



Global Flyway Network: progress report for 2007



Toddler in Iwik, Banc d'Arguin, Mauritania, discovering the power of a telescope and the beauty of individually recognizable, colour-ringed Sanderling. Photos by Jeroen Reneerkens.

TABLE OF CONTENTS

Executive summary	3
Introducing the <i>Global Flyway Network</i>	5
Developments in 2007	7
Annotated focal species list: most recent population developments	8
Population status update for East Asian-Australasian Flyway	11
Summary of the activities of Patricia M. González	14
Monitoring at Rio Grande, Tierra del Fuego, Argentina	18
Monitoring at San Antonio Oeste, Rio Negro, Argentina	22
Male-biased mortality in Red Knots <i>Calidris canutus rufa</i>	27
Southward migration of <i>C. c. rufa</i> : the Mingan Archipelago	29
Progress report by Chris Hassell	32
STOP PRESS: satellite tagging of Bar-tailed Godwits in 2008	36
The <i>Pacific Shorebird Migration Project</i> : results from 2007	41
Molecular cloning and characterization of MHC genes in Red Knots	46
Migratory Ruffs have prolonged stopovers in spring	54
Migration routes of Sanderling: insights after a year of colour-ringing	62

Appendices:

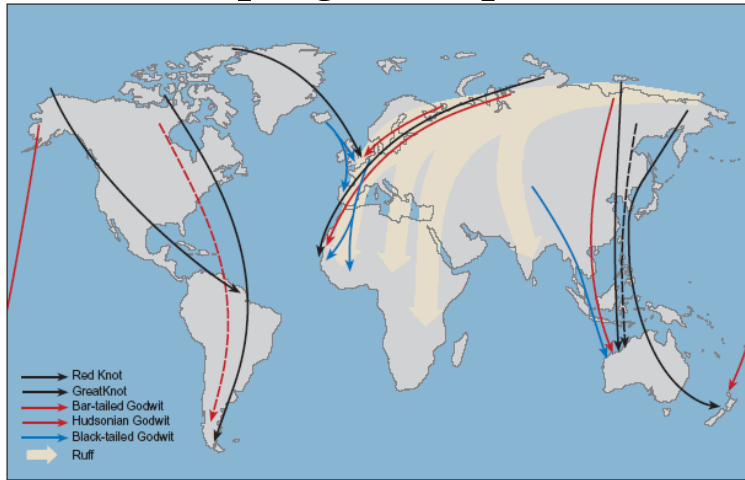
A. published paper by T. Piersma in *Journal of Ornithology* in 2007 in which the comparative approach to shorebird biology, demographics and conservation was outlined, and the *Global Flyway Network* formula introduced, based on a plenary lecture at the International Ornithological Congress in Hamburg in August 2006.

B. a paper by P.M. González *et al.* published in *Hornero* in 2007 on the population consequences of individual variations in stopover timing and progress of Red Knots *Calidris canutus rufa* in Argentina

C. paper by P.W. Atkinson *et al.* published in the *Journal of Applied Ecology* in 2007 on the role of horseshoe egg declines in Delaware Bay with respect to the ongoing population decline of Red Knots *Calidris canutus rufa* based on an analysis of individual body mass trajectories.

D. published paper in the *Wader Study Group Bulletin* in 2007 by J. Gill *et al.* on a conservation-inspired comparison between the continental subspecies of the Black-tailed Godwit *Limosa limosa limosa* (in steep decline) and its Icelandic counterpart that is doing well, *Limosa limosa islandica*. This paper was the outcome of a workshop organised during the 2007 International Wader Study Group Conference in La Rochelle, France.

Global Flyway Network: the second progress report – for 2007



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

Executive summary

1. With funding support from BirdLife Netherlands (Vogelbescherming Nederland), the *Global Flyway Network* formally started its activities in 2007. 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. 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, and in 2007 we also helped Dr Sergio Pereira (Royal Ontario Museum, Toronto) to decipher the MHC complex in Red Knots — a set of key, disease-resistance related — genes that may play an important role during and after population bottlenecks.
3. In 2007 intense field work on the endangered *rufa* subspecies of Red Knots was carried out at the two key sites in Argentina, in Delaware Bay, and during southward migration in the Gulf of St. Lawrence in Canada. Reports of these activities are presented here. In Roebuck Bay, northwest Australia, much groundwork was laid by additional individual marking of good cohorts of the target species and many resightings were made, also during northward migration in China. Finally, 2007 was a very successful year for the satellite tagging of Bar-tailed Godwits and Bristle-thighed Curlew under the umbrella of the Pacific Shorebird Migration Project.
4. With respect to the state of the monitored populations, there is little hopeful news to report. The ongoing reclamation of Saemangeum in South Korea already has led to measurable declines in Great Knot numbers in northwest Australia. This was to be expected in view of the reliance of this species on this area. The ongoing demographic work will tell us more about the demographic background of the decline (heightened mortality, reduced recruitment, or both).
5. A couple of new and important publications resulting from the worldwide research team that represents the *Global Flyway Network* have seen the light of day, and these are enclosed in the report as Appendices.

Introducing the *Global Flyway Network*

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. 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 2007, the first operational year of the network, being the second. (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 now planned to be organised in October 2009 in California in conjunction with the Pacific Shorebird Migration Project and with additional support from the Packard foundation.
- (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. Tomas 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* and some of them represented in this report. All this work should underpin our sentinel services and story-telling contributions.

List of contributing scientists and institutions

	Affiliation(s)	Specialization (flyway, species or trade)	% funded by GFN
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 Ntiamo-Baidu	WWF/Univ. Ghana, Ghana	East Atlantic, ecology/conservation	p.m.
Field technician			
Chris Hassell	GFN/NIOZ, 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	
Nathan Senner	Cornell University, Ithaca, USA	Hudsonian Godwits	
Dr R.I. Guy Morrison	Canadian Wildlife Service, Canada	West Atlantic, Red Knot	
Grant B. Pearson	Bennelongia, 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	
Drs Yvonne I. Verkuil	Univ. of Groningen, Netherlands	Ruff	
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	

Developments in 2007

In 2007 the *Global Flyway Network* started in earnest. With financial support from BirdLife Netherlands (Vogelbescherming Nederland) we employed two long-established key-workers along respectively the West-Atlantic Flyway (Patricia M. González, San Antonio Oeste, Argentina) and the East Asian-Australasian Flyway (Chris Hassell, Broome, Australia) for the full year. In addition, we helped to support the work of Dr Sergio Pereira at the Royal Ontario Museum in Toronto, who is making steep progress on deciphering what we believe is a key gene complex (also to address conservation issues), the MHC complex in Red Knots. The Major Histocompatibility Complex is a set of disease-resistance related genes that may play an important role during and after population bottlenecks.

In 2007 intense field work on the endangered *rufa* subspecies of Red Knots was carried out at the two key sites in Argentina, in Delaware Bay, and during southward migration in the Gulf of St. Lawrence in Canada. In Argentina, not only did Patricia M. González continue the demographic monitoring of the seriously endangered *rufa* population of Red Knots, she also organised very labour intensive fieldwork to document the food resource base at the San Antonio Oeste staging site, trained many students and rangers in the process and helped establish the Shorebird Interpretation Centre “Vuelo Latitud 40”, opened to the public on 8 December 2007. To top up her activities, Patricia continued her work in Delaware Bay and took part in the expedition to the Mingan Archipelago, to establish the importance of this site in the Gulf of St. Lawrence during southward migration.

In Roebuck Bay, northwest Australia, much groundwork was laid by additional individual marking of good cohorts of the target species and many resightings were made. During the northward migration times, Chris Hassell travelled to China and visited all key locations there, interacting with the local scientists and conservationists, helping during the counts and trying to see as many individual birds and read as many individual colour-band combinations as possible.

Finally, 2007 was a very successful year for the satellite tagging of Bar-tailed Godwits and Bristle-thighed Curlew under the umbrella of the *Pacific Shorebird Migration Project*, work that has been continued as part of the *Global Flyway Network* agenda in 2008, and a summary accounts of both the 2007 efforts and the beginnings of the one in 2008 are presented below.

One of the aims of the *Global Flyway Network* is to foster cooperation among members of the worldwide community of shorebird demographers, and between this community and the conservation folks. As part of the annual conference of the International Wader Study Group in La Rochelle, France, from 29-31 September 2007, a well-attended workshop (over 100 present) was held to evaluate the population biology and conservation of the two European subspecies of Black-tailed Godwits, one of which, *Limosa limosa limosa*, is in steep decline and the other, *Limosa limosa islandica*, which, unique among shorebirds, is doing quite well. The contrasts between the historical ecologies of the two species was very informative, and demonstrated the current dependence of Black-tailed Godwits on human created landscapes. The resulting summary paper is enclosed in this report.

Annotated focal species list: most recent population developments

Based on the worklist of focal species and subspecies (including sites of focus, ecological characteristics and whether the populations are on a trajectory of increase or decline), we here, this time *very briefly*, summarize our latest accumulated insights in how these birds are doing, as an alerting service to the BirdLife International community.

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	Increasing but 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

1. Red Knot *Calidris canutus canutus* — Preliminary calculations of population size of this West-African wintering and Siberian breeding population based on ring densities of Banc d'Arguin marked individuals (B. Spaans *et al.* in prep.), does not suggest further declines in recent years.

2. Red Knot *Calidris canutus piersmai* — The latest population estimate for this population (Wetlands International) was ca. 30,000. Based on the counts in NW Australia in the context of the MYSMA project we have no evidence for further declines in recent years (see report by D.I. Rogers below).

3. Red Knot *Calidris canutus rogersi* — No changes in reported status.

4. Red Knot *Calidris canutus roselaari* — This subspecies has remained enigmatic in its occurrence, and good evidence to link possible wintering areas around the Caribbean (southeastern states of the USA and northern Brasil) with breeding areas in Alaska and Wrangel Island was lacking. Now information has become available from Baja California, winter 2007-2008, suggesting that the *roselaari* population from Alaska and Wrangel Island winters in that region (including colour-banding sightings; H.P. Sitters pers. comm.). The precise subspecific status of the “Caribbean-winterers” remains to be resolved.

5. Red Knot *Calidris canutus rufa* — During the 2007-2008, after three years of fairly stable wintering numbers in Tierra del Fuego, numbers seem to have declined by a third, both based on counts at Rio Grande by the *Global Flyway Network* team (A.J. Baker pers. comm.) as during the overall aerial surveys in Tierra del Fuego (Chile and Argentina) carried out by R.I.G. Morrisson and R.K. Ross (pers. comm.).

6. Red Knot *Calidris canutus islandica* — At present the population seems to be in slow decline (B. Spaans *et al.* in prep.).

7. Great Knot *Calidris tenuirostris* — Of the total world population of 340,000 Great Knots, in May 2007 70,000 went missing from the Korean coast after the reclamation of the Saemangeum key site. This translated itself in a decrease of 20,000 birds on the northwest Australian wintering grounds. See the detailed report by D.I. Rogers that follows this chapter.

8. Bar-tailed Godwit *Limosa lapponica lapponica* — Whilst the subspecies seems on the increase in the Dutch Wadden Sea (SOVON counts), its wintering numbers are decreasing in the German part of the Wadden Sea.

9. Bar-tailed Godwit *Limosa lapponica taymyrensis* — On the basis of ring-density estimates of godwits on Banc d’Arguin, Mauritania, birds that are ringed during stopover in the Dutch Wadden Sea, the estimate of their population size is about 200,000 birds lower (!) than what is the currently accepted population figure of 540,000 birds (B. Spaans *et al.* in prep.).

10. Bar-tailed Godwit *Limosa lapponica menzbieri* — No evidence for very recent declines.

11. Bar-tailed Godwit *Limosa lapponica baueri* — A subspecies in decline, but no further known change of population status.

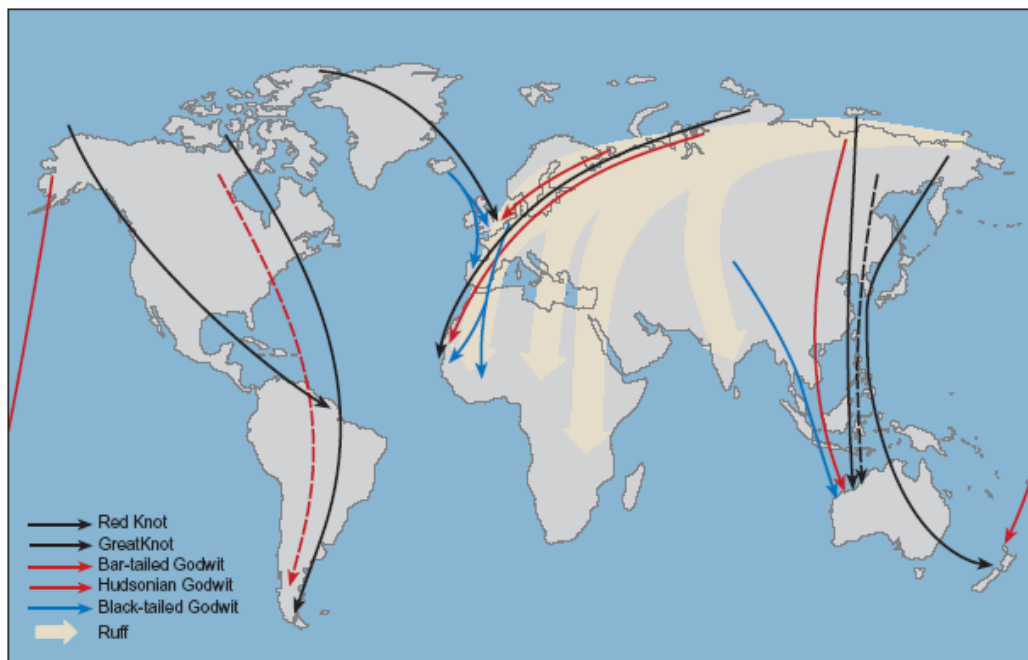
12. Hudsonian Godwit *Limosa haemastica* — No known recent change in population status.

13. Black-tailed Godwit *Limosa limosa limosa* — In spring 2007 on the Friesland breeding study area, many birds were reported back from the West African breeding grounds that were subsequently not reported breeding. This suggests that in some years a fair proportion may skip breeding, and this will have serious repercussions for their demography. We have no reason to believe that population decline has stopped recently, but population size estimates certainly need reassessment.

14. Black-tailed Godwit *Limosa limosa islandica* — The increase of this subspecies is either slowly continuing or has halted over the past few years.

15. Ruff *Philomachus pugnax* — Although numbers staging in Friesland during northward migration seem to be in decline, we don't know whether these reflect total population numbers. See update by Verkuil *et al.* in this report.

16. Sanderling *Calidris alba* — Other than a suggested increase in the numbers using the Dutch Wadden Sea, no evidence for population status changes have come forward. See summary of recent colourringing work by Reneerkens and Koomson in this report.



Population status update for East Asian-Australasian Flyway

Danny I. Rogers

Much of the shorebird migration that occurs in the East Asian – Australasian Flyway (EAAF) is funnelled through the Yellow Sea. It has been an area of concern to shorebird conservationists for some time, given the huge human population in this region (many of them making a living from the tidal flats) and the extensive reclamation of tidal flats (c. 40% of Chinese and 50% of Korean tidal flats have been reclaimed in the last 50 years).

The most controversial reclamation project has been the ongoing work at Saemangeum, on the west coast of south Korea, which was formerly the single most important site of staging shorebirds in the EAAF. It is now the site for the largest reclamation project ever undertaken (involving construction of a 33 km sea-wall through intertidal and subtidal waters, and resulting in the loss of over 400 km² of tidal flat). Concern about Saemangeum led to the development of two projects using counts to assess effects of the reclamation: (1) the Saemangeum Shorebird Monitoring Project (SSMP) involves censuses of birds in Saemangeum and two adjacent natural sites, the Geum Estuary and Gomso Bay; (2) The Monitoring Yellow Sea Migrants in Australia (MYSMA) aims to monitor shorebird populations in the key non-breeding areas of North-western Australia, and also to develop techniques to analyse such count data. As will be seen below, this data is complementary to the demographic data obtained through the GFN.

Red Knot *Calidris canutus piersmai*

The latest population estimate for this population (Bamford & Watkins 2007) was c. 30,000 birds. A large proportion of these birds spend the non-breeding season in sites in north-western Australia which are censused annually by the MYSMA project. The Saemangeum reclamation was not expected to have large effects on *piersmai*, as most are thought to follow a migration route up the western side of the Yellow Sea and few stage in Korea. Results from the summer 2007-08 survey, combining counts from northern Roebuck Bay, Bush Point and a 60 km stretch of Eighty-mile Beach (see Rogers *et al.* 2006 for methodology) suggest there was a slight increase in numbers in 2007 (Table 1). The effect was not statistically significant but may have been real nevertheless, as age-ratios within non-breeding flocks suggesting breeding success had been high. Despite this encouraging result, it should be remembered that north-western Australian counts of Red Knots were considerably higher in the 1980's, suggesting the longer-term population trend of this subspecies is a decline.

Great Knot *Calidris tenuirostris*

A decline in numbers of Great Knots in 2007 was anticipated because of the deterioration of Saemangeum. Saemangeum used to be a site of particular importance to this species; nearly 30% of the world population of c. 340,000 used to stage there on northwards migration. In 2006, SSMP surveys established that Saemangeum was still a stronghold for Great Knots, with a build-up in numbers from mid-April to late May before a late departure indicating that the area was used as a launching point for a long-distance flight to Siberian breeding grounds. The Saemangeum sea-wall was officially closed on April 21st, reducing the tidal range inside from over 6 m on spring tides to less than half a metre, and causing a massive shellfish die-off. This die-off was

exploited by Great Knots (and a number of other shorebird species) which fed on dying and dead bivalves as they gaped open on the surface. As a result they probably managed to fuel and migrate on schedule in 2006. A bivalve can only die once, so no such resource was available in 2007, when tidal range in Saemangeum had declined further, to less than 20 cm. Instead of increasing in numbers during the migration season, Great Knot numbers decreased during April and May. In mid-May 2006 there had been 88,000 Great Knots in Saemangeum; in mid-May 2007 there were only 3,500. There were increases in numbers at the adjacent Geum Estuary and Gomso Bay, but they were not sufficient to account for all birds lost from Saemangeum, and 70,000 Great Knots were “missing”.

Given the difficulty of breeding grounds access, and of counting large areas of the Yellow Sea concurrently during the brief period of northwards migration, determining the fate of these missing 70,000 birds is only practical on the non-breeding grounds. Colour-band resightings by the SSMP had previously demonstrated that Saemangeum is visited by large numbers of birds from north-western Australia, and also by large numbers of birds from eastern Australia. Counts undertaken in eastern Australia in the austral summer of 2007/08 have yet to be compiled and analysed, but data from MYSMA surveys on north-western Australia are already available (Table 1). These show that numbers had decreased significantly, by some 20,000 birds, since the austral summer of 2005/06 (the last season of north-western Australian counts pre-Saemangeum reclamation). Saemangeum therefore seems to have caused a large increase in annual mortality of Great Knots (especially when bearing in mind that not all of the 70,000 “missing” birds from Saemangeum were from north-western Australian non-breeding grounds). The band-recapture data being collected by the global flyways network will allow a direct calculation of this increase in annual adult mortality to be made in 1-2 years time (for statistical reasons, a follow-up season of colour-band resightings is required to obtain a satisfactory estimate of mortality in a given year).

Bar-tailed Godwit *Limosa lapponica menzibieri*

MYSMA surveys showed no evidence for immediate declines in this subspecies. The Saemangeum population of Bar-tailed Godwits was never very large (c. 5,000 birds) and colour-band and flag resightings indicated that although *menzibieri* do pass through in the area in April, the great majority of the birds there are subspecies *baueri* from eastern Australia and New Zealand.

REFERENCES

- Rogers, D.I., N. Moores and P.F. Battley. 2006. Northwards migration of shorebirds through Saemangeum, the Geum Estuary and Gomso Bay, South Korea, in 2006. *Stilt* 50: 73-88.

Table 1. MYSMA counts of shorebird numbers in selected sites of north-western Australia: (1) the northern beaches of Roebuck Bay; (2) Bush Point (southern roebuck Bay) and (3) A 60 km stretch of Eighty-mile Beach. Two austral-summer surveys are carried out each season between late October and early December; count methodology and the method used to calculate standard errors are outlined in detail in Rogers *et al.* 2006. Note that the 2006 surveys below were complicated by disturbance to a section of Eighty-mile Beach, and corrections for these effects have yet to be carried out; the 2006 numbers may therefore be revised in future.

Season	Red Knot, <i>Calidris canutus piersmai</i>		Great Knot, <i>Calidris tenuirostris</i>		Bar-tailed Godwit, <i>Limosa lapponica menzbieri</i>	
2004	11,427	± 2,495	92,450	± 10,287	70,335	± 6,624
2005	12,702	± 2,445	96,620	± 12,157	72,513	± 6,450
2006	12,671	± 1,944	83,031	± 6,939	87,358	± 8,077
2007	13,259	± 3,400	76,501	± 7,149	70,444	± 5,869



Summary of the activities of Patricia M. González

Patricia M. González



Coordination

Coordination of field teams in San Antonio Oeste (SAO) from February to April 2007 (Inalafquen students and volunteers, environmental rangers, and international researchers: Allan Baker and Guy Morrison) to run simultaneous censuses, scans of color-banded birds, cannon netting, and food and feeding studies.

Under WHSRN Monitoring of Red Knot project in Patagonia, coordination of censuses and scans of color banded knots at Rio Grande wintering grounds, Rio Gallegos and Peninsula Valdes during northern migration (this is with matching funds provided by GFN for the season).

Coordination of Rio Grande 9th International Shorebird Banding Expedition in November 2007.

Training

Training of students from Rio Gallegos in scanning and resightings (April 2007)

Training of rangers and Inalafquen volunteers in cannon netting shorebirds (March 2007 in San Antonio Oeste and November 2007 in Río Grande).

Course for future rangers about Shorebirds and Conservation, December 2007.

Public awareness

First presentation of the building for Shorebird Interpretation Center “Vuelo Latitud 40”, opened to public on 8 December 2007. Scientific advisor for the exhibition under

“Multinational project for Red Knot Conservation at 3 sites in Patagonia” funded by Neotropical Migratory Bird Conservation Act from USA, a private owner, Fundacion Inalafquen and Ocasión Turismo.



Scientific advisor for the updated version of documentary video “Una historia de viajeras” (*A tale from travellers*) from Juan Pablo Chillón and the shorebird video film for the Interpretation Center.

Fieldwork in San Antonio Oeste, Argentina

25 simultaneous censuses from 5 February to 2 May 2007.

2500 sightings of individually colour-banded knots.

4900 Red Knots scanned for proportion of banded birds.

Red Knots scanned for % breeding plumage, abdominal profiles, proportion of juveniles.

Waypoint records of feeding flocks.

Catches: 164 Red Knots caught on 22 March 2007 at Mar Grande (19 of them retraps from other expeditions) plus 1 Hudsonian godwit.

Feeding ecology during northern migration in SAO (see attached report)

At Banco Reparo sandflats

Benthos sampling with 2 corers in each of 129 pk for a big grid (see attached graphs I got from Maru today) in the middle of the season.

Sampling with 5 corers in each of 25 pk three times (Feb, March, April) at hot spots.

Dropping collected in March and April (Total 383 droppings), they were already weighed and sieved, from some of them, condroforos of Darina were separated.

Extra benthos sampling was done at 7 waypoints where birds were seen feeding.

Some *Darina* and *Travisia* were dried for future estimates of AFDM and Ash Mass.

At restinga

A total of 65 samples of mussels (N= 8710) were taken at 5 waypoints (having information from previous years) in the restinga, three times during the season. Shell length of mussels were already measured (not computerized yet). Fraction of the sediment was separated by size class (>300 microns and < 300 microns). An extra sampling of clams was taken at place where knots were found feeding on them in the low intertidal. Four to seven pictures of all pk at restinga were taken.

A total of 345 droppings were collected during February and March (sorry I don't have here the number of samples). Some mussels were dried up for estimates of AFDM and Ash Mass.

Benthos sampling in December in SAO (when knots are in wintering areas)

Sampling with 5 corers in each of 25 pk in Banco Reparo sandflats.

A total of 12 samples of mussels (N = 2096) were taken at 6 waypoints in the restinga (having information from previous years).

Other work and resighting efforts

In Delaware Bay, USA

From 17 May to 29 May 2007, a total of 613 sightings of individually color-banded knots and 3468 Red Knots scanned for proportion of banded birds were taken at New Jersey and Delaware shores (trip funded by ROM).

In Mingan Archipelago, Quebec, Canada

Participant in the resighting and shorebird banding expedition organized by Royal Ontario Museum and Canadian Wildlife Service between 19 August to 5 September 2007 (see attached report).

In Rio Grande, Tierra del Fuego, Argentina

General coordinator of the Red Knot banding expedition and food & feeding sampling from 6 to 14 November 2007. See attached report.

In La Coronilla, Uruguay

Two days of visit from 16 to 17 November 2007 to the north shore of Uruguay between La Coronilla and El Chuy, with Joaquín Aldabe from Birdlife Uruguay and Allan Baker. The objective was to see the areas where a mass mortality of Red Knots occurred in the past April, interview witnesses, and monitor number of Red Knot presents (only 22 juveniles as total) as part of a cooperative effort with Birdlife Uruguay to design a monitoring plan for 2008 migration season.

Manuscripts

Licenciatura Thesis defense on 13 March 2007 at Univ. Buenos Aires :

Population decline of a long distance migrant Red Knot Calidris canutus rufa, (Scolopacidae): the role of sex-specific survival and migratory strategies.

Director: Allan J. Baker

Codirector: Juan Carlos Rebores

MS for publication

González P. & Baker A.J. *Male biased annual survival associated with population decline of a long distance migrant Red Knot Calidris canutus rufa, (Scolopacidae): the role of migratory strategies.*

Published paper

González, P.M., A.J.Baker & M.E. Echave. 2006. 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. *Hornero* 21:109-117. This paper is included in this report as Appendix B

Presentation in Wader Study Group Annual Conference,

La Rochelle, France, 28 September to 1st October 2007

Quality vs Profitability: Bimodal selection of mussel sizes by Red Knots Calidris canutus rufa when soft prey were available during the 2006 northward migration at San Antonio Oeste, Río Negro, Argentina

Patricia M. González, María Eugenia Echave, Mirta Carbajal, Luciana Barzola & Paula Zaidman.

Monitoring of the declining *rufa* Red Knots at Río Grande wintering site, Tierra del Fuego, Argentina

Patricia M. González, Allan J. Baker & Luis Benegas



Other participants

Gastón Tolosa (Fishery technician student Univ. of Comahue, Argentina)

Matías Suárez (Fishery technician student Univ. of Comahue)

and participants of the shorebird banding expedition

Introduction

Río Grande in Tierra del Fuego (TDF), Argentina, is at the southern tip of the West Atlantic flyway where *rufa* Red Knots spend their nonbreeding season from late September to early March. Along with the major wintering site at Bahía Lomas in Chile, a total of 18,000 birds winter in TDF. Río Grande is a city placed at the mouth of the Río Grande river and hosted 5000 to 6000 Red Knots before the dramatic decline in population size in the period 2000-2001 to almost 3000 knots in years 2006-2007 (González *et al.* 2004, Morrison *et al.* 1989, 2004, aerial censuses from CWS). From 6 to 15 November 2007 we ran the 9th International shorebird banding expedition in Río Grande coordinated by PMG, AJB and LB with the objectives of 1) to collect recapture and resighting data of previously banded birds and to capture a new cohort and mark and release them for ongoing annual survival estimates, 2) to measure the condition of birds (body mass, percentage of breeding plumage, body molt and primary molt status), 3) to estimate local population size, and 4) to evaluate food supplies at the local scale and prey selection by the birds.

On 8 November, 2007 we caught 670 knots of which 325 were processed (120 recaptures from former expeditions in Río Grande & San Antonio Oeste in Argentina, and Delaware Bay in USA, + 205 new birds) while 345 were released. Average body mass of adults was the lowest ever recorded in an expedition there (Fig. 1).

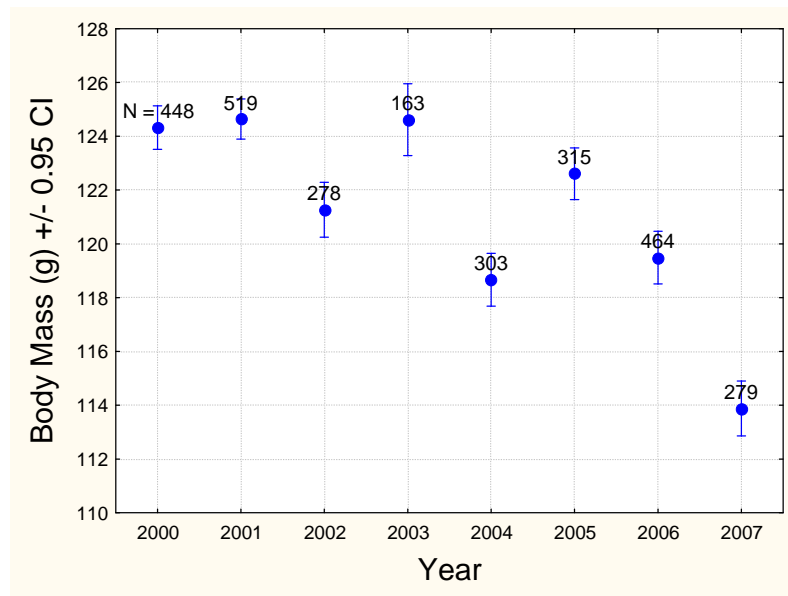


Fig. 1. Average body mass of adult *rufa* Red Knots in annual catches in November/December at Rio Grande ($p < 0.001$) (from Baker *et al.* 2005 & unpublished data).

Previous studies of feeding ecology of Red Knots in Rio Grande in February 1995 (T. Piersma & P. de Goeij unpublished) and January 2000 (G.B. Escudero & T. Piersma unpublished) have shown that the main prey of knots were the clam *Darina solenoides* in the intertidal sandflat and the mussel *Mytilus edulis* on the “restinga” (rocky flat). These authors found that in diet reconstruction from faeces the ingested shell length of *Darina* ranged from 15 to 32 mm, and visually estimated that sizes of ingested mussels ranged from 10 to 25 mm. Our preliminary analysis of the benthos at 60 sampling points in the feeding areas for Red Knots in Rio Grande in 2007 revealed that the mode of the size distribution of harvestable clams was located in small sizes, far below those selected in 1995 & 2000. While smaller clams are likely better quality food than bigger clams they are less profitable (Fig. 2A). The opposite was observed for mussel size distribution on restinga (Fig. 2B).

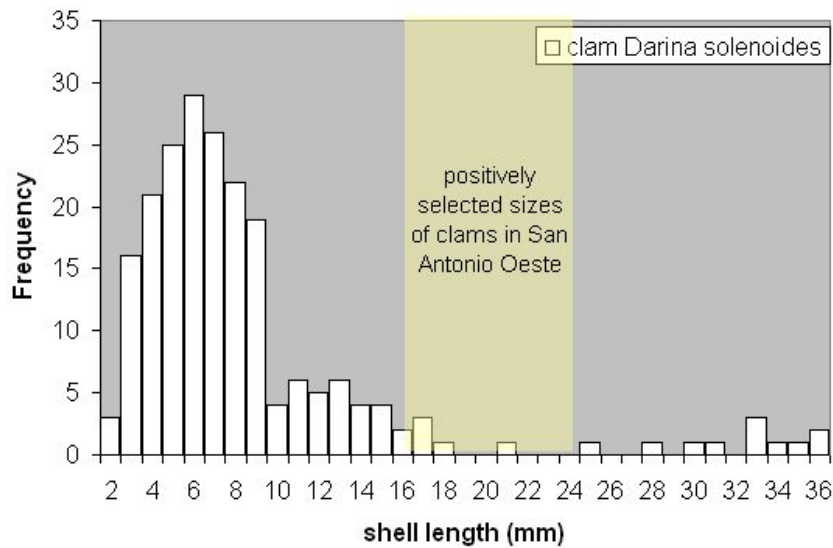


Fig. 2A. Size distribution of the clam *Darina solenoides* in 5 cm top layer in Río Grande sandflat in November 2007. If knots in Río Grande positively select same sizes as in SAO, then availability of positively selected sizes is remarkably low.

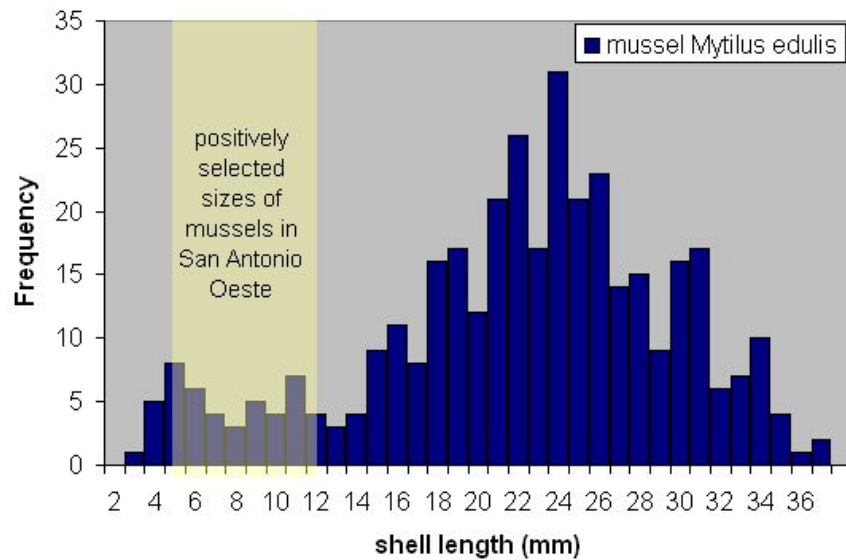


Fig. 2B. Size distribution of mussels on Río Grande upper and medium intertidal restinga. Range of positively selected sizes of mussel *Brachidontes rodriguezi* in San Antonio Oeste is shown; if knots in Río Grande positively select same sizes as in SAO, then appropriate shell lengths for knots are poorly represented in November 2007.

Calorific determinations of mussel and clam samples plus diet reconstruction from 400 faeces collected during this expedition will be carried out in the near future to provide more insight on feeding energetics, but these preliminary results suggest that the low average body mass of knots in RG in 2007 is related to low availability of appropriate prey sizes for knots. Visual observations of knots feeding on mobile polychaetes near the sewage discharge of the water treatment plant of the city supports this conclusion. On the other hand the number of Red Knots censused this year was only 1200 birds, less than half of the number recorded the previous year. Future aerial censuses and analyses of annual survival of individually color marked birds will let us know if this decrease corresponds to a redistribution of the birds to better feeding conditions elsewhere, or to a broader and more serious decrease in their survival in TDF.

At present we have begun to analyze this situation with the provincial and city authorities of Río Grande to elucidate potential reasons for this problem. In particular we consulted with staff of the Mayor's office to try and halt development of the small remaining part of the Beach where the Knots roost at high water. If the building of a new hotel and other other building go ahead then this site will be destroyed as a favoured high water roost for the birds.

Acknowledgements

We thank Tabaré Barreto, Walter Alejandro, Juan Pablo Suárez, Erika Tavares, Sarah Frey, Alejandra Varisco, Lesley Howes, Joaquín Aldabe, Miguel Isla, Silvia Gigli and Cristian Pantoja who helped to collect and sort benthos and dropping samples as well to catch and band Red Knots.

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Food and feeding of the declining *rufa* Red Knots at its major austral stopover: San Antonio Oeste, Río Negro, Argentina

Patricia M. González



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Introduction

San Antonio Oeste (SAO) is the first major stopover site for the declining *rufa* Red Knot population during the northwards migrating from Tierra del Fuego to their Arctic breeding grounds. Located only 1450 km from the southern tip of the continent, SAO hosts from 25 to 50 % of the wintering population every year from February to April, thus in the years 2005 and 2006 around 9,500 knots of the ca 18,000 censused by Canadian Wildlife Service in Tierra del Fuego stopped in this site. Although SAO is a natural area protected by provincial law (2670 /2003), in recent years it was developed at an accelerated rate without systematic planning for tourism, housing, and recreation. Development threatens the roosting and feeding areas for Red Knots, and a Soda Ash factory placed adjacent to one of the knot feeding areas began to work in 2005/6. The dramatic decline of Red Knots in last 10 years (Morrison *et al.* 2004) has been related to a limitation of their food, horseshoe crab eggs (*Limulus polyphemus*), due to overfishing of adult horseshoe crabs at Delaware Bay, USA, their last stopover site before reaching their breeding grounds in the Arctic, as well as the late arrivals from the birds coming from South America (Baker *et al.* 2004). Birds arriving late in SAO also arrived later in Delaware Bay (González *et al.* 2006), and was shown to have subsequent fitness consequences.

Food and feeding of Red Knots might be expected to affect their condition and migratory strategies, and thus are key aspects to monitor at San Antonio Oeste. Studies before the decline (González *et al.* 1996, Sitters *et al.* 2001) showed that knots during day feed mainly on mussels that they find at rocky flat surfaces known as "restinga", and at night on San Antonio Bay mudflats. However field observations from the 2004 and 2005 migration seasons showed atypical use of feeding places where knots were foraging on sand flats on Banco Reparo near the new Soda Ash factory.

Our objectives were establish food availability at a local scale, feeding behavior and prey selection that could be related with other variables like bird condition, stopover duration and number of Red Knots present during the northern migration in 2006 and 2007 to further relate with migratory strategies and annual survival. Study area and grid sampling points are shown in Fig. 1.



Fig. 1. Location of San Antonio Oeste area. Big grids showing poskeys (sampling points) as red dots every 200 m at Banco Reparo (128 pk) and the restinga (81 pk). A small grid for bigger sampling effort with 100 m between poskeys at Banco Reparo (25 pk) is shown in yellow.

Results from the 2006 season showed that knots fed mostly in the sandflat not because of the lack of mussel availability in the restinga but the good availability of the polychaete *Travisia olens* in Banco Reparo. This prey is a good quality food because it is unshelled, has low mobility, and burrows near the surface of the sediment where knots can easily detect and reach it. In terms of food availability, the restinga provided an average of 7.7 g Ash Free Dry Mass (AFDM)/m² of mussel meat kept constant throughout the stopover period. However, the sandflat offered 5.4 g AFDM/m² of *T. olens* on 13 March that was already depleted to 1.3 g AFDM/m² by 25 March 2006 ($p < 0.001$). Both at the beginning and later in the season, when knots have just arrived and ready to leave, respectively, they used only the sandflat. This is the time when

birds might have reduced guts after and just before long distance flights. At this stage knots cannot process a big amount of shell mass such as mussels have, thus polychaetes are the best choice.

During the 2007 season knots fed mainly on restinga mussels. While the availability of mussel meat was similar to 2006, the availability of *T. olens* offer in 2007 was lower than in early March 2006, constant from 23 February to 10 April 2007 with an average of 1.5 g AFDM/m².

Feeding behavior of knots could be explained by the size of their gizzards. Studies of Jan van Gils, Theunis Piersma and other authors (e.g. Piersma 1997, van Gils 2004) have shown that Red Knot is a digestively constrained migrant with high phenotypic variability of organ sizes within the same individual: small gizzards have lower ability to process shell mass than bigger gizzards unless the prey item is soft (like *T. olens*). Thus bigger gizzards have the benefit of a higher rate of processing shell mass but the compromise of several days to get built it up after arriving from a long distance flight with a small gut; on the other hands Red Knots with small gizzards only can choose high quality prey with small amount of ballast relative to digestible biomass.

Resightings of color banded knots from different origins in 2006 (Rio Grande and Bahia Lomas in Tierra del Fuego, San Antonio Oeste in Argentina and Delaware Bay in USA) showed that the likelihood to resight a bird banded in San Antonio Oeste was higher in Banco Reparo than in the restinga ($p < 0.003$), in other words, this group of knots preferred to feed on the sandflat. These birds that have been banded here exhibit a higher fidelity compared with birds from other origins (Gonzalez *et al.* unpublished), thus they know the place better. Birds feeding mainly on soft food might have a small gizzard, as consequently if they decide to feed on the restinga they have to choose smaller sizes of mussels with a higher ratio of AFDM/shell. Diet reconstruction from faeces collected on the restinga showed a bimodal size distribution of ingested mussels, then suggesting two groups of feeding knots: one with smaller and another with bigger gizzards (Fig. 2 A). However, in 2007 all ingested sizes of mussels corresponded to birds with big gizzards (Fig. 2 B), as was found in a study in 1992.

Capture-recapture analysis of turnover showed that 9,500 knots passed through SAO in 2006, but only 7,500 knots stopped in 2007. As the population size of wintering knots in Tierra del Fuego was similar in both years (aerial censuses by CWS), it is possible that differences in the availability of mussels of a suitable size and high quality polychaetes impacted migration strategies and affected decisions of individual knots including the choice to skip SAO as a stopover site. In this context the size of gizzards of arriving birds may play an important role in refuelling strategies at stopover sites with associated fitness consequences. Our objective in 2008 and the following years is to relate feeding behavior of individually marked birds with their short term seasonal survival and annual survival. The big database of resightings and the cohorts of knots caught in SAO during 2006 and 2007 will provide the baseline.

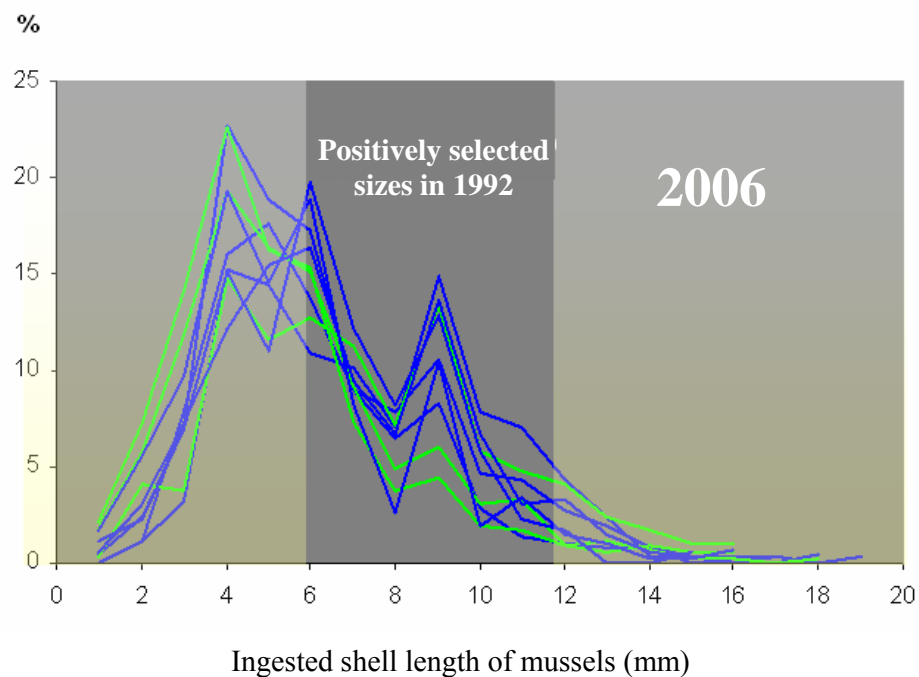


Fig. 2A. Relative frequency (%) of ingested sizes of mussels in droppings of Red Knots feeding on the restinga in 2006. Blue lines with bimodal distribution represent samples taken in March and early April 2006; green lines represent samples taken on 22 April 2006, four days before a big departure on migration. The size distribution shows two samples with a depressed mode in larger sizes, and one

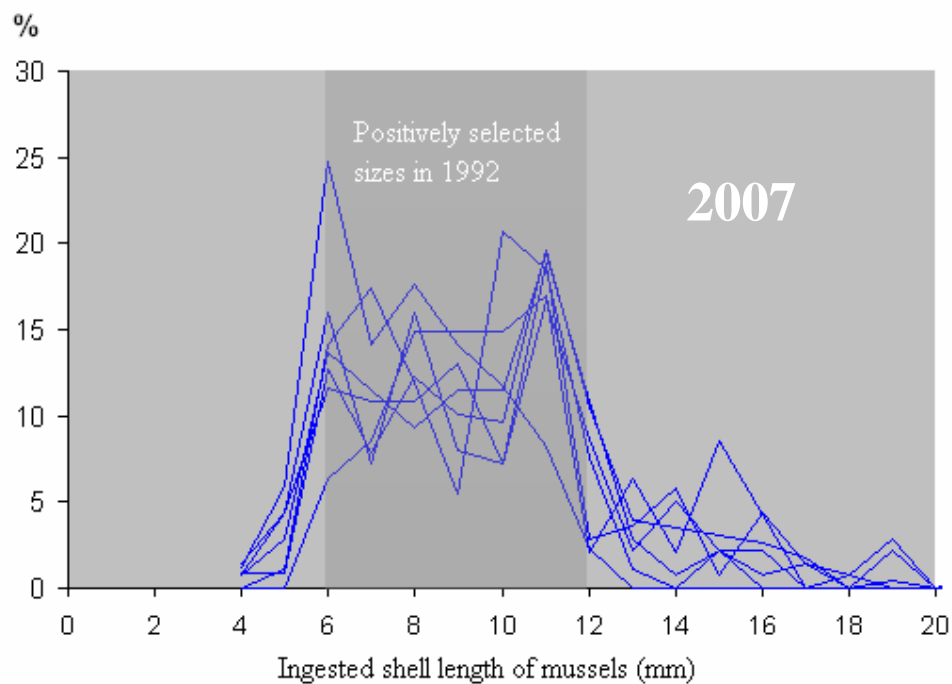


Fig. 2B. Relative frequency (%) of ingested sizes of mussels in droppings of Red Knots feeding on the restinga in 2007.

Acknowledgements

We are very grateful to Theunis Piersma, Petra de Goeij and Allan Baker for their advising in this study. The Institute of Marine Biology “Alte. Storni” provided a lab to analyze samples and their researchers provided advice to the students in this project. Environmental rangers, Guy and Susan Morrison helped with the collection of droppings. Binocular microscope and supplies were provided by Dirección de Fauna de Río Negro. Calcinations were made at INTA lab in Bariloche, Argentina. Funding provided by Birdlife Netherlands to Aves Argentinas-Fundación Inalafquen (2006) and GFN (2007).

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Male-biased mortality associated with a large population decline of a long distance migrant Red Knot *Calidris canutus rufa*, (Scolopacidae): the role of migratory strategies

Patricia M. González & Allan J. Baker



The new world *rufa* subspecies has suffered a dramatic 45% decline from 2000 onwards: population numbers in 2003 were about 30 000 compared to 67 500 in the mid-1980s (Morrison *et al.* 2004, González *et al.* 2004). This decline was related to a limitation of their food, the eggs of horseshoe crabs (*Limulus polyphemus*), because of overfishing of this species at Delaware Bay, USA, and possible late arrival of adult knots at this last stopover site before reaching their breeding grounds (Baker *et al.* 2004).

In this study we investigated whether (1) this decline was associated with a differential sex specific survival,)2) migratory strategies are different between males and females, and)3) if migration patterns and condition dependent variables may explain changes in annual survival.

Capture-recapture analysis with Barker's model of 221 banded and molecularly sexed knots in year 1998 (before the decline) in San Antonio Oeste, Argentina, shown that average survival of males ($\Phi = 0.57$ 95% CI [0.48 - 0.66]) was lower than females ($\Phi = 0.74$ 95% CI [0.66 - 0.81] in period 1998-2000, with no significant differences between survival of males ($\Phi = 0.87$) and females ($\Phi = 0.97$) in the period 2000-2004 (after the decline). As result the adult sex ratio measured on annual catches in their wintering ground of Rio Grande, Tierra del Fuego, became biased in favor of females in December 2000 (N = 92, male ratio = 0.38 $p < 0.05$) and November 2001(N = 222, male ratio = 0.41 $p < 0.05$) , thus contributing to the population decline.

In the Arctic, precocial chicks are under care of males, thus on average successful breeders leave the breeding grounds three weeks earlier than females. However, arrival time in the Tierra del Fuego wintering grounds inferred from the progress of primary molt did not show sex-specific differences, suggesting that phenology of males had a compressed timing during southern migration. Males as well exhibited a delay in acquiring the basic plumage and underwent a higher rate of body mass increment before

starting the annual molt of flight feathers, compared with females. Once flight feather molt begun, primary molt progress explained a decrease in body mass in both sexes (p males < 0.001 , p females < 0.05); while body molt intensity was negative correlated only in males ($p < 0.014$).

When arriving in the wintering grounds, males exhibit a delay in acquiring the basic plumage ($p < 0.01$). However during northern migration in San Antonio Oeste, they are ahead of females in getting the alternate (breeding) plumage ($p < 0.001$).

From February to April 2006 during northern migration in San Antonio Oeste, male ratio from resightings of knots that have been individually marked and sexed in previous expeditions showed that males migrate on average earlier than females (male ratio Feb = 0.73, $N = 26$, $p < 0.05$; male ratio March and April = 0.44, $N = 53$, $p > 0.05$). This pattern have been observed as well in catches on migration in Lagoa do Peixe, Brazil, during early April 1997 (male ratio = 0.61, $N = 111$, $p < 0.01$).

Compared with other migrant Red Knot subspecies around the World, *rufa* knots have to confront a more compressed migration timing, and our results indicate that males had to evolve molt and migration strategies under higher natural selection pressure than females, to be able to adjust to the constraints of a longer breeding season as a result of their mating and parental care system.

Consequently, in annual migration cycles when birds refuel inadequately or are late in breeding this translates into increased fitness consequences for males, as reflected in the biased sex ratio favouring females after the big population decline in 2000-2002. This suggests that different migration strategies of males and females have evolved as a result of sexual conflict in adult survival.

Monitoring annual survival and recruitment in the endangered Red Knot population refuelling on the southward migration at Mingan Archipelago, Quebec, Canada

Allan J. Baker, Patricia M. González & Yves Aubry

To further investigate causes of the continuing decline of the endangered Red Knot in Canada our team monitored the fall migration through the newly discovered refuelling site in Mingan Archipelago National Park in the Gulf of St. Lawrence in 2007 (Fig. 1, 2). Our objectives were (1) to estimate the numbers of Red Knots stopping in the Park to refuel for the onward southern migration, (2) to scan flocks of birds with spotting scopes for studies of annual survival of individually banded adults, (3) to determine the stopover durations and sexes of these individuals and (4) to obtain an annual index of the recruitment of juveniles from the 2007 breeding season.

A total of 23,327 adults were counted in daily censuses, with a peak count of 2,200 on August 8. Corresponding counts for juveniles were 705 in total and a peak of 214 on October 9. Mean stopover durations ranged from 12 to 2 days, suggesting that the population refuelling in the Park was about 5,000 birds. Resightings were made of 500 individually recognizable knots banded in Argentina, Chile, Maranhao in northern Brazil, and Delaware Bay, Florida and Virginia in the USA. Two distinct waves of birds arrived at Mingan composed of both sexes, unlike in 2006 when females leaving the Arctic after the clutch hatched were followed later by males that tended young until fledging. This probably indicates that the breeding season in 2007 was later than in 2006. Body masses of 11 recaptured birds were all above 160g with one reaching 246g, and thus they likely have enough reserves at departure to migrate nonstop to South America or Florida. One knot (B95) surviving the big decline since the year 2000 was resighted in Mingan in 2007 and recaptured in Tierra del Fuego 2 months later, and is estimated have flown the distance to the moon and is now on the way back (Fig. 3).

Knots arriving early in Mingan had higher body masses and had begun primary moult when captured soon after arrival in TDF, whereas late birds at Mingan had lower body masses and had not commenced wing moult. These are condition-dependent differences that have been shown to affect fitness. The hemispheric population is expected to decline significantly following the death of at least 1,300 birds migrating through Uruguay, as evidenced by 40% less birds at Rio Grande in TDF. Adult survival was estimated at 80% in the past, and juvenile recruitment is apparently not high enough for population recovery. Further declines increase the risk of extinction, and continued annual monitoring of the Mingan population has to be a conservation priority for recovery planning.



Fig. 1. Google Earth map showing the location of the Mingan Archipelago National Park Reserve of Canada in the Gulf of St. Lawrence.



Fig. 2. Google Earth map showing the study area in the western part of the Park where the Red Knots are concentrated.

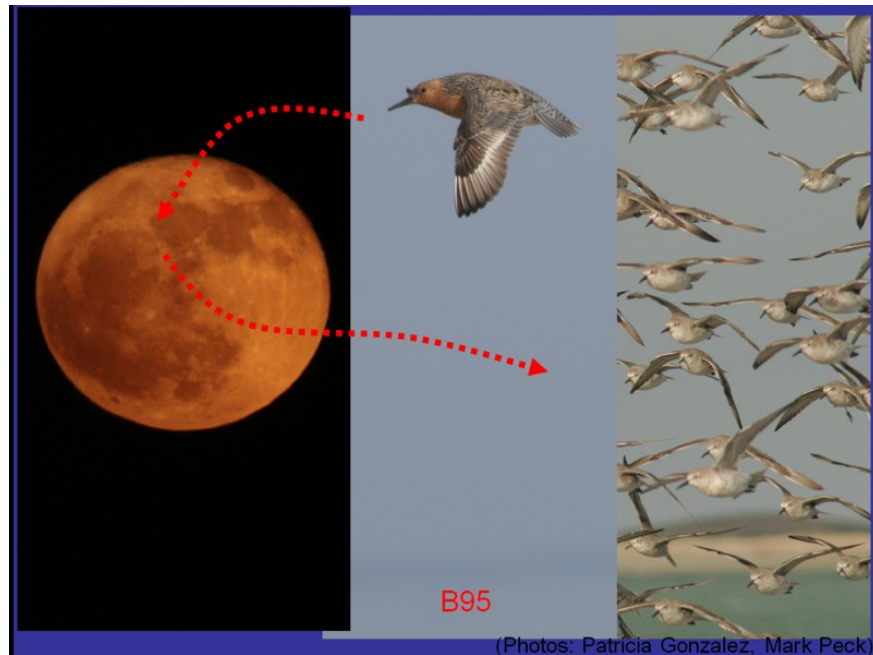


Figure 3. Male Red Knot with an orange flag inscribed with B95 was originally captured as an adult in Tierra del Fuego in 1995, and is at least 15 years old. He is estimated to have flown the distance to the moon and in on his return trip to Earth.



Figure 4. B95 recaptured in Rio Grande, Tierra del Fuego on November 8, 2007, two months after been seen in Mingan, Quebec, Canada.

Progress report by Chris Hassell

Chris Hassell

Another successful year has finished for the GFN/AWSG collaborative north west Australia colour-banding project. Volunteer participation was high with both experienced local people contributing heavily and novices being introduced to the wonders of shorebird research, mostly via the Broome Bird Observatory's guests.

1901 shorebirds were caught in 8 successful cannon net catches of these 199 were Bar-tailed Godwit, 752 Great Knot and 204 Red Knot. And of these the numbers colour-banded are shown in table 1 below.

Table 1.

DATE	SITE	BTG	RK	GK	TOTAL
17/02/2007	SV	40	0	1	41
1/06/2007	2D	22	1	24	47
8/07/2007	WS	17	20	18	55
12/08/2007	RP	0	60	43	103
19/08/2007	CS	18	3	65	86
4/09/2007	SV	11	0	1	12
16/09/2007	CS	0	65	0	65
14/10/2007	2D	8	4	25	37
TOTALS		116	153	177	446

In addition to the work done by the local Broome team 126 birds were colour-banded during the AWSG Shorebird and Tern banding expedition 2007. Shown below in table 2.

Table 2.

DATE	SITE	BTG	RK	GK	TOTAL
11/11/2007	RP	0	0	23	23
12/11/2007	TR	1	0	25	26
13/11/2007	2D	20	0	0	20
14/11/2007	RP	16	0	7	23
26/11/2007	SV	25	0	0	25
27/11/2007	WQ	0	9	0	9
TOTALS		62	9	55	126

These 572 birds bring the total birds with individual colour-band combinations to 873. These marked birds have now yielded a total, over two years, of 3086 re-sightings. Table 3 shows the 2007 totals month by month. Tables 4 to 9 at the end of the document show the species breakdown and re-sighting locations in more detail.

Table 3.

NUMBER OF MARKED BIRDS RE-SIGHTED BY MONTH		
Year	Month	N
2007	1	26
2007	2	157
2007	3	103
2007	4	58
2007	5	126
2007	6	0
2007	7	170
2007	8	230
2007	9	162
2007	10	615
2007	11	85
2007	12	197
TOTAL		1929

One Bar-tailed Godwit we caught on October 14th was a re-trap and we placed an individual colour combination on her. When I got home and punched the band number in to the database I could hardly believe my eyes 'banded **02/09/1981**'. I rang Clive Minton and asked him to check the field data sheet to make sure this was correct and sure enough it was. It was banded on the first ever expedition to Broome. Only four cannon net catches were made on that trip as counting and exploring this new-found (to ornithologists) region was the priority. This is the oldest recorded Bar-tailed Godwit she is now 27 years and 3 months old (having been age 2 at banding) and beats the previous record holder by some 6 years. This bird has been seen alive and well 5 times since she was colour-banded.

Another exciting record was of a Great Knot '1BBBR' caught at Chongming Dongtan Nature Reserve (CDNR), Chongming Dao, Shanghai on April 5 2007 (see attached image). This bird was banded August 27th 2006 at the western end of the northern shores of Roebuck bay and then only ever been recorded at Coconut Well Beach 20KM north of its banding site, prior to its capture in China. This bird has been seen back at Coconut Well on 3 occasions since November 1st 2007. I was at CDNR when this bird was re-trapped but I was not at the banding boat at the time as I was looking for colour-banded birds in a different part of the reserve! The team leader of the shorebird banding at CDNR, Ma Qiang, has subsequently joined me in Roebuck Bay on the AWSG Shorebird and Tern banding expedition 2007.

A particularly pleasing aspect of this years work was the number of Red Knot colour-banded, this species is relatively difficult to catch at Roebuck bay but this year we got 2 excellent catches during the southward migration period which will, and has already, yield useful information. The connection between Roebuck Bay and New Zealand in relation to the two Red knot populations occurring in the East Asian-Australasian Flyway (*rogersi* and *piersmai*) is still not well understood despite the amount of research done at both locations and in Victoria south east Australia.

Already during this project 4 Red Knot with Broome colour combinations have been seen in NZ, including one in the South Island which was an unusual record. During the GFN/AWSG catches in Broome we also caught a Red Knot previously banded at Miranda in the north island of NZ, the first ever caught in Western Australia, this bird was presumably (but not definitely!) of the *rogersi* sub-species returning to NZ via Broome, not the regular route to our knowledge. Another first during my field work, in May, was the record of a Red Knot with an engraved flag from Miranda NZ. Presumably (but not definitely!) a bird on its journey to the Arctic breeding grounds. As our knowledge accumulates on this fascinating species so do the questions!

During my trip to China in March and April 2007 I did not record any Red Knot from the project but just after I left one of my Chinese colleagues, Yan Hong Yen, saw one near Tianjin, Bohai Wan. Hopefully this region will yield more re-sightings this year although the inter-tidal mudflats there are under great pressure from reclamation, as I witnessed during my visit.

Further north in China at Yalu Jiang National Nature Reserve on the border with North Korea 3 Bar-tailed Godwit and 2 Great Knot from the project were seen. This remarkably important area will surely yield many more records in the years to come.

I hope that the northward migration season in the Yellow Sea will yield more resightings this year as the project now has more birds marked and many of the birds that have previously been marked as first and second year birds will be undertaking their first migrations. I will spend three weeks in Korea during May 2008 to further relationships with researchers in the Yellow Sea region and to search for marked birds from both Broome and the GFN marked birds from NZ.

Table 4.

SEEN OR UNSEEN?			
SPECIES	N	SEEN?	%
Bar-tailed Godwit	98	no	29.34
Bar-tailed Godwit	236	yes	70.66
TOTAL	334		100

Table 5.

STATUS OF MARKED BIRDS			
SPECIES	N	STATUS	%
Bar-tailed Godwit	98	NOT SEEN	29.34
Bar-tailed Godwit	38	SEEN AT 80MB	11.38
Bar-tailed Godwit	195	SEEN AT RB	58.38
Bar-tailed Godwit	3	SEEN OS	0.9
TOTAL	334		100

Table 6.

SEEN OR UNSEEN?			
SPECIES	N	SEEN?	%
Red Knot	77	no	36.84
Red Knot	132	yes	63.16
TOTAL	209		100

Table 7.

STATUS OF MARKED BIRDS			
SPECIES	N	STATUS	%
Red Knot	77	NOT SEEN	36.84
Red Knot	14	SEEN AT 80MB	6.7
Red Knot	113	SEEN AT RB	54.07
Red Knot	5	SEEN OS	2.39
TOTAL	209		100

Table 8.

SEEN OR UNSEEN?			
SPECIES	N	SEEN?	%
Great Knot	93	no	28.01
Great Knot	239	yes	71.99
TOTAL	332		100

Table 9.

STATUS OF MARKED BIRDS			
SPECIES	N	STATUS	%
Great Knot	93	NOT SEEN	28.01
Great Knot	21	SEEN AT 80MB	6.33
Great Knot	210	SEEN AT RB	63.26
Great Knot	4	SEEN AT CW	1.2
Great Knot	4	SEEN OS	1.2
TOTAL	332		100

NOT SEEN = marked bird not seen since banding

SEEN AT 80MB = seen at 80 Mile Beach 165 to 220KM south west of Roebuck Bay

SEEN AT RB = seen in Roebuck Bay including Bush Point

SEEN OS = seen overseas in either New Zealand, China or Korea

SEEN CW = seen at Coconut Well Beach 25KM north west of Roebuck Bay

Early in 2008 Chris has established a Global Flyway Network website! Visit him and us at:

<http://www.globalflywaynetwork.com.au/>

STOP PRESS: satellite tagging of Bar-tailed Godwits in 2008

Chris Hassell

Introduction

As one aspect of the Pacific Shorebird Migration Project during February 2007, in New Zealand, 16 Bar-tailed Godwits (*Limosa lapponica baueri*) were implanted with satellite transmitters (PTTs) to gather data on their northward migration. This study went better than could have been hoped for with the batteries lasting, not only until the birds reached their breeding grounds in Alaska, but all through the southward migration. This wonderful result proved once and for all that the Alaskan breeding Bar-tailed Godwit undertakes the longest single non-stop migration in the avian world. This was best illustrated by the now famous 'E7' as she covered a 29,000 km round trip from Miranda Shorebird Centre, Firth of Thames on the North Island of New Zealand to staging sites in the Yellow Sea and on to breeding areas in western Alaska before the epic journey back across the Pacific Ocean.

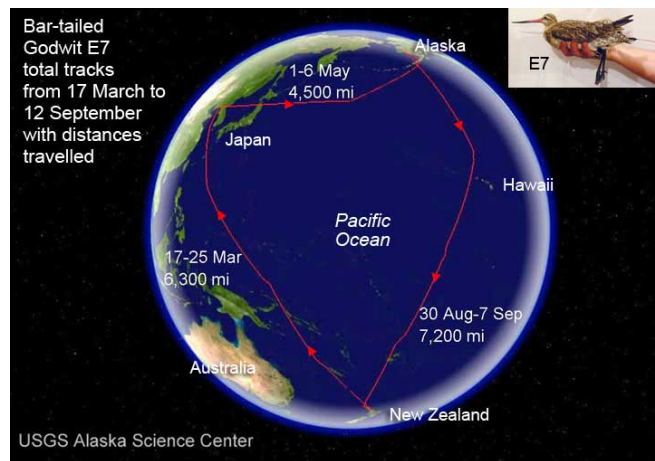


Image USGS Alaska Science Centre

After the success of the 2007 work, consultations began between Nils Warnock of PRBO Conservation Science (PRBO), Bob Gill and Lee Tibbitts of the United States Geological Survey, Alaska Science Centre (USGS), Clive Minton of the Australasian Wader Studies Group (AWSG), Theunis Piersma of the Netherlands Institute for Sea Research (NIOZ) and Chris Hassell of the Global Flyway Network (GFN) to extend this work to the *menzbieri* sub-species that spends the non-breeding season in north-west Australia and breeds in the Yakutia region of Eastern Siberia. With the continued generous funding from the David and Lucile Packard Foundation the talk became action and a team of researchers gathered at the Broome Bird Observatory (BBO) to undertake the work between February 18 and 23 2008.

Field work

The birds to be implanted with PTTs were captured by cannon net in 4 catches, one of which yielded no godwits. The weather during February is very hot and humid with regular rain. We were lucky in that catching was not restricted too much by heavy rain.

The first catch was a regular catch with the net set just above high tide and with limited twinkling we caught 116 birds. Seven Bar-tailed Godwits had surgery, performed with great expertise by veterinarians Dan Mulcahy of USGS and Brett Gartrell of Massey University, New Zealand. All birds were successfully released 2-3 hours after surgery. For this catch we had a TV crew with us filming for the ABC's Stateline programme. They got some excellent footage and interviews; the segment went to air on the last night of our field work and was watched by us all with great interest.

The second day's catch was less successful with repeated bird of prey disturbances over the catching area. We only caught 3 birds and none were Bar-tailed Godwits.

The third day's catch was a tricky affair with very heavy overnight rain persisting in to the morning and delaying the setting of the net. Eventually we went out with the whole team ready to set a net and catch promptly. We set the net well below high tide and with twinkling, decoys, luck (and no little skill!) we made a catch of 12 birds. They were many more close to the net but as I waited for them to walk in to the catching area heavy rain started to fall so I took what was available. I had expected to catch about 30 birds but the net and its sand covering were very wet and the net went slowly. Ten of the total were Bar-tailed Godwits and five underwent successful implant surgery. The remaining birds were transported back to BBO and processed in the Shade House out of the inclement weather. All birds flew well on release.

We had only planned for 3 catching days due to tides and tight travel arrangements for the overseas researchers, however we had 3 PTTs left and so some hasty rearranging of flights saw us out on the northern shores of Roebuck Bay for a fourth attempt. Once again we set the net well below high tide, some 30 metres, as it was a high tide of 8.63M and on such tides the birds do not stay on the beaches but roost at inaccessible locations in and beyond the mangroves.

We started twinkling very early on and had a possible catch soon afterwards but within seconds of firing all the birds flew. After some more skilled work from Maurice and Adrian we once again had birds close to the net and eventually they were catchable as the tide pushed them close enough. I fired and a good catch of 97 was made. Extraction and getting birds in to cages was hectic, with only a small team and due to the fast moving spring tide, but was accomplished successfully.

The final three PTTs were implanted in birds and all went strongly on release.

There were some old birds among the re-traps with Great Knots at 15, 14 and 11+ (this bird is now individually colour-banded). We also now have Bar-tailed Godwits at 18+, 14+ and 12+ colour-banded and others at 18+ and 15+ with engraved leg flags from this latest field work.

Two of the birds carrying PTTs were retraps and are 13 and 5+ years of age as they set off with their precious cargo.



Image Adrian Boyle.

Catch details below.

February 19 2008					
SPECIES	NEW	RETRAP	1ST YEAR	ADULT	TOTAL
Bar-tailed Godwit	48	12	14	46	60
Curlew Sandpiper	2	0	2	0	2
Great Knot	39	12	6	45	51
Red Knot	3	0	1	2	3
TOTALS	92	24	23	93	116

February 20 2008					
SPECIES	NEW	RETRAP	1ST YEAR	ADULT	TOTAL
Curlew Sandpiper	1	0	0	1	1
Great Knot	0	2	0	2	2
TOTALS	1	2	0	3	3

February 21 2008					
SPECIES	NEW	RETRAP	1ST YEAR	ADULT	TOTAL
Bar-tailed Godwit	9	1	1	9	10
Greater Sand Plover	1	0	0	1	1
Terek Sandpiper	1	0	0	1	1
TOTALS	11	1	1	11	12

February 22 2008

SPECIES	NEW	RETRAP	1ST YEAR	ADULT	TOTAL
Bar-tailed Godwit	33	17	0	50	50
Black-tailed Godwit	1	0	0	1	1
Curlew Sandpiper	1	0	0	1	1
Great Knot	29	13	2	40	42
Ruddy Turnstone	2	0	1	1	2
TOTALS	66	30	3	93	96

As of March 12 2008 all 15 PTTs are communicating effectively with the ARGOS satellites and providing data about the birds' whereabouts in Roebuck Bay. During regular colour-band re-sighting field work 7 of the birds have been seen in the field at roost sites looking strong and healthy. In addition to the thin aerial protruding from their feathers they can be identified by their large black flags engraved through to white with a single letter and a single digit.

The immediate future

In mid-March 2008 the PTTs will automatically switch on their regular reporting schedule of 6 hours on and 36 hours off. This should allow the batteries to last at least until the birds arrive on their Arctic breeding grounds. Any additional data received after mid-June (i.e. after approximately 400 hours of transmission time) will be a bonus. You will be able to follow the migrations of the Roebuck Bay Bar-tailed Godwits by following the links from Chris Hassell's Global Flyway Network site <http://globalflywaynetwork.com.au/>, Broome Bird Observatory <http://www.broomebirdobservatory.com/standard/index.html> or directly to the USGS Migration page http://alaska.usgs.gov/science/biology/shorebirds/barg_updates.html

Acknowledgements

Projects such as this take an enormous amount of money and effort, not just in the field work stage but during all the meticulous planning. Please bear with me while I thank the many people involved. The considerable financial contributions from David and Lucile Packard Foundation, PRBO Conservation Science, USGS Alaska Science Centre, US Department of Interior and are gratefully acknowledged. Microwave Telemetry Inc is thanked for the development and manufacturing of the PTTs used in this study. To BirdLife Netherlands (Vogelbescherming-Nederland), thanks for funding my full-time position. The team in the field did a great job, having my Broome team with me fills me with confidence so thanks to Adrian Boyle, Maurice O'Connor, Helen Macarthur, Andrea Spencer, Yindi Newman and Jan Lewis. Also Mavis Russell, Petra de Goeij, Grant Pearson and Theunis Piersma (all honorary Broome team members). Bob Gill, Nils Warnock, Lee Tibbitts, Colleen Handel for field work and being instrumental in getting the project going here in Broome. To the highly skilled Vets Dan Mulcahy and Brett Gartrell. To John Curran for veterinary assistance and vital support with medication supplies. To Andrea Spencer, Maurice O'Connor and Helen Macarthur for wonderful food and plenty of it! The BBO wardens Pete Collins and Holly Sitters for hosting us and for field work. To Annie Tibbitts for field work. To Graeme Hamilton, Alison Russell-French and Rob Davis of Birds Australia for field work. To

Jan van de Kam for images of all the birds. To the AWSG committee for support of this initiative. And last but not least to Clive Minton for continuing his unfailing support of me over the past 12 years.



The Pacific Shorebird Migration Project: results from 2007

Robert E. Gill, Jr, Nils Warnock & Phil F. Battley

In 2006, PRBO Conservation Science (PRBO) and U.S. Geological Survey (USGS) received funding from the David and Lucile Packard Foundation (supplemented with funding from the Department of Interior, USGS, and PRBO) to initiate a broad-scale study of the migration of curlews and godwits (large shorebirds of the tribe Numeniini) throughout the Pacific Basin. The results from this collaborative effort have been beyond expectations (Fig. 1) and have produced findings that both refine—and in some instances challenge—several accepted components of optimal migration theory and provide knowledge crucial for developing and implementing effective conservation strategies for migratory shorebirds.

During the 2007 phase of the Pacific Shorebird Migration Project (PSMP) we employed the latest satellite telemetry technology to document the southbound migration of the Bristle-thighed Curlew (*Numenius tahitiensis*) and Long-billed Curlew (*N. americanus*) and both the south- and northbound migrations of the Bar-tailed Godwit (*Limosa lapponica baueri*). Female Bar-tailed Godwits and male and female Bristle-thighed Curlews had battery-powered satellite transmitters (Platform Transmitting Terminals or PTTs) surgically implanted in their abdominal cavities while male and female Long-billed Curlews and male godwits were fitted with externally mounted, solar-powered PTTs. All three taxa are of high conservation concern as determined by the United States and Canadian Shorebird Conservation plans.

Objectives of the project:

1. Determine the migratory pathways of Pacific Basin Bar-tailed Godwit, Bristle-thighed Curlew, and Long-billed Curlew.
2. Identify intermediate stopover and staging areas and estimate the length-of-stay at each site.
3. Evaluate inter-relationships of stopover and staging sites around the Pacific Basin.
4. Compare migratory strategies of different Numeniini species migrating different distances.
5. Identify key threats specific to Pacific Basin populations of Bar-tailed Godwit, Bristle-thighed Curlew, and Long-billed Curlew and develop conservation frameworks for mitigating these threats.
6. Improve public awareness of conservation issues pertaining to Numeniini and other shorebirds through outreach including Web pages (e.g. USGS and PRBO websites), presentations, and publications.

<http://alaska.usgs.gov/science/biology/shorebirds/index.html>

Understanding the migratory movements of the large shorebird species in the Pacific Basin and their requirements on the breeding and non-breeding grounds (in terms of habitat and periods of use) will not only help develop more effective conservation strategies for this group but also help scientists and conservationists to better understand

the effects of global-scale threats to shorebirds, including habitat destruction, climate change, and the spread of infectious diseases.

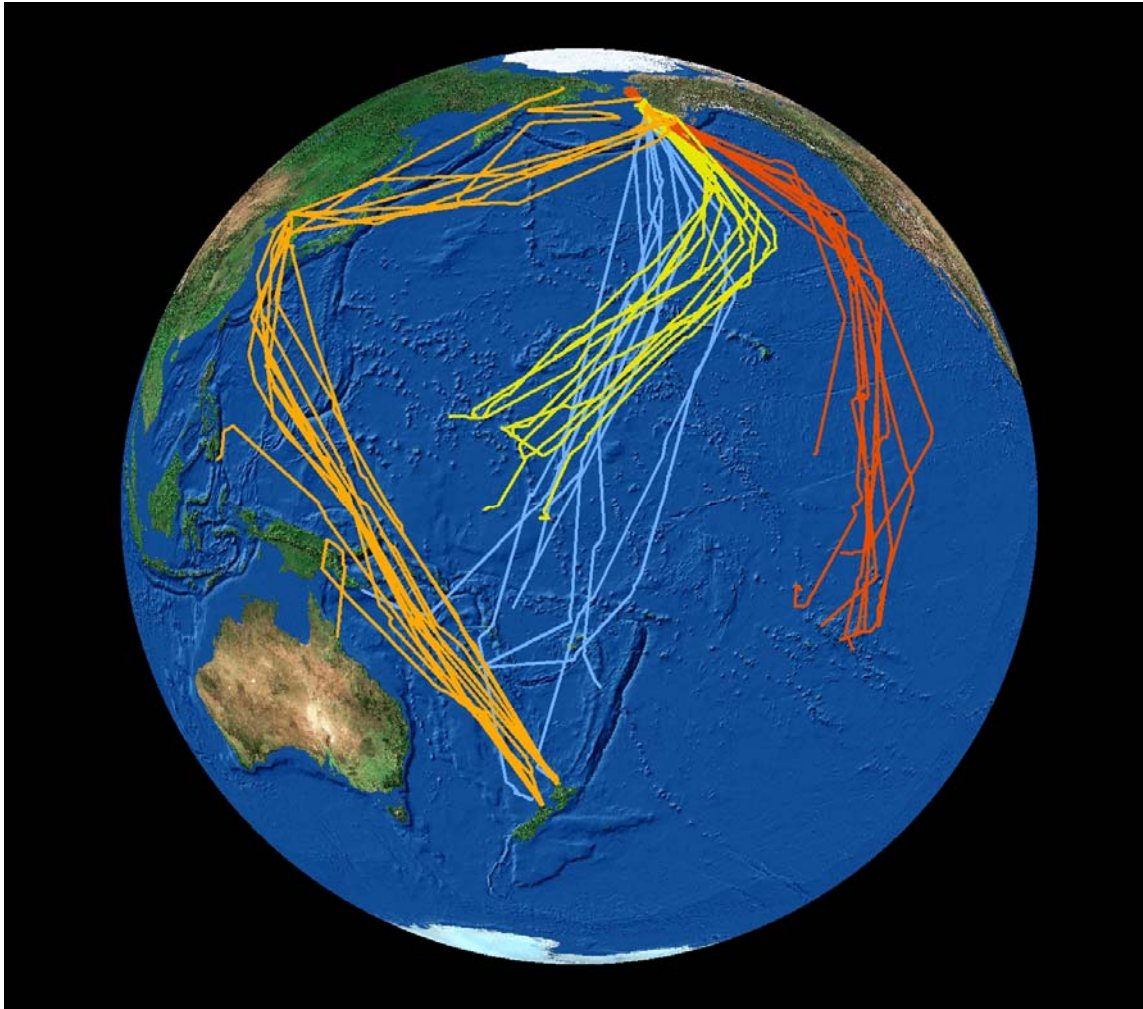


Fig. 1. Bristle-thighed Curlews and Bar-tailed Godwits tracked with satellite telemetry in 2006-2007. Golden tracks = Bar-tailed Godwits, northward migration, 2007; blue tracks = Bar-tailed Godwits, southward migration, 2006 & 2007; orange tracks = Northern breeding Bristle-thighed Curlews, southward migration, 2006; yellow tracks = Southern breeding Bristle-thighed Curlews, southward migration, 2007.

Specific finding from the effort in 2007

BAR-TAILED GODWITS. Sixteen godwits of the *baueri* subspecies were captured in New Zealand (4 males and 4 females at Farewell Spit and 4 males and 4 females at Miranda) in early February and fitted with PTTs. Thirteen of 16 godwits were tracked on migration (Fig. 1), leaving in two distinct pulses, 16–20 March (10 birds) and 31 March–1 April (3 birds). All departures were towards the northwest in conjunction with pronounced tail winds.

Of the female godwits, six were tracked on non-stop flights directly to the Yellow Sea

(a great-circle distance of about 10,000 km), representing some of the longest documented nonstop flights ever recorded in birds. [A seventh female last reported about 250 km southeast of Okinawa and has not been heard from or seen since.] After a 5- to 6-week stay in the Yellow Sea all females then migrated to Alaska. These flights also were nonstop along a wind-aided course that initially took birds east well into the Pacific before they turned north-northeast towards Alaska. Four of the six females apparently attempted to nest or did nest based on suites of signals received from fixed locales over prolonged periods. Five of six females were tracked to the Kuskokwim Shoals on the YKD in July and August, reinforcing the importance of this staging area to the population.

The most remarkable part of this story is that the batteries in the PTTs in these five females then lasted into autumn and all five birds were subsequently tracked on southward migration. Among these was godwit E7 who proved to be the exemplar of non-stop bird flight. Not only was she apparently the first long-distance migrant shorebird to be tracked throughout an annual cycle, but in doing so she flew some 29,000 km, including a record setting nonstop leg from Alaska to New Zealand that entailed 8.2 days of flight along a track totalling 11,700 km.

The migration history of male godwits was more problematic than that of females, with only a single bird being tracked to the breeding grounds. The markedly different tracking patterns we obtained between female and male godwits could be related to at least two factors. First would be the attachment method of the PTT (females received implants, male's harnesses). In early February, when the PTTs were attached, the birds had already begun to fuel for their long migrations and had robust body profiles. The PTTs on males were attached to their legs with a figure-8 harness made of Teflon, elastic, or combinations of each, but leaving a finger-width's of slack beneath the PTT to accommodate anticipated additional fattening. The PTTs appeared securely attached when the birds were released and the birds subsequently completed long, nonstop flights of between 4,000 and 7,000 km before either no longer reporting or making landfall. Those that stopped reporting over open ocean were easily within a day's flight of land (and the next scheduled reporting period for the PTT). We suspect that the loss of mostly fat that is used to fuel such long initial flights significantly changes body morphology and thus the harness becomes much looser than when applied. This would have facilitated PTTs either being shed in flight or birds walking out of them shortly after reaching land. It is also possible that with a change in morphology the harness loosened and allowed the PTT to shift position in flight, creating drag that adversely affected flight performance. Such birds may have responded by changing course to reach the nearest land (where they walked out of the harnesses) or they simply depleted fuel and perished at sea. Through autumn 2007 and winter 2007–2008, efforts will be made in New Zealand and Queensland to re-sight individuals from this cohort of marked males with the hope that some of them survived after shedding their PTTs (e.g., one of the males tracked to Melanesia and seen later in Queensland had shed its PTT).

BRISTLE-THIGHED CURLEWS: Satellite tracking confirmed what previous molecular and biometric data suggested, in that the two disjunct breeding populations in Alaska likely occupied different portions of the nonbreeding range. Indeed, curlews nesting on the Seward Peninsula of Alaska (the northern population) were tracked in 2006 to the east-central Pacific; curlews from the Andreafsky Wilderness (southern population) were

tracked in 2007 to the west-central Pacific in western Kiribati, the Marshall Islands, and Nauru, with a single bird stopping in the Northwest Hawaiian Islands (Fig. 1). Both cohorts of marked birds first migrated southeast into the trade wind belt that in turn provided winds favorable for flights back to the southwest and the nonbreeding grounds. Flights to nonbreeding destinations were nonstop, requiring between 4.5 and 8.5 days and covering distances between 4,400 and 8,300 km.

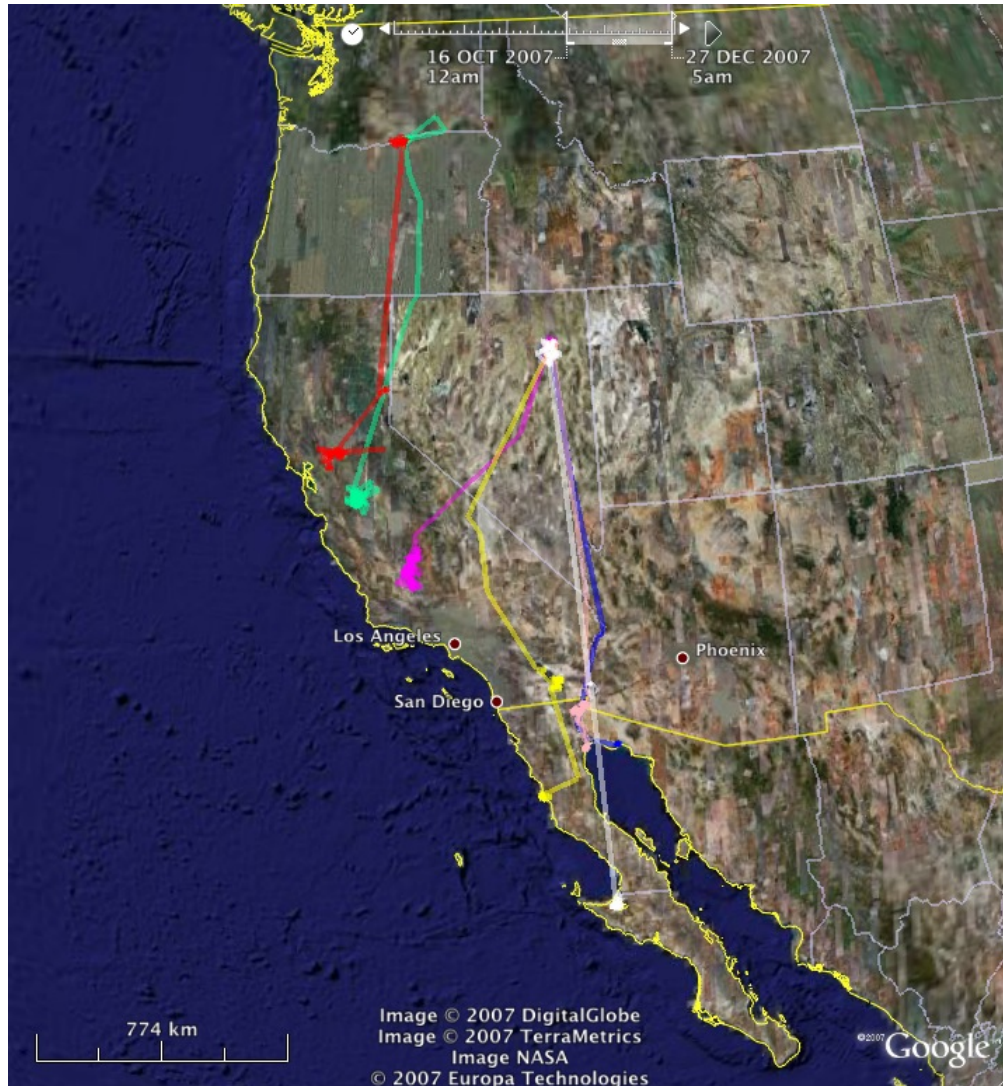


Fig. 2. Long-billed Curlews tracked with satellite telemetry, May – July 2007.

LONG-BILLED CURLEWS: In late April and early May 2007, seven Long-billed Curlews were fitted with ~20 g solar-powered, harness-attached PTTs at two sites in the western United States, Boardman, Oregon (two birds) and Ruby Valley, Nevada (five birds) (Fig. 2).

All birds were tracked on flight south of their capture site. The two Oregon birds migrated to agricultural areas in the Central Valley of California, about 900 km south of their nesting area. Four of five birds from Nevada migrated to nonbreeding areas along

the Baja California peninsula or Gulf of California (900-2,000 km south of Ruby Valley); the fifth bird was tracked to the southern San Joaquin Valley, California, 600 km south of its nesting area. As of early January 2008 all seven curlews still carried their PTTs and were being tracked at their nonbreeding sites. The success we have had with harness-attached PTTs on Long-billed Curlews contrasts markedly with that of male Bar-tailed Godwits (see above). We suspect that Long-billed Curlews retain harnesses because they are relatively short-distance migrants whose body mass does not fluctuate greatly between seasons thus allowing the harness to remain snug.

Plans for 2008

In January we will travel to Chile to work there with colleagues on Hudsonian Godwits (*L. haemastica*). This species is too small to be fitted with implantable PTTs and, since this species of godwit is also a long-distance migrant, likely with long, nonstop legs to their flights, they may have problems retaining harness-attached solar PTTs (see under Bar-tailed Godwit, above). For this reason we plan to modify our methods slightly to include use of smaller archival tags while we continue exploring attachment methods so we can effectively use PTT technology.

In February 2008 we will travel to both New Zealand and Western Australia to continue work on Bar-tailed Godwits. In New Zealand we will try to capture a sample of the largest males of the *baueri* subspecies so that we may use implantable PTTs to follow their northward migration. In Western Australia we will capture both males and females of the *L. l. menzbieri* subspecies and track their northward migration—hopefully to the breeding grounds and if possible on the return migration south (see previous chapter to this report by Chris Hassell)

Lastly, in May 2007 we will begin work on the small population of Marbled Godwits (*L. fedoa beringiae*) that nests on the Alaska Peninsula.

Details of all aspects of the project can be found at:
<http://alaska.usgs.gov/science/biology/shorebirds/index.html>

Progress report on the molecular cloning and characterization of MHC genes in Red Knots (*Calidris canutus islandica*)

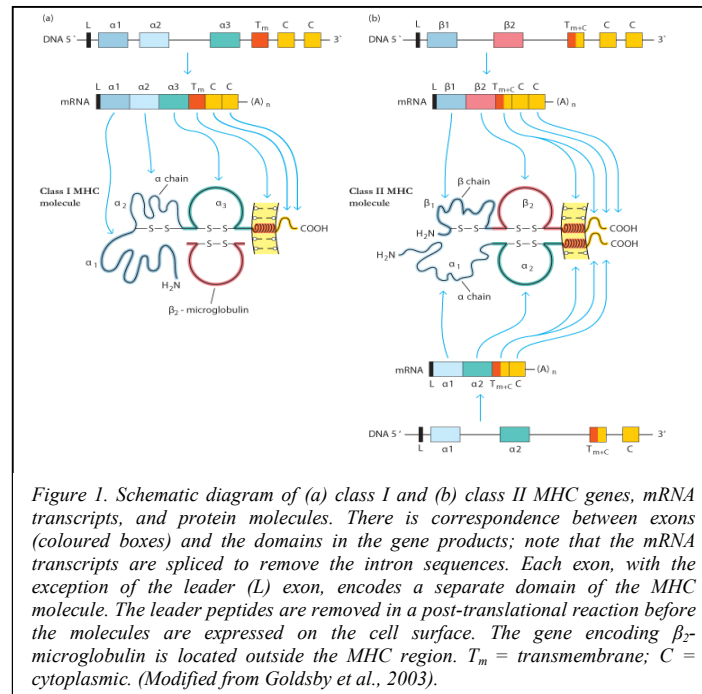
Sergio L. Pereira

Genes of the major histocompatibility complex (MHC) are important components of the immune system, and have been used as molecular markers in ecology and evolutionary biology because of their association with disease resistance, mate choice, sexual selection, survival, and other life-trait parameters. We have successfully cloned and characterized for the first time most of the MHC-II gene in the Red Knot *Calidris canutus islandica*. Preliminary results indicate that the peptide-binding region of Red Knot MHC-II genes has high allelic diversity, and are under strong selection for amino acid substitutions involved in detection of pathogens. The high allelic diversity we found in MHC-II argues against the hypothesis that Red Knots have suffered a recent population bottleneck as suggested by mitochondrial and nuclear markers. The results obtained with MHC-II has opened up new a venue of collaborative research on Red Knots among members of the Global Flyway Network. More specifically, we will (1) study the correlation between the allelic diversity and survival of populations of Red Knots around the world, and (2) compare the organization and allelic diversity of MHC-II in other species and subspecies within the genus *Calidris*. Because all *Calidris canutus* subspecies perform continental migration biannually, they are constantly threatened by pathogens in breeding and wintering grounds in different parts of the world. Hence, our pioneer work on MHC in Red Knots will be an important tool for other members of the *Global Flyway Network* to address issues on survival of the R0ed Knot populations, which are declining worldwide.

The Major Histocompatibility Complex as tools in ecology and evolutionary biology of Red Knots

The *Major Histocompatibility Complex* (MHC) is a region of the vertebrate genome that harbors a multigene family of highly polymorphic loci that encodes receptors on the surfaces of a variety of immune and nonimmune cells. These receptors bind fragmented peptides from foreign pathogens, triggering an immunological response against foreign pathogens. Three distinct classes of MHC genes have been characterized. Class I and Class II MHC genes (hereafter MHC-I and MHC-II, respectively) are structurally and functionally similar, and are responsible for encoding glycoproteins that present antigenic peptides to T cells. MHC-I and MHC-II are expressed, respectively, in nearly all nucleated cells and in antigen-presenting cells (macrophages, dendritic cells, and B cells). Class III MHC genes encode a series of products, including components of the complement system and molecules involved in inflammation, and have unrelated structural and functional properties compared to MHC-I and MHC-II genes. Figure 1 shows the genomic organization of MHC-I and MHC-II genes, their corresponding mRNA and representation of MHC proteins. In brief, each exon encodes a functional domain (α and β chains, transmembrane segment and cytoplasmic tail) in the MHC protein. In both MHC-I and MHC-II, the distal domains contain the peptide-binding cleft, and the proximal domains are related to immunoglobulin families. MHC molecules within a species and within an individual are highly diverse due to the presence of multiple alleles at a given locus within a species, and to the presence of two or more copies of each gene within an individual. The tight association between MHC

and diseases in chicken has driven the characterization of MHC structure and allelic variation in a diversity of non-model bird species to study (a) the association of MHC alleles and resistance to parasites (Bonneaud *et al.*, 2006; Westerdahl *et al.*, 2005), (b) allelic diversity in natural populations (Bonneaud *et al.*, 2004), (c) correlation between alleles and mate choice (Ekblom *et al.*, 2004; Westerdahl, 2004), and (d) genomic organization and evolution of highly polymorphic MHC genes (Alcaide *et al.*, 2007; Shiina *et al.* 2004).



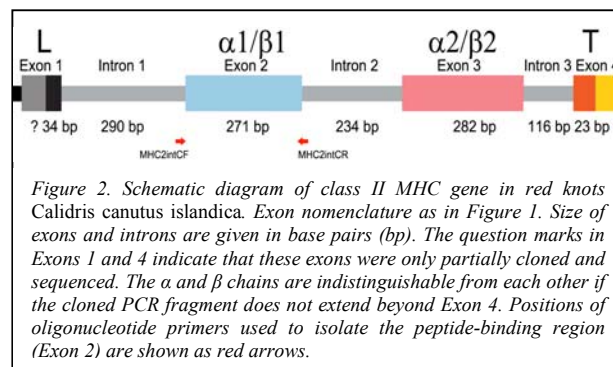
The Global Flyway Network, under the directive efforts of Dr. Allan Baker of the Royal Ontario Museum (Canada) and Dr. Theunis Piersma of the University of Groningen and the Royal Netherlands Institute for Sea Research (NIOZ) (The Netherlands), put forward an integrative project combining MHC genomics and ecology to understand the natural history of Red Knots. The Red Knot *Calidris canutus* is a medium sized shorebird that breeds in the Arctic regions of North America and Eurasia. Six subspecies are recognized based on plumage colour, body size, and migration route. However, only three subspecies are genetically distinct (*C. c. canutus*, *C. c. piermai*, and *C. c. rogersi*), while the remaining three (*C. c. islandica*, *C. c. roselaari*, and *C. c. rufa*) likely colonized North America only recently, and hence have not yet established unique genetic differences (Buehler and Baker, 2005; Buehler *et al.*, 2006).

Migration routes in Red Knots vary between 4,000 and 15,000 kilometers (Buehler *et al.*, 2006). Long-distance migrants (*C. c. rogersi* and *C. c. rufa*) are expected to have higher mortality rates due to higher physiological demands compared to short-distance migrants (*C. c. islandica*). Red Knot populations have been declining worldwide mainly due to anthropogenic habitat disturbance (Baker *et al.*, 2004; van Gils *et al.*, 2006), and because long-distance migrants may not be able to adjust their migration schedule to maximize individual fitness in changing environments (Both and Visser, 2001). Hence,

we are using MHC genes as a molecular tool to address diverse issues in ecology and evolutionary biology of declining natural populations of Red Knots. Specifically, we are targeting MHC genes to (1) characterize the genomic structure of MHC-I and MHC-II in different subspecies of Red Knots, (2) compare the genomic organization of MHC genes in Red Knots with other birds, especially shorebirds, (3) evaluate the allelic diversity found in natural populations of Red Knots, (4) study the association between survival and MHC alleles. Goals (1) and (3) are underway and the progress achieved so far with the molecular work performed at the Royal Ontario Museum is detailed below.

Molecular characterization of MHC genes in Red Knots

To characterize the genomic structure of MHC genes, we optimized the experimental conditions (oligonucleotide primer combination, reaction temperatures, buffer composition, etc) to isolate and amplify each class of MHC genes of *Calidris canutus islandica* using the polymerase chain reaction (PCR). Because MHC genes occur in multiple copies within the same individual and are part of an ubiquitous gene family (immunoglobulin), the isolated PCR products are, in fact, a pool of all the alleles for all the loci present in the targeted specimen. Hence, after the target gene was isolated by PCR, we sequenced the PCR product without performing further separation of the alleles to certify that we have isolated and amplified MHC genes, and not any other member of the immunoglobulin family. When direct sequencing proved that we obtained the desired target, we performed further separation of the alleles by cloning different alleles using bacterial plasmids, or by separating alleles in an SSCP gel (details below).



The isolation of MHC-I in *Calidris canutus islandica* has shown to be particularly difficult, with most PCR and sequencing experiments resulting in false positive so far. The exons bearing the peptide (antigen) binding sites (α_1 and α_2 in Fig. 1) have enough sequence similarity at priming sites to prevent isolation with PCR, yet are too variable to be isolated using cross-specific primers. Plasmid cloning of MHC-I have been obscured by the presence of the ubiquitous immunoglobulin domain (exon α_3 in Fig. 1), which resulted in the isolation of unrelated genes. These results are in agreement with the paucity of MHC-I genes used in ecological and evolutionary studies in the ornithological literature. We are now screening a *Calidris canutus islandica* cDNA library to isolate expressed MHC-I alleles that can be used to design primers specific for isolating MHC-I and avoid the contamination with other immunoglobulin-like genes.

We successfully isolated and characterized for the first time most of the MHC-II gene in two individual of *Calidris canutus islandica* using PCR, cloning and direct sequencing (Fig. 2). We obtained complete genomic sequences for the region extending from intron 1 to intron 3, including intron 2 and exons 2 and 3. Because the sequencing upstream from exon 1 and downstream from exon 4 are very variable, and locus-specific oligonucleotide primers has proven ineffective to isolate and characterize these regions, exons 1 and 4 were partially sequenced, and attribution of sequences to locus α or β is unattainable at this moment. The organization of MHC-II in *Calidris canutus islandica* is similar to that of the chicken and quail (Kaufman *et al.*, 1999; Shiina *et al.*, 2004), and gulls (Cloutier and Baker, pers. comm.). One MHC-II pseudogene was cloned during the process, which included a transposable element upstream of exon 4.

Allelic diversity of MHC-II in Red Knots

After we characterized the genomic MHC-II region, we were able to select primers to isolate the MHC-II exon 2 specifically, which harbors the peptide-binding region of the MHC-II molecule (red arrows in Fig. 2). MHC-II exon 2 is of particular biological interest because its polymorphic alleles are associated with disease resistance, mate choice, sexual selection, survival, and other life-trait parameters. We are screening 31 *Calidris canutus islandica* collected in Friesland in 1988 and 1997 to access the allelic diversity of this subspecies. The oligonucleotide primers used to isolate MHC-II exon 2 encompass a region of about 280 base pairs (bp), and amplify all the alleles of loci α_1 and β_1 . To separate these alleles from each other, we have been applying the Single Strand Conformational Polymorphism (SSCP) technique, which is quicker and more affordable than plasmid cloning. This technique is based on the principle that once denatured to become single-stranded, each DNA molecule undergoes a 3-dimensional folding and may assume a different conformational state according to the nucleotide sequence. Hence, different MHC-2 exon 2 alleles will assume a distinct conformation and migrate at variable speeds on a polyacrylamide gel, even though the number of nucleotides in both DNA strands is the same.

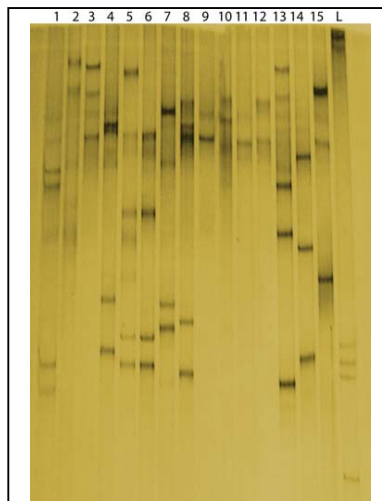
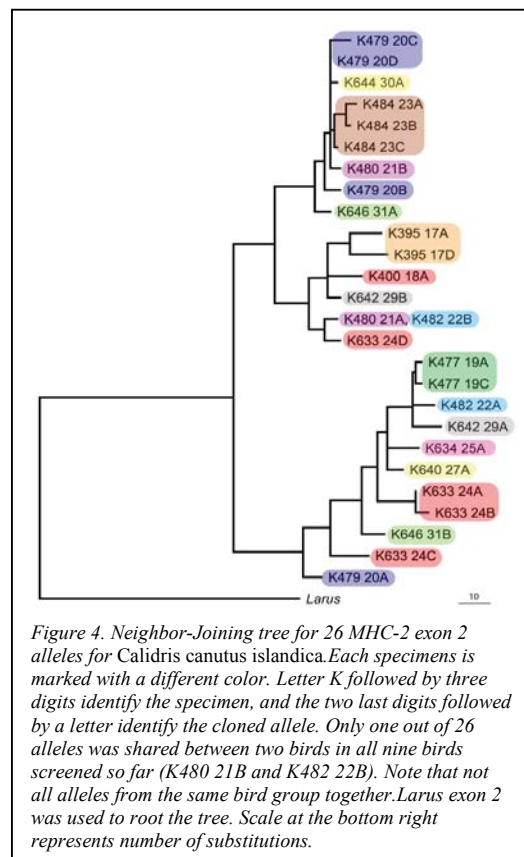
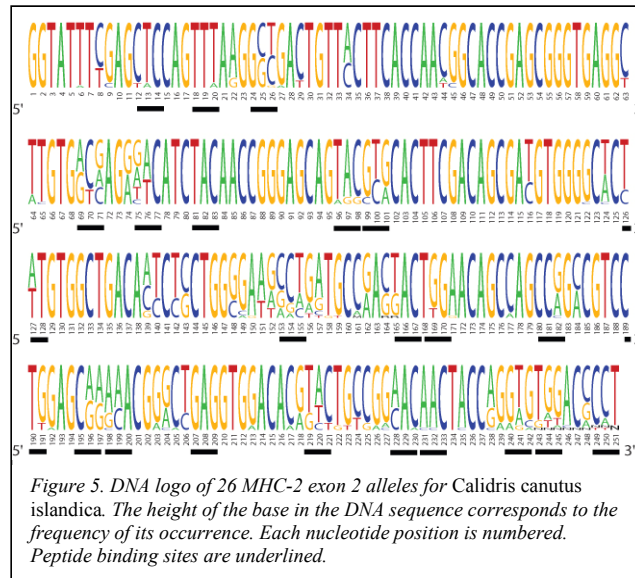


Figure 3. SSCP gel, after silver staining. Numbers on top of each lane identify different birds. L identifies the lane with the molecular ladder. Different alleles assume a distinctive conformation structure, allowing them to separate from each other in the SSCP gel. Homozygous birds at both loci should have only two bands.

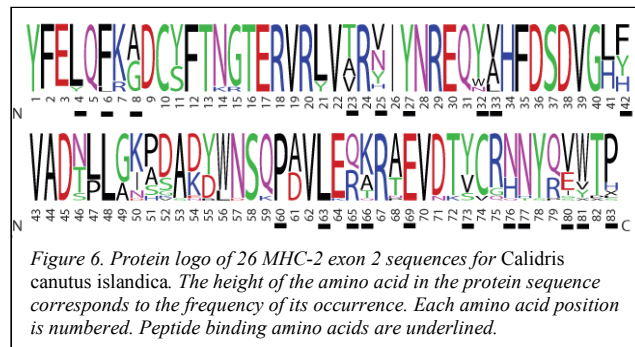
We optimized the conditions for proper separation of MHC-II exon 2 alleles in SSCP gels. Figure 3 illustrate one of the gels obtained for 15 *Calidris canutus islandica*. Each individual had between 2 and 5 bands. If a specimen is homozygous for all loci, only two bands should be identified, corresponding to each single DNA strand. A total of 43 bands from 15 individuals were recovered from the SSCP gel and sequenced. Except for two birds whose sequence quality was below the expected standard, sequencing for the other 13 birds revealed a total of 26 distinct alleles (Fig. 4). Each specimens had between one and four different alleles, implying that at least two MHC-II loci exist in the nuclear genome of *Calidris canutus islandica*, as found in other birds (Alcaide *et al.*, 2007; Ekblom *et al.*, 2004; Shiina *et al.*, 2004; Wittzell *et al.*, 1999). Only two specimens share the same allele, and four birds have one single allele each, implying that the may be homozygous at both loci (Fig. 4). However, we cannot discard the possibility that the priming sites are variable and, hence, some alleles will go undetected under the current experimental conditions.



The results also indicate that *Calidris canutus islandica* has high allelic diversity. This is an interesting finding because the *C. c. islandica* separated from *C. c. roselaari* and *C. c. rufa* since the Last Glacial Maximum about 20000 year ago, and these three subspecies are not genetically distinguished as yet (Buehler and Baker, 2005). This argues against the hypothesis of a genetic bottleneck in the recent past.



A further investigation of the distribution of the variation in MHC-II exon 2 shows that most of the nucleotide variation lies within peptide-binding region (PBR), although some PBR were invariable (Fig. 5). The estimated rates of synonymous (d_s) and non-synonymous (d_N) substitutions for the PBR were 0.24 ± 0.08 and 0.33 ± 0.07 , respectively. The d_N/d_s ratio > 1 indicates that the PBR is experiencing strong selection for amino acid substitutions involved in detecting pathogens. For sites not involved in peptide binding, d_s and d_N were 0.13 ± 0.03 and 0.08 ± 0.02 , respectively, showing that they are effectively neutral ($d_N/d_s < 1$). This is a critically important finding for Red Knots because populations are declining in many parts of the world, and pathogens are in part implicated in mortalities. The distribution of variation centred in PBS and the pattern of d_N/d_s ratio observed in Red Knots, allied with the absence of stop codons and frameshift mutations along the sequence, and no amino acid shifts in traditionally conserved regions (Fig. 6) suggest that all these 26 alleles are likely expressed in *C. c. islandica*. However, the possibility that some alleles have become inactive recently and yet preserved sequence similarity at the nucleotide and amino acid level cannot be ruled out.



Short to long-term expectations

In the short term, we will finish screening allelic diversity in a population of *Calidris canutus islandica*. We will also fully characterize the MHC-II gene and screen allelic diversity of the other five *Calidris canutus* subspecies (*Calidris c. canutus*, *C. c. piersmai*, *C. c. rogersi*, *C. c. roselaari*, and *C. c. rufa*), and possibly in other *Calidris*

species if primers used are conserved enough to amplify MHC-II alleles in the short term. Thus, this powerful molecular tool important in survival will be made available for other members in the Global Flyway Network to study different species, and will allow us to compare the genomic organization of MHC-II gene in the genus *Calidris*. The data gathered by us in this project will also be compared to published data available for other avian groups.

In the medium term, we will screen individuals of *C. c. islandica*, *C.c. canutus*, and *C. c. rufa*, for which we have survival data and investigate whether greater allelic diversity is correlated with long survival range in Red knots, and whether specific alleles provide a fitness advantage in survival.

In the long term, we will continue working towards the isolation and characterization of MHC-I genes in Red Knots to complement the studies with MHC-II. Initially, a cDNA library will be screened to look for expressed MHC-I alleles that can be used to isolate and amplify MHC-I alleles from genomic DNA.

Acknowledgements

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Migratory Ruffs have prolonged stopovers in spring

Yvonne Verkuil, Jos Hooijmeijer, Jan Wijmenga, Kathryn Hine & Theunis Piersma

Knowledge of stopover timing in migratory birds allows us to understand (1) a species' migrating strategy and (2) the population dynamics at a particular stopover site along the flyway. The Ruff is an inland migratory shorebird, well studied for its reproductive behaviour but its migration is poorly known. We monitored turnover and population size during stopover in The Netherlands, by colour-marking and radio-tagging Ruffs individually. Using capture-recapture analysis, we estimated day to day survival, staging duration, staging numbers and new arrivals throughout the season. Our estimates revealed patterns not visible in normal census data.



Introduction

One of the great challenges in migration biology is getting reliable estimates on (changes) in population size and structure (Gwinner 1977). Large scale counts provide valuable information on migrating bird populations. However, these data on numbers and timing usually only provide limited information on a population at a certain point in time, and thus neglect the continuous nature of migration. On staging sites, there is a constant process of new individuals entering the staging population and other individuals leaving, en route to and from the breeding grounds (Schaub *et al.* 2001). This turnover prevents accurate counts of population size and stopover duration. Only when individual stopover time is taken into account, we can get a better insight on the underlying demographics, such as total population size and proportions of different

subgroups. The last decades, the use of colour rings with a unique code and radiotags has provided us with information on dispersion, survival and age distribution of individual birds. So far, most studies have used colour rings especially to understand more of the population dynamics over years. However, a number of recent studies has applied the technique to estimate stopover duration and to estimate volume (Lee *et al.* 2007; Schaub *et al.* 2001; Schaub *et al.* 2004; Schaub & Jenni 2001).

The Ruff (*Philomachus pugnax*) is a species which behaviour has been well studied but which migratory behaviour and demography are unknown. This gregarious wader breeds from temperate to sub arctic areas from Western Europe to Eastern Siberia, and winters from Western and Southern Europe up to South-Africa and India. It has migration routes through Eastern and Western Europe, but it is unknown how the world population is divided along the migration routes and how the routes connect to breeding and wintering areas. Census data show that in some years at least 50.000 take a route along the meadows of Southwest Fryslân in The Netherlands in spring (Wymenga 1999).

In this study we aim to estimate the survival within a spring migration season at a stopover site, i.e. the stopover time, use the survival estimates to calculate population size changes throughout the season at the stopover site and test whether two different capture-mark-recapture techniques, colour rings and radio telemetry, give the same survival and population estimates (Bachler & Schaub 2007; Salewski, Thoma & Schaub 2007). We want to test the following hypotheses:

- (1) Day to day survival varies between years
- (2) Resighting probabilities do not vary between years (using Automatic receiving stations ARTS).
- (3) Day to survival varies with body mass at capture: heavier birds stay shorter.
- (4) Day to day survival does not vary between encounter techniques: colour-marks or radio transmitters.
- (5) Estimates of population size based on survival data will exceed census counts.

Methods

Each Ruff was marked with a unique combination of five colour rings, one being a flag. Additionally in 2005 and 2007, 46 and 48 adult male Ruffs were equipped with a radio transmitter. The transmitters weighed 2.8 g transmitters, a maximum of 2% of the birds' total body mass, and were glued to clipped feather bases and skin on the plateau below the spine on the lower back. The transmitters fall off at the next moult. Automatic receiving stations (ARTS) were put up such that they covered the nine most important roosting sites. The ARTS gathered information at 20 min intervals, 24 hours a day. Foraging and roosting Ruffs were checked daily for colour rings using binoculars and telescopes. Our resighting effort covered all known foraging and roosting site in the study area.



Application of a radio-tag on an adult male Ruff

Given the low number of females that were caught and colour ringed, data presented here are only for males. Estimation of stopover duration is done by combining two capture-mark-recapture models. Local, apparent survival (ϕ), the change that individuals will be alive and present in the area after capture ($i+1$), is estimated with Cormack-Jolly-Seber models (CJS models, Lebreton *et al.* 1992). Seniority (γ), the change that an individual was already present at the site before capture ($i-1$) is estimated with the Pradel model (Pradel 1996). These estimations were done in program MARK (White and Burnham 1999). We tested different models that would explain our data, including parameters as time in season, year, body mass at capture. These candidate models were ranked based on the modified Akaike information criterion (AICc), which accounts for overdispersion and sample size (Burnham and Anderson 1998). The most parsimonious survival and seniority model were then used to estimate the time spent by male Ruff in the area before and after time i , using SODA (Schaub *et al.* 2001). The sum of the two components then represents the total stopover duration. The ARTS data were pooled over three day intervals, the colour-mark data over 15 day intervals.

We tested with a global model $\{\phi(t)p(t)\}$ whether our data fitted the general assumptions of the CJS model. GOF TEST 3 results showed that our data did not differ significantly from the assumption that all marked individuals have the same probability for survival ($X^2=5.9115$, $df=11$, $p=0.8792$). TEST2 however yielded an significant result ($X^2=229.7423$, $df=36$, $p<0.001$, indicating that our marked birds did not have an equal probability to be resighted, which is expected as birds are at a stopover and have to leave before the end of the season: non-random emigration.

Results

Day to day survival and resighting probability of radio-tagged Ruffs

The ARTS data for 2005 and 2007 were analysed jointly to test for differences between years in day to day survival. We tested which was the best model to estimate day to day survival. The most parsimonious model with a high AICc weight included the parameters time and year, $\phi(t)p(y)$. That means that day to day survival varied with date and the probability of resighting a bird varied with year (Table 1).

Table 1. Model selection for radio-transmitter re-encounter data of Ruffs in 2005 and 2007. The model that best explained the data stated that the day to day survival (ϕ , phi) varies of days (t), but not over years (y). The re-encounter probability p did vary between years.

Model	AICc	Delta AICc	AICc Weight	Model Likelihood	#Par	Deviance
$\phi(t)p(y)$	964.12	0.00	0.92505	1.0000	22	918.214
$\phi(t*massmass2)p(y)_{ci}$	970.268	6.15	0.04277	0.0462	30	906.712
$\phi(t*massmass2)p(y)_{cs}$	971.242	7.12	0.02628	0.0284	21	927.505
$\phi(t)p(.)$	974.504	10.38	0.00514	0.0056	21	930.767
$\phi(y*t)p(y)$	978.376	14.26	0.00074	0.0008	41	889.649
$\phi(y*t)p(.)$	987.137	23.02	0.00001	0.0000	40	900.743
$\phi(t)p(t)$	990.666	26.55	0.00000	0.0000	40	904.272
$\phi(y)p(y)$	1002.333	38.21	0.00000	0.0000	4	994.261
$\phi(y*t)p(t)$	1007.307	43.19	0.00000	0.0000	59	874.975
$\phi(y*t)p(y*t)$	1033.017	68.90	0.00000	0.0000	76	856.481

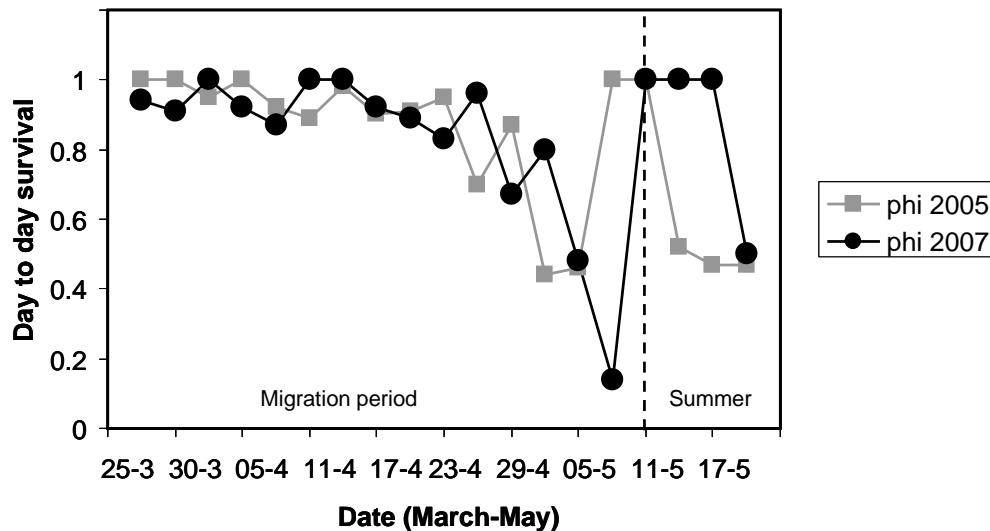


Fig. 1. Estimates of day to day survival as yielded by the model $\phi(t)p(y)$ Data are from ARTS stations and radio-tagged Ruffs in 2005 and 2007.

The day to day survival did not vary significantly between years and was on average 0.82, varying from 0.96 (± 0.03) early in the season to 0.45 (± 0.16) in the first week of May (Table 1, Fig. 1). Halfway May most birds have left and estimates start to fluctuate largely, with se increasing to 0.37 (not shown). Resighting probabilities were significantly different between years, being 0.73 (± 0.03) in 2005 and 0.86 (± 0.02).

Day to day survival in relation to phenotypic parameters.

To test whether individual covariates affect survival estimates we included wing length, as a measure of structural size, and body mass in the model and tested them against the other less parameterized models (Table 1). Wing length yielded very inadequate model estimates, $AICc > 1100$ (not shown). Models including body mass were more adequate but the difference with the first, most parsimonious model was $\Delta AICc = 6.15$. The best model predicted a constant ϕ for body mass (Fig. 2).

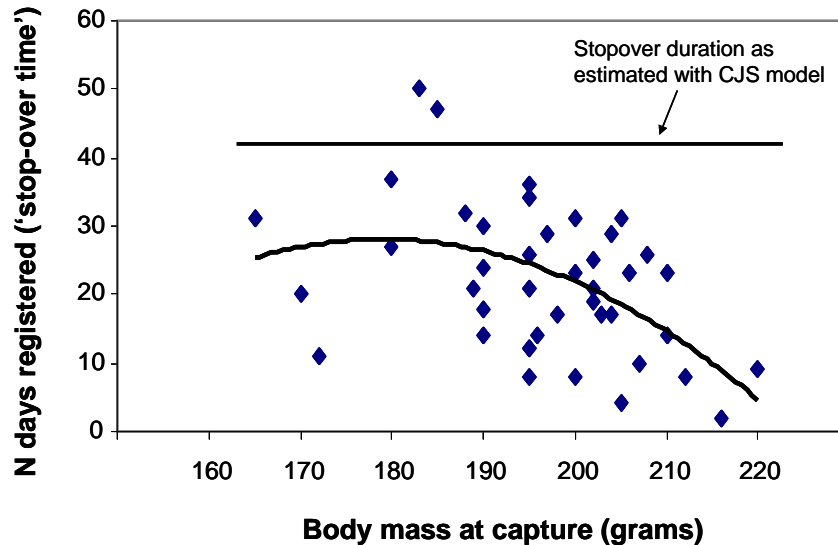


Fig. 2. Days registered at an ARTS station correlated with body mass at capture (lower line). The most parsimonious CJS models for day to day survival did not include body mass. The estimate of stopover duration was constant with body mass (upper line).

Day to day survival for different encounter methods

For the years 2005 and 2006 we performed preliminary day to day survival analyses with colour-mark data. In both years the most parsimonious model was $\phi(t)p(\cdot)$, indicating that survival varies with date but not the resighting probability (p). Models including individual covariates as age, structural size and body mass are currently tested. Because p is much smaller for colour-marked (CM) birds than for radio-tagged Ruffs we pooled CM data over 15 day intervals to increase the fit of the models. The difference in estimate day to day survival is significant. For 2005 the ARTS data yielded much higher estimates than the CM data (Fig. 3).

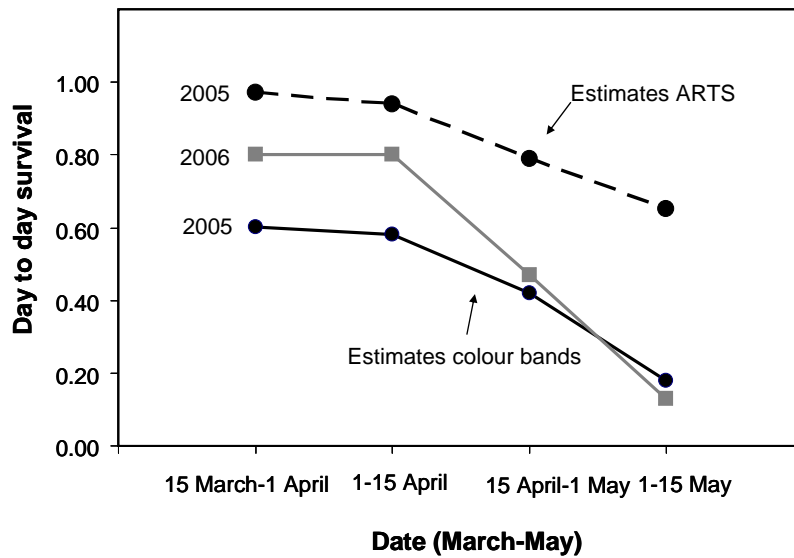


Fig. 3. Effect of encounter technique on estimates of day to day survival: ARTS data and colour-mark data.

Estimates of population size (volume)

The day to day survival was very high from late March to half April, leading staging duration estimate of 42 days (Wijmenga *et al.* in prep.). This implies that almost all the birds arriving in that time period are still present when the numbers start declining (Fig. 4).

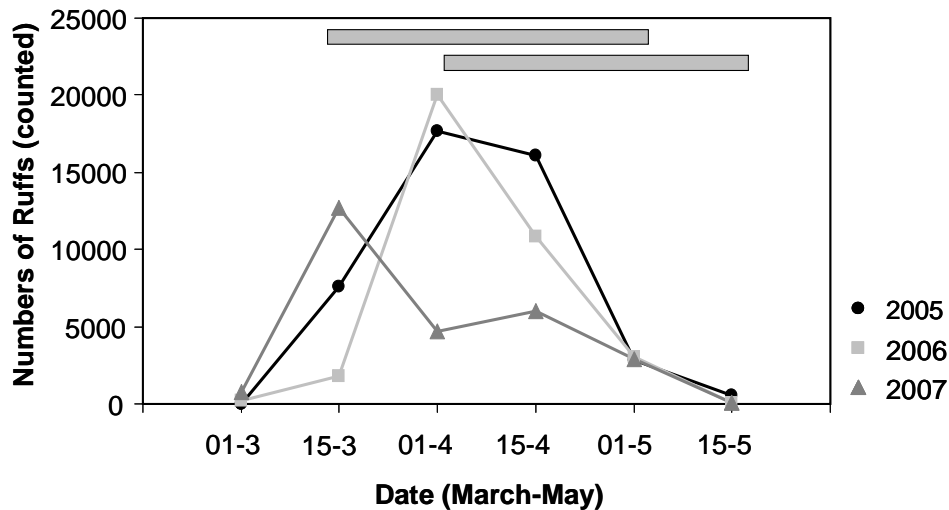


Fig. 4. Census data of the population of Ruffs staging in Southwest Fryslân. Day to day survival estimates from colour-mark data in 2006 yielded a total staging time estimate of 42 days (indicated by grey bars).

We actually could not detect any arrival of new birds after the 1st of April (Fig. 5), except for 2007. The ARTS data in 2007 did not detect the decline in numbers between 15 March and 1 April, most probably since we only started radio-tracking the first birds after March 25. High day to day survival estimates yielded volume estimates not very different from the maximum counts during the census.

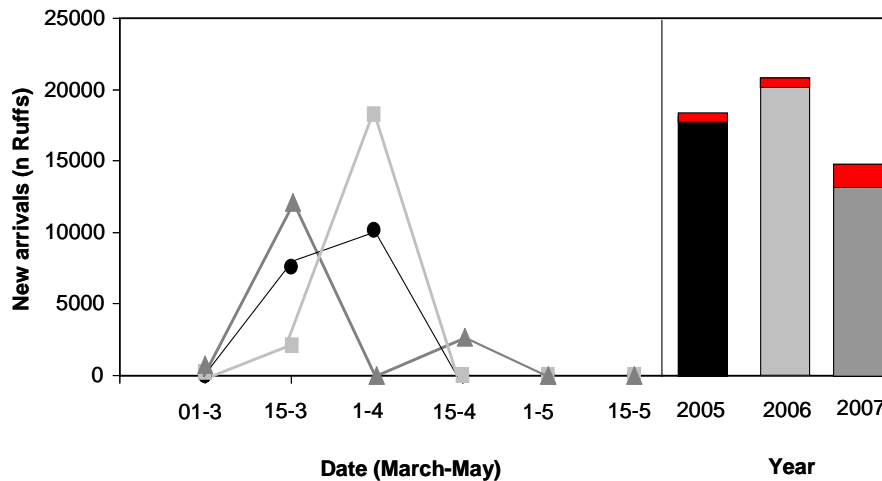


Fig. 5. Estimates of new arriving Ruffs staging in our study area in Southwest Fryslân. Total volume estimates and maximum counts during the census are depicted in the right panel.

Conclusions

We found day to day survival to be very high (ca. 0.95), which means that there was almost no turnover of Ruffs in the study area. The birds arriving in between early March/early April stay for approximately 40 days and leave gradually from half way April. There is however a difference in phenotype in the birds arriving in early March and the birds arriving late March/early April, with late birds being smaller (unpublished data).

Day to day survival (ϕ) did not vary between years, although spring 2005 was much colder and wetter than 2007 when it was exceptionally warm and dry. We found however a remarkable difference in resighting probability (p), being much lower ($\Delta p = 0.13$) in 2005. The ARTS stations were build on the major roosts along Lake IJsselmeer and set-up in the exact same way in both years and were functioning without a flaw. We actually had one station less in 2007 but still a higher p estimate. An explanation could be that Ruffs in 2005 spent less time at the roosts than in 2007. The meadows in 2005 were wet and maybe better foraging habitats than in 2007 when birds tend to stay near the coast of Lake IJsselmeer (Verkuil & de Goeij 2003).

The presented analyses of stopover timing did not reveal any individual covariates to play a role in staging time. Important phenotypic characteristics as wing length and

body mass were not included in the best survival models. This means either that we have to refine our models, or that Ruffs have a very rigidly set migratory schedule.

Survival estimates differed remarkably between encounter methods. An explanation can be that the colour-mark data included both adult and juvenile male Ruffs. The much lower resighting probability (p) should not affect estimates of ϕ , as in demonstrated with the ARTS data sets of 2005 and 2007, where very different p yielded equal estimates of (ϕ). The colour-mark analyses are still being refined.

Estimates of population size only add a small number of Ruffs to the census counts as Ruffs tend to stopover in the study area for a remarkably prolonged time of 42 days. Only in 2007 we had small influx of new birds in April, after a very early departure in early April (Fig. 5). Birds probably left the study area early because the fields surrounding the roosts were too dry to forage.

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Migration routes of Sanderling: insights after a year of colour-ringing

Jeroen Reneerkens & Edward Koomson

Sanderling *Calidris alba* are probably the most omnipresent shorebirds in the world. Outside the breeding season it is a bird of temperate and tropical beaches. During reproduction Sanderlings are high arctic, breeding only on the northernmost parts of the circumpolar tundra. Important areas with high densities of breeding pairs occur on the High Arctic Canadian archipelago west of Ellesmere Island, northeast Greenland and the Taimyr peninsula of Siberia (Cramp 1998). The latitude at which Sanderling spend the non-breeding season thus varies a lot and for Sanderlings that use the East-Atlantic Flyway ranges from as far south as South Africa to Ireland and Scotland in the north. Although Sanderlings invariably occur on sandy beaches where they feed on benthic prey in the surf and, opportunistically, on fish remains and insects, winter habitats at different latitudes (might) differ in terms of predation pressure, food availability, disease risk and ambient temperature. Furthermore the distance between breeding and wintering areas differs with a few thousand kilometres for birds wintering in the extreme south or north of the species' non-breeding range. This requires different migration strategies in terms of timing of departure, physiological condition before departure, the number of stop-overs and the length of stay at stop-over sites for Sanderlings wintering at different latitudes.

Despite the fact that Sanderlings are widespread, reasonably common, usually not very shy to human observers and often the favourite species of bird watchers, much basic information about the biology of Sanderlings is still not available. Sanderlings that use the East Atlantic Flyway breed in Greenland (and possibly NE Canada, but see Lyngs 2003) and Siberia. The available ring recoveries suggest that, unlike other shorebird species such as the Red Knot *Calidris canutus*, Nearctic and Siberian Sanderlings spend the non-breeding period mixed along the coasts of West Europe and the whole west coast of Africa, but much about the population structure is still largely unknown. Gudmundsson & Lindström (1992) analysed ringing data from Sanderlings migrating through Iceland. Of the 66 birds that were reported in winter (November-February), 63 were from Great Britain, one from the Wadden Sea and two from Ghana. This could mean that the majority of Greenlandic Sanderlings winter in Britain. However, ringing activities and colour-ring reading occurs much more intensively in western Europe compared with Africa. Therefore, our knowledge of the non-breeding area of Sanderlings from Greenlandic as well as Siberian origin will be biased. More ring(reading) activities in to the African part of the potential wintering range of Sanderlings are needed.

An intensive colour-ringing effort of Sanderlings along the East-Atlantic Flyway under the umbrella of the Global Flyway Network was recently set up to study demography at different wintering areas of which two in western Africa (Ghana and Mauritania, Koomson 2007). In addition, a study of migration strategies at a spring stop-over site in Iceland and a study to the reproductive output in relation to disease risk and immune defense in northeast Greenland was started in 2007 (Reneerkens unpubl.). For the latter two projects Sanderlings were colour-ringed as well. Despite the recent start, these

projects yielded a great amount of resightings already (table 1). Here we show some first results.

Number of Sanderlings ringed

Sanderlings were individually colour-ringed on three wintering sites; Esiam beach in Ghana, Iwik village in the Banc d'Arguin national parc of Mauritania and on the North Sea beach of Vlieland, The Netherlands. The birds were caught with mist nets in Ghana, with a canon-net in The Netherlands and with a small clapnet for the majority of Sanderlings in Iwik. During spring migration in May we caught Sanderlings with a canon-net on the several small beaches of Sandgerdi in SW Iceland. All breeding birds on the breeding grounds of Zackenberg, NE Greenland, were caught with small clapnets placed over the birds' nests, whereas chicks were picked up after chasing them by foot. Sanderlings were marked with a red flag (extended colour-ring) in Ghana, a white flag in Mauritania, a yellow flag in The Netherlands and a green flag for Iceland and Greenland but on different positions in relation to the other colour-rings for the latter two countries. The advantage of using different colours of flags for each country where we worked is that the origin of a resighted bird can usually be traced back, also when an observer was unable to read the full combination.

Site fidelity and resighting probabilities

Sanderlings are very site faithful to their wintering grounds as appeared from yearly resightings in Iwik, Mauritania (Spaans 2006), and which is later confirmed by us in Ghana and The Netherlands (unpubl. data). This makes Sanderlings very appropriate for careful survival analysis since resighting probabilities are high and, as a consequence, true survival can accurately be distinguished from permanent emigration.

Birds ringed in the non-breeding grounds in Ghana, Mauritania and The Netherlands are mainly resighted in winter very close to the original catching location due to very intensive colour-ring reading on those locations to obtain survival estimates. In addition, we have received reports of colour-ringed Sanderling observations during spring and autumn migration by European bird watchers in different countries than where they were caught in winter (Table 1).

Table 1. Number of Sanderlings colour-ringed and resighted from different study sites along the East Atlantic Flyway. Only birds caught before autumn migration in 2007 are included. In total 86 and 101 Sanderling have been caught in August – December 2007 in Ghana and Mauritania, respectively.

Country	Year	# colour-ringed	# re-sighted abroad	%
Greenland	2007	63	9	14.3
Iceland	2007	155	28	18.1
The Netherlands	2007	16	1	6.3
Mauritania	2002 - 2006	462	29	6.3
Ghana	2007	56	2	3.6
Total		752	68	9.0



Juvenile Sanderling with the colourcode G5WWWG was ringed on 22 July 2007 as a 16-day old chick in Zackenberg, NE Greenland, and was reported on Skagens Gren, northern Jutland, Denmark on 23 September 2007. On both occasions a picture of this birds was taken.

Results and Discussion

In total we have colour-ringed 752 Sanderlings on different locations along the East Atlantic Flyway between NE Greenland and Ghana (Table 1) before autumn migration in 2007. This has yielded already 68 resightings (9.0 %) on locations other than where the birds were ringed. This is a lot, given the size of the birds and the fact that, next to ringing activities in Mauritania since winter 2002, the project runs only less than a year! These recoveries already provide some first insights into the connection between breeding and non-breeding areas of Sanderlings, which is mapped in Fig. 1.

Because the majority of resightings during migration of Sanderlings that were ringed in Mauritania and Ghana were resighted in West-Europe, it is impossible to say whether these birds breed in Siberia or Greenland. The migrating birds ringed in Iceland and Greenland during migration and reproduction, respectively, are therefore more informative when it comes to knowledge about the wintering areas of Greenlandic Sanderlings, presuming that Sanderlings that pass through Iceland in spring all breed in Greenland (cf. Gudmundsson & Lindström 1992, Lyngs 2003).

Our data confirm that Greenlandic Sanderlings spend the non-breeding season in Western Europe but also that they winter in western Africa. Two Sanderlings colour-ringed in winter in Mauritania were observed during autumn migration in SW Iceland where they stayed for at least 4 and 14 days, respectively. Both birds were resighted in Mauritania in the following winter. Also the appealing observation of a sanderling on the remote island of Arel in the Banc d'Arguin, Mauritania that was caught on a nest with four eggs in Zackenberg, NE Greenland confirms that part of the Greenlandic birds winter in West-Africa. A report of a sanderling with a green flag in Walvisbaai, Namibia, of which unfortunately the flag position or the colour of any other colour-ring were not identified, shows that Greenlandic sanderlings might winter as far south as Namibia. If the green flag was correctly observed, this would be the southernmost resighting or ring recovery of a Greenlandic Sanderling (Lyngs 2003). Given the much higher intensity of bird watching and colour-ring reading in Europe it is likely that many more Sanderlings winter in Africa than we currently know. More expeditions for colour-ring reading to African areas with high numbers of Sanderlings would probably yield interesting information about population structure, and by determining ring densities could also lead to good estimates of population size (cf. Reneerkens *et al.* 2005, Spaans 2006).

Interestingly, many birds from Iceland and Greenland were resighted in Brittany, France. Where Gudmundsson & Lindström (1992) noticed that the great majority of the birds caught in Iceland on spring passage to Greenland winter in Great Britain, our data additionally also show that a remarkable proportion of birds also stop over on autumn migration and spend the non-breeding period in Brittany.

Unfortunately, we have only received a single resighting of a colour-ringed Sanderling east of the Wadden Sea. Such birds are most likely from Siberian origin. That observation of a bird in Latvia that had spent the winter in Mauritania suggest that, as other studies based on ringing recoveries have suggested, birds from Greenlandic and Siberian origin winter together on beaches on the west coast of Africa (and Europe).

We have collected a small wing feather (median covert) of each colour-ringed Sanderling that is moulted in the wintering area and is composed of the the local food sources and, therefore, may be a unique signature of isotope ratio. By this means, we will try to trace back the non-breeding grounds of each sanderling that we caught in Iceland and Greenland. The feathers from the birds caught in Ghana, Mauritania and The Netherlands in winter will form a useful reference collection and we expect that the isotope signature of the Sanderlings resighted in winter will be a unique, additional way to check the accuracy of the stable isotope method, that often is lacking in studies where stable isotopes re used to trace back the winter ranges of migratory birds (e.g. Hobson 2003). If this method proves useful, it will be possible to determine to a greater extent the proportion of Greenlandic Sanderlings that spend the non-breeding season in Africa and Europe, respectively. The same can be done for the birds on migration through the Wadden Sea and Iceland and will show whether there is a difference in timing of migration between Sanderlings wintering at different latitudes.

In the future, we also hope to get a better grip on the population structure and relate sex, age and condition (e.g. health status and immune defence) to migration strategies and non-breeding habitat. An interesting, preliminary result indicating a strongly skewed sex-ratio was found in Iwik, Mauritania, where in 2005 195 Sanderlings were caught of which 135 (69 %) were male. By continuing colour-ring marking and resighting a lot of sanderlings along the East Atlantic Flyway, individuals of which we collect a lot of additional information on health status, sex and age, we are convinced that we have a strong tool in hand to unravel a lot of interesting biological questions of a intriguing, but still mysterious, species.

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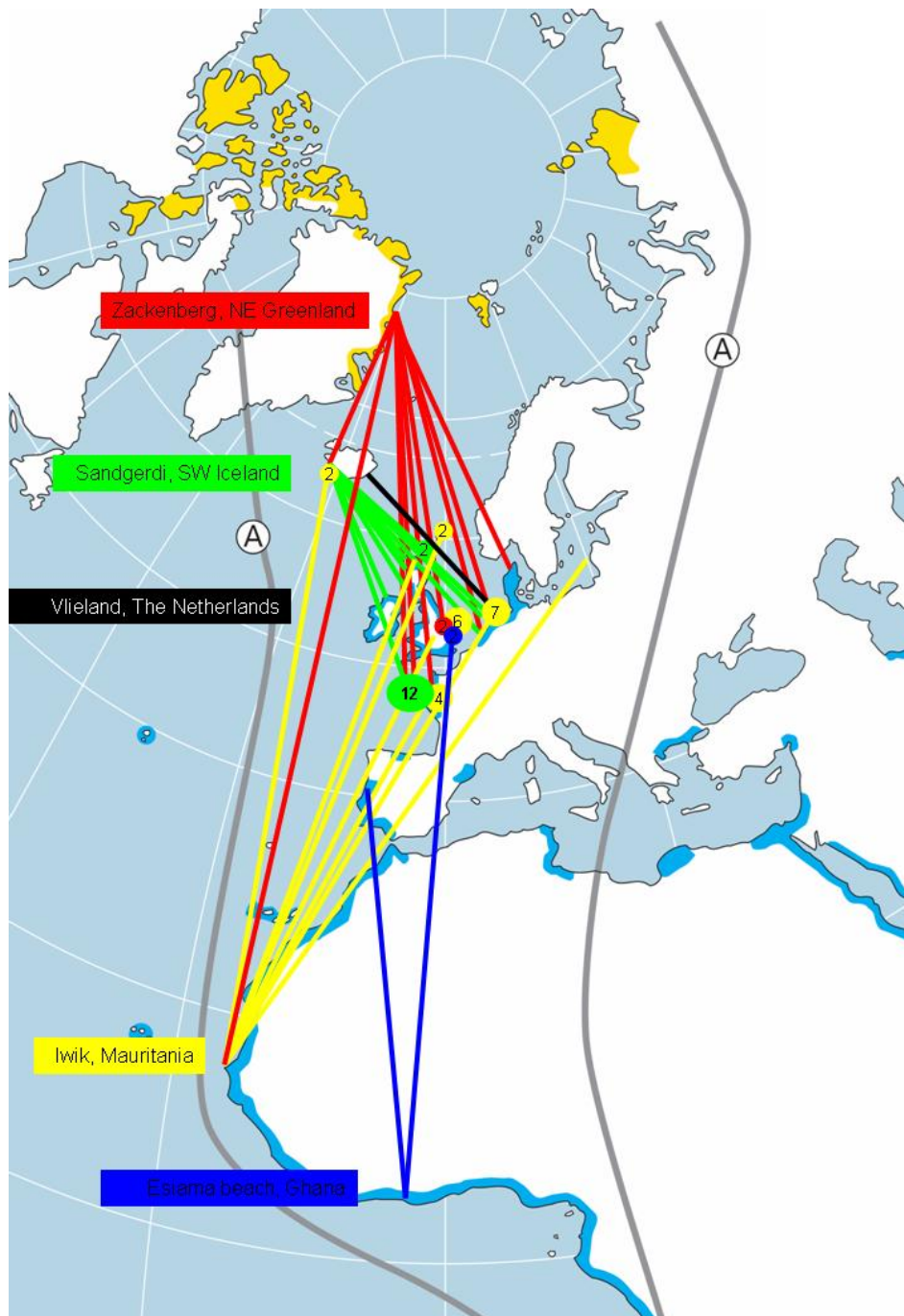


Fig. 1. Resightings of individually colour-marked Sanderlings in other areas than the original catching site. Red lines connect resighting locations with the place of ringing at Zackenberg, NE Greenland, green lines with Sandgerdi, Iceland, the black line with Vlieland, The Netherlands, yellow lines with Iwik, Mauritania and blue lines with Esima beach, Ghana. More than one resighting in a certain area are depicted with a circle indicating the number of resightings. The size of the circle corresponds to the number of individual birds on that location. Yellow areas indicate known breeding areas of Sanderling, blue areas indicate known non-breeding areas, where the grey line (indicated with an 'A') indicates the East Atlantic Flyway. The map is copied from Van de Kam *et al.* (2004).



Some colour-ringed Sanderling in a flock on the beach of Sandgerdi, SW Iceland on 28 May 2005.



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Appendix A

Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide

Theunis Piersma

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Abstract Shorebirds, or waders, form an ecologically (but not phylogenetically) homogenous group of birds that, despite this homogeneity, exhibits clear correlated contrasts in habitat use and migration distance between closely related species pairs. In addition, within species there is distinct variation in breeding and wintering latitudes, i.e. migration distance. I examine here such contrasts at different taxonomic levels and evaluate what we can learn about selective forces on habitat selection and the evolution of migration strategies in birds. My primary example is the worldwide migration system of the Red Knot *Calidris canutus*. These sandpipers breed only on high arctic tundra (65–83°N), but they move south from their disjunct, circumpolar breeding areas to nonbreeding sites on the coasts of all continents (except Antarctica), between latitudes 58°N and 53°S. Due to their specialized sensory capabilities, Red Knots generally eat hard-shelled prey found on intertidal, mostly soft, substrates. As a consequence, ecologically suitable coastal sites are few and far between, so they must routinely undertake flights of many thousands of kilometres. In contrast to prediction, Red Knots at tropical intertidal sites have lower fuelling rates than birds at more southern or northern latitudes. This leads to greater time–

stress in the southernmost wintering populations that not only have to cover over 14,000 km in single migrations, but also cannot rely on tropical regions to make refuelling stops. Rapid human-caused losses of the food-base in staging areas during both north- and southward migrations have been demonstrated to have caused rapid declines in several Red Knot populations. Detailed worldwide eco-demographic research on these extreme long-distance migrants, as embodied in, for example, the recently established Global Flyway Network, yields a two-pronged benefit: (1) on the basis of the unintended large-scale experiments carried out by humans, we rapidly come to grips with the selection pressures moulding the migration strategies of migrant birds, and (2) in applied contexts, the work gives instantaneous feedbacks on the conservation consequences of man-made alterations to wetland environments at the relevant global spatial scales.

Keywords Annual cycle · Conservation · Flyways · Foraging · Migration · Seasonal schedules · Waders

Introduction: comparisons are the backbone of biology

Biodiversity is the wellspring for comparisons, and insightful comparison is the basis for much of our understanding in biology (Wilson 1992). The development of biological research fields as divergent as genetics, functional morphology, nutrition, communication, behavioural and other kinds of ecology is based on comparison: comparisons between (aspects of) individuals, between groups and populations living in different places and different environments, between species and between higher taxa, between habitats (e.g. Schmidt-Nielsen 1964; Krebs and Davies 1987; Aulsebrook 1994; Wainwright and Reilly 1994;

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Klasing 1998; Marler and Slabbekoorn 2004). Needless to say, “the comparative approach... was Darwin’s favoured technique” (Harvey and Pagel 1991).

Birds, so visible, audible and ubiquitous, so variable yet structurally uniform, so inspiring in numbers and behaviour and so inviting to study, have been exceptionally well studied compared with other vertebrate groups and have thus become a major focus for comparative work on life histories and mating systems (Bennett and Owens 2002). Among the birds of open landscapes, the shorebirds—or waders—form an ecologically quite homogeneous guild, but not a monophyletic clade, within the order Charadriiformes (Paton et al. 2003). The approximately 217 shorebird species belonging to 14 families (Jacanidae, Rostratulidae, Dromadidae, Haematopodidae, Ibisornithidae, Recurvirostridae, Burhinidae, Glareolidae, Pluvianellidae, Charadriidae, Scolopacidae, Pedionomidae, Thinocoridae and Chionidae) have received a great deal of scientific attention (see relevant chapters in del Hoyo et al. 1996), at least the common species living in parts of the world with an ornithological tradition (Piersma et al. 1997). Shorebirds exhibit great variability, both within and between families, in the degree of sexual size and plumage dimorphism and in mating system (van de Kam et al. 2004), and this has invited several comparative analyses of sexually selected traits in relation to ecology, migration and mating system (Pitelka et al. 1974; Figuerola 1999a; Jukema and Piersma 2000; Piersma and Baker 2000; Székely et al. 2004, 2006).

The plovers Charadriidae (with 66 species and 105 distinct populations or subspecies) and the sandpipers Scolopacidae (with 86 species and 134 subspecies units) are not only the two most diverse families among shorebirds, they also show the greatest diversity with respect to migration propensity and migration distance. There are plover and sandpiper species where individuals never move more than several 100 m away from their natal areas (see, for example, Miskelly 1999), but the plovers and the sandpipers also count among their ranks champion seasonal migrants that cover entire ocean basins in single flights (see, for example, Johnston and McFarlane 1967; Gill et al. 2005). Rather than providing a wide-ranging comparative analysis of ecological correlates of migration behaviour among shorebird species (in fact, I believe that at present this is not the best taxonomic level for insightful analyses), I will build on the considerable intraspecific variation in migration distances among extant populations of the Red Knot (*Calidris canutus*) to investigate how ecological factors may have moulded migration distance. Of course, these ecological, season-specific selection pressures will shape all aspects of the annual cycle, i.e. fuelling, flight and moult (Buehler and Piersma 2007). Several such selection

pressures have recently been brought to light as a consequence of rapid, man-made alterations of habitats, and these will be discussed. However, it is their use of very specific habitats year-round that we first have to consider: why do Red Knots and other migrant birds breeding in the High Arctic tend to winter in marine or saline habitats?

Covariation between breeding and wintering habitat: a life-history gradient generated by differential disease pressures?

Red Knots breed in the high arctic, about as far north as one can get. Outside the breeding season, one finds Red Knots only in marine coastal habitats, usually large wetlands with extensive intertidal foreshores (Piersma et al. 2005). Red Knots are also particular because they are a specialized molluscivore (see below) but shift to eat surface arthropods during the summer months on high arctic tundra. Thus, as they are able to live off intertidal bivalves as well as surface arthropods, there is no obvious reason based on their trophic specialization why Red Knots should restrict themselves to tundra during the breeding season (they should be able to find such arthropod prey in temperate meadows as well; see Schekkerman et al. 2003) and coastal intertidal habitats during the nonbreeding season (they should also be able to use freshwater wetlands with shellfish resources, such as the Niger floodplains in Mali; Zwarts et al. 1999, 2005).

Expanding the comparison, other high arctic breeding shorebirds, such as Grey Plover (*Pluvialis squatarola*), Sanderling (*Calidris alba*), Purple Sandpiper (*Calidris maritima*) and Bar-tailed Godwit (*Limosa lapponica*) also winter in marine coastal wetlands, a striking contrast with their more southerly breeding congeners (respectively, for example, Eurasian Golden Plover *Pluvialis apricaria*, Temmick’s Stint *Calidris temminckii*, Dunlin *Calidris alpina* and Black-tailed Godwit *Limosa limosa*) that tend to additionally, or uniquely, rely on freshwater wetlands during the nonbreeding season. Piersma (1997) put these interspecific associations to formal statistical tests and was able to confirm the empirical linkages between the degrees of northerly breeding and the use of marine or coastal nonbreeding habitats. However, this association does not stop at shorebirds. Comparisons among gulls, terns and allies (Lari), ducks, Anatidae and passerines (Table 1) all suggest that the far-northern breeders tend to use coastal or saline habitats, re-emphasizing that the biogeographic pattern is not coupled to some sort of trophic specialization. Then and now, the only relevant covariate that I could dream up is the possibility of a relative paucity of disease organisms or their vectors in both arctic and marine habitats (Piersma 1997, partially inspired by Ridley 1993).

Table 1 Evidence for linkages between latitude of breeding and degree of coastal/marine wintering habitat in various groups of birds

Group	Evidence for linkage
Sandpipers Calidridinae	Significant association between breeding latitude and relative use of marine wintering habitats
Shorebirds Charadrii	In 11 pairwise, within-genus comparisons, ten cases confirmed the association between arctic breeding and marine wintering
Gulls and allies Lari	Obligate open sea wintering skuas (Stercorariidae) all breed in boreal and arctic habitats, whereas the closely related tern family (Sternidae), especially species with a more southerly breeding distribution, also use nearshore and inland freshwater wetlands (e.g. to roost)
Sternidae	The two northernmost and the southernmost breeding tern species (respectively, Arctic <i>Sterna paradisaea</i> , Aleutian <i>Sterna aleutica</i> and Antarctic tern <i>Sterna vittata</i>) only winter in marine habitats
Laridae	The northernmost breeding gulls (Glaucous Gull <i>Larus hyperboreus</i> , Ivory Gull <i>Pagophila eburnea</i> , Ross's <i>Rhodostethia rosea</i> and Sabine's Gull <i>Xema sabini</i>) are all limited to marine environments in the nonbreeding season
Ducks and geese Anatidae	The two most northerly breeding species of duck (Long-tailed Duck <i>Clangula hyemalis</i>) and goose (Brent <i>Branta bernicla</i>) strictly winter in marine and coastal habitats
Songbirds Passeriformes	The two most northerly breeding passerines (Snow Bunting <i>Plectrophenax nivalis</i> and Lapland Longspur <i>Calcarius lapponicus</i>) tend to especially use coastal and saline wintering habitats

The shorebird examples are from Piersma (1997)

High arctic breeding species may represent one end of a continuum of decreasing investments in immunity, a strategy that would ecologically be enabled by low disease pressure and which in turn makes it possible for the birds to show high levels of energetic performance (high growth, storage and thermoregulatory rates).

There is an increasing body of evidence indicating that disease organisms—blood parasites in particular—and/or their vectors are indeed relatively sparse in both high arctic and marine/saline habitats compared to temperate and tropical freshwater habitats (e.g. Bennett et al. 1992; Figueroa 1999b; Jovani et al. 2001; Mendes et al. 2005). However, any of the contrasts in overall immune investments, or aspects of immunity, between high arctic/marine species and with lower latitude/freshwater species—contrasts that would logically follow from the differential exposure to disease pressures during either the egg- or chick-phase or later during life—have as yet proven to be difficult to investigate and to confirm (Mendes et al. 2006a, b).

A corollary of the disease-based covariation hypothesis of Piersma (1997) is that drastic historic population bottlenecks, ones extreme enough to lead to the loss of genetic variation in the genes coding for the immune system (i.e. genes coding for antigen recognition sites and for natural antibodies; see O'Brien and Evermann 1988), would have been tolerated by species under relaxed disease pressures—i.e. the high arctic breeders and marine wintering ones (Piersma 2003). During periods of rapid climate change (disappearance of tundra, loss of intertidal wintering habitats during fast sea level changes), these species would be

especially susceptible to habitat loss and population bottlenecking (Piersma 2003). Consistent with this, Red Knots indeed show quite low levels of neutral genetic variation, Dunlin (an intermediate species) has been reported to show intermediate levels of genetic variation and Ruff (*Philo-machus pugnax*, quite southerly breeding and a marine averse calidrid sandpiper), supposedly show high levels of genetic variation (Segre et al. 1970; Baker et al. 1994; Aulsebrook 2000; Buehler and Baker 2005).

On this basis, I suggested that there might be historical feedbacks in the generation of contrasts between the low and high end of the immunity/habitat selection gradient (Piersma 2003). As shown in Fig. 1, if an increased susceptibility to disease has indeed restricted the range of suitable habitats [e.g. birds having to avoid areas with ample food but many (vectors for) debilitating diseases, such as mosquitoes carrying avian malaria], we have a system with a strong positive historical feedback link. This is rather more exciting than a system where historical ecological constraints have simply led to a loss of genetic variation for disease resistance; that is, lowered disease resistance being just a *consequence* (and not also a cause) of population bottlenecks due to temporary restrictions in habitat availability.

In this scenario then, habitat selection, population size, migration strategies and disease resistance are all linked in one historical web of causality. In fact, there are several additional biological contrasts that may be relevant: the more pronounced seasonal plumage dimorphism in the high-latitude breeding species (Jukema and Piersma 2000) and their greater apparent organ flexibility (Piersma 1998) as well as

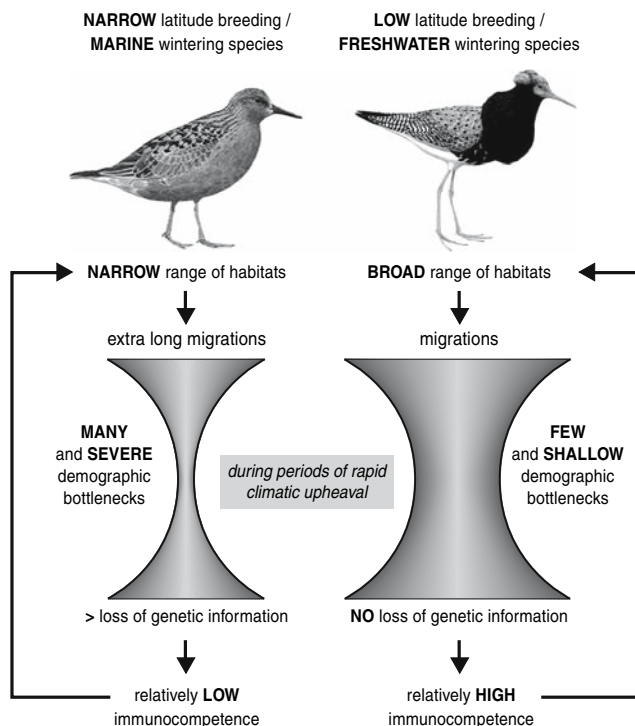


Fig. 1 Schematic overview of the contrasts between latitudinal migrant shorebird species that breed at high latitudes and spend the winter in marine (saline) habitats and those that breed at lower latitudes and spend the winter in freshwater (including grassland) habitats and the possible consequences and positive feedbacks induced by population bottlenecks. Based on Piersma (2003)

the finding that freshwater species first migrate northwards from the circa-tropical wintering areas at earlier ages than the coastal species (D.I. Rogers, personal communication). Also, freshwater species of shorebirds appear to have a lower ‘lifespan energy potential’ (spend less energy per maximum lifetime) than marine species (Goede 1993).

Intraspecific comparisons: introducing a long-distance migrating, molluscivore shorebird

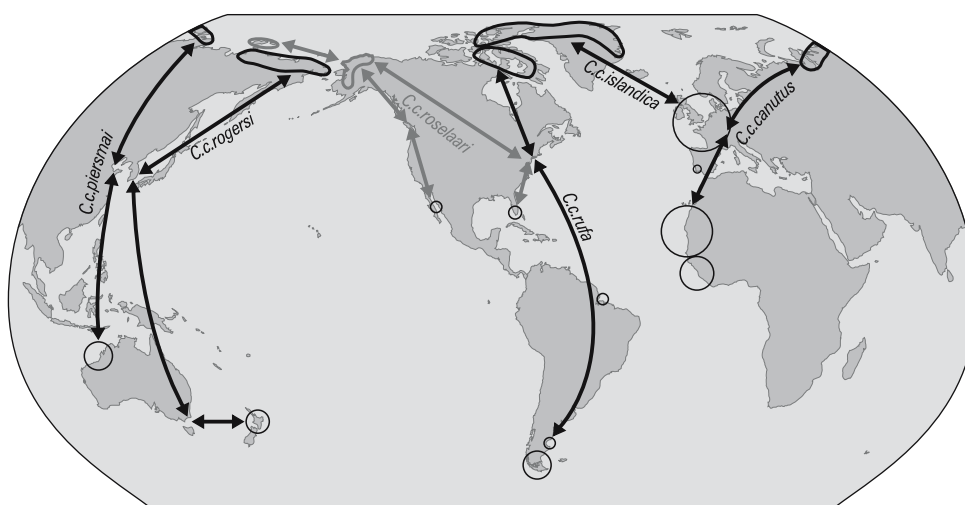
Returning to the point made at the start of the previous section—that Red Knots uniquely breed on high arctic tundra and only use extensive coastal wetlands during the nonbreeding season—I can now add spatial and temporal details. The discontinuous circumpolar breeding range of Red Knots incorporates breeding areas of at least six populations (Fig. 2), populations that are morphologically sufficiently distinct to count as subspecies (Roselaar 1983; Tomkovich 1992, 2001). The subspecies certainly are distinct when it comes to their migratory trajectories and the seasonal timing of their movements (Piersma and Davidson 1992; Piersma et al. 2005; Buehler and Piersma 2007). The populations show little (Tomkovich and Riegen 2000) or

no overlap at the final wintering¹ destinations, and only limited overlap during south and northward migration. The subspecies *islandica* and *canutus* co-occur in the Wadden Sea during the southward migration (Nebel et al. 2000) and less so during the northward migration (Prokosch 1988). The subspecies *piersmai* and *rogersi* coming from wintering areas in northwest Australia and southeastern Australia/New Zealand, respectively, both migrate through the Yellow Sea in spring (Battley et al. 2005; Piersma et al. 2005). Red Knots wintering from Georgia to northern Brazil are distinct from the *rufa* knots wintering in southernmost South America (Baker et al. 2005; Atkinson et al. 2005) and may represent an eastern group of *roselaari* birds, or an undescribed separate population that co-occurs with *rufa* knots during the northward migration in Delaware Bay (Atkinson et al. 2005, 2007). Another population of *roselaari* knots is now known to connect wintering areas in northwestern Mexico and staging areas in southwestern Alaska (R.E. Gill Jr, P.S. Tomkovich, H.P. Sitters and N.A. Clark, personal communication). In the case of *canutus*, a previously existing transequatorial wintering area in southern Africa seems to have been abandoned from the 1990s onward (R.W. Summers and L.G. Underhill, personal communication). Arguably the most fascinating aspect of the whole substructuring of the world’s Red Knots is the suggestion, based on genetics, that all of the world’s six or seven subspecies have diversified recently from a single founder population that survived the last glacial maximum of approximately 20,000 years ago (Baker et al. 1994; Piersma 1994; Buehler and Baker 2005; Buehler et al. 2006); if true, the subspecies of Red Knots have very shallow phylogenetic roots.

Although, as we have seen, the apparently strict non-breeding habitat requirement of Red Knots (extensive and open coastal intertidal areas) may relate to the avoidance of pathogens, it may also relate to the avoidance of predators (Piersma et al. 1993a, b; van den Hout et al. 2007), and it certainly relates to their trophic specialization. Studies on their diet have revealed that Red Knots eat hard-shelled molluscs (Prater 1972; Piersma 1991; Piersma et al. 1993b, 1994; González et al. 1996; van Gils et al. 2005c), sometimes supplemented with easily accessed softer prey, such as crustaceans (Alerstam et al. 1992; van Gils et al. 2005b) and even polychaetes (P.M. González, personal communication). This is not because Red Knots necessarily prefer hard-shelled molluscs (in fact, they do not when given the choice; van Gils et al. 2005a), but because they are specialized in finding and processing such prey, even at the detriment of being able to find actively crawling soft-

¹ Taking a knot-o-centric view (i.e. that of a bird born in the northern hemisphere in summer), I see only benefits in talking about *wintering* areas, even if wintering takes place during the southern summer.

Fig. 2 Global distribution of the six recognized subspecies of Red Knots during the breeding and nonbreeding season, with schematic south- and northward migration routes, and information on migration distances and approximate population sizes. The contours in the Arctic delimit the approximate breeding areas and circles indicate wintering areas. The size of the circle indicates the relative number of birds using the respective ‘wintering’ areas. This figure is modified after Buehler and Piersma (2007) and is an update of the original synthesis by Piersma and Davidson (1992)



	<i>C. c. piersmai</i>	<i>C. c. rogersi</i>	<i>C. c. roselaari</i>	<i>C. c. rufa</i>	<i>C. c. islandica</i>	<i>C. c. canutus</i>
Total migration distance (km)	10400	15000	7500	15000	4650	9000
Max. single flight distance (km)	6300	6500	5600	8000	2830	5100
Breeding latitude	75–78°N	67–70°N	65–75°N	64–76°N	76–85°N	75–80°N
Population size	30000	100000	35000	30000	400000	300000

bodied worms and small crustaceans that other sandpipers specialize on (Gerritsen and Meijboom 1986). In fact, Red Knots have a unique sensory capacity—which to date has not described for any other animal—that uses self-induced pressure gradients around hard objects in wet soft sediments (Piersma et al. 1998; Fig. 3). The “remote detection” of buried hard-shelled prey is probably enabled by their bill-tip organ, the dense conglomerations of pressure sensors (Herbst’ corpuscles) clustered in forward pointing “sensory pits” in the outside surfaces of the tips of both upper and lower mandible (Piersma et al. 1998).

Unlike molluscivore shorebirds that remove the flesh from the shell with their stout bill, such as oystercatchers Haematopodidae (Hockey 1996), but just as molluscivore diving ducks (Kehoe and Ankney 1985; Barnes and Thomas 1987; Goudie and Ryan 1991), Red Knots ingest their prey whole, crushing the shell in the muscular part of the stomach, the gizzard (the glandular stomach is rudimentary; Piersma et al. 1993c). Crushed shell material is not usually voided as pellets (as is the habit of a related shorebird, the Dunlin *Calidris alpina*; Worrall 1984), but as faeces (Dekinga and Piersma 1993). As a consequence of

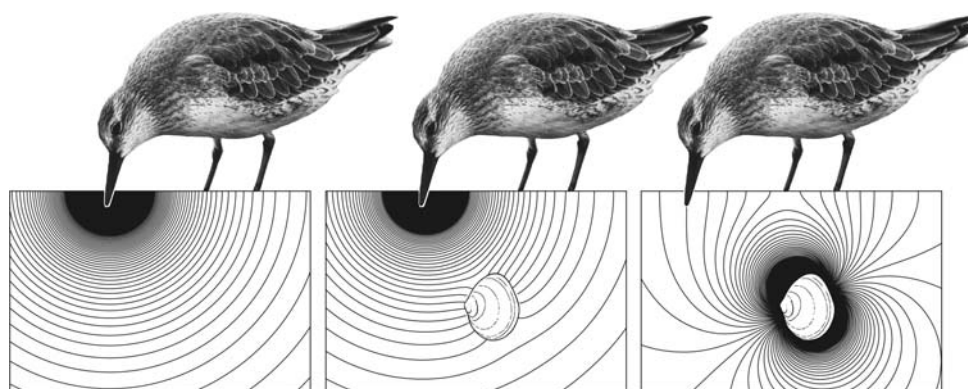


Fig. 3 Cross section through a tidal flat showing hypothetical pressure fields created when a Red Knot probes the upper surface of the wet sediment. In the *left-most* cross section there are no hard objects present to disrupt the pressure field. In the *middle* cross section, a buried bivalve prevents the interstitial water from rapidly moving away from the pressure exerted by the repeatedly probing bill.

This results in an increased water pressure around the bivalve that allows the knot to detect it from several centimetres away (cross section at *right*, showing contours of pressure differences between the ideal spherical pressure landscape on the *left* and the disturbed pressure landscape in the *middle*). Based on Piersma et al. (1998)

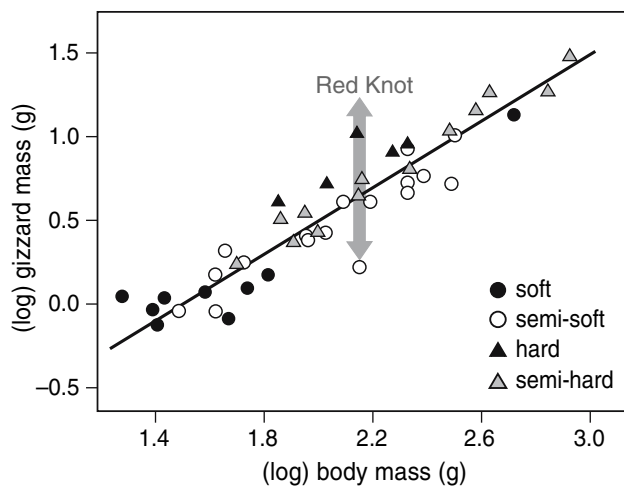


Fig. 4 Allometry of the fresh gizzard mass in 41 species of shorebird from four different families, assigned to four different diet 'hardness' categories. For the Red Knot, the vertical line additionally indicates the great variation in gizzard mass that can occur even within individuals. After Battley and Piersma (2005)

the work that the gizzard and intestine have to do on the shell material, and perhaps to prevent wear and tear inflicted by shell fragments on the sensitive intestinal wall, both gizzard and intestine are relatively heavy in hard-shelled-prey-eating shorebirds (Battley and Piersma 2005). In an allometric comparison among 41 shorebirds, the Red Knot came out as the species with the largest gizzard for its body mass (Fig. 4). Experimental work has shown that gizzard size determines the shell-processing capacity of a bird and thereby limits instantaneous food intake rates (van Gils et al. 2003).

A heavy digestive tract is a burden for well-travelled birds that would best be off with low flight costs, and it is therefore no surprise that at every stage of the annual cycle, Red Knots seem to keep the gizzard to the locally possible minimum (Piersma et al. 1999a, b; van Gils et al. 2003, 2005c, 2006a). When fed soft trout-food pellets in captivity, wild-captured Red Knots, which had eaten bivalves up to that point, lost half of the gizzard mass within about 1 week (Dekinga et al. 2001). This loss could be reversed by a return to a diet of hard-shelled mollusc prey. Building on an extensive set of dedicated laboratory experiments, gizzard mass in free-living Red Knots (measured non-invasively by ultrasound; Dietz et al. 1999; Starck et al. 2001) can be predicted quite accurately for different months, years and sites (Fig. 5) on the basis of energetic requirements, the length of the working day, the quality (the flesh to shell mass ratio) of the prey and whether birds are trying to maintain energy balance (*satisficing*) or rather fuel as fast as they can (*net rate maximizing*; van Gils et al. 2003, 2006a). This gives us a context to examine gizzard mass, prey quantity and quality requirements and energy

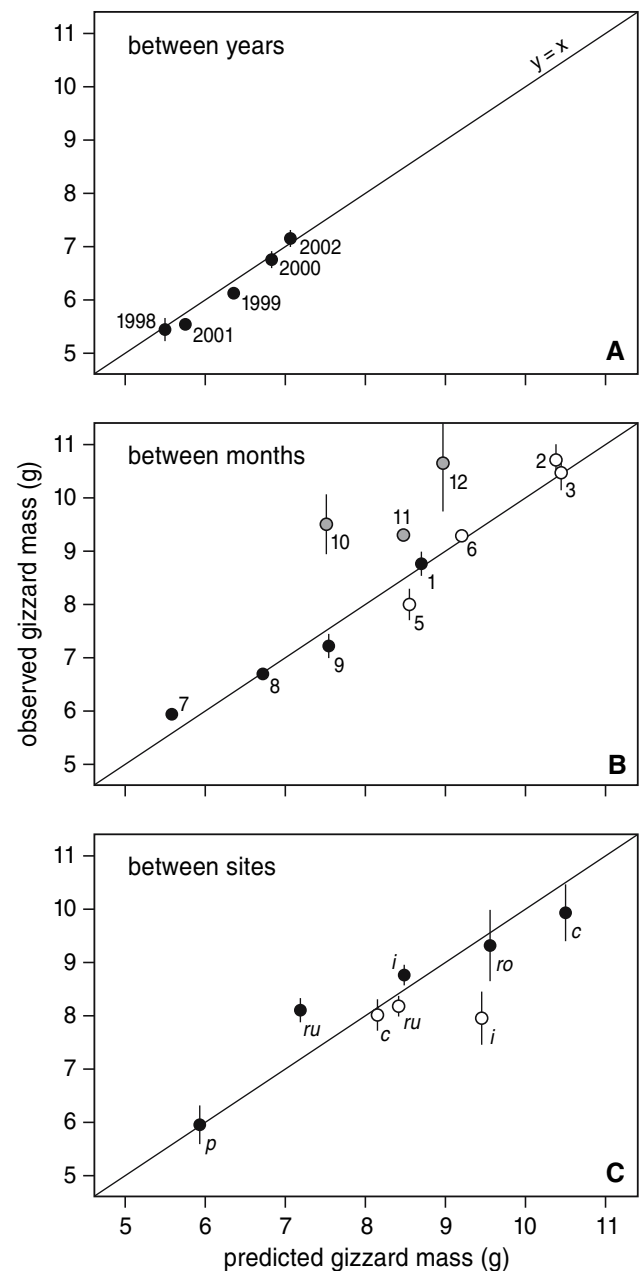


Fig. 5 Relation between observed gizzard mass and predicted gizzard mass at various temporal and spatial scales: **a** between years (Dutch Wadden Sea during late summer), **b** between months (Dutch Wadden Sea; 1–12 indicate the months January–December), **c** between sites (worldwide; letter indicates subspecies: *c* *canutus*, *i* *islandica*, *p* *piersma*, *ro* *rogersi*, *ru* *rufa*). In all plots, black dots indicate samples from wintering periods when *satisficing* gizzards are predicted; in **b, c** open dots indicate fuelling periods when *rate-maximizing* gizzards are predicted; additionally, in **b**, grey-filled dots (underestimations by 1.6–2.0 g) indicate those months in early winter (October–December) when Red Knots were assumed to be *satisficing* but actually were building up a small peak in body mass. Diagonal lines give $y = x$ lines and bars give standard errors. From van Gils et al. (2006a)

requirements as factors potentially constraining the fuelling and migration performance of Red Knots (Battley et al. 2005; van Gils et al. 2006b).

Do ecological constraints shape seasonal plumage changes and other annual cycle characteristics?

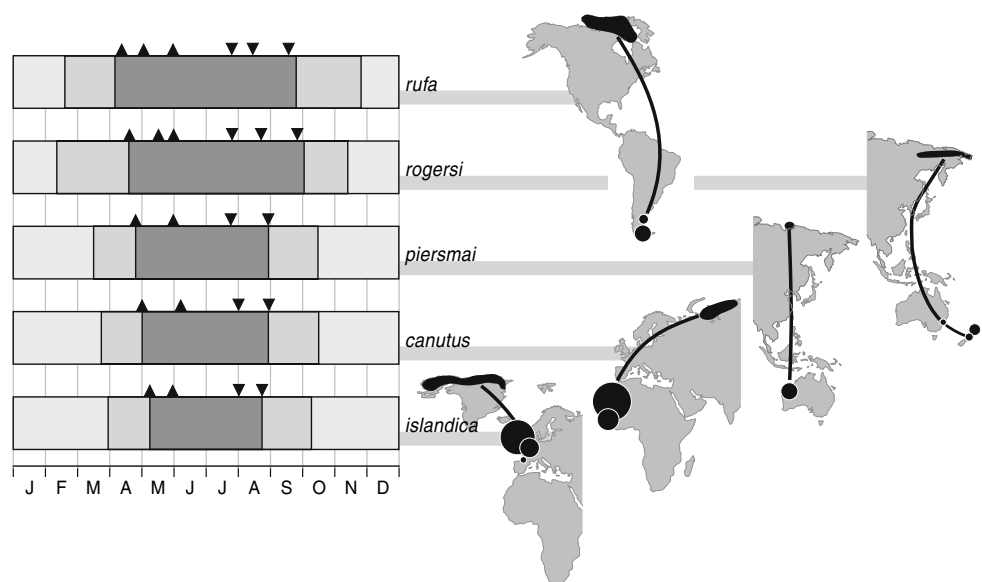
An examination of the seasonal timing of moults and long-distance flights of the five best-known subspecies (Fig. 6) indicates two groups with similar patterns. The two subspecies *rufa* and *rogersi*, which both winter south of the Equator, make three non-stop northward and three non-stop southward flights and carry the alternate (breeding) plumage for no fewer than 6–7 months (Piersma et al. 2005). The first northward flights do not take them very far from the wintering areas—*rufa*, from Tierra del Fuego to northern Patagonia (Baker et al. 2001); *rogersi*, from New Zealand to eastern Australia (Battley 1997; Battley and Piersma 1997). In both subspecies, this is followed by very long flights across the Equator to north temperate staging grounds in eastern North America and around the Yellow Sea, respectively. The three subspecies *piersmai*, *canutus* and *islandica*, which winter in or north of the tropics, each make two non-stop north- and two southward flights and carry the alternate (breeding) plumage for a shorter time, 3–4 months. In all subspecies, much of the moult from the basic to the alternate plumage takes place before the first northward flight, i.e. on the wintering areas (although some subspecies, especially *rufa*, do a fair amount of ‘touching-up’ at the staging sites during the northward migration, and some moult back to the basic plumage at stopover sites during southward migration; González et al. 2006; personal observation).

Note that the ordering in two “migration-types” does not reflect what we currently know about their phylogenetic relatedness (Buehler and Baker 2005; Buehler et al. 2006). For example, *piersmai* (“northern” winterer, two flights, short alternate plumage season) and *rogersi* (transequatorial,

three flights, long alternate plumage season) would be more closely related to each other than to either *canutus* or *rogersi* (of respectively either type). Similarly, *rufa* (the transequatorial champion) appears to be the closest relative of *islandica*, the only subspecies wintering in the north-temperate zone. The suggestion that migration schedules of Red Knots are not deeply rooted in their phylogeny echoes similar findings of evolutionary lability of migration in passerines, where closely related species or subspecies may also show stark divergences in migratory versus sedentary behaviour (Helbig 2003; Outlaw et al. 2003; Outlaw and Voelker 2006; Pérez-Tris et al. 2004; Winker and Pruett 2006).

Apart from this timing-of-moults-and-flights correlate of migration distance, the extent and relative intensity of the rusty-redness of the alternate plumage of each subspecies is also correlated with migration distance (Fig. 7; Buehler and Piersma 2007). The subspecies that winter in or north of the tropics (*canutus*, *islandica* and *piersmai*) are the ‘darker’ subspecies, whereas the transequatorial *rogersi* and *rufa* have lighter bellies than both *roselaari* and *piersmai*; *rufa* is also the palest of all in overall plumage. This relatively lower investment in melanin-based colouration of contour feathers by the transequatorial wintering subspecies may indicate that they cannot invest so much energy in moult. For both *rogersi* and *rufa*, we know that the wintering grounds offer relatively rich food resources (P.F. Battley, unpublished data; G.B. Escudero et al., unpublished data), a feature of their environment that is actually reflected in their decent fuelling rates before northward departure (Piersma et al. 2005). The *piersmai* subspecies, wintering just south of the Equator in north-western Australia, shows slow rates of fuelling before northward migration (Piersma et al. 2005), and it migrates

Fig. 6 Timing of plumage changes and of the northward (upward pointed triangles) and southward flights (downward pointed triangles) in the five best known subspecies of Red Knot, along with approximate migration routes and the relative population size of the wintering populations. In these diagrams, the time that Red Knots carry the grey-coloured basic plumage is indicated by the light shading, the time they carry the rusty-red alternate plumage is indicated by the darkest shading and the periods that they moult contour feathers to go from one to the other plumage type by the intermediate shading



very late (Battley et al. 2005). In view of these arguments, it seems most likely that lack of time at the southern wintering grounds curtails investments in this—sexually selected (Jukema and Piersma 2000; Piersma and Jukema 1993; Battley et al. 2006)—trait. The subsequent increased survival of individual *rufa* birds showing a ‘touch-up’ contour feather moult during their stopover in San Antonio Bay, northern Patagonia, in March 1998 relative to that of non-moulting individuals (González et al. 2006) suggests that relative plumage redness within populations is a honest quality signal, perhaps correlated with health, disease resistance and/or age (Piersma et al. 2001a, b; Drent et al. 2003; Battley 2007). Note that as male Red Knots of all subspecies are usually somewhat brighter and more extensively rufous than females (personal observation), females may not have as much need to advertise their quality.

In this context one wonders why Red Knots that winter as far south as Tierra del Fuego (*rufa*) and New Zealand (*rogersi*) do not, or hardly, use tropical coastal wetlands as stopovers; after all, such areas are found en route. For example, why do *rufa* not make the time to refuel at the Maranhão coast in northeastern Brazil (see Baker et al. 2005), an area used by “eastern *roselaari*” (Fig. 2)? I believe that an answer is suggested by the very low rates of fuelling before northward flights in tropical wintering areas (Piersma et al. 2005). The fuelling rates of 1 g/day or less at wintering sites in West Africa and in north-western Australia were surprising because, everything else being equal, the warm climates and low maintenance costs at such tropical sites (Wiersma and Piersma 1994) should enable higher rather than lower fuelling rates. Tropical constraints may relate to both the high ambient heat loads during the fuelling period (preventing hard work; Battley et al. 2003) and the mediocre quality of the prey (van Gils et al. 2005c). In summary, I propose that although tropical coastal wetlands with reasonable shellfish stocks can be used as wintering areas (because birds have the time to get away again; Zwarts et al. 1990), they fall short of providing the conditions for rapid en route refuelling by the transequatorial migrants. This means that the ultra-long, transequatorial migrants face the severest time constraints in carrying out seasonal functions, such as the moults, which are then reflected in their phenotype (Fig. 7).

The identification of selection pressures in a rapidly changing world

Perhaps more than any other habitat, wetlands suffer at the hands of ever-expanding and affluent human populations (Boere et al. 2006). In many parts of the world water

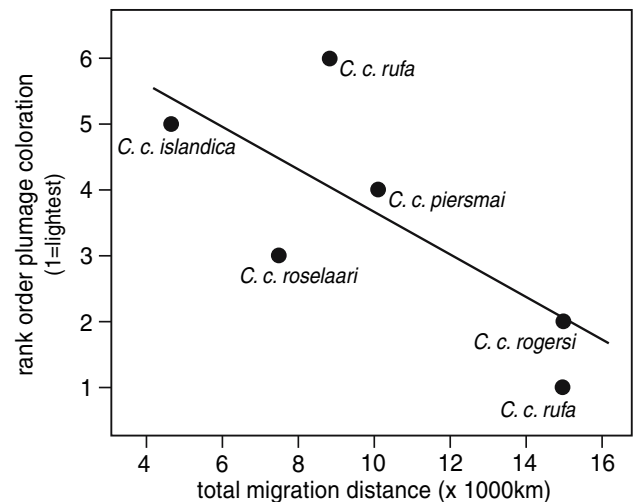


Fig. 7 Intraspecific correlation based on subspecific averages between the colouration of the alternate (breeding) plumage coloration and the overall migration distance for a one-way journey in Red Knots. Here, for breeding plumage, a *six* signifies the darkest colouration [taking into account both overall extent of redness and depth of colour (after Buehler and Piersma 2007; plumage data from Tomkovich 1992, 2001)]. Pearson correlation $r = 0.751$; $P = 0.04$, one-tailed test

resources are taken away from the wetlands to sustain agriculture. The preservation of wetlands has not been helped by a long-standing mindset that wetlands are mere wastelands. In coastal regions, wetlands were—and are still—reclaimed to satisfy increasing demands for harbour, industrial, housing and agricultural space; that most of the world’s humans live close to the coast intensifies the conflict, as does the demand for the marine resources harvested from the remaining areas. In this light it is no surprise that a recent survey by the international Wader Study Group showed that of 207 shorebird populations with known population trajectories (out of a total of 511 known shorebird populations), almost half (48%) were in decline, whereas only 16% were increasing (International Wader Study Group 2003; Stroud et al. 2006). With threefold more populations in decline than increasing, shorebirds belong to the most globally endangered segment of the migrant birds of the world.

We can, and should, lament the loss of wetland habitat and the migrant birds that make use of these wetlands. Equally, and as part of the scientific underpinning of conservation efforts, we can use well-studied cases of habitat modification to decipher the selection pressures that mould the variety of migration strategies just described for a single highly specialized migratory shorebird species, the Red Knot. As it happens, all populations of Red Knots are now in decline (Wetlands International 2006, personal observation) and, in a few cases, direct causal links have been established between human-induced habitat changes

at wintering and stopover sites and changing bird numbers at the population level. What do these cases tell us?

The first case concerns *rufa*, the southernmost wintering subspecies. The non-breeding population in Tierra del Fuego was over 67,000 birds in surveys carried out 1982–1985, but declined to around 18,000 in January–February 2005–2007 (Morrison et al. 2004; R.I.G. Morrison, personal communication). The decline was particularly steep from 2000 to 2002, with wintering numbers in Tierra del Fuego dropping from 51,000 to 27,000. In the absence of evidence for great changes in either the wintering or southern stopover areas, or from the Arctic breeding grounds, all of the evidence suggests a serious refuelling problem in the major staging site during northward migration, Delaware Bay, at the New Jersey–Delaware coast of northeastern USA (Baker et al. 2004). Here Red Knots feed and fuel on a single prey type, the eggs of horseshoe crab *Limulus polyphemus* (Tsipoura and Burger 1999; Haramis et al. 2007), which are superabundant and easily accessed in May when the horseshoe crabs come to spawn at the bay's beaches in great numbers. However, from the early 1990s onwards, the harvesting of horseshoe crabs for bait and the biomedical industry underwent an order of magnitude increase (Walls et al. 2002) and, consequently, the large masses of spawning crabs that characterized so many beaches around Delaware Bay (Myers 1986) became a pretty rare and localized sight. From 1997 to 2002, an increasing proportion of knots failed to reach threshold departure masses of 180–200 g. Reduced nutrient storage, especially in late-arriving birds, possibly combined with reduced sizes of intestine and liver during refuelling, had severe fitness consequences for adult survival and the recruitment of young in 2000–2002 (Baker et al. 2004); problems of food availability have become even more serious since (Atkinson et al. 2007). From 1997 to 2002 known survivors in Delaware Bay were heavier at initial capture than birds never seen again, and annual survival of adults decreased by 37% between May 2000 and May 2001 (Baker et al. 2004); annual survival showed the decline a year later for the segment of birds stopping over in San Antonio Bay, northern Patagonia (González et al. 2006). As they began to leave Delaware Bay for the breeding grounds with suboptimal stores, breeding success of Red Knots was also impoverished, with the number of second-year birds found in wintering flocks declining by 47% from 2000 to 2001 (Baker et al. 2004).

The decline of *rufa* knots around at the turn of the millennium can thus clearly be attributed to a food—or rather a fuelling—constraint acting on the last stopover site before the flight into the breeding grounds, the ‘launching pad’ so to speak. The studies that span research workers and areas at the two American continents have thus demonstrated how critical it is for these migrants to reach

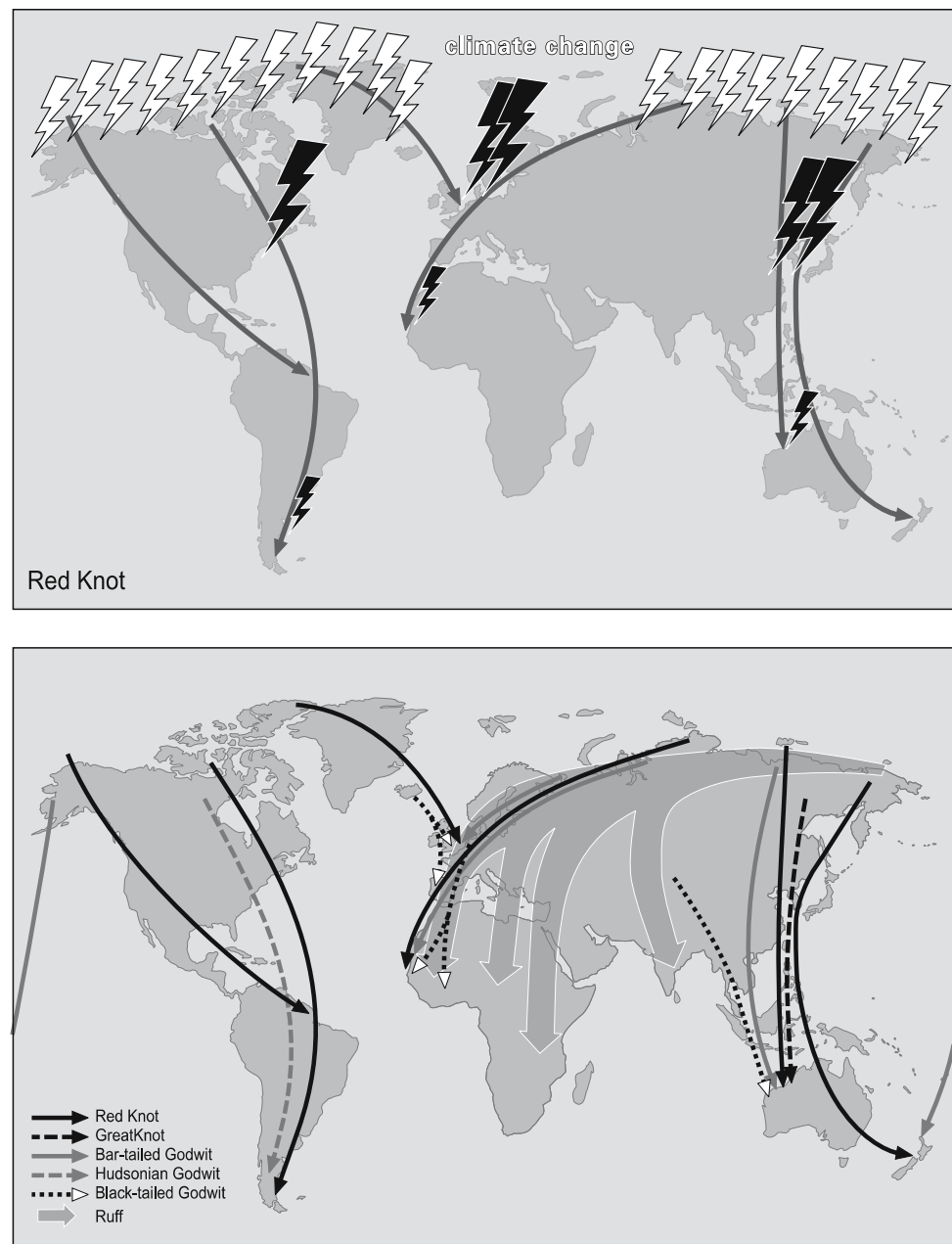
high threshold body masses at departure to the breeding grounds (compare Morrison et al. 2005). Threshold mass levels can be reached by fast fuelling on a reliable and abundant food supply, or by arriving early enough to compensate. The latter, as we have seen, is likely to be a problem for a time-stressed migrant such as *rufa* that comes from the far end of the other hemisphere and, in fact, late arrivals in recent years may also represent individual adjustments to local fuelling difficulties encountered in previous years (Atkinson et al. 2007).

In summary, for the case of the *rufa* subspecies encountering serious refuelling problems during its stopover before the direct flight to the breeding grounds, we now have hard evidence that below average mass gains at staging sites during northward migration negatively impacts subsequent survival. As predicted (e.g. Piersma 1987; Gudmundsson et al. 1991), fuelling performance and speed of migration are selected for. Similarly, after early summers in the early 1970s, when *islandica* knots ran into icy conditions on the breeding grounds, the heaviest birds during stopover in Iceland had the greatest chance to survive (Morrison 2006; Morrison et al. 2007).

Implicit in this whole argument is the issue of inter-seasonal carry-over effects: birds that encounter problems during some stage of the annual cycle may only come to pay the reproductive or survival price at some later stage (Piersma 1987; Piersma and Baker 2000). In the case of *rufa* knots, those that were captured light or late in the San Antonio Oeste area in northern Patagonia were less likely to ever be encountered again (González et al. 2006).

How factors acting in subsequent seasons can determine the fate of individuals can also be demonstrated with research on *islandica* knots that arrive in late summer in the Dutch Wadden Sea to moult and spend the winter (van Gils et al. 2006c). In this particular case, the returning Red Knots in 1998–2003 encountered serious declines in both prey quantity and quality as a result of the destructive mechanical harvesting of edible cockles *Cerastoderma edule* in the best feeding areas (Piersma et al. 2001a, b; van Gils et al. 2006c; Kraan et al. 2007). From 1998 to 2002, the fraction of the 250-km² of intertidal flats in the western Dutch Wadden Sea that was too poor for Red Knots to obtain a threshold intake rate of 4.8 W (based on food requirements at that time of year; Piersma et al. 1995) increased from 66 to 87% (van Gils et al. 2006c). Diet quality declined by 11.7% per year and to compensate for such reductions in prey quality the knots increased gizzard mass. Despite this increase in gizzard size over the years, resightings of individually colour-banded birds in which the gizzards were measured before release with ultrasonography (Dietz et al. 1999) demonstrated that individuals not seen again in our study area had undersized gizzards; individuals that we subsequently did see again had gizzards

Fig. 8 a Summary of the currently recognized ecological problems encountered by the various subspecies of Red Knots worldwide (see text), including major problems (*big lightning bolts*), such as overharvesting of benthic resources in Delaware Bay and the Dutch Wadden Sea and reclamations around the Yellow Sea, and smaller problems (*smaller bolts*) related to increased disturbance by humans in wintering areas in Patagonia, Mauritania and northwestern Australia, as well as the imminent habitat changes following from global warming (*repeated lightning bolts over the Arctic*). **b** A sentinel system for the world's long-distance migrant shorebird, the Global Flyway Network, that combines all research efforts to follow the demographics of a comprehensive set of long-distance migrating shorebird populations (see Table 2) in the context of studies on the ecological conditions at their wintering and staging grounds



large enough for a balanced daily energy budget (van Gils et al. 2006c). Local annual survival rate (calculated from resighting rates of colour-ringed birds) increased with year-specific food quality. Individually colour-ringed knots that disappeared from the western Dutch Wadden Sea may have died or, perhaps more likely for a wide-ranging migrant, emigrated to other areas, such as the estuaries in the UK. Here they probably paid a mortality cost due to the extra travel and/or due to uncertainties in the food supply at their new destination. Whatever happened to them, the steep decline in numbers of Red Knots wintering in the Dutch Wadden Sea can be explained satisfactorily by these documented population- and individual-level effects of

declining food conditions (van Gils et al. 2006c). The local disappearance from the western Dutch Wadden Sea accounted for much of the 25% decline of the entire NW European wintering population over the same period.

This example, then, shows that birds arriving from the tundra breeding areas with a gizzard that was too small needed more time to adjust their gizzard than their remaining energy stores allowed them: they would face starvation unless they left the area promptly. Were they to have left the tundra at higher body masses, with bigger gizzards, or not have encountered opposing winds en route, they would have found ways to survive and adjust to a Dutch Wadden Sea where food conditions had become

Table 2 Summary table of the long-distance migrating shorebird species and subspecies studied in concerted ways within the context of the Global Flyway Network and in combination with the areas where they are presently studied most intensively (i.e. where marking

and resighting efforts are concentrated), two ecological characteristics (habitat and diet types used), and an indication of whether the populations are currently on a trajectory of increase or decline

Species	Subspecies	Core study site(s)	Habitat	Diet	Population change
Red Knot <i>Calidris canutus</i>	<i>canutus</i>	Mauritania	Coastal	Molluscs	Negative
Red Knot	<i>piersmai</i>	NW Australia	Coastal	Molluscs	Negative
Red Knot	<i>rogersi</i>	New Zealand	Coastal	Molluscs	Negative
Red Knot	<i>roselaari?</i>	NW Brasil	Coastal	Molluscs	Negative
Red Knot	<i>rufa</i>	Argentina & USA	Coastal	Molluscs	Negative
Red Knot	<i>islandica</i>	Netherlands	Coastal	Molluscs	Negative
Great knot <i>Calidris tenuirostris</i>		NW Australia	Coastal	Molluscs	Negative
Bar-tailed Godwit <i>Limosa lapponica</i>	<i>lapponica</i>	Netherlands	Coastal	Worms	Positive?
Bar-tailed Godwit	<i>taymyrensis</i>	Netherlands & Mauritania	Coastal	Worms	Negative
Bar-tailed Godwit	<i>menzbieri</i>	NW Australia	Coastal	Worms	Negative
Bar-tailed Godwit	<i>baueri</i>	New Zealand	Coastal	Worms	Negative
Hudsonian Godwit <i>Limosa haemastica</i>		Argentina	Coastal	Worms	Stable?
Black-tailed Godwit <i>Limosa limosa</i>	<i>limosa</i>	Netherlands	Inland	Worms	Negative
Black-tailed Godwit	<i>islandica</i>	Iceland, UK, France	Coastal	Worms & molluscs	Now stable
Ruff <i>Philomachus pugnax</i>		Netherlands	Inland	Arthropods	Negative
Sanderling <i>Calidris alba</i>		Ghana, Mauritania, Netherlands, Iceland	Coastal	Worms & arthropods	Variously stable and negative

A graphical representation of the research network is provided by Fig. 8b

poor due to human economic activities². The encounter of such conditions is part of the migrants' life story. I would argue that the extent and the rapidity of human-caused changes (often for the worse, and certainly not helped by any drastic climate change; Fig. 8a) enable us to pin down ecological cause–effect relationships (if we bother to study the processes).

Conservation-relevant prospects: widening the scope of the comparisons

Based on the preceding arguments, I feel very encouraged that sustained efforts in studying the varying fates of some of the world's long-distance migrant shorebirds will continue to yield fundamental biological insight and at the same time provide precisely the information that well-meaning governmental and non-governmental organizations need to galvanize efforts to protect these very migratory phenomena and the networks of wetlands on which they depend. It would be particularly rewarding to

extend the comparisons among the world's populations of a shellfish-specialist dwelled on here to comparisons between subspecies in differently tropically specialized species (e.g. the worm-eating Godwit *Limosa*) and between different ecologically specialized species themselves (shellfish specialists, such as the two knot species versus the three godwit species that have a much more varied diet, notably polychaete worms). Returning to the contrast between high Arctic/marine versus lower latitude/freshwater species, comparisons between the ecology and demographics of, on the one hand, pure freshwater habitat specialists as the Ruff and the *limosa* subspecies of the Black-tailed Godwit (*Limosa limosa*) and, on the other hand, species only using coastal marine nonbreeding environments might prove very insightful.

Luckily for science and conservation, shorebirds worldwide have, for a long time, attracted considerable attention from researchers working in both amateur and professional capacities (Piersma and Baker 2000). To bring the dreams just outlined to practice, we have endeavoured to amalgamate many of the existing demographic research initiatives into a truly *worldwide observatory* of the changing fates of the world's shorebird populations and their habitats (Fig. 8b). We have named this the *Global Flyway Network, the shorebird ecological demographics and conservation initiative*. The programme intends to combine and coordinate the efforts of a worldwide

² Ironically, the intertidal mud- and sandflats in the Dutch Wadden Sea belong to the best formally protected areas in The Netherlands, having received multiple conservation agreement assignments. Despite this, the government issued permits for novel industrial forms of shellfish harvesting on the basis of the argument that these represented extensions of old fishing rights.

consortium of well-established shorebird scientists that over the past decade have demonstrated productive collaborations at several different levels. Covering all major flyways, it is our aim to cover the changing world with a system of continuous critical observations on the ecology, demography, body condition, health status and relevant genetic variability in 16 (or more) distinct populations of long-distance migrant shorebirds.

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, i.e. 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 the monitoring of 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 who can make a difference to the fate of the habitats and populations under threat; (3) to further the science, including an understanding of the historical background and the current demographic processes and ecological, genetic and immunological constraints that determine whether populations flourish or flounder. The species selected (Table 2) cover all major flyway systems, have a tenfold range in body size, represent declining as well as (a few) increasing or stable populations and show contrasts in sensory and ecological specializations and in general habitat use. From a conservation point of view, this sentinel system covers declining populations and others under threat (those using geographical flyways under siege from overexploitation or habitat destruction, e.g. staging areas around the Yellow Sea, Wadden Sea and Delaware Bay, wintering areas in Sahel).

In summary, detailed worldwide eco-demographic research on these extreme long-distance migrants, as embodied in the Global Flyway Network, yields a two-pronged benefit: (1) on the basis of the unintended large-scale experiments carried out by humans, we rapidly come to grips with the selection pressures moulding the migration strategies of migrant birds, and (2) in applied contexts, this type of work gives instantaneous feedbacks on the conservation consequences of man-made alterations to wetland environments at the relevant global spatial scales.

Acknowledgments Giving an IOC plenary is as much a challenge as it is an opportunity, and I am very grateful to the Scientific Programme Committee, especially Jacques Blondel, Susan Hannon, Franz Bairlein and Pat Monaghan, for giving me the chance. I have been extremely fortunate to be able to accumulate considerable experience with several of the world's shorebirds and their habitats, and I thank Rudi Drent and many others for helping to make this possible. Key financial support came from my parent institutions and through timely grants from the Netherlands Organization for Scientific Research (an NWO-PIONIER research award, NAP and WOTRO grants), the Swedish Academy of Sciences, National

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Appendix B

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

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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 under-appreciated. Through banding studies and censuses along the flyway from Tierra del Fuego 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, Argentina, where 25–50% of the Tierra del Fuego Red Knots 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 San Antonio Oeste earlier in March arrived in Delaware Bay on average before those marked 15 days later. Additionally, early migrating knots with active body moult in San Antonio Oeste 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 site. These domino effects indicate that there are fitness consequences to individual migration strategies adopted by birds at austral summering and stopover sites, which can be amplified by compressed timing in Delaware Bay when food is depleted at this final stopover site.

KEY WORDS: *Calidris canutus*, domino effects, migration, population decline, Red Knot, stopover ecology.

RESUMEN. REDUCCIÓN DE LA SUPERVIVENCIA ANUAL DEL PLAYERO ROJIZO (*CALIDRIS CANUTUS RUFA*) EN SU ESCALA MIGRATORIA DE SAN ANTONIO OESTE, ARGENTINA, POR EFECTOS DOMINÓ DE LLEGADA TARDÍA Y DEPRESIÓN DEL RECURSO TRÓFICO EN BAHÍA DELAWARE.— 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 crías, el papel de los sitios de escala como limitante del tamaño poblacional es escasamente conocido. Mediante estudios de anillado y censos a lo largo de la ruta de vuelo desde Tierra del Fuego 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 (Bahía Delaware, EEUU) y la llegada tardía de las aves. En San Antonio Oeste, Argentina, donde se congrega el 25–50% de la población de Tierra del Fuego 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 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 Bahía Delaware. Estos efectos dominó indican que las estrategias de migración individuales originadas en las áreas de estadía austral y en los sitios de escala migratoria tienen consecuencias sobre la adecuación biológica y que éstas pueden ser amplificadas por la reducción en el tiempo de estadía en Bahía Delaware cuando el recurso trófico es escaso en este sitio.

PALABRAS CLAVE: *Calidris canutus*, declinación poblacional, ecología de escala migratoria, efecto dominó, migración, Playero Rojizo.

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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 and Pienkowski 1984, Evans et al. 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). Although less is known about long distance migrants, 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.

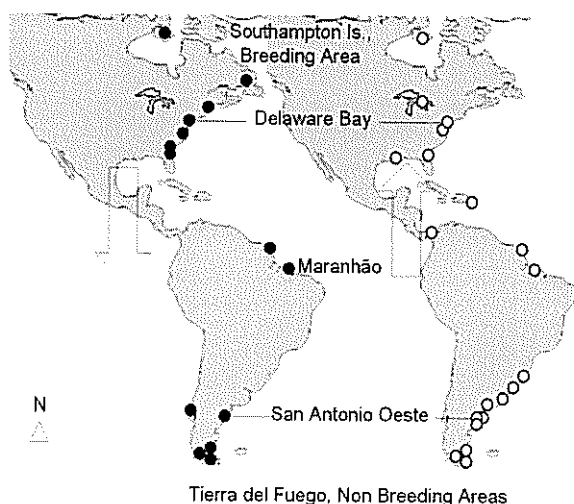


Figure 1. Red Knot flyway depicted on the basis of resightings of individuals colour-banded in Argentina from 1995 onwards. Black dots indicate resighting places during southern migration and white dots during northward migration. Key stopover study sites are indicated (González et al., unpublished data).

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, *Calidris canutus rufa* travels the longest migration of about 16000 km twice a year between their breeding grounds in the Arctic and their summering (= northern wintering areas) 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 the 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 (Atkinson et al. 2005, Baker 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 (Morrison 1975, 2006, Boyd 1992), 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, studies that captured and colour-banded northbound Red Knots (9851 individuals) 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 colour-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 have 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 (González et al. 2004, Morrison et al. 2004); such a rapid decline may seriously threaten the viability of this 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 (3644 individuals) 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 three-year period to 2000–2001. Recruitment, as measured by the proportion of second-year birds, comprised 19% of annual catches of 500–600 Knots in Tierra del Fuego 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 *Calidris canutus 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 in Argentina, the main stopover site on the coast of Patagonia for Red Knots, where 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. San Antonio Oeste is located at 40°45'S, 64°55'W in Río Negro Province of Argentina, and hosts 25–50% 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) is the mussel *Brachidontes rodriguezi* that they find on a rocky intertidal habitat locally 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

Table 1. Details of Red Knots catches (number of individuals) made at San Antonio Oeste, Río Negro, Argentina, in March, 1998. Retraps indicates knots banded previously in this or other expeditions. Analyses were based only on the 906 colour-banded birds.

Date	Juveniles	Retraps	With standard combination	With individual combination	Total colour marked	Total catch
5 March	5	12	270	33	303	321
13 March	6	5	79	39	118	124
16 March	5	24	241	7	248	280
20 March	5	23	137	17	154	178
28 March	7	10	53	30	83	97
Total	28	74	780	126	906	1000

in San Antonio Oeste. As part of an international research project on Red Knot populations throughout the flyway, a banding expedition to San Antonio Oeste 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). Age class (juvenile or 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" (distinctive combinations for 5 and 13 March, 16 and 20 March, and 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": knots colour-banded during 5 and 13 March) and the second half ("late cohort": knots colour-banded during 16 and 20 March) of March 1998. To keep resighting probabilities approximately equal for the two time cohorts the sample from 28 March was not included in the analysis. Three observers 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 Regression with dependent variable (1: banded; 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 assumptions according to Choquet et al. (2001). Survival analyses were run in Mark 3.2 (White and Burnham 1999) using Cormack-Jolly-Seber models by cohort. Model selection was based on the Akaike Information Criterion. Binary Logistic Regression with logit link and sigma-restricted parameterization 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

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 San Antonio Oeste in 1998 ($n = 19884$) increased through

the season (Day $b = 0.064$, $SE = 0.02$, $P < 0.001$; Fig. 2), either because birds from the unbanded Maranhão or Florida summering populations were leaving or more banded knots from San Antonio Oeste were present at the end of the season, or both. Despite the similar numbers of birds banded at San Antonio Oeste in both time cohorts, the late cohort had a lower return rate than the earlier banded cohort (Fig. 2), 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. Red Knots from San Antonio Oeste were more represented on the shores of Delaware than New Jersey (Shore $b = 0.36$, $SE = 0.10$, $P < 0.0001$), but the same trend in true detection rates was apparent in both states.

Apparent survival

Because we have shown previously (Baker et al. 2004) that a two time period model (1998-1999 to 2000-2001) was the best-fitting model for the Tierra del Fuego population, we compared this model for the 1998 San Antonio Oeste cohort with another that allowed a one

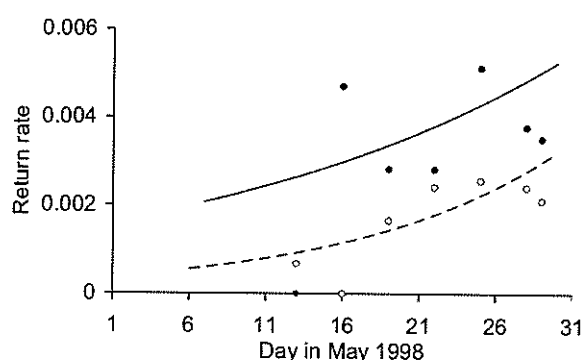


Figure 2. Return rates in Delaware Bay of "early" (filled circles) and "late" (open circles) cohorts of Red Knots banded at San Antonio Oeste, Río Negro, Argentina. The time dependent model of the return rate of colour-banded knots during the first half of March 1998 (early cohort, solid line; $n = 421$, $b = 0.049$, $SE = 0.024$, $P < 0.043$) is compared with the model for those banded in the second half of March 1998 (late cohort, dashed line; $n = 402$, $b = 0.092$, $SE = 0.034$, $P < 0.007$). Number of checked birds was 19884.

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 San Antonio Oeste 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% confidence intervals of the estimates of annual survival in the San Antonio Oeste 1998 cohort model before and after 2001 partly overlap because of the relatively small size of the colour-banded 1998 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 San Antonio Oeste 1998 knots according to the Akaike Information Criterion included the effect of both day of initial capture and presence of body moult they were undergoing ($P < 0.0001$). The probability for a 1998 cohort bird to be seen in the following years was negatively correlated ($b = -0.090$, $SE = 0.025$) with day of initial capture ($P < 0.0001$), 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 ($b = 4.43$, $SE = 0.277$, $P < 0.0001$), 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 ($b = -0.412$, $SE = 0.16$, $P < 0.01$; number of birds seen again = 57, number of birds not seen again = 171). A model including only body mass and presence

Table 2. Apparent survival of the San Antonio Oeste 1998 cohort from Cormack-Jolly-Seber capture-recapture analysis: (A) model selection, (B) real function parameters of the best-fitting model for individually colour-banded Red Knots. AIC: Akaike Information Criterion, ϕ : apparent survival, p : probability of recapture or resighting, (.): constant model, (t): time dependent model, t_1 : 1998–2001, t_2 : 2001–2002, t_3 : 1998–2000, t_4 : 2000–2002. Model selection based on correction for over-dispersion with $\hat{c} = 1.509$.

(A)

Model	AIC c	δ AIC c	AIC c weights	Model likelihood	Number of parameters	Deviance
$\phi(t_1, t_2)p(.)$	442.3	0	0.2943	1	3	24.14
$\phi(t_3, t_4)p(.)$	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
$\phi(t_1, t_2)p(t)$	444.6	2.28	0.0943	0.32	7	18.08
$\phi(t_3, t_4)p(t)$	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

(B)

Model	Parameter	Period	Estimate	SE	95% confidence interval
$\phi(t_1, t_2)p(.)$	$\phi 1$	1998–2001	0.803	0.037	0.721–0.866
	$\phi 2$	2001–2002	0.659	0.112	0.420–0.838
	p	1998–2002	0.508	0.045	0.421–0.595

of body moult as independent variables was not significant for body mass because late cohort knots were heavier than early cohort birds (128.0 ± 0.9 g, $n = 122$, and 123.7 ± 1.0 g, $n = 106$, respectively, mean \pm SE; ANOVA: $F_{1,226} = 13.66$, $P < 0.0003$). However, moulting birds were heavier on average than non-moulting birds (127.2 ± 0.8 g, $n = 191$, and 122.5 ± 1.7 g, $n = 37$, respectively; ANOVA: $F_{1,226} = 6.26$, $P < 0.0130$). These results suggest that later captured Red Knots stayed later at the San Antonio Oeste 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 food supplies at Delaware Bay, the last stopover site before the flight to the High Arctic breeding grounds, limited the Patagonian wintering population of Red Knots. 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 was 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 San Antonio Oeste 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 Tierra del Fuego potentially could have fitness consequences, as northbound knots arriving later at their first southern stopover site in San Antonio Oeste 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 San Antonio Oeste could be related to habitat condition in Tierra del Fuego 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 San Antonio Oeste does not necessarily reflect departure date, as some earlier arrivals left in a few days while others remained until the end of the season in April, and thus late arrivals might depart together with some early birds (González et al., unpublished data). The rate of storage of nutrients at the San Antonio Oeste stopover site is around 0.5 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 San Antonio Oeste 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 San Antonio Oeste 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 San Antonio Oeste, 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 San Antonio Oeste Red

Knots have a broader window of time where individual strategies can be employed.

Apparent survival estimates for the San Antonio Oeste 1998 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 San Antonio Oeste 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 Tierra del Fuego 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 *Calidris canutus islandica* departing from their last stopover site 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. 2006). 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 San Antonio Oeste, 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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Appendix C

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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Summary

1. Millions of shorebirds migrate each year through a small number of highly productive staging areas where they often conflict with fisheries interests. Delaware Bay, USA, is a major shorebird stopover site where, in spring, many thousands of shorebirds undergo rapid mass gain by feeding on the eggs of commercially harvested horseshoe crabs *Limulus polyphemus*.

2. Environmental factors may cause deviations from the best migration schedule. We used within-year mass gain data from red knot *Calidris canutus* caught in Delaware Bay between 1998 and 2005 to determine the degree of flexibility individuals have to vary migration speed.

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 among the highest ever recorded among vertebrates (5–7 × basic metabolic rate).

4. A total of 36–62% of the variation in observed rates of energy deposition between 1998 and 2002 was 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 two to three times higher than birds of similar mass in mid-May, indicating that birds were attempting to achieve a certain mass by a certain date. In 2003 and 2005, this relationship broke down as a result of lower densities of eggs.

5. *Synthesis and application.* The maintenance of high densities of crab eggs required for high rates of mass gain in red knot requires severe cuts in, or the complete cessation of, the crab harvest, reduced human and raptor-related disturbance as well as 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.

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

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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-minimizers that aim to arrive at the breeding grounds as fast as possible, energy maximizers that arrive at breeding grounds with excess fuel stores, or birds that followed no strategy, termed random. Ålerstam & Lindström (1990) predicted that time-minimizers should show a positive relationship between fuel deposition rate and departure mass. Across northward migrating red knot populations world-wide, there is indeed a positive relationship (Piersma *et al.* 2005) and a comparison of five subspecies of red knot showed that they time-minimized 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 stopover 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 suboptimum 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 (Piersma *et al.* 1999; van Gils *et al.* 2005b; Selman & Evans 2005; Stein *et al.* 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 (Piersma *et al.* 1999; Dekinga *et al.* 2001; McWilliams & Karasov 2005). 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 switched rapidly 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 thermoregulatory 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 north-east 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 United States (Florida and Georgia) before birds reach their Arctic breeding areas. Individuals make stopovers in the bay of 12–14 days (S. Gillings *et al.* unpublished data) and fatten rapidly 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; Gillings *et al.* 2007; G.M. Haramis *et al.* 2007). It is predicted that the knots need to depart at between 180 and 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) hypothesized that body mass should be divided into the 'structural' part and 'stores'. The structural part consisted mainly of water and fat-free lean mass (bone, muscle, etc.), whereas the stores consisted mainly 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, measured easily, 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 programme, 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 0.1 g . Although no special efforts were taken to recapture birds again during the same season, 178 birds in their second year or older were recaptured and their mass recorded for a second time.

DETERMINING THE COMPOSITION OF BODY STORES

A total of 61 red knot were collected from catches over 3 years (1998: 24 birds; 1999: 24 birds; 2000: 13 birds). These birds were taken at random from cannon net catches on dates spread out through the spring migration season. Birds were killed humanely using cervical dislocation and, after weighing to the nearest gram, placed in airtight plastic bags and frozen at -20°C .

As the red knot that pass through Delaware Bay come from a mix of wintering populations, we identified their wintering location based on the stable isotope ratios of carbon and nitrogen in their flight feathers. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were obtained from the sixth primary covert, measured ascendantly, using continuous flow isotope ratio mass spectrometry (CF-IRMS). Atkinson *et al.* (2005) showed that there was a clear division in the values of $\delta^{15}\text{N}$ between birds wintering in Patagonia and Tierra del Fuego ($\delta^{15}\text{N} > 13.5\text{‰}$, termed 'southern' birds) and elsewhere ($\delta^{15}\text{N} < 13.5\text{‰}$, termed 'northern' birds). Northern birds comprise two geographically distinct populations from the southeastern United States and Brazil, but the isotope signatures of birds from each overlap. $\delta^{13}\text{C}$ values were checked to ensure that no subadult birds were included. These birds, hatched the previous year, would have a carbon isotope signature typical of the freshwater systems ($\delta^{13}\text{C} < -19.5\text{‰}$) where their feathers were grown. None were found among the specimens.

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

To determine the point at which birds deposit fat stores, the total fat mass of each specimen was plotted against the total mass and a two-phase (broken stick) regression model applied using the inbuilt function of SIGMAPLOT version 10. The slopes of the two regression lines reflect the proportion of fat being stored as total mass increases and the breakpoint indicates the point at which that relationship changes.

The energy deposition of fat and protein was calculated as follows. The mass change between captures above and below the breakpoint was multiplied by the 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?

Generalized 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 (AIC) corrected for small sample size (cAIC) was calculated in each case $\{-2 \times \log \text{likelihood} + 2k + [2k \cdot (k + 1)] / (n - k - 1)\}$, where n is the sample size and k the number of estimable parameters. cAIC operates on the basis of parsimony by selecting the best-fitting model while minimizing 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 2 (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 1 h 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 correlated negatively 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 day^{-1}), mean mass gain per day was positive and approximately constant thereafter, averaging 4.3 g day^{-1} up to 14 days after first capture (Fig. 1). This lower initial rate was likely to be a capture effect and we have therefore excluded birds with retrap intervals of 1 day as well as 2 birds with missing data from the analysis, thus leaving 166 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

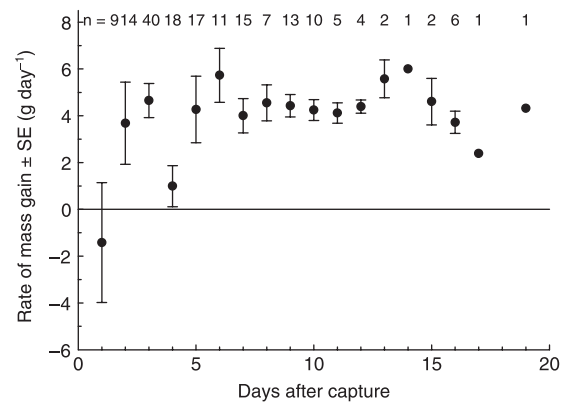


Fig. 1. Rate of mass gain ± 1 SE of red knot retrapped during the same season in Delaware Bay in relation to the number of days after capture. Sample size appears at the top of the graph.

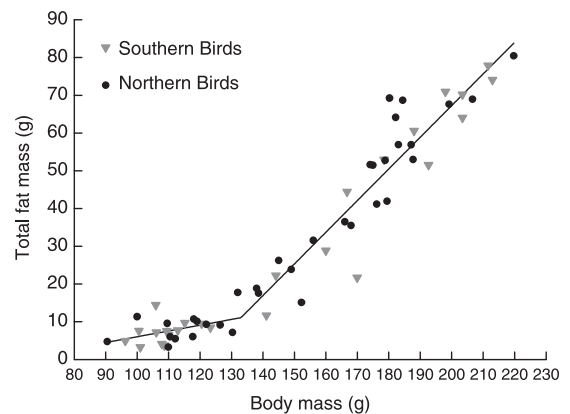


Fig. 2. The relationship between the total mass of individual birds and the amount that is fat. A two-phase regression line is shown. Northern birds are those that winter in northern Brazil and the south-eastern United States; southern refers to those wintering in Patagonia and Tierra del Fuego.

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 day^{-1} , the mean mass gain from the 166 retraps. If a bird's predicted mass exceeded 190 g it was excluded from this analysis. This removed a further 25 birds, leaving 141. Where means are given these are quoted ± 1 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.

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 data set using all birds. Model structure: Y = year (1998–2005, eight-level factor), M = mass (linear variable), D = number of days after 1 May (linear variable). k = number of estimable parameters, × = interaction term

Model no.	Model structure	Energy deposition			Mass gain			
		k	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

RATE OF ENERGY DEPOSITION AND MASS GAIN IN RELATION TO DATE, INITIAL MASS AND YEAR

The average rate of energy deposition of all 166 retrapped birds was $119.1 \text{ kJ day}^{-1}$ (95% CI: -193.7 – $322.9 \text{ kJ day}^{-1}$). In terms of mass gain, this represented an average rate of $4.05 \pm 0.32 \text{ g day}^{-1}$ and ranged between -14.4 and 18.8 g day^{-1} . The most rapid mass gain of 18.8 g day^{-1} (514 kJ day^{-1}) was exhibited by a bird caught in 2003 at 117 g on 25 May and retrapped 3 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 related inversely 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 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 fitted 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 0.59, Table 1). When the birds which were predicted to be $> 190 \text{ g}$ 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 $Y \times D$ and $Y \times M$ 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 interaction terms 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 (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.

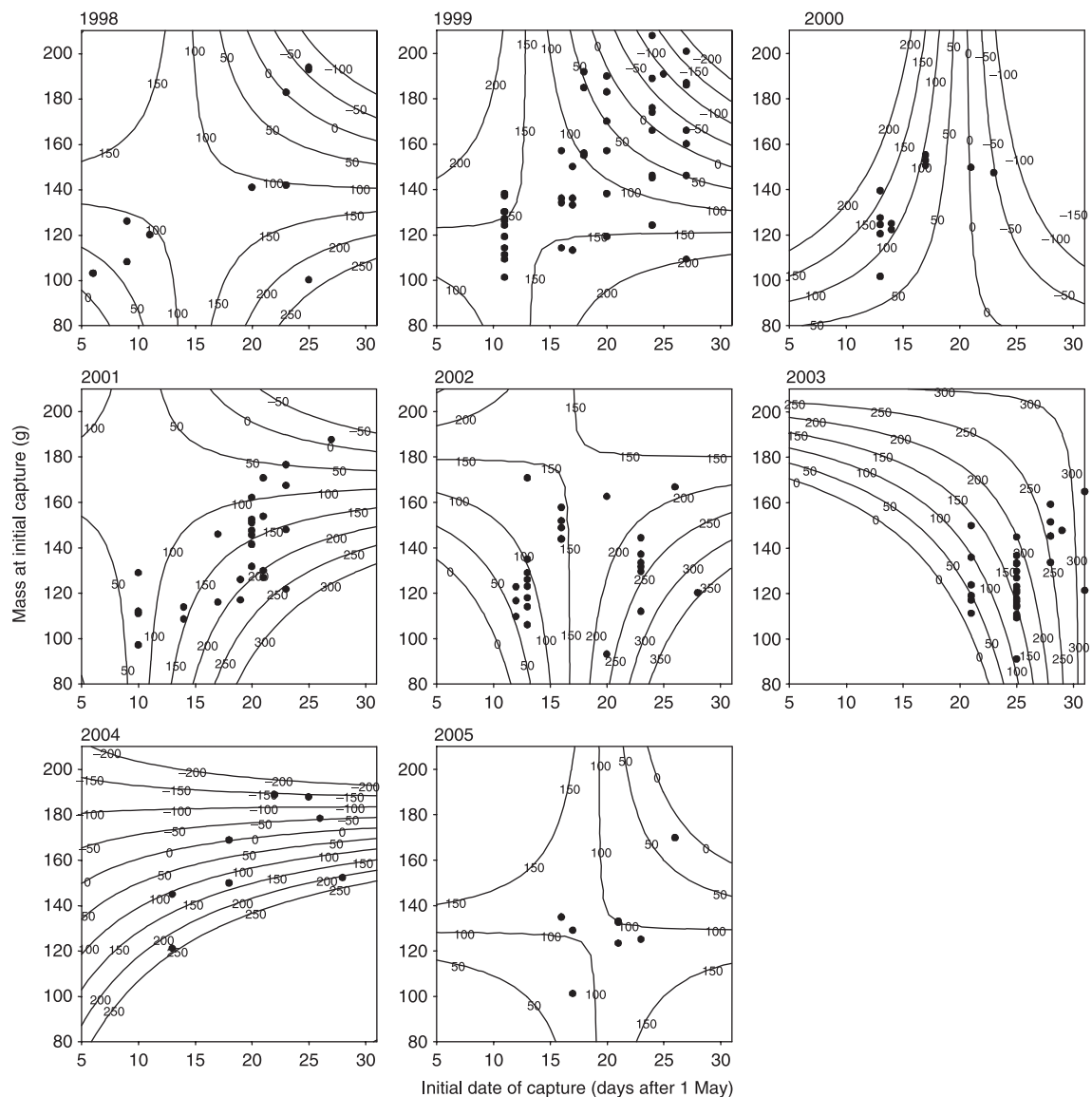


Fig. 3. Contour plots of the rate of energy deposition (kJ day^{-1}) of red knot based on retrapped birds in relation to the date at initial capture and their initial mass. Dots represent individual birds and refer to date and mass at initial capture. To avoid predicting outside the available data, contours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

The rates of energy deposition are among the highest observed in the animal kingdom. With maintenance and activity requirements of a minimum of $200\text{--}250 \text{ kJ day}^{-1}$ (Piersma 2002), which includes a basal metabolic rate (BMR) component of $c. 80 \text{ kJ day}^{-1}$ (Wiersma & Piersma 1994), birds were assimilating energy at an average equivalent to $5\text{--}5.6 \times \text{BMR}$. At the upper confidence limit this was raised to $6.5\text{--}7.2 \times \text{BMR}$ and two individuals with energy deposition rates greater than 500 kJ day^{-1} probably exceeded $9 \times \text{BMR}$.

These rates reflect those observed in captive shorebirds, where soft-shelled food (mealworm larvae) was provided *ad libitum* and available 24 h a day (Kvist & Lindström 2003). The authors acknowledged that the high energy assimilation rates ($10.4 \times \text{BMR}$ 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 $10.4 \times \text{BMR}$ 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 2 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 also important 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

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, eight-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

years (Baker *et al.* 2004), indicating negative fitness consequences associated with departing late and light from Delaware Bay.

ARE RED KNOTS TIME-MINIMIZERS?

The results from this study have indicated that the migration strategy is more complex than assumed previously. Fuelling rates among 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 two to three times later in May. This raises the question of why birds arriving earlier do 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 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 unlikely to explain the patterns fully. 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; MacLeod *et al.* 2005a, MacLeod *et al.* 2005b), 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

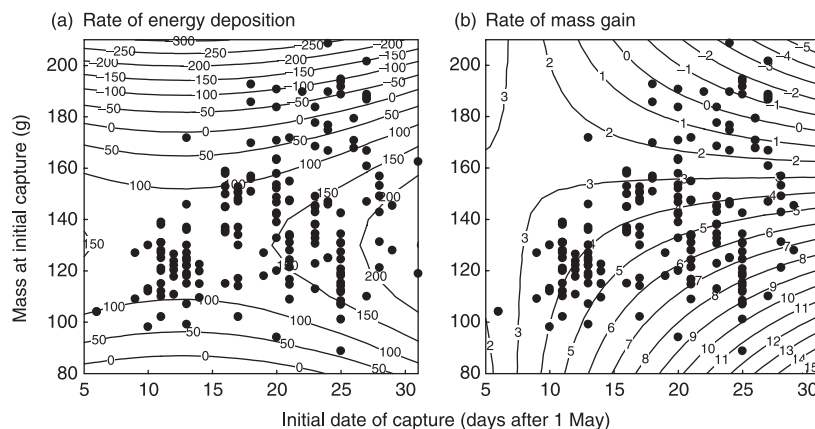


Fig. 4. Contour plots of the average rate of (a) energy deposition (kJ day^{-1}) from model 1 and (b) mass gain (g day^{-1}) from model 4 in relation to the date a bird was initially caught and its mass at initial capture, excluding any year effects. Model number refers to Table 1.

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 *C. mauri* (Cabanis) at their last stopover before reaching the Arctic breeding area (the Copper River Delta in Alaska, USA) was related inversely 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 suboptimal masses, or leaving at optimum masses achieved by a greater rate of mass gain. Although these studies do not address specifically 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 (L.J. Niles, unpublished) 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 day^{-1} , and these did not fit 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 2 of the past 3 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 been restricted recently 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, an increase in the number of lightweight 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 understand more clearly the increase in later arrivals.

Peak numbers of red knot have declined in Delaware Bay (L.J. Niles *et al.*, unpublished), 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 personal communication). Birds from wintering areas in northern Brazil and also the south-eastern United States (both populations in the order of 7500–10 000 birds) also pass through Delaware Bay (Atkinson *et al.* 2005) and there has been no evidence of similar declines in these groups of birds (L.J. Niles *et al.*, unpublished).

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 areas of birds passing through the Bay in 2004 and 2005 were determined (Atkinson *et al.* 2006). 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 mainly short-distance migrants from wintering areas in the south-eastern United States, 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 al.* 2003, 2005b). The harvest of spawning crabs over the past decade will have reduced egg loads within beaches. It is likely that the bulk of shorter-distance migrants feeding on mussels (which does not enable such high fuelling rates, van Gils *et al.* 2005a) would, through earlier arrival compared with longer-distance migrants, still be able to fatten successfully. Reducing egg densities would have a disproportionately higher impact on longer-distance migrants. Indeed, when staging in the Wadden Sea in spring, knots with the smallest gizzard size, which may be those that have travelled the

longest distance, were found to suffer the highest mortality rate. This increased mortality rate was due to the large-scale harvesting of the knots' food resources by the commercial fishing industry (van Gils *et al.* 2006).

Conclusion

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

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Appendix D

Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations

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In recent decades, the West European population of Black-tailed Godwits, *Limosa limosa limosa*, has declined in size at a quite alarming rate, while the Icelandic population, *L. l. islandica*, has undergone a rapid increase in population size. These two populations have been the subject of a great deal of research, much of which has been focused on understanding the causes and consequences of the contrasting population trends. In 2007, a workshop was held during the annual conference of the International Wader Study Group at La Rochelle, France, with the aims of identifying the likely causes of the population changes and providing recommendations for future actions to improve the conservation of both populations. The available evidence strongly suggests that changes in productivity as a consequence of agricultural intensification are the most likely driver of the decline in *L. l. limosa*, although the concentration of much of the population in just a few sites in winter and spring is likely to exacerbate their vulnerability to future habitat changes. Agricultural and climatic changes are implicated in the expansion of *L. l. islandica*, and the availability of both intertidal mudflats and wet grasslands as foraging habitats appears to be very important across much of the winter range of this population. A series of recommendations for actions to conserve both populations are provided, including improving agricultural land management and protecting key passage and winter sites and habitats.

The last three decades have seen widespread declines in the population size of many species of shorebird (International Wader Study Group 2003). While research has strongly implicated the loss and degradation of breeding habitats in

these declines, largely through drainage of wetlands and conversion to intensive agriculture (Thorup 2006), efforts to reverse declining population trends have met with little success. The West European population of Black-tailed Godwits,



Limosa limosa limosa, provides one of the clearest examples of this problem. The great majority of this population breed in the Netherlands where, after increasing in the first half of the 20th century (Bijlsma *et al.* 2001), it was a widespread and common meadow bird in the 1960s, numbering up to 250,000 individuals (Mulder 1972, Piersma 1986). However, since then this population has declined severely, and now numbers only around 50,000 breeding pairs (BirdLife International 2004).

Attempts to reverse this population decline (and similar declines in many other meadow-breeding bird species) have focused on implementing agri-environment schemes (AES) on farmland in breeding areas to improve breeding success (Beintema *et al.* 1997, Kleijn *et al.* 2001, van Brederode & Laporte 2006, Verhulst *et al.* 2007). Despite the area covered by AES aimed at conserving meadow birds increasing from c.20,000 ha to c.150,000 ha of farmland in the Netherlands by 2006, and schemes costing in excess of 30 million Euro per year, no discernible improvement in the population so far has been apparent (Kleijn *et al.* 2001). In fact, the national population trends of meadow birds in the period 2000–2004 have declined even more rapidly (by approximately 3.5%) than trends in the period 1990–2000 (Teunissen & Soldaat 2006). In addition to agri-environment initiatives, the creation and management of nature reserves for meadow birds has also occurred but on relatively small areas (c.18,000 ha, Schekkerman *et al.* subm. b). Although population declines are less steep in reserves than in the wider countryside, there is much variability between reserves (Teunissen & Soldaat 2006).

By contrast, the population of Black-tailed Godwits that breeds in Iceland, *Limosa limosa islandica*, has undergone a rapid increase over the same time period, from an estimated 2,000–3,000 individuals around 1900 to c.50,000–75,000 at present. This population has expanded from breeding locations in south-west Iceland and now occurs virtually throughout lowland Iceland (Gunnarsson *et al.* 2005a).

Both the *limosa* and *islandica* subspecies of Black-tailed Godwits have been the subject of extensive research studies in recent years, mostly focused on the causes and consequences of population changes (e.g. Beintema 2007, Both *et al.* 2006, Gill *et al.* 2001a, Groen & Hemerik 2002, Gunnarsson *et al.* 2005b, Roodbergen *et al.* subm., Schekkerman *et al.* 2005, subm. a,b, Schekkerman & Verhulst *et al.* 2007). In order to bring together the available information on both populations, a workshop was held at the International Wader Study Group conference at La Rochelle, France in 2007. This workshop aimed to:

- compare current knowledge of the Icelandic and West European *L. limosa* populations
- inform potential explanations for the divergent population trajectories
- highlight research gaps and potential future collaborations
- recommend conservation measures.

Here we report on the findings of this workshop, particularly focusing on identifying the likely drivers of changes in demography and distribution of both populations, highlighting the key issues influencing each population and providing a series of recommendations for future conservation and research efforts. The workshop attracted c.100 participants with a wide range of expertise and knowledge of these birds

and their habitats. This meeting was therefore a unique and exciting opportunity to compare two subspecies with widely diverging population trajectories, and to discuss causes of changes and prioritise future actions.

The workshop comprised a series of comparative talks which detailed current knowledge of the key processes influencing breeding and non-breeding season distribution and demography, and patterns of connectivity between seasons and sites, for the two populations. During the workshop, information from each talk was used to complete a summary table of current status, drivers of change and potential impact for a series of demographic, distribution and habitat issues (Tables 1 & 2). The key issues arising from this summary are discussed below.

CURRENT DISTRIBUTION AND HABITAT USE OF *L. L. LIMOSA*

The West European breeding population of Black-tailed Godwits breeds throughout the Netherlands, with smaller numbers in Germany, Belgium, Denmark, France and the UK, and migrates via France and Iberia to winter grounds in Senegal, Guinea-Bissau and Guinea in sub-Saharan West Africa (Beintema & Drost 1986, Kuijper *et al.* 2006).

Key breeding season issues

This population depends on grasslands with high groundwater levels as breeding sites, and on wetlands as passage and winter foraging sites (Wymenga *et al.* 2006). Over the last 50 years, both of these habitats have undergone extensive modification. The core of the recent breeding range of this population is on clay-on-peat and peat soils, but the historical distribution also included blanket bogs and wet moorland, which were abandoned as the population expanded into agricultural habitats in the first half of the 20th century (Bijlsma *et al.* 2001). Since then, drainage, urbanisation and conversion of grasslands to arable crops have created drier and highly fragmented breeding habitats (SOVON 2002). The remaining grasslands are generally farmed very intensively, with mowing dates having advanced by one month over the last century, most grasslands now being mown more than twice per year, and livestock number per unit grassland area being the highest of all European countries (Statistics Netherlands, Statline). In addition, there is evidence that changes in predator control and environmental contamination, and landscape changes such as road-building and tree-planting, have altered predator abundance and distribution, and consequently increased nest and chick predation rates (Schekkerman *et al.* subm. a, Teunissen *et al.* 2006, Teunissen & Willems 2004).

When the population size was higher, godwits bred on grasslands in areas of peat, clay and sandy soils. The population decline has been characterised by a contraction into largely peat areas, although levels of degradation now appear similar across all soil types. AES initiatives to reverse the population decline have focused on delaying mowing dates and improving nest protection. However, there is no strong evidence that these schemes have improved breeding densities (Kleijn *et al.* 2001, Kleijn & van Zuijlen 2004, Verhulst *et al.* 2007, Willems *et al.* 2004), despite evidence that delayed mowing saves nests and improves chick survival (Schekkerman & Müskens 2000, Schekkerman *et al.* 2005, subm. b). Godwits preferentially choose areas with high groundwater levels as breeding sites (Kleijn & van Zuijlen



2004, Verhulst *et al.* 2007); although clay soils with relatively low ground water levels can also be used. Current AES do not, however, include management of groundwater levels, as this is a contentious issue for farmers. Successful management is also likely to require fields with tall, open and structurally diverse swards within the matrix of more intensively farmed fields throughout the breeding season. This provides chicks hatched throughout an area with access to high quality foraging sites as well as shelter from predators (Schekkerman *et al.* subm. b).

Key non-breeding season issues

On passage and at wintering sites in Iberia and West Africa, wetlands have been extensively drained and dammed since the 1960s, to facilitate energy production, water storage and agriculture (Kuijper *et al.* 2006). Rice production is now widespread, and rice fields provide an alternative habitat which, when flooded, is wet enough to allow birds such as godwits to forage. Godwits have been reported foraging on rice fields in winter since at least the 1970s (Altenburg *et al.* 1985, Tréca 1984, van der Kamp *et al.* 2007), and recent studies of godwits in Iberia and Africa have shown that

the birds primarily consume rice seeds (along with smaller amounts of invertebrate food) during the months in which rice fields are used (Tréca 1994). Godwits typically forage on molluscs, worms and other invertebrates, and the consequences of this largely plant-based diet through much of the winter and spring are currently unknown.

Godwits begin to arrive in West Africa in July, and they use rice fields extensively, particularly during planting (Jul–Aug) and harvest (Nov–Dec) (Kuijper *et al.* 2006, van der Kamp *et al.* 2007). When the African rice fields are dried out and harvested during December, the birds begin to migrate north to use rice fields in Spain and Portugal (Sanchez-Guzman *et al.* 2007, Zwarts *et al.* in press). At this time they can be highly concentrated, with up to 50,000 birds in the Doñana National and Natural Park, SW Spain, in December, up to 25,000 in Extremadura, W Spain, by early February and up to 45,000 around the Tagus and Sado estuaries, W Portugal, by late February. Passage sites in Morocco were formerly used in autumn and spring but few birds use these sites now. Drainage of Moroccan wetlands may have influenced this shift in passage site use, as may recent increases in rice production in Spain. Similarly, use of French sites on spring migration may have declined in recent years, although overlap

Table 1. Summary of the current status of the demography, distribution and habitat use of the West European Black-tailed Godwit population, *Limosa limosa limosa*, together with likely drivers of changes and estimates of the proportion of the population experiencing these conditions.

	Status of <i>limosa</i> population	Drivers of changes	Potential population impact
Population size	c.60,000 breeding pairs		
Population trend	Severe decline at c.5%p.a.	Primarily due to declining productivity	Population-wide
Nest survival	Intermediate to low and variable.	Earlier mowing and increased predation	Population-wide
Chick survival	Low. Declines since 1980s	Earlier mowing, reduced habitat heterogeneity and increased predation	Population-wide
Productivity trend	Decline since 1980s from c.0.7 to 0.2 fledged young /pair	Loss of grasslands with high water tables, intensification of remaining grasslands	Population-wide
Juvenile survival	Estimates from 40% to 68%	Hunting of juveniles on migration could be significant	Higher estimate from one site only (Workumerwaard)
Adult survival	Annual estimates = 81–96%	Unknown	Probably population-wide
Breeding habitat	Grasslands with high ground water levels in open landscapes	26% loss to urbanisation and arable conversion since 1960s. Severe decline in quality through drainage and intensification	Population-wide
Breeding locations	Grassland in Netherlands, Germany, Belgium and Denmark	Unknown as degradation of all soil types appears similar	Population wide
Breeding trend	Declining and contracting in range	Declining habitat quality, fragmentation	Population-wide
Autumn habitat	Wetlands, mudflats, saltpans, rice fields	Unknown	Unknown
Autumn locations	France (Jun–Nov), Iberia (Jun–Nov) and W Africa (Jul–Nov)	Reduced wetland area in Morocco and S Europe and/or changes in site quality	Most adults fly direct to Africa. Juveniles may use European sites
Autumn trend	Earlier departure and reduced use of Morocco	Early departure correlated with poor breeding success and deferral of breeding	Unknown
Winter habitat	Rice fields and wetlands	Increased use of rice following widespread conversion of wetlands	Population-wide
Winter locations	Senegal and Guinea Bissau (Nov–Dec), Iberia (Dec–Feb)	Large-scale damming, drainage, water storage and agriculture in Senegal delta	Population-wide
Winter trend	Possible earlier departure from Africa for Iberia	Departure follows drying of rice fields – changing rainfall patterns may be involved	Population-wide
Spring habitat	Rice fields, saltpans and wetlands	Conversion of wetlands to rice fields	Population-wide
Spring locations	Iberia (Dec–Feb), France (Feb–Mar) and Netherlands (Mar–Apr), reduced use of Morocco and France	Reduced wetland area in Morocco and France and/or changes in site quality	Population-wide
Spring trend	Possible earlier departure from Iberia but arrival in Netherlands unchanged	Switch to rice-seed diet	Unknown
		Unknown	Unknown



between the two subspecies at this time of year makes this difficult to assess.

POSSIBLE CAUSES OF THE POPULATION DECLINE IN *L. L. LIMOSA*

These extensive habitat changes throughout the range of *L. l. limosa* allow several plausible causes of the severe population decline to be identified:

- declining habitat quality and availability in the breeding season may have resulted in reductions in productivity;
- changes in winter and spring diet may have altered the body condition or survival probability of fully-grown birds;
- habitat and climatic changes in the Sahel region may have altered habitat availability, and consequently body condition or survival of fully-grown birds.

The demographic evidence presented at this workshop strongly suggests that reductions in productivity are the most likely driver of the population decline. Changes in productivity through the period of breeding habitat change have been severe, declining from *c.*0.7 chicks per pair (range: 0.5–1) in

the 1980s to *c.*0.2 chicks per pair (range: 0.1–0.7) at present (Schekkerman *et al.* 2005, subm b). Changes in the timing and frequency of mowing, affecting both direct nest and chick losses and the foraging conditions for chicks (Schekkerman & Beintema 2007), are strongly implicated in driving these declines. In addition, the abundance of nest and chick predators and their impact on an increasingly fragmented and exposed (through loss of cover by early mowing) population appears to be growing. In recent years, there has also been evidence from one site for deferral of breeding by up to half of the adults returning to the breeding grounds.

The widespread use of rice as food in winter and spring may affect adult body condition but there is currently no evidence for any declines in adult survival rates, in fact adult survival appears to have increased in recent decades (Zwarts *et al.* in press). Recent colour-ring studies suggest high adult annual survival rates of *c.*81–96% (Both *et al.* 2006, Roodbergen *et al.* subm., J. Schröder in prep.), though national estimates from ring-recoveries suggest annual survival rates of *c.*80% (van Noordwijk & Thomson subm.). Recent reductions in the length of the hunting season in France are likely to have reduced hunting pressure, and numbers of hunting recoveries of ringed birds have declined in recent years (Zwarts *et al.* in press). Mortality of juveniles on autumn migration may

Table 2. Summary of the current status of the demography, distribution and habitat use of the Icelandic Black-tailed Godwit population, *Limosa limosa islandica*, together with likely drivers of changes and estimates of the proportion of the population experiencing these conditions.

	Status of <i>islandica</i> population	Drivers of changes	Potential population impact
Population size	<i>c.</i> 50,000–75,000 individuals		
Population trend	Rapid increase, from <i>c.</i> 2600 around 1900	Warmer temperatures and agricultural expansion in Iceland	Population-wide
Nest survival	50–75% of nests hatch	Unknown	Unknown
Chick survival	20–80% pairs fledge at least one chick. Productivity likely to be <i>c.</i> 0.5–0.8 chicks/pair	Population expansion may have reduced average productivity	Unknown
Productivity trend	Unknown	Unknown	Population-wide
Juvenile survival	<i>c.</i> 60% from ringing to fledging and <i>c.</i> 50% post-fledging to first autumn	Unknown	Population-wide
Adult survival	Annual estimates = 87–99%, highest in winter and lowest during spring migration	Survival increased in late 1990s. Some evidence of recent declines	Probable regional variation in survival trends
Breeding habitat	Lowland marshes and dwarf-birch bogs	Suitability of dwarf-birch bogs as breeding sites may have increased	Population-wide
Breeding locations	Expansion from SW to NE Iceland	Expansion into colder parts of Iceland with more dwarf-birch bog	Population-wide
Breeding trend	Increasing and expanding distribution	Average productivity likely declined but number of pairs increased	Population-wide
Autumn habitat	Estuarine mudflats, occasional use of river valleys and gravel pits	None	Most use of freshwater habitats by juveniles
Autumn locations	Most in UK, Ireland and France (Jul–Sep).	None	Population-wide
Autumn trend	Expansion into E and NW England moulting sites	Population size increase	<i>c.</i> 30% of population in new sites
Winter habitat	Estuarine mudflats and grasslands. Saltpans in Iberia	Grassland use more extensive in recently occupied sites	<i>c.</i> 80% on mudflats and <i>c.</i> 20% on grasslands
Winter locations	UK, Ireland, France and Iberia (Oct–Feb)	Population size increase	Population-wide
Winter trend	Recent expansion into E and NW England	Population size increase	<i>c.</i> 10% of population in new sites
Spring habitat	Estuarine mudflats and grasslands. Some use of saltpans (France & Iberia) and rice fields (Iberia)	Grassland use more extensive in recently occupied sites	<i>c.</i> 30% on mudflats and <i>c.</i> 70% on grasslands
Spring locations	Netherlands (Iberian and French birds), Ireland (Irish birds), UK (UK and Irish birds) (Mar–Apr)	Increase in use of Netherlands and E England grasslands	<i>c.</i> 50–60% of the population uses Netherlands and E England sites
Spring trend	Increasing use of grasslands on spring passage. Earlier arrival in Iceland	Changing rainfall. Population increase and/or warmer springs	Earlier arrival trend may be more apparent in the earliest birds



be higher as they appear to use European passage sites more than adults, and may thus be exposed to hunting pressures in France. The available national ringing recovery data, together with a recent colour-ringing study from one site, suggest that juvenile survival is not particularly low, but these estimates may not be representative of the whole population.

Habitat structure and composition in Iberia and West Africa have clearly changed dramatically since the 1950–1960s, especially in the Senegal delta, but again there is little evidence for negative impacts on survival rates, at least in recent years. Mortality rates do appear to be a little higher in years with low rainfall in the Sahel, possibly as a consequence of birds occurring at high densities in the remaining wet areas, especially during the post-breeding arrival period when conflict with rice farmers can make the godwits vulnerable to hunting pressure (Zwarts *et al.* in press). However, although there is no strong evidence for climatic or habitat changes in the non-breeding season driving the population declines, there is clear concern that these processes could exacerbate the declines, as such a high proportion of the population is dependent upon relatively small areas of rice fields at key times of year.

CURRENT DISTRIBUTION AND HABITAT USE OF *L. L. ISLANDICA*

The Icelandic population of Black-tailed Godwits breeds primarily in Iceland, with small numbers in the Faeroes, Lofoten and Shetland Islands. In Iceland they breed in lowland areas, primarily on coastal marshes and dwarf-birch bogs (Gunnarsson *et al.* 2006a).

Key breeding season issues

In both marshes and dwarf-birch bogs, Icelandic Black-tailed Godwits are strongly associated with shallow pools, often surrounded by sedges, which support foraging adults. Chicks feed mostly on invertebrates gleaned from vegetation, and seek out tracts of grassland which are rarer in the dwarf-birch bog habitats. The expansion from SW Iceland (around 1900) to the major basins in the north and west (1920s–1940s) and then the east and north-east of Iceland (1970s–1980s) was characterised by an increase in the proportion of dwarf-birch bog sites occupied (Gunnarsson *et al.* 2005a). The most recently occupied sites are also colder than the traditionally occupied southerly sites (Gunnarsson *et al.* 2006b). The lowland areas of Iceland have seen widespread drainage of wetlands and increases in numbers of hayfields since the 1960s, and godwits are now frequently recorded feeding on hayfields during the breeding season.

Key non-breeding season issues

After the breeding season, Icelandic godwits migrate south to the UK, Ireland and France. Small numbers of birds also appear to migrate directly to Portugal from Iceland. The moulting sites in the north-west and east of England have seen particularly large increases in use in recent decades, especially the Wash, Humber and Dee estuaries. The vast majority of Icelandic godwits use estuarine mudflats during the autumn months. By winter many birds have moved south to estuaries in France and Portugal and, in Ireland and England, they start to forage on grasslands. The number of Icelandic godwits wintering in the UK, Ireland and France is

well reported, but the number wintering in Iberia is difficult to assess because the subspecies overlap there, particularly during January and February when both wintering and migratory continental godwits are present.

In spring, most godwits from Portugal and France migrate to the Netherlands or eastern England, where they forage primarily on grasslands. At the same time, many birds from coastal sites around the UK move inland to forage on flooded grasslands. Studies of energetic intake rates on mudflats and grasslands suggest that godwits move to grasslands when estuarine food supplies are no longer sufficient to support them, and that they frequently use both mudflats and grasslands throughout winter and spring. This seems to be particularly common in the northern part of their range, where estuarine prey are often subject to strong seasonal depletion (e.g. Gill *et al.* 2001b) and where grassland foraging appears to be a necessary addition to compensate for insufficient estuarine food supplies.

POSSIBLE CAUSES OF THE POPULATION INCREASE IN *L. L. ISLANDICA*

The drivers of the population increase in Icelandic godwits are not fully identified, but there are several plausible candidates:

- climatic amelioration in Iceland may have improved breeding conditions and increased the area available for breeding godwits;
- changes in habitat structure in Iceland may have improved breeding conditions;
- climatic and habitat changes in the non-breeding range may have improved survival and condition for breeding;
- changes in hunting pressures may have improved survival rates.

The initial increase in godwit numbers around the 1920s coincided with a period of rapid warming in Iceland, suggesting that climatic amelioration may have been involved, at least in the early stages of population growth. From the 1930s to the 1980s, the rate of colonisation of Iceland is correlated with the number of drainage ditches installed, indicating that large-scale habitat changes may have positively influenced godwit breeding distribution. The common observation of godwits foraging in hayfields, especially those close to dwarf-birch bogs, suggests that the presence of hayfields as foraging habitats may have improved the quality of dwarf-birch bogs as breeding sites.

In recent decades, the primary habitat change in lowland Iceland has been the development of afforestation schemes, many of which are focused on marsh habitats, in addition to house-building in lowland areas. Since the 1980s, there has been a strong positive correlation between Iceland spring temperatures and the index of Icelandic godwits wintering in the UK (as recorded by the Wetland Bird Survey, Banks *et al.* 2006). Colour-ring information has shown that the majority of the UK population increase has involved birds from the recently occupied east and north-east of Iceland (Gunnarsson *et al.* 2005b); strongly suggesting that recent climatic amelioration has allowed these coldest parts of the country to be occupied.

In the non-breeding range, there are few indications of improvements to habitat quality, but changing rainfall pat-



terns may be altering the timing of availability of grassland foraging sites. This may be particularly true of sites in eastern England and the Netherlands, use of which has increased substantially in recent years (Gerritsen & Tijssen 2003, Gill *et al.* 2001). The reduced frequency of cold winters in NW Europe also may be influencing survival rates.

The role of hunting pressure in driving population changes in Icelandic godwits is difficult to assess. Historically, there are records of godwits being considered a delicacy, having been described as “highly esteemed for the table” and “both shot and taken by snares” (Morris 1897). It is possible that reductions in hunting pressure, and the associated disturbance levels, may have influenced the population changes, but there are currently no data with which to explore this issue. At present, the only country in which Icelandic godwits are shot is France, and the lack of accurate bag statistics precludes calculation of the impact of this hunting pressure. Although the Icelandic population is increasing, it is still small and restricted in range, and the impact of hunting is therefore difficult to predict should conditions change.

CONTRASTING *LIMOSA* AND *ISLANDICA* POPULATIONS

Despite the current contrast in the fortunes of these two populations, comparison of their demography and distribution has revealed intriguing similarities, which we hope will help to focus current and future conservation and research efforts. In both Iceland and the Netherlands, it seems evident that agricultural intensification has played a role in driving population expansions and contractions over the last century. Wetlands and heathlands have been converted into agricultural habitats in which productivity has increased through fertilisation and reduction of flooding intensity, while frequent cutting and mowing maintains an open sward structure. This seems to have benefited several large, ground-nesting shorebird species, probably through higher abundances of soil macrofauna and improved access to these resources (Beintema 1986, Beintema *et al.* 1987). Throughout Europe this process began in the first half of the twentieth century, but so far the area converted and the level of intensification have been much greater in the more populated countries of NW Europe than in Iceland. In both Iceland and the Netherlands, there is evidence that populations of Black-tailed Godwit, along with other similar species, may have been able initially to increase and expand their distribution in response to this habitat conversion and increase in productivity.

In the Netherlands, the agricultural landscape is now so intensively managed that the area suitable for breeding godwits has declined dramatically, such that the population is now probably lower than it was prior to the 1950s. By contrast, the Icelandic population appears to be still benefiting from changes in agricultural practice that have created a landscape in which grass production and moderate levels of horse grazing have given rise to the complex sward structure necessary for breeding, alongside areas suitable for foraging. The extent to which these habitat changes have driven the population increase in Iceland is not currently clear, and there may yet be scope for further population expansion in Iceland. However, the Netherlands experience would strongly suggest that further intensification, such as increasing grazing intensities, are likely to be very detrimental to godwits and other ground-nesting birds. In addition, land-use changes in Iceland, such as the current widespread afforestation programmes, are a major

threat to the internationally important shorebird populations of lowland habitats.

While habitat changes may be the primary driver of population changes over the last century, climatic changes have the potential to be an equally important issue in the near future. Temperature increases and changing precipitation patterns are both implicated in the *islandica* population increase, and there is some recent evidence for deferral of breeding in *limosa* in particularly dry years, although warm conditions are also likely to improve chick growth and survival. The timing of spring rainfall and the magnitude of temperature changes in the future are therefore likely to be very important in determining the impact of climate change on breeding success. The dependence of most of the *limosa* population on relatively small areas of flooded rice fields in Africa and Iberia is also likely to make them highly vulnerable to changing rainfall patterns. The recent drought in the Sahel region (Dai *et al.* 2004) is of particular concern for the maintenance of suitable foraging areas for these birds. Rice production is also dependent upon global markets and, in Iberia, on European Union agricultural support mechanisms, further increasing concern over the persistence of these key habitats.

A more immediate threat to the godwits that depend on rice fields and mudflats in Portugal is the proposed development of a new airport near Lisbon. One potential location for this airport is in the vicinity of the Tagus Estuary Nature Reserve, with approach routes that are likely to cross the main rice field areas in the Tagus and Sado estuaries, which are used by tens of thousands of godwits during January and February, and the corridor linking the Tagus and Sado mudflats which are used by godwits throughout the non-breeding season. Such a development could seriously impact on a very large proportion of the godwit population at a critical time of year, and would therefore be very likely to exacerbate already severe population declines.

The historical context of the population changes, and concern about future conditions for godwits and other similar bird species, led the workshop participants to identify the key recommendations that we believe it will be necessary to implement in order to conserve Black-tailed Godwits effectively in Iceland and W Europe.

CONSERVATION RECOMMENDATIONS FOR *L. L. LIMOSA*

1. Improve prescriptions and targeting of AES in the breeding range, focusing efforts in areas with high groundwater levels and open landscapes to attract godwits and avoid high predator densities, in order to have the potential to improve overall productivity. Include raising groundwater levels in the Netherlands AES prescriptions (as is the case in the UK, Denmark and Germany)
2. Incorporate the creation of small-scale habitat mosaics into management prescriptions, to provide both foraging and predator avoidance options throughout the season.
3. Improve conservation of key wetland habitats in Iberia and Africa, either through maintenance of support for rice production or restoration of wetlands, as well as designation of more sites under relevant national legislation and international treaties (EU Birds and Habitats Directives, Ramsar Convention etc.).
4. In view of the severe continuing declines of this population, take a precautionary approach and ban hunting of godwits, at least temporarily, where there is any risk that birds from



this population could be involved (especially late migrating juveniles in autumn), until productivity is increased to a level that can sustain a certain amount of additional mortality of adults and immatures.

CONSERVATION RECOMMENDATIONS FOR *L. L. ISLANDICA*

1. Improve conservation of winter habitat mosaics, particularly in areas, such as Ireland, England and France, where grasslands, coastal lagoons and salinas may be necessary to maintain populations when estuarine food supplies are depleted.
2. Reduce impact of afforestation and building developments in Iceland on godwits and other shorebird species, by conserving key breeding areas.
3. Improve protection of coastal habitats in areas where development and associated disturbance levels are high (especially in Ireland).

KEY RESEARCH GAPS FOR *L. L. LIMOSA*

1. Improve estimates of juvenile survival, causes of mortality and distribution prior to recruitment.
2. Improve survey information on the distribution and abundance of Black-tailed Godwits in the West African wintering grounds.
3. Improve understanding of the importance of the Doñana National and Natural Park area for protecting *L. l. limosa* during spring migration.
4. Explore the potential impact of hunting on the *limosa* population, and work with hunting organizations to develop better methods of recording accurate bag statistics in France.
5. Explore the impact of the increasing time-lag between godwit arrival in the Netherlands and the commencement of breeding, and the frequency of deferral of breeding attempts.
6. Improve understanding of the location, timing and duration of use of passage sites in Europe and Africa, and habitat use and diet within these sites.

KEY RESEARCH GAPS FOR *L. L. ISLANDICA*

1. Improve understanding of the role of agricultural intensification in Iceland.
2. Identify the key drivers of productivity in different habitats in Iceland.
3. Improve survey data for Iberia and France during the passage period of January to March, when there is the greatest overlap between the subspecies.
4. Explore the factors influencing the quality and availability of grassland habitats.
5. Explore the consequences of seasonal matching (individual use of similar quality habitat in both breeding and wintering areas) for population processes and identification of key areas for conservation.
6. Explore the potential impact of hunting on the *islandica* population.

FINAL COMMENT

The workshop provided an exciting and hopefully very valuable means of exploring the causes of population change in two closely related subspecies. The large group of experts provided an ideal forum for both highlighting key issues and using expert opinion to identify and prioritise the conservation recommendations. This process would undoubtedly have been helped were information available on the eastern population of *L. l. limosa* and the eastern subspecies, *L. l. melanuroides*. Our final recommendation is therefore to encourage the collation and presentation of information on these two populations.

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