would consistently migrate to the breeding grounds earlier than adults, particularly if there was selection against this (as suggested by the absence of pale birds in recaptures between years in the Netherlands; this could also be

explained by lower site-fidelity of immatures rather than lower survival). Perhaps the timing of migration of immatures represents the genetic breadth of the population, which includes early departures that are cropped by mortality in some years but could allow early breeding in others (when conditions are amenable). Such early arrival by naïve youngsters could provide a mechanism by which the population as a whole could adjust the timing of breeding towards an increasingly early optimal breeding date (Both and Visser 2001). Alternatively, immatures could migrate in shorter flights than adults, refuelling en route at sites that thaw earlier than the actual breeding grounds that later adults fly directly to, or some pale birds could even be very old, experienced individuals that no longer undergo a full moult. It is all too easy to speculate on such topics; it is probably wiser to refrain until stronger datasets exist.

High parasite loads in young birds are not unusual (Borgsteede et al. 1988), and there is not necessarily any direct functional link between parasite loads and extent of moult in either male (Drent et al. 2003) or female (Piersma et al. 2001) bar-tailed godwits. Such analyses in the future will need to explicitly account for age effects.

The logistics of studying trans-hemispheric migrants will always be challenging, but a full understanding of how individuals schedule their migrations demands such large-scale approaches (Marra et al. 1998, Norris et al. 2004, Gunnarsson et al. 2005). Inferences about migrants from stop-over sites in the absence of information from the initial fuelling sites can lead to dubious conclusions. While 'risky deserters' may exist in migratory bird populations, there is as yet no evidence for their existence in bar-tailed godwits. And if the pale birds recorded on migration are indeed young birds, then conclusions based on the assumption that all birds on migration are adult (implicit in Piersma and Jukema 1993) may need revisiting.

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Appendix F1

ANNUAL SURVIVAL OF RED KNOTS (*CALIDRIS CANUTUS RUFA*) USING THE SAN ANTONIO OESTE STOPOVER SITE IS REDUCED BY DOMINO EFFECTS INVOLVING LATE ARRIVAL AND FOOD DEPLETION IN DELAWARE BAY

REDUCCION DE LA SUPERVIVENCIA ANUAL DEL PLAYERO ROJIZO (*CALIDRIS CANUTUS RUFA*) EN SU ESCALA MIGRATORIA DE SAN ANTONIO OESTE, ARGENTINA, POR EFECTOS DOMINO DE LLEGADA TARDÍA Y DEPRESIÓN DEL RECURSO TRÓFICO EN DELAWARE BAY, USA

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Short Title: DOMINO EFFECTS AT STOPOVER SITES IN KNOTS

ABSTRACT

Ecological conditions in breeding and non-breeding areas of migrant birds have been linked to their annual survival and production of young, but the role of stopover sites is underappreciated. Through banding studies and censuses along the flyway from Tierra del Fuego (TDF) to the Canadian Arctic, the drastic decline in 2000-2001 of Red Knots (*Calidris canutus rufa*) population summering in southern South America in the northern winter was shown to be related to the overharvesting of Horseshoe Crabs (*Limulus polyphemus*) in Delaware Bay, USA, their last stopover site before reaching their breeding grounds, and to the late arrival of the birds at this site. In San Antonio Oeste (SAO), Argentina, where 25 to 50% of the TDF knot population congregates every northward migration season, annual survival of the cohort of experienced birds banded in March 1998 was impacted a year later than the general decline. Knots marked at SAO earlier in March arrived in Delaware Bay on average before those marked 15 days later. Additionally, early migrating knots with active body moult in SAO exhibited a higher return rate in the following years than late and non-moulting birds. Since the decline, birds arriving late in Delaware Bay have been at increased risk of not being able to refuel properly or on time because food is no longer superabundant at that stopover. These domino effects indicate that there are fitness consequences to individual migration strategies adopted by birds at austral summering and stopover sites, and can be amplified by compressed timing in Delaware Bay when food is depleted at the final stopover.

Keywords: migration, domino effects, population decline, Red Knots, stopover ecology

RESUMEN

Si bien se ha relacionado la condición de las áreas de estadía no reproductiva y reproductiva de las aves migratorias con su supervivencia y producción de jóvenes, aún el papel de los sitios de escala como limitante del tamaño poblacional es escaso. Mediante estudios de anillado y censos a lo largo de la ruta de vuelo desde Tierra del Fuego (TDF) hasta el Ártico de Canadá, hemos relacionado la drástica declinación de la población de Playero Rojizo (*Calidris canutus rufa*) ocurrida durante 2000-2001 con la sobrepesca del Cangrejo Herradura (*Limulus polyphemus*) en su última escala en la migración hacia el norte, la Bahía Delaware, USA, y la llegada tardía de las aves. En San Antonio Oeste (SAO), Argentina, donde se congrega del 25 al 50% de la población de TDF durante la migración al norte, el seguimiento de aves experimentadas de la cohorte anillada en marzo de 1998 permitió estimar que su supervivencia fue afectada un año más tarde que la declinación general. Las aves marcadas más temprano en marzo, llegaron antes a la Bahía Delaware en promedio que las marcadas 15 días después. Además las aves tempranas con presencia de muda activa de plumaje corporal mostraron una tasa de retorno significativamente mayor en años posteriores que las aves sin muda activa. Desde la declinación, las aves tardías incrementaron el riesgo de no acumular reservas apropiadamente o a tiempo, debido a que el recurso trófico dejó de ser superabundante en Delaware Bay. Estos efectos dominó indican que existen consecuencias en el fitness de estrategias de migración individuales originadas en las áreas de estadía austral y sitios de escala migratoria y pueden ser amplificadas por la compresión de su cronología en Delaware Bay, cuando el recurso trófico es deprimido en la escala final.

Palabras clave: migración, efecto dominó, *Calidris canutus*, declinación poblacional, ecología de escala migratoria.

The role of the condition of birds in non-breeding staging areas, breeding sites, or both in limiting long-term or year-to-year population sizes in migrants has been the subject of many studies in different bird taxa, especially in shorebirds (e.g. Evans et al. 1984, Evans and Pienkowski 1984, Pienkowski and Evans 1985, Newton 2004). In some species, habitats occupied in wintering areas (also known as "austral summering areas" in the southern hemisphere) and migration flyways, and their associated food supplies, can influence the body condition, migration dates and subsequent breeding success of migrants (Marra et al. 1998, Drent et al. 2003). Similarly, the numbers of young produced in one region could, through density-dependent processes, affect subsequent overall mortality in another region (e.g. Goss-Custard et al. 1995). Thus, events in breeding, migration and "wintering areas" are interdependent in their effects on bird numbers (reviewed in Newton 2004). However, less is known about long distance migrants, but we hypothesize that population size might be limited by intra- or interspecific competition at key stopover sites if they face low food availability, higher predation risk, and increased disturbance or poor quality roosting places.

One of the best known shorebird species is the Red Knot *Calidris canutus* (Scolopacidae) which has a circumpolar breeding distribution in the northern hemisphere comprised of six discrete populations that are recognized as subspecies on the basis of differences in morphometrics and plumage (Piersma et al. 2005). Of these subspecies, *C. c. rufa* travels the longest migration of about 16 000 km twice a year between their breeding grounds in the Arctic and their summering (= northern wintering) sites in Tierra del Fuego and Patagonian Argentina (Morrison and Harrington 1992, Piersma and Davidson 1992, Harrington 2001, Tomkovich 2001). During their journeys, they congregate at scarce wetlands extensive

enough to support large flocks of birds. Such wetlands occur thousands of kilometres apart in the Atlantic flyway, like San Antonio Oeste at Río Negro Province in Argentina, Rio Grande do Sul and Maranhão in Brazil, and Delaware Bay in USA (Fig. 1).

The majority of adults in the Tierra del Fuego population make a stopover in Delaware Bay every May, and mix with separate populations that spend the non-breeding season in Maranhão in northern Brazil and Florida, respectively (Baker et al. 2005, Atkinson et al. 2005). Until 2000 Red Knots and other migrant shorebirds fed almost exclusively on a superabundant supply of eggs of spawning Horseshoe Crabs (*Limulus polyphemus*) (Castro and Myers 1993, Tsipoura and Burger 1999), enabling them to store nutrients quickly and almost double their body mass for the final leg of migration to the Arctic breeding grounds. Extra stores are carried not only so that the birds can survive poor weather or lack of food after arrival, which can cause high levels of mortality (Boyd 1992, Morrison 1975, 2006), but also to enable the birds to undergo a series of physiological transformations from a state suitable for migration to one for breeding (Morrison et al. 2005). Beginning in 1990 and peaking in 1995/1996, there was a dramatic increase in commercial fishing to provide bait for eel and conch fisheries (Walls et al. 2002), which resulted in a six-fold decline in the numbers of horseshoe crabs caught in survey trawls in Delaware Bay (S. Michels, unpublished data, cited in Andres 2003). Since 2000, crab eggs are no longer superabundant in Delaware Bay.

Several lines of evidence suggest linkages between events at stopover sites in San Antonio Oeste and Delaware Bay and the breeding grounds. First, we provide the following review of previous research. Studies that captured and colour-banded northbound Red Knots ($N = 9\,851$) in Delaware Bay during each May from 1997 to 2002 showed that fewer Red Knots reached threshold departure masses of 180–200 g (Baker et al. 2004). As the abundance of crab eggs declined from 1997/1998 to 2001/2002 the predicted proportion of well-conditioned Knots (200 g or greater) in Delaware Bay near departure time on 28 May

decreased significantly by 70% (Baker et al. 2004). In the 2-3 days before the peak departure for the Arctic, mean body masses declined significantly from 183 g in 1997 to 162 g in 2002. Return rates of northbound adults caught in Delaware Bay also showed that Red Knots known to survive to a later year by being recaptured or resighted throughout the flyway were significantly heavier at initial capture than birds never seen again (Baker et al. 2004). Second, emerging evidence suggests that northbound birds from Tierra del Fuego may be arriving in Delaware Bay later in the spring than in earlier years, and that late birds are increasingly delaying departure for the breeding grounds (Baker et al. 2004). Late arrival on the breeding grounds often confers a strong reproductive disadvantage; late arrivals are predicted to have a lower probability of surviving and producing offspring if they attempt to breed. Resights of color-banded birds showed that arrival time of the Tierra del Fuego birds in Delaware Bay relative to the more northerly summering birds in Florida and Maranhão has differed over time, although in most years the former on average arrive later in Delaware Bay than birds from northern Brazil or Florida. In 2000 and 2001 the highest proportion of Tierra del Fuego birds occurred at or after the peak aerial count, meaning that Florida and Maranhão birds may have departed earlier, or there were more late arrivals from Tierra del Fuego, or both (Baker et al. 2004).

Fitness consequences of reduced adult survival and recruitment are consistent with the alarming decline in population size of Red Knots in Tierra del Fuego from 51 000 to 27 000 in 2000–2002 (Morrison et al. 2004, González et al. 2004); such a rapid decline may seriously threaten the viability of the *rufa* subspecies. Annual survival of adult birds at Delaware Bay arriving from Tierra del Fuego and northern South America decreased by 37% between May 2000 and May 2001. In addition, annual survival estimated from captured and marked birds (N = 3 644) from 1995 to 2003 in San Antonio Oeste and in Tierra del Fuego declined significantly from an average of 85% in the three migration years from 1994/1995 to

1997/1998 to 56% in the ensuing 3-year period to 2000/2001. Recruitment as measured by the proportion of second-year birds comprised 19% of annual catches of ca. 500–600 Knots in TDF in 1995, 16% in 2000 and 10% in 2001 (Baker et al. 2004).

In this paper we examine the role of two key stopover sites in the flyway of *C. c. rufa* and assess the possible flow-on or domino effects (Piersma 1987) that can accrue after the birds leave the austral summering sites in Tierra del Fuego and migrate northwards en route to the breeding grounds. These sites are (1) San Antonio Oeste (SAO) in Argentina, the main stopover site on the coast of Patagonia for Red Knots where the most adults undergo body moult into breeding plumage before undertaking long flights northwards, and (2) Delaware Bay in USA, the critical final spring refuelling site where they must accumulate large stores of nutrients before departing for the breeding grounds in the Arctic. SAO is located at 40° 45' S, 64° 55' W in the Río Negro Province of Argentina, and hosts 25% to 50 % of the total population from Tierra del Fuego during northward migration from late January to April (González et al. 2004). Here the primary food for Red Knots during the day (Sitters et al. 2001) are the mussels *Brachidontes rodriguezi* that they find on a rocky intertidal habitat known as "restinga" (González et al. 1996). Specifically, our objectives were to investigate whether habitat conditions and the timing of migration at a stopover site in the southern end of the flyway might be exacerbated by the declining food supplies in Delaware Bay, and the flow-on fitness consequences of decreased refuelling rates on late arriving Red Knots at this penultimate staging site.

METHODS

We analyzed arrival time of Red Knots in Delaware Bay in relation to their banding time in San Antonio Oeste (SAO). As part of an international research project on Red Knot populations throughout the flyway, a banding expedition to SAO lead by the Fundación

Inalafquen and Royal Ontario Museum was organized in 1998 (Baker et al. 1999, 2001, Piersma et al. 2005), during which knots were caught with cannon nets in five catches on 5, 13, 16, 20 and 28 March during the peak of migration ($n = 1000$, Table 1). Two age classes (juvenile and adult), body mass, body moult activity on the breast, and percentage of breeding plumage were recorded on captured birds. In addition to a metal numbered band most knots ($n = 780$) were banded with standard combinations of two colour bands and a coloured flag to identify 'time cohorts' (orange flag right tibia, blue over red band on left tarsus, for 5 & 13 March; orange flag right tibia, red band right tarsus, blue band left tarsus for 16 & 20 March; red band over orange flag on right tarsus, blue band on left tarsus for 28 March), while 126 birds were marked with individual schemes of orange flag and four colour bands.

In May 1998 we compared the return rates in Delaware Bay of birds previously colour-banded at San Antonio Oeste during the first half (early cohort) and the second half (late cohort) of March 1998 (see below). We regularly carried out scans of the flocks of Red Knots at different sites on the shores of Delaware Bay in New Jersey and Delaware and recorded the numbers of banded individuals relative to the numbers of unbanded birds. To avoid any biases introduced by the visual attraction of colour-banded birds, we made sure that all observed birds received scores as we examined as many different parts of feeding flocks as possible. We analyzed the data for each 'time cohort' using binary logistic regressions with dependent variable (1 = banded vs 0 = non-banded) on independent categorical variables (shore, observer) and day as a continuous variable.

In subsequent years from 1999 to 2003, resighting efforts of individually colour-banded adults at San Antonio Oeste were used to estimate annual apparent survival of the "1998 year cohort". The data conformed to Cormack/Jolly/Seber (CJS) assumptions according to the program Ucare v.1.3 (Choquet et al. 2001). Survival analyses were run in

Mark 3.2 (White and Burnham 1999) using CJS models by cohort. Model selection was based on the Akaike information criterion (AIC). Binary logistic regression with logit link and sigma-restricted parameterization (Statsoft Inc, STATISTICA 6) was used to analyze the return rate in the six following years (1 = seen again, 0 = not seen again) from recapture and resighting of banded birds ($n = 228$) related to the presence of active body moult, percentage of breeding plumage (categorical independent variables), body mass and day of initial capture (continuous independent variables).

RESULTS

SAO 1998 cohort arrival times in Delaware Bay

Return rates in Delaware Bay estimated from resightings or recaptures of both early and late cohorts of Red Knots banded in SAO in 1998 increased through the season (Fig. 2), either because birds from the unbanded Maranhao or Florida summering populations were leaving or more banded knots from SAO were present at the end of the season, or both. Despite the similar numbers of birds banded at SAO in both time cohorts, the ‘late cohort’ had a lower return rate than the earlier banded cohort, indicating that the late cohort was on average arriving later in Delaware Bay, that at least some birds had not reached the Bay by the end of May, or that a higher proportion of the late cohort used sites other than Delaware Bay, or a combination of these factors (Fig. 2). Red Knots from SAO were represented more highly on the shores of Delaware than New Jersey (Delaware relative to New Jersey regression coefficient $\exists = 0.36$ SE 0.10, $P < 0.000$, Day $\exists = 0.064$ SE 0.02, $P < 0.001$, n checked birds 19 884), but the same trend in true detection rates was apparent in both states.

Apparent survival (Φ) of "1998 year cohort"

Because we have shown previously (Baker et al. 2004) that a two time period model (1998/99 to 2000/01) was the best-fitting model for the TDF population, we compared this model for the 1998 SAO cohort with another that allowed a one year lag in survival effects between the periods 1998-2001 and 2001-2002. We also computed standard time dependent and constant survival and resighting probability models to check for goodness of fit. The model with the one year lag in the decline of annual survival and with a constant resighting probability was the best model (Table 2A). Annual survival of the SAO 1998 cohort was estimated to drop from 80.3% between 1998 and 2001 to 65.9% between 2001 and 2002, one year after the general population passing through Delaware Bay had suffered a similar drop in annual survival (Table 2B). Although the 95% CI of the estimates of annual survival in the SAO 1998 cohort model before and after 2001 partly overlap because of the relatively small size of the colour-banded 1998 year cohort ($n = 126$), there is no indication of a decline in annual survival before 2001.

Variables explaining return rates

The best logistic regression model for return rates of SAO 1998 knots according to the AIC was the two effects of day of initial capture and presence of body moult they were undergoing ($P < 0.000$). The probability for a 1998 year cohort bird to be seen in the following years was negatively correlated ($\Xi = -0.090$, SE 0.025) with day of initial capture ($P < 0.000$), indicating that birds captured late in March were less likely to be seen again than those captured in the early half of the month. Red Knots in body moult had a higher probability of being seen in future years than birds that were not moulting ($\Xi = 4.43$, SE

0.277, $P < 0.000$), thereby relating the condition of the bird to an indirect measure of survival. Although percentage of breeding plumage and body mass are indices of body condition and thus we would expect that redder-plumaged and heavier birds exhibit a higher probability of survival, these variables are collinear (positively correlated) with day of initial capture through the season. Thus, a model with percentage of breeding plumage and presence of body moult showed that redder Knots had a lower likelihood of being seen in following years ($\beta = -0.412$, SE 0.16, $P < 0.01$). (n seen again = 57, n not seen again = 171). A model including only body mass and presence of body moult as independent variables was not significant for body mass because late cohort knots were heavier (body mass $\bar{\mu} = 128$ g SE 0.94 $n = 122$) than early cohort birds (body mass $\bar{\mu} = 123.7$ g SE 1.0 $n = 106$; one way ANOVA: $F(1, 226) = 13.662$, $P < 0.0003$). However, moulting birds were heavier on average ($\bar{\mu} = 127.2$ g SE 0.77 $n = 191$) than non-moulting birds ($\bar{\mu} = 122.5$ g SE 1.7 $n = 37$; one way ANOVA $F(1, 226) = 6.2604$, $P < 0.0130$). These results suggest that later captured Red Knots stayed later at the SAO stopover site to gain mass and complete the acquisition of redder breeding plumage than did earlier captured Red Knots.

DISCUSSION

Domino effects at stopover sites

Baker et al. (2004) argued that the food supplies at Delaware Bay, the last stopover site before the flight to the High Arctic breeding grounds, had limited the Patagonian wintering population of Red Knots *C. c. rufa*. The new analyses presented here further suggest that different segments of the population may be differently affected by staging site problems; in particular the late migration strategy adopted by some individuals is now associated with

greater risks of mortality than in the past. Long-distance migrants from the Red Knot population in southern South America are more restricted in their timing of migration into Delaware Bay than are northern populations. On average they arrive later in Delaware Bay than do northerly wintering Knots as shown here for the migration season of 1998, when conditions in Delaware Bay were good (see also Baker et al 2004). In the years of severe food limitation that occurred in Delaware Bay after 2000, we predicted that Red Knots would suffer potentially drastic consequences on survival and recruitment. Prior to 2000, knots refuelling in Delaware Bay departed *en masse* for the Arctic in the period May 28-30, but as the supply of Horseshoe Crab eggs has been depleted in subsequent years more birds have been delaying their departure by 7-14 days (Baker et al. 2004, pers. obs). A domino effect between the two stopover sites in SAO and Delaware Bay has thus appeared and been exacerbated mainly by poor refuelling conditions in the final stopover site. Drent et al. (2003:274) emphasized the “critical role of the final take-off site” of pink-footed geese (*Anser brachyrhynchus*) as suggested by a positive relationship between en route body condition and subsequent breeding success.

Fitness consequences of individual migration strategies

The migration schedules of the austral summering population in TDF potentially could have fitness consequences, as northbound knots arriving later at their first southern stopover site in SAO on average also arrive later in Delaware Bay and thus have compressed refuelling time and later departure for the breeding grounds. However, arrival timing in SAO could be related to habitat condition in TDF or differences in individual strategies of Red Knots or both, rather than to a limitation from poor quality stopover. This is because day of initial capture at SAO does not necessarily reflect departure date, as some earlier arrivals left

in a few days while others remained to the end of the season in April, and thus late arrivals might depart together with some early birds (González et al. unpublished). The rate of storage of nutrients at the SAO stopover site is around 0.50 g/day (Piersma et al. 2005), which is very low compared with the average 4.6 g/day that Knots achieve at Delaware Bay, the highest recorded among the world's subspecies and staging sites (Piersma et al. 2005). Thus, birds departing from SAO in early March are likely to have lower body mass than those that remain until the middle of April. Birds that are minimizing the cost of energy transport are expected to stop at all useful sites along the route to carry the smallest possible fuel loads (Gudmundsson et al. 1991, Alerstam and Hedenström 1998); while our results suggest that early cohort knots in SAO are following this general strategy, late cohort knots in contrast seems to adjust to time-selected migration, where birds should accrue substantial fuel loads to minimize migration time to Delaware Bay.

These differences in individual migratory strategies indicate why body mass could not explain the likelihood of return rates at SAO, whereas at Delaware Bay it is a significant explanatory variable. While Red Knots at Delaware Bay appear more synchronized in migration timing for refuelling and departures because the Arctic breeding grounds are only available during a short period in the year, at SAO Red Knots have a broader window of time where individual strategies can be employed.

Apparent survival estimates for the "SAO 1998 year cohort" indicate that birds in this cohort did not suffer the decline that the average adult passage population in Delaware Bay did between 2000-2001, but instead had a lag until one year later when they had a significant drop in survival. We interpret this to mean that early migrating and experienced birds in the SAO 1998 cohort (whose survivors would have been older than the general population in 2000-2001) were able to avoid mortality better than the general population in TDF which includes younger adult birds, and only were affected late in the population decline.

Role of stopover sites in population limitation

The importance of the last stopover as a refuelling site before departing for the breeding grounds and of late arrival has been shown to have fitness consequences in birds (Alerstam and Hedenström 1998, Madsen 2001, Drent et al. 2003, Morrison 2006). Morrison (2006) found that *C. c. islandica* Red Knots departing from their last stopover in Iceland in better than average condition had a higher probability of being seen again following a series of years with difficult weather conditions in the Arctic. This shows that being in superior condition was linked with higher survival; in this case conditions were normal at the final stopover area but the birds encountered unusually difficult conditions on the breeding grounds. The situation in Delaware Bay again demonstrates the link between condition and survival; birds were unable to reach suitable departure condition because of a reduction in the available food supplies resulting in reduced survival. In the Wadden Sea, reduction in food stocks for shorebirds due to overharvesting in the cockle fishery has resulted in a concomitant reduction in bird numbers, providing another example of how human activities can severely impact population sizes in migratory shorebirds (Stroud et al. *in press*). Under conditions of food depletion in Delaware Bay there can be a domino effect from the timing of refuelling in southern stopover sites in South America like SAO, as birds arriving late in the USA will then be delayed further in their departure or be underfuelled, resulting in overall lower breeding success and increased mortality in the population. This emphasizes the migratory connectivity of populations of knots at these and other sites as well as the role of individual migration strategies. An integrated flyway-wide approach to management and recovery is required for effective conservation of this rapidly declining population. In the absence of effective management at sites throughout the flyway we can expect the worldwide decline in

shorebird numbers to continue, and face the grim prospect of extinction of populations or species at an accelerating rate.

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Table 1.

Details of Red Knots catches made at San Antonio Oeste in March, 1998. Retraps indicates knots banded previously in this or another expeditions. Analyses were based only on the 906 colour banded birds.

Date	<i>n</i> Juvenile Knots	<i>n</i> Retraps	<i>n</i> Knots with standard combination ¹	<i>n</i> Knots with individual combination	Total colour marked	Total Catch
5-Mar-98	5	12	270	33	303	321
13-Mar-98	6	5	79	39	118	124
16-Mar-98	5	24	241	7	248	280
20-Mar-98	5	23	137	17	154	178
28-Mar-98	7	10	53	30	83	97
TOTALS	28	74	780	126	906	1000

Table 2

Apparent survival of the San Antonio Oeste 1998 year cohort from Cormack/Jolly/Seber capture-recapture analysis: (A) model selection and (B) real function parameters of the best-fitting model for individually colour-banded Red Knots. Φ = apparent survival, p = probability of recapture/resighting, $(.)$ = constant model, (t) = time dependent model, $t1$ = 1998-2001, $t2$ = 2001-2002, $t3$ = 1998-2000, $t4$ = 2000-2002. Model selection based on correction for over-dispersion with $\hat{c} = 1.509$.

Table 2A

Model	AICc	Delta AICc	AICc Weights	Model Likelihood	Number of Parameters	Deviance
$\Phi(t1,t2) p(.)$	442.3	0	0.2943	1	3	24.14
$\Phi(t3,t4) p(.)$	443.4	1.04	0.1747	0.59	3	25.18
$\Phi(.) p(t)$	443.6	1.30	0.1535	0.52	6	19.21
$\Phi(.) p(.)$	444.4	2.06	0.1049	0.36	2	28.25
$\Phi(t) p(.)$	444.4	2.11	0.1026	0.35	5	22.18
$\Phi(t1,t2) p(t)$	444.6	2.28	0.0943	0.32	7	18.08
$\Phi(t3,t4) p(t)$	445.4	3.09	0.0629	0.21	7	18.89
$\Phi(t) p(t)$	448.6	6.27	0.0128	0.04	9	17.81

Table 2B.

Model	Parameter	Period	Estimate	Standard Error	Lower 95%	Upper 95%
					CI	CI
$\Phi(t1, t2) p(.)$	$\varphi 1$	1998-2001	0.803	0.037	0.721	0.866
	$\varphi 2$	2001-2002	0.659	0.112	0.420	0.838
	p	1998-2002	0.508	0.045	0.421	0.595

Figure Captions

Figure 1.

Red Knots flyway depicted on the basis of resightings of Red Knots colour-banded in Argentina from 1995 onwards. Black dots indicate resighting places during southern migration and white dots during northward migration. Key stopover study sites are shown. (González et al. unpublished).

Figure 2.

Return Rates in Delaware Bay of "early" vs "late" cohorts of banded Red Knots at San Antonio Oeste. Time dependent model of the Return Rate of colour-banded knots during the first half of March 1998 ("early cohort": filled symbols and solid line, $n = 421$, $\beta = 0.049$ SE 0.024, $P < 0.043$) compared with those banded in the second half of March 1998 ("late cohort": unfilled symbols and dashed line, $n = 402$, $\beta = 0.092$ SE 0.034, $P < 0.007$). Number of checked birds 19 884, n observers = 3. To keep resighting probabilities approximately equal for the two time cohorts the sample from 28 March was not included in the analysis.

Figure 1

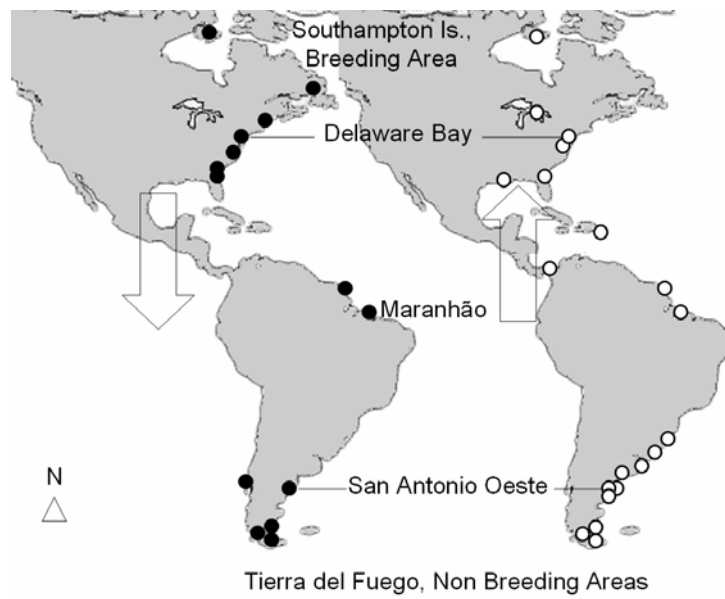
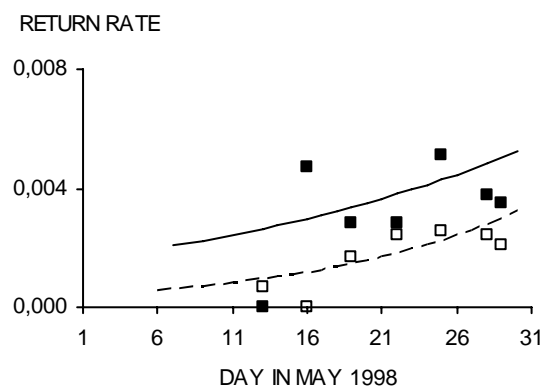


Figure 2



Las aves migratorias.

Las preguntas de la ida y vuelta de los chorlos y playeros entre los Hemisferios Sur y Norte. Su estadía temporaria en el Área Natural Protegida “Bahía de San Antonio” y su reconocimiento como “Sitio Internacional”. Estudio de su potencial ecoturístico. La declinación.

Por: **Patricia González**

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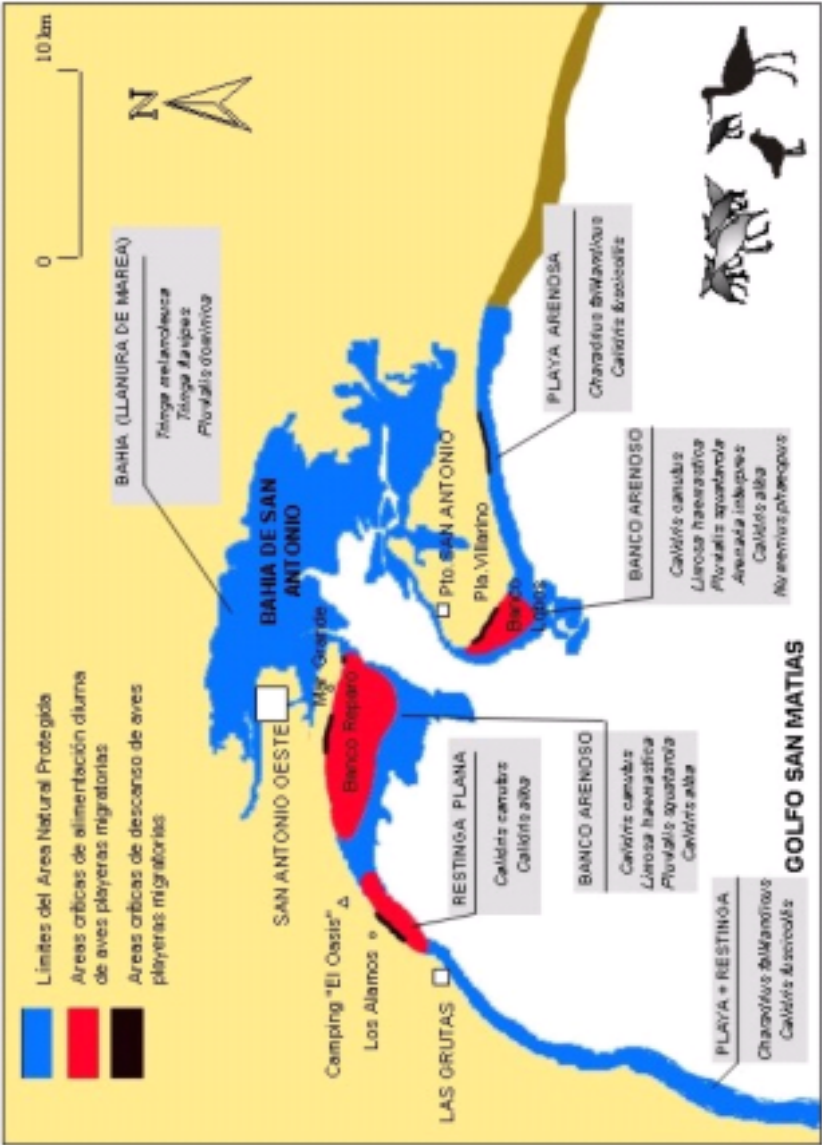
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Agradecimientos

Nota sobre la autora.

Mapa 1.

Area Natural Protegida “Bahía de San Antonio” y distribución de las especies de Aves Playeras típicas de cada unidad ambiental litoral comprendida hasta la línea de bajamar. *Charadrius falklandicus* y *Calidris fuscicollis* sólo se mencionan en los ambientes en los cuales no se han registrado otras especies típicas, pero son comunes en todos las unidades.



Las aves migratorias. Las preguntas de la ida y vuelta de los chorlos y playeros entre los Hemisferios Sur y Norte. Su estadía temporaria en el Área Natural Protegida "Bahía de San Antonio" y su reconocimiento como "Sitio Internacional". Estudio de su potencial ecoturístico. La declinación.

Por: **Patricia González**

El título de este estudio puede parecer extenso, sin embargo, resultó el adecuado para enunciar con exactitud un tema que, al interior del equipo de investigación Las Mesetas Patagónicas, se presentaba como relevante, dado que es de aquellos que le otorgan una identidad distintiva a «Bahía de San Antonio» . Este es el criterio, devenido en meta, en la selección de los micro espacios regionales elegidos para investigarlos pluridisciplinariamente en éste y en los otros libros de esta serie editorial.

1. Las aves playeras migratorias

"- Dicen que el clima está cambiando..."

-¡Son miles de aves!... seguro que algo va a ocurrir..."

Estas son algunas de las muchas frases de los turistas oídas en el Balneario Las Grutas, Pcia. de Río Negro, ante el encuentro con bandadas de miles de aves playeras migratorias.

Hace apenas diez años atrás sólo unas pocas personas, en su mayoría pescadores deportivos y artesanales de San Antonio Oeste, habían experimentado estos encuentros con los llamados «teritos de mar», y conocían de su ocurrencia estacional y congregación en unos pocos sitios costeros como las playas de Los Álamos, Mar Grande y Punta Villarino (Mapa 1). Aún no sabían mucho más de ellas. En aquellos tiempos no existían numerosos accesos al mar ni estaban difundidos los vehículos todo terreno como en la actualidad, mientras la presencia humana masiva se limitaba a las playas del Balneario Las Grutas sólo durante los meses de vacaciones estivales.

¿De qué aves se trata? ¿de dónde vienen y adónde se dirigen?

Lo cierto es que sólo con el comienzo de la utilización de técnicas de captura y anillado de aves silvestres apenas 100 años atrás (Preuss 2001) la humanidad comenzó a descubrir los desplazamientos de numerosas especies de Aves. Entre ellas los «teros» y «teritos de mar» también llamados chorlos (Flia. Charadriidae) y playeros (Flia. Scolopacidae) que en cada temporada hacen escala en el rincón noroeste del Golfo San Matías sobre las costas de la Bahía de San Antonio y aledañas sobre este golfo (González 1991, González 1996 a); foto 1 (de Guy Morrison) ver en sección fotos color del libro.

Así descubrimos que algunas de estas especies son migratorias de larga distancia. Nidifican en áreas tan lejanas como el Ártico de Norte América durante el verano boreal, migrando hasta sus sitios de estadía austral en el Hemisferio sur –como Tierra del Fuego- para permanecer desde la primavera al verano. Se las conoce como «migrantes neárticas».

Otras se reproducen en el sur de la Patagonia durante la primavera y verano austral, para luego migrar al norte hasta sitios como Bahía de San Antonio o llegando incluso a Brasil donde permanecerán durante el invierno. Se las conoce como «migrantes australes» o de la «corriente patagónica».

¿Por qué el Área Natural Protegida Bahía de San Antonio es importante para las aves migratorias?

Por sus características geológicas y geomorfológicas (Angulo et al. 1981, González Díaz y Malagnino 1984) el área ofrece grandes extensiones intermareales que ofrecen estacionalmente una fuente de alimento en cantidad y calidad suficiente para que las aves playeras migratorias puedan almacenar reservas suficientes para llegar a su próxima escala. Los chorlos y playeros se alimentan de invertebrados como mejillines, poliquetos y pequeños crustáceos que capturan cuando la marea descubre las áreas intermareales.

No se trata de hechos aislados, los humedales de la región son importantes pues brindan numerosos beneficios a las comunidades humanas en términos de metabolización de efluentes orgánicos y producción de nutrientes base para las cadenas y tramas alimentarias; son sitios de cría de numerosos organismos marinos así como de aves marinas y costeras; además sus sedimentos retienen tóxicos tales como metales pesados (Canevari et al. 1999).

20 especies de chorlos y playeros han sido registradas en el Área (González 1991, González 1999) (Tabla 1 al final del estudio) siendo ésta de especial importancia para el Playero Rojizo (*Calidris canutus rufa*) por el número de ejemplares que realiza escala aquí.

“Cada año entre el 25 al 50 % de la población total de 30.000 ej. de Playero Rojizo cuya estadía austral transcurre en Tierra del Fuego” (González et al. 2003), “...utiliza el Área Natural Protegida Bahía de San Antonio como primer escala principal en la migración al norte que transcurre entre Febrero y Abril” (González et al. 2004).

Por esta razón ha sido declarada Área Natural Protegida Provincial en 1993 (Ley 2670, Río Negro) y en Agosto del mismo año reconocida en el Continente como “Sitio Internacional” por la Red Hemisférica de Reservas para Aves Playeras, mapa 1 ver en pagina 322 (cfr. trabajo sobre ANP de D.Paz Barreto en este libro).

Descubriendo la ruta migratoria del Playero Rojizo

De las seis subespecies de Playero Rojizo reconocidas en el mundo, la subespecie «*rufa*» es la que migra mayores distancias recorriendo cada año unos 16.000 km de ida y otro tanto de regreso entre Tierra del Fuego y sus áreas reproductivas en el Este del Ártico Canadiense (Piersma y Davidson 1992, Tomkovich 2001) (Mapa 2 ver al final del estudio en página 346).

Los avistajes de playeros marcados con combinaciones de banderillas y anillos de colores (fotos de Mark Peck y P. González, ver en sección fotos color del libro) durante las campañas organizadas por la Fundación Inalafquen (SAO) y el Royal Ontario Museum de Toronto junto al Consejo Provincial de Ecología y Medio Ambiente de Río Negro en los años 1997, 1998 y 2003 en las playas de Los Álamos y Península Villarino, muestran que su ruta migratoria es predominantemente atlántica como se observa en el Mapa 3, página 346. Pero las aves se concentran en determinados sitios críticos separados miles de kilómetros entre sí: se trata de escasos humedales productivos que las aves unen en sus migraciones.

2. La migración de larga distancia

¿Por qué migrar?

¿Y por qué no? ...después de todo las aves tienen alas para volar y entonces tal vez la pregunta debería formularse al revés: ¿por qué existen aves que no migran? (Fretwell 1980).

Lo cierto es que a lo largo del proceso evolutivo la Migración de Larga Distancia se desarrolló independientemente no sólo en las aves sino también en muchos organismos como los cetáceos, reptiles, peces e insectos entre otros. Por otra parte no sólo han ocurrido procesos de evolución positiva hacia la migración, también han ocurrido en el sentido contrario; en los últimos miles de años luego de las glaciaciones, ha habido especies con patrones migratorios que se convirtieron a la residencia (Alerstam et al. 2003). Esta gran flexibilidad evolutiva es sorprendente si se piensa que la migración es una propiedad compleja que requiere instrucciones genéticas sobre el calendario y la duración del movimiento en el programa temporal/circanual del organismo. Del mismo modo para las adaptaciones fisiológicas para el depósito de sustancias de reserva (grasa y proteínas) que serán el combustible para llegar al siguiente lugar de escala en el viaje y el metabolismo que lo acompañe; las adaptaciones del comportamiento para responder a condiciones ambientales variables (viento, meteorológicas), y asimismo para el control de la orientación y navegación. (Berthold 2001).

Se piensa que en general la migración es una adaptación primaria para la explotación de picos estacionales de abundancia de recursos evitando paralelamente las épocas del año en que estos están deprimidos (Alerstam et al. 2003). En otras palabras se realiza una utilización temporal de hábitats de manera de aprovecharlos en el tiempo del año en que estos ofrecen mayores beneficios a las especies. Por ejemplo en el momento en que la disponibilidad de las presas que son alimento para los adultos es mayor, o bien

cuando el ambiente ofrece la mejor calidad de alimento para los juveniles, ya que no necesariamente demandan el mismo tipo de presas que los adultos. Pero esto también debe ajustarse a otros factores: así la muda anual de las plumas de vuelo de las alas no sólo requiere un sitio con buena oferta de alimento sino también una baja presencia de predadores (halcones, búhos, zorros) porque las aves tienen disminuida su maniobrabilidad de vuelo mientras las plumas crecen.

¿Cómo organizar el viaje?

A manera de piezas de un rompecabezas, además de la estacionalidad ya mencionada, existen numerosos factores ecológicos y evolutivos que estructuran la migración. En otras palabras, la migración ha debido «co-evolucionar» concertadamente con otros elementos de la historia natural de los playeros como los siguientes (ver revisión en Alerstam et al. 2003):

-- El costo del transporte

Las aves necesitan un tiempo determinado para reproducirse así como para mudar sus plumas de vuelo dejando en consecuencia un tiempo limitado para otras actividades, incluida la migración, tanto más si se trata de larga distancia. Transportarse entre escalas migratorias tiene un costo en energía y en tiempo. Así el tiempo de migración se reduce cuando la velocidad de transporte (vuelo) es mayor, la tasa de acumulación de reservas (grasa y proteínas) durante las escalas migratorias es mayor, y el costo de locomoción es menor (Hedenström y Alerstam 1997). Por lo tanto se espera que las aves migratorias de larga distancia exhiban estas adaptaciones (Weber y Hedenström 2001).

-- La presencia de barreras geográficas como océanos y montañas.

En respuesta a su presencia las especies o poblaciones de aves podrían utilizar diferentes estrategias como rodearlas, sobrevolarlas, o incluso podrían decidir no atravesarlas.

-- El tamaño del ave.

Las más pequeñas son capaces de acumular mayores reservas relativas a su tamaño para la migración que las aves grandes y por lo tanto cubrir mayores distancias sin bajar a tierra (Hedenström y Alerstam 1992), aunque las aves grandes lo compensan con alas relativamente más largas (Rayner 1988). Además la duración de los eventos reproductivos y de la muda de plumaje incrementa con el tamaño de las aves, dejando menos tiempo para completar la migración de retorno en el contexto del presupuesto de tiempo anual (Hedenström y Alerstam 1998).

-- Competencia

La competencia por alimento o espacio con aves de la misma o de diferentes especies, residentes o migratorias, que comparten el hábitat en el mismo momento del año (ver revisión en Hedenström y Alerstam 1998).

Por ej. hay especies de aves playeras en las cuales los individuos «dominantes»

(machos y/o adultos) se «apropian» de rutas de migración más cortas y cercanas a los sitios de reproducción en el Ártico mientras los individuos «subordinados» (hembras y/o juveniles) se ven desplazados a migrar a sitios alejados hacia el sur.

-- Parásitos e inmunología.

La elección de ambientes libres de la presencia de patógenos o parásitos ha sido sugerida como una razón importante para la migración de larga distancia en aves playeras (Piersma 1997) porque los costos ecológicos asociados a las aves huéspedes de parásitos son altos. Así la selección natural favorecería comportamientos migratorios que eviten la permanencia en ambientes con alta carga parasitaria tal como los trópicos y ecosistemas interiores. Esto es posible en sistemas de migración como el del Playero Rojizo que alterna la tundra ártica para la reproducción con ambientes costeros marinos el resto del año.

-- Predadores

La presencia de predadores en determinados sitios y momentos del año son un factor de presión para que los playeros modifiquen su ruta o cronograma de migración (Lank et al. 2003).

-- Mecanismos fisiológicos y comportamiento

Indudablemente las aves playeras requieren la capacidad de disponer de mecanismos fisiológicos que les permitan orientarse y enfrentar los desafíos de trasladarse largas distancias. Por otra parte las respuestas del comportamiento migratorio pueden ser heredadas (genéticas) y también aprendidas.

El beneficio para una especie que logra acomodar las piezas del rompecabezas de la migración se manifiesta en el aumento de su supervivencia anual y producción de jóvenes.

La subespecie *rufa* de Playero Rojizo pertenece al reducido grupo de migratorias de Larga Distancia

Unen el Continente Americano de extremo a extremo al viajar desde Tierra del Fuego hasta la tundra de los alrededores del Círculo Polar Ártico donde nidifica. No sólo sus áreas reproductivas se encuentran a mayores latitudes que las de muchas otras especies de aves playeras que prefieren los pastizales y bosques de la taiga del Hemisferio Norte, sino que además llega en su migración al Hemisferio Austral, mucho más al sur que esas mismas especies. La Becasa de Mar (*Limosa haemastica*) es otro ejemplo de ave migratoria de larga distancia.

3. El Playero Rojizo

a) La reproducción

¿Por qué reproducirse en el Ártico?

Una de las ventajas del verano en la tundra es la gran oferta estacional de insectos y

arañas que constituyen un excelente alimento tanto para los pichones como para los adultos, pero además se trata de una oferta abundante y predecible acompañada por una baja densidad de parejas de aves playeras por lo cual la competencia por el recurso parecería despreciable (Piersma et al. 1996).

Considerando que el resto del año sólo visitan áreas costeras intermareales donde consumen principalmente bivalvos como almejas, mejillines o mejillones, la tundra ártica implica un dramático cambio a ambientes interiores e ítems alimenticios totalmente diferentes que obligan a los playeros a desarrollar otras técnicas para su captura. Esto implica que los playeros deben disponer tanto de flexibilidad fisiológica como de comportamiento.

La importancia de llegar a tiempo

Sin embargo para poder aprovechar estas ventajas de la tundra ártica, no sólo deben recorrer largas distancias, sino que además deben llegar en el tiempo justo. Los playeros no deben llegar mucho antes que los hielos comiencen a derretirse, para no comprometer su supervivencia pues se enfrentarían a una escasez de alimento e importantes gastos energéticos en termoregulación (mantenimiento de la temperatura corporal). Tampoco deberían llegar demasiado tarde, porque la ventana temporal de explosión de insectos es limitada y los pichones, además de nacer, deben completar su desarrollo durante ese período.

El verano ártico con sus días de luz interminable es corto, peligrosamente corto.

En términos de supervivencia y producción de descendencia la selección natural parece favorecer a los individuos que llegan «temprano», pero ¿es así con todos? Ser un playero rojizo que llega temprano al ártico en un año en que los hielos manifiestan un derretimiento demorado no parece un acontecimiento prometedor. Pero tal vez este playero rojizo está en muy buenas condiciones porque dispone de reservas de grasa y proteínas remanentes luego de su última migración y no sólo eso, además posee un sistema inmune fuerte. De esta manera podrá sobrevivir los primeros tiempos en el ártico hasta que las condiciones ambientales sean más favorables, o incluso podría decidir demorar su llegada al Artico a medida que avanza en la última etapa de su migración (Drent et al 2003, Baker et al. 2004).

Los «mejores machos» intentarán llegar temprano, así podrán disponer de un territorio que defenderán de otros machos hasta la llegada de las hembras. Los despliegues de cortejo incluyen vocalizaciones y vuelos particulares. Todo ocurre muy rápido, en pocos días las parejas están constituidas (Piersma et al. 1996).

Este es el único lugar y momento del año en que los playeros rojizos no muestran su comportamiento gregario de formar grandes bandadas y requieren privacidad.....

La reproducción

Una vez conformadas, las parejas y sus nidos están tan aislados unos de otros, 500m a 2 km o más de distancia entre sus territorios, que los investigadores tienen muchas dificultades para encontrarlas (Larry Niles in litt.).

No es fácil para los humanos trasladarse en grandes parajes sin caminos y llenos de lagunas y corrientes producidas por el derretimiento de los hielos. Además los playeros poseen un plumaje rojizo críptico que los confunde con el medio y el nido es apenas una depresión en terrenos áridos y rocosos de la tundra, razón por la cual es difícil encontrarlos. Como si esto no fuera suficiente, su estrategia ante la presencia de un depredador (como podría serlo un humano) se diferencia del comportamiento de escape utilizado en el resto de la ruta migratoria. La respuesta en el Ártico es permanecer inmóvil sobre el nido para sólo reaccionar escapando ruidosamente en el último momento, cuando el acercamiento es ínfimo, de unos pocos decímetros (Guy Morrison in litt).

Generalmente la puesta consta de 4 huevos que ambos padres incuban por turnos. En unas tres semanas los polluelos nacen y éste es el momento en que la hembra abandona el nido y su progenie. Hasta esta instancia ella ha invertido nutrientes y energía en la formación de los huevos, llegó el momento de recuperarse antes de la migración al sur. Mientras tanto el macho se hará cargo de los pichones hasta que sean capaces de volar.

Los playeros rojizos tienen polluelos «precociales», esto significa que pocas horas luego de nacer son capaces de caminar y buscar su propio alimento. Pero no son capaces de regular su temperatura corporal hasta aproximadamente una semana más tarde, requiriendo periódicamente el resguardo del calor del padre, aun así son capaces de sobrevivir las bajas temperaturas en las cuales pichones de otras especies de aves playeras que nidifican a menores latitudes morirían rápidamente. Pero la «precocialidad» implica que estos pichones crecerán 3 a 4 veces más lentamente que los de otras taxa de aves cuyos padres alimentan a sus polluelos en el nido (Piersma et al. 1996, Van de Kam et al. 2004).

Los juveniles

Luego de unas tres semanas los «juveniles» ¡están listos para volar! Durante este período el padre los protegió con gritos de alarma para que permanezcan inmóviles ante la cercanía de zorros u otros predadores. Pero muy pronto el padre también partirá en su migración al sur, antes aún que los juveniles hayan podido almacenar reservas para el viaje, es el momento en que los jóvenes playeros comienzan a reunirse con otros de la misma edad, no sólo playeros rojizos sino también de otras especies. Estas primeras bandadas migrarán al sur algo más tarde que los adultos y los investigadores piensan que la dirección general del vuelo que emprenderán está impresa en su información genética. Sin embargo disponer sólo de la información genética no alcanza, necesitan aprender y su falta de experiencia los lleva muchas veces a desviarse del rumbo apropiado o a tomar decisiones incorrectas que pueden costarles la vida. Decidir es la clave y su vida estará llena de decisiones. En un año «normal» sólo alrededor de 1 a 2 de los cuatro huevos llega a convertirse en un juvenil que llega a volar, de ellos generalmente no más del 50% llegarán al primer año de vida. (Piersma et al. 1996, V. de Kam et al. 2004).

Sólo unos pocos juveniles llegan en su primera migración hasta Tierra del Fuego, el resto pasará su primer verano austral en el norte de Sudamérica o en sitios distribuidos

a lo largo de la costa atlántica hasta el norte de la Patagonia Argentina. (Baker et al. 2004).

b) ¿Cómo orientarse y llegar a destino?

Estas son preguntas que por muchos años han desvelado a los investigadores. Sabemos que los playeros prefieren partir antes del anochecer, momento ideal porque disponen de múltiples herramientas de orientación simultáneamente como los patrones de polarización de la luz en el cielo y la posición del sol poniente y las estrellas. Junto al campo magnético del Planeta y las «marcas» de referencia terrestre constituyen herramientas para establecer la posición y el rumbo en diferentes condiciones de visibilidad (ver revisión en Alerstam et al. 2003 y Alerstam 1996):

Las alas del viento

La dirección del viento y su velocidad es esencial, hay estudios realizados en la subespecie *canutus* de playero rojizo que muestran que estos prefieren migrar con asistencia de viento de cola. Sólo en años de ausencia de vientos de altura del sur, los playeros que migran desde Mauritania en Africa, hasta el Mar de Wadden en Holanda, se ven obligados a descender en las costas francesas (Dick et al. 1987), (ver mapa 2)

En Bahía de San Antonio los grandes cambios en los números presentes de la subespecie *rufa* debidos tanto a las aves que partieron en migración como a las recién llegadas desde el sur, suelen manifestarse posteriormente a la ocurrencia de frentes fríos del sur durante la migración al norte (F. Inalafquen no publicado). En el año 1999, durante la migración desde la costa norte de Sudamérica hasta la Bahía Delaware (unos 4500 km de distancia), ocurrieron infrecuentes vientos en contra desde el norte; en esa temporada se recibieron excepcionalmente avistajes de playeros en sitios del Caribe y de la costa de USA donde no se habían registrado regularmente con anterioridad. Ese año la llegada de las aves a la Bahía Delaware también se vio demorada y no sólo los playeros sufrieron retrasos, los aviones comerciales también debieron enfrentar estos vientos en contra haciendo uso de un mayor gasto de combustible y tiempo de vuelo (Baker et al. 2001, Int. Shorebird Banding Project Team in litt.).

Es que al igual que el efecto producido sobre los ciclistas, la asistencia de viento de cola no sólo contribuye a aumentar la velocidad de traslado, también disminuye los costos energéticos implicados en el transporte.

Así los playeros, aves capaces de volar en promedio a unos 70 km/h, pueden alcanzar velocidades relativas a la superficie terrestre mucho mayores utilizando los fuertes vientos de altura (Piersma y van de Sant 1992). Estudios realizados en túneles de viento en laboratorio, avistajes de aves anilladas y simulaciones de modelos matemáticos, muestran que los playeros Scolopácidos son capaces de volar 40 a 175 horas ininterrumpidamente (e.g. Pennycuik 2003).

Altura de vuelo

Los radares muestran que los playeros se desplazan a alturas crucero de alrededor de 3000 m pero pueden alcanzar los 6000m y aún más de 8.000 m como lo hacen las especies que sobrevuelan el Himalaya. A más altura pueden adquirir mayor velocidad debido a las poderosas corrientes de viento, pero deben enfrentar las demandas metabólicas provenientes de la escasez de oxígeno y las temperaturas de 20 C a 30 C bajo cero , en tanto a menor altura el balance es opuesto (Piersma et al. 1996).

Por lo tanto uno de los factores que los playeros deben tener en cuenta a la hora de decidir el momento de la migración, tiene que ver con el juzgamiento de las condiciones meteorológicas óptimas para la partida. Lamentablemente existen indicios que señalan que las aves no pueden predecir las condiciones meteorológicas que encontrarán kilómetros más adelante durante su vuelo, y posiblemente esto explique que eventualmente se encuentren playeros desviados de su ruta hasta incluso 1000 km (Piersma et al. 1996). Pero además implica que las aves deben estar del mejor modo preparadas para enfrentar contingencias durante el vuelo acumulando suficientes reservas de grasa y proteínas durante sus escalas migratorias.

Estudios de presupuesto energético en otras especies como la Becasa de Mar (*Limosa lapponica*) cuando migra 4500 km entre el Banc d'Arguin en Africa y el Mar de Wadden en Holanda en su ruta a Siberia, muestran que sólo pueden alcanzar esta autonomía de vuelo las aves más pesadas, es decir aquellas con gran almacenamiento de grasa y proteínas, pero sólo pueden lograrlo si disponen de la asistencia de viento de cola (Piersma y Jukema 1990).

c) ¿Cómo almacenar reservas de grasa y proteínas, el combustible para la migración?

--¿Dónde se alimentan las «Aves de playa....» ?

Los playeros rojizos no nadan, aunque pueden hacerlo excepcionalmente como escape a predadores, altas temperaturas o desvíos de sus rutas que los llevan a posarse en el mar, pero no pueden sobrevivir en condiciones de mar encrespado por el oleaje. Definitivamente son aves playeras, «aves de playa» y buscan su alimento caminando....

--¿Qué comen?

Aunque pueden consumir poliquetos (gusanos de mar), pequeños crustáceos, insectos, larvas y hasta semillas, los playeros rojizos son especialistas en alimentarse de moluscos bivalvos y gasterópodos (caracoles) (Piersma et al. 1996) que obtienen preferentemente en extensas áreas costeras intermareales arenoso-limosas, muchas de ellas localizadas en estuarios y bahías protegidas.

--¿Cómo encuentran sus presas?

Habitualmente su presas se encuentran enterradas y no demuestran gran movilidad,

¿cómo detectarlas sin verlas? Para esto los playeros rojizos disponen conjuntos de órganos sensoriales ubicados en cavidades del extremo del pico, llamados «corpúsculos de Herbst». Estos órganos funcionan como sensores remotos, capaces de detectar ondas de presión que se producen en el agua intersticial cuando el ave introduce su pico «probando» en el sedimento húmedo, si las ondas encuentran elementos duros como lo son los bivalvos, la presión cambia informando al playero de su posición y tamaño (Piersma et al 1998).

De este modo los playeros rojizos pueden alimentarse en llanuras intermareales tanto de día como de noche pues no utilizan la vista para detectar los organismos que son su alimento.

Para un búsqueda eficiente, el sustrato debe poseer características especiales de granulometría y debe estar húmedo, los sensores no funcionan en sustratos secos. Como los playeros detectan tanto piedras como bivalvos pero no pueden distinguir entre ellos, nunca los veremos alimentándose en sustratos con clastos de tamaños similares a los bivalvos que ellos consumen.

La excepción a la regla puede observarse en Bahía de San Antonio.

Justamente por ser *Calidris canutus* una especie absolutamente especializada en este tipo de ambientes, sorprende que en Bahía de San Antonio no sea así: su principal sitio de alimentación se encuentra en las restingas planas de la Formación Patagonia ubicadas en las playas del norte de Las Grutas hasta las cercanías del Aeropuerto Saint Exupéry. Geomorfológicamente son plataformas de abrasión labradas por el mar. Se trata de superficies intermareales rocosas lisas sobre las cuales se asientan manchones de mejillines *Brachidontes rodriguezi*, principal presa de los playeros rojizos en esta localidad (González et al. 1996 b).

Este cambio de hábitat hace en primera instancia que los playeros deben utilizar su vista para encontrar sus presas y esto implica que no pueden alimentarse de noche en estos ambientes. En efecto, estudios realizados con radiotransmisores demostraron que los playeros rojizos se alimentaron de noche en la llanura intermareal de la Bahía de San Antonio (Sitters et al. 2001)

Los playeros necesitan agua para ingerir los mejillines, por esa razón nunca se los verá forrajeando en zonas intermareales desecadas temporalmente durante la bajamar como es habitual luego de una larga exposición al sol o a fuertes vientos del Norte o del Oeste. Los bivalvos son ingeridos enteros y luego convertidos en fragmentos por el fuerte estómago muscular de las aves, en tanto la masa de la carne de la presa es digerida y asimilada, los restos de las valvas son desechados con las heces. Estudiando las heces es posible reconstruir la dieta, de este modo sabemos por ejemplo que los playeros rojizos sólo consumen los mejillines cuyas tallas varían entre 5 a 20 mm de longitud, pero prefieren los de 10 a 13 mm (González et al. 1996 b).

Aunque los playeros rojizos también consumen otras presas en la región (la almeja *Darina solenoides* ciertas especies de poliquetos, pequeños crustáceos y hasta insectos) que obtienen principalmente en los bancos intermareales Reparo y Banco Lobos

(Mapa 1), estos recursos sólo parecen ser utilizados como alternativos y su uso no es regular año a año (González P. no publicado). Por lo tanto las restingas son de importancia vital para la supervivencia de las poblaciones de playeros que realizan escala en Bahía de San Antonio.

El incremento de masa corporal previo a la migración

Los playeros rojizos son capaces de aumentar su peso desde 100 g hasta más de 200 g aunque se han registrado pesos tan bajos como 84 g y tan altos como 248 g (Int. Shorebird Banding Project in litt), (ver fotos 2, izq. y der. en sección foto color del libro). Pero esta habilidad no significa que la tasa de incremento de masa corporal sea la misma en todos los sitios de escala o de estadía austral. Es que en esencia se trata del resultado del balance de un presupuesto entre la energía que ingresa a través del alimento y la energía que se gasta (Tasa metabólica basal –es decir la energía que se consume en reposo para el mantenimiento de las funciones metabólicas– ; termoregulación; muda de plumaje; actividades). También intervienen regulaciones hormonales que se relacionan con la duración del fotoperíodo (horas luz por día) a través de “relojes internos” (Gwinner 1996). Por lo tanto la oferta de alimento es fundamental para un balance positivo.

En cada sitio la «disponibilidad» de las presas no es necesariamente la misma que en otro, además puede variar año a año e incluso hasta dentro de la misma temporada migratoria. Que las presas estén «disponibles» para los playeros significa que:

--Las presas deben poder ser alcanzadas.

Por ej. muchos organismos bénticos (asociados a los fondos intermareales) como las almejas, se desplazan a mayores profundidades a medida que crecen, quedando fuera del alcance de los picos de los playeros. En las restingas los mejillines asentados en los fondos de las pozas intermareales quedan sumergidos aún durante la bajamar, de manera que no pueden ser alcanzados por las aves playeras. Hay otras formaciones de restingas en Río Negro que poseen bancos de mejillines cuya fijación al sustrato es sustancial y los playeros, aunque pueden alcanzarlos, no pueden desprenderlos.

--Las presas deben ser detectables

Como ya se ha mencionado anteriormente, en sedimentos desecados las aves no pueden utilizar los corpúsculos de Herbst para detectar las presas. Análogamente de noche no pueden detectar visualmente los mejillines en la restinga (Sitters et al. 2001).

--Las presas deben poder ser ingeridas.

El tamaño y forma de las presas es crucial. En los bivalvos la dimensión limitante es la circunferencia más que la longitud pues presas muy grandes podrían dañar el esófago de los playeros o provocarles muerte por asfixia. Asimismo bivalvos con exofauna adherida tal como Cirripedios (“Dientes de Perro”) tampoco son consumidos.

--Las presas deben poder ser digeridas.

Romper las valvas de caracoles y bivalvos en el estómago requiere gran energía, por esta razón los playeros rojizos tienen un estómago casi dos veces más pesado que el de

otras aves playeras de similar tamaño que consumen presas blandas. El material inorgánico de las valvas no es digerido pero ayuda en la digestión de la carne de las presas.

--Las presas deben ser aprovechables.

Por ej., los playeros rojizos rechazan los mejillines de tallas muy pequeñas porque les aportan muy poca carne en relación al tiempo invertido en buscarlos y en manipularlos para ingerirlos.

“La disponibilidad de las presas depende de factores naturales pero también se encuentra condicionada por las actividades humanas”. (Van de Kam et al. 2004)

¿Incremento de masa muscular sin ejercicio físico?

Si existe una capacidad asombrosa y poco conocida en la naturaleza, ésta es la habilidad que tienen los playeros rojizos para cambiar el tamaño de sus órganos.

Para maximizar su tasa de incremento de masa corporal los playeros rojizos necesitan disponer de una maquinaria digestiva eficiente y son capaces de realizar cambios reversibles en el tamaño de sus órganos. Así pueden desarrollar el tamaño de los órganos del sistema digestivo como estómago, hígado e intestinos luego de llegar a una escala migratoria. (Piersma et al. 1999) Además la hipertrofia del estómago será mayor cuando las presas tengan valvas más duras (Dekinga et al. 2001)

Inversamente, a medida que van aumentando de peso los playeros comienzan a preparar su maquinaria para el vuelo: paulatinamente los órganos del sistema digestivo comienzan a disminuir de tamaño, el estómago va perdiendo su fuerza y las aves ya no pueden digerir eficientemente presas duras como los bivalvos, debiendo cambiar su elección a presas con exoesqueletos más blandos (van Gils et al. en prensa). tal como pequeños cangrejos Paralelamente los músculos pectorales de vuelo comienzan a aumentar de tamaño.

Esta flexibilidad permite que los playeros ahorren energía de mantenimiento metabólico tanto durante la escala migratoria como durante el vuelo migratorio porque reducen el tamaño de los órganos que no utilizan.

Curiosamente para los humanos, este incremento de masa muscular transcurre sin necesidad de ejercicio físico, por eso a medida que las aves engordan cada vez invierten menos tiempo en actividades de forrajeo (alimentación) y dedican más horas al descanso. Durante una migración de larga distancia el playero disminuirá su masa corporal debido a la oxidación de las grasas que le proporcionarán energía para el vuelo, pero además disminuirán la masa muscular, tal vez porque sus proteínas son necesarias para la metabolización de esas grasas (Battley et al. 2000).

Solo recientemente con el advenimiento de estudios no invasivos como las ecografías en las aves, se ha comenzado a conocer estos procesos. Seguramente no pasará mucho tiempo hasta que los investigadores decidan desentrañar sus secretos para poder darles aplicación humana.

Si fuera una mujer de 50 kg., aumentaría 4,8 kg por día.

Las aves playeras son los organismos que denotan la mayor tasa de asimilación de energía excediendo incluso la reportada para vertebrados durante períodos de alta

demanda (como frío o reproducción). Entre ellas, el playero rojizo ha mostrado una de las más altas tasas de aumento de masa corporal: 9,6 % de su masa inicial por día (Kvist y Lindström 2003).

d) La atracción de un buen traje

La condición corporal y rol de Bahía de San Antonio en la selección sexual

Las variaciones anuales en la calidad y cantidad de la oferta de recurso trófico (presas alimento de los playeros) pueden «leerse» en la condición de las aves. Así en «buenos años» los playeros incrementan su masa corporal más rápido y asimismo su intensidad de muda corporal.

Durante su escala en la migración al norte en Bahía de San Antonio, la mayoría de los playeros rojizos mudan su plumaje corporal claro, no reproductivo, al plumaje rojizo reproductivo (Baker et al. 2001). En este sentido Bahía de San Antonio es un sitio clave para este proceso (Foto 1 en sección foto color del libro). Sin embargo, la muda corporal de algunas aves puede iniciarse en Tierra del Fuego y en algunas temporadas un escaso porcentaje aún muestra muda activa cuando están en la Bahía Delaware (EEUU).

En líneas generales los playeros rojizos que están en mejor condición física mudan más rápido y adquieren colores más brillantes. Un buen plumaje es una señal honesta hacia los miembros del sexo opuesto que así los preferirán o «seleccionarán» como compañeros sexuales (González et al. 2003).

e) Los sitios de reposo y Bahía de San Antonio

En Bahía de San Antonio los mejillines y otras presas sólo están disponibles cuando las mareas descubren las superficies intermareales, ese es el momento que las aves deben aprovechar al máximo para alimentarse. Por lo tanto sólo pueden descansar durante las pleamares, las cuales ocurren a diferentes horas cada día.

A medida que la marea sube, los playeros se van congregando para descansar en sus sitios de reposo ubicados en las playas del ex Centro Minero Los Álamos, Península Villarino o La Mar Grande. (Mapa 1)

Los sitios de reposo no son elegidos al azar y deben cumplir determinadas características: deben ser áreas amplias y abiertas de modo que los múltiples ojos de la bandada puedan ejercer su vigilancia ante cualquier peligro y las rutas de escape estén libres; deben estar en lo posible cerca de los sitios de alimentación pero al mismo tiempo lejos de los refugios de predadores (aves rapaces diurnas y nocturnas, zorros, perros); además deben ofrecer protección frente a las condiciones meteorológicas adversas o poco confortables. Por ej., en Bahía de San Antonio preferirán la Península Villarino en los días de altas temperaturas o con vientos cálidos o tormentas de polvo y arena. Además, dentro de los sitios de reposo preferirán los sectores más cercanos a la orilla del mar o aquellos microambientes protegidos cuando existan inclemencias (pendientes, detrás de piedras o resaca, etc.). Los cantos rodados funcionan como importantes acumulado-

res de calor y tenderán a ser evitados en los días cálidos en Bahía de San Antonio pero serán preferidos en los sitios de reposo de Tierra del Fuego cuando las bajas temperaturas y los vientos son extremos.

f) La ventaja de estar en bandada

La búsqueda colectiva en bandadas de alimentación favorece el encuentro de las presas, organismos bentónicos que generalmente se distribuyen espacialmente de manera agrupada como si fueran manchones (van Gils 2004) y las aves más jóvenes se benefician y aprenden de la experiencia de las de mayor edad. Cuantos más individuos tenga la bandada, mayor es la velocidad de encuentro de los manchones de presas.

Pero al mismo tiempo la distancia entre los playeros debe responder a un balance, la cercanía excesiva a otro individuo podría implicar competencia intraespecífica por el recurso trófico. Las distancias entre individuos en el comportamiento de las bandadas que se alimentan parecen depender del número de aves y la interferencia de unas con otras, de la densidad y disponibilidad de las presas, y del tipo de presa (su digestibilidad). (Van de Kam et al. 2004, van Gils 2004).

Mil ojos ven más que dos y estar en bandadas también representa mayor seguridad ante la aparición de peligros tanto en los sitios de reposo, como en los sitios de alimentación. Sin embargo los playeros deben encontrar un balance entre el tiempo dedicado a la vigilancia (gasto de energía) y el tiempo cuya atención está puesta en alimentarse (ganancia de energía) (van Gils 2004). Por ej. en la mala temporada ocurrida en Delaware Bay durante 2003, la escasez de huevos de cangrejo herradura, alimento de los playeros, obligó a las aves más delgadas a poner toda su atención y tiempo en la actividad de forrajeo, disminuyendo la vigilancia. Por primera vez esa temporada se observaron gaviotas (*Larus argentatus*) capturando playeros para su propia alimentación, los cuales fueron presa fácil debido a esta inusual situación (Phil Atkinson com.pers).

El vuelo en bandadas compactas conformando una unidad gigantesca, parece oficiar como un mecanismo para desconcertar a los predadores. Los movimientos sincronizados son similares a los producidos por las ondas de espectadores en los estadios (Piersma et al. 1996) y permiten una disrupción del color de la bandada al tiempo que los individuos exhiben sus dorsos oscuros o bien sus vientres más claros “*desapareciendo en el aire*”.

g) La conectividad migratoria

El tamaño poblacional de las aves playeras migratorias es muy sensible a las variaciones en la supervivencia de los adultos y por lo tanto la conservación de estas especies requiere la protección de las áreas no reproductivas, es decir de los sitios clave que utilizan para alimentación y descanso a lo largo de su ruta de vuelo.

Los playeros rojizos eligen sus sitios de escala migratoria de acuerdo a la experiencia de la bandada en cuanto a la calidad de las presas disponibles, de manera de maximizar la velocidad de la migración, pero también de acuerdo a su condición corporal en la escala previa, y asistencia de vientos.

Estos sitios no son abundantes a lo largo de la ruta migratoria, su degradación y pérdida se traduce en la disminución de la tasa de incremento de masa corporal de los playeros que no les permite alcanzar una masa corporal previa a la migración adecuada para enfrentar sus viajes de miles de kilómetros, y el riesgo de parasitosis e infecciones por depresión del sistema inmunológico.

Estos factores limitantes en la biología de los playeros migratorios de larga distancia se manifiestan en una cadena de eventos “dominó” que se desarrollan a lo largo de la ruta de vuelo llevando a la disminución de la tasa de supervivencia de los adultos y éxito reproductivo.

“En otras palabras, lo que ocurra en un sitio, repercutirá en el resto”. (Baker et al. 2001; González et al. 2003, Piersma & Baker 2000).

h) La declinación

Declinación del tamaño poblacional

Por medio de censos aéreos (Morrison et al. 2004) y estudios de captura–recaptura de aves anilladas (González et al. 2004), se establecieron los tamaños poblacionales de playero rojizo en las áreas de estadía austral en Tierra del Fuego señalando una alarmante declinación de alrededor del 50% de 52.000 ejes. a partir de Febrero de 2000. Esta declinación está vinculada con la sobrepesca del Cangrejo Herradura (*Limulus polyphemus*) –cuyos huevos constituyen el alimento principal de los playeros rojizos en Delaware Bay, USA, última escala antes de volar a sus áreas reproductivas en el Artico– y tal vez con la posible llegada tardía de playeros rojizos al hemisferio norte. Ambos sucesos repercuten negativamente porque los playeros no alcanzan el umbral de masa corporal necesario para su supervivencia y producción de jóvenes (Baker et al. 2004).

Contracción biogeográfica en sus áreas de estadía austral

Luego de la declinación los playeros rojizos dejaron de utilizar Patagonia continental como sitio de estadía austral concentrándose sólo en Tierra del Fuego (Morrison et al. 2004). La contracción de los números de playeros rojizos de «Patagonia y Tierra del Fuego» a solo áreas en «Tierra del Fuego» señala entonces la importancia de los sitios de esta última como áreas críticas para la supervivencia de la subespecie; en tanto los de Patagonia parecen ofrecer alternativas secundarias para los requerimientos de la temporada de estadía austral.

Vulnerabilidad ecológica

Además de los peligros ecológicos que enfrentan, los playeros rojizos presentan baja variabilidad genética debido a un cuello de botella evolutivo (reducción de su tamaño poblacional) sufrido en el Pleistoceno tardío y por esta razón su vulnerabilidad frente a estos peligros se encuentra incrementada (Piersma y Baker 2000).

Vulnerabilidad evolutiva

Como si los riesgos ecológicos no fueran suficientes, desde el punto de vista evolutivo, el tamaño efectivo de la población de *C.canutus rufa* en el largo plazo es de alrededor de sólo 2000-4000 hembras. Estos números representan el promedio del número de hembras que dejan descendencia por generación, si consideramos que por debajo del umbral de $N = 1500$ hembras, la población corre el riesgo de extinción por fijación de mutaciones letales por un proceso conocido como «deriva genética», entonces existe una necesidad urgente de incrementar el número de parejas reproductivas en la población para evitar su extinción. (Baker 2003).

Estas investigaciones (junto a los censos aéreos de Morrison et al. 2004) han sido utilizadas como fundamentación para la solicitud del pasaje de la subespecie *Calidris canutus rufa* del Apéndice 2 al Apéndice 1 (P.González en Marzo de 2004) elevada al Comité Científico de la Convención de Especies Migratorias conocida como Convención de Bonn y aprobada por el mismo en su XII reunión de Marzo de 2004.

¿Qué peligros enfrentan en Bahía de San Antonio?

En Bahía de San Antonio una de las principales actividades económicas es el turismo de playa con 160.000 turistas anuales concentrados en temporada estival. Este centro ha contado con escasa planificación, con el consecuente avance irrestricto de visitantes sobre los sectores críticos de descanso y alimentación de aves migratorias y sobre el recurso natural en general.

Apenas diez años atrás los Playeros Rojizos y otras especies de aves playeras disponían de tres a cuatro sitios de descanso mientras que en la actualidad sólo disponen de dos, uno de ellos, Los Álamos, disturbado altamente durante las mareas altas por la presencia de vehículos en la playa, personas caminando, perros, e incremento de aves de presa que utilizan las estructuras altas (como las antenas) a modo de perchas. El principal sitio de alimentación, la restinga intermareal que se extiende a lo largo de unos 9 km de costa al norte del Las Grutas está sufriendo el deterioro creciente producido por el aplastamiento por vehículos todo terreno (4 x 4) de los manchones de mejillines, mientras que las aves que se alimentan son disturbadas y alejadas de sus manchones preferenciales por personas, perros, redes de pesca colocadas a modo de paredes sobre su superficie y sonidos de que circulan sobre los médanos y la playa. Además ha sufrido modificaciones con la construcción de piletas recreativas excavadas en la roca que han provocado la disminución de la superficie del mejillinar disponible para la alimentación de las aves. Cada pileta en sí misma no ofrece una superficie de pérdida importante, en cambio el conjunto de la superficie acumulada de todas ellas puede hacerse significativo y producir impacto de pérdida de hábitat para las aves si su construcción se continuara en el tiempo.

En este marco se destaca la iniciativa llevada a cabo por la Secretaría de Turismo de la Municipalidad de San Antonio Oeste junto al Consejo Provincial de Ecología y

Medio Ambiente de RN y la Fundación Inalafquen de implementación del cuerpo de Guardias Ambientales. Se trata de personal apostado en sitios críticos para las aves playeras durante la temporada estival y hasta el mes de Abril, fin del pasaje migratorio, con el objeto de brindar protección a las aves y explicar a los visitantes la importancia del Area Natural Protegida Bahía de San Antonio.

La construcción de la fábrica de Soda Solvay en la Punta Delgado y muelle aledaño (ver Anexo en este libro) ha hecho desaparecer uno de los antiguos sitios de descanso allí ubicado. Aún se desconocen los efectos potenciales de la puesta en marcha de este emprendimiento sobre las comunidades bentónicas alimento de las aves playeras y el recurso natural en general del cual dependen.

4. Las aves playeras como recurso turístico.

La tendencia mundial del turismo es buscar lugares ecológicamente limpios donde el turista es partícipe de actividades físicas e intelectuales con interés en la cultura local. Además evita los destinos con problemas ambientales o sociales (Organización Mundial de Turismo). Por ej. en los últimos años ha incrementado en los Estados Unidos el turismo de observación de aves (Pullis La Rouché 2003) y cada vez más comunidades de USA y Canadá se han beneficiado con la realización de festivales durante la temporada migratoria de las aves playeras.

Los estudios regionales en el área costera patagónica reafirman la tendencia mundial en el sentido que la motivación principal la constituyen los atractivos naturales (Plan de Manejo Integrado de la Zona Costera Patagónica – Fundación Patagonia Natural - 1995).

Con el objetivo de conservar las aves playeras y sus hábitats, desarrollar un nuevo producto ecoturístico, y crear conciencia en la comunidad sobre la importancia global del Area Natural Protegida Bahía de San Antonio, se iniciaron experiencias de turismo y educación para evaluar las posibilidades de un programa de turismo sostenible. Así se ha ofrecido desde 1998 la observación de aves playeras como producto a turistas a través de experiencias piloto conducidas desde la Municipalidad de San Antonio Oeste conjuntamente con la Fundación Inalafquen y desde el año 2000 entre esta última y la empresa Ocasión Turismo.

La metodología respondió a un esquema exploratorio cualitativo con aplicación de estímulos basados en la información. Los grupos experimentales fueron alumnos de escuelas y turistas; se trabajó bajo asesoramiento científico en diferentes meses del año según la presencia de aves migratorias. En los grupos de alumnos con información heterogénea, ante la presencia de aves, la respuesta fue altamente positiva con respecto a la valoración del recurso, el interés por ampliar conocimientos y la motivación para repetir la experiencia. En tanto en los más informados se observó especificidad en el requerimiento de conocimientos sobre las aves. Despertó interés general la relación humana con los científicos. Los grupos de turistas que participaron en la temporada estival (sin aves migratorias) con otra motivación y nivel de información bajo, fueron en su mayoría «sorprendidos por el recurso y las investigaciones científicas»; algunos

lo asociaron al lugar de origen. En todos los grupos se destacó el interés por el uso de prismáticos y telescopios que fueron facilitados por la Fundación Inalafquen. No se registraron importantes experiencias negativas. Los estudios de la demanda han demostrado un importante incremento en la variable motivación “observación de aves” sin haber realizado promoción turística de ninguna clase. Del mismo modo ha aumentado la demanda desde el sector educativo a un punto en que el recurso humano y la infraestructura disponible no alcanza a satisfacer. En este contexto debe mencionarse que en la Argentina no está difundida la figura del “birdwatcher” (observador de aves) típico de Norte América o Europa, el cual posee óptica propia y facilidad de fuentes de información, pues en nuestro país la mayor parte de la población no tiene acceso a los conocimientos para identificar aves, guías de aves ni instrumentos adecuados para su observación. En este sentido las experiencias piloto aquí desarrolladas son innovadoras.

Estos resultados despertaron la atención del sector turístico. Es indispensable para su continuidad: estimar la capacidad de carga del recurso, instalar un Centro de Interpretación, incrementar la cantidad de guías intérpretes capacitados y el apoyo de instituciones educativas y científicas.

“La única manera de realizar un turismo de observación de la naturaleza sustentable es conservando el recurso mediante pautas de manejo con base científica”. (Sawicki et al. 2003)

5. Conexión humana y pérdida de la biodiversidad

Las Aves Playeras están declinando a lo largo y ancho del Planeta.

Entre las aves playeras, el Playero Rojizo es una de las más estudiadas del mundo. De las 439 poblaciones de aves playeras que existen en el mundo pertenecientes a las familias Charadriidae, Scolopacidae, Haematopodidae, Recurvirostridae, Rostratulidae y Thinocoridae, 100 poblaciones (22,9%) que representan 60 especies (32%) son Neotropicales, se distribuyen en América del Sur y Caribe. Para el 51% de éstas últimas no existen estudios que provean estimaciones de sus tendencias poblacionales. La mitad del 49% restante, es decir aquellas para las cuales existe información, se encuentra en declinación, incluyendo 1 especie posiblemente extinta (*Numenius borealis*, Playero Esquimal). En América, las poblaciones Neárticas, migratorias de larga distancia que se reproducen en el Hemisferio Norte (65%), están más estudiadas que las Neotropicales de migración intracontinental o residentes (33%). La razón es que la mayor parte de la financiación para proyectos de investigación, monitoreo y conservación proviene de Norte América.

Por otra parte existe un mayor número de poblaciones Neárticas en declinación que Neotropicales (58% de N=33 vs 38% de N=16 respectivamente), debido a la historia de vida y alta dependencia de sitios críticos a lo largo de la ruta migratoria de las primeras.

En algunas áreas las aves playeras migratorias se encuentran amenazadas por contaminación, turismo y desarrollo descontrolado, manejo inadecuado de los recursos acuáticos y cambios de hábitat producidos por la ganadería y la agricultura. (González y Blanco

2003).

En el año 2002, los líderes mundiales expresaron su deseo de alcanzar “*una reducción significativa en la tasa actual de pérdida de diversidad biológica*” hacia el año 2010. Apenas el año anterior los Jefes de los Estados europeos expresaron su intención de “*que la declinación de la biodiversidad debería detenerse ... hacia 2010*”. Información reciente presentada en la Conferencia Internacional del Wader Study Group realizada en Cádiz, España, en 2003 indica que una significativa proporción de las poblaciones de aves playeras están en declinación y sugiere que, al menos para estas aves, será un desafío extremo alcanzar estos objetivos sin que los gobiernos de todos los continentes realicen inversiones importantes y altamente focalizadas en actividades de conservación (Wader Study Group 2003).

La nueva declinación

Al momento del cierre de este estudio, una nueva declinación de la población de playero rojizo de Tierra del Fuego ha tenido lugar. Los censos aéreos del Canadian Wildlife Service de enero de 2005 detectaron una nueva y drástica reducción de unos 30.000 ej. en 2004 a poco menos de 18.000 ej. De ellos, más de 9.000 playeros rojizos han hecho escala posteriormente en Bahía de San Antonio durante su migración al norte, entre Febrero y Abril. En otras palabras significa que la mitad de la población total depende de su supervivencia de Bahía San Antonio, de nuestro compromiso y responsabilidad.

Reconocimiento a los primeros

Poul Pedersen, ya conocía los sitios de concentración de aves playeras antes que cualquier estudio fuera realizado y tuvo la generosidad de enseñarlos.

Oswaldo Baraschi, viviendo al lado de uno de los principales sitios críticos para aves playeras, apoyó la creación del Area Natural Protegida Bahía de San Antonio y junto a su familia respaldó las primeras tareas de investigación y conservación del área.

Héctor Piacentini, fue el primero en documentar en video y fotografía el pasaje de las aves playeras y gracias a su material y artículos periodísticos fue posible comunicar a la comunidad y sus autoridades la importancia del sitio.

Vanessa Calvo, siendo estudiante secundaria, respaldó la creación del Área Natural Protegida Bahía de San Antonio en el III Congreso de la Juventud Rionegrina de Junio de 1993. Además consiguió llevar a la práctica la impresión del primer folleto existente sobre aves playeras del Área.

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Tabla 1.

Lista de las especies de chorlos y playeros del Área Natural Protegida Bahía de San Antonio. Se indica el nombre común entre paréntesis según Narosky e Izurieta 2003

Familia Scolopacidae (Playeros)

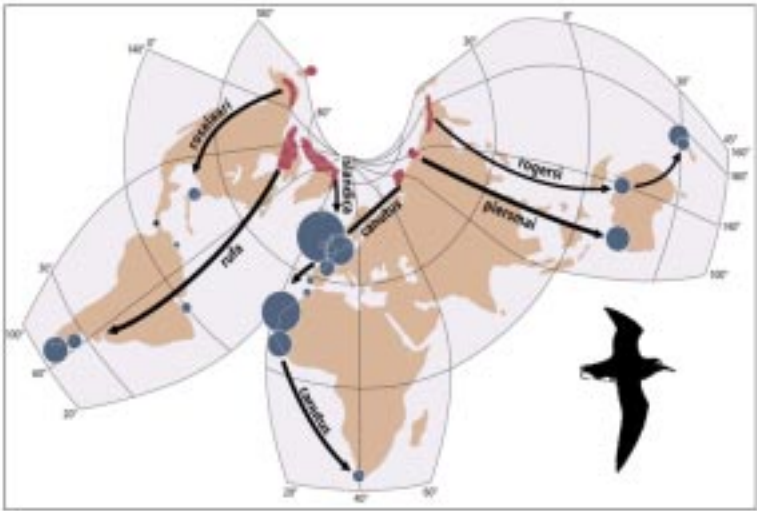
* <i>Aphriza virgata</i>	(Playero de rompiente)
<i>Calidris fuscicollis</i>	(Playerito de rabadilla blanca)
* <i>Calidris bairdii</i>	(Playerito de rabadilla parda)
<i>Calidris canutus</i>	(Playero rojizo)
<i>Calidris alba</i>	(Playero blanco)
* <i>Calidris pusilla</i>	(Playerito enano)
<i>Limosa haemastica</i>	(Becasa de mar)
<i>Arenaria interpres</i>	(Vuelvepiedras)
<i>Tringa melanoleuca</i>	(Playero grande de patas amarillas)
<i>Tringa flavipes</i>	(Playero chico de patas amarillas)
* <i>Numenius phaeopus</i>	(Playero trinador)

Familia Charadriidae (Chorlos)

<i>Pluvialis dominica</i>	(Chorlo dorado)
<i>Pluvialis squatarola</i>	(Chorlo ártico)
<i>Charadrius falklandicus</i>	(Chorlito de doble collar)
* <i>Charadrius collaris</i>	(Chorlito de collar)
* <i>Charadrius semipalmatus</i>	(Chorlito semipalmado)
* <i>Charadrius modestus</i>	(Chorlito pecho canela)
<i>Pluvianellus socialis</i>	(Chorlito ceniciento)
* <i>Oreophollus ruficollis</i>	(Chorlo cabezón)
<i>Vanellus chilensis</i>	(Tero común)

(*) raras.

Mapa 2. Rutas de migración de las seis subespecies de Playero Rojizo *Calidris canutus* reconocidas en el Mundo al presente. Los círculos señalan las áreas de estadía no reproductiva (estadía austral) y las zonas en rojo las áreas reproductivas. (Gentileza de Theunis Piersma).



Mapa 3. Ruta de migración de la subespecie *rufa* de Playero Rojizo, y principales áreas de concentración de aves.



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Nota sobre la autora.

Patricia María González. *Fundación Inalafquen*

Nació en la ciudad de Buenos Aires en 1958. Estudió Biología en la Universidad de Buenos Aires. Sus investigaciones proveyeron el fundamento científico para la creación del Área Natural Protegida “Bahía de San Antonio” y su posterior reconocimiento como “Sitio Internacional” de la Red Hemisférica de Reservas para Aves Playeras (RHRAP) en 1993. Entre los premios por sus trabajos sobre conservación e investigación de Aves Playeras se destaca por ser la primer galardonada con el Premio “Pablo Canevari” de la RHRAP en el año 2000. Actualmente se desempeña como Coordinadora del Programa “Humedales” de la Fundación Inalafquen. Organiza y participa de trabajos de investigación, educación y conservación de aves playeras a lo largo del continente americano, incluyendo campañas de anillado de aves playeras en cooperación con instituciones locales e internacionales de Argentina, Chile, Brasil, USA, Canadá, Gran Bretaña y Holanda. Forma parte del Consejo Ejecutivo del Wader Study Group por Sudamérica; especialista de la Unión Internacional para la Conservación de la Naturaleza; es miembro del Consejo Científico de la RHRAP. Participa ad honórem en el presente libro.

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