

Shorebird ecology and conservation in
the Western Hemisphere



Peter Hicklin, Editor-in-chief

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Shorebird ecology and conservation in the Western Hemisphere

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in conjunction with the IV Neotropical Ornithology Congress
in Quito, Ecuador

Peter Hicklin, Editor-in-chief
Anthony J. Erskine, Assistant Editor
Joe Jehl, Assistant Editor

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Front cover: Red Knots on northward migration at Peninsula Valdés, Argentina (photo by R.I.G. Morrison)

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Foreword

Shorebirds make up a very important group of birds, a group that has been the subject of intensive study and conservation initiatives in recent years in the Western Hemisphere. With their long-distance migrations, shorebirds connect habitats and people across the American continent.

The first obvious connection is their use of habitats along the hemisphere. Most species of shorebirds (sandpipers, plovers and relatives) depend upon wetlands for their survival. Recent studies have documented the astonishing rate at which the wetlands of the Americas continue to be drained and filled or otherwise rendered unsuitable for use by shorebirds. Not surprisingly, the precarious relationship between shorebirds and their habitats has not escaped the attention of the conservation community. In the past decade, conservation efforts focusing on wetlands (and specifically shorebirds) have increased dramatically. Our ability to conserve wetlands and shorebirds will be a measure of our ability to ensure our own survival as a species.

The second important connection that shorebirds provide is among researchers. Throughout the years, I have witnessed encounters between researchers who often handle the same individual birds but work in different countries. The need for interactions among researchers working on shorebirds throughout the Americas is paramount. Yet the opportunities for these interactions are rare.

The present volume is the result of a symposium organized to help close this gap. The symposium on the ecology and conservation of shorebirds in the Western Hemisphere was organized as part of the IV Neotropical Ornithology Congress held in Quito, Ecuador, in November 1991. This event served as a forum where the latest research in shorebird migration, ecology and conservation was discussed. What is more important is that the symposium provided a great opportunity to forge scientific partnerships among researchers from many parts of the hemisphere. Simultaneous translations (English-Spanish) were available at all times during the workshop in order to facilitate these exchanges.

Finally, and most importantly, shorebirds connect people. Many efforts to protect shorebirds and their habitats are succeeding because the people of the Americas are working together towards this goal. The linkages that shorebirds provide serve as an inspiration to many people in the hemisphere working to preserve the environment. Maintaining the splendour of the shorebirds' annual migratory flights will be the ultimate recognition to conservationists in North, Central and South America.

The present publication represents the work of many scientists. Collectively, their wide-ranging research interests and efforts, wisely invested in the advancement of our knowledge of shorebird ecology and conservation, are truly monumental. This volume is in recognition of these valiant efforts.

Gonzalo Castro
Chair, Organizing Committee

Preface

The opportunity to attend a symposium on 'Shorebird ecology and conservation in the Western Hemisphere' was an interesting experience in itself, but to have this same meeting as part of the IV Neotropical Ornithology Congress, with its varied membership, and in the beautiful city of Quito in Ecuador, made for a most memorable experience. I shall remember those days in Quito very warmly; the fascinating conversations with my South American colleagues (with and without the assistance of Spanish interpreters/translators...) will vividly remain with me for a long time. These proceedings present you with only part of this experience, but, as you will see, the papers herein make for a most important contribution to our knowledge of shorebirds, north and south of the equator.

You will note that some papers are presented in full, whereas others are presented only as expanded abstracts. This is because, at the time of the presentation of these papers, some were either already in press or soon due to be submitted for publication. Hence, those specific papers are published herein as expanded abstracts.

You will also note that many references are shown in the References sections as being in press, while in reality they have been published since this symposium was held. There are a number of reasons for this: first of all, at the time I write this (September 1995), it has been over three and a half years since this meeting was held. The need for translations (Spanish/English) as well as other work duties slowed down the process, but I hope that, like me, you will find that it was worth the wait. Also, when the presentations were made, the papers were indeed not yet in print, and to seek them all out now, so long after the symposium was held, simply was not possible. However, you will note that some references published after 1991 were added by the authors as the symposium papers went through numerous reviews and drafts.

Each year, many species of shorebirds migrate across the Western Hemisphere. Those of us who study them do not often have the same opportunity to meet with colleagues who study the same populations in different, distant reaches of this hemisphere. For me, and many others who attended this meeting, Quito gave us the opportunity to flex our wings, cross the flyways and exchange views that had, for too long, been in storage.

Peter Hicklin
Canadian Wildlife Service
Editor-in-chief.

Acknowledgements

The editors wish to thank the National Science Foundation, the Canadian Wildlife Service and the Western Hemispheric Shorebird Reserve Network for sponsoring the symposium. Grateful thanks are also tendered to the International Waterfowl and Wetlands Research Bureau for financial support. The editor-in-chief is indebted to assistant editors Dr Joe Jehl and Dr Anthony J. (Tony) Erskine for their invaluable assistance with reviewing the first drafts of the manuscripts (AJE) and the expanded abstracts (JJ). Dr Michel Sallaberry compiled the South American contributions.

The members of the organizing committee that made this event possible were Gonzalo Castro (chair), Julie Sibbing, Humberto Alvarez-López, Pablo Caneveri, Brian Harrington, Peter Hicklin, Nancy Higert de Benavides and Marshall Howe. But all members wish to acknowledge that Julie Sibbing really made it all happen.

The organizers are most grateful to invited speakers Dr Raymond McNeil, Dr R.I.G. Morrison, Dr Theunis Piersma and Dr Michel Sallaberry for their presentations and valuable participation in discussions throughout the course of these meetings.

Participants and organizers are also grateful to the staff of Universidad Católica del Ecuador for the comfortable accommodations where the symposium was held.

This publication was produced by the Scientific and Technical Documents Division of the Canadian Wildlife Service. The following people were responsible: Patricia Logan, Chief — coordination and supervision; Sylvie Larose, Computer Publishing Specialist — layout; Marla Sheffer, Contract Editor — scientific editing; and Gilles Bertrand, Production Officer — printing. The editor-in-chief thanks them for their careful and caring work throughout the long production process. Funding for the publication was provided by the Canadian Wildlife Service (Atlantic Region and Latin American Program).

Part I

Populations, habitat use and breeding biology of shorebirds in North America

Alaska and its importance to Western Hemisphere shorebirds

Robert E. Gill, Jr. & Stanley E. Senner

Gill, R.E., Jr., & Senner, S.E. 1996. Alaska and its importance to Western Hemisphere shorebirds. *International Wader Studies* 8: 8-14.

Thirty-seven species of shorebirds breed in Alaska, and six overwinter in its subarctic regions. The coastal habitats of Alaska provide critical staging areas during spring and fall migrations; 51 sites qualify within the three categories of shorebird reserves listed by the Western Hemisphere Shorebird Reserve Network (Hemispheric, International and Regional). Studies on Alaskan shorebirds span 50 years, although the largest number of field studies have been undertaken over the past 20-year period.

En Alaska se reproducen treinta y siete especies de aves costeras, seis de las cuales pasan el invierno en esas regiones subárticas. Los hábitats costeros de Alaska son zonas cruciales para las escalas durante las migraciones de primavera y otoño; 51 sitios están comprendidos en las tres categorías de reservas de aves costeras incluidas en la lista de la Red de Reservas de Aves Costeras del Hemisferio Occidental (hemisféricas, internacionales y regionales). Los estudios de las aves costeras en Alaska se remontan a 50 años, aunque la mayoría de los estudios sobre el terreno se han llevado a cabo en los últimos 20 años.

Trente-sept espèces d'oiseaux de rivage se reproduisent en Alaska et six hivernent dans ses régions subarctiques. Les habitats côtiers de l'Alaska constituent des aires de repos vitales durant les migrations printanières et automnales; 51 sites appartiennent à l'une des trois catégories (hémisphérique, internationale et régionale) du Réseau de réserves pour les oiseaux de rivage dans l'hémisphère occidental. Les études sur les oiseaux de rivage de l'Alaska couvrent 50 ans, quoique la plupart des études de terrain portent sur les deux dernières décennies.

Robert E. Gill, Jr., *Alaska Fish and Wildlife Research Center, National Biological Survey, 1011 E. Tudor Rd, Anchorage, Alaska 99503, USA.*
Stanley E. Senner, *International Council for the Protection of Birds — United States Section, PO Box 101193, Anchorage, Alaska 99501, USA. (Present address: National Audubon Society, 4150 Darley, Suite 5, Boulder, Colorado 80303, USA.)*

Introduction

In 1977, when the last major symposium on Western Hemisphere shorebirds was held, Frank Pitelka solicited from researchers a broad synthesis of information about coastal habitats in Alaska and their importance to shorebirds (Pitelka 1979). Unfortunately, none was forthcoming; at that time, there were too few data, and the information available was of limited geographic coverage. In the ensuing 15 years, a considerable body of information has been gathered on shorebirds and their ecology. Here we present an overview of the work that has been done in Alaska. Although our focus on shorebirds within a single state may seem somewhat provincial, Alaska is a distinct feature of the hemisphere in terms of prominent land-forms and land-cover. Alaska not only serves as the terminus of several major migratory bird flyways but also supports a unique shorebird fauna that has evolved within the region. One of our primary goals in this paper is to acquaint our colleagues in Central and South America with the importance of

Alaska to shorebirds during the austral winter. We also hope to promote international co-operative research leading to more effective conservation and management of shorebirds and their habitats throughout the Western Hemisphere.

The region and physical setting

By most standards, Alaska is a huge region. Its borders span 20 degrees of latitude and 57 degrees of longitude, distances comparable to those between the Canadian and Mexican borders and the Pacific and Atlantic coasts of the United States. Alaska's area is equal to that of Peru and Ecuador combined (Figure 1). The coast of Alaska is unusually convoluted and encompasses about 55,000 km of shoreline, a distance equal to about 40% of the coast of the entire conterminous United States and exceeding that of the coastline of South America (Hall 1988). In this region, more so than at most temperate and tropical latitudes, tides greatly influence the extent and quality of habitats available to shorebirds. Tidal amplitudes range

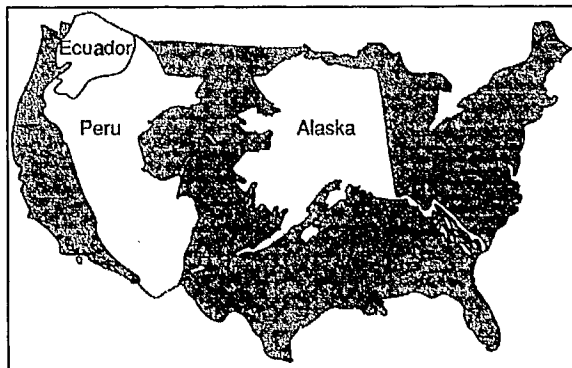


Figure 1. Alaska's area compared with those of the conterminous United States and Ecuador and Peru.

from less than 0.3 m along the Beaufort Sea coast to almost 9.0 m in portions of south-central Alaska. The mean tidal range among 55 sites within Alaska that have been identified as being important to shorebirds (see below) is 3.0 ± 2.2 m (SD). Consequently, Alaska has more vegetated and unvegetated littoral habitat than the rest of the United States and Mexico combined (Hall 1988).

The shorebirds in Alaska

About 80 species of shorebirds (Charadrii) regularly breed in the Western Hemisphere, of which about two-thirds are migratory (Pitelka 1979; Hayman, Marchant & Prater 1986; Sibley & Monroe 1990). Among the migratory species, 47 (89%) occur in Alaska, and 37 of these, plus three additional races, regularly breed there (Page & Gill 1994). Information available on population size and distribution for 17 of these taxa allowed us to estimate the relative proportions of the global and Western Hemisphere breeding populations that occur in Alaska (Table 1). Alaska hosts almost the entire breeding population of three species (*Numenius tahitiensis*, *Arenaria melanocephala* and *Calidris mauri*) and four subspecies (*C. alpina pacifica*, *C. ptilocnemis ptilocnemis*, *C. p. couesi* and *Limnodromus griseus caurinus*). Probably 75% of the world population of *Aphriza virgata* and *C. ptilocnemis tschuktschorum* and 100% of the Western Hemisphere populations of *Pluvialis fulva*, *Limosa lapponica baueri* and *C. canutus roselaari* also breed in Alaska (Table 1). Alaska is important to yet a third group, albeit one for which we have little or no information. For these taxa (*Haematopus bachmani*, *Heteroscelus incanus*, *N. phaeopus hudsonicus* and *L. haemastica*), Alaska may support as much as half of their respective Western Hemisphere populations (Table 1).

Where do Alaska's breeding shorebirds disperse during the boreal winter? Pitelka (1979), Boland (1991) and, more recently, Page & Gill (1994) have summarized the wintering distributions of shorebirds in various regions of the Western

Hemisphere. A summary of the non-breeding distributions of shorebirds that breed in Alaska is shown in Table 2. Only seven species regularly spend the boreal winter in Alaska, all within ice-free subarctic regions. These include *H. bachmani*, *A. melanocephala*, *A. virgata*, *C. alba*, *C. ptilocnemis*, *C. alpina* and *Gallinago gallinago*. Six species winter primarily in temperate North America, 13 have ranges that include portions of both North and South America, 10 winter in South America, 3 winter in Oceania and Asia and 5 have populations that winter in Oceania, in Asia and throughout the Americas (Table 2).

Important sites for shorebirds in Alaska

Alaska is important to shorebirds of the Western Hemisphere not only for its extensive breeding grounds but also for its provision of critical staging areas during spring and fall migrations. One measure of the importance of Alaskan coastal habitats is the number of sites within the region that qualify for inclusion in the Western Hemisphere Shorebird Reserve Network (WHSRN) (Figure 2). To date, only one site in Alaska, the Copper River Delta, has been formally dedicated within the WHSRN system. A second site, the central Yukon-Kuskokwim River Delta, has formally been nominated as a WHSRN site. Both sites qualify as Hemispheric reserves (Senner, West & Norton 1981; Senner & Howe 1984; Gill & Handel 1990).

Based on preliminary data (R. Gill & L. Tibbitts, unpubl. data), we have identified an additional 4 sites in Alaska as Hemispheric reserves, 4 sites as either Hemispheric or International reserves, 8 sites as International reserves and 33 sites as Regional reserves (Figure 2). Proposed Hemispheric reserves include the southern Yukon-Kuskokwim River Delta and Montague Island in Prince William Sound. Most Bering Sea islands qualify as either Hemispheric or International reserves based on the percentage of populations of *C. ptilocnemis* breeding there (Figure 2). The preponderance of sites in western and south-western Alaska is strongly correlated with the greater tidal ranges and larger expanses of littoral habitat, specifically the invertebrate-rich mud- and sand-flats in these areas that are used by migrant shorebirds. Major breeding areas along the coast, and perhaps in the poorly studied interior of Alaska, may also qualify for inclusion within the WHSRN. For example, the well-defined Arctic Coastal Plain provides critical nesting habitat for several Arctic-nesting species, and discrete breeding areas on the Seward Peninsula and Norton Sound (Figure 2) have been identified for *N. tahitiensis* (Gill, Lancot & Handel 1991) and *L. fedoa* (Gibson & Kessel 1989).

Table 1. Alaska's contribution to global and Western Hemisphere populations of selected shorebird species. Note that the information required to make the following estimates was available for only 14 of 37 nesting species.

Species	% of breeding population ^a		Source
	Global	Western Hemisphere	
<i>Haematopus bachmani</i>	60	60	1,2,3
<i>Pluvialis fulva</i>	?	100	1,2,4
<i>Heteroscelus incanus</i>	50	50	1,6
<i>Numenius tahitiensis</i>	100	100	2,7
<i>N. phaeopus hudsonicus</i>	50	50	1,5,6
<i>Limosa haemastica</i>	30-50	30-50	1,5,6
<i>L. lapponica baueri</i>	20-40	100	3,8,9
<i>Arenaria melanocephala</i>	100	100	1,10
<i>Aphriza virgata</i>	75	75	1,2,11,12
<i>Calidris mauri</i>	95	100	1,13
<i>C. ptilocnemis ptilocnemis</i>	100	100	1,9,14
<i>C. p. couesi</i>	100	100	1,9,14
<i>C. p. tschuktschorum</i>	75	100	1,9,14
<i>Calidris alpina pacifica</i>	100	100	1,13,14
<i>Tryngites subruficollis</i>	20-50	20-50	1,6,15
<i>Limnodromus griseus caurinus</i>	100	100	1,14

^a These represent best estimates based on known distributions and applicable studies: 1 = American Ornithologists' Union (1957); 2 = Campbell *et al.* (1990); 3 = Page & Gill (1994); 4 = Connors (1983), Connors, McCaffery & Maron (1993); 5 = Morrison & Ross (1989); 6 = Hayman, Marchant & Prater (1986); 7 = Gill, Lanctot & Handel (1991); 8 = Lane (1987); 9 = R. Gill (unpubl. data); 10 = Handel & Gill (1992a); 11 = Norton *et al.* (1990); 12 = P. Martin (unpubl. data); 13 = Senner, West & Norton (1981); 14 = Gabrielson & Lincoln (1959); 15 = Lanctot & Slater (1992, unpubl. data).

We stress that the data supporting designations of WHSRN sites in Alaska are quite varied in quality and quantity. We anticipate that designations of some sites may shift up or down with better information. Some sites have not been looked at since the 1970s, others only from the air and yet others during periods of less than optimal use by shorebirds. For example, upper Kachemak Bay, in south-central Alaska, certainly qualifies as an international site based on the large numbers of *C. mauri* that occasionally stop there in spring (Senner, West & Norton 1981). Upon further study, this site may prove to be of hemispheric importance.

Studies past and present

Although published information on Alaskan shorebirds dates to the late 1700s, most of the earlier reports focused on occurrence and distribution, primarily as part of comprehensive faunal studies of various regions of the state (see Gabrielson & Lincoln 1959 for review). Given the size of the state, the length of its coastline and its comparative paucity of roads, such studies will likely continue to reap great benefits well into the next century. Studies directed specifically at shorebirds in Alaska, however, did not really begin until the middle of this century and have occurred in three distinct phases (Figure 3). Some of the earliest studies, such as those by William Conover in the early 1940s, involved examination of museum specimens to resolve questions on the taxonomy of Alaskan shorebirds (*i.e.* *P. dominica*, *Tringa solitaria*, *A. interpres*, *C. canutus*, *C. alpina*, *C. ptilocnemis* and

Limnodromus spp.). Field research did not begin until the 1950s, when Frank Pitelka and his students began what proved to be a 30-year investigation of the reproductive and social biology of species nesting on the North Slope and Yukon-Kuskokwim River Delta. Other major field studies of shorebirds in this early phase occurred at only six sites in the state (Figure 3). These addressed various aspects of distribution, habitat use, migration ecology and behaviour (see Handel *et al.* 1981 for a review of studies in Alaska prior to 1980).

Spurred by the advent of modern mineral exploration in Alaska in the 1960s and an increasing level of environmental awareness, studies of shorebirds entered their most productive era (Figure 3). From 1976 to the mid-1980s, a host of shorebird studies was initiated in Alaska. The great majority occurred along coastal areas in response to impending widespread exploration for oil and natural gas on the continental shelf. Most of these studies were designed to assess the seasonal dependence of shorebirds and other marine avifauna on coastal habitats. A few studies examined in more detail the breeding and migration ecology of particular species.

The past decade has seen yet a third phase of shorebird studies in Alaska (Figure 3). This period is characterized by studies at fewer locations but generally of longer duration, such as those of Troy (1992, this volume) and Moitoret & Walker (1993). Recent studies have focused on monitoring communities of shorebirds in regions of ongoing or

Table 2. Principal 'wintering' regions of shorebird species breeding in Alaska.

Species	Wintering region ^a				Asia-Oceania/ Bicontinental
	North America	Bicontinental	South America	Asia-Oceania	
<i>Haematopus bachmani</i>	x ^b				
<i>Pluvialis squatarola</i>		x			
<i>P. dominica</i>				x	
<i>P. fulva</i>					x
<i>Charadrius semipalmatus</i>		x			
<i>C. vociferus</i>		x			
<i>Tringa melanoleuca</i>		x			
<i>T. flavipes</i>		x			
<i>T. solitaria</i>				x	
<i>Heteroscelus incanus</i>					x
<i>Actitis macularia</i>		x			
<i>Bartramia longicauda</i>				x	
<i>Numenius tahitiensis</i>					x
<i>N. phaeopus hudsonicus</i>					x
<i>Limosa lapponica</i>					x
<i>L. fedoa</i>	x				
<i>Arenaria interpres</i>					x
<i>A. melanocephala</i>	x ^b				
<i>Aphriza virgata</i>		x ^b			
<i>Calidris canutus</i>		x			
<i>C. alba</i>					x ^b
<i>C. pusilla</i>		x			
<i>C. mauri</i>		x			
<i>C. minutilla</i>		x			
<i>C. fuscicollis</i>				x	
<i>C. bairdii</i>				x	
<i>C. melanotos</i>				x	
<i>C. ptilocnemis</i>	x ^b				
<i>C. alpina pacifica</i>	x ^b				
<i>C. a. sakhalina</i>					x
<i>C. himantopus</i>				x	
<i>Tryngites subruficollis</i>				x	
<i>Limnodromus scolopaceus</i>	x				
<i>L. griseus caurinus</i>		x			
<i>Gallinago gallinago</i>		x ^b			
<i>Phalaropus lobatus</i>				x	
<i>P. fulvicaria</i>				x	

^a Modified from Pitelka (1979), Boland (1991) and Page & Gill (in press).

^b Species with populations that regularly spend the boreal winter in Alaska.

planned development, such as the North Slope, or on species of particular concern, such as *N. tahitiensis*. Throughout all earlier phases of shorebird research in Alaska, studies in the interior region or in upland habitats of the state have been virtually absent. This trend finally appears to be changing. Within the past five years, long-term projects were initiated on *P. fulva* and *P. dominica* (Connors, McCaffery & Maron 1993; Johnson *et al.* 1993; S. Gunther, unpubl. data), *N. tahitiensis* and *N. phaeopus* (Gill, Lanctot & Handel 1991; McCaffery, this volume) and *Tryngites subruficollis* (Lanctot & Slater 1992, unpubl. data). With greater emphasis on species that migrate to the Neotropics, our knowledge of shorebirds breeding in non-coastal areas of Alaska should increase substantially.

Information known and research needs

Since the 1977 symposium in Monterey, California, a wealth of new information has been gathered about shorebirds in Alaska. As expected, much of this information pertains to the seasonal use of habitats by species while in Alaska, especially during the non-breeding period, when birds are particularly dependent on coastal areas (*e.g.* Shields & Peyton 1979; Gill & Handel 1981; Lehnhausen & Quinlan 1981; Senner, West & Norton 1981; Woodby & Divoky 1983; Gill, Handel & Connors 1985; Andres 1989; Gill & Handel 1990; Norton *et al.* 1990; Johnson, Wiggins & Wainwright 1992; M. Bishop & C. Iverson, unpubl. data). Other studies

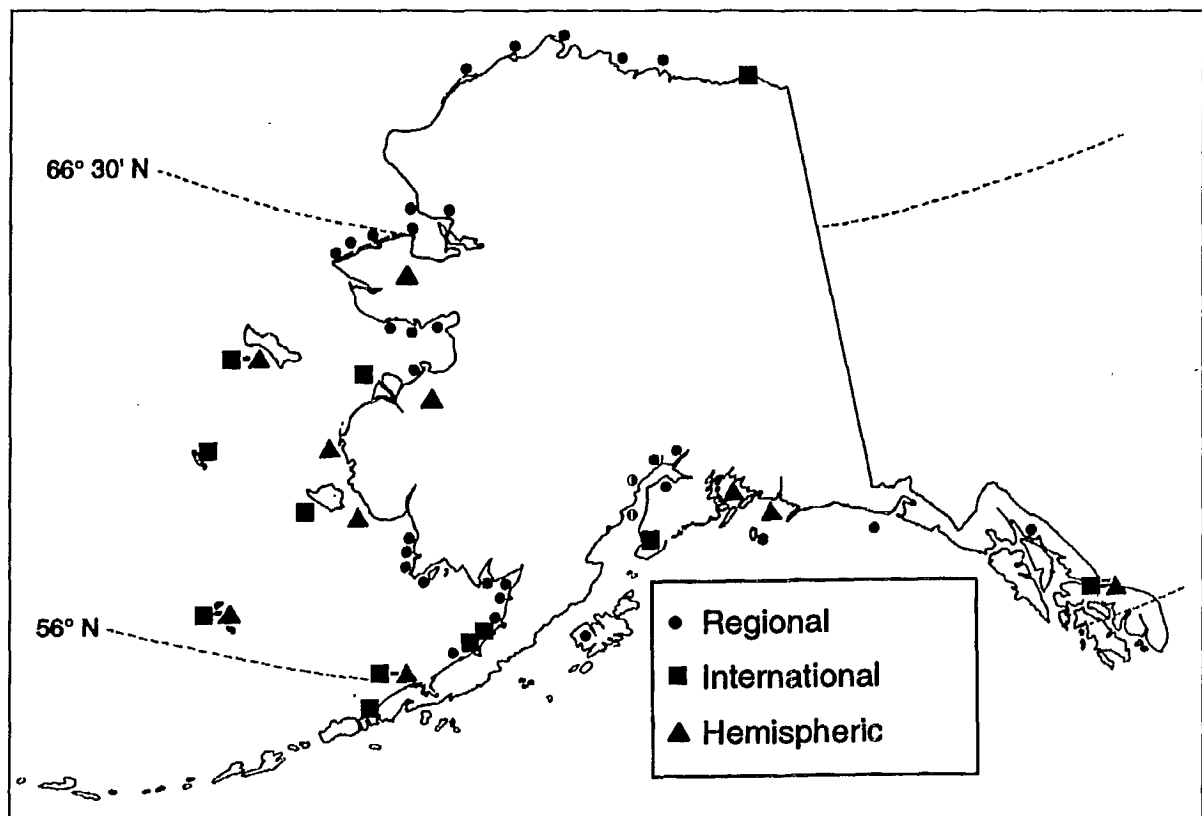


Figure 2. Current and potential Western Hemisphere Shorebird Reserve Network sites for shorebirds using coastal habitats in Alaska (R. Gill & L. Tibbitts, unpubl. data).

have focused on the status and size of populations (Handel & Gill 1992a; Gill & Redmond 1992; Troy 1992, this volume), and some have clarified or raised questions about taxonomic problems (Connors 1983; Tomkovich 1986; Gibson & Kessel 1989; Browning 1991; Piersma & Davidson 1992; Connors, McCaffery & Maron 1993). Yet other studies have addressed specific aspects of breeding ecology (Ashkenazie & Safriel 1979; Smith 1980; Handel 1982; Schamel & Tracy 1987; Gill, Lanctot & Handel 1991; McCaffery & Gill 1992; Johnson *et al.* 1993), foraging ecology (Senner, Norton & West 1989) and migration ecology (Senner, West & Norton 1981; Senner & Martinez 1982; Handel & Dau 1988; Johnson & Herter 1990; Handel & Gill 1992b).

While the foregoing represents an impressive body of knowledge, much information is still required for conservation and management initiatives, especially those in the international arena. Data on population sizes, geographical ranges during various phases of the annual cycle and locations of staging and stop-over sites are indispensable in these efforts. However, greater emphasis needs to be placed on linking discrete breeding, staging and wintering areas at the population and subpopulation levels.

For instance, we have good information on discrete non-breeding areas for only 6 of 37 species of

shorebirds that nest in Alaska (Table 3). For four other species, we suspect certain linkages exist between particular breeding and non-breeding areas. For the remaining 27 species, however, we know little more about distributional patterns than what appears in field guides. We cannot hope to understand the factors influencing population levels of different shorebird species or begin to monitor their numbers and trends without basic information on the existence of subpopulations and related migrational patterns. We especially need this type of information for species that nest across the Nearctic and spend the boreal winter in the Southern Hemisphere.

Specific issues for co-operative study

Based on the current state of knowledge of shorebirds and their ecology in Alaska, we here suggest several projects that may benefit from co-operative studies among researchers in Alaska, Canada and the Southern Hemisphere. Various methods may be used, but analysis of genetic material in comparison with results of large-scale colour-marking programmes appears best suited to resolving most issues.

- (1) Determine if *L. haemastica* using the Chiloe region belongs to the population breeding in Alaska, as suggested by Morrison & Ross (1989).

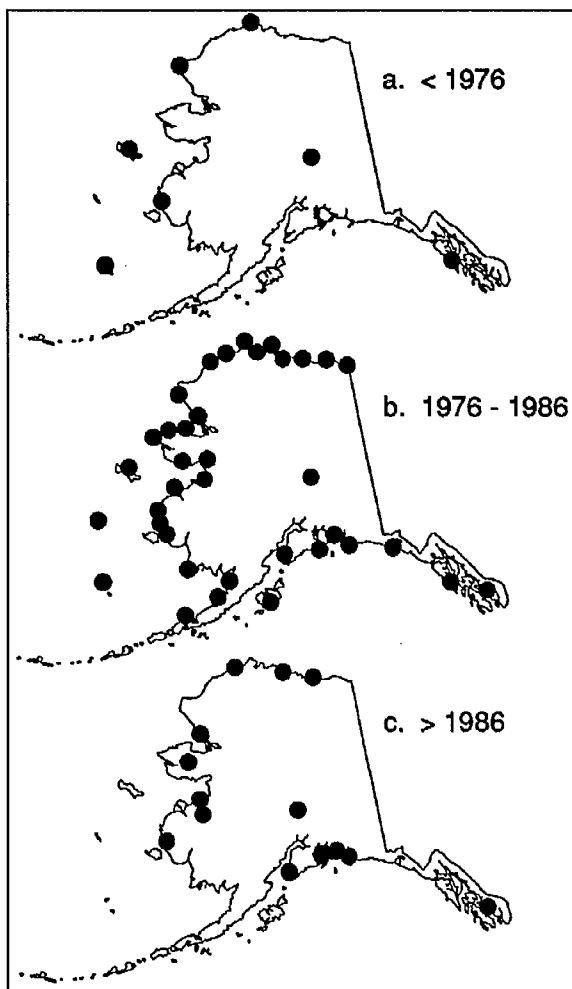


Figure 3. Sites in Alaska at which shorebirds were the principal or a major focus of study.

Recent studies in Alaska have shown that numbers of this species can be captured and marked on post-breeding staging areas.

- (2) In conjunction with ongoing studies of *T. subruficollis* in Alaska, in which populations are being monitored and birds are being marked, initiate similar studies in the Canadian Arctic and develop monitoring programmes on the non-breeding grounds in South America.
- (3) Assess the existence of discrete populations of *A. virgata*. Recent studies in Alaska have identified areas where the majority of the population stages during early May.
- (4) Determine the subspecific status and non-breeding season distribution of *C. canutus* breeding and staging in Alaska. Recent studies have linked Alaska and Wrangel Island breeding populations (Tomkovich, in Piersma & Davidson 1992), but their wintering distribution remains unclear.

Table 3. Status of knowledge of discrete non-breeding areas of Alaska-produced shorebirds.

Generally known	Suspected	Unknown
<i>Calidris alpina</i>	<i>Limosa lapponica</i>	27 species
<i>Calidris ptilocnemis</i>	<i>Numenius tahitiensis</i>	
<i>Calidris mauri</i>	<i>Arenaria interpres</i>	
<i>Limosa fedoa</i>	<i>Calidris pusilla</i>	
<i>Arenaria melanocephala</i>		
<i>Pluvialis fulva</i>		

Biologists studying non-game species (and shorebirds in particular) have had a history of coping with limited funds and personnel. Because many of the problems we face are now global in scope, no one person or group can do justice to them. We hope that from the Quito conference we will establish some long-lasting, international partnerships so that we can identify and solve our resource problems together.

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Population dynamics of breeding shorebirds in Arctic Alaska

Declan M. Troy

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Shorebird populations were monitored in 9 of 11 years between 1981 and 1991 near Prudhoe Bay, north Alaska, USA. Weather, predation, habitat changes and events away from the breeding grounds were considered as possible determinants of population change. Densities of Semipalmated Sandpiper *Calidris pusilla*, Dunlin *C. alpina* and Red Phalarope *Phalaropus fulicaria* (the most common philopatric species) fluctuated synchronously, although these species overwinter in widely disparate areas. This suggests that population regulation occurs in the breeding areas. Population trends of these species were correlated with hatching success two years earlier. Hatching success was determined primarily by the intensity of nest predation by arctic foxes. Shorebird eggs were an alternative prey used by foxes following crashes in microtine rodent (lemming) populations. These fluctuations in productivity have long-term implications on population size. Adverse weather on the breeding grounds had its greatest effect on nest initiation; in years of delayed snow-melt or cold temperatures, birds nested later. However, in most years, a proportion of shorebirds on the breeding grounds did not attempt to nest. Non-breeding appeared to be related to the severity of the weather. Occasional catastrophic population changes may be attributable to climatic events, but the best-documented cases have occurred away from the breeding areas. For example, phalarope densities were lower following the El Niño in 1982-83.

Se observaron las poblaciones de aves costeras durante 9 de los 11 años comprendidos entre 1981 y 1991 en las cercanías de Prudhoe Bay, en el norte de Alaska, EE.UU. Como posibles determinantes del cambio poblacional se analizaron factores tales como las condiciones climáticas, la conducta predatoria, los cambios de hábitat y los sucesos alejados de los criaderos. La densidad de los playeros semipalmados *Calidris pusilla*, las alondras de mar *C. alpina* y los falaropos rojos *Phalaropus fulicaria* (las especies filopátridas más comunes) fluctuaron sincrónicamente, a pesar de que esas especies pasan el invierno en zonas muy separadas. Ello parece indicar que la regulación de la población ocurre en los criaderos. Las tendencias poblacionales de esas especies se correlacionaron con el éxito de la incubación dos años antes. El éxito en materia de incubación se determinó principalmente en base a la intensidad de la predación de los nidos por parte de los zorros del Ártico. Los huevos de las aves costeras fueron una presa alternativa de los zorros como resultado de las abruptas disminuciones de las poblaciones de roedores micrótidos (lemmings o ratón de Noruega). Esas fluctuaciones en la productividad tienen implicaciones a largo plazo para el volumen de la población. Las condiciones climáticas adversas sobre los criaderos tuvieron su mayor efecto sobre el inicio de la nidificación; en años en que se retrasa el deshielo o que las temperaturas son frías, las aves anidaron más tarde. Sin embargo, en la mayoría de los años, se observó en los criaderos cierto porcentaje de aves costeras que no trataron de anidar. La evitación de la reproducción parecía estar relacionada con la inclemencia de las condiciones climáticas. Los ocasionales cambios catastróficos en la población podrían obedecer a las condiciones climáticas, pero los casos mejor documentados han ocurrido en puntos alejados de los criaderos. Por ejemplo, la densidad de los falaropos fue inferior después de El Niño en 1982-83.

Les populations d'oiseaux de rivage de la région de Prudhoe Bay dans le nord de l'Alaska, aux États-Unis, ont été étudiées au cours de neuf des onze années de la période 1981-1991. Ont été considérés comme agents potentiels de changement de la population : les conditions météorologiques, la prédation, la modification des habitats et des phénomènes se produisant à l'extérieur des aires de reproduction. Les densités de Bécasseau semipalmé *Calidris pusilla*, de Bécasseau variable *C. alpina* et de Phalarope roux *Phalaropus fulicaria*, les espèces philopatriques les plus courantes, ont fluctué de façon synchrone, même si ces espèces hivernent dans des régions très variées. Cela semble indiquer que la régulation des populations se produit dans les aires de reproduction. On a établi, pour ces espèces, des corrélations entre les tendances démographiques et le succès d'éclosion, déterminé deux ans auparavant, essentiellement en fonction de l'intensité de la prédation des nids par les renards arctiques. En effet, les renards se sont nourris d'oeufs d'oiseaux de rivage après l'effondrement des populations de Microtinés (lemmings). Ces fluctuations de productivité ont des effets à long terme sur la taille des populations. Les conditions météorologiques défavorables à la reproduction ont l'effet le plus important au moment de la construction des nids; ainsi, lorsque la fonte des neiges est tardive ou que le temps est

particulièrement froid, les oiseaux nidifient plus tard que d'habitude. Toutefois, la plupart des années, une portion des oiseaux de rivage n'a pas cherché à nidifier; on pense que cela tient aux rigueurs du climat. Il arrive à l'occasion que des changements catastrophiques de population soient attribuables à des phénomènes climatiques, mais les cas les mieux étudiés se sont produits à l'extérieur des aires de reproduction. Les densités de phalaropes, par exemple, étaient plus faibles après le passage d'El Niño en 1982-1983.

Troy Ecological Research Associates, 2322 E. 16th Ave., Anchorage, Alaska 99508-2905, USA.

Introduction

This review summarizes information on the fluctuations in bird use at a study area near Prudhoe Bay along the Beaufort Sea coast of the Alaska North Slope (Figure 1). This study area, the Point McIntyre Reference Area (PMRA), is near the Prudhoe Bay oilfield but is relatively isolated from oilfield facilities. Field sampling was conducted during nine summers between 1981 and 1991 (no sampling was undertaken in 1983 and 1985). The study plots were originally established as part of a control area for a study to monitor the effects of an oilfield expansion 4 km to the east. The layout of the plots was determined by that study; however, sampling in this area continued long after its original role was ended. This sampling has provided a time series of data showing natural variations in populations of birds using coastal tundra along the central Beaufort Sea. The variables used to quantify bird use included nest densities, timing of nest initiation, nest success and breeding season bird densities.

In this paper, temporal changes in shorebird densities and nesting biology are described, and trends in nest densities are correlated with several environmental (snow cover and temperature) and biotic variables in order to determine the factors causing population fluctuations. Space limitations prevent a complete presentation of all the analyses conducted and discussion of the results. This summary provides an overview of the study and some of the more interesting findings.

The breeding bird community

The species composition of breeding birds near Prudhoe Bay was dominated by shorebirds (Figure 2). Population levels of all species in the tundra bird community were monitored and trends determined. Data summaries of the ten most numerous nesting species (eight of which were shorebirds) are presented below. These species were King Eider *Somateria spectabilis*, Lesser Golden-Plover *Pluvialis dominica*, Semipalmated Sandpiper *Calidris pusilla*, Pectoral Sandpiper *C. melanotos*, Dunlin *C. alpina*, Stilt Sandpiper *C. himantopus*, Buff-breasted Sandpiper *Tryngites subruficollis*, Red-necked Phalarope *Phalaropus lobatus*, Red Phalarope *P. fulicaria* and Lapland Longspur *Calcarius lapponicus*.

These ten species accounted for 92% of the approximately 4,500 nests (600 from this investigation) that we have found on study plots in the Prudhoe Bay area. The results and discussion concentrate primarily on shorebirds, but data on the King Eider and Lapland Longspur are also included in the summary tables.

Methods

Birds and nests

The results obtained from ten study plots (each measuring 100 m × 1,000 m [or 10-ha plots], for a total area of 1 km²) provided most of the information for this report. The habitat composition was not considered when these plots were originally established, except that large, deep lakes were avoided.

All the results presented herein are based on data obtained during breeding season censuses. In our sampling protocol, the breeding season comprised Census Periods 2-5 (Table 1). All plots were censused during each period (2-5; note that Census Period 1 occurs prior to most nesting activity), and an attempt was made to locate every nest that might be associated with any of the birds using the plots. To aid in nest location, a rope was dragged (50-m swaths) by two biologists in order to flush right-sitting birds during Census Periods 3 and 4. Additional visits were scheduled to monitor nests. As hatching approached, an attempt was made to visit the nests every other day.

Following the completion of monitoring, three parameters (hatching success, nest initiation date and re-nest status) were determined for each nest. A nest was considered to be successful if at least one egg hatched. Evidence used in evaluating *nest success* included (1) the length of time the nest had been active since initiation, (2) evidence of predation (broken eggs, fox scats or urine), (3) the presence of hatching eggs, chicks or egg bits (tiny fragments remaining from hatching) and (4) re-nesting attempts. If the outcome of a nest attempt could not be determined by these criteria, the reproductive success was coded as *unknown*.

The *nest initiation date* was the date the first egg was laid. This date could rarely be determined directly. If the nest was found during egg laying, the initiation date was determined by subtracting one

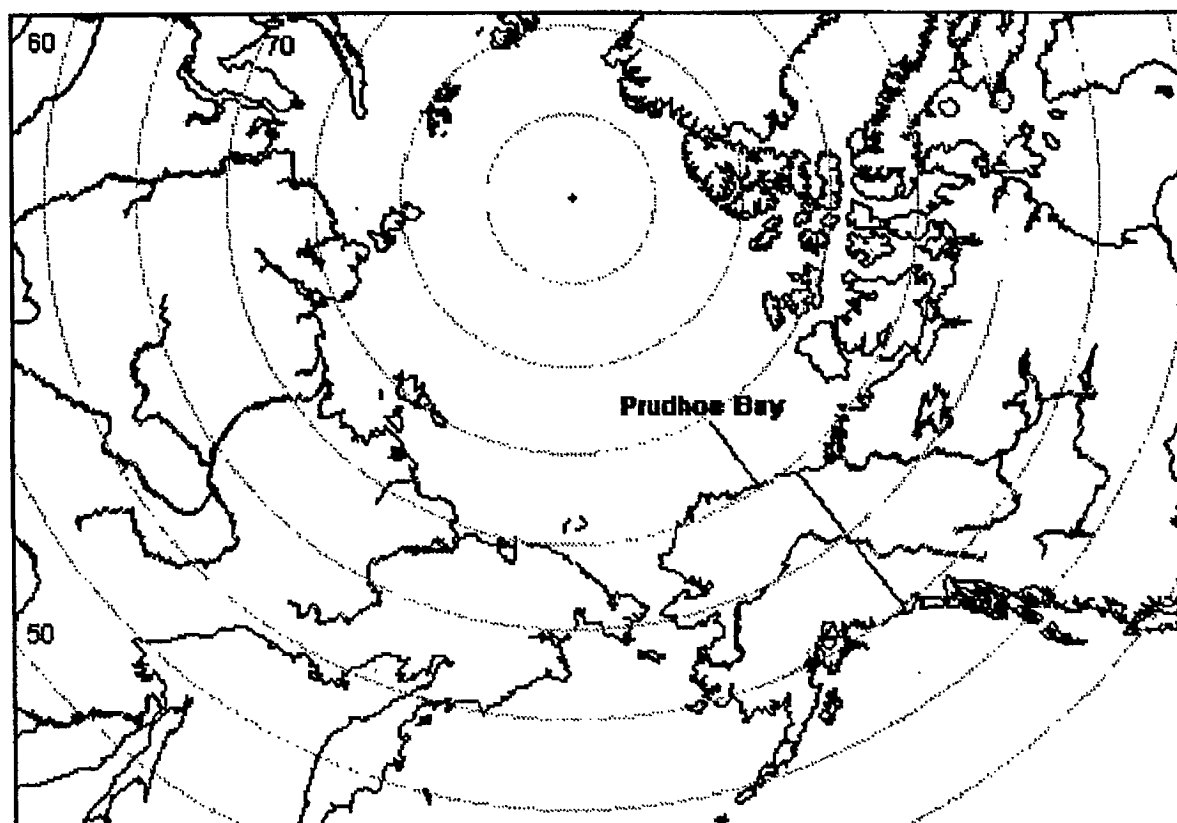


Figure 1. Polar view of the Arctic showing location of Prudhoe Bay, Alaska, where sampling for this study took place.

day for each egg back to the first egg, assuming that one egg is laid each day. For nests found during the incubation period, the date of initiation was estimated only for those having a known hatching date. The initiation date was derived by back-calculating from the hatching date and subtracting the average incubation period and the clutch size to the first egg.

A *re-nest* was a second nesting effort by a pair of birds that failed a prior attempt. A nest initiated shortly after another one failed in the same general location (within approximately 100 m) indicated re-nesting. Such nests were excluded from the analysis of densities and nest initiation dates.

Environmental measures

Temperature measurements were obtained from records at Deadhorse Flight Service Station, approximately 20 km SSW of the PMRA, where weather measurements were recorded hourly. These records were averaged to provide a daily value. Depending on the specific analyses, these data were further summarized to provide an overall measure for the breeding season as a whole (1 June – 18 July) or for particular census periods of interest. Temperature deviation, as used in the analyses, was the difference between average temperature on a given day and the average temperature for that date for the years 1981–1991

(including 1983 and 1985). Each deviation was added to yield a cumulative value that indicated the total energy input (in degree-days) up to that date (from 1 June) relative to other years. An 'average' year would have a negative value.

Starting in 1986, snow cover estimates were made during the censuses. The percentage of tundra covered in each 50 m × 50 m unit of the plots (40 estimates per plot per visit) was estimated and recorded during maintenance activities and censuses. Differences in the timing of melt among years were evaluated by comparing the percent snow cover during Census Periods 2 and 3.

Statistical analyses

The principal analytical techniques used in this report examined changes in densities of birds or nests among years. Nest densities were based on the numbers of nests found in the plots (excluding re-nests) each year. Annual densities of birds were determined by averaging the four censuses conducted during each breeding season. Changes in density over years were evaluated using the Friedman test. The sample units (ten plots) were considered to be blocks subjected to nine treatments (years). Calculations of nest initiation dates and nest success are based on information from all nests monitored in the reference area. The Kruskal-Wallis test was used to detect significant differences

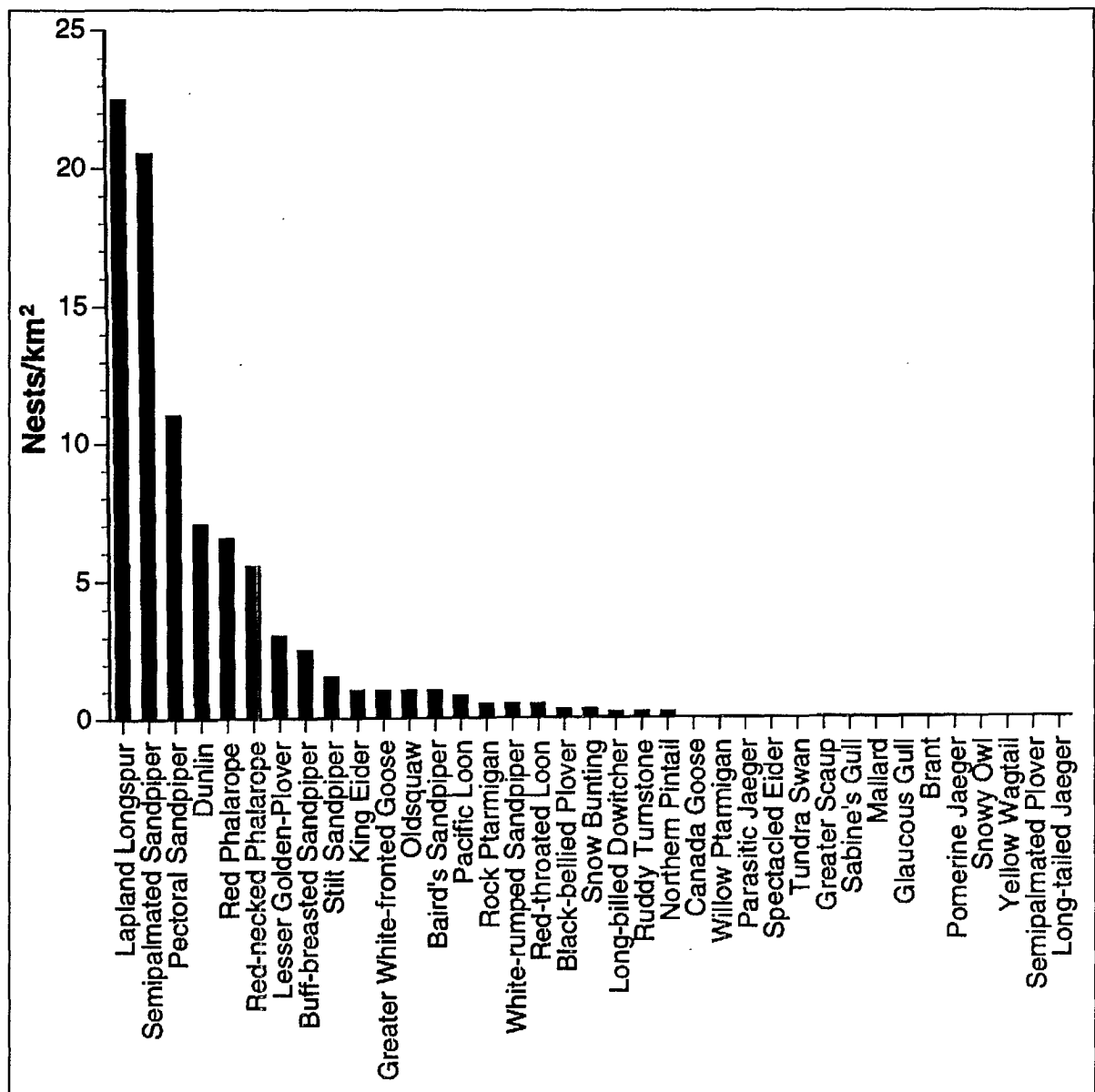


Figure 2. Species composition of the Prudhoe Bay area tundra bird community based on nests on over 200 study plots scattered throughout the region. The PMRA is the subset of these plots that received the most continuous sampling and contributed 13% of the total nests studied.

Table 1. Plot census periods for determining breeding season bird densities.

Period	Timing	Dates
2	Early June	9-13 June
3	Mid-June	14-27 June
4	Early July	28 June - 10 July
5	Mid-July	11-18 July

in nest initiation dates among years, and the χ^2 goodness-of-fit test was used to test for differences in nest success among years. Pearson correlation coefficients were used to document covariation

among measures of the environment, nest variable and measures of bird abundance.

A significance level of $p = 0.05$ was used for all tests except the screening of correlations among bird and environmental variables, where a more restrictive criterion of $p = 0.01$ was used.

Results and discussion

Nest densities

Among-year differences in nest densities were significant only for Pectoral Sandpiper and Lapland Longspur (Table 2). The Pectoral Sandpiper was the most variable species. Much of this variability

Table 2. Nest densities in Point McIntyre Reference Area, 1981–1991. Test results (probabilities) of Friedman analyses for among-year changes in nest density are listed. In all cases, the degrees of freedom for the test statistics are 8 (9 years - 1).

Species	Nest densities (no. of nests/km ²)									p
	1981	1982	1984	1986	1987	1988	1989	1990	1991	
King Eider	2	3	0	3	1	1	0	0	2	0.951
Lesser Golden-Plover	1	3	1	2	2	3	3	3	4	0.974
Semipalmated Sandpiper	12	13	12	11	10	11	15	19	10	0.237
Pectoral Sandpiper	7	1	7	4	7	9	3	33	6	0.006
Dunlin	8	8	10	3	6	5	9	10	8	0.469
Stilt Sandpiper	0	0	1	1	0	1	0	0	3	0.997
Buff-breasted Sandpiper	2	3	0	0	1	0	0	2	1	0.952
Red-necked Phalarope	0	0	0	0	0	2	1	3	2	0.938
Red Phalarope	10	9	4	3	2	5	6	11	6	0.321
Lapland Longspur	15	10	22	20	6	22	6	13	22	0.008
Totals	57	50	57	47	35	59	43	94	64	–

Table 3. Median dates of nest initiation within the Point McIntyre Reference Area. Test results (probabilities) of Kruskal-Wallis analyses for among-year changes in the median date of nest initiation are listed.

Species	Median date of nest initiation									p
	1981	1982	1984	1986	1987	1988	1989	1990	1991	
King Eider					21 June					
Lesser Golden-Plover	16 June	13 June	15 June	22 June	26 June	24 June	23 June	1 June	18 June	0.054
Semipalmated Sandpiper	15 June	21 June	11 June	18 June	14 June	15 June	22 June	4 June	14 June	0.000
Pectoral Sandpiper	15 June	29 June	16 June	23 June	24 June	24 June	15 June	8 June	17 June	0.000
Dunlin	11 June	18 June	11 June	15 June	14 June	12 June	11 June	7 June	9 June	0.003
Stilt Sandpiper			10 June		16 June		14 June	2 June	13 June	0.253
Buff-breasted Sandpiper	14 June	28 June	23 June		2 July			3 July	1 July	0.317
Red-necked Phalarope		28 June		25 June	23 June	22 June	18 June	6 June	18 June	0.160
Red Phalarope	19 June	23 June	14 June		21 June	16 June	20 June	10 June	21 June	0.002
Lapland Longspur	14 June	16 June	10 June	18 June	20 June	13 June	12 June	9 June	16 June	0.000

resulted from the exceptionally high nest density of 1990. Pectoral Sandpipers are thought to be nomadic, changing nesting areas between years for unknown reasons (Pitelka 1959). Because their regional abundances can fluctuate considerably among years, it is not unexpected that large inter-annual changes in density were recorded. The magnitude of their invasion into the Prudhoe Bay area in 1990 was of greater amplitude than any fluctuation previously experienced.

Although not showing statistically significant differences among years, several species exhibited more gradual, but regular, density shifts. The common philopatric shorebirds, such as Semipalmated Sandpiper, Dunlin and Red Phalarope, are most notable in this regard. Following the presentation of major trends in other aspects of the breeding status of these species, density fluctuations of site-tenacious species and correlations among nest densities and other measures are also discussed.

Nest initiation

Nesting is often thought to occur in a highly synchronous fashion in the Arctic. However, median nest initiation dates were found to vary considerably among species (Table 3). For example, median initiation dates in 1990 encompassed the period from 1 June to 3 July (Lesser Golden-Plover and Buff-breasted Sandpiper, respectively). Within species, there was also considerable variability as to when nest initiation occurred across years. Lesser Golden-Plovers, for example, initiated their nests 25 days earlier in 1990 than in 1987. Five species exhibited significant variability among years in the timing of nesting (Table 3).

Years promoting early or late nesting tended to affect many species in unison. Except for the Buff-breasted Sandpiper, all other species had their earliest nest initiation in 1990. Four pairs of initiation dates were significantly correlated with each other: Lesser Golden-Plover with Stilt Sandpiper ($r = 0.992$, $p = 0.001$), Pectoral Sandpiper

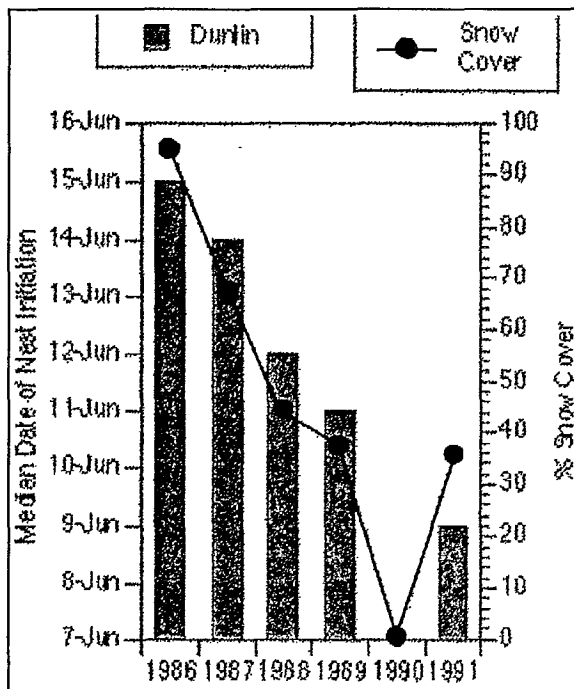


Figure 3. Trend in nest initiation dates of Dunlin in relation to percent snow cover during early (9-13) June.

with Dunlin ($r = 0.911$, $p = 0.001$), Pectoral Sandpiper with Red-necked Phalarope ($r = 0.960$, $p = 0.001$) and Dunlin with Red-necked Phalarope ($r = 0.920$, $p = 0.003$). The species in these correlations included both early- and intermediate-season nesters. The timing of nest initiation of the late-nesting Buff-breasted Sandpiper was not in synchrony with any of these species. Conspicuously absent from this group are some of the most common nesting species: Lapland Longspur, Semipalmated Sandpiper and Red Phalarope.

Snow-melt was thought to be the environmental factor of greatest potential influence on nest initiation, but the short time series of this parameter prevented as rigorous a statistical evaluation of its importance as was possible for the other environmental variables. Dunlin nest initiation data and snow cover exhibited a significant relationship ($r = 0.955$, $p = 0.003$), with initiation being late in years of delayed snow-melt (Figure 3). Most species (except the late-nesting Buff-breasted Sandpiper) had relatively high correlations between nest initiation date and snow cover, and several of these will no doubt prove statistically significant as the period of monitoring becomes longer.

Nest success

Nesting success varied both among species and among years (Table 4). Statistically significant differences among years were detected for the Semipalmated Sandpiper and the Lapland Longspur and for all species combined ($c = 38.990$,

30.592 and 54.067, respectively; $p < 0.001$ for all tests). Nest success, especially that of Semipalmated Sandpiper, was lowest in 1986. A single best year was not as evident, although both 1981 and 1988 had, overall, high nest success.

Semipalmated Sandpiper nest success was correlated with the success of all the species pooled ($r = 0.964$, $p < 0.001$; Figure 4). The significance of this correlation suggests that nest success varies (relatively) synchronously across all species. Because Semipalmated Sandpipers accounted for only 19% of the total nests monitored, there is a minor element of self-correlation; the greater proportion of the total success did not involve this species. For most species taken individually, our annual measures of nest success in the PMRA are variable owing to small samples. This correlation showed that patterns of variation in our best-monitored species were mirrored in all species combined. Variations in nest success were more or less synchronous for all species, and the measure for all species pooled best characterized conditions for a given year.

Many factors may influence nest success; these include predation (by arctic fox *Alopex lagopus*, jaegers, Glaucous Gull *Larus hyperboreus*, Common Raven *Corvus corax* and others), desertion (perhaps weather-related) and trampling by caribou. Trends in nest success were not found to be significantly correlated with any environmental or biotic variable. The largest single source of nest loss appeared to be nest predation by arctic foxes. My working hypothesis, the 'Alternative Prey Hypothesis' first advanced by Summers & Underhill (1987), is that arctic fox population levels fluctuate in response to the availability of their primary prey, which in this study are presumed to be lemmings. Following precipitous declines in lemming abundance, arctic foxes switch to alternative food sources, in particular bird nests. This leads to episodic periods of low nest success until fox populations decrease or the availability of the primary prey increases.

Breeding season populations

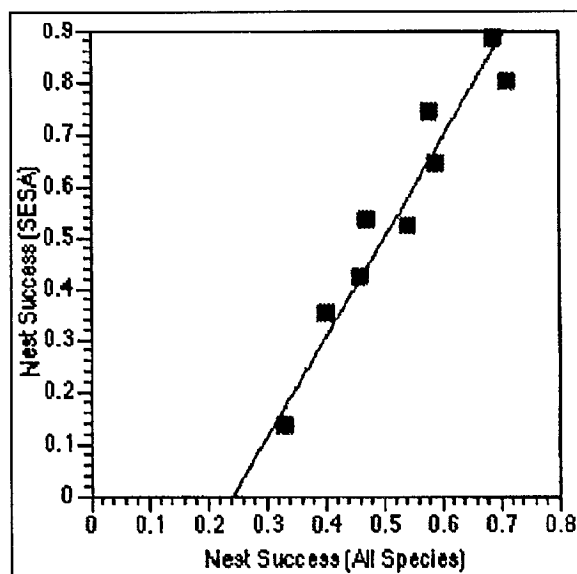
Densities

The population densities of five of the ten species under study varied significantly between years. These species were Pectoral Sandpiper, Buff-breasted Sandpiper, Red-necked Phalarope, Red Phalarope and Lapland Longspur (Table 5). The nest densities of the Pectoral Sandpiper and Lapland Longspur also varied significantly between years (Table 2), and the changes found here probably reflect changes in breeding effort.

Breeding season population densities of three species (Pectoral Sandpiper, Buff-breasted Sandpiper and Red Phalarope) were strongly correlated

Table 4. Proportion of nests hatching at least one egg in the Point McIntyre Reference Area, 1981–1991. Only species of which at least 100 nests were monitored are detailed.

Nest success	% of nests hatching ≥ 1 egg									
	1981	1982	1984	1986	1987	1988	1989	1990	1991	All years
Semipalmated Sandpiper	0.80	0.35	0.52	0.13	0.74	0.88	0.42	0.64	0.53	0.60
Pectoral Sandpiper	0.83	0.75	0.56	0.50	0.44	0.77	0.75	0.58	0.41	0.57
Dunlin	0.33	0.36	0.38	0.60	0.66	0.70	0.42	0.53	0.45	0.50
Lapland Longspur	0.90	0.41	0.56	0.51	0.72	0.67	0.31	0.66	0.61	0.59
All species	0.71	0.40	0.54	0.33	0.58	0.69	0.46	0.59	0.47	0.54

**Figure 4.** Semipalmated Sandpiper (SESA) nest success in relation to nest success over all species.

with the densities of their nests ($r = 0.937$, $p < 0.001$; $r = 0.815$, $p = 0.007$; $r = 0.983$, $p < 0.001$; respectively). Perhaps the most significant feature of these correlations is that similar relationships were not found for other species. That a relationship exists between bird densities and nest densities is often assumed in population assessments based on bird counts alone (e.g. line transects), but, as evidenced here, this may not always be a valid assumption. The only species showing this relationship were those with the most variable abundances in the Prudhoe Bay area. Two of these species, the Pectoral Sandpiper and Buff-breasted Sandpiper, are nomadic and exhibit little philopatry. The Red Phalarope, although somewhat philopatric, owes its variability to a dramatic population decrease in the mid-1980s. Both species of phalaropes decreased markedly in abundance between 1982 and 1984 (there was no sampling in 1983), corresponding to the severe El Niño that may have induced losses on the wintering grounds. None of the species exhibiting a high correlation between nest and bird densities is monogamous, and all have uniparental incubation systems. *A priori*, these species might have been expected to

have the weakest correlations between nest and bird densities, because early departure of the non-incubating birds affected census results. The importance of mating systems in these correlations is uncertain.

Most species that are philopatric, and thus have more stable numbers, showed little relationship between bird and nest densities. This lack of relationship between birds and nests of most philopatric species suggested that non-breeding birds were present in some years. This prompted the use of a non-breeding index as an analytical tool for understanding patterns of density variation in nests and birds.

The non-breeding index

The non-breeding index is defined here as the ratio of the number of birds counted during the breeding season per nest found. Ideally, this index might be expected to be close to 2 if there was an equal sex ratio, if all nests were found and if all birds were breeding. In practice, some deviation from 2 would be expected because of the overlap of migration and nesting. For example, many shorebirds commence migration prior to fledging of their young or even the hatch of their eggs. This is particularly true of species with uniparental care, such that one sex, female phalaropes for example, may be absent during some breeding season censuses. Hence, an index less than 2 might be expected. Disproportionate sampling of nesting and foraging habitats or failure to locate some nests could also contribute to departures from an index value of 2. However, within a species, the index should remain relatively stable over years if most birds were nesting. Our results revealed that non-breeding indices were not constant over years; they showed considerable variability (Table 6). In the two common monogamous species, the Semipalmated Sandpiper and the Dunlin, the minimum value of the index was 1.8; this is close to the expected value of 2 if all birds nested.

Several correlations were found involving non-breeding indices, but they were not strongly associated with any single class of measurement. Findings of potential biological significance

Table 5. Average breeding season density of birds in the Point McIntyre Reference Area. Test results (probabilities) of Friedman analyses for among-year changes in breeding season bird density are listed.

Species	No. of birds/km ²									p
	1981	1982	1984	1986	1987	1988	1989	1990	1991	
King Eider	3.8	10.5	4.3	1.3	1.8	1.5	3.3	2.0	2.25	0.158
Lesser Golden-Plover	16.5	8.8	6.3	6.0	5.5	5.3	3.3	6.3	11.0	0.106
Semipalmated Sandpiper	30.3	30.5	28.3	23.5	30.5	34.0	28.0	33.5	27.5	0.240
Pectoral Sandpiper	38.3	22.5	29.5	17.0	30.0	36.5	18.5	65.8	22.8	0.000
Dunlin	23.3	25.3	20.8	17.0	18.8	16.0	17.3	20.3	14.5	0.072
Stilt Sandpiper	0.0	0.3	1.0	2.8	2.0	2.8	3.3	2.3	1.75	0.136
Buff-breasted Sandpiper	8.8	14.0	3.8	4.3	4.3	4.3	0.5	5.8	1.25	0.001
Red-necked Phalarope	10.3	2.8	5.0	1.5	2.8	5.5	6.8	18.0	9.0	0.024
Red Phalarope	21.3	20.0	5.3	3.5	3.8	7.3	10.5	28.0	6.5	0.000
Lapland Longspur	92.5	67.3	71.3	57.0	44.0	72.5	31.3	54.5	58.5	0.000

Table 6. Yearly non-breeding index scores for the Point McIntyre Reference Area. Empty cells indicate that no nest was found that year.

Species	Non-breeding index score (no. of birds/no. of nests)								
	1981	1982	1984	1986	1987	1988	1989	1990	1991
King Eider	1.9	3.5		0.4	1.8	1.5			1.1
Lesser Golden-Plover	16.5	2.9	6.3	3.0	2.8	1.8	1.1	2.1	2.8
Semipalmated Sandpiper	2.5	2.3	2.4	2.1	3.1	3.1	1.9	1.8	2.8
Pectoral Sandpiper	5.5	22.5	4.2	4.3	4.3	4.1	6.2	2.0	3.8
Dunlin	2.9	3.2	2.1	5.7	3.1	3.2	1.9	2.0	1.8
Stilt Sandpiper			1.0	2.8		2.8			0.6
Buff-breasted Sandpiper	4.4	4.7			4.3			2.9	1.3
Red-necked Phalarope						2.8	6.8	6.0	4.5
Red Phalarope	2.1	2.2	1.3	1.2	1.9	1.5	1.8	2.6	1.1
Lapland Longspur	6.2	6.7	3.2	2.9	7.3	3.3	5.2	4.2	2.7

included the following: (1) weather appeared to be important to Semipalmated Sandpipers, because non-breeding was correlated with low temperature ($r = -0.874$, $p = 0.002$; Figure 5), (2) non-breeding by Dunlins was associated with low nest densities ($r = -0.874$, $p = 0.002$), but (3) non-breeding was associated with high breeding season bird densities for both the Lesser Golden-Plover ($r = 0.836$, $p = 0.005$) and the Red Phalarope ($r = 0.865$, $p = 0.003$).

These results indicate that reductions in nesting effort may arise from environmental factors such as temperature. However, high non-breeding scores should not always be viewed as having negative implications for breeding. In the case of the Lesser Golden-Plover and the Red Phalarope, these indices increased with breeding season bird densities and, in the case of the Red Phalarope, with nest densities (which were correlated with bird densities). In these cases, adult birds apparently made greater use of the area, perhaps for staging prior to migration.

The non-breeding indices and the presence of non-breeding birds are important for several reasons. First, they highlight the use of the Arctic

Coastal Plain by birds for purposes other than nesting. Among arctic shorebirds, the presence of non-breeding birds on the breeding grounds is rarely considered. In contrast to waterfowl, especially geese, where subadult birds return to the Arctic, even though they do not nest, non-breeding shorebirds are frequently thought to remain in their wintering ranges. Occasional sightings of non-breeding shorebirds in the Arctic have been reported during extreme conditions when nesting fails to take place. However, our results suggest that a variable proportion of non-breeding birds may be present in many years.

Second, the presence of non-breeding birds helps to explain why population densities and nesting densities are so poorly correlated for many species during the breeding season. Nest densities and population densities correlated only for those species with the greatest fluctuations in their use of the area, most notably the nomadic species, including Pectoral and Buff-breasted sandpipers. The other species, including most of the philopatric species, are predominantly represented by monogamous species. Evidently, variations in

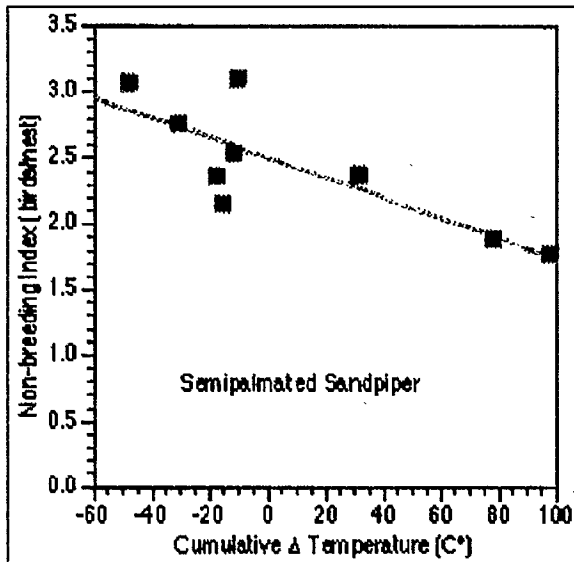


Figure 5. Semipalmated Sandpiper non-breeding index in relation to breeding season temperatures.

environmental variables can exert a considerable influence on the nesting effort of these species, resulting in a lack of synchronization between densities of birds and nests.

Variation in nest densities of North Slope shorebirds

In this section, the data series describing annual trends in nest densities is compared with trends found for other measures of nesting and environmental conditions in order to find common

patterns. Two approaches were taken. First, a specific hypothesis, that breeding density is determined by prior nest success, was investigated. Support for this hypothesis would indicate that changes in nest density reflected actual population changes, at least for philopatric species. Second, the roles of environmental conditions and non-breeding, as determinants of nesting densities, were evaluated. If fluctuations in nest density were related to weather or non-breeding, these density changes may not necessarily have had population-level implications.

Nest success as a predictor of future nest densities

The major changes in nest densities, such as those for the Pectoral Sandpiper, are the easiest to detect with statistical verification. However, additional and more subtle density changes also occur. Nest density trends of the three most common philopatric species — the Semipalmated Sandpiper, the Dunlin and the Red Phalarope — appeared to change synchronously (Figure 6). The similarities in those trends suggested that some common factor was contributing to density changes in all three species. Semipalmated Sandpipers winter in coastal South America, primarily along the coast of Suriname (Morrison & Ross 1989). Dunlin from Alaska's Arctic Coastal Plain spend the winter around the South China Sea and the Sea of Japan (MacLean & Holmes 1971). Red Phalaropes are marine birds during the winter, and those nesting in Alaska are thought to winter at sea off Peru and Chile (Marchant, Hayman & Prater 1986). Because these birds migrate to such different areas, it is

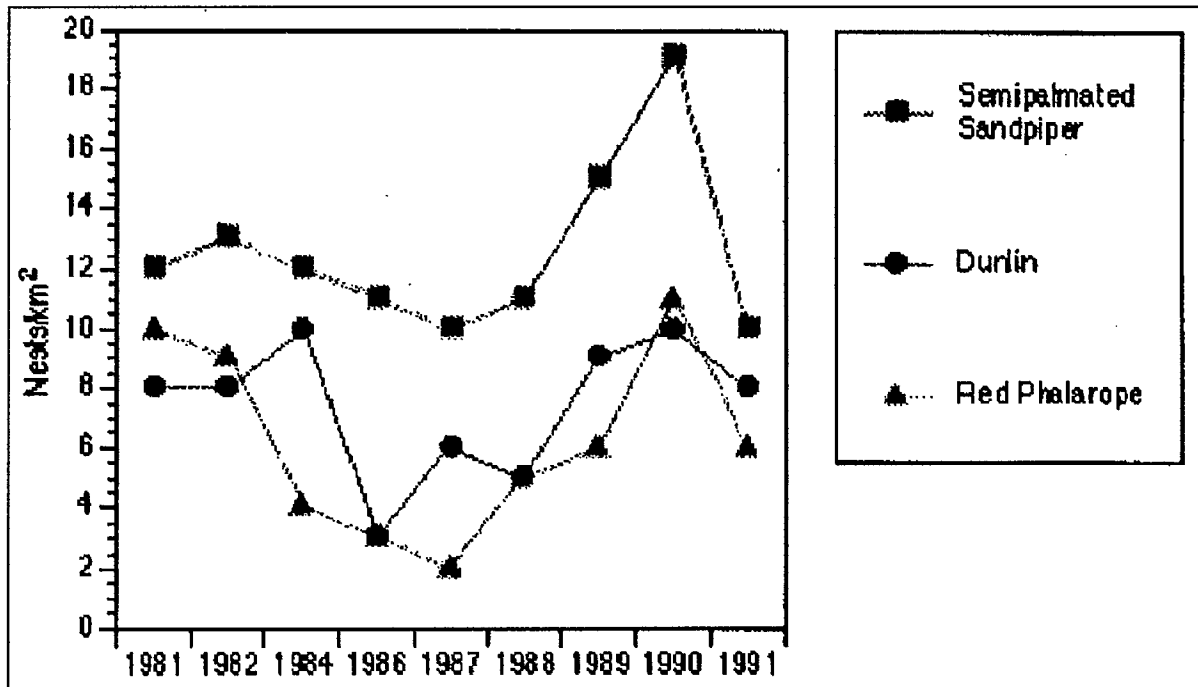


Figure 6. Trends in nest densities of the common philopatric shorebirds in the PMRA.

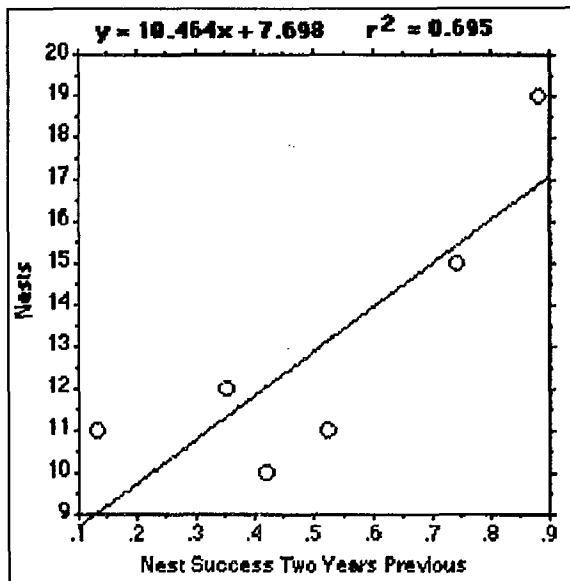


Figure 7. Results of regression of Semipalmated Sandpiper nest density on their nest success two years earlier.

unlikely that the synchronous population trends can be attributable to factors operating on the separate wintering grounds. These species occur together only on the breeding grounds; therefore, the cause for their parallel changes in abundance most likely occurs where they nest.

Recruitment appears to be a factor in determining the direction of nest density changes. Nest densities of the Semipalmated Sandpiper were significantly correlated with nest success two years earlier (Figure 7; $F_{1,4} = 0.097$, $p = 0.04$, $r = 0.833$). Dunlin and Red Phalaropes were not sufficiently numerous to provide reliable estimates of nest success for individual species. However, evidence presented earlier indicated that the trends in nest success appeared to vary in parallel across all species. If nest success is a leading indicator of nest densities, as appears to be the case, we would expect similar patterns in density fluctuations across all site-tenacious species. This was indeed the pattern that we observed. It is simplistic to expect nest densities to be entirely dependent on nest success. Realistically, nest success should (with all other things being equal) influence the direction of change but not the absolute value. The breeding population in any year (y) would depend on population size during the preceding year ($y-1$) with some allowance for mortality (m) plus recruitment of new birds into the breeding population. Recruitment would depend on the nesting population two years earlier ($y-2$) times nest success in that year to give production of young. Some allowance needs to be made for survival (s) before entering the breeding population. Additional allowances need to be made for such factors as partial non-breeding during years of adverse weather. Because of non-breeding,

nests $_{y-1}$ may underestimate the size of the breeding population, especially as population size is used to calculate the survivorship component of the model described above. Eventually, we hope to incorporate all these factors into a model of population trends. At present, nest success alone appears to explain a large amount of the annual fluctuations in nest densities.

Other shorebird populations may be regulated by nest success. Sanderling *Calidris alba*, Curlew Sandpiper *C. ferruginea* and Ruddy Turnstone *Arenaria interpres* populations wintering in South Africa follow a three-year cycle (Summers & Underhill 1987; Summers *et al.* 1987). The major component of these changes was the proportion of first-year birds (*i.e.* nest success during the preceding summer). This cycle correlated with fox and lemming abundances on the Taimyr Peninsula in Russia, where many of these shorebirds breed. Following crashes in lemming populations, the foxes apparently preyed on bird nests, thus resulting in low nest success and low proportions of young birds on the wintering grounds.

Our results agree with the hypothesis that nest success is determined by variable predation rates and that success in turn drives the rate of recruitment, which determines the size of the breeding populations of philopatric shorebirds. Field studies are now in progress to ascertain that trends in nest success in the PMRA indeed correspond with changes in microtine abundance.

Influences of environmental factors Snow

Our results have shown that nest initiation was delayed during years of persistent snow cover, especially for the Dunlin (Figure 3), as shown for this species and others in earlier studies. Meltofte (1985), in Greenland, found a strong negative correlation between Dunlin nest initiation and early June snow cover. He concluded that delayed nesting resulted from poor feeding conditions and increased risk of nest predation. Nest initiation by Greater Golden-Plovers *Pluvialis apricaria* was also influenced by snow-melt (Byrkjedal 1980). Before nesting, the birds apparently waited until a considerable amount of snow-free area was available. Significantly greater predation on artificial nests occurred early in the season, when predators (primarily red foxes *Vulpes vulpes*) could systematically search restricted snow-free areas for nests. Byrkjedal (1980) concluded that vulnerability to predation was the factor ultimately controlling the timing of nest initiation.

Temperature

Temperature, as represented by the cumulative deviation from average temperature summed over the entire breeding season, was the best environmental predictor of nest densities. In particular, the

nest density of the Semipalmated Sandpiper was positively correlated with temperature ($r = 0.906$, $p = 0.001$). A related result was that the non-breeding index of Semipalmated Sandpipers was inversely related to breeding season temperatures (Figure 5). In aggregate, these relationships suggested that fewer Semipalmated Sandpipers attempted nesting in cold years. The birds were present but not all nesting.

In an average year ($\Delta\text{temp.} = 0$), the non-breeding index is approximately 2.5 (Figure 5), which suggests that on the order of 20% of Semipalmated Sandpipers do not nest (assuming that an index of 2.0 represents complete nesting). This could be interpreted as indicating that the Prudhoe Bay area is colder than optimum for breeding Semipalmated Sandpipers. If so, higher nest densities would be expected in warmer areas. Regional comparisons are difficult, because most study areas differ more than in temperature alone. Much higher densities, approximately 50 nests/km², have been recorded from subarctic areas such as in Churchill, Manitoba (Gratto, Morrison & Cooke 1985). However, even there, Gratto-Trevor (1991) reported years when fewer than half of the Semipalmated Sandpipers present actually nested.

The numbers of non-breeding Dunlin and Semipalmated Sandpipers were examined in relation to the annual temperature summaries shown in Figure 8. As reported earlier, the incidence of non-breeding in Semipalmated Sandpipers increased in association with lower temperatures. The data for Dunlin indicated a similar relationship, the principal difference being that this species had higher non-breeding indices (especially in 1986). The Dunlin is an earlier-nesting species than the Semipalmated Sandpiper and thus may be more affected by adverse conditions such as delayed snow-melt.

The negative association between nest densities and non-breeding or weather for species such as the Semipalmated Sandpiper and Dunlin indicates that we can expect some error in our measures of both current and past population sizes based on nest densities. For the Dunlin, nest density was very low in 1986 owing to the high incidence of non-breeders. These birds were still part of the population in 1987 and allowed for an apparent increase in nest density greater than might have been predicted based on recruitment alone.

Environmental factors appeared to have a pronounced influence on some measures of nesting. Our data suggest that temperature was the best predictor of variability in breeding biology for a given year; however, the timing of snow-melt also appeared to be important. These environmental factors are related (as snow tends to melt earlier when temperatures are above average), but the

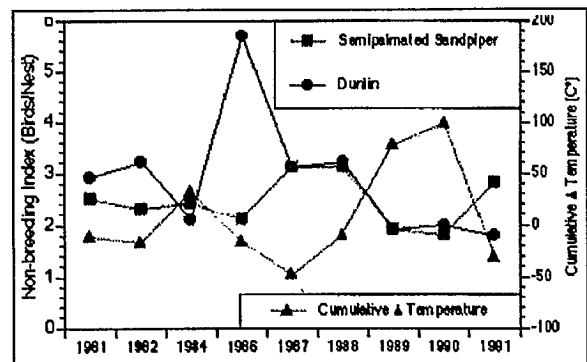


Figure 8. Trends in non-breeding indices of Semipalmated Sandpiper and Dunlin and of annual cumulative temperature deviations (1 June - 18 July).

analyses indicated that the shorebird population data correlated better with temperature over the entire breeding season than with temperature up to when most of the snow had melted (end of Census Period 2). Therefore, the influence of temperature appears to extend beyond its role in snow-melt. Environmental conditions exerted their greatest influence on the timing of nest initiation and the related measure of non-breeding (the ultimate in delayed initiation) as measured by the non-breeding index. Under conditions that we would expect to be adverse, *i.e.* delayed snow-melt or cold temperatures, nesting is delayed or not attempted.

Other correlates of nest density

Several correlations were found between nest densities and variables other than environmental measures. Predominant in these relationships were correlations involving Pectoral Sandpiper nest densities. The numbers of Pectoral Sandpipers have long been known to vary markedly from year to year at breeding locations (Pitelka 1959), but explanations for this variation have been elusive. The nest density of the Pectoral Sandpiper was highly correlated with four measurements describing tundra bird breeding biology: Semipalmated Sandpiper nest initiation, Red Phalarope nest initiation, Pectoral Sandpiper density and Red-necked Phalarope density.

Two correlations involved nest initiation. High nest densities of Pectoral Sandpipers corresponded to years of early nesting by Semipalmated Sandpipers and Red Phalaropes. Two independent correlations with nest initiation suggested that the conditions favourable for early nesting also favoured settling by Pectoral Sandpipers. Of interest are the species involved in these correlations. Besides the Pectoral Sandpiper, four species were common breeding birds in the PMRA: the Dunlin, the Semipalmated Sandpiper, the Red Phalarope and the Lapland Longspur. The Dunlin and the Lapland Longspur are early-nesting species whose nest initiations appear to be strongly influenced by the timing of snow-melt. The Semipalmated Sandpiper and the

Red Phalarope, along with the Pectoral Sandpiper, are mid-season nesters. Nesting of these species is not as affected by snow-melt and, in the case of the Semipalmated Sandpiper, appears to be influenced by temperature. The abundance of nesting Pectoral Sandpipers appears to be related to whatever regulates the timing of these mid-season nesters. In all cases, the relationship was greatly influenced by the outlying data point corresponding to the high 1990 nest density, but the same general trends appeared to be present even when that data point was excluded.

Summary

In summary, several interesting associations between nest densities and other measures were detected. Correlations involving environmental measures were infrequently detected directly; only the correlation between the Semipalmated Sandpiper and temperature met our criterion for statistical significance. Species having the greatest among-year variability in nest densities, especially nomadic species such as the Pectoral Sandpiper, were found to have significant correlations between bird and nest densities. This was not found for other species. The lack of correlation implies that nest and bird densities were out of synchrony, with the only possible conclusion that some birds that were not associated with nests were present. The non-breeding index, a measure of surplus birds, was found to vary inversely with nest densities of the early-nesting Dunlin, indicating that there were excess non-breeding birds during years of low nesting densities. This excess probably accounted for the rapid rebounds we recorded after years of nesting depressions. Reductions in nesting effort appeared to be related to environmental factors: low temperatures in the case of the Semipalmated Sandpiper and persistent snow cover for the Dunlin. Although the factor or factors that induced high nesting densities of Pectoral Sandpipers remain unknown, high nest densities of this species were correlated with early nesting in the Semipalmated Sandpiper and the Red Phalarope, two other species characterized by mid-season nest initiation dates.

Conclusions

Arctic shorebirds are sometimes characterized as having two breeding strategies (Pitelka, Holmes & MacLean 1974). One group comprises *conservative* species, such as Semipalmated Sandpiper and Dunlin, which have stable breeding densities, with breeding birds spaced relatively uniformly so that the birds can expect to find the resources they need within their 'territories'. The second group includes *opportunistic* species, such as Pectoral Sandpiper, which are nomadic and alter their local abundances markedly in response to changing environmental conditions. Our results supported a general dichotomy of philopatric versus nomadic species

but otherwise indicated that the breeding biology of these tundra birds is somewhat more complicated. Our results showed that the nesting populations of conservative species were much more variable than has been previously reported. Indications are that these species do not regulate their densities by spacing behaviour but rather that these populations are perpetually recovering from population depression caused by poor recruitment. The magnitudes of the population fluctuations are significant — on the order of two- to three-fold — although the densities of these species are still much more stable than those of the nomadic species.

Environmental conditions were also found to be important in the population dynamics of tundra birds. The most important role was in causing birds to forego breeding during years of adverse conditions. Our results indicated a much greater degree and regularity of non-breeding in arctic shorebirds than has been previously reported. Snow cover and temperatures appeared to be important environmental conditions influencing the incidence of nesting. The abundance of nomadic species appeared to be related to conditions that promoted early nesting.

In summary, our preliminary findings indicate that populations of philopatric shorebirds were regulated by recruitment, with episodic years of intense nest predation followed, two years later, by population depressions due to low recruitment. The trends predicted by this relationship are moderated by the influences of environmental conditions that discourage a variable proportion of the breeding population from attempting to nest each year.

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The status of Alaska's large shorebirds: a review and an example

Brian J. McCaffery

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Western Alaska supports five breeding species of large sandpipers (*Numenius* and *Limosa*). Three of these, Hudsonian Godwits *L. haemastica*, Marbled Godwits *L. fedoa* and Whimbrels *N. phaeopus*, winter in the Western Hemisphere. Breeding distributions and breeding biology of these forms are poorly known, and details on their staging grounds, migration routes and wintering grounds are fragmentary. A population of Whimbrels in western Alaska exhibited low breeding density, site fidelity and fledging success in 1988–1990. Reproduction was particularly poor in 1990. Hypotheses to explain the reproductive failure cannot be evaluated, nor can the geographical scale of the decline be ascertained from existing data. The decline at this one site may not be symptomatic of a more general trend. These uncertainties highlight the low priority given to the study of large sandpipers.

La region oeste de Alaska aloja 5 especies reproductoras de aves playeras grandes (*Numenius* y *Limosa*). Tres de estas: la limosa ornamentada *L. haemastica*, la limosa canela *L. fedoa* y el zarapito cabezirrayado *N. phaeopus* pasan el invierno en el hemisferio occidental. Se conoce poco respecto a las distribuciones y la biología de la reproducción de estas formas y se tienen conocimientos parciales respecto a los terrenos de estancia, rutas de migración y terrenos de invernación. Una población de zarapitos cabezirrayados en Alaska occidental exhibió una densidad reproductora baja, fidelidad al sitio y éxito en la crianza en el periodo 1988–1990. La reproducción fue particularmente baja en 1990. A partir de los datos existentes no se pueden evaluar las hipótesis para explicar al fracaso reproductivo, ni tampoco se puede calcular la escala geográfica del descenso. El descenso demográfico en este sitio puede no ser sintomático de una tendencia más general. Estas incertidumbres indican el bajo nivel de prioridad otorgado al estudio de las aves playeras grandes.

On trouve dans la partie occidentale de l'Alaska cinq espèces de barges et de courlis nicheurs (des genres *Numenius* et *Limosa*), dont trois, la Barge hudsonienne *Limosa haemastica*, la Barge marbrée *L. fedoa* et le Courlis corlieu *Numenius phaeopus*, hivernent dans l'hémisphère occidental. Les aires de nidification et la biologie de la reproduction de ces formes sont mal connues et les données sur les aires de repos et d'hivernage et les voies migratoires sont fragmentaires. Une population de Courlis corlieu de la partie occidentale de l'Alaska examinée entre 1988 et 1990 présentait une faible densité de reproduction, une fidélité au site et un succès d'envol. La reproduction a été particulièrement faible en 1990. On ne peut évaluer les hypothèses visant à expliquer l'échec de la reproduction ni l'ampleur spatiale du déclin à partir des données existantes. Le déclin observé à cet endroit n'est pas nécessairement le signe d'une tendance plus générale. Ces incertitudes révèlent la faible priorité accordée à l'étude des courlis et des barges.

US Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, PO Box 346, Bethel, Alaska 99559, USA.

Introduction

Five species of large shorebirds nest in western Alaska: Whimbrel *Numenius phaeopus*, Bristle-thighed Curlew *N. tahitiensis*, Hudsonian Godwit *Limosa haemastica*, Bar-tailed Godwit *L. lapponica* and Marbled Godwit *L. fedoa* (Gabrielson & Lincoln 1959; Kessel & Gibson 1978; Gibson & Kessel 1989; Kessel 1989). Our knowledge of the habitats, migration routes and geographical areas used by these species in Alaska during their annual cycle is extremely fragmentary compared with that for smaller shorebird species in Alaska (Holmes 1966, 1971; Senner 1979).

Hudsonian Godwits, Marbled Godwits and Whimbrels breed in Alaska and winter in the Western Hemisphere (American Ornithologists' Union 1983), but we lack basic information on their life histories, distributions and population dynamics. With few exceptions (e.g. Hagar 1966; Skeel 1983), the same can be said of most populations breeding in Canada. In this paper, I review knowledge of the Alaskan populations of these species through the year and describe a recent reproductive failure in a local Alaskan Whimbrel population. Large shorebirds in the Western Hemisphere should receive much more attention

than they currently do from shorebird biologists and wildlife managers.

The status of Alaska's large shorebirds

Hudsonian Godwits

Hudsonian Godwits breed around Cook Inlet in south-central Alaska (Williamson & Smith 1964) and probably in western Alaska (Kessel & Gibson 1978; Kessel 1989; B. McCaffery, unpubl. data). The maximum spring count at Alaskan staging areas is 204 birds. Recent (1992) sightings of up to a thousand post-breeding birds at a single site on Cook Inlet (G. Balogh, pers. commun.) suggest an Alaskan population in the low thousands.

Breeding birds arrive in Alaska nearly a month earlier than breeding birds at Churchill, suggesting a different migration route (Kessel & Gibson 1978) and perhaps a discrete wintering area. The large population on Chiloe Island off Chile's west coast (Morrison & Ross 1989) may include Alaskan breeders, but this is speculation.

Marbled Godwit

The race *L. fedoa beringiae* apparently nests only on the Alaska Peninsula (Gibson & Kessel 1989), along 30–40 km of coastal tundra between Ugashik Bay and Cinder River and perhaps 60 km west to Port Heiden. Its breeding biology has not been studied, and the breeding population size, evidently very small, is unknown.

In winter, a few Marbled Godwits are found on the coast of Washington and Oregon, but most members of this race occur on the coast of California north of San Francisco Bay (Gibson & Kessel 1989). Between 5,000 and 10,000 Marbled Godwits overwinter within the range known for this form (LeBaron 1991), but many may be of other races.

Whimbrel

In Alaska, the broad outlines of the Whimbrel's breeding range and the major fall staging areas are fairly well known (Gabrielson & Lincoln 1959; Handel & Dau 1988). The fall population may exceed 10,000, but there are no data linking specific breeding populations with particular staging areas.

Wintering Whimbrels on the Pacific coast of Latin America may include Alaskan birds, but this has not been confirmed. The small numbers of this race wintering in New Zealand (Pratt, Bruner & Berrett 1987) might also originate in Alaska.

Case study: a Whimbrel population decline

Study site and methods

During a study of Bristle-thighed Curlews, data on breeding Whimbrels were collected in 1987–1991 on the Yukon Delta National Wildlife Refuge, Alaska. The habitat mosaic included dwarf shrub meadows on flat or gently sloping mesic terrain, dwarf shrub mat along ridgelines and steep xeric slopes and shrub thickets on steep moist slopes and drainages (Kessel 1979). Whimbrels occupied both dwarf shrub habitats, which were characterized by an abundance of berry-producing shrubs. Overwintered berry densities reached 200,000/ha in late spring, and crowberries *Empetrum nigrum* alone accounted for 80% of this total (B. McCaffery, unpubl. data).

Data on nesting phenology, nest density, clutch size and reproductive success were collected near the Archuelinguk River (62°16'N, 162°30'W) on 26 May – 13 July 1987. In 1988–1990, similar data were collected at Curlew Lake (62°22'N, 163°30'W) from early May to mid-July for Whimbrels, as well as for Pacific Golden-Plovers *Pluvialis fulva*, Bristle-thighed Curlews and Long-tailed Jaegers *Stercorarius longicaudus*. In 1991, breeding densities for these four species were determined during 5–30 May.

In 1988, four adult Whimbrels and eight adult Bristle-thighed Curlews were captured and colour-banded to assess breeding site fidelity in subsequent seasons. In 1989 and 1990, faeces deposited by foraging *Numenius* were collected when defecation was observed; *Numenius* faeces not assignable to species were ignored. Each sample was analysed for the presence of invertebrate fragments, fruit parts and *E. nigrum* seeds and was classified as consisting primarily (>50%) of either invertebrate fragments or fruit remains (excluding seeds). Although some studies have determined the percentage of several categories in faecal remains to the nearest 10% (e.g. Herrera & Jordano 1981), I was not confident in my ability to achieve this level of resolution. Chi-squared contingency tables using SPSSPC+ (SPSS 1988) were used to assess interspecific and interannual differences in faecal contents. The alpha level for tests of significance was 0.05.

Results

Nesting density, site fidelity and reproductive success

In 1988–1991, the mean number of Whimbrel breeding pairs in a 5-km² area was 5 (Table 1). Bristle-thighed Curlews occurred at slightly higher mean densities (Table 2). Six of eight Bristle-thighed Curlews banded in 1988 returned as

Table 1. Whimbrel productivity in 5-km² Curlew Lake study area, 1988–1991.

	1988	1989	1990	1990 ^a	1991
Nests	8	6	2	5	4
Nests hatched ^b	6	4	2	3	— ^c
Eggs	26	22	6	18	— ^c
Eggs hatched	19	14	6	7	— ^c

^a Totals from expanded 9-km² area.

^b Hatched nest = ≥1 egg hatched.

^c Data not collected.

Table 2. Number of breeding pairs of Pacific Golden-Plovers, Bristle-thighed Curlews and Long-tailed Jaegers in Curlew Lake study area, 1988–1991^a.

Species	1988	1989	1990	1991	Mean
Pacific Golden-Plover	7	8	4	5	6.0
Bristle-thighed Curlew	6	5	6	6	5.8
Long-tailed Jaeger	4	5	3	6	4.5

^a The area searched for Bristle-thighed Curlews was 7.5 km². Approximately 9.0 km² were searched for Pacific Golden-Plovers and Long-tailed Jaegers.

breeders in 1990, whereas none of four Whimbrels did.

Approximately two-thirds of Whimbrel nests reached the hatching stage (68% observed, 66% calculated; Mayfield 1975), and 61% of the eggs hatched. However, no more than 3 of 24 nests fledged young, and I confirmed fledging (1 young) in only one instance.

The 1990 reproductive failure

Pairs were seen within 2 days of the first aerial displays by territorial males in all years, and the first nests were initiated 9, 12 and 14 days following the birds' arrival in 1988, 1989 and 1990, respectively. Mean initiation dates were 12, 15 and 20 days after arrival, respectively. Thus, nest initiation was later in 1990, although snow-melt and plant leaf-out in 1990 were comparable to those in 1988 and earlier than those in 1989.

Only two nests were initiated in the study area in 1990 (Table 1). Both had only three eggs, whereas all other complete clutches ($n = 17$) had four eggs. A search of an additional 4 km² adjacent to the main study area in 1990 located three more nests.

The percentage of eggs hatching averaged 69% in 1988 and 1989 but fell to 39% in 1990 (Table 1). All eggs hatched in both three-egg clutches in 1990, but two of the four-egg clutches in the supplementary area were depredated. At the third nest with four eggs, only one egg hatched. Of the other three eggs, one was soft and unpigmented, and the adults

attempted to remove it from the nest. Another egg disappeared, and the third was found, cracked and empty, outside of the nest.

Faecal analysis

Seven and 21 Whimbrel faeces were collected in 1989 and 1990, respectively. Four of the 1990 samples were collected earlier than any in 1989; these were excluded from the analysis. Sixty-five and 37 Bristle-thighed Curlew faeces were analysed in the two years, respectively. Overall, 100% of Whimbrel faeces included fruit parts, and 82% included invertebrate remains. For Bristle-thighed Curlews, 97% contained fruit parts, and 60% had invertebrate remains.

The relative contribution of these dietary components varied between the two years for both species. The proportions of Whimbrel and Bristle-thighed Curlew faeces composed primarily of invertebrate remains declined significantly in 1990 ($\chi^2 = 8.80$ and 6.095 , $p = 0.003$ and 0.0136 , respectively). Similarly, the proportions of faeces containing crowberry seeds increased significantly in 1990 for both Whimbrel ($\chi^2 = 11.31$, $p = 0.0008$) and Bristle-thighed Curlews ($\chi^2 = 3.94$, $p = 0.0470$). The data suggested that Whimbrels selected invertebrates more often and berries less often than did Bristle-thighed Curlews.

Significantly fewer Whimbrel faeces were dominated by berries in 1989 ($\chi^2 = 22.38$, $p < 0.0001$), and more included invertebrates in 1990 ($\chi^2 = 4.62$, $p = 0.0315$).

Breeding status of co-occurring species

Like Whimbrels, the breeding densities of Pacific Golden-Plovers and Long-tailed Jaegers reached their four-year low in 1990 (Table 2), and mean clutch size for Long-tailed Jaegers fell from 1.8 in 1988 ($n = 4$) and 1.6 in 1989 ($n = 5$) to 1.0 in 1990 ($n = 3$). Among the four breeding charadriiforms at Curlew Lake, only Bristle-thighed Curlews did not exhibit lower numbers in 1990 (Table 2).

Discussion

The breeding density of Whimbrels at Curlew Lake was an order of magnitude lower than in 'good' habitat at Churchill, Manitoba (11 pairs/km²) and only 20–25% of nesting densities in 'poor' habitat there (Skeel 1983). Breeding densities in Shetland were even higher, up to 21 pairs/km² (Grant 1991). At Curlew Lake, Whimbrel breeding site fidelity was markedly lower than that for Bristle-thighed Curlews, as well as lower than that for Whimbrels in both Manitoba (Skeel 1983) and Shetland (Grant 1991). Whimbrel nest success at Curlew Lake was intermediate between that for Whimbrels in good and poor habitat, respectively, at Churchill (Skeel 1983) and not significantly different from either.

Egg hatching success at Curlew Lake was similar to that determined in Shetland (Grant 1991), but fewer than 13% of breeding pairs fledged young. Even if all potentially successful pairs fledged the maximum number of young, fledging success of the Curlew Lake study population was no more than half that of Whimbrels in Shetland (Grant 1991).

Whimbrel reproduction in 1990 stood out as particularly poor. Nesting was delayed, nesting density was lower, clutches of fewer than four eggs were detected for the first time and the percentage of eggs hatching declined. Why did the reproductive failure occur in 1990? Factors operating on or away from the breeding grounds, or both, could have been responsible.

Factors on the breeding grounds

Evans & Pienkowski (1984) suggested weather and predation as the most important factors limiting shorebird productivity. However, at Curlew Lake, weather was decidedly mild in 1990. Relative to other years, predation pressure was also low. The 1990 breeding season was the only year in which Common Ravens *Corvus corax* did not nest near the study area, where adult ravens with dependent young had been the most serious predator of *Numenius* eggs and young (B. McCaffery, unpubl. data).

Whimbrels may have fared poorly in 1990 owing to a decline in the availability of invertebrate prey. Both Whimbrels and Bristle-thighed Curlews appeared to consume fewer arthropods in 1990. This was not a response to an increase in alternative foods (*i.e.* berries), as overwintered fruit abundance did not increase between 1989 and 1990 (B. McCaffery, unpubl. data).

Pacific Golden-Plovers and Long-tailed Jaegers are primarily insectivorous at Curlew Lake, and both also declined in 1990. Only Bristle-thighed Curlews did not decline in 1990, perhaps owing to their greater reliance on berries.

Neither the availability of invertebrate prey nor those foraging behaviours correlated with variation in food abundance (*e.g.* Hutto 1990) were quantified, and the sample sizes of faeces were very small. Thus, although the pieces of the puzzle are consistent with the food limitation hypothesis, the analytical rigour required for confident inference is clearly lacking.

Factors away from the breeding grounds

The soft, unpigmented egg and the cracked empty egg were the only evidence implicating chemical contamination, the source of which must be away from the breeding grounds, as Curlew Lake is both a designated and a *de facto* wilderness. If factors outside of Alaska are responsible, declines at

wintering sites may be detected. However, we do not know where these Alaskan birds winter.

There are very few long-term trend data for any wintering Whimbrel populations. The International Shorebird Survey (ISS) detected a statistically significant decline in Whimbrels along the Atlantic coast between 1972 and 1983 (Howe, Geissler & Harrington 1989). However, that survey sampled migrants, presumably from different breeding areas and possibly destined for different wintering areas, which precludes the detection of population trends at any geographic scale below the flyway. In addition, the ISS Whimbrel sample size was small, leading the authors to question the biological significance of the decline (Howe, Geissler & Harrington 1989).

Christmas Bird Count data provide some information on the Whimbrels that winter in North America, but these are only a small fraction of the total, as most Whimbrels winter in Middle and South America (American Ornithologists' Union 1983; Morrison & Ross 1989).

Conclusions

Although the size and productivity of the breeding Whimbrel population at Curlew Lake declined between 1988 and 1990, the data gathered there preclude conclusions regarding causation. It is impossible to assess the relative significance of the local decline at Curlew Lake, which might be merely a local phenomenon rather than revealing a wider trend.

This example illustrates how little we know about our large shorebird populations. North American species of the genera *Numenius* and *Limosa* should receive more attention than at present from both shorebird biologists and wildlife managers. Increased banding and monitoring of large shorebirds at sites with concentrations in Alaska will be helpful for determining the migration routes and wintering distributions of birds that breed or stage in Alaska. Potential sites for monitoring include Humboldt Bay and the Eel River mouth in California for Marbled Godwits, the Bay of Panama for Whimbrels and Chiloe Island in Chile for both Whimbrels and Hudsonian Godwits.

We also need better information on the breeding distribution and breeding biology of all three species in Alaska. Additional surveys and the accumulation of natural history information are imperative but scarcely adequate for managing these (or any other) wildlife populations responsibly (Nichols 1991). We need to move beyond descriptive studies and begin testing hypotheses to explain the behaviour, ecology and population dynamics of large shorebirds. Such

rigour will challenge biologists' ability to design studies and especially to obtain adequate sample sizes, because these species occur at relatively low densities. These studies will require a level of funding previously unavailable to most shorebird researchers.

Finally, an assessment of critical sites for possible inclusion in the Western Hemisphere Shorebird Reserve Network is required. Few designated reserves support, or were designated because of, large numbers of *Numenius* and *Limosa*.

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Protection of shorebirds and their habitats on Alaska's North Slope

Michelle Gilders

Gilders, M. 1996. Protection of shorebirds and their habitats on Alaska's North Slope. *International Wader Studies* 8: 33.

BP Exploration (Alaska) Inc., PO Box 196612, 900 E. Benson Blvd, Anchorage, Alaska 99519-6612, USA.

To minimize environmental effects on tundra wildlife and habitat, oil exploration activities on the North Slope of Alaska are conducted during the winter, using ice pads and ice roads. However, the construction of gravel roads and pads needed to support the infrastructure of the oilfields results in unavoidable alterations to local habitats. These include the impoundment of water along roads and possible disturbance effects from humans, vehicles and noise. Gravel 'habitats' created in the five currently producing fields (Prudhoe Bay, Kuparuk, Milne Point, Endicott and Lisburne) now cover 2,660 ha, or 0.0001% of approximately 23 million hectares in the North Slope region classified as wetlands. By examining the changes associated with site development, it is possible to evaluate their effects on individual species.

In intensive studies of shorebirds in the Prudhoe Bay oilfield in 1986, D. Troy (unpubl. data) reported the same species that would be expected to occur in undeveloped regions: Semipalmated Sandpiper *Calidris pusilla*, Pectoral Sandpiper *C. melanotos*, Dunlin *C. alpina*, Stilt Sandpiper *C. himantopus*, Long-billed Dowitcher *Limnodromus scolopaceus*, Red-necked Phalarope *Phalaropus lobatus* and Red Phalarope *P. fulicaria*. He found no changes owing to fragmentation of habitat, although the use of areas near roads was somewhat affected by altered habitat. In narrow corridors along the roads, the density of some species was reduced, but this had no detectable population effect.

D. Troy and T.A. Carpenter (unpubl. data) mapped nest sites at the new production pad location in 1988, before the production pad was built. The principal species of interest were Semipalmated and Pectoral sandpipers, Dunlin and Buff-breasted Sandpiper *Tryngites subruficollis*. Nest success of

birds displaced was similar to that of undisturbed individuals. Baird's Sandpiper *C. bairdii*, absent before construction, nested in altered habitats in 1989. On a population basis, effects from gravel displacement and pipeline construction were limited and probably transitory.

D. Troy also examined bird use of abandoned peat roads, which were built in the 1960s and are susceptible to thermal subsidence (now all roads rest on gravel, to insulate the permafrost layer). He found that shorebird densities were often higher and more stable than in undisturbed areas and that some species appeared to prefer disturbed sites. The increased diversity of terrain, resulting from the peat roads and subsequent thermokarst, was attractive to birds, as it provided a variety of habitats for foraging and nesting that are unavailable or relatively rare in undisturbed areas.

Another study found that more shorebird species (and individuals) used abandoned gravel pads for feeding and resting than used undisturbed tundra or river-bar sites; these pads also created nesting habitat for Baird's Sandpipers. Impoundment areas with the emergent grass *Arctophila fulva* were particularly attractive to Red Phalaropes. These impoundments appear to be highly productive, particularly with respect to chironomids, and thus may represent significant habitat for shorebirds.

These studies demonstrated that the presence of oilfield structures and activities changes the local boundaries of available habitats but has no discernible effect on the regional population levels of shorebirds. Shorebirds use habitats within operational oilfields, and their numbers fluctuate within the bounds of natural variability.

Recruitment and the role of reconnaissance in Spotted Sandpipers

Lewis W. Oring & J. Michael Reed

Oring, L.W. & Reed, J.M. 1996. Recruitment and the role of reconnaissance in Spotted Sandpipers. *International Wader Studies* 8: 34.

Ecology, Evolution, and Conservation Biology Program, RWF, 1000 Valley Rd, University of Nevada, Reno, Nevada 89512, USA.

One critical issue in population dynamics is understanding factors affecting immigration to particular populations. We addressed this issue for a subset of immigrants in a population of polyandrous Spotted Sandpipers *Actitis macularia*. Data were collected from 1974 to 1990 for a population in northern Minnesota, USA. After peak arrival of breeding birds, and before peak departure at the end of the breeding season, there were many short-term visitors (transients) (present for <4 days) to the study site. Many of these transients returned the subsequent year to breed. We used step-wise discriminant function analysis (DFA) to determine the importance of absolute sex ratio (males/female), sex of the transient bird, number of nests and number of breeding males and females, during the week of visit, in predicting whether or not a visiting bird would return the following year. In addition, we used multiple regression to determine how much variability in the number of transient birds returning in subsequent years could be explained by annual values, during the year of transience, for numbers of breeding males and females, numbers of eggs laid and hatched and absolute sex ratio.

The DFA showed that transient females returned more often than transient males and that the number of transients returning in subsequent years was positively associated with the absolute sex ratio (males/female) during the week visited. When the sexes were analysed separately, none of the weekly variables significantly discriminated female return, but sex ratio was positively associated with male return. However, low male return rates diminish the significance of this result.

Regression showed that the number of transient birds returning in subsequent years was positively associated with the number of male breeders at our study site during the year a bird visited. Per cent return the year following transience was positively associated with the number of eggs laid at our study site during the year a bird visited. When females were analysed separately, the higher the number of male breeders during the year a bird visited, the greater the number of female transients returning in subsequent years.

Annual recruitment of foreign adults ranged from 1 to 20 birds, of which 0–56% were seen visiting in previous years. Female recruits were more likely than males to have been observed previously as transients. Twenty-two chicks hatched at our study site returned and bred for the first time more than one year after hatching. Of these, nine (41%) were seen as transients between the year of hatch and breeding.

Based on our results, we suggest that transient birds were searching for better breeding areas for future breeding and that intrasexual competition in this polyandrous species made this information more important to females than to males. The behavioural conspecific attraction exhibited by adults would result in large populations increasing; small populations, then, would have reduced immigration. Reconnaissance for future breeding sites and conspecific attraction could be important aspects of local population dynamics for other species, as well.

Local and regional differences in habitat utilization by Dunlins *Calidris alpina* as revealed by radio-telemetry: conservation implications

Nils Warnock

Warnock, N. 1996. Local and regional differences in habitat utilization by Dunlins *Calidris alpina* as revealed by radio-telemetry: conservation implications. *International Wader Studies* 8: 35–38.

In northern California (USA), radio-tagged Dunlins demonstrated differences in habitat utilization on both local and regional levels. Causes for these differences may include temporal variability in availability of feeding and roosting habitat owing to changing tide levels or differing degrees of physical isolation of lagoons where Dunlins winter. Other factors, such as disturbance, predation and individual preference, may also contribute to the differences observed but are not discussed in this paper. The conservation of suitable wintering habitat for Dunlins and other shorebirds requires site-specific information on movement patterns of populations of birds. The use of radio-telemetry is one way to begin to gather these types of data.

En el norte de California, EUA, las observaciones de alondras de mar a las que se habian colocado indicadores radioactivos indicaron diferencias en la utilizacion del habitat, tanto a nivel local como regional. Esas deferencias podrian obedecer a varias causas, tales como la variabilidad temporal en la disponibilidad de los habitats en que se alimentan y anidan debido a variaciones en los niveles de las mareas, o los diferentes grados de aislamiento fisico de las laguna en que inviernan las alondras de mar. Otros factores que pueden contribuir tambien a las deferencias observadas, tales como las perturbaciones, la depredacion y las preferencias individuales no se examinan en este articulo. La conservacion de los habitats apropiados para la invernacion de las alondras de mare y ontras aves de ribera requiere informacion acerca de los patrones de desplazamiento de las poblaciones de aves en sitios especificos. El empleo de la radiotelemetria es un primer paso para comenzar a obtener esos tipos de datos.

Dans le nord de la Californie, l'étude de Bécasseaux variables munis de radio-émetteurs a révélé des différences d'utilisation des habitats tant à l'échelle locale qu'à l'échelle régionale. Ces différences pourraient s'expliquer par la variabilité temporelle des habitats d'alimentation et de repos disponibles selon les mouvements de la marée ou le degré variable d'isolement des lagunes où ils hivernent. D'autres facteurs, dont il n'est pas question ici — perturbations, prédation et préférences individuelles — peuvent aussi expliquer les différences observées. Pour assurer la conservation des habitats d'hivernage des Bécasseaux variables et d'autres espèces d'oiseaux de rivage, il faut disposer d'information sur les caractéristiques des déplacements des populations d'oiseaux pour des sites particuliers. L'utilisation de la radio-télémetrie semble un moyen d'y parvenir.

Biology Department, San Diego State University, San Diego, California 92182, USA. (Present address: Wildlife and Fisheries Biology, University of California, Davis, California 95616, USA.)

Introduction

Within California, approximately 90% of wetlands have been destroyed, including 70% of coastal wetlands (Page *et al.* 1990). The effect of this habitat destruction on the distribution and abundance of shorebird populations is poorly understood (Goss-Custard 1979; Senner & Howe 1984; Smit, Lambeck & Wolff 1987; Howe, Geissler & Harrington 1989). Radio-telemetry has the potential to further our understanding of shorebird distribution patterns significantly (*e.g.* Wood 1986).

In this paper, I present preliminary data on movement patterns of radio-tagged Dunlins *Calidris*

alpina at two study sites in northern California (Figure 1).

Study sites

The Bodega Harbor study site is a 320-ha lagoon on the north-central coast of California (for description, see Ruiz *et al.* 1989). The Bolinas Lagoon study site is a 570-ha lagoon approximately 50 km south-east of Bodega Harbor (for description, see Page, Stenzel & Wolfe 1979).

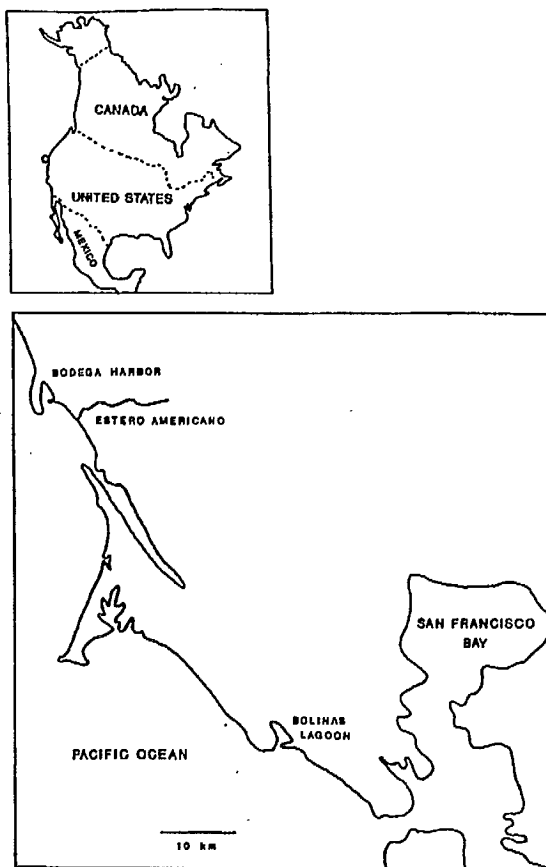


Figure 1. Study area, identified by circle on small map.

Methods

Bodega Bay

In December 1989, a preliminary radio-telemetry study was conducted at Bodega Bay. Four ~1.3-g radio-transmitters (Holohil Systems Ltd., 3387 Stonecrest Rd, Woodlawn, Ontario K0A 3M0, Canada) were glued to the upper backs of Dunlins with cyanoacrylate (Superglue®). Additionally, each bird was banded with a unique combination of colour bands and a numbered aluminium US Fish and Wildlife Service (USFWS) band and measured. These Dunlins were radio-tagged in mid-December and followed sporadically until the second week of January. Estuaries within a 50-km radius were checked for marked birds on an irregular basis.

Bolinas Lagoon

In January 1991, 10 Dunlins were outfitted with radio-transmitters and released at Bolinas Lagoon. Radio-transmitters were glued to the lower backs of the Dunlins just above the uropygial gland (see Hill and Talent 1990), using a waterproof epoxy (#332 Epoxy Adhesive, Titan Corp., 5629 208th St. SW, Lynnwood, WA 98036, USA) manufactured specifically for attaching radio-transmitters on birds. To reduce their visibility, each transmitter

was coloured brown, and the trailing antenna was coloured a flat black. Additionally, each bird received a unique combination of colour bands and a USFWS band and was measured.

I attempted to locate all active radio-tagged birds approximately two times per day ($\bar{x} = 2.3 \pm 1.1$ times/day, range = 0-5, n = 29 days). Resighting efforts were concentrated within 3 km of Bolinas Lagoon.

Each radio-tagged Dunlin was recorded as roosting, foraging/moving or unknown. The signals from radio-tagged Dunlins that were moving/feeding were found to be erratic. These behaviours were confirmed with birds that were visually located. Birds were considered to be roosting if the radio signal remained steady between radio fixes or if the birds were visually located.

Data from the first two days after a tagged bird was released were not used except in calculating the total number of days the radio ran. Observations of the same individual within two hours of each other were not used in the analyses in order to ensure independence of observations. Frequency data were tested using Pearson's Chi Square test (STATA, Santa Monica, CA).

Tides between -0.6 and 0.0 m were classified as low tides; tides between +0.1 and +0.9 m as medium tides; and tides greater than 0.9 m as high tides.

Results

Bodega Bay

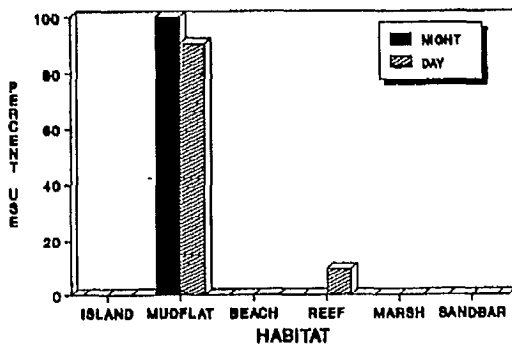
Of the four birds radio-tagged in Bodega Bay, two were killed by avian predators within seven days of being released. One bird was never detected again.

The fourth bird was followed for 14 days. On 21 December at 21:30, it was located roosting in a small *Salicornia* marsh in Bodega Harbor, and the next morning at 09:30 it was resighted midway up Estero Americano about 5 km from Bodega Harbor (Figure 1). This bird was relocated in Bodega Bay on 31 December, but not on three subsequent search days.

Bolinas Lagoon

The fates of ten Dunlins radio-tagged at Bolinas Lagoon were as follows. One bird was predated after two days; one bird was not seen after the first day; and two birds' radios fell off within the first six days. Data on behaviour and habitat use were collected on the remaining six Dunlins. The mean time that these radios emitted signals was 18.8 ± 4.1 days (range = 12-24 days).

HABITAT TYPES USED BY FORAGING DUNLIN AT BOLINAS LAGOON



HABITAT TYPES USED BY ROOSTING DUNLIN AT BOLINAS LAGOON

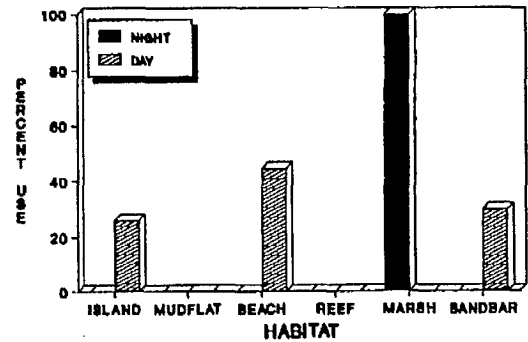


Figure 2. Habitat types used by radio-tagged Dunlins at Bolinas Lagoon according to behaviour (foraging and roosting) and time of day.

The radio-tagged Dunlins used different habitats within the area for different activities ($\chi^2 = 168.0$, d.f. = 5, $p < 0.001$; see Figure 2). All locations for foraging radio-tagged Dunlins were at mudflats within Bolinas Lagoon ($n = 107$) and on an outer-coast reef 1 km north of the mouth of the lagoon ($n = 7$). Locations of roosting birds were at an island beach within the Bolinas Lagoon ($n = 7$), the outer-coast beach ($n = 12$), a sand-bar within the lagoon ($n = 8$) and a marsh also within the lagoon ($n = 18$).

Habitats used by foraging and roosting Dunlins in the Bolinas Lagoon area during the day differed significantly from habitats used during the night ($\chi^2 = 50.9$, d.f. = 5, $p < 0.001$). Dunlins were located foraging on the mudflats during both the day ($n = 67$) and the night ($n = 40$) (Figure 2). They foraged on the outer-coast reef during the day ($n = 7$) but were never located there at night. Night-roosting Dunlins were located only in the marsh within Bolinas Lagoon ($n = 18$) (Figure 2). During the day, they roosted on the other sites (island beach, $n = 7$; coast beach, $n = 12$; sand-bar, $n = 8$).

Use of the different habitat types by roosting and foraging Dunlins varied significantly with the tide height ($\chi^2 = 93.6$, d.f. = 10, $p < 0.001$) (Figure 3). The island, outer beach, marsh and sand-bar habitats were never used on low tides, whereas the outer-coast reef was used mainly on low tides. Mudflats were the habitat most frequently used by the radio-tagged Dunlins on all tides.

Daily monitoring of radio-tagged Dunlins within the Bolinas area showed few movements away from the lagoon. All birds except one were located every day while their radios were active. One bird was not found on 3 of the 20 days its radio was active.

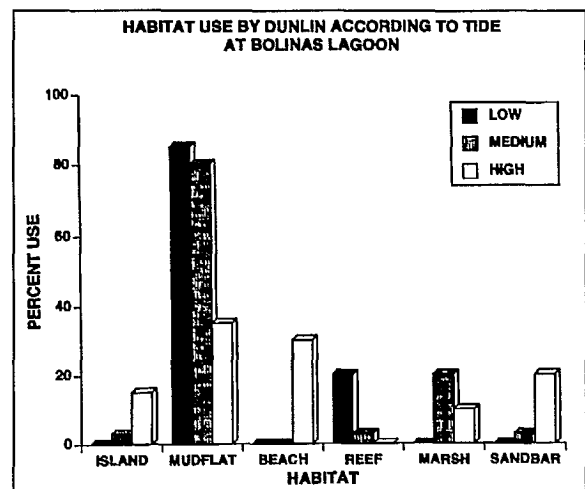


Figure 3. Habitat types used by radio-tagged Dunlins at Bolinas Lagoon according to tide height: low tide = -0.6 to 0 m; medium tide = +0.1 to +0.9 m; high tide = +1.0 to +1.8 m.

Discussion

Differences in habitat utilization by Dunlins on a temporal scale of 1–24 hours were clearly demonstrated by radio-tagged Dunlins on Bolinas Lagoon. Not surprisingly, the tide cycle affected where Dunlins were likely to be found, but the differences in where Dunlins were found during the day versus during the night were more unexpected. Habitat types within the Bolinas Lagoon area were also differentially used by radio-tagged Dunlins. Mudflats were the most frequently used feeding substrate by these Dunlins, yet a coastal reef was also utilized by foraging birds during the daylight hours. These types of data are needed for the successful conservation of shorebird habitat. Knowledge of local spatial and temporal patterns of distribution allows one to rank the importance of different habitats to shorebirds. By knowing when and where shorebirds are likely to occur within an

estuary, action can be taken to minimize disturbance to shorebird populations and to conserve the required habitats.

My study of habitat use and movement patterns of two nearby yet different groups of Dunlins suggests that habitat use on a regional level can be quite varied. At Bodega Harbor, one Dunlin used a series of lagoons within a 12-km radius during its daily/weekly activities. This bird was frequently not found in Bodega Harbor, and it was located once feeding in an estuary approximately 6 km away after having been located 12 hours earlier roosting in Bodega Harbor. Similarly, Dunlins colour-banded in Bodega Harbor have been frequently resighted in the estuaries surrounding the Bodega area (P. Connors, per. commun.). The proximity of suitable estuaries and lagoons to Bodega Harbor may make it energetically advantageous for Dunlins to capitalize on tidal differences between estuaries and lagoons by extending their foraging time (Ruiz *et al.* 1989; P. Connors and J.L. Maron, unpubl. data). For instance, by leaving Bodega Harbor on a rising tide and flying to Estero Americano (Figure 1), a Dunlin could extend its feeding time by at least three hours owing to the time lag in tides between the two areas (P. Connors and J.L. Maron, unpubl. data).

Radio-telemetry work and resightings of colour-marked Dunlins at Bolinas Lagoon indicated that Bolinas Dunlins were quite site-faithful¹. The geographical isolation of Bolinas Lagoon may make it energetically detrimental for Dunlins to use other lagoons during daily activities.

Despite my small sample sizes, my analysis of Dunlins' movement patterns allows one to appreciate the complexity of the habitat requirements of wintering shorebird populations (see also Page, Stenzel & Wolfe 1979). Bolinas Dunlins used a single estuary almost exclusively during their daily activities, but at Bodega at least one Dunlin utilized a series of lagoons and estuaries during its daily activities.

Acknowledgements

All aspects of this study benefited from the advice and help of Sarah Griffin. Financial support from San Diego State University and the University of California at Davis is gratefully appreciated. Logistic support from the Point Reyes Bird Observatory, Bodega Marine Laboratory and Margaret Greene was also critical in this study. Finally, Gonzalo Castro and Julie Sibbing deserve credit for making the shorebird symposium happen.

This is Contribution 545 of the Point Reyes Bird Observatory.

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¹ Radio-telemetry work in Bolinas Lagoon in 1992 revealed a different pattern from that in 1991. Following the first significant rainfall of the season (there were no rainstorms in 1991 while the radios were active), some of the radio-tagged birds flew between San Francisco Bay and Bolinas Lagoon, a distance of 12-14 km, sometimes on a daily basis. There was also heavy raptor predation in 1992.

Population status of the threatened/endangered Piping Plover in 1991

Susan M. Haig & Jonathan Plissner

Haig, S.M. & Plissner, J. 1996. Population status of the threatened/endangered Piping Plover in 1991. *International Wader Studies* 8: 39-41.

US Fish and Wildlife Service, South Carolina Cooperative Fish and Wildlife Research Unit, Behavior, Ecology and Conservation Biology Program, G08 Lehotsky Hall, Clemson University, Clemson, South Carolina 29634, USA.

In 1991, biologists from Canada, the United States, Mexico and various Caribbean nations collaborated in a census of all known Piping Plover *Charadrius melodus* breeding and wintering sites. The goals of the census were to (1) establish current population levels, (2) survey additional potential breeding and wintering sites and (3) assess the status of the species relative to past population estimates.

Observers conducted censuses by walking and driving along a predetermined stretch of beach or sandflat and recording the number and location of Piping Plovers at each site. The winter census was conducted from 12 to 20 January 1991, along the Gulf coast of the United States and Mexico and the southern Atlantic coast of the United States, Cuba and several other Caribbean countries (Figure 1, Table 1). The breeding census was carried out across the species' range (Figure 1, Table 2) from 1 to 9 June 1991. Nests, eggs and chicks were not counted. More precise methods for the winter and breeding censuses are summarized in Haig & Plissner (1994).

Over 850 observers from ten nations participated in the census. Approximately 2,095 sites were surveyed, resulting in total numbers of 5,482 breeding adults and 3,451 wintering birds. The number of wintering birds comprised 63% of the breeding birds counted (Tables 1 & 2). The majority of wintering birds (55% or 1,898 birds) were found in Texas. Among areas where birds were found, 51% (1,762 birds) occurred on ocean beaches, 43% (1,486) used sandflats or algal flats in protected bays and 6% (203) used areas where protected bays met ocean beaches.

The 1991 breeding census represented a complete census of all known Piping Plover breeding sites. Currently, Piping Plovers are widely distributed in small populations across their breeding range (Figure 1). The majority of adults (63.2%) are found in the northern Great Plains and Prairies of the United States and Canada, whereas the numbers of birds and breeding sites on the Great Lakes remain small (Table 2). Piping Plovers breed in a variety of habitat types. On the Atlantic coast, 93.9% (1,854) of breeding birds were found on ocean beaches, and the remainder used protected bays. All Great Lakes birds used Great Lakes beach shoreline. In the northern Great Plains and Prairies, 59.6% (2,068) of Piping Plovers used shorelines around alkaline lakes, 24.6% (854) used reservoir beaches, 13.4% (466) used river islands and sand-pits, 2% (68) occupied large freshwater lake beaches and 0.4% (13) were found along the shores of industrial ponds.

Birds were found in areas where they had not been reported previously, including the Missouri River Coteau region of Saskatchewan, a number of areas in northeastern Montana and the Prewitt Reservoir in Colorado. Piping Plovers have all but disappeared on the Great Lakes and on the Lake of the Woods in Minnesota, Ontario and Manitoba. Numbers on the Atlantic coast remain stable, perhaps because of unprecedented efforts to protect Piping Plover there.

Reference

- Haig, S.M. & Plissner, J.H. 1994. The 1991 International Piping Plover Census in the United States, Mexico, and the Caribbean: breeding and winter populations. *Can. Wildl. Serv. Occas. Pap.* 82: 48-51.

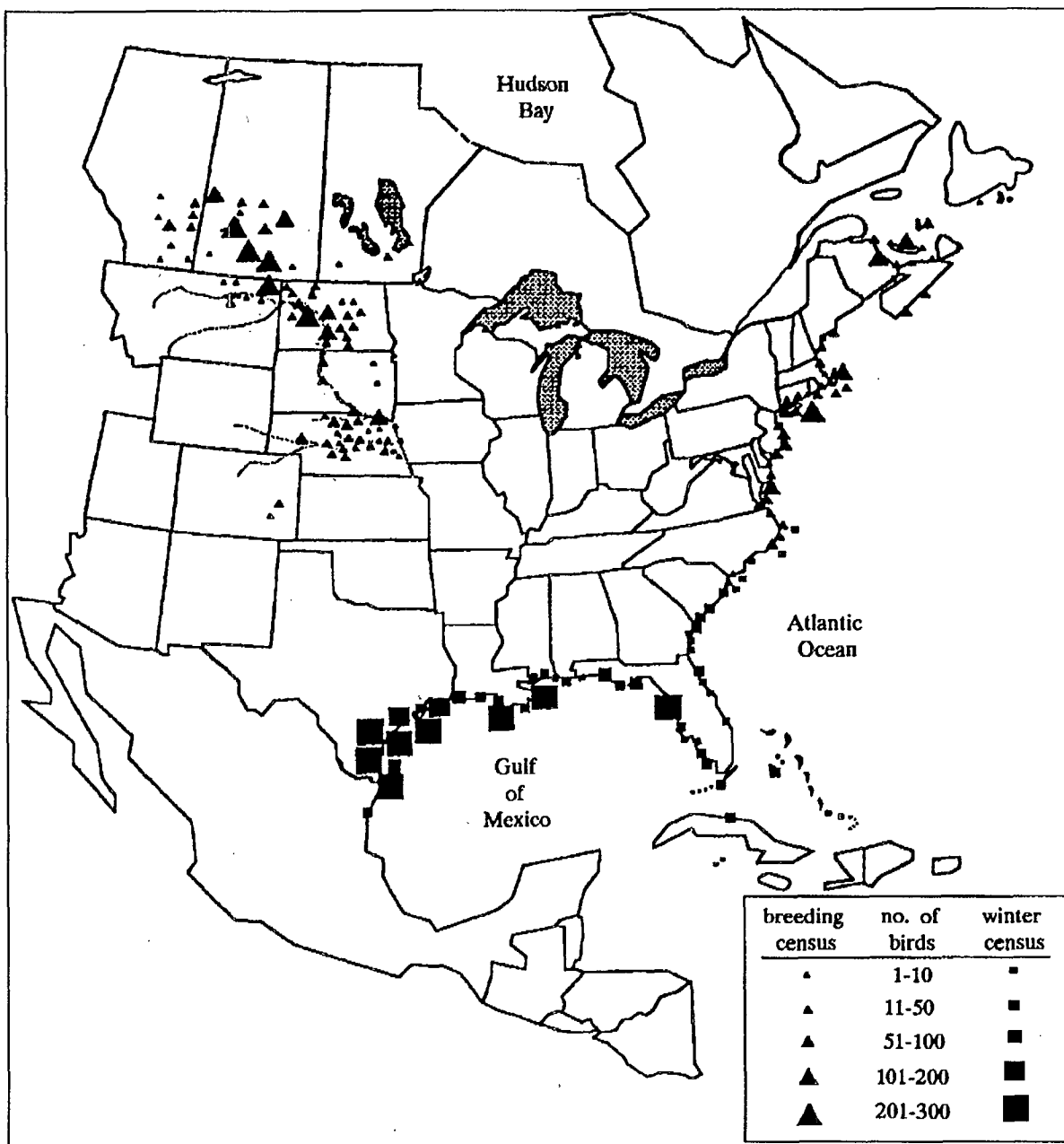


Figure 1. Distribution of birds reported from the 1991 International Piping Plover Census.

Table 1. Results from the 1991 International Piping Plover winter census.

Location	No. of birds	Total no. of sites	No. of plover sites
<i>Total USA</i>	3,384	325	156
US Atlantic	178	132	30
US Gulf	3,206	193	126
<i>Gulf of Mexico</i>	27	18	4
<i>Caribbean</i>	40	11+	2
Bahamas	29	1	1
Turks and Caicos	0	1	0
Cuba	11	2	1
Jamaica	1	^a	0
Puerto Rico	0	5	0
Cayman Islands	0	^a	0
Total winter	3,451	354+	162

^a Unknown number of sites surveyed in Cayman Islands and Jamaica.

Table 2. Results from the 1991 International Piping Plover breeding census.

Location	No. of adults	No. of pairs	Total no. of sites	No. of plover sites
<i>Total Prairie Canada & US Great Plains</i>	3,467	1,486	1,121+	425
Prairie Canada	1,437	589	561	111
US Great Plains	2,030	897	560+	314
<i>Total Great Lakes</i>	40	17	47	15
<i>Total Atlantic</i>	1,975	938	573	288
Atlantic Canada	513	236	234	92
US Atlantic	1,462	702	339	196
Total Canada	1,950	825	795	203
Total USA	3,532	1,616	946+	525
Total census	5,482	2,441	1,741+	728

Preliminary study of shorebird habitat and feeding conditions at Lobos Bay, Sonora, Mexico

Mauricio Cervantes Abrego & Rocio E. Muratalla Contreras

Cervantes Abrego, M. & Muratalla Contreras, R.E. 1996. Preliminary study of shorebird habitat and feeding conditions at Lobos Bay, Sonora, Mexico. *International Wader Studies* 8: 42.

Institute for Technology and Advanced Studies (Monterrey campus), Guaymas, Mexico.

Lobos Bay and the Yaqui River Delta in southern Sonora, Mexico (27°30'N, 110°35'W), which have a surface area of 60,000 ha, are composed of extensive marshlands with a system of lagoons and small natural salt-marshes adjoining a shallow bay, separated from the Gulf of California by a dune island (Lankford 1977). Some inlets and marshes are dammed and flooded for the year-round extraction of salt. An equable climate [BW (h') hw(e); Garcia 1973] favours development of micro-organisms on which aquatic larvae, insects, fish and higher vertebrates feed. Preliminary surveys of climate, topography and invertebrate life in 1990–1991 also showed the area to be used by a variety of shorebirds, mainly migratory species. Seasonal use by the various species has not yet been determined, as visits were made only in May through October. A maximum number of 2,100 birds, composed of 21 species, was counted on 5 July. The most common species were Least Sandpiper *Calidris minutilla* (800), Western

Sandpiper *C. mauri* (500) and Willet *Catoptrophorus semipalmatus* (300). Shorebirds foraged by day on mudflats around mangrove thickets, where a variety of invertebrates (Polychaeta: 53%, Crustacea: 23%, Mollusca: 18%, others: 6%) occurred. At dusk, they resorted to the shallow water of evaporation pits at the Lobos Bay salt plant, where prey was artificially concentrated and a profusion of shore flies (Ephydriidae) provided easy foraging.

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Part II

Ecology of migrant and resident shorebird populations in Central and South America

The impact of foraging by sandpipers (Scolopacidae) on populations of invertebrates in the intertidal zone of Chomes Beach, Gulf of Nicoya, Costa Rica

Ana I. Pereira

Pereira, A.I. 1996. The impact of foraging by sandpipers (Scolopacidae) on populations of invertebrates in the intertidal zone of Chomes Beach, Gulf of Nicoya, Costa Rica. *International Wader Studies* 8: 44–51

Foraging by sandpipers in the intertidal zone of Chomes Beach in Costa Rica affected populations of invertebrates upon which they fed during the 1986–1987 wintering period. Significant differences were found in the numbers of invertebrates inside and outside exclosures that were constructed on the mudflats where the sandpipers foraged. There was an inverse relationship between the numbers of crustacean- and bivalve-eating sandpipers and the differences in the numbers of crustaceans and bivalves found inside and outside the exclosures. Similarly, the abundances of *Uca* crabs varied inversely with the numbers of sandpipers. However, as with the other invertebrates, crab abundance did not diminish at the end of the season. Overall, no relationship was found between the total numbers of sandpipers foraging in the area and the differences in the total numbers of invertebrates found inside and outside the exclosures.

Se determinó que el forrajeo de los correlimos en la zona de entremareas de la playa de Chomes, Costa Rica, afectó las poblaciones de invertebrados durante el periodo de invernación 1986–1987. Se encontró diferencias significativas en el número de invertebrados dentro y fuera de las áreas protegidas del forrajeo de los correlimos. Este mismo resultado se encontró al analizar el número de individuos de las especies de invertebrados más comunes del área, dentro y fuera de las áreas protegidas. Existe una relación inversa entre el número de correlimos comedores de crustáceos y bivalvos y las diferencias encontradas entre las áreas protegidas y fuera de ellas en número de individuos de estos de invertebrados. Sin embargo, no se encontró relación entre el número total de correlimos que forrajearon en el área y la diferencia de invertebrados dentro y fuera de las áreas. La abundancia de cangrejos está relacionada inversamente con el número de correlimos que se alimentan de ellos. Sin embargo, al igual que con el resto de los invertebrados, no disminuye la abundancia al final de la época.

Les habitudes alimentaires des Scolopacidés dans la zone intertidale de la plage Chomes au Costa Rica ont eu des répercussions sur les populations d'invertébrés qui leur ont servi de nourriture durant la période d'hivernage de 1986–1987. On a observé des différences significatives entre le nombre d'invertébrés à l'intérieur d'exclos érigés sur les slikkes où s'alimentent les Scolopacidés, d'une part, et à l'extérieur de ceux-ci, d'autre part. On a en effet découvert que le nombre de crustacés et de bivalves dénombrés à l'intérieur et à l'extérieur des exclos était inversement proportionnel au nombre de Scolopacidés s'en nourrissant. De même, l'abondance de crabes *Uca* variait en proportion inverse du nombre de Scolopacidés. Toutefois, comme pour les autres invertébrés, l'abondance de crabes n'a pas diminué à la fin de la saison. Globalement, on n'a pas trouvé de rapport entre le nombre total de Scolopacidés s'alimentant dans la région et le nombre total d'invertébrés se trouvant à l'intérieur et à l'extérieur des exclos.

School of Biology, University of Costa Rica, Costa Rica.

Introduction

After reproducing at high latitudes in the north, sandpipers migrate southward, where they concentrate along the coasts of Central and South America. There, they spend the overwintering period foraging on polychaetes and bivalves and a variety of other invertebrates (see Schneider 1983).

In several studies carried out at wintering sites in extra-tropical areas, a reduction in populations of the prey of sandpipers was found as a result of the birds' intense foraging activities. At the mouth of the Tees River, Evans *et al.* (1979) discovered a 90% reduction in harvests of *Hydrobia* and an 80% reduction in those of *Nereis* as a result of foraging by sandpipers. Such reductions have not been found in the tropics (Duffy, Atkins & Schneider 1981; Schneider 1983).

In Costa Rica, the mudflats along the Gulf of Nicoya support large populations of sandpipers. One such area is Chomes Beach, which is used as both a stop-over and wintering site (Stiles & Skutch 1989).

The main objective of this research was to determine whether foraging by the sandpipers that use Chomes Beach affected invertebrate populations and whether the availability of these food resources diminished over the wintering period.

Materials and methods

This research was undertaken from September 1986 to August 1987 in the intertidal zone between the Chomes and Coco inlets at Chomes Beach (10°N and 85°W) on the Pacific coast of Costa Rica (Figure 1). The study area (50 ha) had a soft mud substrate characterized by the presence of polychaete and Diopatra tubes typically adorned with bits of leaves and shells, which are abundant in the area. There were also some patches of sandy substrate. Above the tide line there was a small sandy beach that bordered a mangrove swamp consisting principally of *Laguncularia racemosa* and *Avicennia germinans*.

In order to determine the impact of foraging by sandpipers on invertebrate populations, three 25-m² portions of the intertidal area were enclosed, 100 m apart, at a distance of 50 m from the mangrove swamp. Wooden stakes, connected by nylon rope at heights of 5, 10, 15, 20 and 25 cm from the substrate, delineated each quadrat. These exclosures prevented sandpipers, but not other predators, such as fish, from entering those specific portions of mudflat.

Invertebrates were sampled every two weeks at low tide. During the first eight sampling periods, two random samples of mud were taken inside and outside each exclosure using a 10-cm-diameter core pushed to a depth of 15 cm. Beginning in January, a 5.5-cm-diameter core was used, and the number of samples increased to six inside and outside each exclosure. Each mud sample was placed in a plastic bag containing a solution of 10% formalin in sea water with Bengal red to preserve and tint the invertebrates. The samples were then passed through a 1-mm mesh sieve to separate organisms equal to or greater than that diameter and then placed in vials with 70% alcohol and subsequently identified.

The densities of crabs were determined by using ten 4-m² quadrats along each of three 100-m-long transects, 50 m apart and perpendicular to the edge of the swamp (Figure 1). Quadrats were placed every 10 m along each transect, and, after a three-minute wait, the crabs inside each quadrat

were counted. Each count was undertaken at a distance of 6 m from the quadrat using 7 × 50 binoculars to avoid interfering with the crabs' activities.

Following each sampling period, I surveyed a 1-km-long transect parallel to the beach between the Chomes and Coco inlets to determine how many sandpipers were present.

Results

A total of 27 species of Charadriiformes was observed in the study area (Table 1). The Gull-billed Tern *Sterna nilotica* and the first 18 species listed in Table 1 all foraged there. Up to 14 species, totalling 713 individuals, were observed during a single count (Figure 2). Although the number of species remained relatively constant until the end of April, the numbers of birds present in the area began to decline as early as February and March. Numbers continued to decline until August 1987. Throughout that period, in 18 of 23 invertebrate samples, larger numbers of invertebrates were found inside the exclosures (Table 2, Figure 3).

In order to determine if there were significant differences between the numbers of different species of invertebrates in the exclosures and the control areas, the Wilcoxon Test was applied to the data (Siegal 1972). Using this test, separate analyses were done on samples taken during the wintering period and those taken during periods after most of the sandpipers had migrated to the breeding grounds.

The numbers of invertebrates were significantly larger inside the exclosures than outside ($W = 55$, $n = 23$, $p < 0.01$) (Figure 3A). The same was true for samples taken during the sandpiper wintering period, which runs from September to March ($W = 12$, $n = 13$, $p < 0.01$); in the samples taken during their absence from the area, from April to August, on the other hand, the differences were not significant ($W = 13.5$, $n = 10$, $p > 0.05$). Nevertheless, the resource was not depleted, as the numbers of invertebrates did not decline throughout the period (Figure 3).

The same results were found when analysing for differences in the numbers of polychaetes inside and outside the exclosures for (1) all samples ($W = 51$, $n = 23$, $p < 0.01$); (2) samples taken during the wintering period ($W = 16$, $n = 13$, $p < 0.05$); and (3) samples taken after the wintering period ($W = 11$, $n = 10$, $p > 0.05$) (see Figure 3). For bivalves, significant differences were found only in samples taken during the wintering period ($W = 17.5$, $n = 13$, $p < 0.05$); for crustaceans, no significant differences were found.

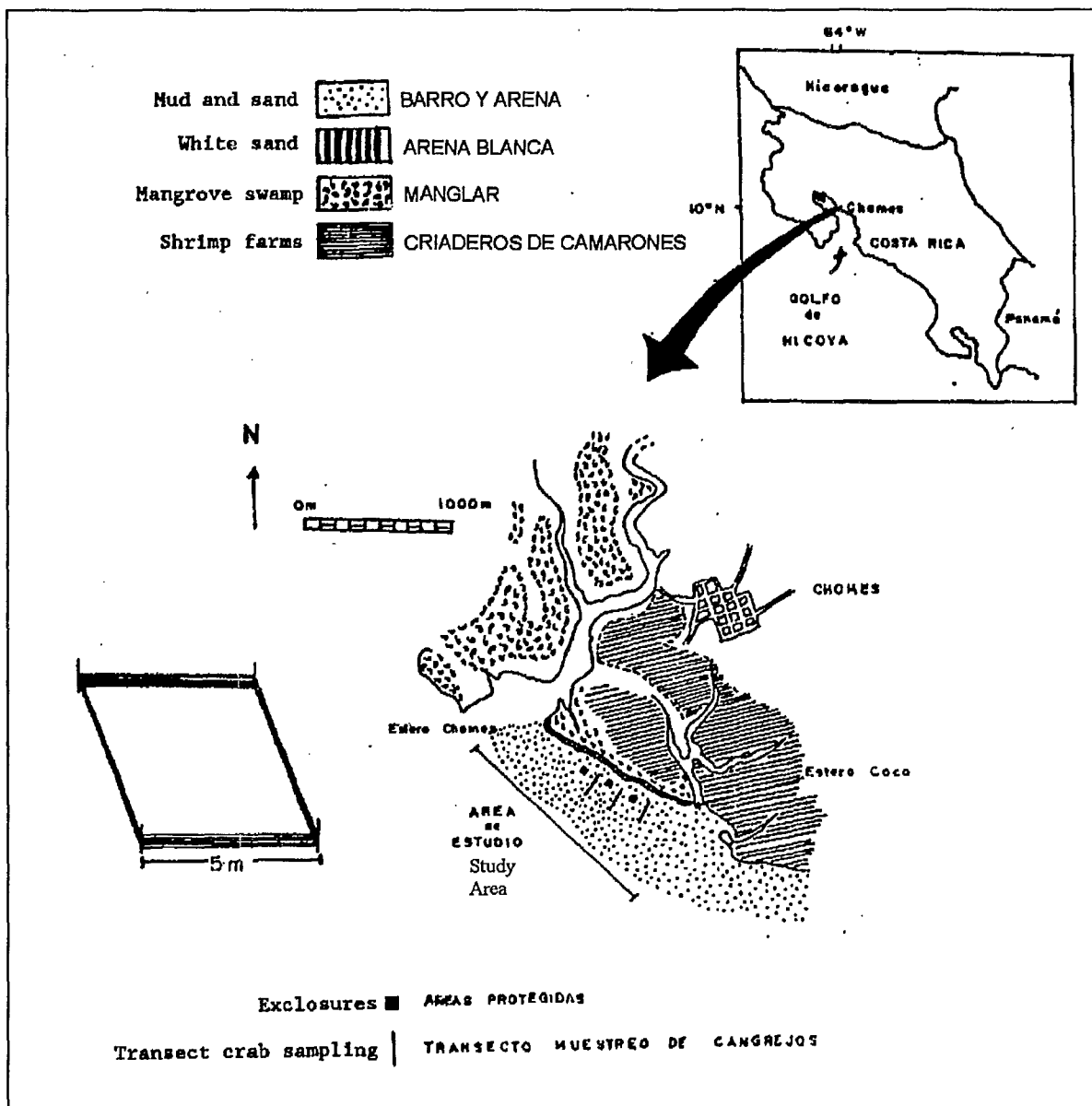


Figure 1. Study area, located in the intertidal zone of Chomes Beach, Gulf of Nicoya, Costa Rica.

Table 1. Charadriiformes sighted on Chomes Beach, Gulf of Nicoya, Costa Rica, between September 1986 and August 1987. Diet is shown in parentheses, where P = polychaete, C = crustacean, B = bivalve, F = fish and I = insects.

<i>Haematopus palliatus</i> (Temminck) (B)	<i>Numenius americanus</i> (Bechstein) (C,P)
<i>Pluvialis squatarola</i> (Linnaeus) (P)	<i>Limosa fedoa</i> (Linnaeus) (P)
<i>Charadrius semipalmatus</i> (Bonaparte) (P)	<i>Limnodromus griseus</i> (Gmelin) (P,B)
<i>Charadrius wilsonia</i> (Ord) (C)	<i>Himantopus mexicanus</i> (Muller) (C,I)
<i>Tringa melanoleuca</i> (Gmelin) (P)	<i>Larus atricilla</i> (Linnaeus) (F,B)
<i>Tringa flavipes</i> (Gmelin) (P)	<i>Larus pipixcan</i> (Wagler) (F)
<i>Actitis macularia</i> (Linnaeus) (C)	<i>Chlidonias niger</i> (Linnaeus) (F,C)
<i>Catoptrophorus semipalmatus</i> (Gmelin) (C,B)	<i>Sterna nilotica</i> (Gmelin) (C)
<i>Arenaria interpres</i> (Linnaeus) (B)	<i>Sterna maxima</i> (Boddaert) (F,C)
<i>Calidris canutus</i> (Linnaeus) (B)	<i>Sterna sandvicensis</i> (Latham) (F,C)
<i>Calidris minutilla</i> (Vieillot) (C,I)	<i>Sterna caspia</i> (Pallas) (F,C)
<i>Calidris mauri</i> (Cabanis) (C)	<i>Sterna antillarum</i> (Lesson) (F,C)
<i>Calidris alba</i> (Pallas) (C)	<i>Rynchops niger</i> (Linnaeus) (F,C)
<i>Numenius phaeopus</i> (Linnaeus) (C)	

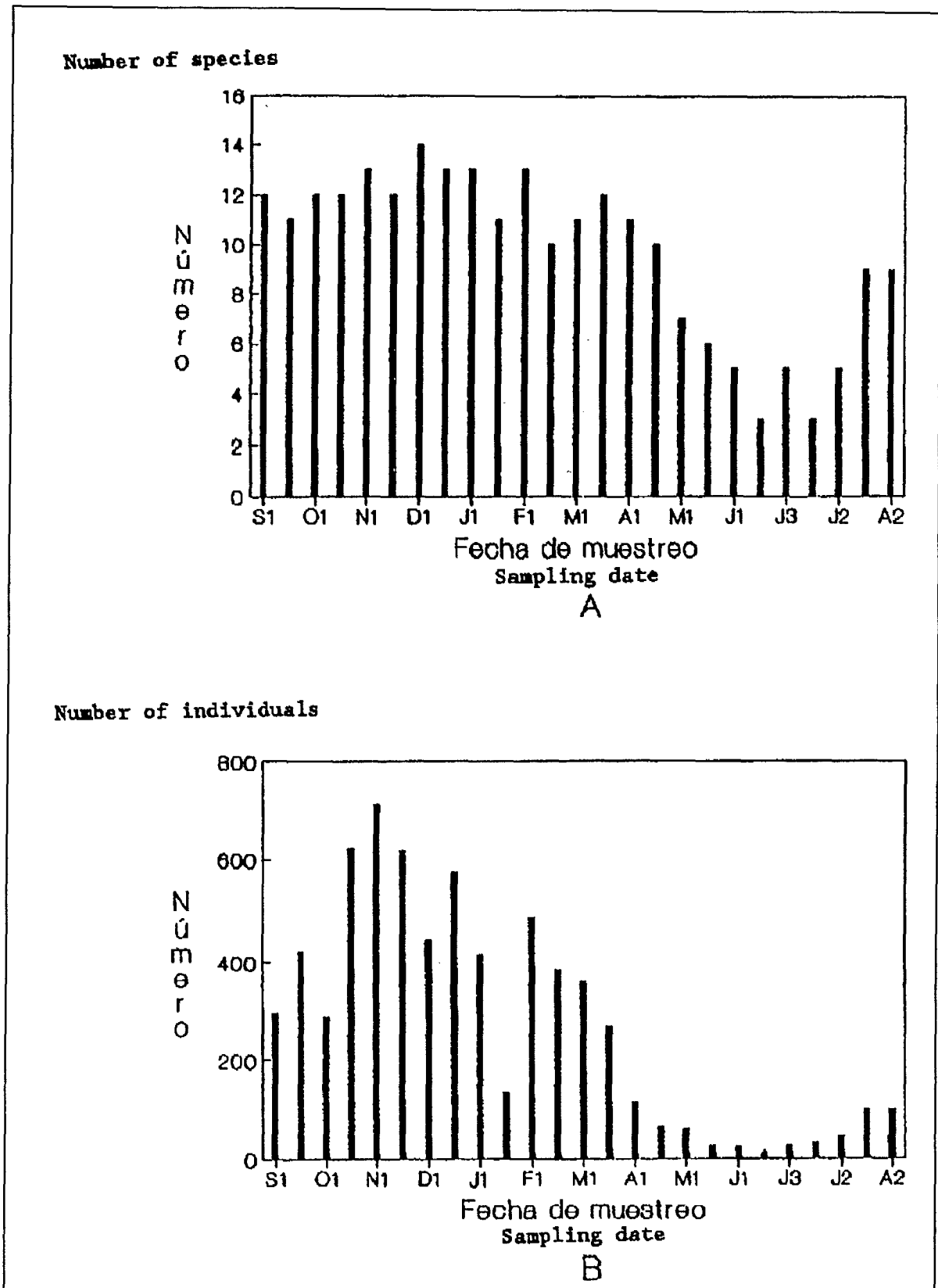


Figure 2. Number of species (A) and number of individuals (B) of sandpipers present during the 1986–1987 wintering period in Chomes Beach, Gulf of Nicoya, Costa Rica.

Table 2. Number of individuals from each invertebrate species found inside and outside exclosures during and after the wintering period, Chomes, Costa Rica. P = Polychaeta, B = bivalves, C = crustaceans, E = Echinodermata, Br = brachiopoda, F = filtered, AD = part of sediment, CA = carnivore, OM = omnivore.

	During wintering period		After wintering period	
	Inside	Outside	Inside	Outside
<i>Owenia collaris</i> (P-AD)	250	172	100	84
<i>Notomastus hemipodus</i> (P-AD)	67	54	18	9
<i>Ophiophiolis geminata</i> (E-AD)	53	40	41	34
Paraonidae sp. 1 (P-AD)	46	35	9	5
<i>Armandia salvadoriana</i> (P-AD)	42	34	10	13
<i>Mediomastus californiensis</i> (P-AD)	43	24	49	49
Nematoda	31	23	2	1
<i>Phlytiderma phoebe</i> (B-F)	31	18	14	26
<i>Glottidia audebarti</i> (Br-F)	22	25	8	15
<i>Tharyx parvus</i> (P-AD)	17	20	6	10
Polynoidae sp. 1 (P-AD)	17	19	27	17
<i>Calyptraea mamillaris</i> (C-F)	10	17	13	9
Nemertino sp. 1 (CA)	16	18	11	9
<i>Hemipodus borealis</i> (P-CA)	12	15	2	9
<i>Pitar perfragilis</i> (B-F)	13	13	26	21
<i>Glycinde armigera</i> (P-CA)	11	12	8	10
<i>Sinelmis albini</i> (P-AD)	15	7	8	8
<i>Tellina tumbezensis</i> (B-F)	16	6	16	14
Sipunculidae sp. 1	8	12	6	7
<i>Linopherus spiralis</i> (P-CA)	15	4	9	19
<i>Pectinaria californiensis</i> (P-AD)	12	6	2	2
<i>Neanthes</i> sp. 1 (P-CA)	11	6	8	2
<i>Parapinnixa</i> sp. (C-OM)	8	7	3	6
<i>Macra thracioides</i> (B-F)	10	4	10	3
<i>Encope estokessi</i> (E-AD)	8	6	12	8
<i>Tagelus bougeoisae</i> (B-F)	7	7	12	7
<i>Lumbrineris tetraura</i> (P-AD)	4	9	7	6
<i>Ceratonereis</i> sp. (P-CA)	5	8	6	4
<i>Tellina</i> sp. (B-F)	11	2	6	10
<i>Pinnixa valerii</i> (C-OM)	7	6	3	10
<i>Ancistrosyllis</i> sp. (P-AD)	4	5	8	10
<i>Tellidora burneti</i> (B-F)	4	5	10	12
<i>Corbula obesa</i> (B-F)	8	0	7	15
<i>Loimia medusa</i> (P-AD)	5	2	11	5

The more common and abundant invertebrates also occurred in significantly higher numbers inside the exclosures during the wintering period ($z = -2.78$, $n = 32$, $p < 0.01$), whereas afterwards the differences were no longer significant ($z = -0.85$, $n = 32$, $p > 0.05$). The species that contributed most to these differences were the polychaetes *Owenia collaris*, *Mediomastus californiensis*, *Notomastus hemipodus* and *Linopherus spiralis*, the bivalve *Phlytiderma phoebe* and the starfish *Ophiophiolis geminata*, most of which represented the most abundant species. The birds *Limnodromus griseus*, *Charadrius semipalmatus* and *Pluvialis squatarola* fed on polychaetes; the stomach contents of several *L. griseus* collected in the area included large quantities of bivalve remains.

The Spearman Rank Correlation test was used to determine whether there was any relation between the differences in the numbers of invertebrates inside and outside the exclosures and the numbers

of sandpipers present on the beach during the same period (P) and between the average numbers of birds sighted during the same period and during the previous period (P, P-1). This was done to correct for the effect of prior consumption and the delay in recovery of invertebrate populations.

The differences found in the numbers of invertebrates inside and outside the exclosures bore no relation to the numbers of birds foraging on the beach ($r_s = 0.17$ and $r_s = 0.10$, $n = 21$, $p > 0.05$, respectively, for P and P, P-1). Nor was there any relationship between the numbers of birds foraging on polychaetes and the differences in the numbers of these invertebrates between the two areas ($r_s = 0.25$ and $r_s = 0.21$, $n = 21$, $p > 0.05$, respectively, for P, P-1). However, an increase in the numbers of birds feeding on bivalves and crustaceans produced a greater increase in the differences between the numbers of both taxonomic groups, inside and

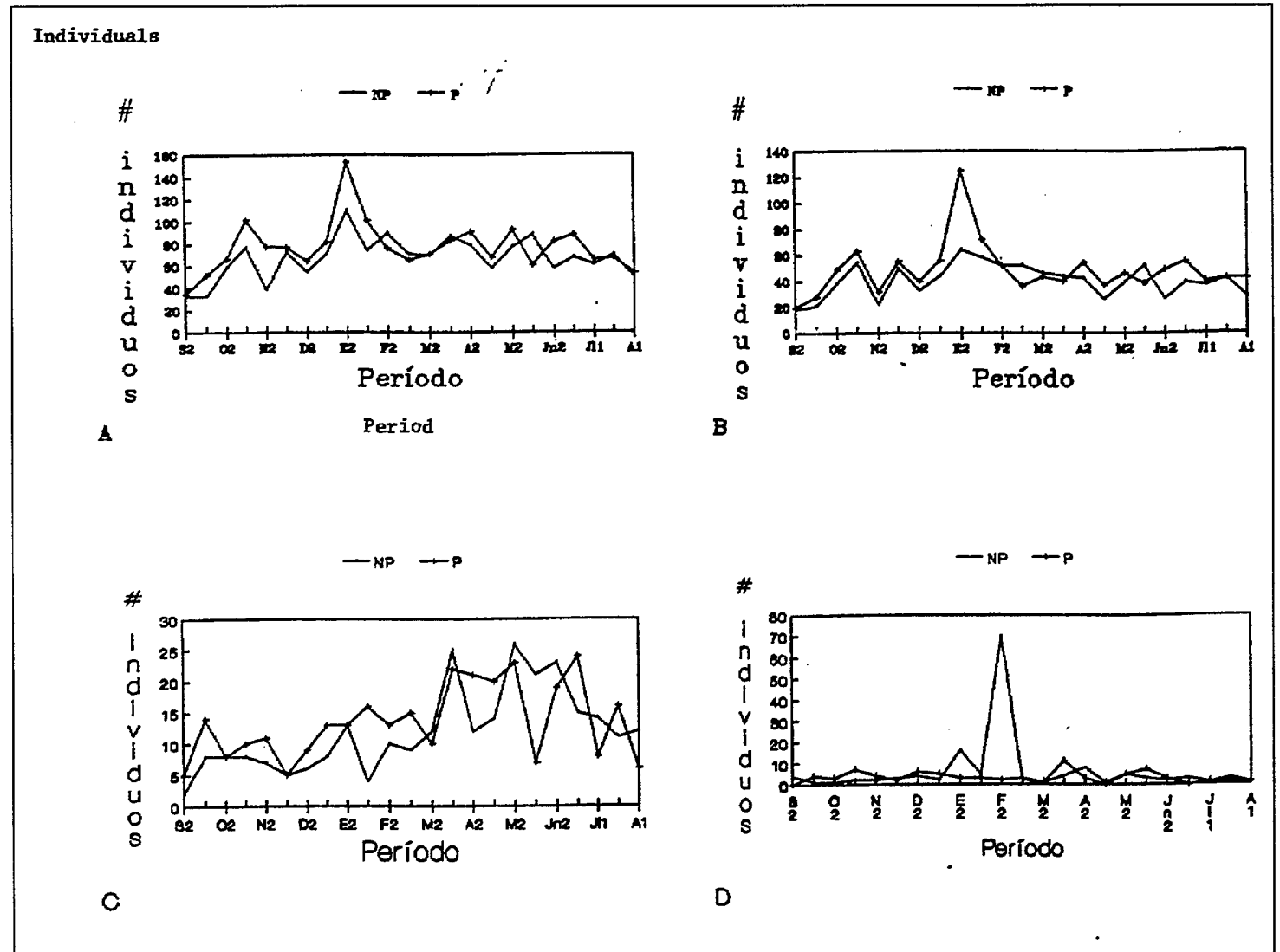


Figure 3. Number of invertebrates (A), polychaetes (B), bivalves (C) and crustaceans (D) present inside and outside enclosures in the intertidal zone of Chomes Beach, 1986-1987, Gulf of Nicoya, Costa Rica. P = enclosures; NP = control areas.

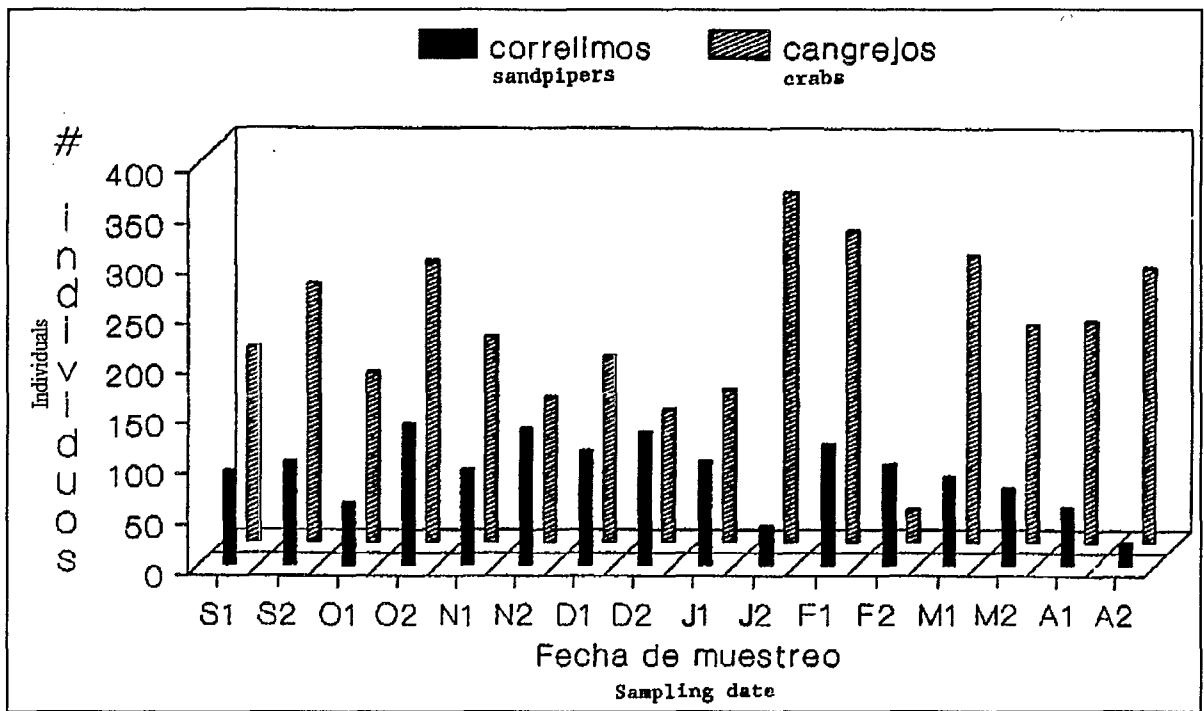


Figure 4. Number of crab-eating sandpipers and number of crabs present in each sample, Chomes.

outside the enclosures ($r = 0.38, p < 0.05$ and $r = 0.30, p > 0.05$; $r = 0.39, p < 0.05$ and $r = 0.38, p < 0.05$, for bivalves and crustaceans for periods P and P-1, respectively).

To determine whether there was any relation between foraging by *Numenius phaeopus*, *Catoptrophorus semipalmatus*, *Charadrius wilsonia*, *Actitis macularia* and *Sterna nilotica* and the crab populations upon which they fed, the Spearman Rank Correlation test was applied between the total numbers of individuals of all five species and the numbers of crabs sampled in each period (transect method). This was repeated with the average number of sandpipers present during the same period and the previous period.

Together, these birds caused a significant decrease in crab populations ($r_s = -0.61, n = 15, p < 0.05$; Figure 4). This effect was seen when we considered the average numbers of birds present during the same period and during the previous period. If we take into account the effect of these birds in each period, the same trend presents itself, although not to a significant degree ($r = -0.32, n = 16, p > 0.05$; Figure 3).

Most crabs caught by *Numenius phaeopus* and *Charadrius semipalmatus* were between 0.6 and 1.0 cm long. Crabs under 0.5 cm were infrequently captured by the birds.

Discussion

Foraging by sandpipers significantly affected the invertebrates upon which they fed. However, the foraging resources of these birds were not depleted in the latter months of the wintering period, as has been reported in other regions (Goss-Custard 1976, 1977, 1978, 1980; Evans 1979; Pienkowski 1981, 1983; Peer, Linkletter & Hicklin 1986). This may be attributable to the fact that breeding by invertebrates in the tropics is not confined to a particular season, as occurs in the extra-tropical areas, where most of these studies were undertaken.

Seasonality is present in the reproductive cycles of organisms in the tropics (Broom 1984; Cruz 1984; Vargas 1988), but different species breed at different times of the year (Vargas 1988). In a study carried out on a mudflat 2 km from the study area, Vargas (1988) found that organisms such as *Mediomastus californiensis* experienced breeding peaks during the dry season, whereas *Paraprionospio pinnata* had them during the rainy season; other species, such as the decapod *Pinnixa valerii*, showed peaks at breeding intervals of over a year. Hence, invertebrate species bred throughout the sandpipers' wintering period. This could compensate for depredation losses and may be one of the reasons why no decreases were found in the numbers of invertebrates at the end of the wintering period.

Crane (1975) reported that crab species of the genus *Uca*, which were abundant in the study area, reproduce throughout the year in the tropics. In a

study of zooplankton done near the study area, Dittel (1989) found *Uca* crab larvae throughout the entire year.

Of the species of *Uca* reported in the study area, the sizes of the adults ranged between 0.53 and 2.5 cm (Crane 1975); individuals smaller than 0.6 cm were considered to be juveniles. *Numenius phaeopus* and *Charadrius semipalmatus* caught crabs that were usually between 0.6 and 1.0 cm long. This may explain why, although foraging by sandpipers affected crab populations, the latter were not in decline, because the sandpipers captured mainly adult individuals, thus allowing juveniles to remain in the population (see also Goss-Custard 1977, 1978; Hartwick & Blaylock 1979; Pienkowski 1983; Zwartz 1985, cited in Piersma 1987).

If food resources for sandpipers were not being depleted, why were there not more birds foraging in the area? One explanation might be the aggressive territorial behaviour of certain species, such as *Catoptrophorus semipalmatus*, *Numenius phaeopus* and *Charadrius wilsonia*. *Catoptrophorus semipalmatus* commonly defended areas of the beach against conspecifics and other species such as *Limnodromus griseus*. *Numenius phaeopus* and *Charadrius wilsonia* were less aggressive birds but frequently pursued or vocalized threats at conspecifics coming to forage or simply flying by.

It should be kept in mind that the enclosures used in this research prevented birds from foraging in specific areas but did not bar access to other predators, such as fish and macroinvertebrates, a problem present in the methodology used by other researchers. Sedimentation and stream flow problems that might have affected the results of the experiment (Quammen 1981) were absent as well.

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Segregation of roosting habitat in migratory shorebirds on the Pacific coast of Colombia

Luis G. Naranjo & Jaime E. Mauna

Naranjo, L.G. & Mauna, J.E. 1996. Segregation of roosting habitat in migratory shorebirds on the Pacific coast of Colombia. *International Wader Studies* 8: 52-54.

During fall migration in 1990, we conducted visual counts of shorebirds along the sandy shoreline of Punta Soldado (Valle, Colombia). Although this location is not regularly used as a feeding site by shorebirds, about 5,000 shorebirds of different species congregate on a limited portion of the beach. We mapped the location of these birds in relation to the tide line. We found that the most numerous species, *Actitis macularia*, used the innermost portions, which were covered with various grasses. *Charadrius wilsonia* and *C. semipalmatus* preferred a different section, which was covered with organic and inorganic detritus, and *Calidris mauri* showed a marked preference for the wet outer beach. We discuss the importance of resting sites as a limited resource for migrant shorebirds.

Durante la migración de otoño de 1990, realizamos censos visuales de aves playeras en el litoral arenoso de Punta Soldado (Valle, Colombia). Aunque esta localidad no es usada regularmente como sitio de alimentación por estas aves, durante la noche se congregan en un sector limitado de la playa cerca de 5 000 individuos de diferentes especies. Durante los censos, mapeamos la ubicación de las aves contadas determinando su distancia con respecto a la línea de rompeolas. Encontramos que *Actitis macularia*, dominante numéricamente en la comunidad, utilizó la parte más interna, cubierta por vegetación rastrera y gramíneas, mientras que *Charadrius wilsonia* y *C. semipalmatus* prefirieron el segmento inmediatamente siguiente cubierto por detritus orgánicos e inorgánicos y por último, *Calidris mauri* mostró una marcada preferencia por la playa externa húmeda. Discutimos la importancia de los sitios de descanso como recursos limitantes para aves playeras migratorias.

Les auteurs ont effectué des dénombrements visuels d'oiseaux de rivage durant la migration automnale à partir du rivage sablonneux de Punta Soldado, à Valle, en Colombie. Même s'il ne s'agit pas d'une aire d'alimentation utilisée régulièrement, quelque 5 000 oiseaux de rivage de diverses espèces s'y rassemblent. Nous avons cartographié l'emplacement de ces oiseaux par rapport à la laisse de marée. Nous avons découvert que l'espèce la plus abondante, *Actitis macularia*, se nourrissait des diverses graminées de l'arrière-plage. *Charadrius wilsonia* et *C. semipalmatus* préféraient une autre section de la plage, couverte de débris organiques et inorganiques, et *Calidris mauri* avait une nette préférence pour l'avant-plage humide. On traite de l'importance des aires de repos comme ressource limitée pour les oiseaux de rivage migrateurs.

Dept. Biología, Univ. del Valle, AA 25360, Cali, Colombia¹.

Introduction

The Buenaventura Bay on the Pacific coast of Colombia (03°48'N, 77°10'W) has been shown to be important both as a stop-over area and as wintering grounds for populations of several species of Nearctic shorebirds (Franke 1986; Naranjo *et al.* 1987). Banding of several hundred shorebirds in the area during the last seven years has indicated strong site fidelity for all species, with several sites around the bay supporting different populations of sandpipers and plovers.

One of these sites is the Punta Soldado Island. Since 1985, we have found this site to be used as a

feeding area only by a few shorebirds at a time; at the same time, however, large numbers of roosting shorebirds congregate there. As there is no other locality around the bay where this phenomenon occurs, and as the roosting sites are restricted points of the beach of Punta Soldado, we sought to determine whether spatial segregation among species might be occurring. If such segregation can be demonstrated and if special features of the habitat are related to the pattern of occupation of discrete sectors of the coastline, the availability of suitable roosting sites may be a limiting resource for wintering shorebirds.

¹ This paper is contribution No. 01 of CALIDRIS, Asociación para el Estudio y Conservación de Aves Marinas y Playeras en Colombia.

Study area and methods

Punta Soldado is located at the north-western end of the Buenaventura Bay. The island is separated from the mainland by a network of channels and mudflats partially covered by mangroves, but its outer shore is mostly a continuous sand beach. Tidal fluctuations are wide (up to 4 m), and during the high waters only a narrow tongue of this external beach is exposed.

We conducted visual counts of shorebirds and evaluated the roosting site at the peak of the 1990 fall migration. Birds were counted four times on 27 October using a 40× spotting scope, and their locations were mapped relative to a grid (10 m × 10 m squares) of wooden markers planted on the ground, from the surf line to the inner boundary of the beach, naturally marked by grasses and shrubs.

On 28 October, we measured the total area of the roosting site and determined the boundaries between microhabitats according to substrate texture and humidity, accumulation of debris and the slope of the beach measured with a clinometer located on a 10-m-long string tied to poles and parallel to the substrate.

Habitat selection and spatial segregation were examined by a chi-squared test for randomness of the location of each particular species.

Results

The roosting site can be divided into four zones parallel to the shoreline. The outermost zone (number 1 in Table 1) corresponded to the shoreline proper and could be recognized by both texture (fine-grained sand) and humidity. Its width (perpendicular to the shoreline) was 20 m, and its slope was 2°. The second zone (number 2 in Table 1) was not directly affected by the surf, and the relatively dry sand in that zone contained a few pieces of debris. This segment, 100 m wide with a slope of 1.8°, was densely occupied by crabs (*Ocypode gaudichaudii*) and their burrows. The third zone (number 3) was the most distinct of all because of the loose coarse sand and the heavy deposition of debris. It was completely flat (slope = 0°), and its width averaged 20 m. Immediately after this zone, the beach ends in a fourth zone (number 4), 5 m wide with a slope of -0.14°, formed by fine-grained sand and locally humid because of the drainage of fresh water from inland. The inner edge of the beach was abrupt and coincided with a bank of mixed (sand-clay) texture. Bordering this bank, an additional zone of variable width was recognizable because of its dense cover of grasses and shrubs.

A total of seven species of shorebirds was recorded on the roost. We counted a few Whimbrels *Numenius phaeopus*, Willets *Catoptrophorus semipalmatus* and Sanderlings *Calidris alba* along the shoreline, but the roost proper (zones 1–4) was occupied only by Western and Spotted sandpipers (*Calidris mauri* and *Actitis macularia*) and Semipalmated and Wilson's plovers (*Charadrius semipalmatus* and *C. wilsonia*).

Adding up the numbers of shorebirds in discrete flocks arriving at the roosting site, we estimated that approximately 5,000 individuals spent the night on the beaches of Punta Soldado. This figure is realistic: during our first banding night at the roost, 99 birds were captured, and, although several banded birds were observed the following day, none of the 75 birds captured the second night was banded.

The results of four diurnal censuses carried out in 1990 are presented in Table 1. The Spotted Sandpiper is not included in our analyses, because these birds occupied the roost only at night and began to disperse before we had enough light to conduct our censuses. As the counts progressed, some movement between zones and from other sites along the beach to and from the roost was apparent for all species. Western Sandpipers moved towards the outermost zone following the retiring surf line while feeding; Semipalmated Plovers were leaving the roost at the same time, and Wilson's Plovers tended to concentrate around freshwater ponds at the innermost zone of the beach.

The regularity of the microhabitat choice was also evident. Testing the null hypothesis of random occupancy of the different sectors, by means of a chi-squared test, yielded significant rejection in all cases (for censuses 1–4, respectively, $\chi^2 = 356.81, 290.75, 471.02$ and $315.1, p < 0.001$).

Discussion

Although we do not have information on inter-specific territoriality for the roost, this pattern of occupation strongly suggested selection for particular features of the microhabitat. Whereas the Western Sandpiper favoured the outer beach exposed to wave action, as well as the second band of humid sand, and the Wilson's Plover definitely preferred the innermost part of the beach, the Semipalmated Plover occupied all four zones. This pattern could be interpreted in terms of differential activity among species. Whereas the Western Sandpiper alternated roosting and comfort behaviour with variable bouts of feeding along the humid shoreline and the Wilson's Plover did the same around freshwater ponds, Semipalmated Plovers remained lying on their bellies,

Table 1. Roosting shorebird abundances across the beach of Punta Soldado in October 1990. For a description of zones, see text.

Species	Beach zone	Counts at different times of the day			
		07:00	07:30	08:00	08:30
Western Sandpiper	1-2	50	57	182	80
	3	54	58	31	0
	4	0	0	0	0
Semipalmated Plover	1-2	255	150	0	0
	3	107	37	0	0
	4	135	135	58	0
Wilson's Plover	1-2	0	0	0	0
	3	34	68	0	0
	4	211	211	200	235

camouflaged amid pieces of wood, dry leaves and inorganic litter. In addition, the presence of large numbers of Spotted Sandpipers roosting at night at the innermost zone of the beach also suggested habitat selection for roosting.

Because our censuses were made at a time of day when the birds had begun to fly towards the mudflats inside the bay, the numbers used for the analyses represent only a sample of the total populations. Nevertheless, we assume that our figures reflect the pattern of occupation of the roost, judging from observations of birds settling down on the beach during the evening.

The importance of the site as a restricted roost is further inferred from the fact that, although the beach continues towards the south-west, we have not detected a single flock spending the night at a different spot. Taking this into account, it is also important to note that there are no other sites with similar characteristics of width at high tide, slope and deposition of litter around the mouth of Buenaventura Bay. A similar trend was noted by Morrison & Ross (1989) for the Colombian Pacific coastline around Guapi, where sandy points of the beach were heavily occupied by small shorebirds at high tide. However, these authors failed to detect important numbers of peeps in the sector, which included our study area, although their survey was also made during high tide. Whereas the aerial surveys of Morrison & Ross (1989) yielded a total of only 181 shorebirds in our study area at the peak of migration, our lowest diurnal count (when most birds had left the roost) amounts to 315 birds!

Taking into account these facts, it thus seems likely that not only the area around Buenaventura Bay but also the rest of the sandy Pacific coastline of

Colombia support a population of shorebirds much larger than has been reported in the literature. Conservation efforts concerning the fate of migrant shorebirds in the Neotropics must take into account the existence of such restricted roosts as limiting resources. Beach sectors of a few hundred square metres may be particularly vulnerable to destruction owing to natural processes like erosion and plant succession and to human disturbance. An adequate evaluation of populations at these sites must be given top priority in the next few years if we want to preserve the ever-fascinating miracle of shorebird migration in the continent.

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Conservation of Charadriiformes on the Peruvian coast

Victor Pulido, Jaime Jahncke, Patricia Makamatsu & Cecilia Flores

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On the Pacific coast of Peru, the order Charadriiformes is represented by 75 species, of which 16 are resident and 59 migrate from the Nearctic and Austral regions and the Galapagos Islands. On the basis of studies done on shorebirds between 1982 and 1991, suggestions are put forward for modifying the criteria for the establishment of Hemispheric, International and Regional reserves within the Western Hemisphere Shorebird Reserve Network along the coasts of the southern Pacific. Also proposed is a strategy to be followed for the conservation of migratory birds on the coasts of Peru.

En la costa del Pacifico en Peru, el orden de los Charadriiformes esta representado por 75 especies, de las cuales 16 son residentes y 59 migran de las regiones nearctica y austral y de las islas Galapagos. En base a estudios hechos sobre aves playeras entre 1982 y 1991, se plantean sugerencias para modificar los criterios para el establecimiento de reservas hemisfericas, internacionales y regionales en el marco de la Red de Reservas de aves Playeras del hemisfero Occidental a lo largo de las costas del oceano Pacifico sur. Tambien se propone una estrategia para la conservacion de aves migratorias en las costas de Peru.

Sur la côte pacifique du Pérou, l'ordre des Charadriiformes compte 75 espèces, dont 16 y nichent et 59 y migrent depuis les régions néarctiques et australes et les îles Galapagos. Sur la foi d'études d'oiseaux de rivage effectuées entre 1982 et 1991, on propose des modifications aux critères d'établissement, pour les côtes du Pacifique Sud, des réserves hémisphériques, internationales et régionales du Réseau de réserves pour les oiseaux de rivage de l'hémisphère occidental. On recommande aussi l'adoption d'une stratégie de conservation des oiseaux migrateurs des côtes du Pérou.

Instituto Nacional de Investigación Agraria y Agroindustrial, Dirección de Investigación y Vida Silvestre [National Institute for Agricultural and Agroindustrial Research, Research and Wildlife Division], Apdo. Postal 11-0150 Lima 11, Peru.

Introduction

Until 1980, few studies had been done in Peru on the Charadriiformes that inhabit the Peruvian coast (e.g. Hughes 1968, 1970, 1976, 1979; Tovar & Ashmole 1970). Only part of studies conducted by the Peruvian Oceanic Institute (IMARPE) included Charadriiformes. In 1982, the Wildlife Directorate of the former National Wildlife Authority (INFOR), together with the Pan American Shorebird Program, the Philadelphia Academy of Science and other Peruvian non-governmental organizations, undertook the first studies on bird migration. In September 1982, under the leadership of J.P. Myers, a census of shorebirds was undertaken, and Sanderlings *Calidris alba* were banded on the sandy seashore of the Mejia resort area on the southern coast of Peru (Pulido 1983a, 1983b).

In March of the following year, censusing and banding of migratory shorebirds continued in the Mejia Lagoons National Bird Sanctuary and in the Paracas National Reserve. In 1983 and 1984, new

research was begun in Paracas and in the Villa beaches and Paraiso Lagoon by E. Ortiz and G. Castro, respectively. These studies later extended to work on the ecology and conservation of areas important to shorebirds (Castro 1984; Castro & Myers 1987; Castro, Myers & Bertochi 1988; Castro, Ortiz & Bertochi 1990).

In 1985, under a letter of agreement between the Canadian Wildlife Service of Environment Canada and the former INFOR, a collaborative programme was set up to study the feeding habits and ecology of the Common Tern *Sterna hirundo* (Pulido 1987). In February 1986, the first aerial census of shorebirds was done along the entire Peruvian coast between Tumbes and Tacna. The resulting data were used by R.I.G. Morrison and R.K. Ross in the *Atlas of Nearctic shorebirds on the coast of South America* (Morrison & Ross 1989).

In 1987, 1989 and 1991, the Wildlife Research Directorate of the Instituto Nacional de Investigación Agraria y Agroindustrial (INIAA),

with the support of national and international organizations, organized workshops on research and conservation of wild birds, which included banding campaigns in the Paracas National Reserve. Nearly 1,600 specimens of various species of shorebirds were banded. Further banding campaigns took place in Paracas in 1990 and 1991.

Field studies undertaken along the Peruvian and the entire Pacific and Atlantic coasts have made it possible to standardize the banding of migratory shorebirds using metal bands and coloured flags and bands (Myers *et al.* 1987a, 1987b; Pulido 1989) and to establish avenues for research (Castro 1985; Castro & Sallaberry 1986).

This study covers certain aspects of shorebird migration along the Pacific coast of Peru, including (1) the results of banding done over five years from 1987 to 1991, (2) the identification of those areas important to the conservation of shorebirds in Peru and (3) suggestions for the establishment of shorebird reserves by the Western Hemisphere Shorebird Reserve Network (WHSRN).

Shorebird migrations along the Pacific coast of Peru

Many migrant shorebirds that stop over on the coast of Peru come from the Nearctic region (Canada and the United States), the Galapagos Islands (Ecuador) and the Austral region (South Pole and Chile) by horizontal migration. Others migrate vertically when descending from the Andes to the Pacific coast or the Amazon region.

Of the 11 families that make up the order Charadriiformes, 10 occur in Peru (Parker, Parker & Plenge 1982; Hayman, Marchant & Prater 1986) (Table 1). These 10 families comprise 86 species, of which 75 (87%) inhabit Peru's coasts either temporarily or permanently. Of the 75 coastal species, 16 species are resident, whereas 59 are migratory species originating from the Nearctic region (48), the Austral region (6), the Galapagos Islands (1) and the Peruvian Andes (4) (Table 2).

Of the 10 families that occur in Peru, Scolopacidae is represented by 27 species (all of them Nearctic and migratory), followed by Laridae with 22 species (7 resident and 15 migratory) and Charadriidae with 11 species (4 resident and 7 migratory). The 7 remaining families include between 1 and 5 species.

Banding of shorebirds from 1987 to 1991

Six banding campaigns were carried out in the Paracas National Reserve in 1987 through to 1991. Shorebirds were banded in March 1987 (395), March

1989 (474), February and March 1990 (138 and 312 birds, respectively) and March and April 1991 (81 and 160, respectively). Overall, 1,560 specimens were banded: 568 Semipalmated Sandpipers *Calidris pusilla*, 519 Western Sandpipers *Calidris mauri*, 439 Sanderlings, 19 Short-billed Dowitchers *Limnodromus griseus*, 14 Semipalmated Plovers *Charadrius semipalmatus* and 1 Black-bellied Plover *Pluvialis squatarola* (Table 3).

Both the recapture and recovery rates were very low. For recaptured birds, the percentage did not exceed 2% of total birds banded for that campaign. For recoveries, the percentage on one occasion rose exceptionally high to 12%, pointing to a certain degree of site fidelity in migratory birds wintering in Paracas.

Important areas for shorebird conservation in Peru

The Peruvian coast is an arid strip, 3,080 km long and up to 200 km wide, which extends along the maritime littoral between Boca Capones in the north and Concordía in the south (Peñaherrera 1989). Its topography is varied; it includes 53 major rivers, vast expanses of coastal desert, cropland and hill formations. Throughout is a series of wetlands important to the conservation of Charadriiformes.

Of the most important wetlands along the Peruvian coast, only three are protected: the National Tumbes Mangrove Swamp Sanctuary (2,972 ha), the Paracas National Reserve (335,000 ha, of which 217,594 ha are marine) and the Mejia Lagoons National Bird Sanctuary (690.6 ha). Among the unprotected wetlands are the Virrilá Estuary, the San Pedro mangrove swamps, the Lambayeque coasts and the Paraiso Lagoon. Of all these areas, only the Paracas National Reserve has been recognized by the WHSRN, designated as a Regional reserve in September 1991.

Other wetlands of national importance on the Peruvian coast include the Ramón Lagoon, the mouth of the Chira River, the mouth of the Piura River, the mouth of the Eten River, the Medio Mundo Lagoons, the Villa Swamps Reserve, the mouth of the Lurín River, the Puerto Viejo Lagoons, the mouth of the Chíncha River, the mouth of the Pisco River, the Agua Santa Lagoons, Punta Lomitas, Asma, the Tilimaco Lagoons, the Pucchún Lagoons, the mouth of the Camaná River, the mouth of the Tambo River, Punta Coles, the mouth of the Locumba River, the Ite Lagoons and the beaches of Tacna. All these wetlands of recognized importance to migratory birds are interconnected in various ways by means of avian migration routes. The distances between them range from a few kilometres to not more than 100 km. It is therefore important to protect most of these aquatic

Table 1. Species of Charadriiformes and their status on the Peruvian coast. R = resident, A = Austral (migratory), S = southern, An = Andes (migratory), G = Galapagos (migratory) and N = Nearctic.

Family/Species	Common name	Status
Haematopodidae		
<i>Haematopus palliatus</i>	American Oystercatcher	R
<i>Haematopus ater</i>	Blackish Oystercatcher	R
Charadriidae		
<i>Vanellus resplendens</i>	Andean Lapwing	An
<i>Pluvialis squatarola</i>	Black-bellied Plover	N
<i>Pluvialis dominica</i>	Lesser Golden-Plover	N
<i>Charadrius semipalmatus</i>	Semipalmated Plover	N
<i>Charadrius alexandrinus</i>	Snowy Plover	R
<i>Charadrius alticola</i>	Puna Plover	An
<i>Charadrius collaris</i>	Collared Plover	R
<i>Charadrius vociferus</i>	Killdeer	R
<i>Charadrius wilsonia</i>	Wilson's Plover	N
<i>Charadrius modestus</i>	Rufous-chested Dotterel	A
<i>Oreopholus ruficollis</i>	Tawny-throated Dotterel	R
Scolopacidae		
<i>Aphriza virgata</i>	Surfbird	N
<i>Arenaria interpres</i>	Ruddy Turnstone	N
<i>Tringa solitaria</i>	Solitary Sandpiper	N
<i>Tringa flavipes</i>	Lesser Yellowlegs	N
<i>Tringa melanoleuca</i>	Greater Yellowlegs	N
<i>Actitis macularia</i>	Spotted Sandpiper	N
<i>Heteroscelus incanus</i>	Wandering Tattler	N
<i>Catoptrophorus semipalmatus</i>	Willet	N
<i>Calidris canutus</i>	Red Knot	N
<i>Calidris minutilla</i>	Least Sandpiper	N
<i>Calidris bairdii</i>	Baird's Sandpiper	N
<i>Calidris fuscicollis</i>	White-rumped Sandpiper	N
<i>Calidris melanotos</i>	Pectoral Sandpiper	N
<i>Calidris pusilla</i>	Semipalmated Sandpiper	N
<i>Calidris mauri</i>	Western Sandpiper	N
<i>Calidris alba</i>	Sanderling	N
<i>Calidris alpina</i>	Dunlin	N
<i>Calidris ferruginea</i>	Curlew Sandpiper	N
<i>Calidris himantopus</i>	Stilt Sandpiper	N
<i>Tringites subruficollis</i>	Buff-breasted Sandpiper	N
<i>Philomachus pugnax</i>	Ruff	N
<i>Bartramia longicauda</i>	Upland Sandpiper	N
<i>Numenius phaeopus</i>	Whimbrel	N
<i>Limosa haemastica</i>	Hudsonian Godwit	N
<i>Limosa fedoa</i>	Marbled Godwit	N
<i>Limnodromus scolopaceus</i>	Long-billed Dowitcher	N
<i>Limnodromus griseus</i>	Short-billed Dowitcher	N
Recurvirostridae		
<i>Himantopus mexicanus</i>	Black-necked Stilt	A
<i>Recurvirostra andina</i>	Andean Avocet	An
Phalaropodidae		
<i>Phalaropus fulicaria</i>	Red Phalarope	N
<i>Phalaropus lobatus</i>	Red-necked Phalarope	N
<i>Phalaropus tricolor</i>	Wilson's Phalarope	N
Stercorariidae		
<i>Catharacta chilensis</i>	Chilean Skua	A
<i>Catharacta maccormicki</i>	South Polar Skua	A
<i>Stercorarius pomarinus</i>	Pomarine Jaeger	N
<i>Stercorarius parasiticus</i>	Parasitic Jaeger	N
<i>Stercorarius longicaudus</i>	Long-tailed Jaeger	N
Burhinidae		
<i>Burhinus superciliaris</i>	Peruvian Thick-knee	R

Continued

Table 1. (Cont'd) Species of Charadriiformes and their status on the Peruvian coast. R = resident, A = Austral (migratory), S = southern, An = Andes (migratory), G = Galapagos (migratory) and N = Nearctic.

Family/Species	Common name	Status
Thinocoridae		
<i>Thinocorus rumicivorus</i>	Least Seedsnipe	R
Laridae		
<i>Larus modestus</i>	Grey Gull	A
<i>Larus belcheri</i>	Peruvian Tern	R
<i>Larus dominicanus</i>	Kelp Gull	R
<i>Larus atricilla</i>	Laughing Gull	N
<i>Larus cirrocephalus</i>	Grey-hooded Gull	R
<i>Larus serranus</i>	Andean Gull	An
<i>Larus pipixcan</i>	Franklin's Gull	N
<i>Xema sabini</i>	Sabine's Gull	N
<i>Creagrus furcatus</i>	Swallow-tailed Gull	G
<i>Cheidonias niger</i>	Black Tern	N
<i>Gelochelidon nilotica</i>	Gull-billed Tern	N
<i>Sterna hirundinacea</i>	South American Tern	R
<i>Sterna hirundo</i>	Common Tern	N
<i>Sterna paradisaea</i>	Arctic Tern	N
<i>Sterna trudeaui</i>	Trudeau's Tern	A
<i>Sterna fuscata</i>	Sooty Tern	R
<i>Sterna albifrons</i>	Little Tern	N
<i>Sterna lorata</i>	Peruvian Tern	R
<i>Sterna maxima</i>	Royal Tern	N
<i>Sterna elegans</i>	Elegant Tern	N
<i>Sterna sandwicensis</i>	Sandwich Tern	N
<i>Larosterna inca</i>	Inca Tern	R
Rynchopidae		
<i>Rynchops niger</i>	Black Skimmer	R

Table 2. Numbers of resident and migratory species of Charadriiformes on the Peruvian coast. R = resident, A = Austral (migratory), S = southern, An = Andes (migratory), G = Galapagos (migratory) and N = Nearctic (migratory).

Family	R	N	A	G	An	Total species
Haematopodidae	2	-	-	-	-	2
Charadriidae	4	4	1	-	2	11
Scolopacidae	-	27	-	-	-	27
Recurvirostridae	-	-	1	-	1	2
Phalaropodidae	-	3	-	-	-	3
Stercorariidae	-	3	2	-	-	5
Burhinidae	1	-	-	-	-	1
Thinocoridae	1	-	-	-	-	1
Laridae	7	11	2	1	1	22
Rynchopidae	1	-	-	-	-	1
Total species	16	48	6	1	4	75

environments using the legal instruments available to the Peruvian government.

Suggestions for the establishment of shorebird reserves as part of the WHSRN

Some of the criteria for establishing International, Hemispheric and Regional shorebird reserves within the WHSRN may need to be modified in the

case of areas that do not meet the criteria established to date, such as those along the coast of the southern Pacific.

In principle, the same parameters should be used to establish Hemispheric, International or Regional reserves for the Nearctic region as for the Neotropical region. However, the farther away wintering grounds are located, the fewer species and individuals reach them (Rappole *et al.* 1983),

Table 3. Shorebirds banded in Paracas.

Species	Status	87/3	89/3	90/2	90/3	91/3	91/4	Total
<i>Calidris alba</i>	1	118	37	9	66	51	158	439
	2	1	0	0	0	0	4	5
	3	11	2	0	4	5	12	<u>34</u>
								478
<i>Calidris mauri</i>	1	100	216	59	114	30	0	519
	2	5	0	0	3	1	0	9
	3	5	2	5	9	0	0	<u>21</u>
								549
<i>Calidris pusilla</i>	1	165	211	69	123	0	0	568
	2	2	0	0	3	0	0	5
	3	6	2	5	10	8	9	<u>40</u>
								613
<i>Charadrius semipalmatus</i>	1	1	9	0	3	0	1	14
	2	0	0	0	0	0	0	0
	3	0	1	0	0	0	0	1
								15
<i>Limnodromus griseus</i>	1	11	1	1	5	0	1	19
	2	0	0	0	1	0	0	1
	3	1	0	0	1	0	0	<u>2</u>
								22
<i>Pluvialis squatarola</i>	1	0	0	0	1	0	0	1
	2	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	<u>0</u>
								1
Total banded		395	474	138	312	81	160	1,560
Total recaptured		8	0	0	7	1	4	20
Total recovered		23	7	10	24	13	21	98
Total captured		426	481	148	343	95	185	1,678

although they may be essential habitats for those that do.

In the Nearctic region, in both pre-breeding and post-breeding periods, large numbers of plovers and shorebirds concentrate at key sites, such as Delaware Bay and the Bay of Fundy on the Atlantic coast, San Francisco Bay and the Copper River Delta on the Pacific coast and Stillwater, Great Salt Lake and Cheyenne Bottoms in continental areas.

There are also sites with high concentrations of shorebirds on the coasts of the southern Atlantic: the large populations of (1) Semipalmated Sandpiper on the coasts of Suriname (about 80% of the world population), (2) Wilson's Phalarope *Phalaropus tricolor* and Red-necked Phalarope *P. lobatus* in the Mar Chiquita Lagoon in Argentina and (3) Red Knot *Calidris canutus*, White-rumped Sandpiper *C. fuscicollis* and Hudsonian Godwit *Limosa haemastica* in Tierra del Fuego. Generally speaking, those species that breed farther north occupy overwintering areas farther south (Myers *et al.* 1987a). In contrast, on the Pacific coast, smaller concentrations of birds are dispersed over a wide area.

Another factor is that shorebird populations in the Nearctic region are close to attaining the optimal

numbers of birds in relation to their reproductive capacity. Furthermore, these populations include juveniles that have opted not to migrate south, adults that have bred and those birds born in the boreal summer of the year. In the south, only part of the population that began the post-breeding migration actually reaches the wintering grounds, *i.e.* some of the juveniles, immature birds and breeding adults. From this total must be subtracted the number of birds that die during the post-breeding migration to the wintering grounds and those that die at the wintering grounds from depredation or other climatic factors or because of the destruction of their habitat, which affects birds concentrating in small areas during migration.

This means that the possibility of a population of migratory birds disappearing with the passage of time is greater at wintering sites. This is fundamentally due to the destruction of habitats, which is occurring more rapidly every year in South America as a result of anthropogenic activities.

Time is another factor. As the breeding period is relatively short (from June to August), birds are forced to have a greater sense of timing in the north, particularly those migrating great distances from the Arctic (Myers *et al.* 1987a). This exerts pressure on birds to obtain certain advantages and to locate

better nesting sites to ensure breeding success. The result is a longer wintering period, which also includes pre- and post-breeding travel.

It is also likely that a greater destruction of northern areas supporting habitats for these birds is causing a greater concentration of birds in particularly productive sites. Senner & Howe (1984) showed that birds do not have the option of locating in other areas given the availability of food and habitats precisely in those specific locations. With regards to food supply, food is abundant in the north, which makes large concentrations of birds possible, especially at particular times, such as at the end of May in Delaware Bay (Myers 1986). Along the coast of the southern Pacific, on the other hand, maximum advantage is taken of available food. In the first case, the limiting factor is space, and in the second, it is food. With regards to habitat in the United States, by 1978 close to 40% of all aquatic and continental habitats had been lost (Horwitz 1978). Although no quantitative data are available, the destruction of wetlands in South America has probably not yet reached that extent, which should make a wider dispersion of birds possible, as there is more habitat available. Then there is the fact that some populations spend a relatively short period of time at each wintering site. It is therefore important to conserve not one location but several locations near each other along the coast, as is the case in coastal Peru.

A different survival strategy is adopted by birds in the south than in the north. While in the north, they survive to nest and thus ensure breeding success; in the south, they survive to recover from the post-breeding migratory effort and to store sufficient energy during the wintering period to reinitiate the return on pre-breeding flights.

Although the criteria for establishing reserves by the WHSRN are appropriate for North America and for the Atlantic coast of South America, they need to be modified for the southern Pacific. The WHSRN, in addition to taking into account the number of birds in a given place, must also stress other aspects such as species diversity, strategic staging sites along migration routes, the natural and pristine state of aquatic environments and their importance as conservation areas for resident and migratory species.

On the Pacific coast of Peru and northern Chile, the presence of the Humboldt Current ensures the existence of numerous coastal areas with an appreciable food supply. However, basic factors such as human intervention and pollution and the destruction and disappearance of wetlands could be forcing birds to fly to different wintering areas. The low recovery rates of banded shorebirds would appear to confirm this.

The Mejia Lagoons, for instance, constitute one of the most important wetlands of the Pacific coast of Peru. One of the largest Sanderling populations is concentrated here. Even so, the number of birds of this species is not sufficient to include the Mejia Lagoons in any of the WHSRN's categories. Nonetheless, in this single protected area of 690.6 ha, 172 species have been recorded, or one species for every 4 ha (Pulido 1987; Pulido & Myers 1987). Also, 64 species of Charadriiformes were found on 10 km of beach, or between 6 and 7 species per kilometre.

For this reason, the appropriate strategy for the conservation of migratory shorebirds must necessarily include the establishment of a series of protected areas along the Peruvian coast. First, the establishment of such areas must be approved and supported by the Peruvian government. Second, efforts must be concentrated on managing these areas. This means not only applying protective measures but also developing a plan for the comprehensive management of wetlands. To this end, it is necessary to consider important factors such as staging sites, feeding grounds, variations in water levels and habitat diversity in such management areas. Only in this way will it be possible to ensure the conservation of wetlands along the Peruvian coast so that shorebirds from different latitudes may find a safe place to stop along the way in the yearly migration to their overwintering areas.

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Migratory bird activity in the bay of Lake Titicaca, Puno, Peru

Angel G. Canales

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Apeco-Puno, Casilla 448, Peru.

Lake Titicaca is located between Peru and Bolivia at an altitude of 3,808 m and covers an area of 8,167 km². This aquatic ecosystem is a very important habitat for both resident and migrant species of birds. The first migrants arrive around mid-August. They remain in the area until April, when they begin the northward migration to their breeding areas.

Field work for the present study was undertaken between, and including, January and March 1990, in a feeding and staging area of 40 ha known as 'Chejona', south of the city of Puno.

The aim of this study was to determine the foraging habitats used most by two species of tattlers (Greater Yellowlegs *Tringa melanoleuca* and Lesser Yellowlegs *Tringa flavipes*), one calidrine sandpiper (Baird's Sandpiper *Calidris bairdii*) and one phalarope (Wilson's Phalarope *Phalaropus tricolor*).

The study area was surveyed twice monthly with binoculars. The area was subdivided into three distinct foraging habitats: (1) the water surface, (2) the lakeshore and (3) marshes.

Phalaropus tricolor was the most abundant species, with an average number per visit of 280 birds, but a daily maximum of 1,200 phalaropes was also recorded (Table 1). *Calidris bairdii* was the least abundant species, with a daily average of 28 birds recorded and a peak number of 49. At most times, all species foraged together, along with many ducks, geese and swans. The only exception to this was *Tringa melanoleuca*; some individuals were occasionally seen to forage alone.

As shown in Table 2, the four species spent 36–72% of their foraging time at the lake shore and the remainder in the marshes. Some phalaropes were seen on the water surface, but it was not a commonly used foraging habitat. Rather, the phalaropes spent 64% of the time in the marshes.

Most of the birds' foraging occurred during the early morning hours, although all species continued to feed extensively at mid-day and only slightly less during the late afternoon/early evening hours (Table 2).

Table 1. Maximum numbers of birds seen over the study period and average number of birds seen per visit in the study area.

Species	Maximum number	Average number
<i>Tringa melanoleuca</i>	79	32
<i>Tringa flavipes</i>	160	75
<i>Phalaropus tricolor</i>	1,200	280
<i>Calidris bairdii</i>	49	28

Table 2. Foraging habitats used by shorebirds in the Chejona area of Lake Titicaca between, and including, January and March 1990.

Species	Habitat ^a			% time in habitat		
	WS	L	W	06:00–08:00	12:00–14:00	16:00–18:00
<i>T. melanoleuca</i>	0	72	28	96	93	84
<i>T. flavipes</i>	0	56	44	97	95	87
<i>C. bairdii</i>	0	46	41	98	96	94
<i>P. tricolor</i>	13	36	64	93	90	82

^a WS = water surface; L = lake shore; W = wetland.

Analysis of Red Knot *Calidris canutus rufa* banding data in Brazil

Paulo T.Z. Antas & Inêz L.S. Nascimento

Antas, P.T.Z. & Nascimento, I.L.S. 1996. Analysis of Red Knot *Calidris canutus rufa* banding data in Brazil. *International Wader Studies* 8: 63-70.

During the first two weeks in April, most Red Knots captured in Lagoa do Peixe in Brazil moulted their contour feathers to attain full breeding plumage; primaries and tail feathers were moulted in November, when the birds first arrived at the wintering grounds. Body masses increased over the first two weeks in April, although mean body masses varied considerably between years. Red Knots in Lagoa do Peixe originated from southern Argentina and Chile and migrated north to Punta Rasa and the coast of Rio Grande do Sul, to Maranhão state in northern Brazil and subsequently to Delaware Bay and Cape May, New Jersey. Southward migrants into Brazil originated from South Carolina and Massachusetts in July and August and Guyana in September.

Durante las dos primeras semanas de abril, la mayoría de los canutos rojos (también conocidos como 'correlimos gordo') capturados en Lagoa do Peixe en Brasil mudaron sus plumas de contorno para cambiar a un plumaje de reproducción; mudaron las plumas primarias y caudales en noviembre, cuando las aves llegan primero al territorio de invierno. La masa corporal aumentó en las primeras dos semanas en abril, si bien la masa corporal media varió considerablemente de un año a otro. Los canutos rojos en Lagoa do Peixe vienen del sur de Argentina y Chile y migran al norte a Punta Rasa y la costa de Rio Grande do Sul, al estado de Maranhão en el norte de Brasil y posteriormente a la bahía Delaware y Cabo May, Nueva Jersey. Las aves que migran hacia el sur a Brasil provienen de Carolina del Sur y Massachusetts en julio y agosto y de Guyana en septiembre.

Au cours des deux premières semaines d'avril, la plupart des bécasseaux maubèches capturés dans le Lagoa do Peixe au Brésil perdaient leurs plumes de contour pour acquérir leur plumage nuptial complet. Les rémiges primaires et les plumes de la queue étaient tombées en novembre lorsque les oiseaux sont arrivés aux aires d'hivernage. Leurs masses corporelles ont augmenté au cours des deux premières semaines d'avril, quoique les masses corporelles moyennes varient considérablement d'une année à l'autre. Les bécasseaux maubèches du Lagoa do Peixe proviennent du sud de l'Argentine et du Chili; au cours de leur migration vers le nord, ils sont passés par Punta Rasa et la côte du Rio Grande do Sul, ainsi que par l'État de Maranhão dans le nord du Brésil, avant d'arriver dans la baie du Delaware et au cap May, dans le New Jersey. Les oiseaux migrant vers le sud, vers le Brésil, sont partis de la Caroline du Sud et du Massachusetts en juillet et août, et de la Guyane en septembre.

Centro de Pesquisas para Conservação das Aves Silvestres (CEMAVE), Parque Nacional de Brasília, Via EPIA, S.M.U.-Brasília, CEP 70.63, Brazil.

Introduction

The Red Knot *Calidris canutus rufa* is one of the Nearctic subspecies of knots breeding in the central Canadian Arctic. Its wintering grounds in the Western Hemisphere are scattered from western Florida in the United States to Tierra del Fuego and Patagonia in Argentina and Chile (Morrison & Harrington 1992). Morrison & Ross (1989) found the largest wintering concentration in the Chilean sector of Tierra del Fuego. In Brazil, wintering flocks occur along the northern coast, the delta of the Amazon River (Morrison & Ross 1989; Morrison, Ross & Antas 1989; Morrison & Harrington 1992) and at Lagoa do Peixe National Park (31°10'S, 51°00'W) in southern Brazil (Belton 1984). Staging areas utilized by knots during spring and fall migrations are located at Rio Grande do Sul

(Belton 1984; Harrington, Antas & Silva 1986) and along the Maranhão coastline in northern Brazil (R.I.G. Morrison & P.T.Z. Antas, unpubl. data). During the breeding season, small numbers of non-breeders remain in Rio Grande do Sul and Lagoa do Peixe National Park (Belton 1984).

Because of the importance of Lagoa do Peixe for the conservation of coastal birds, including high numbers of Nearctic and Patagonian shorebirds, the Brazilian government established it as a national park in November 1986. The area was also proposed by the Instituto Brasileiro do meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) as an International reserve in the Western Hemisphere Shorebird Reserve Network (WHSRN) in March 1990. The proposal was accepted by the WHSRN Council in April 1991.

This paper summarizes the recapture/recovery data obtained from Red Knots marked and banded in Brazil and also data collected on moult and body mass.

Materials and methods

From April 1984 through to April 1991, 1,087 Red Knots were banded in Lagoa do Peixe National Park plus 3 at the mouth of the Amazon River, for a total of 1,090 birds. The birds captured in the Amazon were netted on a small island (25 ha) surrounded by mudflats. The tidal amplitude in this portion of the Brazilian coastline reaches 6 m, and the birds foraged on the available mudflats and roosted on sandy beaches during high tide.

All the birds were captured at night with mist nets erected over shallow water. Each bird received a CEMAVE (Centre for Research and Conservation of Wild Birds) metal band, either stainless steel or aluminium, as well as colour bands. From 1986 to 1991, colour band combinations were assigned by the Pan-American Shorebird Program (PASP). In that same time period, the birds were also colour-marked with a picric acid solution. Volunteers throughout Brazil and North America provided details of sightings made of these birds, and recoveries of metal bands were also reported to CEMAVE.

Data on body mass were obtained by using 300-g Pesola scales, and the birds were also examined for moult during weighing. Based on the examination of the plumages (see Prater, Marchant & Vuorinen 1977; Hayman, Marchant & Prater 1986), each bird captured was classified as (1) young-of-the-year, (2) sub-adult, (3) adult-non-breeding, (4) adult-intermediate and (5) adult-full-breeding. The data collected were lumped by week (cohorts), such that all the birds captured in the same week were treated as a single unit. In the tables and figures included in this paper, the first weekday of each week is used to represent the full week's data.

Results

Moult schedule

Although there was variation between years in the percentage of birds that had completed the moult of contour feathers, a general pattern was found (Figure 1). Most birds captured in the first week of April (1987 and 1988) were actively undergoing the moult of the contour feathers; 21% of the birds were not moulting and were already in breeding plumage. As April progressed, the percentage of non-moulting knots increased, thus showing that full breeding plumage was attained during the first two weeks of April for most of the population. The new red feathers have a dull tip, and its wear

renders the plumage brilliant red at the belly, which is noticeable in some individuals by late April or early May.

However, within the same period, the moulting schedule varied from year to year, as was shown in our 1986 sample, when 84% of the birds were not moulting. In the third week in April, 42% of the birds in 1991, 59% in 1985 and 65% in 1990 were also not moulting. The only sample available from the southward migration (the first week of November in 1986) showed that some birds were still in the process of moulting the contour feathers to the eclipse or non-breeding plumage at that time of the year, although the majority had already moulted.

Outside of the first-year cohort, which was recognized in April by the birds' completely dull plumage, very worn primaries and greenish-yellow tarsus plus light body mass, no adult or sub-adult knots were moulting flight feathers or tail feathers. This moult occurs earlier, beginning around the time the birds arrive on their wintering grounds, as the November sample suggested; four of ten knots were then moulting primaries (numbers 3-7). A similar pattern of primary moult was found in the Semipalmated Sandpiper *Calidris pusilla* wintering in north-eastern Brazil, with the adults moulting the primaries from September until December/January (Antas & Nascimento 1990). The same was also true for Sanderling *Calidris alba* wintering in Pernambuco in north-eastern Brazil (Nascimento, Antas & Azevedo-Junior 1990). In west Africa, the wintering population of *C. c. canutus* begins to moult primaries soon after its arrival in Banc d'Arguin, Mauritania (Piersma, Prokosh & Bredin 1992).

Body mass

The average body mass of the samples also showed variable patterns between years (Figure 2). The average body masses ranged from 120 to 205 g. The second-week samples showed a slight increase in average body mass over the first-week birds, except in the 1987 sample.

When the maximum individual body masses in any week over all years were compared, the general pattern was the occurrence of a plateau, which varied annually, even when comparing the same months (Figure 3). The widest difference in maximum body masses between the first and second weeks occurred in 1988, when the maximum in week 1 was 145 g and the maximum for week 2 was 244 g (Figure 3). On the other hand, in 1986, the maximum body mass in week 2 was lower than the maximum mass recorded in week 1 (Figure 3). Over all years, the lowest body mass was 140 g.

Increases in maximum body masses between weeks 1 and 2 in 1988 (see Figure 3) were probably due to

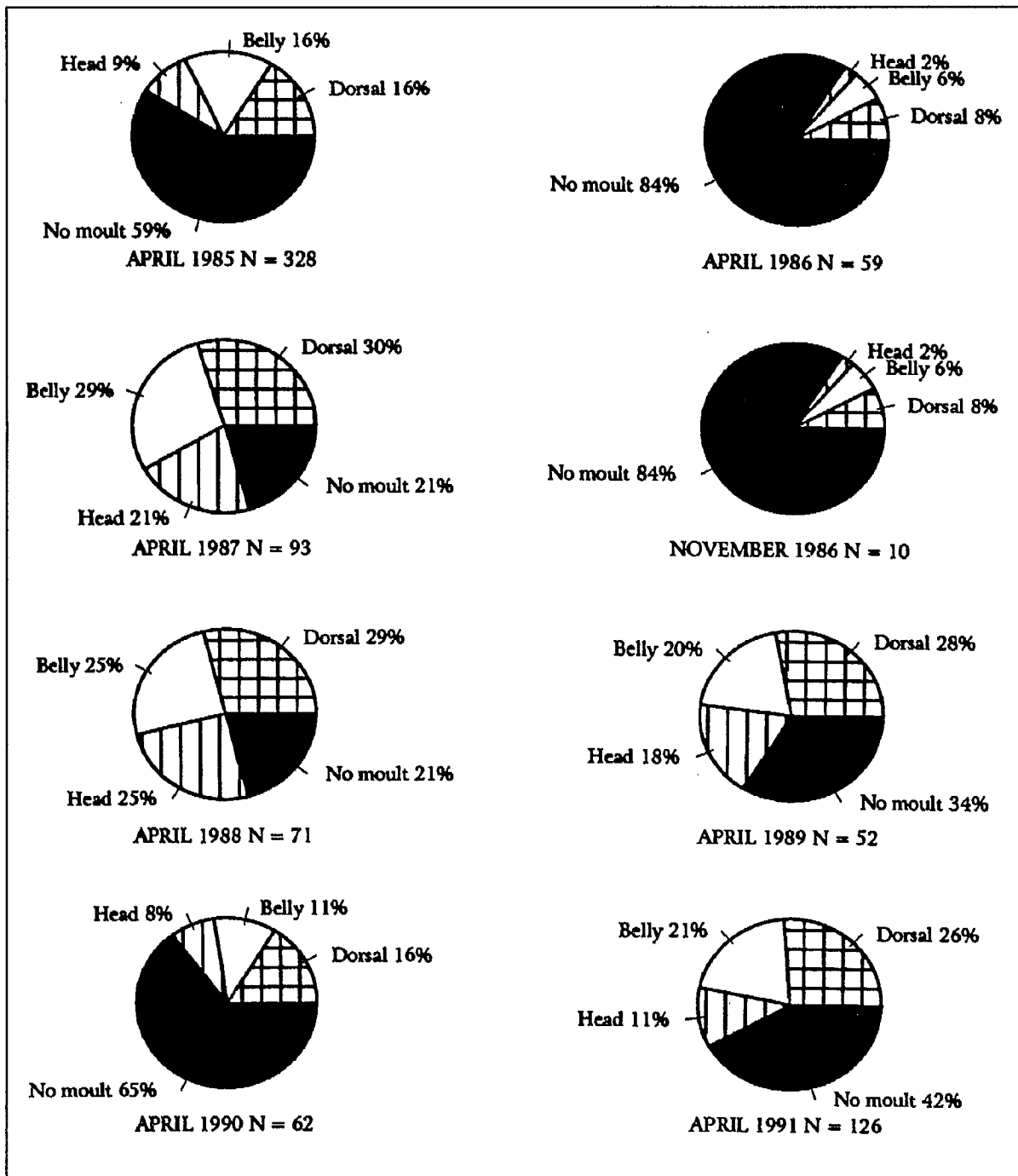


Figure 1. Body moult of *Calidris canutus* in Lagoa do Peixe National Park in Brazil.

birds coming from more southerly locations and thus arriving in Lagoa do Peixe with exceptionally high body masses. We interpreted the 1986 decrease as being due to the departure from the area by the birds with the highest body masses. The year 1986 was a year of severe drought, which was followed by very heavy rainfall. Hence, there was exceptional run-off of fresh water into the habitat, such that the lagoon contained primarily fresh and brackish water. Most of the birds that favoured a marine habitat moved from the lagoon to the seashore.

Band recoveries and sightings of colour-marked birds

To date, 144 bands and sightings of colour-marked knots that were banded or marked in Lagoa do Peixe have been reported. Only four bands were actually recovered. Of the sightings of colour-marked birds, 46 were of unknown individuals and 94 were resightings of the same birds. There were no retraps of banded birds. The annual recovery rates are shown in Table 1.

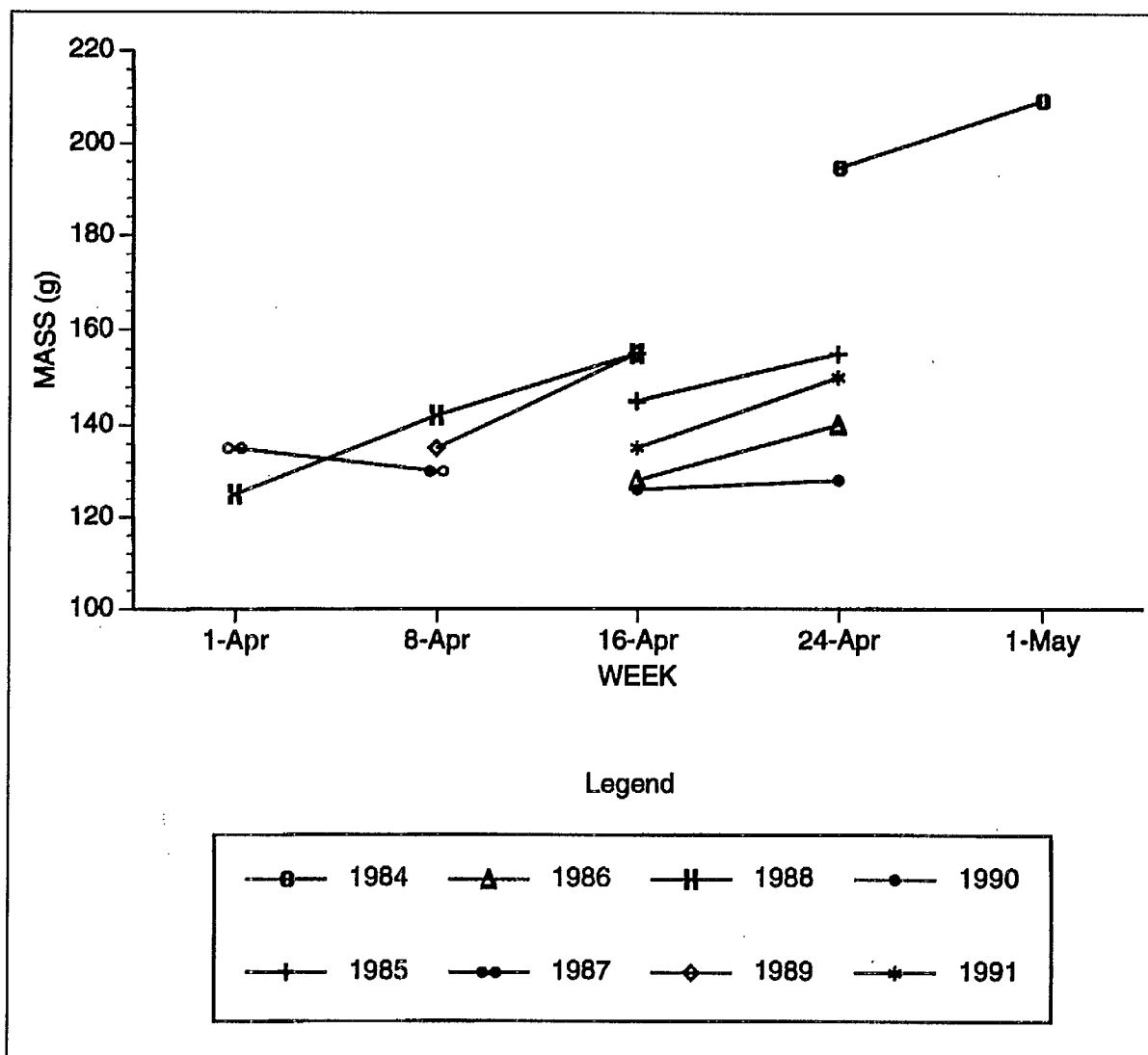


Figure 2. Average body masses of *Calidris canutus* in Lagoa do Peixe National Park, Brazil.

Northward migration

Most of the knots at Lagoa do Peixe in March, April and May originate from the southernmost portions of South America. Those birds banded and marked in Lagoa do Peixe were sighted in Punta Rasa, Buenos Aires Province, in Argentina and along the coast of Rio Grande do Sul. Knots banded in Lagoa do Peixe in April and May were subsequently seen in the northern parts of Rio Grande do Sul and south of Santa Catarina by mid-May (Figure 4). The next known stop is the Turiaçu beaches in Maranhão state in northern Brazil, again in mid-May. The time period from mid- to late May is when knots occur in Delaware Bay near Cape May. Beyond the eastern United States, there has been one sighting of our colour-marked knots, at Presqu'île Provincial Park on Lake Ontario, Canada (Figure 5).

Southward migration

The first post-breeding return came from South Carolina on 28 July 1986, when two birds were seen (Figure 6). Other birds recorded in the United States were in Massachusetts in mid-August, and two birds were seen in the Berbice area of Guyana in mid-September. There were no other records south of Lagoa do Peixe to allow us to trace the migratory path to the wintering grounds.

Discussion

The data suggest that most of the knots at Lagoa do Peixe National Park came from southerly wintering grounds in Argentina or Chile, although a small proportion overwintered there (Belton 1984).

Two lines of evidence suggest that the knots at Lagoa do Peixe moved slowly northward as April progressed. There were sightings of the previous year's colour-marked birds at Cassino beach near

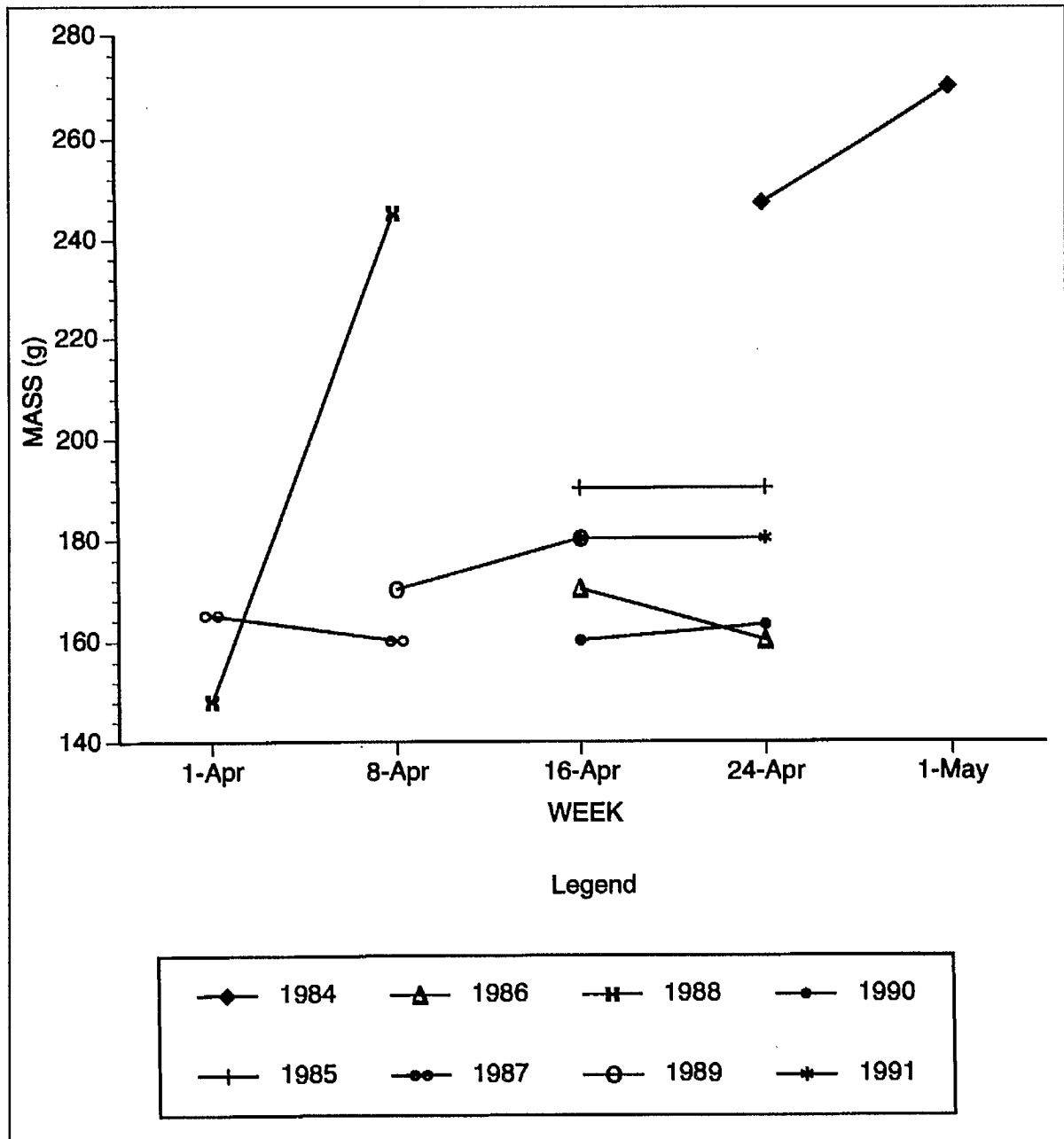


Figure 3. Maximum individual body masses of *Calidris canutus* in Lagoa do Peixe National Park, Brazil.

Rio Del Grande in mid-April. One of these birds was resighted the following year in Lagoa do Peixe. In 1991 and 1992, some birds were north of Rio Grande do Sul near Pinhal at the end of April. These last observations were significant, as the picric acid dye is lost when the birds moult their contour feathers. Those birds seen near Pinhal in 1991 and 1992 were certainly dyed earlier in those same years. The lack of retraps of marked birds in Lagoa do Peixe suggests a rapid turnover of knots.

At the end of April and in early May, the birds increased their fattening rates and departed on the long migratory flight; some birds stopped along the Maranhão state coastline, although most of the

birds likely continued on to Cape May. Table 2 shows the straight-line distances between stops, the minimum body masses required for each non-stop flight and the time necessary to fly these distances. The minimum body masses and the times shown in Table 2 are conservative applications of the formulae derived for shorebirds by McNeil (1970) and modified by us with hypothetical values for flight speeds estimated at 60 km/h. Theoretically, the average body mass of knots in Lagoa do Peixe in mid-April was sufficient only to reach the Maranhão coastline. The early May sample had too little fuel to accomplish the non-stop flight to the United States. The individual maximum body

Table 1. The numbers of knots banded at Lagoa do Peixe and sightings of colour-marked birds between 1984 and 1991, inclusive.

Year	Number banded	Number sighted	Recovery rate (%)
1984	281	10	3.6
1985	332	27	8.1
1986	69	20	29.0
1987	94	44	46.8
1988	70	14	20.0
1989	51	13	25.5
1990	64	16	25.0
1991	126	-	-
Total	1,087	144	13.2

Note: The number individually colour-marked under PASP was 474 (43.6%).

masses suggest that some knots could accomplish the flight with perhaps a quick stop at Maranhão.

The stop-over in Delaware Bay includes birds from Lagoa do Peixe; one of our colour-marked birds seen on the coast of Maranhão in 1987 was subsequently resighted in Delaware Bay in 1988 and 1990. The maximum stop-over interval confirmed by observations of colour-marked birds in Delaware Bay was seven days.

Coastal areas at Rio Grande do Sul must provide a rich source of food for knots. At Lagoa do Peixe, knots feed on polychaetes, the snail *Littorina*, *Emerita* spp., *Donax* spp. and adult mosquitoes. Food items may vary from year to year owing largely to differences in precipitation. In years when waters are brackish, salt-water invertebrates flourish. In years with heavy rains, these species do not occur in large numbers; they also become unavailable to the knots, as the birds cannot reach them because of the deeper waters. The abandonment of the lagoon by knots in 1986 is an example of such a situation.

Lagoa do Peixe is one of the major staging areas for knots in Rio Grande do Sul. When birds are present, there is a constant northward movement of knots through the area. Another major concentration of knots occurs at Pinhal in early May. The entire state coastline appears to be important, as it supplies knots with sufficient energy for moult and fat deposition in preparation for the long flight northwards.

This same coastline is also used by other species. However, like many other similar beaches in many parts of the world, the increasing human population uses these same beaches for recreational purposes. The creation of the Lagoa do Peixe National Park provided some control of human uses of the area, and its inclusion in the WHSRN gave further support to control disturbance.

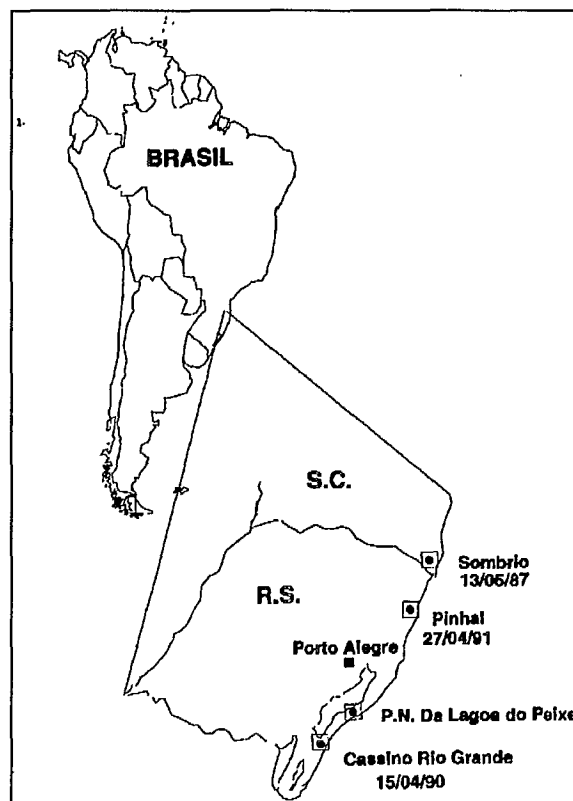


Figure 4. Recoveries of knots banded in Lagoa do Peixe and found in Rio Grande do Sul (R.S.) and Santa Catarina (S.C.) state coastlines.

However, the entire coast of the state needs attention.

Another significant threat to the area from human sources is oil spillage. This is unfortunately common in the northern portion of the state coast, where an oil terminal is located. A major oil spill in late April or early May could be catastrophic for migrating knots. The long distance from southern Brazil to the next two northern stops in the course of the birds' migration makes that coast crucial for the future of this subspecies.

Acknowledgements

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Figure 5. Northward migration of knots using Rio Grande do Sul, based on band recoveries and literature.

us observations of colour-marked birds. The WHSRN provided a grant to Inêz Nascimento to present this paper to the IV Congreso de Ornitologia Neotropical in Quito, Ecuador, in 1991.

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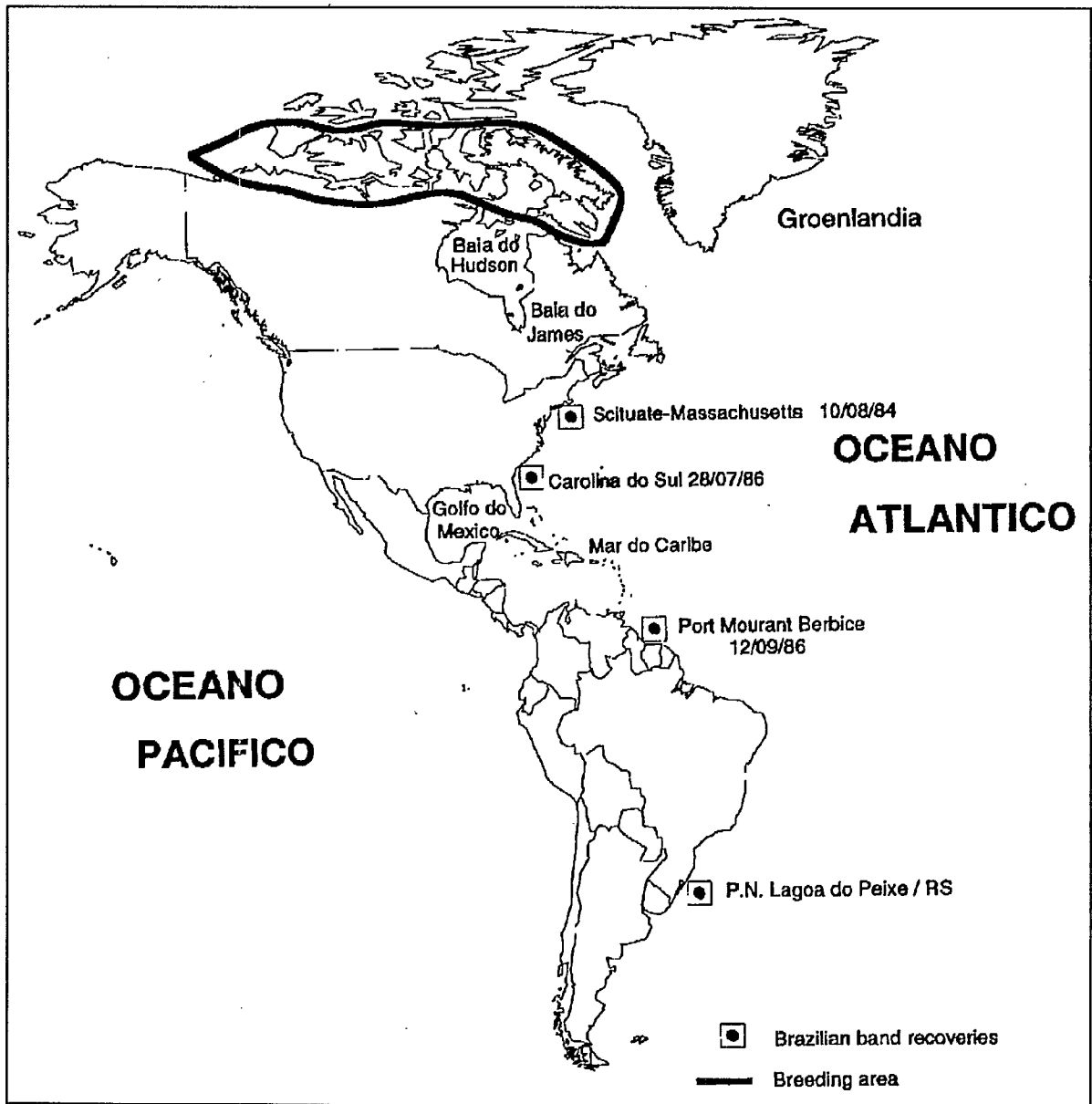


Figure 6. Southward migration of knots using Rio Grande do Sul coastline, based on recoveries.

Table 2. Hypothetical estimations of the minimum mass required for an individual knot to fly between known stop-over areas during the northward migration.

	Distance (km)	Minimum mass (g)	Estimation of flight time (h)
Lagoa do Peixe → Maranhão	3,200	145	42 ± 48
Maranhão → Delaware	5,000	200	66 ± 72
Delaware → Arctic	3,200	145	42 ± 48

Piersma, T., Prokosh, P. & Bredin, D. 1992. The migration system of Afro-Siberian Knots *Calidris canutus*. *Wader Study Group Bull.* 64, Suppl.: 52-63.

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The Chilean Shorebird Network (RECAP)

M. Sallaberry, E. Tabilo, C. Klesse & J. Abarca

Sallaberry, M., Tabilo, E., Klesse, C. & Abarca, J. 1996. The Chilean Shorebird Network (RECAP). *International Wader Studies* 8: 71–78.

The importance of Chile's coastline for long-distance migratory shorebirds is broadly known. Every year, thousands of shorebirds migrate south from their northern breeding grounds and congregate at coastal sites in Chile. Since the creation of the Chilean Shorebird Network (RECAP) in 1989, research on shorebirds in Chile has increased. Study sites currently span more than 3,000 km from Arica (18°S) to Concepción Bay (37°S), including Coquimbo, Quinteros and Santo Domingo. Each of these areas supports a high concentration of shorebirds, and each is a centre of investigation. RECAP has over 30 active members who are associated with 6 different universities. The scientific studies conducted at each research centre are varied and include research on populations and community ecology, as well as management and conservation strategies for long-distance migratory species.

Ya es ampliamente sabido la importancia de las costas de Chile para las aves migratorias de larga distancia, ofreciendo áreas de descanso y de permanencia durante la época no reproductiva para las aves. En estas áreas cada año se concentran miles de chorlos y playeros provenientes del Hemisferio Norte. Desde el origen de la Red Chilena de Aves Playeras (RECAP) en 1989, los estudios en este grupo de aves en el país se han intensificado cubriendo actualmente más de 3 000 km de distancia entre la localidad de Arica (18 lat. sur) hasta la Bahía de Concepción (37 lat. sur), pasando por Coquimbo, Quintero y Santo Domingo, las que concentran gran abundancia de Playeros y son nuestros Centros de Investigación. RECAP cuenta con más de 30 participantes activos afiliados a 6 diferentes instituciones. Los estudios científicos que se realizan en cada uno de estos Centros de Investigación son variados abarcando desde estudios poblacionales, ecología de comunidades, hasta manejo y conservación de las especies migratorias de larga distancia.

L'importance de la côte du Chili pour les oiseaux de rivage qui migrent sur de longues distances est largement connue. Ainsi, tous les ans, des milliers d'oiseaux de rivage migrent vers le Sud depuis leurs aires de reproduction du Nord et se rassemblent à divers endroits de la côte du Chili. Depuis la création en 1989 du Réseau chilien d'étude des oiseaux de rivage (RECAP), la recherche sur les oiseaux de rivage s'est accrue dans ce pays. À l'heure actuelle, les secteurs étudiés couvrent une région qui va d'Arica (18°S) à la baie Concepción (37°S), soit plus de 3 000 km, et qui comprend Coquimbo, Quinteros et Santo Domingo. Chacun de ces secteurs, qui abrite des concentrations élevées d'oiseaux de rivage, constitue un centre de recherche. Le réseau RECAP compte plus de 30 membres actifs affiliés à 6 universités différentes. Les études scientifiques effectuées à chacun des centres sont variées et comportent des études sur les populations et l'écologie des communautés, ainsi que sur les stratégies de gestion et de conservation des espèces de migrants au long cours.

M. Sallaberry, Depto. de Ciencias Ecológicas, Fac. de Ciencias, Universidad de Chile, Las Palmeras 3425, Santiago, Chile.

E. Tabilo, CONAF, Illapel, Chile.

C. Klesse, Depto. de Zoología, Universidad de Concepción, Concepción, Chile.

J. Abarca, Depto. de Zoología, Universidad de Tarapaca, Arica, Chile.

Introduction

The shorebirds (Charadrii) are a typical group of long-distance migratory birds and are widespread throughout the world. This group comprises 166 species, divided into 8 families (Johnsgard 1981). The most diversified families are Scolopacidae and Charadriidae, with 83 and 61 species, respectively.

In South America, there are 65 shorebird species, of which 37 migrate from the Northern Hemisphere. The most diversified families are the sandpipers (Scolopacidae), with 29 species, and the plovers

(Charadriidae), with 6 species (Table 1) (Prater, Marchant & Vuorinen 1977).

Chile is located entirely on the western watershed of the Andes. It extends over more degrees of latitude than any other country in the world, from Arica (18°S) to Cape Horn (56°S). It is bordered by Peru and Bolivia to the north and north-east and by Argentina to the east. The geography of continental Chile is altogether remarkable. It is an extremely long and narrow strip of land, 4,160 km long and 320 km wide, narrowing in places to less than 96 km. It is bordered on one side by mountains

Table 1. Diversity of species per family and migratory species in North and South America.

Family	North America		South America		Migratory species
	Genus	Species	Genus	Species	
Jacaniidae	1	1	1	1	-
Rostratulidae	-	-	1	1	-
Haematopodidae	1	2	1	3	-
Charadriidae	3	13	8	16	6
Scolopacidae	21	57	15	34	29 ^a
Recurvirostridae	2	2	2	2	2
Burhinidae	1	1	1	2	-
Thinocoridae	-	-	2	4	-
Chionidae	-	-	1	2	-
Total	29	76	32	65	37

^a Only the five species belonging to the genus *Gallinago* are not migratory.

6,096 m above sea level and on the other by the sea. The total area of continental Chile is 480,000 km². The ecological and climatological features of the country are also remarkable, from the driest desert in the world to cold antarctic weather. The country also has many isolated islands in the Pacific Ocean.

Because of its geography, Chile is an important country for migratory shorebirds from North America, with over 4,000 km of coastal environment and many high-altitude lakes where the shorebird densities are appreciable. Nevertheless, few studies have been undertaken to estimate the diversity and numerical variation of birds in these environments. Recently, a very good study estimating the abundance of shorebird species along the coast of Chile has been done by Morrison & Ross (1989). A total of 50 species of shorebirds is reported in Chile, of which 62% are migratory species from North America. Many of these species are accidental, but the Sanderling *Calidris alba*, Ruddy Turnstone *Arenaria interpres*, Baird's Sandpiper *Calidris bairdii* and Whimbrel *Numenius phaeopus* are very important species in Chile (Araya & Millie 1986).

Since 1982, Chile has been a member of the Pan-American Shorebird Program (PASP). The long-term objective of the programme in Chile has been to band shorebirds on the wintering grounds and to link Chilean sites with other locations critical to the conservation of specific populations (Myers & Sallaberry 1983; Myers *et al.* 1990; Sallaberry & Tabilo 1990).

In 1989, the first Field Workshop for studies of long-distance migratory shorebirds was held in Coquimbo. Since then, research on shorebirds has increased. Knowing the large extent of coastline that should be covered in studies on these migratory birds, Chile organized the Chilean Shorebird Network, or RECAP (Red Chilean para Aves Playeras).

In Chile, we are gradually developing a conservationist attitude regarding wildlife, specifically in relation to birds (Sallaberry 1989; Rottmann & Lopéz-Callejas 1992). To develop and disseminate such knowledge to different levels of our society, it is necessary to know and understand thoroughly the general biology of the species concerned. Furthermore, it is imperative to develop a good exchange of information among people, communicating the results to the general public and reaching a broad spectrum of interest levels, from scientists to schoolchildren. A preliminary strategy for conservation of long-distance migratory shorebirds in the Western Hemisphere has been developed by Myers *et al.* (1987).

The purpose of this paper is to summarize the different studies devoted to long-distance migratory shorebirds in Chile under the co-ordination of RECAP.

Methodology

We gathered information from the different working groups in Chile. We summarized principally the objectives, methodology and results of each project. In many cases, the methods used were conventional and are described elsewhere. More specific methodology is described with regards to each paper to which it applies. The preliminary results of these projects are discussed in relation to the overall scope of RECAP. We present some original tables and figures of specific papers in preparation.

Results and discussion

Figure 1 locates the centres of research for long-distance migratory shorebirds in Chile, spanning more than 4,000 km from Arica to Punta Arenas. A large variety of projects is being developed at each site with the co-ordination of RECAP. Unfortunately, not all the sites have the same level of

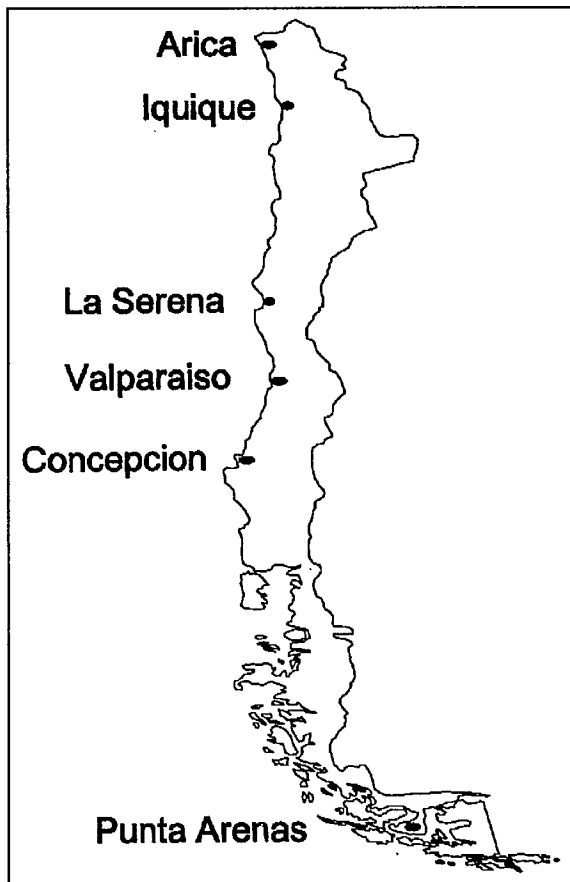


Figure 1. Migratory shorebird research centres in Chile.

research, but there is a shared interest in the movement of the populations during migration to the wintering grounds.

Another interest of RECAP is to co-ordinate workshops on migratory birds in Chile. Already we have held three workshops in different localities. The first one was held in Coquimbo in 1989, the second in Iquique in 1990 and the third in Puerto Montt in 1991. It is very important that this process be continued and that the next workshop be organized with participants from all over the country.

The different projects at each locality are summarized in Table 2; these include five ongoing projects and two under review. The funding for these projects comes from different sources, including private funds. As is evident, research ranges widely from preliminary surveys and censuses to detailed studies of foraging ecology and the environmental impacts of human activities. The scientific studies conducted at each research centre vary; these include surveys and censuses of populations, community ecology and management and conservation strategies for long-distance migratory species.

Because RECAP extends over almost the whole length of the country, it has to collaborate with many other national institutions (Table 3). To minimize problems and to speed up the work in different localities, it is always important to involve graduate students and their universities. This has proven to be the best and most productive association for RECAP.

Below are brief summaries of each of the projects (except Quintero, for which details were not received).

Diversity and abundance of shorebirds at Arica Bay (I Region) during the austral summer

Arica is the northernmost city of Chile, close to the border with Peru. Very little information on the shorebird community has been gathered until now. During the months of January and February 1991, we censused Arica Bay, which is separated in the middle by the city of Arica. This allowed us to census two well-defined areas, the north and south zones, respectively. The northern section is a sandy beach, whereas the southern section has a rockier environment. The methodology used for this study was conventional: walking along the beach with binoculars (10 × 40 mm) and a spotting scope while counting and identifying the birds. Figure 2 shows the numbers and species of birds in both sections of Arica Bay during the austral summer.

Fifteen species were recorded in the northern section. The most common were Franklin's Gulls *Larus pipixcan* and Sanderlings, each accounting for more than 1,500 birds. Next followed the Whimbrels and Grey Gulls *Larus modestus*, with 300 and 100 birds, respectively.

Only 13 species of coastal birds were recorded in the southern section. Franklin's Gull was the most abundant species in this section, followed by the Elegant Tern *Sterna elegans*, the Grey Gull and the Willet *Catoptrophorus semipalmatus*. The data collected suggest that the Willet population winters largely in northern Chile.

Workshops for the study and conservation of long-distance migratory shorebirds in Chile

To date, we have organized three field workshops in different parts of the country. Advanced students from universities, professors and professionals employed in government positions attended the workshops. The results of these activities have been excellent, motivating a great number of students to develop their theses on topics related to the study of long-distance migratory shorebirds. The next step is to obtain funds for these students to support them through

Table 2. List of projects of the Chilean Shorebird Network.

A. Ongoing projects			
Locality	Latitude	Investigator	Title
Arica	18°21'S	M. Sallaberry	Diversity and abundance of shorebirds at Arica Bay (I Region) during the months of austral summer.
Iquique	20°00'S	J. Abarca E. Tabilo M. Sallaberry V. Farias	Workshops for the study and conservation of long-distance migratory shorebirds in Chile.
Coquimbo	29°32'S	E. Tabilo R. Jorge	Conservation of wetlands and shorebirds on the coastline of Coquimbo.
Quintero	32°45'S	M. Sallaberry C. Gonzalez	Human impact on the shorebird community at Quintero Bay (V Region), Chile.
Concepción	36°40'S	M.C. Klesse M. Sallaberry	Foraging behaviour of Sanderling <i>Calidris alba</i> on Roquant Island, Concepción Bay.
B. Projects under review			
1. Title: Population studies in <i>Calidris alba</i> and other long-distance migratory species in Chile. Principal investigator: Dr Michel Sallaberry A. Co-investigator: Lic. Cristina Klesse M.			
2. Title: Study of the coastal environment of southern Chile (X Region) as a wintering ground for long-distance migratory shorebirds. Principal investigator: Prof. Luis Espinoza G.			

Table 3. National institutions with which RECAP collaborates.

1. CONAF Corporación Nacional Forestal
2. UNORCH Unión de Ornitólogos de Chile
3. Universidad Arturo Prat (Iquique)
4. Universidad de La Serena (La Serena)
5. Universidad Católica del Norte (Coquimbo)
6. Universidad de Chile (Santiago)
7. Universidad de Playa Ancha (Valparaíso)
8. Universidad Católica de Valparaíso (Valparaíso)
9. Universidad de Concepción (Concepción)

their graduate studies. These workshops are always accompanied by local media publicity.

The second workshop for migratory shorebirds was held in Iquique in 1990. Fifteen students attended the meeting. Now we have a small group studying the annual variation in shorebird numbers at Iquique Bay.

We realize that these activities are very important to motivate both undergraduate and post-graduate students. It is the best way to recruit new young students interested in public education and conservation relating to migratory birds. We must continue with these activities in the future.

The conservation of wetlands and shorebirds in Coquimbo Bay

This project is the follow-up of Tabilo's thesis on the annual variation, diversity and habitat preferences of shorebird species in Coquimbo Bay. At the completion of this study, we presented a new

project to the government in relation to the management and conservation of long-distance migratory shorebirds (Tabilo, Sallaberry & Myers 1990).

Figure 3 shows the proposed study site in our research proposal. We suggested dividing the bay into three areas as follows: a **recreational area** in the extreme south; an **educational area** in the centre of the bay; and, finally, a **protected area** in the extreme north of the bay (this area to be used only for scientific purposes). Each of these areas is about 4,000 m long.

An alternative project will be developed for the educational area. We are planning to (1) produce a field guide on the birds of the area, (2) present seminars and (3) hold other ecological and conservational activities for students and the general public.

Discussions on this proposal with the government are ongoing.

Foraging behaviour of Sanderling on Roquant Island, Concepción Bay

This project is C. Klesse's graduate thesis. The general purpose of this work is to study the annual variation in numbers and habitat preferences of the Sanderlings at Concepción Bay and to compare these data with the food availability and foraging ecology of Sanderlings in the area. Two years of observations have been completed, and at this time Klesse is in the final stage of writing his thesis.

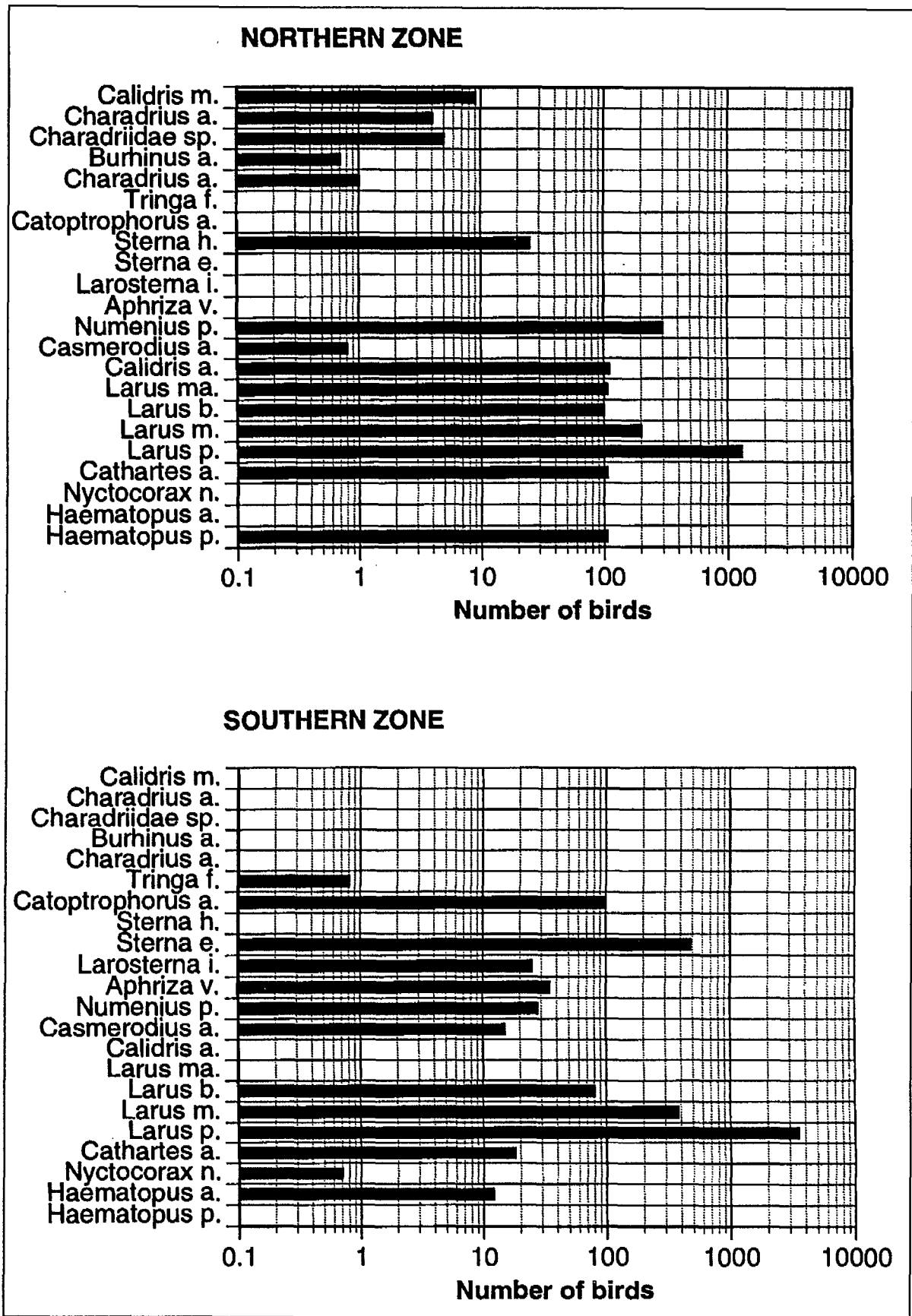


Figure 2. Species and numbers of shorebirds in both sections of Arica Bay during the austral summer.

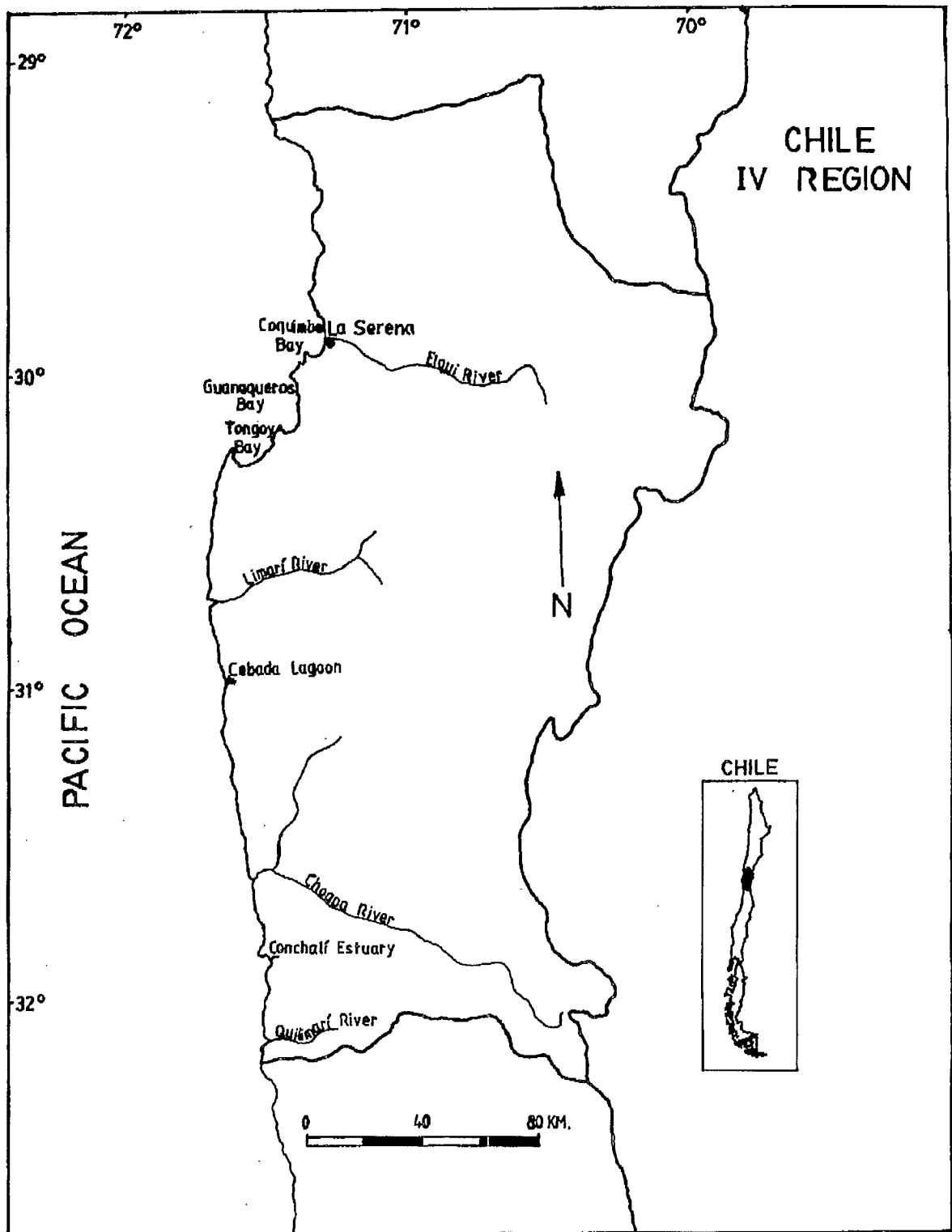


Figure 3. The proposed study site in Coquimbo Bay.

Figure 4 illustrates the monthly variations in Sanderling numbers over two years. These data show that Sanderlings start arriving in the area in August and September and that large numbers of birds remain on the beach during the (austral) summer. Then, in the months of April and May,

there is a second peak, suggesting that southern populations use this beach as a staging area during the northward migration.

Table 4 summarizes the data on the foods consumed by 72 Sanderlings on Roquant Island.

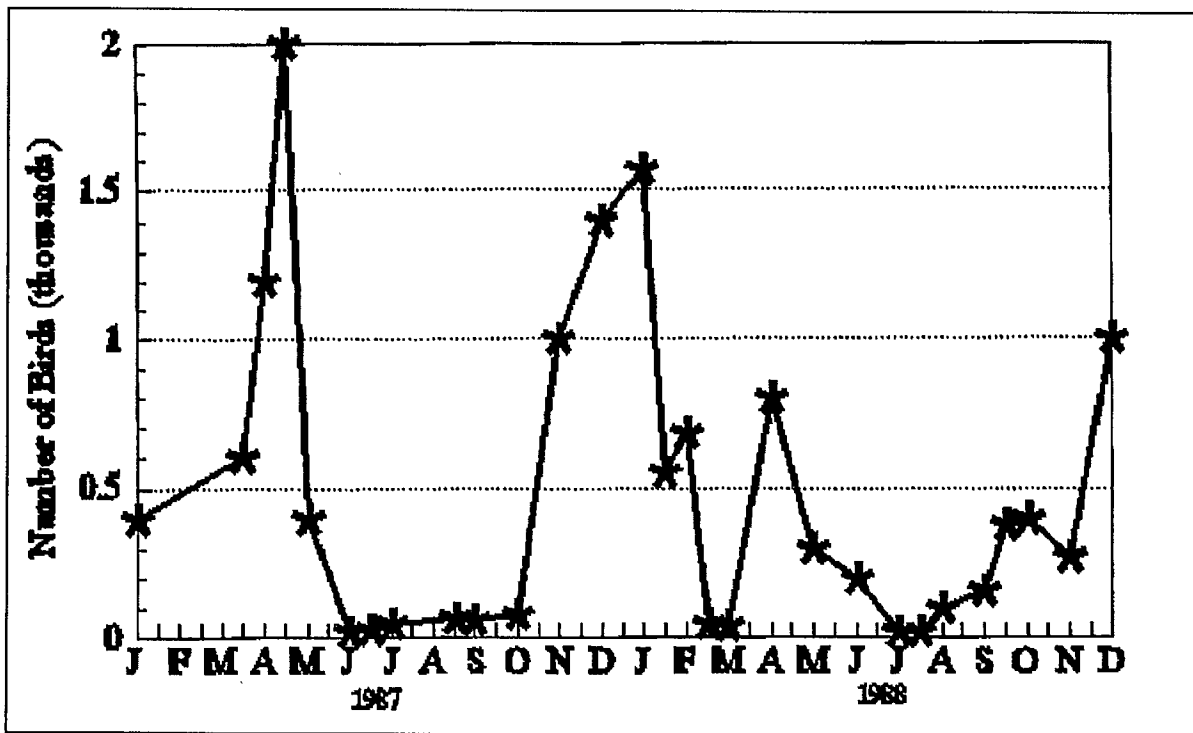


Figure 4. Monthly numbers of Sanderling in 1987 and 1988.

Table 4. Analysis of stomach contents of 72 Sanderlings *Calidris alba* at Roquant Island, Chile.

Type of prey	Prey composition		Frequency	
	Number	%	Number	%
Annelida				
<i>Malacoceros glutaeus</i>	6	0.75	5	6.94
<i>Perinareis vallata</i>	135	16.83	18	25.0
<i>Scolecopsis squamata</i>	18	2.24	17	23.61
Crustacea				
<i>Cancer setosus</i>	548	68.33	36	50.0
<i>Emerita analoga</i>	6	0.75	5	6.94
<i>Exirolana hirsuticauda</i>	8	1.0	4	5.55
<i>Lepidopa chilensis</i>	8	1.0	5	6.94
Insecta				
Carabidae	6	0.75	4	5.55
Coleoptera (no identif.)	11	1.49	11	15.27
Ligacidae	2	0.25	2	2.77
Mollusca				
<i>Aulacomya ater</i>	5	0.62	5	6.94
<i>Littorina araucana</i>	14	1.74	5	6.94
<i>Mulinia edulis</i>	14	1.74	9	12.5
<i>Nassarius gayi</i>	7	0.86	3	4.16
<i>Semimytilus algosus</i>	13	1.62	4	5.55

The two items most important to their diet were *Perinareis vallata* (Annelida) and *Cancer setosus* (Crustacea). These prey were compared with those available on the beach.

It is hoped that this research will be published in detail in a scientific journal.

Conclusions

- (1) Because of the importance of Chile's coastline for shorebirds and the peculiar biology of long-distance migratory birds, it is necessary to co-ordinate efforts from different parts of the country in order to understand the movement of shorebird populations on their wintering grounds.
- (2) Through RECAP and the production of regular bulletins, people are more aware of the research and new information obtained in different parts of the country.
- (3) With regards to future conservation and habitat protection, it is imperative to know and understand thoroughly the general biology of the species in the ecosystem. It is also necessary to develop a good exchange of information between scientists and the government.

Acknowledgements

First, we acknowledge all members of RECAP for increasing our knowledge of the migratory shorebirds along our coast. We also thank the Western Hemisphere Shorebird Reserve Network (Wetlands for Americas) and the Wildfowl and Wetlands Trust, UK, for supporting us with many of our projects. We also acknowledge the help of all government and non-government institutions that support our local research.

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Management and conservation of the habitats used by migratory shorebirds at Coquimbo, Chile

E. Tabilo, R. Jorge, R. Riquelme, A. Mondaca, C. Labra, J. Campusano, M. Tabilo, M. Varela, A. Tapia & M. Sallaberry

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Migratory shorebirds in Chile are concentrated mainly in Patagonia, Chiloe Island and some areas in the northern part of the country. One of these areas is the Coquimbo coastline, with 350 km of coast and 80 km of beaches and lagoons that annually receive hundreds of Nearctic and austral shorebirds. These habitats are under constant pressure owing to human activity. The characteristics of the annual life cycle of migratory birds make them very vulnerable to habitat deterioration. In order to design conservation strategies, it is very important to know areas of concentration and to understand annual rhythms of abundance as well as the environmental problems associated with the habitats that the birds occupy. This study describes the habitats used by migratory shorebirds in Coquimbo, population fluctuations and sources of environmental impact. The information obtained by Coquimbo RECAP (the Chilean Shorebird Network) is being used to design strategies for the management and conservation of these birds and their habitats in the area of Coquimbo, Chile.

En Chile los Chorlos y Playeros migratorios se concentran mayoritariamente en la Patagonia, Isla de Chileo y algunos puntos del Norte del país. Unos de estos sitios es el litoral de Coquimbo con unos 350 km de costa y 80 km de playas y lagunas que reciben anualmente a cientos de Chorlos neárticos y australes. Estos ambientes están siendo sometidos a una permanente presión ambiental por actividades humanas. Las características del ciclo de vida anual de un ave migratoria las hace muy vulnerable al deterioro ambiental. Conocer las áreas de concentración, ritmos de abundancia anual y los problemas ambientales asociados al lugar son claves en la hora de diseñar estrategias de conservación. Este trabajo describe los ambientes usados por Chorlos y Playeros migratorios en Coquimbo, fluctuaciones poblacionales y las fuentes de impacto ambiental. La información obtenida por RECAP Coquimbo se está usando para diseñar una estrategia de conservación y manejo de estas aves y sus ambientes en Coquimbo, Chile.

Au Chili, les oiseaux de rivage migrateurs se concentrent essentiellement en Patagonie, aux îles Chiloe et dans certaines régions du nord du pays, notamment la région de Coquimbo. À cet endroit, la côte s'étire sur 350 km, dont 80 de plages et de lagunes, et reçoit tous les ans des centaines d'oiseaux de rivage néarctiques et australs. Les activités anthropiques exercent des pressions constantes sur ces régions. À cause des caractéristiques propres à leur cycle annuel de vie, les oiseaux de rivage sont particulièrement sensibles à la détérioration des habitats. Afin de pouvoir élaborer des stratégies de conservation, il faut connaître les secteurs de concentration des oiseaux et les rythmes annuels d'abondance, ainsi que les problèmes environnementaux associés aux habitats de prédilection des oiseaux. La présente étude décrit les habitats qu'utilisent les oiseaux de rivage dans la région de Coquimbo, les fluctuations démographiques et les sources potentielles d'impact sur l'environnement. Les résultats de l'étude réalisée dans le cadre du RECAP pour la région de Coquimbo servent à élaborer des stratégies de gestion et de conservation de ces oiseaux et de leurs habitats dans la région de Coquimbo au Chili.

E. Tabilo, Corporación Nacional Forestal, IV Región - Chile.

R. Jorge & R. Riquelme, Depto. Biología Marina, Univ. Católica del Norte, Coquimbo.

A. Mondaca, C. Labra, J. Campusano, M. Tabilo, M. Varela & A. Tapia, Depto. Biología, Univ. de La Serena, La Serena, Chile.

M. Sallaberry, Depto. Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile.

Introduction

Many authors have described sites of large concentrations of long-distance migratory shorebirds in Chile (Myers *et al.* 1984, 1985, 1990;

Tabilo 1987; Tabilo & Noton 1987, 1989; Tabilo *et al.* 1987; Morrison & Myers 1989; Morrison & Ross 1989; Sallaberry & Tabilo 1990; M. Sallaberry & J. Abarca, pers. commun.). These sites are located on Tierra del Fuego, Chiloe Island and the coastlines of

Concepción, Valparaíso, Coquimbo, Mejillones and Arica.

The special characteristics of the biological cycles of these species make them very sensitive to environmental disturbance (Myers *et al.* 1987), because these birds use environments desired for human development, recreation, agricultural needs and industry (Smit, Lambeck & Wolff 1987). These kinds of disturbances produce accumulative effects on the wetlands (Harris 1988; Risser 1988; Weller 1988), which are evident in structural changes in the bird community and in biodiversity (Hutto 1989), with displacement of species with highly specialized habitat requirements, such as migratory shorebirds, by generalist species (Myers *et al.* 1987). This deterioration of the environment will produce loss and fragmentation and a decrease in the biodiversity of the aquatic ecosystem.

Shorebirds in Chile experience serious deterioration of their habitats, due especially to the pollution of the coastline. Bore, Pizarro & Cabrera (1986) suggested that in Chile the contamination of the coastline is very high but localized. Great amounts of human and industrial residues are released into the ocean without any treatment. In the northern part of Chile, there is a large amount of contamination by the mining companies. In the central part, the contamination is due to the big cities, in the southern part, mainly chemicals or products of the forestry companies, and in the extreme south, petroleum companies.

The Coquimbo coastline, approximately 350 km long, is an important area, both nationally and internationally, for Sanderlings *Calidris alba* and Whimbrels *Numenius phaeopus* (Myers *et al.* 1984, 1985, 1990; Tabilo 1987; Morrison & Ross 1989). Unfortunately, these wetlands receive industrial, domestic and petroleum contamination. The accelerated urbanization of the coastline owing to increased tourism is also a problem. Coastal highways and tourist complexes have been built right on the beach. In 1987, Tabilo & Noton published a *Management field guide*, which contained the scientific bases that support the conservation of these habitats. They proposed a series of management activities, among them that the Coquimbo coastline be included in the Western Hemisphere Shorebird Reserve Network as a Regional reserve for migratory shorebirds.

Attempts to arouse interest in protecting these environments have been relatively successful. The existence of abundant and solid biological information about these habitats and the migratory shorebirds that use them is the key to securing support for our efforts. Permanent and updated information, including wetland inventories, shorebird counts and knowledge of habitat deterioration, is needed in order to propose

conservation strategies, management and sustainable use of the coastline. With this information, it will be possible to visualize the general situation and prioritize conservation activities (what to do and where to do it) in the wetlands.

The purpose of this paper is to describe the aquatic environment of the Coquimbo coastline, the species of shorebirds that use the wetlands and the environmental impact variables associated with each site. We also propose mechanisms for conservation and management of these habitats.

Methodology

Monthly counts of aquatic birds were carried out from March 1990 through April 1991 between Coquimbo Bay to the north and the southern tip of Playa Changa to the south (Figure 1), according to standardized counting methods (Tabilo 1987). In this study, we put special emphasis on the comparative richness, abundance and diversity (Hair 1987) of Charadriidae and Scolopacidae. The coastline was inspected for 71 different sources of environmental impact (Smit, Lambeck & Wolff 1987; Bojórquez & Ortega 1989) at each wetland site.

For analysis of the data, we compared only the percentages of the 71 environmental impact variables that applied at each wetland site. From this information, we assessed the conservation status of migratory shorebirds, and we proposed management activities for each wetland site along the coast of Coquimbo, Chile. For the bird list, we used the field guide *Guía de Campo de las Aves de Chile* (Araya & Millie 1988), and for the wetland classification, we followed Ramsar (1990) criteria.

Study site

The Coquimbo coastline (29–32°S, 71–72°W) is characterized by extensive beaches, cliffs, peninsulas and estuaries (Figure 1). With regard to climate, it is a transitional zone under strong influences, both from the desert to the north and from mediterranean habitats to the south, that affect the physiognomy of the landscape. Interannual climatic variations are marked. There is a predominance of xerophytic vegetation, which classifies the region as arid mediterranean, in which the arid aspect is less pronounced than in equivalent latitudes elsewhere, owing to the existence of the cold Humboldt Current (Di Castri & Hajek 1976).

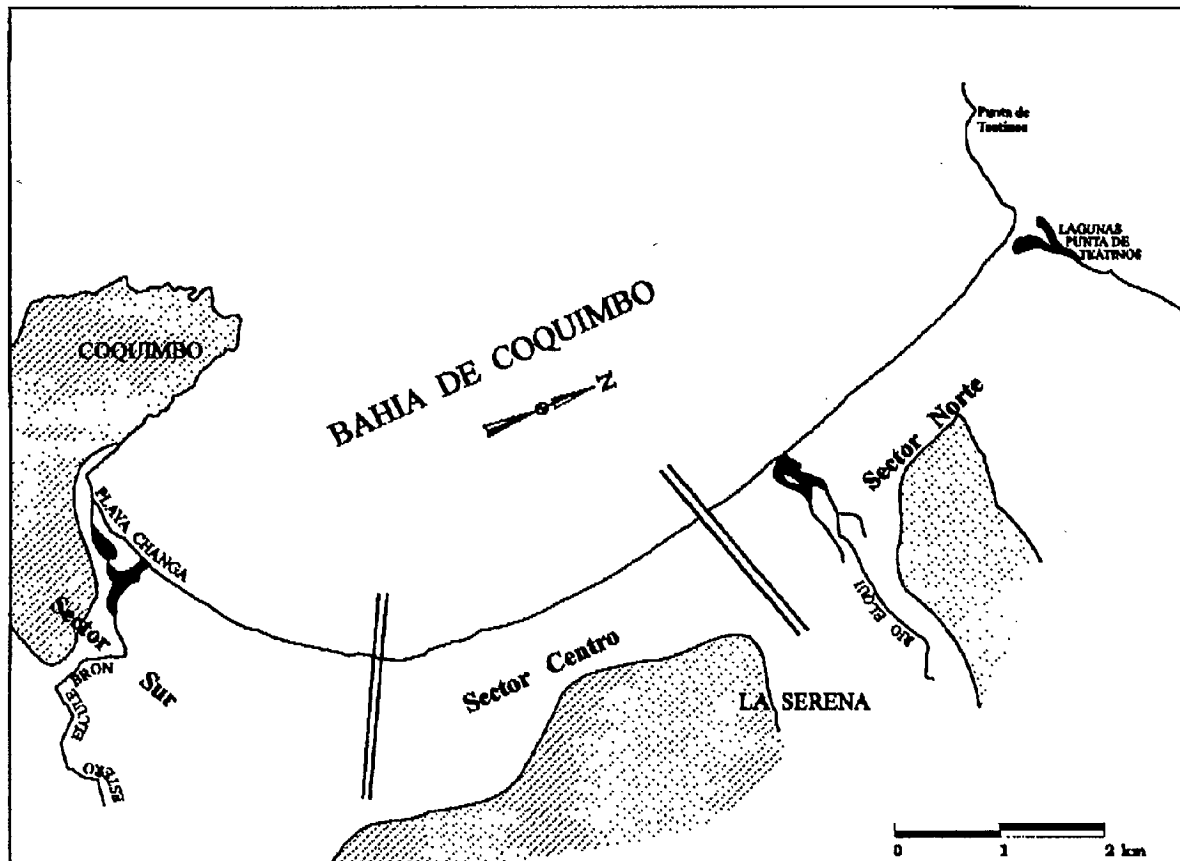


Figure 1. Coquimbo Bay in Chile showing the south (sur), central (centro) and north (norte) sections (sector) described in this study.

Results and discussion

Bird biology

Of the birds counted, the resident plovers showed higher relative abundance. The Southern Lapwing *Vanellus chilensis* was observed at all wetland sites along the Coquimbo coastline. It is a common species near humid sites throughout the country (Araya & Millie 1988). Owing to its flexibility in use of habitats and its abundance, we considered this species to have no conservation problems in the area.

The Snowy Plover *Charadrius alexandrinus* was relatively common and used the sandy beaches as nesting and feeding sites. Lagoons were used as roosting sites. Nevertheless, we speculate that this species will present conservation problems in the future (R. Jorge, pers. commun.), because of the fact that it is very specialized in its habitat and highly sensitive to environmental disturbance. This species has modified its distribution patterns in the area as a result of the ongoing loss of nesting sites. As an example, in Coquimbo Bay, with its 18 km of sandy beaches, this plover is concentrated along the last 6 km of beach at the northern part of the bay. The birds are continuously disturbed by people,

vehicles and dogs, and many of their nests are destroyed.

The Banded Plover *Charadrius collaris* is considered a resident species. Hayman, Marchant & Prater (1986) described the status of this plover as unclear. However, it was common to observe small flocks throughout the year along the Coquimbo coastline, where the species is even known to nest (R. Jorge & A. Mondaca, unpubl. data).

All the austral migrants occurred in small groups between March and September each year, and they were distributed throughout all the aquatic environments along the coastline.

Nearctic migratory shorebirds, such as the Black-bellied Plover *Pluvialis squatarola*, occurred in small numbers during the summer months at the wetland sites near Tongoy. The Semipalmated Plover *Charadrius semipalmatus* occurred in small flocks almost exclusively at lagoons to the south of Coquimbo Bay.

Yellowlegs (*Tringa* spp.) were commonly observed in small groups in the lagoons and bays of Coquimbo and Tongoy. The Ruddy Turnstone

Arenaria interpres seemed to move about a great deal within the area, and it was normally present in all coastal habitats of the Coquimbo coastline, occasionally in large numbers.

The Common Snipe *Gallinago gallinago* used only those wetland sites that included abundant vegetation. This species has almost completely disappeared from the lagoons near Coquimbo Bay, because these sites have been severely affected by coastal urbanization.

Sanderlings and Whimbrels are the most common and abundant shorebirds of the Coquimbo coastline. Tabilo (1987) pointed out that Sanderlings are especially abundant in Coquimbo Bay, and the same is true for Whimbrels in Tongoy Bay. In spite of this, Sanderlings have shown a continued decrease in abundance in Coquimbo Bay during the last five years. We suspect that this is due to the decline of the environmental quality of the bay.

Another group of shorebirds occurred in the area irregularly and in low numbers (see Table 1; where abundance = 1). We believe that these shorebirds stopped in the area to rest for a few weeks while they accumulated reserves to continue their migration. They used the beaches and lagoons of the region sporadically, coinciding with their migratory patterns. Other species, such as Red Knot *Calidris canutus* and Hudsonian Godwit *Limosa haemastica*, were seen only occasionally, and we suspect that those sightings were of birds that had strayed off their usual routes.

From the above results, we conclude the following:

- (1) The regular visits of small flocks of austral and boreal migratory shorebirds in this area could be explained by the need of these birds for high-quality and safe overwintering sites. Destruction and loss of their traditional environments could cause an ongoing decline in the numbers of those birds that stop off at these sites each year.
- (2) Some occasional visits could be of birds that use the Pacific corridor by mistake. They could also be due to birds that normally use this corridor but do not overwinter at Coquimbo. These birds are observed as they use the site for short stops to refuel before continuing their migrations.
- (3) We suspect that abundant species such as Sanderling will have serious conservation problems in the near future owing to the current rate of deterioration of the aquatic ecosystems. For example, the Snowy Plover is faced with nesting difficulties, and Sanderlings show a population decrease. Resident shorebirds move

locally up and down the coast, and it is increasingly difficult for them to find sites in good condition for feeding, roosting and nesting requirements.

Wetlands

The bays of Coquimbo and Tongoy present the greatest variety of different aquatic micro-environments locally. This could be the reason why Tongoy (Table 2) showed the greatest bird diversity as well as a relatively low environmental impact index (58%). This situation will change greatly in the future with increasing coastal urbanization for tourism. Currently, the major environmental impacts are seen during the summer and are associated with an excess of people and vehicles on the beach and near the lagoons. Tourism is a fundamental part of the region's economy, and improved urban infrastructure is needed in these areas to take advantage of their economic potential.

Coquimbo Bay presented the greatest species richness and highest abundance of shorebirds in the area, but it had an alarming 92% environmental impact index. This was to be expected, as both the Port of Coquimbo and the city of La Serena are located on the bay. This urban centre includes a human population of nearly 400,000 and almost all of the industry of the IV Region. Tourism is also a very important activity in the area and has led to the construction of coastal highways and condominiums. As a result of these activities, wetlands have been destroyed, drained, fragmented and contaminated. Our data indicate that, in the southern part of the bay, specialist bird species are being replaced by more generalist species.

Owing to factors beyond our control, it proved impossible to realize counts in Guanaqueros Bay, and thus information for this area is lacking. It showed an environmental impact index of only 54% in the summer months, mostly because of the construction of buildings at the edge of the beach.

With regards to lagoons, the mouth of the Limari River showed the highest species diversity of shorebirds as well as the greatest number of different aquatic microhabitats. It is an environment that is relatively little altered. The northern edge of the river-mouth borders Fray Jorge National Park, and it thus is constantly watched by park personnel. The greatest bird abundance was observed at Conchali Stream, the area that also presented the highest environmental impact index because of a nearby highway and summer camping. The rest of the coastal environments (Cebada and Quilimari) showed low bird abundance, probably because these areas are poor in alternative aquatic microhabitats. On the other hand, this series of small coastal lagoons may become important if we analyse them on a regional scale.

Table 1. Wader species in Coquimbo coastline, IV Region of Chile.

Species	Status	Type of migrants	Season	Occurrence	Relative abundance
Fam. Charadriidae					
<i>Vanellus chilensis</i>	R			R	2
<i>Pluvialis squatarola</i>	M	B	S	R	1
<i>Charadrius semipalmatus</i>	M	B	S	R	1
<i>C. alexandrinus</i>	R			R	3
<i>C. falklandicus</i>	M	A	W	R	1
<i>C. collaris</i>	R			R	1
<i>C. modestus</i>	M	A	W	R	1
Fam. Scolopaciidae					
<i>Tringa flavipes</i>	M	B	S	R	1
<i>T. melanoleuca</i>	M	B	S	R	1
<i>Catoptrophorus semipalmatus</i>	M	B	S	I	1
<i>Numenius phaeopus</i>	M	B	S	R	3
<i>Limosa haemastica</i>	M	B	S	I	1
<i>Arenaria interpres</i>	M	B	S	R	2
<i>Calidris canutus</i>	M	B	S	I	1
<i>C. bairdii</i>	M	B	S	I	1
<i>C. alba</i>	M	B	S	R	3
<i>C. melanotos</i>	M	B	S	O	1
<i>C. pusilla</i>	M	B	S	I	1
<i>C. fuscicollis</i>	M	B	S	I	1
<i>Gallinago gallinago</i>	R			R	2

Status: R: resident; M: migratory. Type of migrants: B: boreal; A: austral. Season: S: summer; W: winter. Occurrence: R: regular; I: irregular; O: occasional. Relative abundance: 1: scarce; 2: regular; 3: abundant.

Table 2. Comparison of different variables among beaches and lagoons of the Coquimbo coastline: different microhabitats (Ramsar 1990), number and abundance of shorebirds, Shannon-Weaver index of diversity (H) and percentage of the environmental impact variables of relevance at each site.

Habitat	Microhabitat	No. of wader spp.	Abundance	H	Environmental impact index (%)
Bays					
Coquimbo	6	21	18.052	2.2	92
Guanaqueros	4				54
Tongoy	6	18	9.630	2.6	58
Lagoons					
Limari	7	11	1.478	2.5	34
Cebada	3	12	0.289	1.8	38
Conchali	4	15	2.070	2.0	41
Quilimari	4	11	0.739	2.0	37

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The Neotropical plovers of Estero El Yali in central Chile

Yerko A. Vilina & M. Victoria López-Calleja

Vilina, Y.A. & López-Calleja, M.V. 1996. The Neotropical plovers of Estero El Yali in central Chile. *International Wader Studies* 8: 85–92.

Five species of Neotropical plovers using the delta of the river El Yali in central Chile were censused in 1989, 1990 and 1991. The species observed were the Southern Lapwing *Vanellus chilensis*, Two-banded Plover *Charadrius falklandicus*, Rufous-chested Dotterel *C. modestus*, Collared Plover *C. collaris* and Snowy Plover *C. alexandrinus*. The Southern Lapwing is a year-round resident, and, between early May and late September, the other four species collectively attained numbers of 206, 545 and 753 birds.

Se realizaron censos en 1989, 1990 y 1991 de cinco especies de chorlito neotropicales que emplean el delta del río El Yali, en la zona central de Chile. Las especies observadas fueron el tero *Vanellus chilensis*, el chorlito de doble collar *Charadrius falklandicus*, el chorlo de pelo colorado *C. modestus*, el chorlito de collar *C. collaris* y el chorlitejo patinegro *C. alexandrinus*. El tero reside en esas regiones durante todo el año; entre comienzos de mayo y fines de septiembre, se observaron 206, 545 y 753 ejemplares de las otras cuatro especies.

Cinq espèces de pluviers néotropicaux se trouvant dans la région du delta de la rivière El Yali, dans le centre du Chili, ont été dénombrées en 1989, 1990 et 1991. Les espèces observées étaient le Vanneau téro *Vanellus chilensis*, le Pluvier des Falkland *Charadrius falklandicus*, le Pluvier d'Urville *C. modestus*, le Pluvier d'Azara *C. collaris* et le Gravelot à collier interrompu *C. alexandrinus*. Le Vanneau téro y séjourne toute l'année; entre le début mai et la fin septembre, on a dénombré au total pour les quatre autres espèces 206, 545 et 753 individus respectivement, pour ces trois années.

Y.A. Vilina, Unidad de Biología de la Reproducción, Departamento de Biología Celular y Genética, Facultad de Medicina, Universidad de Chile, Casilla 70061-7, Santiago, Chile.

M.V. López-Calleja, Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 365, Santiago, Chile.

Introduction

The delta of the river El Yali (33°47'S, 71°23'W) is a wetland with as high a diversity of avian species as is found anywhere along the central Chilean coastline. A maximum of 96 species has been recorded (Vilina & López-Calleja 1992). Scott & Carbonell (1986) indicated that this area contains a waterfowl community fully representative of this part of Chile. More importantly, the area has also been described as an important gathering site for both Nearctic and Neotropical shorebirds. Twelve species of resident and migrant shorebirds have been recorded here (Philippi 1940, 1951; Reed & Larrain 1943; Johnson & Ewer 1969; Chang *et al.* 1989; Vilina & Drouilly 1990).

In this paper, we assess the importance of this wetland as a wintering area for Neotropical plovers by (1) documenting the species present and their relative numbers and (2) describing the habitat preferences of both resident and southern migrants over three consecutive winter seasons.

Study area

The river El Yali is near Villa Alhué (34°02'S, 71°06'W) in the province of Melipilla. The river stretches approximately 60 km to its outlet, where it can attain depths of 4 m. Seven lagoons are formed from underground streams and rainfall; one of them, the coastal lagoon, is simply part of the river bank. All the lagoons have muddy banks, and only the Matanza and El Rey lagoons have tall aquatic vegetation (Juncaceae and Cyperaceae). El Convento is a human-made salt-marsh for occasional mining of salt. The coastline is primarily sandy beach.

Materials and methods

In the winters of 1989, 1990 and 1991, we conducted monthly censuses from May to August inclusive. Each census followed linear transects, and all birds observed within a 200-m-wide sampling zone were recorded. We used 8 × 30 field glasses and conducted the surveys between 07:30 and 10:30. A spring census was undertaken in late September, and similar observations were carried out

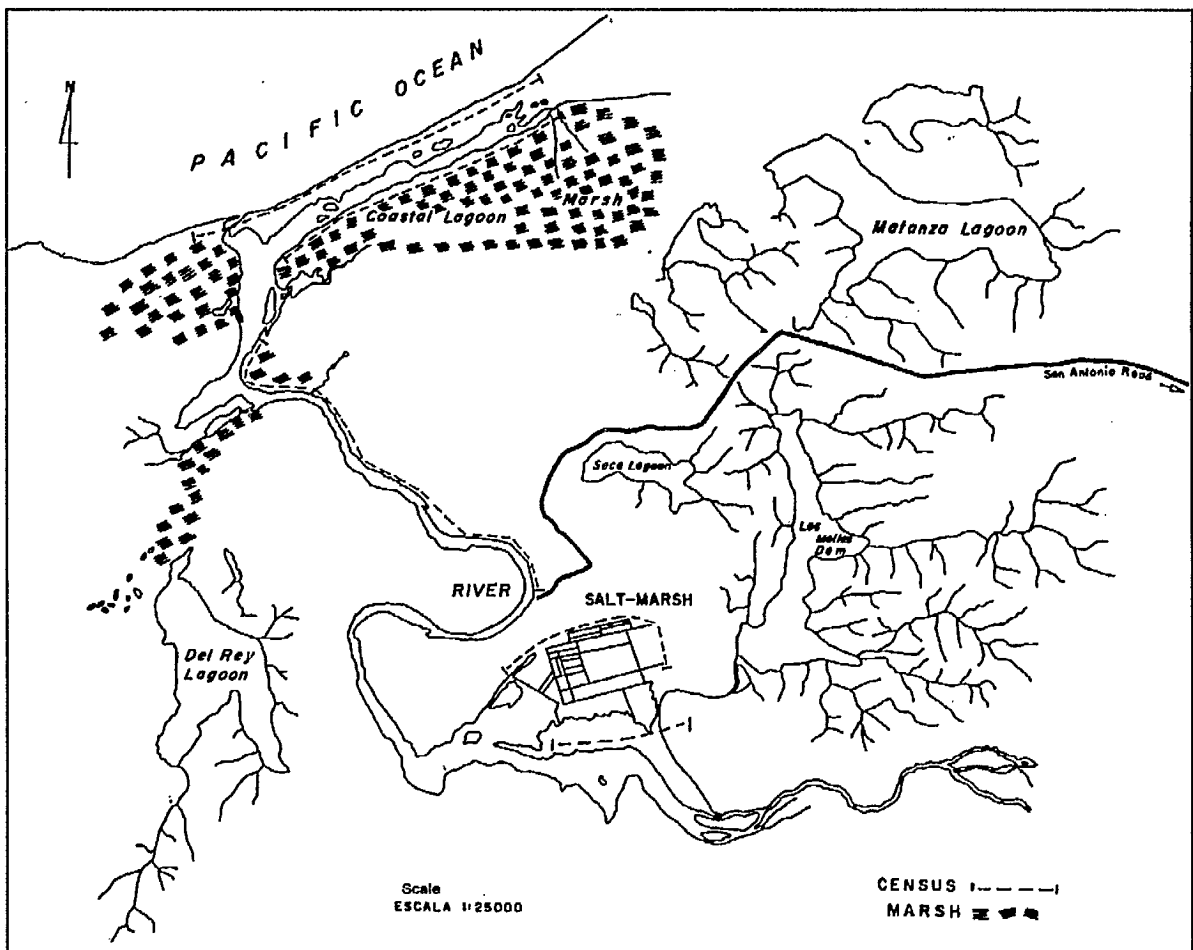


Figure 1. The El Yali wetland in central Chile.

periodically during the summer. All transects were done in representative wetland habitats: the El Convento salt-marsh, the El Yali river shoreline, the coastal lagoon and sandy beach (Figure 1). At each site, we determined species diversity and counted the Neotropical plovers present. We omitted from our analysis the Southern Lapwing *Vanellus chilensis*, because its presence cannot be directly associated with wetland habitats. Precipitation records from the meteorological station of San Antonio (33°34'S, 71°37'W) were correlated with species diversity and abundance.

Results

Our surveys revealed the occurrence of five species of Neotropical plovers in our study area: the Southern Lapwing, Two-banded Plover *Charadrius falklandicus*, Rufous-chested Dotterel *Charadrius (Zonibyx) modestus*, Collared Plover *Charadrius collaris* and Snowy Plover *Charadrius alexandrinus*. *Vanellus chilensis* and *C. falklandicus* were resident, *C. modestus* was seasonal and *C. collaris* and *C. alexandrinus* were seen only occasionally.

Over three field seasons, the migrants from Tierra del Fuego (Hayman, Marchant & Prater 1986), Rufous-chested Dotterel and Two-banded Plover, were the most abundant species, with 722 and 688 individuals seen over the three survey years (see Tables 1, 2 & 3). The largest numbers of *C. falklandicus* (97) and *C. modestus* (147) occurred during the month of July in 1991. Although the same species were recorded each winter, the total numbers of birds in the winters of 1989 (Table 1) and 1991 (Table 3) were about three times higher than in 1990 (Table 2). In each of the three years, the numbers declined as summer approached and the summer migration ensued.

The highest species richness values and the larger individual concentrations of birds were observed on the coastal lagoon (Figures 2, 3 & 4), mainly on those sections where the mudflats were most extensive. Most species, except the Snowy Plover, also occupied the stream banks, although in lesser numbers. The beach itself was not particularly attractive to shorebirds, probably owing to the fact that erosion had impoverished the substrate (Vargas 1990). In 1990, the salt-marsh was the poorest site in terms of bird densities (Figure 3),

Table 1. Numbers and percentages of four species of Neotropical plovers seen on the census transects in 1989.

	May	June	July	August	September	Total
<i>C. alexandrinus</i>	1 5.6%	7 38.9%	7 38.9%	3 16.7%	0 0.0%	18
<i>C. falklandicus</i>	52 16.9%	71 23.1%	72 23.5%	85 27.7%	27 8.8%	307
<i>C. collaris</i>	3 11.1%	8 29.6%	8 29.6%	1 3.7%	7 25.9%	27
<i>C. modestus</i>	26 13.5%	73 37.8%	92 47.7%	2 1.0%	0 0.0%	193
Total	82	159	179	91	34	545

Table 2. Numbers and percentages of four species of Neotropical plovers seen on the census transects in 1990.

	May	June	July	August	September	Total
<i>C. alexandrinus</i>	2 28.6%	5 71.4%	0 0.0%	0 0.0%	0 0.0%	7
<i>C. falklandicus</i>	23 25.0%	31 33.7%	9 9.8%	26 28.3%	3 3.3%	92
<i>C. collaris</i>	3 21.4%	5 35.7%	2 14.3%	0 0.0%	4 28.6%	14
<i>C. modestus</i>	14 15.1%	21 22.6%	19 20.4%	38 40.9%	1 1.1%	93
Total	42	62	30	64	8	206

Table 3. Numbers and percentages of four species of Neotropical plovers seen on the census transects in 1991.

	May	June	July	August	September	Total
<i>C. alexandrinus</i>	2 25.0%	1 12.5%	1 12.5%	4 50.0%	0 0.0%	8
<i>C. falklandicus</i>	54 18.7%	64 22.1%	97 33.6%	58 20.1%	16 5.5%	289
<i>C. collaris</i>	3 15.0%	2 10.0%	7 35.0%	4 20.0%	4 20.0%	20
<i>C. modestus</i>	87 20.0%	139 31.9%	147 33.7%	63 14.4%	0 0.0%	436
Total	146	206	252	129	20	753

because during these months it was unusually dry. Nevertheless, during flooding in 1989 and 1991, this salt-marsh provided a suitable site for these birds before their departure on the southward migration, as well as for Nearctic shorebirds arriving from the north (see Figures 2, 3 & 4).

The remarkable decrease in bird numbers observed during the 1990 winter season may have been due to the drought in northern and central Chile. In the

study area, from May to September 1989, 230.5 mm of rain were recorded; in the same period in 1990, only 154.0 mm were recorded. As a consequence, in 1990, the muddy flats in the salt-marsh became dry, leaving the birds without alternative feeding and resting sites during late winter and early spring. In 1991, when large numbers of plovers were observed using the wetland, the largest amount of rainfall, 442.5 mm, was recorded between May and September (Table 4).

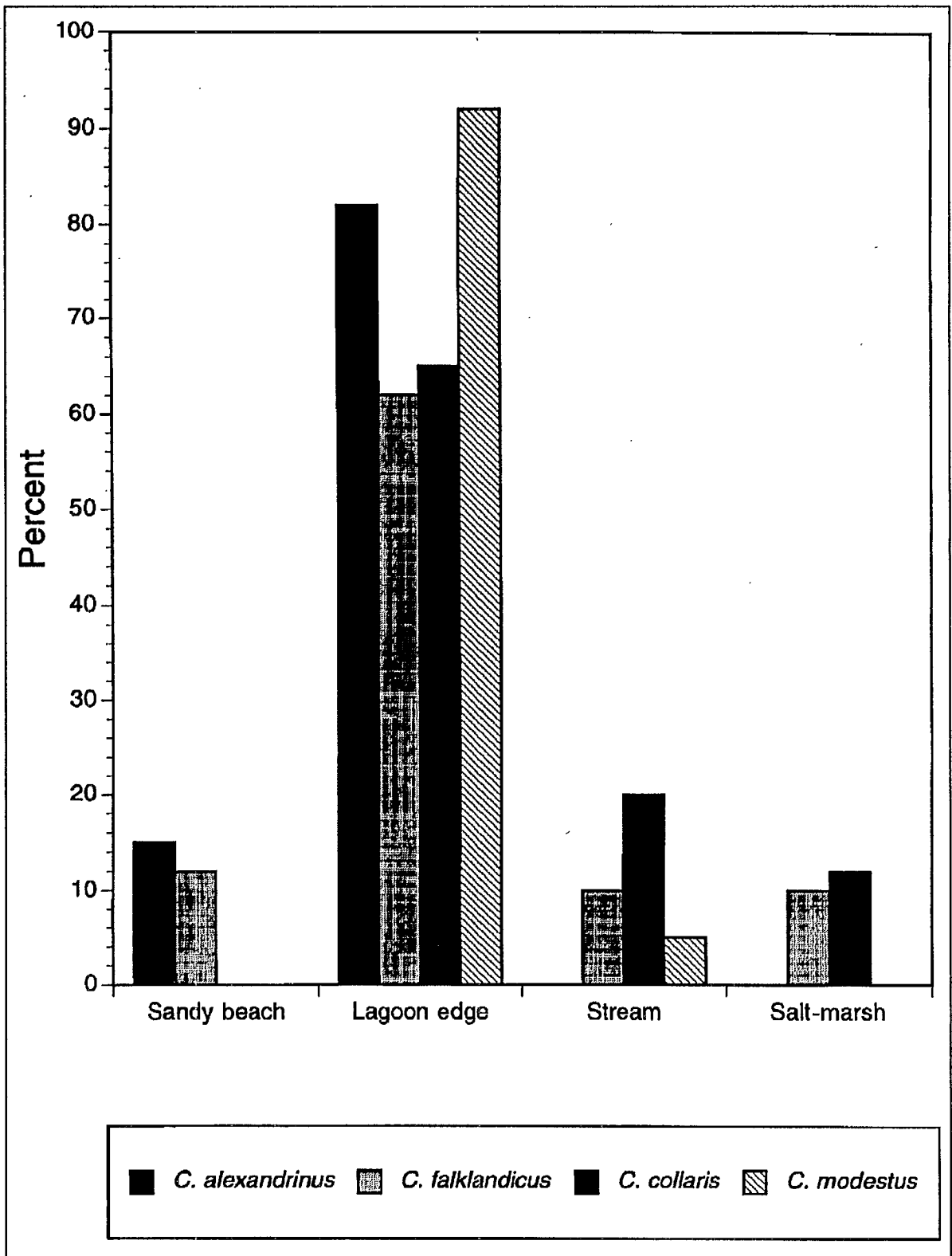


Figure 2. The habitat preferences of Neotropical plovers along the El Yali river in central Chile in 1989.

Species accounts

Rufous-chested Dotterel
 This was the most abundant species. Its southward migration began in August in 1989 and September

in 1990. These dates agree with the dates when they arrived in Tierra del Fuego (Philippi *et al.* 1954). The moult to breeding plumage occurred prior to the southward migration. Dotterels were absent from the study area from late spring and

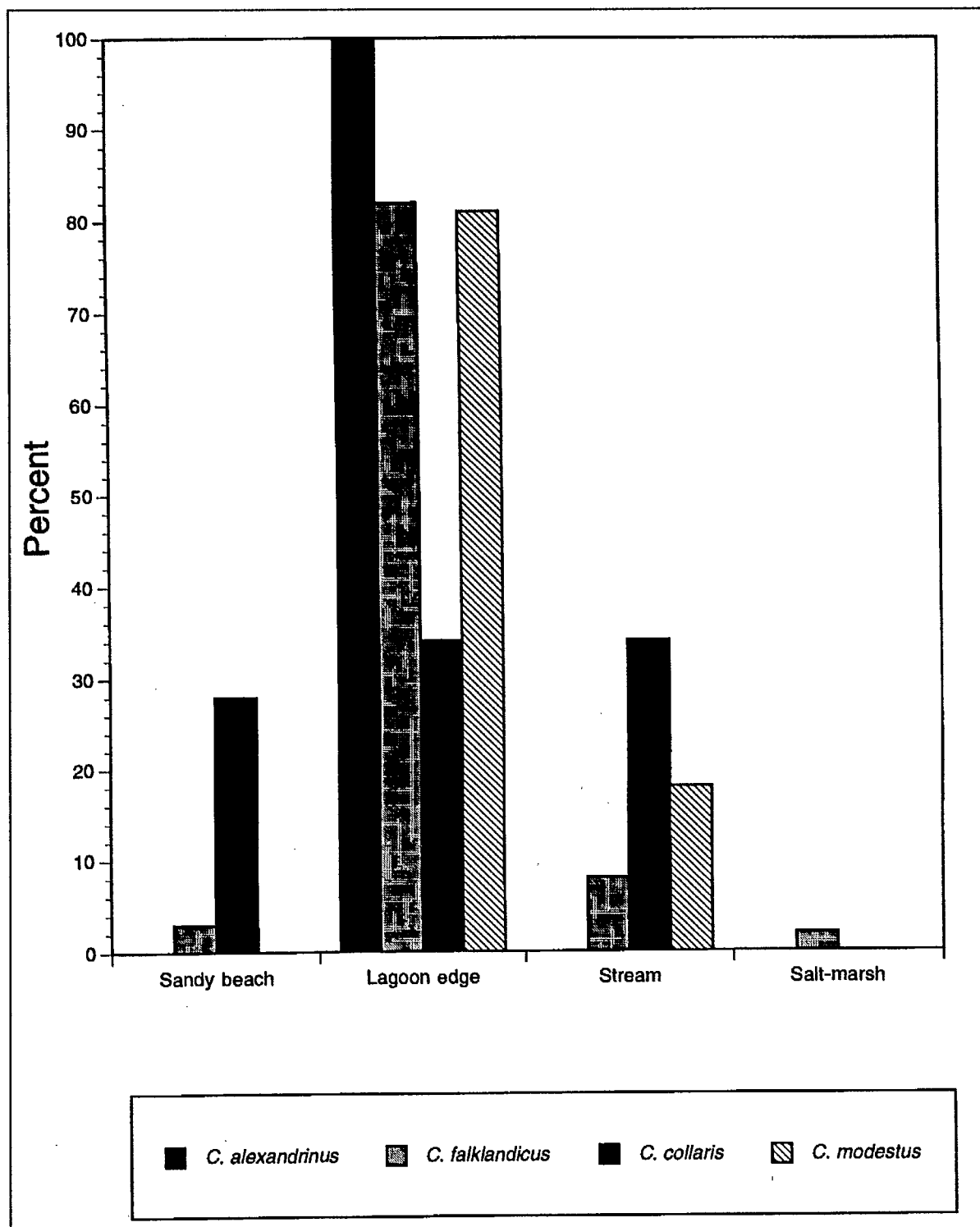


Figure 3. The habitat preferences of Neotropical plovers along the El Yali river in central Chile in 1990.

throughout the austral summer. The preferred habitat was the coastal lagoon, but dotterels were also present, in lesser numbers, along stream banks and occasionally in the salt-marsh. We never detected this species on the sandy beaches.

Two-banded Plover

This species remained all year round in the study area, even though its numbers decreased in spring and summer. In winter, it was possible to detect some birds in breeding plumage; by spring, all were in this condition. This species probably nests in this wetland (Philippi *et al.* 1954). They occupied all four habitats, with marked preference for the

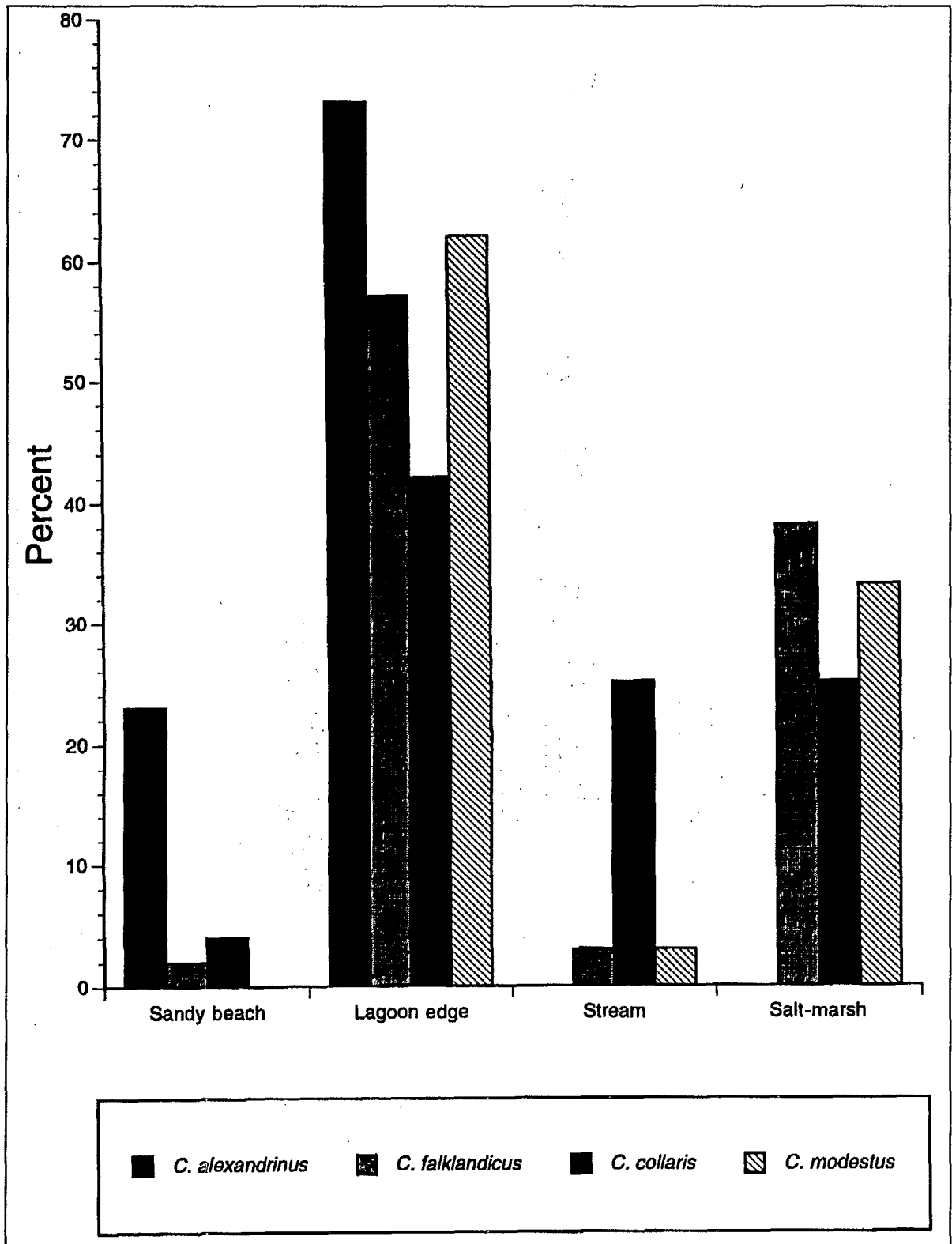


Figure 4. The habitat preferences of Neotropical plovers along the El Yali river in central Chile in 1991.

coastal lagoon, which they shared with the Rufous-chested Dotterel.

Collared Plover

These plovers were usually seen singly or in small flocks at all sites, but always in low numbers. They preferred to feed in small ponds on the northern

Table 4. Cumulative rainfall (mm) in the study area and total numbers of Neotropical plovers in the census transects.

	May	June	July	August	September
1989					
accumulated mm	6.5	28.0	157.5	230.5	230.5
no. of plovers	82	159	179	91	34
1990					
accumulated mm	40.0	44.0	109.5	134.0	154.0
no. of plovers	42	62	30	64	8
1991					
accumulated mm	122.0	311.5	386.5	400.5	442.5
no. of plovers	146	206	252	129	20

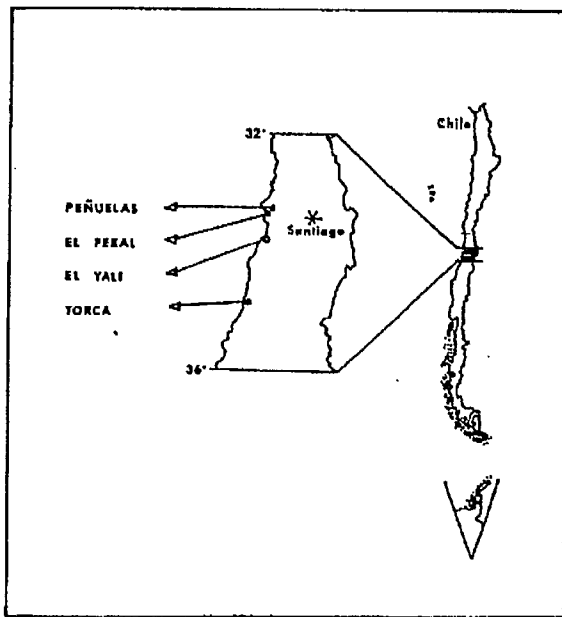


Figure 5. The protected coastal wetlands of central Chile.

shore of the coastal lagoon and also along the stream.

Snowy Plover

Small numbers of this species were occasionally observed in the wetter months. They disappeared in spring. Snowy Plovers preferred the coastal lagoon, and occasionally they were detected on the beach.

Southern Lapwing

Present all year round, this species used all available habitats. In June and July, flocks of more than 1,000 individuals gathered close to the coastal lagoon and the stream.

Discussion

Many coastal wetlands of central Chile are recognized as important gathering and breeding

sites for waterfowl, and some are protected as national wildlife reserves, as is the case for Laguna Torca (34°10'S, 71°38'W), Lago Peñuelas (33°10'S, 71°38'W) and Laguna El Peral (33°30'S, 71°35'W) (Figure 5). The wetland formed by the river El Yali, which will probably also become a wildlife reserve, presents similar conditions (Vilina & López-Calleja 1989, 1992).

As these surveys revealed, the El Yali wetland is an important wintering area for Neotropical plovers. In this wetland, we find five of the six species of Neotropical plovers ascribed to the lowlands of central Chile (Araya & Millie 1986; Hayman, Marchant & Prater 1986). Only the Tawny-throated Dotterel *Oreopholus ruficollis* is absent.

The numbers of these birds in winter, principally the Rufous-chested Dotterel and the Two-banded Plover, seem to depend on the yearly rainfall. During rainy years, the wetland holds a significant number of these birds. In contrast, in dry years, they gather farther south or migrate via the Atlantic coastal route. The option to migrate through the coast of the Atlantic Ocean or Pacific Ocean, depending on climatic conditions, seems to occur in not only Neotropical plovers but also other birds, such as Black-necked Swan *Cygnus melancoryphus* and Coscoroba Swan *Coscoroba coscoroba* (Schlatter *et al.* 1991). This hypothesis should be explored with a banding programme.

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Habitat partitioning and the distribution and seasonal abundances of migratory plovers and sandpipers in Los Alamos, Rio Negro, Argentina

Patricia M. Gonzalez

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Between September 1989 and December 1990, field studies were conducted on the population fluctuations of migratory plovers and sandpipers and on their use of foraging habitats along 4 km of coastline near Los Alamos, San Antonio Oeste, Rio Negro, in Argentina. Eight species were observed, of which four breed in northern North America. The largest flocks (up to 2,550 birds) arrived from the Northern Hemisphere in the second half of November and were present in significant numbers until early April. The greatest number of birds was recorded in March (8,500 birds), when *Calidris canutus* and *C. fuscicollis* were migrating northward. The first month of the southern winter was characterized by the presence of *C. alba* and *Charadrius falklandicus*, common species whose numbers increased substantially thereafter. The most commonly used foraging habitat was rock covered with patches of sandy sediment and water up to 3 cm deep. Similarities in the use of microhabitats are discussed. The most similar species morphologically (*C. alba* and *C. falklandicus*) also showed a positive correlation in time. Nesting and the seasonal variations in the numbers of people, dogs and vehicles were recorded. The Los Alamos coast is considered a 'vital site' (Clark 1974) for the conservation of migratory plovers and sandpipers.

Entre septiembre 1989 y diciembre 1990, se estudiaron la fluctuación poblacional y el uso del hábitat de alimentación de chorlos y playeros migratorios en 4 km de costa con restinga en las cercanías de 'Los Alamos', San Antonio Oeste, Rio Negro, Argentina. Se observaron 8 especies de las cuales 4 se reproducen en el norte del continente americano. Los grupos más conspicuos provenientes del Hemisferio Norte (2 550 ejes.) aparecieron en la 2da. mitad de noviembre registrándose abundancias importantes hasta los 1ros. días de abril. El máximo de aves ocurrió en marzo, cuando el sistema albergó más de 8 500 limícolas simultáneamente: principalmente *Calidris canutus* y *C. fuscicollis* en paso migratorio hacia el Hemisferio Norte. El 1er. mes del invierno austral se caracterizó por la presencia de *C. alba* y *Charadrius falklandicus*, especies frecuentes que entonces exhibieron su mayor abundancia. El ambiente de alimentación más utilizado fue la roca cubierta con películas de sedimentos arenosos en machones y agua hasta 3 cm de profundidad. Se discuten similitudes en el uso de microhábitats; las especies más parecidas estuvieron además correlacionadas positivamente en el tiempo (*C. alba* y *C. falklandicus*). Nidificación y variación temporal en el número de personas, perros y vehículos, fueron registrados. Se estima que la costa de Los Alamos representa un sitio vital (Clark 1974) para la conservación de chorlos y playeros migratorios.

Entre septembre 1989 et décembre 1990, on a étudié sur le terrain les fluctuations de populations de pluviers et de Scolopacides migrants et leur utilisation des habitats d'alimentation sur une portion longue de 4 km du littoral du fleuve Negro dans la région de Los Alamos, San Antonio Oeste, en Argentine. Huit espèces, dont quatre se reproduisent en Amérique du Nord, ont été observées. Les vols les plus importants — 2 550 oiseaux — sont arrivés de l'hémisphère Nord au cours des deux dernières semaines de novembre et y sont demeurés en grand nombre jusqu'au début d'avril. La plus grande concentration a été enregistrée en mars (8 500 oiseaux), au moment où *Calidris canutus* et *C. fuscicollis* migraient vers le Nord. Le premier mois de l'hiver austral a été caractérisé par la présence de *C. alba* et de *Charadrius falklandicus*, des espèces communes dont le nombre a par la suite augmenté. L'habitat d'alimentation le plus fréquemment utilisé était constitué de roches recouvertes de plaques de sédiments sableux et d'au plus 3 cm d'eau. Les auteurs traitent des similitudes dans l'utilisation des habitats. Les espèces morphologiquement les plus semblables (*C. alba* et *C. falklandicus*) ont aussi présenté une corrélation positive dans le temps. On a aussi enregistré la densité de nidification et les variations saisonnières du nombre de personnes, de chiens et de véhicules. On considère que la côte de Los Alamos est une «région vitale» (Clark 1974) pour la conservation des pluviers et des Scolopacides.

Casilla de Correo 84, Pedro Moron 384, 8520 San Antonio Oeste, Provincial de Rio Negro, Argentina.

Introduction

Despite its interesting abundance and diversity of birds, no studies have yet been conducted on the avifauna of the coastal area of Bahia de San Antonio and the coastal zone bordering the Gulf of San Matias, with the exception of censuses carried out by Morrison & Ross (1989).

The objectives of this project were as follows:

- (1) to provide information on the composition and abundances of shorebirds throughout the year along the coast near the Los Alamos Technological Institute of Mining and Groundwaters (ITMAS) in San Antonio Oeste, Rio Negro, and
- (2) to describe the partitioning of foraging habitats by the various species of plovers and sandpipers for purposes of establishing (i) the importance of this site for migratory shorebirds, (ii) the status of shorebird populations prior to the full functioning of a Solvay manufacturing plant, whose construction has been under way for some time in Punta Delgado, and (iii) the biological grounds for seeking political action to minimize the impact of large enterprises and proposing management plans.

Study area

The Los Alamos coast is located on the Gulf of San Matias (64°55'W, 40°45'S), close to the city of San Antonio Oeste and the Las Grutas seaside resort in the District of San Antonio, Province of Rio Negro, Argentina. It is the coastal sector that extends from ITMAS to the entrance of the Antoine de Saint Exupery Airport (Figure 1).

The zone is arid and mesothermic with a mean tidal amplitude of between 0.64 and 8.26 m. On the coast of Los Alamos, the receding tide uncovers a shoal (up to 1 km) perpendicular to the high-water line. It is a horizontal, smooth, slightly convex, greenish-yellow surface, which has fracture joints running in various directions in the limolite of the Patagonia Formation (marine Miocene) (Angulo *et al.* 1981).

The study area that was selected owing to its abundance of birds included the non-sloping coastal sector of the Patagonia Formation. Its upper limit is marked by fixed or shifting dunes 1.5-3 m high, which are higher (10 m) and more unstable in front of ITMAS. The intertidal coastal strip, located between the dunes and the exposed shoal, corresponds to the area included between the high-tide limits during spring and neap tides (Figure 2). It has a variable width of some 50 m,

except in front of ITMAS, where it is about 100 m wide. There are sediment deposits ranging from fine sands to smooth rocks (20 cm diameter) and mollusc shells.

For more information, see Angulo *et al.* (1981), Gonzalez Diaz & Malagnino (1984), Piola & Scasso (1988) and the San Antonio Oeste Environmental Charter (Underdirectorate of the Environment, Department of Economics of Rio Negro).

With respect to continental vegetation, the region is included in the phytogeographic province of El Monte (Cabrera 1976); with respect to ornithogeographics, it falls under the coastal province (Narosky & Yzurieta 1987).

Material and methods

Observations were made every two weeks from September 1989 to December 1990, except for the first two weeks of March, between 3 p.m. and 8 p.m. (later in the summer and earlier in the winter) on clear days with wind speeds under 40 km/h. I observed the birds with 16 × 50 binoculars.

Patterns of distribution and seasonal abundance

The coast was studied at high tide when the shoal was flooded and the species, numbers, behaviour and moulting status (where possible) of shorebirds present were recorded. Pedestrians, dogs, vehicles and other disturbances were also recorded. Passing airplanes were not included.

The reliability of the estimates was substantiated by recounting the birds afterwards or by using photographs. The species were grouped according to where they bred, as described in Myers & Myers (1979).

Partitioning of foraging habitat

Observations were made between 5 November 1989 and 24 November 1990. The zone between the coastal dunes up to 100 m of exposed shoal was selected for observations, as the birds gathered there to feed.

Three homogeneous macrohabitats were recognized. These were subdivided into microhabitats that were temporary because of draining and drying through the tidal cycle. The species and numbers of birds in each microhabitat were recorded under different tidal conditions (given by roman numerals). When possible, notes were made of the number of birds at rest (rest being considered any activity other than foraging).

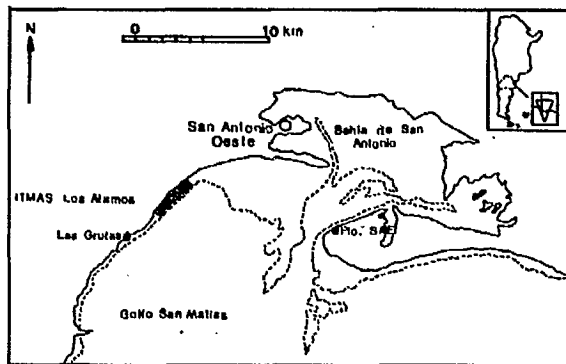


Figure 1. Map of the Bahía de San Antonio and Gulf of San Matías hinterland. The dotted area indicates the Los Alamos coast, and the dotted line shows the low-tide condition.

The macrohabitats were identified with letters and the microhabitats with Arabic numerals. Habitats not used by plovers were marked with a dash.

The specific aspects of the different microhabitats encountered in the study area are shown in Table 1, and the macrohabitats are described below:

Intertidal (S): Described in Study area and shown in Figure 2. The observations were carried out simultaneously along the route used for censusing bird numbers. The tidal conditions were (I) incoming high tide, high tide and slack tide and (II) outgoing high tide without uncovering the shoal.

Typical shoal (A): Represents more than 90% of the upper shoal. Patchy deposits of sand and fine sediments (0–3 cm deep). It faces low dunes with vegetation. The tidal conditions were (III) outgoing tide uncovering 50 m of shoal perpendicular to the coast and (IV) outgoing tide uncovering 100 m of shoal.

Shoal with sediment (B): The remaining surface consists of deposits of sand and fine sediments up to 30 cm thick and decreasing seaward for about 50 m. This macrohabitat faces high, shifting or plant-covered dunes (Figure 2A). The tidal conditions were (III) outgoing tide uncovering 50 m of shoal perpendicular to the coast and (IV) outgoing tide uncovering 100 m of shoal.

Census divisions consisting of 100 m of shoreline reaching back 50 or 100 m from the shore were established according to the height of the tide. The corresponding intertidal surface area of the census divisions was determined by projection. A census was carried out on a total of four divisions shown in Table 1 in the following order: BIII, AIII, BIV and AIV. Macrohabitat B was uncovered first (see Figure 2A).

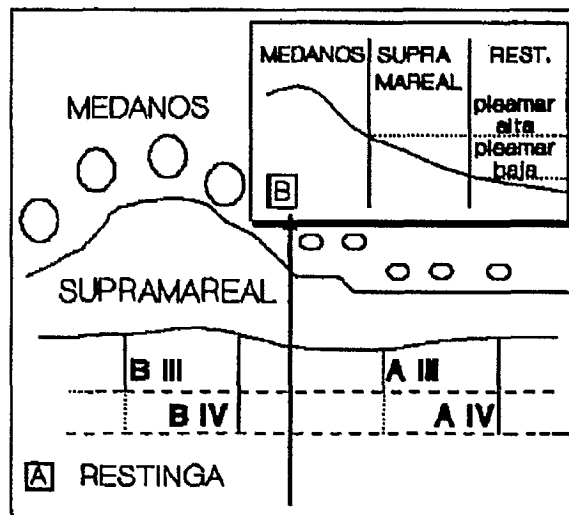


Figure 2. (A) Diagram of the layout of sections in which the habitat division project was carried out. The large circles indicate high, shifting or plant-covered dunes. The smaller circles indicate low, plant-covered dunes. The dotted lines show the height of the tide. (B) Sketch of the outline of the coast (not to scale). medanos = sand dunes; supramareal = intertidal; restinga = shoal; pleamar alta = high tide; pleamar baja = neap tide.

Fortnightly visits were carried out during low tides following a route perpendicular to the coast towards the sea, and the presence or absence of shorebirds and human activity was recorded.

Data processing

The Simpson Diversity Index was used to analyse diversity. I used the Dominance Index to relate the highest number of birds for each species to the total number of birds seen (all species combined). The Bucher and Herrera Index of Relative Importance (Bucher & Herrera 1981) was used as an index to describe the relative numbers of each species in the population.

The Spearman coefficient (r_s) (Southerwood 1971) was used to measure the intensity of association between the annual patterns of different species.

The following index, which is similar to the Bucher and Herrera Index of Relative Importance and which relates the relative intensities of foraging and resting, was used to estimate the feeding activities of each species in the intertidal sector: relative importance (feeding/rest) or RI (f/r) = $(Nf/Nt)(Mf/Mt) 100$, where Nf = the number of birds feeding in all the censuses; Nt = the number of birds in all the censuses; Mf = the number of censuses in which the species is feeding; and Mt = the number of censuses in which the species is present.

The frequency of habitat use by a species was calculated as the number of observations of each

Table 1. Designation of microhabitats. Different numbers for a microhabitat indicate a different spatial location or a different substrate.

Macrohabitats and tide				
SI	SII	AIII-IV	BIII-IV	Microhabitats
1	1	1	1	DRY SEDIMENT
2	2	2	2	DRY BACKWATER (deposits of algae and dry grass)
3				WET BACKWATER
4	8	15	20	BORDER 1: zone alternatively covered and uncovered by waves
5	9	16	21	BORDER 2: deeper than BORDER 1, covered by at least 3 cm of water
6	6			SEMI-PERMANENT POOLS (>5 cm)
	7	13	7	ALGAE recently deposited by the sea
	10	10/11	17	WET SEDIMENT
		12	18	SEDIMENT COVERED IN WATER (0-5 cm deep)
		14	19	ROCK covered in film of sediments in patches and water up to 3 cm deep
				PATCHES OF MUSSELS 10-30 cm wide with variable lengths
				LARGE TIDE POOLS (up to approximately 30 cm deep)
				HIGH ROCK FORMATIONS (up to 100 cm high)
				ROOTED GREEN ALGAE

species in each microhabitat divided by the total number of observations made of this species. The chi-squared test (χ^2) was used to analyse frequency.

The Mean Taxonomic Distance Index (MTD) (Sokal 1965) was used to identify similarities in foraging habitat use among species. The mean linkage technique (Sokal & Sneath 1963) was used for group analysis. Graphic representation was done using dendrograms; the cophenetic correlation coefficient (r) of Sokal & Rohlf (1969) was used to measure distortion between the similarity matrices (Crisci & Lopez Armengol 1983).

The segregation of pairs of species that were very similar in their use of habitat and tide was carried out using the Wilcoxon signed-ranks test (Sokal & Rohlf 1980).

Results

Eight species of shorebirds belonging to the Charadriidae (4) and Scolopacidae (4) were identified.

Patterns of abundance and seasonal distributions

The highest numbers of birds were seen from mid-November to mid-July; there were no numbers exceeding 100 birds/census at other times of the year (Figure 3).

The annual pattern showed three phases: (1) the sudden abundance of birds in November, due mainly to the arrival of *Calidris fuscicollis* from North America, (2) the northern migration of all the

species in early fall and (3) the increase in early winter due to *C. alba* and *Charadrius falklandicus*.

The Simpson Diversity Index ranged between 0.0 and 2.06 on the northern migration. The seasonal variation in dominance showed a definite pattern in the succession of dominant species: *C. fuscicollis* dominated from mid-November to early April (Simpson Diversity Index > 0.93), interrupted only by the arrival of *C. canutus*, which then became dominant (Simpson Diversity Index = 0.79).

Once the migration of the Nearctic plovers had occurred, *C. falklandicus* became dominant until the next season. North American sandpipers (Scolopacidae) dominated from mid-spring to early fall, when plovers (Charadriidae; Patagonian species) exercised full dominance.

The annual balance studied by means of the relative importance values is consistent with the results described above (Figure 4).

Overall, the Scolopacidae occurred in far larger numbers than the Charadriidae (RI = 59.68) owing to the migration of large flocks and not because of a constant movement of sandpipers into the area.

A positive correlation was found between the seasonal patterns of *C. alba* and *C. falklandicus* ($r_s = 0.5937$; $p < 0.01$).

Most of the observers along this coastline were sports fishermen. In the summer, there were larger numbers of tourists during high-tide periods. At low tide, the human presence decreased, and a typical activity at that time was the collection of

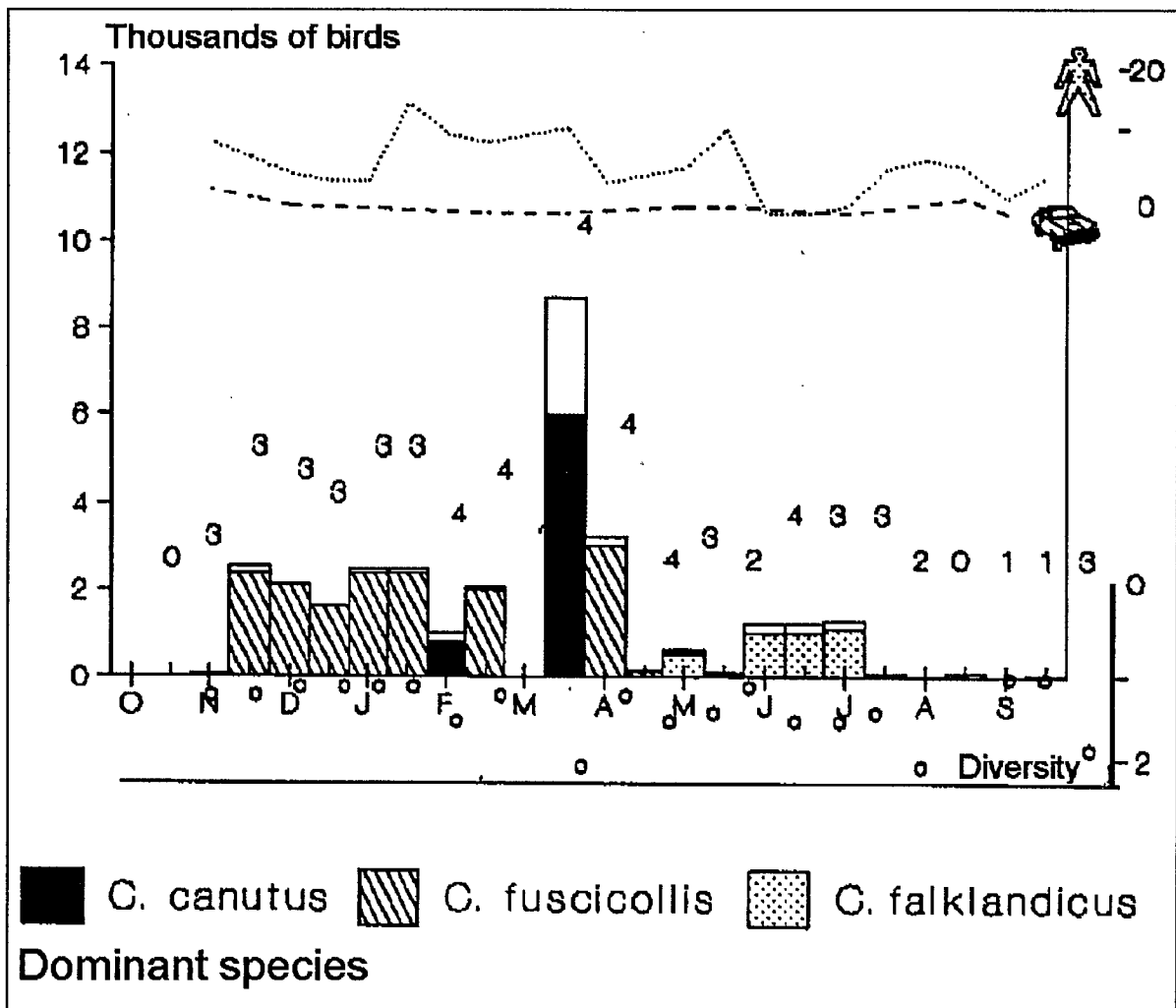


Figure 3. Frequency diagram: Seasonal variation in the total number of plovers and sandpipers, showing the contribution of the dominant species. The number on each bar indicates the number of species present. Lines: Seasonal variation in the number of people and vehicles. Lines were used to indicate possible trends, but the variables are discrete. Points: Seasonal variation in species diversity (Simpson). Observations are for the period between October 1989 and October 1990.

small octopuses. The number of dogs ranged between 0 and 4; 50 goats and 1 boat were also recorded. The groups that interacted most with the birds were passers-by, dogs and vehicles (Figure 3).

Species observations

North American
Family Scolopacidae

Ruddy Turnstone *Arenaria interpres*

One bird in non-breeding plumage was observed on 5 November 1989, and two birds with advanced transitional plumage (verging on breeding plumage) were observed on 15 February 1990.

Sanderling *Calidris alba*

Sanderlings used the study area as a migratory stop on their way south in November and north in March, even though low numbers were often observed in the summer (Figure 4). During the southern fall and winter, there were birds that did not migrate. Similar observations involving juvenile birds were made in Peru by Castro & Myers (1987). Contrary to observations in Peru, the birds did not moult to breeding plumage in Los Alamos, except for one bird sighted on 16 June 1990. These could be sexually immature birds that, like their counterparts in California, did not acquire breeding plumage, although the latter do migrate (Myers *et al.* 1985a, cited in Castro & Myers 1987). The birds sighted in March were beginning a body moult.

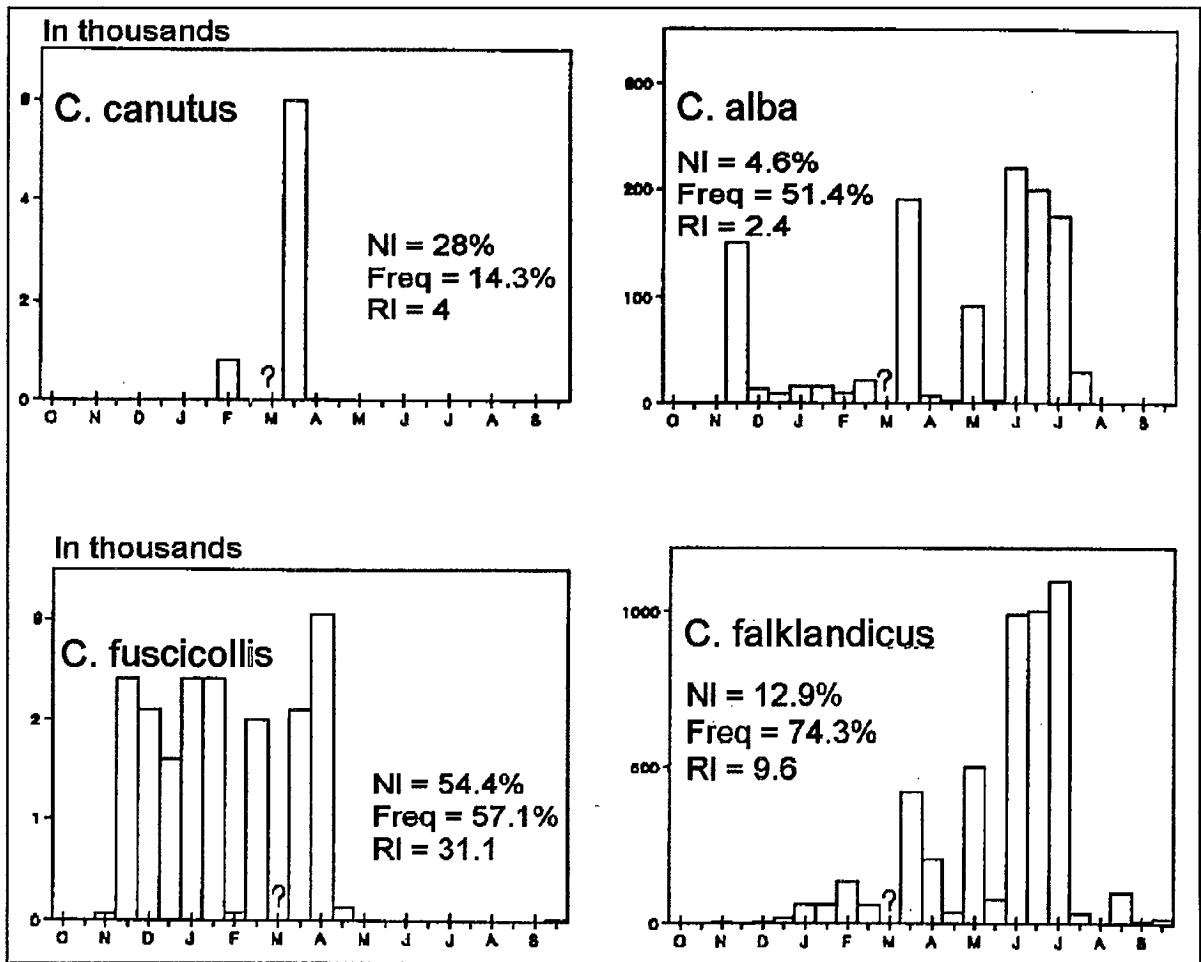


Figure 4. Seasonal variation in the number of individuals for the species with the highest relative importance (RI), indicating numerical importance (NI) and Frequency (Freq.). Observations are for the period between October 1989 and October 1990.

On other beaches in the region, this species was present for a large part of the annual cycle (pers. obs.). In January 1982, Morrison & Ross (1989) reported 490 *C. alba* on the beaches of the east canal that links the Bahia de San Antonio to the Gulf.

Red Knot *Calidris canutus*

The Red Knot was seen in large numbers during the migration to its breeding grounds (Figure 4). Its pattern of seasonal distribution is consistent with that observed by other researchers (Harrington & Morrison 1980; Blanco, Pugnali & Rodríguez Goñi 1988), whereby the species uses different southward and northward migration routes. In February and November, the Red Knots were in breeding plumage. Birds seen in March had begun a body moult (approximately 30% complete). In March, approximately 30 Red Knots with colour bands were sighted; these included birds with orange bands from Punta Rasa, Argentina, birds with dark green bands from the United States and some birds with light green bands from an unknown location.

White-rumped Sandpiper *Calidris fuscicollis*

The White-rumped Sandpiper used this coastline during its northward and southward migrations as well as during the austral summer (Figure 4). Although the large groups appeared in the second half of November (>2,400 birds), the first flocks (7-61 birds) were seen in early November 1989 and in late September 1990. One non-migratory bird was recorded in June.

**Patagonian
 Family Charadriidae**

Tawny-throated Dotterel *Oreopholus ruficollis*

On 1 January 1989, one bird fed for a few minutes in the dry sand at high tide and then flew away (pers. obs.).

Two-banded Plover *Charadrius falklandicus*

This species was recorded in Los Alamos almost all year (Figure 4). Widely fluctuating numbers from the end of January to March and May suggest that at least part of the population consisted of birds migrating north. By contrast, no spring peaks were observed. The winter resident population showed the highest numbers of the year (1,100 birds). The lowest population densities were during the breeding season. Two chicks were observed: one on 31 December 1989 and another on 16 January 1990 (possibly the same bird), confirming that the species was nesting in this area.

Observations were made in September of birds with breeding plumage, which they wore until January, when moulting began. In March and until late April, most birds wore non-breeding plumage. This agrees with the observations of Blanco, Pugnali & Rodríguez Goñi (1988) for Punta Rasa. In May, the plovers showed very advanced transitional plumage, verging on breeding plumage, in contrast with that observed on the previous visit. This possible lack of synchrony in moult could be related to the genetic variability of populations that may alternate in their use of the same site.

Magellanic Plover *Pluvianellus socialis*

A species from the south, it is a resident of the study area during the non-breeding season. Although local records show little latitude in its known range of non-breeding dispersion up to the Valdes Peninsula (Jehl 1975), I have received more recent reports from the southern part of the province of Buenos Aires (Grupo Becasa, San Antonia Ouest, unpubl. data). Three specimens were observed on 18 September 1989; 2 were seen on 18 April, 13 on 16 and 28 June and 9 on 13 July 1990. Out of 13 birds, 7 had yellow feet and whitish spots on the back (juveniles), 2 had reddish-orange feet (older juveniles?) and 4 had red feet (adults).

Brazilian-Paraguayan Family Charadriidae

Collared Plover *Charadrius collaris*

One bird was seen in the wet sand of the intertidal region on 25 September 1990, close to four *C. falklandicus* at rest.

Relationship between foraging and resting birds

Except for the Red Knots, the shorebirds normally rested in groups at high tide and fed on the shoal when it was uncovered by the sea. The knots would rest even with 100–150 m of the shoal still exposed. The proportion of feeding birds was

quantified for the intertidal region at high tide (condition I-II): *P. socialis* and *C. alba* comprised the highest proportion of feeding birds ($RI(f/r) = 27.02$ and 10.20 , respectively). The index relating resting and feeding in *C. canutus* was only 1.50 (very low despite having the highest number of foraging individuals) owing to their lesser significance; at tide condition IV, no more than 360 birds out of 4,800 (7.5%) were feeding. Most of the *C. fuscicollis* remained at rest ($RI(f/r) = 0.19$).

On 16 June and 13 July 1990, *C. alba* and *C. falklandicus* remained at rest, even when tidal waters exposed about 400 m of shoal.

Frequency of feeding habitat use

Intertidal habitat

At high tide (SI), the microhabitat most used ($p < 0.005$) by all species was Border 1 (35%), an environment repeatedly covered and uncovered by waves (Figure 5). *Calidris alba* used the greatest number of resources for the longest time, whereas *C. fuscicollis* and *C. canutus* fed only at Border 1.

When the tide began to ebb (SII), the diversity of foraging habitats increased. The Charadriidae and *C. alba* both significantly preferred to forage on wet sediment ($p < 0.005$). In similar fashion, *C. fuscicollis* preferred Border 1 ($p < 0.005$), and *C. canutus* waded across the border at greater depths ($p < 0.005$).

The shoal

When the shoal was uncovered, the plovers dispersed. For a certain period of time, the water drained from the rock in a laminar flow. As the slope was not steep, the border environments became quite wide and shallow, with small waves. With the shore about 50 m away (condition AIII), *C. fuscicollis* chose algal deposits on the shoal ($p < 0.005$), which were in variable supply. *Charadrius falklandicus* preferred algae deposited by the sea, sediment with water and rock covered in sediment and water ($p < 0.005$), although no significant differences were found in the use of these three environments. *Pluvianellus socialis* used the low border.

In condition AIV (sea at 100 m), the species preferred rock partly covered (>62%) in a film of fine sediment and water up to 3 cm deep (microhabitat 14) ($p < 0.005$ for the sum of individuals of all species and for each individual species).

As the typical shoal was the most available environment and the greatest food supply was in this macrohabitat (microhabitat 14), it was obvious that this was the most important feeding environment in the upper intertidal zone.

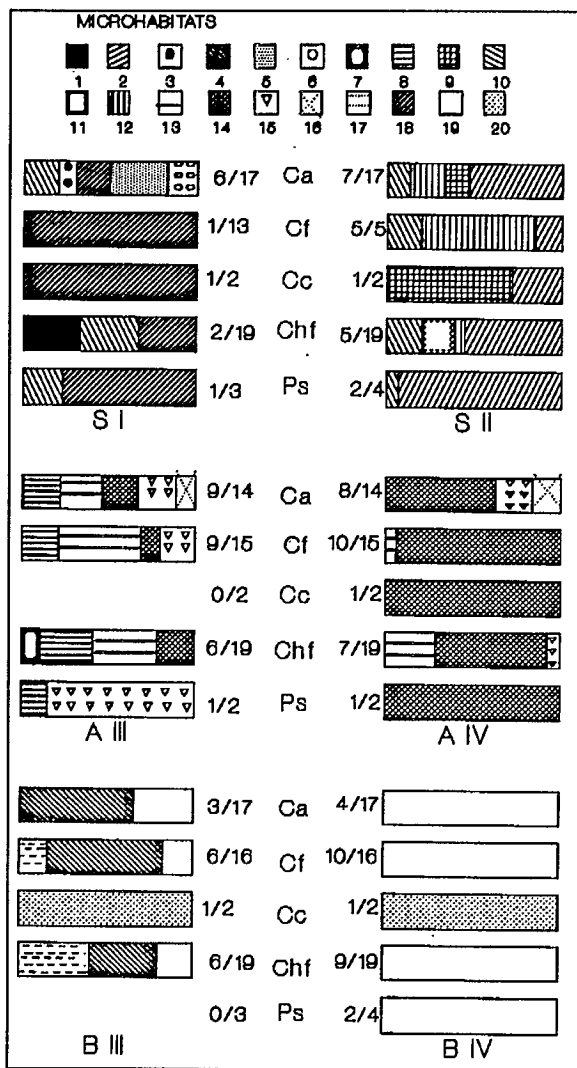


Figure 5. Relative annual use — by species — of feeding microhabitats (Arabic numerals) in various macro-environments (capital letters) and tide conditions (Roman numerals). The fractions point out the relationship between the number of samples in which the species used that habitat and tide condition (numerator) and the total samples in which it was represented (denominator). The species are indicated by the initials of their names; macrohabitats, microhabitats and tide as in Methods. Observations are for the period between 5 November 1989 and 24 November 1990 (from Southerwood 1971; Jehl 1975; Myers & Myers 1979; Harrington & Morrison 1980; Sokal & Rohlf 1980; Myers *et al.* 1987; Narosky & Yzurieta 1987; Piola & Scasso 1988; Morrison & Ross 1989).

In condition BIII, *C. alba* and *C. fuscicollis* fed more on sediment covered with water (microhabitat 18) than on rocks (microhabitat 19) ($p < 0.005$); as the sea went out farther (BIV), the latter microhabitat became more available, and its frequency of use — including *C. falklandicus* and *P. socialis* (which did not use BIII) — increased to levels of over 95%. Only *C. canutus* showed a marked preference for the low border ($p < 0.005$).

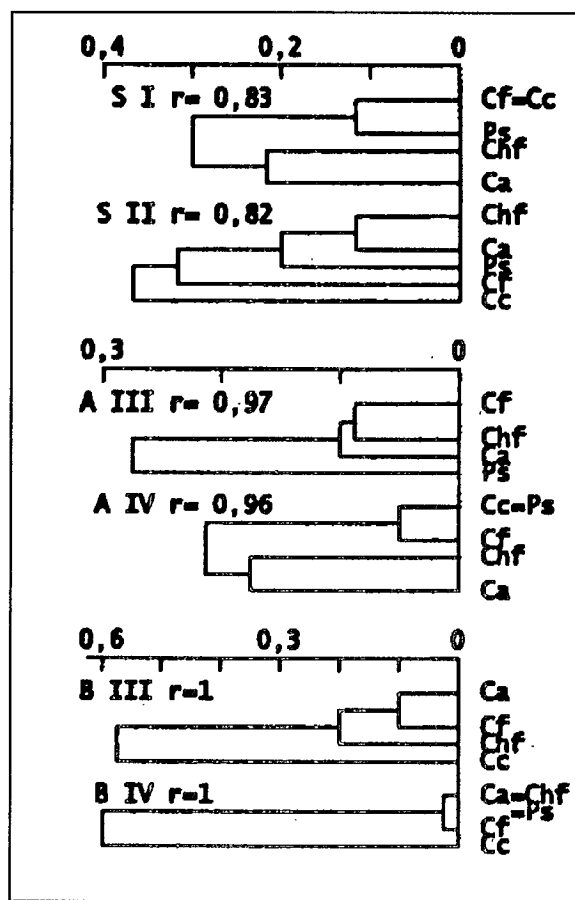


Figure 6. Dendrograms of Similarity (MTD) of feeding habitat use between species for various macrohabitats (capital letters) and tide conditions (Roman numerals). r = cophenetic correlation coefficient; names of species listed by initials; macrohabitats and tide conditions listed in Methods.

In general, *C. alba* used a greater number of microenvironments (17); *C. fuscicollis* and *C. falklandicus* used 15 and 14, respectively; *C. canutus* and *P. socialis* were present in the region for less time, foraging in only 7 environments. Plovers and sandpipers were always present at low tide. Feeding areas were located in the upper, middle and lower intertidal zones.

Similarities between species

The analysis of similarities between pairs of species (Figure 6), which included all the experimental conditions simultaneously, was significant for the following distance relationships (MTD) (note: the species are identified by the initials corresponding to their names):

- Ca-Chf < Ca-Ps (*)
- Ca-Chf < Ps-Chf
- Ca-Cf < Cc-Chf
- Ca-Chf < Ca-Cc
- Ca-Chf < Cc-Chf (*)
- Ps-Chf < Ca-Cc

Ca-Cf < Ca-Cc
 Cf-Chf < Cc-Chf
 Cf-Chf < Ca-Cc

$p < 0.05$ except where marked (*), where $p < 0.025$.

Calidris alba was similar to *C. falklandicus*; *C. canutus* and *P. socialis* were further apart. As there were no significant differences between Ca-Chf and Ca-Cf and no similarity could be drawn between *P. socialis* and *C. canutus*, it is proposed that the species be segregated in the following three groupings that best describe associated and independent species that use the foraging habitat at Los Alamos. These are (1) Ca, Chf and Cf, (2) Ps and (3) Cc.

Discussion

Patterns of abundance and seasonal distribution

The Los Alamos coast is only one of the various sites of shorebird concentrations in the Bahía de San Antonio and the Gulf of San Matías. Could the patterns obtained here be extrapolated to the rest of the region?

This study showed that large numbers of plovers arrived from the north until the second half of November. However, at other sites, peak numbers were reached at the end of September in 1990 (pers. obs.). These observations suggest that plovers used the habitats at different times. Conclusions can therefore not be drawn on habitat use by the plovers based exclusively on the results obtained from Los Alamos.

On 20 and 29 October 1988, about 2,400 *C. fuscicollis* and 400 *C. alba* were recorded at Los Alamos, and similar concentrations were observed near Punta Delgado (pers. obs.). This indicates that patterns may change from year to year. The variation may be due to causes that are internal or external to the system or to the scheduling of the censuses, which may not reflect the actual pattern, as significant numbers of plovers and sandpipers may come and go between censuses.

How many birds depend on the site?

The information obtained suggests that there was some turnover in the numbers of North American species (although it was not quantified) during the non-breeding season. By contrast, the similar numbers of *C. alba*, *C. falklandicus* and *P. socialis* throughout the three consecutive censuses and the distinguishable plumages of shorebirds presumably on their way north indicated that these species were resident during the southern winter.

The figures obtained from the recounts tended towards underestimations, but they offer reliable figures on the minimum numbers of birds using this area.

The results show the importance of the site for the species observed: at least 3,050 *C. fuscicollis*, 6,000 *C. canutus*, 600 *C. alba* and 1,100 *C. falklandicus* used the Los Alamos coast during the 1989–1990 winter.

Feeding habitats

In the course of these field studies, it appeared to me that most birds at rest fed later in the upper intertidal zone. The time during which the birds used this zone, and whether or not shorebirds coming from other roosting sites used it, could not always be determined.

There were similarities in feeding habitat use between the most common species (*C. fuscicollis*, *C. alba* and *C. falklandicus*) and the less common species (*C. canutus* and *P. socialis*), although they remained widely apart. The correlation in the patterns of abundance and seasonal distributions between *C. alba* and *C. falklandicus* is interesting, because these species were not only similar in their use of habitat but also not segregated in time. This leads to the assumption that the habitat and feeding resources were not limiting and that there would thus be no competition; however, it is still unknown whether they were segregated on the feeding axis.

Trophic dynamics

The greatest numbers of plovers and sandpipers were observed during the months of February to April. This is especially relevant, because the highest values of chlorophyll 'a' in the coastal waters of Las Grutas were obtained during that period based on sampling carried out by G.B. Domecq Chantry in 1986 (unpubl. data). Since the period during which the system maintains the most migratory shorebirds coincides with the phytoplankton bloom, this indicates a positive relationship between primary marine productivity and the availability of bottom-dwelling prey for birds.

Conservation

In order to ensure the conservation of migratory shorebirds at the hemispheric level and the critical habitats they require, it is important to determine the significance of this site in Argentina. These birds gather in specific areas at times that are related to the seasonal availability of resources. Plovers make maximum use of the food available at these sites (Evans 1979, cited in Myers *et al.* 1987; Goss-Custard 1979; Schneider & Harrington 1981), which means that birds displaced by habitat degradation will be in a desperate situation by being forced to use sites already used to capacity.

The conservation strategy set out by Myers *et al.* (1987) calls for the protection of important sites used sequentially by shorebirds, thus forming critical links in the international chain. The data presented in this paper demonstrate the significance of this coastline to shorebirds in Los Alamos and the need for the implementation of protection measures in the future.

Conclusions

This study demonstrated the importance of the Los Alamos coastline for migratory shorebirds. According to the guidelines in Clark (1974) regarding the management of coastal areas, it is a 'vital' coastal area, *i.e.* it should be protected because of its role in maintaining the essential ecological processes of this ecosystem. The overall role of the San Antonio Oeste region in the migratory cycles of shorebirds remains to be determined.

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I wish to acknowledge the Ornithological Association of El Plata (AOP), which awarded me the Olrog Scholarship to carry out this project, and Alparamis S.A., which financed it. Partial support was also provided by La Red Hemisferica de Reservas para Aves Playeros (RHRAP) and the Grupo de Aves Limicolas (GAL). Special thanks go to Montserrat Carbonell, whose suggestions and support were invaluable, and to the following individuals and institutions: Eliseo Sepulveda and staff of ITMAS, Luis Curtolo, Daniel Paz and Guillermo Domecq Chantry. Lastly, my special thanks go to Paul Pedersen and Daniel Blanco.

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Observations on migratory and resident shorebirds in lakes in the highlands of north-western Argentina

Claudio D. Laredo

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The highlands located in the extreme north-west of Argentina include several wetlands of significance to Nearctic migratory shorebirds during the southern spring and summer. In addition, resident shorebirds depend on the same habitats for breeding purposes. Since 1989, these birds have been observed at Pozuelos, Vilama, Pufulos, Guayatayoc, Runtuyoc and other locations. Data are now available on the number of species in both groups, their relative abundances, a tentative model of phenology and resource use and the chief threats to the quality of these wetlands. The information obtained shows the importance of the study area to three species of migrants and the less frequent occurrence of a further six species in the same group. Observations of the resident species indicate a probable decline in populations, possibly as a result of human activities; these are primarily disturbances due to cattle and overgrazing, deliberate fires and the clearing of grassland and shrubs.

Las zonas altas ubicadas en el extremo noroccidental de Argentina incluyen varios humedales de importancia significativa para las aves costeras migratorias néárticas durante la primavera y el verano en el sur. Además, las aves costeras residentes dependen de los mismos habitats para su reproducción. Desde 1989, estas aves se han avistado en Pozuelos, Vilama, Pufulos, Guayatayoc, Runtuyoc y otras localidades. Ya existen datos sobre el número de especies en ambos grupos, su abundancia relativa, un modelo fenológico experimental y el uso de recursos, y las amenazas principales a la calidad de estos humedales. La información obtenida muestra la importancia del área de estudio para las tres especies migratorias y para otras seis especies del mismo grupo, avistadas con menos frecuencia. Las observaciones de especies residentes indican una disminución probable de las poblaciones, posiblemente como resultado de actividades humanas; se trata principalmente de perturbaciones debidas al ganado y el pastoreo excesivo, incendios deliberados y el corte de hierba y arbustos.

Les hautes-terres de l'extrême Nord-ouest de l'Argentine abritent plusieurs milieux humides très utilisés par les oiseaux de rivage migrants des régions néarctiques durant le printemps et l'été de l'hémisphère austral. Les espèces résidentes dépendent aussi de ces habitats pour la reproduction. On observe depuis 1989 les oiseaux de rivage à Pozuelos, Vilama, Pufulos, Guayatayoc, Runtuyoc et à d'autres endroits. On dispose maintenant de données sur le nombre d'espèces dans les deux groupes, leur abondance relative, un modèle phénologique et d'utilisation des ressources potentielles et les principales menaces à la qualité de ces milieux humides. Ces données montrent l'importance de la région étudiée pour trois espèces d'oiseaux migrants et la présence occasionnelle de six autres espèces du même groupe. L'observation des espèces résidentes révèle un déclin probable des populations, peut-être associé aux activités anthropiques, surtout les perturbations causées par le bétail et le surpâturage, les incendies délibérés, le défrichage des prairies et la coupe d'arbustes.

Faculty of Natural Sciences and Miguel Lillo Institute, Universidad Nacional de Tucuman, c/o CC 75, Suc. 2, 4000 Tucuman, Argentina.

Introduction

The highlands located in the extreme north-west of Argentina include several wetlands of significance for Nearctic migratory shorebirds during the southern spring and summer. In addition, resident shorebirds depend on the same habitats for breeding purposes. Very little information is available on these birds in the region. There are partial lists, such as those of Correa Luna (1973), Canevari (1985) and others (e.g. Nores 1986, 1988;

Jehl 1988; Laredo 1989), which contain estimates of the number of individuals observed of certain species. Accordingly, presented here are data and observations gathered recently on shorebirds in certain wetlands in north-western Argentina.

Study area

The sources of the information reported here include preliminary observations carried out since 1989 at Lake de los Pozuelos, a natural heritage site.

Table 1. Lakes in north-western Argentina visited in September 1991.

Wetland	Location	Altitude (m)	Area (ha) ^a	Type
Lake de los Pozuelos	22°20'S, 66°00'W	3,500	10,000	Permanent
Lake Larga-Lagunilla	22°21'S, 66°07'W	3,700	300	Permanent
Lake Vilama	22°10'S, 66°55'W	4,400	8,000	Permanent
Lake Pululos	22°40'S, 66°44'W	4,400	700	Permanent
Lake Runtuyoc	22°39'S, 65°41'W	3,400	600	Temporary
Lake sobre Rio Miraflores	23°02'S, 65°52'W	3,600	400	Temporary
Lake Leandro	23°00'S, 65°15'W	4,050	600	Temporary
Lake Blanca	22°58'S, 65°10'W	4,400	600	Temporary
Lake Guayatayoc	23°10'S, 65°33'W	3,660	20,000	Permanent

^a From personal observations and maps.

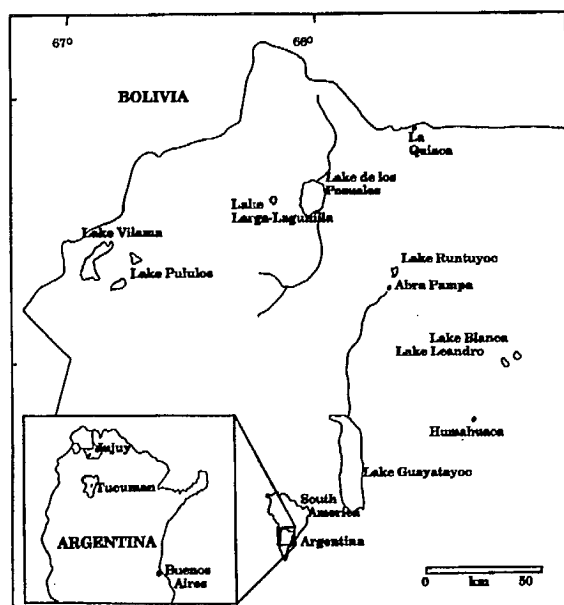


Figure 1. The locations of the wetlands in north-western Argentina considered in this study.

In September 1991, a survey of nine wetlands, including Lake de los Pozuelos, was carried out (Table 1). In addition, intermittent censuses carried out in Lake de los Pozuelos and Lake Larga-Lagunilla in November/December 1989, February 1990 and January 1991 have been used to supply comparative data (Figure 1).

Generally speaking, the lakes visited present similar features. They belong to the major Puna ecosystem (Morello 1983), which lies between 3,500 and 4,500 m above sea level, framed by mountains and attaining higher altitudes at their peaks. The water levels of the lakes vary each year, given the high seasonal variations in precipitation (rain in summer, between September and March) that characterize the region. Waters may be fresh, brackish or saline. The climate is continental, cold and dry (average annual precipitation is 280 mm), with high radiation. Temperatures fluctuate widely during the day, with differences of up to 40 °C. Cold, dry,

blustery and intermittent high winds regularly sweep the western quadrant, which phyto-geographically includes the Andean domain, a subregion of Puna Province (Cabrera 1968).

Three types of habitats were considered to be of interest in observing the shorebirds. These habitats occur frequently in the wetlands visited, so a brief description is in order:

- (1) *Mudflats – shallow waters*: These consist of vast surfaces with very gentle slopes, devoid of vegetation, with patches of saltpetre and clumps of vegetation. Depending on wind direction and velocity, the water may be observed to advance and retreat each day, with frequent changes in humidity and resource availability for fauna. This situation is also apparent at the river-mouths, where the alluvial fans help create rapid habitat variations. Shallow waters are those portions of wetlands where water depths are between 5 and 40 mm and where aquatic plants such as *Potamogeton* and *Zannichellia*, among others, are frequently seen.
- (2) *Grassland–shrubland*: These are located at the periphery of the wetlands behind the mudflats and generally extend throughout dry land in the entire region. Several plant species occupy this habitat, of which *Parastrephia* (shrubs) and *Stipa* (grass) are typical.
- (3) *River-beds*: These include portions of rivers that invade the typical grassland–shrubland landscape and also include large areas of wetlands owing to their alluvial fans. The river-beds are generally of the ravine or canyon type, with depths up to 3 m from the grassland–shrubland levels. Depending on precipitation, the flow in these river-beds varies greatly. In association with rivers not of the canyon type and with springs and streams, swampy lowlands are commonly seen, consisting of communities of phanerogams covered by slowly but continuously flowing water.

Methods

On the mudflat – shallow water habitats, the birds were observed and counted with 8× binoculars and a 40× telescope; in the grassland–shrubland habitat, transects were used; and in river-beds, the birds seen along the shore were counted. In all cases, distances and widths covered were monitored with the use of a Spectrum 500 telemeter (scope 18–457 m and accuracy ±3 m up to 300 m). Directions were taken and corrected by compass. The counts were made between 7:00 a.m. and 5:00 p.m. when atmospheric conditions were sufficiently stable and favourable to achieve reliable observations.

Results

The shorebird species censused were divided into two groups: migrants, having their breeding grounds in the Northern Hemisphere, and residents, breeding in the study area. In the wetlands visited, the occurrence of nine migratory species and ten resident species was recorded (Table 2).

Tables 3, 4 & 5 show the numbers of birds obtained from censuses undertaken on nine wetlands in September 1991 as well as their densities per hectare of habitat and percentage of species that were migrants or residents. As well, these tables contain data collected from Lake de los Pozuelos in November/December 1989, February 1990 and January 1991 and from Lake Larga–Lagunilla in January 1991 for comparative purposes. Table 6 presents values of relative importance (RI) (Bucher & Herrera 1981) for all species counted during the September 1991 censuses in the nine wetland types considered here. These values were calculated using the following formula:

$$RI = \frac{Ni \times Mi}{Nt \times Mt} \times 100$$

where N_i is the number of individuals observed from species i in all samples, N_t is the total individuals for all species, M_i is the number of samples in which species i was present and M_t is the total number of samples.

Below are additional data on the species censused.

Lesser Golden-Plover *Pluvialis dominica*

In the past three years (1989–1991), solitary individuals of this species have been observed beginning in mid-August. The September, November/December and January censuses show compact groups of 15–20 individuals appearing frequently in mudflat – shallow water habitats and infrequently in other habitats. In February, the groups are more numerous, in loose groupings of up to 150 individuals in grassland–shrubland

habitats over 5,000 m from the main wetland. During this period, greater flock mobility was observed as well.

Hudsonian Godwit *Limosa haemastica*

This species is commonly observed in groups of not more than 150 individuals frequenting mudflats – shallow waters, with a few isolated individuals occasionally entering deeper waters. No records earlier than September are available. Beginning in mid-February, some compact flocks of up to 350 individuals were observed in the area adjacent to the mouth of the Cincel River at Lake de los Pozuelos. In late February, some individuals in an advanced state of moult to breeding plumage were observed.

Yellowlegs (*Tringa* spp.)

Both Greater Yellowlegs *Tringa melanoleuca* and Lesser Yellowlegs *Tringa flavipes* are common, although apparently differing in number and disposition. *Tringa flavipes* frequently occurs in compact groups of 15–20 individuals, whereas *T. melanoleuca* appears in loose groupings of 2–5 individuals. Records for both species show little variation between September and February, and occurrences of solitary and scattered individuals also exist for the months of June and July. *Tringa flavipes* has been observed only on mudflats – shallow waters and in temporary ponds, but *T. melanoleuca* is frequently seen in river-mouths and swampy lowlands as well.

Wilson's Phalarope *Phalaropus tricolor*

Very numerous and compact flocks are recorded for this species. Not only does this species frequent mudflats – shallow waters, but high numbers, over 2,500 individuals, have been seen swimming on the waters of Pozuelos, Vilama and Guayatayoc lakes, more than 1,500 m from the shore. Smaller groups of 80–100 individuals are also seen in small temporary ponds. Numerous groups are recorded beginning in late August. Aplomada Falcon *Falco femoralis* hunts large flocks of this species. Beginning in the first half of March, some individuals are moulting to breeding plumage. Isolated and very scattered groups are frequently seen in the months of June and July in Laguna de los Pozuelos.

Baird's Sandpiper *Calidris bairdii*

Large concentrations of birds of this species are recorded beginning in August in Lake de los Pozuelos. In September, flocks of over 1,500 birds are seen massing on mudflats – shallow waters, and groups of up to 400 individuals are regularly scattered over grassland–shrubland habitats. In September, high RI values are recorded for this species, together with *Phalaropus tricolor*, in censuses

Table 2. List of shorebird families and species recorded in the wetlands of the highlands of north-western Argentina.

Family	Migrants	Residents
Recurvirostridae	None	<i>Himantopus himantopus</i> <i>Recurvirostra andina</i>
Charadriidae	<i>Pluvialis dominica</i>	<i>Vanellus resplendens</i> <i>Charadrius alticola</i> <i>Phegornis mitchellii</i> <i>Oreopholus ruficollis</i>
Scolopacidae	<i>Limosa haemastica</i> <i>Tringa melanoleuca</i> <i>Tringa flavipes</i> <i>Phalaropus tricolor</i> <i>Calidris bairdii</i> <i>Calidris melanotos</i> <i>Calidris himantopus</i> <i>Tryngites subruficollis</i>	<i>Gallinago andina</i>
Thinocoridae	None	<i>Attagis gayi</i> <i>Thinocorus orbignyianus</i> <i>Thinocorus rumicivorus</i>

taken in seven of the nine wetlands visited. Flocks of this species are frequently pursued by *Falco femoralis*.

Pectoral Sandpiper *Calidris melanotos*

Birds of this species were observed in small groups of between five and seven individuals beginning in early August. In mid-September, regular flocks of 30–50 individuals are observed, both in mudflats – shallow waters and in grassland–shrubland. Also, single individuals were frequently seen among large concentrations of *Calidris bairdii*.

Stilt Sandpiper *Calidris himantopus*

No sightings earlier than September were recorded for this species. These birds frequent principally mudflats – shallow waters. Smaller groups also enter deeper areas, where they feed by completely submerging their heads and the lower front portion of their bodies. Because of the gentle slopes of the wetlands visited, several birds of this species remained outside the area covered by the censuses (approximately 100 m from the water's edge), given the habitat mentioned earlier. In February, groups gradually grow more numerous, and flocks of over 300 individuals can be seen in early March.

Buff-breasted Sandpiper *Tryngites subruficollis*

A few birds of this species were observed in mudflats – shallow waters; they were always in low numbers and very dispersed. They have also been seen in very loose and small groups feeding in grassland–shrubland with small temporary ponds. Some birds were seen along the roadside adjacent to the wetlands. These groups occasionally amounted

to more than 20 individuals. No records are available earlier than September for this species.

Black-winged Stilt *Himantopus himantopus*

This is undoubtedly the most numerous resident species found in the wetlands visited. It frequents almost exclusively waters near the shore with depths of up to 100 mm. Spindle-shaped groups are very common, comprising more than 2,500 individuals. Also very frequently seen are small loose flocks of 30–50 birds. The larger groups are first seen in late August, and numbers decline substantially by early February. No data are available on nesting in the study area.

Andean Avocet *Recurvirostra andina*

Groups of 15–20 individuals are generally observed in somewhat compact groups, although 2 or 3 birds can often be found feeding at a short distance from one another but isolated from larger groups. Dispersed groups totalling 20 birds almost constantly use the mudflats – shallow waters near the mouth of the Cincel River in Lake de los Pozuelos. Some loose flocks frequent waters up to 80 mm in depth. In February, a nest of this species was found on the narrow beaches of the terraces to the east of Lake de los Pozuelos, located on very irregular ground with vestiges of old swamps. The nest was attacked and destroyed by an Andean Gull *Larus serranus*, despite aggressive attacks by three *R. andina* to repel the gull; one egg, of three in the clutch, was rescued.

Andean Lapwing *Vanellus resplendens*

This species was recorded in every month of the year. Very loose groupings of 15–20 individuals

Table 3. Results of shorebird censuses in Lake de los Pozuelos: (a) mudflats – shallow waters, (b) grassland–shrubland and (c) river-beds and valleys.

Sectors	Variables	Nov.–Dec. 1989	Feb. 1990	Jan. 1991	Sept. 1991
(a) Peninsula N (50 ha)	Total no. birds	2,899	1,680	nc ^a	6,216
	Mean no./ha	58.0	33.6		124.3
	% migrants (no. spp.)	46.4 (9)	70.0 (8)		76.8 (9)
	% residents (no. spp.)	53.6 (5)	30.0 (5)		23.2 (5)
NW (20 ha)	Total no. birds	1,713	nc	nc	3,669
	Mean no./ha	85.6			183.4
	% migrants (no. spp.)	52.2 (8)			80.2 (9)
	% residents (no. spp.)	47.8 (4)			19.8 (5)
NE (60 ha)	Total no. birds	nc	nc	nc	8,709
	Mean no./ha				145.1
	% migrants (no. spp.)				78.4 (7)
	% residents (no. spp.)				21.6 (4)
S (60 ha)	Total no. birds	2,166	1,820	883	6,189
	Mean no./ha	36.1	30.3	14.7	103.1
	% migrants (no. spp.)	49.9 (8)	88.2 (7)	57.7 (6)	94.7 (7)
	% residents (no. spp.)	50.1 (6)	11.8 (5)	42.3 (4)	5.3 (4)
River-mouth Cinzel River (60 ha)	Total no. birds	2,981	2,349	2,333	7,880
	Mean no./ha	49.7	39.1	38.8	131.3
	% migrants (no. spp.)	50.2 (9)	41.3 (9)	74.4 (7)	81.1 (9)
	% residents (no. spp.)	49.8 (4)	58.7 (4)	25.6 (5)	18.9 (4)
(b) Terrazan del E (25 ha)	Total no. birds	521	754	nc	nc
	Mean no./ha	20.8	30.1		
	% migrants (no. spp.)	72.5 (5)	70.1 (8)		
	% residents (no. spp.)	27.5 (5)	29.9 (4)		
NW (20 ha)	Total no. birds	540	nc	nc	2,617
	Mean no./ha	27.0			130.8
	% migrants (no. spp.)	71.1 (3)			95.8 (4)
	% residents (no. spp.)	28.9 (4)			4.2 (4)
S (15 ha)	Total no. birds	256	nc	nc	675
	Mean no./ha	17.0			45.0
	% migrants (no. spp.)	62.1 (3)			93.2 (1)
	% residents (no. spp.)	37.9 (3)			6.8 (4)
(c) River-bed Cinzel River (7.5 ha)	Total no. birds	294	321	nc	nc
	Mean no./ha	39.2	42.8		
	% migrants (no. spp.)	40.8 (3)	26.2 (4)		
	% residents (no. spp.)	59.2 (5)	73.8 (5)		

nc = not censused.

were very frequent in grassland–shrubland and less common in mudflats – shallow waters. Nests were found only in the months of November and January, but chicks, fledglings and juveniles were frequently seen between November and February.

Puna Plover *Charadrius alticola*

From early August to February, some birds of this species occur in the study area in breeding plumage. During this period, only small, widely dispersed flocks are seen, never exceeding 30 birds. Only very few groups frequent grassland–shrubland, as mudflats are the most important of this species' habitats. There, these birds feed on

brine flies (Ephydriidae). Fledglings and juveniles without flight feathers have been seen during the last half of January.

Diademed Sandpiper-Plover *Phegornis mitchellii*

The vernacular name of this species refers to the distinctive crown pattern; it is probably the rarest of the region's shorebirds. These birds were observed only in temporary drainage ditches and swampy lowlands adjacent to Lake Blanca (three birds) in the month of September. However, they were also observed in ditches very close to mudflats south of Lake de los Pozuelos (also three birds) in

Table 4. Results of shorebird censuses in 1991 in Lake Larga–Lagunilla: (a) mudflats – shallow waters and (b) grassland–shrubland.

Sectors	Variables	Jan. 1991	Sept. 1991
(a) SW (32 ha)	Total no. birds	1,021	1,443
	Mean no./ha	31.9	45.1
	% migrants (no. spp.)	64.6 (4)	80.4 (4)
	% residents (no. spp.)	35.4 (5)	19.6 (5)
(b) SW (20 ha)	Total no. birds	75	41
	Mean no./ha	3.7	2.0
	% migrants (no. spp.)	0	0
	% residents (no. spp.)	100.0 (3)	100.0 (4)
E (25 ha)	Total no. birds	52	0
	Mean no./ha	2.0	0
	% migrants (no. spp.)	0	0
	% residents (no. spp.)	100.0 (3)	0
Total no. birds seen		1,148	1,484
Total area censused (ha)		77.0	77.0

Table 5. Results of shorebird censuses conducted in seven wetlands in 1991: (a) mudflats – shallow waters and (c) river-beds and valleys.

Wetland	Area (ha)	Total no. birds	Mean no./ha	% migrants (no. spp.)	% residents (no. spp.)
Lake Vilama					
(a) River-mouth	80	5,932	74.1	94.2 (8) ^a	5.8 (4)
Eastern shore	100	5,250	52.5	89.8 (7)	10.2 (3)
Lake Pululos					
(a) River-mouth	30	3,512	117.0	91.0 (4)	9.0 (4)
Lake Runtuyoc					
(a) NE	60	776	12.9	65.2 (4)	34.8 (4)
Lake Guatatayoc					
(a) N-NW	80	4,175	52.2	89.3 (5)	10.7 (4)
Lake sobre Rio Miraflores					
(a) River-mouth	40	542	13.5	62.3 (7)	37.7 (5)
Lake Leandro					
(a) River-mouth	30	1,497	49.9	81.6 (5)	18.4 (4)
(c) River-bed/valley	15	20	1.3	0	100.0 (5)
Lake Blanca					
(a) River-mouth	30	1,986	66.2	82.3 (4)	17.7 (4)
(c) River-bed/valley	20	72	3.6	0	100.0 (6)

^a Number of species in parentheses.

November. One bird with juvenile plumage was observed in February along the Cincel River.

Tawny-throated Dotterel *Oreopholus ruficollis*

Groups of 10–15 birds were frequently seen in grassland–shrubland near small temporary ponds. In mudflats – shallow waters, only solitary birds were observed very sporadically, although groups of 5–10 birds made short incursions into the beach

from shrubbery close to the water's edge, as observed on the mudflats of the northern peninsula of Lake de los Pozuelos. An important factor in the decline of this species' populations is considered to be the clearing of thickets of *Parastrephia*. Nesting records are available only for the month of September. Juveniles were seen in the second half of December.

Table 6. Values of relative importance (RI) for each shorebird species seen during the 1991 censuses in nine wetlands.

(i) Species	Wetland			
	Lake de los Pozuelos	Lake Larga-Lagunilla	Lake Vilama	Lake Pululos
<i>H. himantopus</i>	8.85	3.75	3.67	5.92
<i>R. andina</i>	0.76	0.78	1.28	0.76
<i>V. resplendens</i>	1.61	1.61	1.76	0.79
<i>P. dominica</i>	1.35	0.08	0.11	—
<i>C. alticola</i>	1.08	1.07	0.32	1.50
<i>P. mitchellii</i>	—	0.02	—	—
<i>O. ruficollis</i>	0.12	0.42	—	—
<i>L. haemastica</i>	0.19	—	0.68	1.48
<i>T. melanoleuca</i>	0.50	0.51	0.67	0.31
<i>T. flavipes</i>	0.76	—	0.38	—
<i>P. tricolor</i>	25.76	18.89	45.71	30.18
<i>C. bairdii</i>	39.54	6.62	35.73	52.67
<i>C. melanotos</i>	2.81	—	3.44	5.21
<i>C. himantopus</i>	0.10	—	0.27	1.13
<i>T. subruficollis</i>	0.21	—	0.07	—
<i>G. andina</i>	0.00	0.65	—	—
<i>A. gayi</i>	0.03	0.04	0.16	—
<i>Thinocorus</i> spp.	0.00	0.04	—	—

(ii) Species	Wetland				
	Lake Runtuyoc	Lake sobre Rio Miraflores	Lake Leandro	Lake Blanca	Lake Guayatayoc
<i>H. himantopus</i>	11.85	12.23	10.01	22.06	4.86
<i>R. andina</i>	6.18	3.32	1.38	7.09	0.88
<i>V. resplendens</i>	6.31	5.16	10.28	7.09	2.68
<i>P. dominica</i>	—	1.29	0.52	1.11	—
<i>C. alticola</i>	10.43	9.59	1.91	1.79	2.13
<i>P. mitchellii</i>	—	—	0.19	0.04	—
<i>O. ruficollis</i>	—	2.95	0.32	—	—
<i>L. haemastica</i>	1.54	0.92	0.19	0.77	0.69
<i>T. melanoleuca</i>	2.19	2.21	0.65	—	1.22
<i>T. flavipes</i>	—	—	—	—	0.04
<i>P. tricolor</i>	39.30	—	47.46	65.35	63.95
<i>C. bairdii</i>	22.16	41.88	31.64	12.14	23.42
<i>C. melanotos</i>	—	15.68	—	—	—
<i>C. himantopus</i>	—	0.18	—	—	—
<i>T. subruficollis</i>	—	0.18	—	—	—
<i>G. andina</i>	—	—	0.13	0.63	—
<i>A. gayi</i>	—	0.36	—	—	0.09
<i>Thinocorus</i> spp.	—	—	0.19	0.04	—

Andean Snipe *Gallinago andina*

This species was very frequently seen in grassland-shrubland habitat. Solitary individuals were sighted in Lake de los Pozuelos and Lake Larga-Lagunilla and valleys close to Lake Blanca. A nest was seen in a gully close to Lake de los Pozuelos in mid-September.

Rufous-bellied Seedsnipe *Attagus gayi*

Birds of this species have been observed in swampy lowlands at river-mouths and along the shores of lagoons with tufted vegetation, which is a common

habitat along the eastern shore of Lake Vilama. Loose flocks of 8–10 birds are frequently sighted feeding in pairs or groups of 3 birds very close to each other. Records are available for almost all months of the year, with the greatest concentrations between the second half of August and the end of April. No data are available on nesting for this species.

Seedsnipes (*Thinocorus* spp.)

Records of both species (Grey-breasted Seedsnipe *Thinocorus orbignyianus* and Least Seedsnipe *Thinocorus rumicivorus*) are very scarce here. These

birds have been observed only in grassland-shrubland with gentle slopes and crossed by vast swampy lowlands. *Thinocorus rumicivorus* has been observed in groups of three or four birds in the underbrush (*Parastrephia*) close to the eastern shore of Lake Larga-Lagunilla. In November, underbrush in this area is completely cleared for agriculture. Records available for *T. orbignyianus* include only a very few solitary birds. During the second half of January, in the grassland-shrubland to the south-east of Lake Larga-Lagunilla, a nest located in a hollow in the ground contained four eggs partially covered with bits of straw. This clutch was attributed to *T. orbignyianus* because of the presence of two birds of this species near the nest.

Discussion

Human activities carried out in the region tend to alter natural conditions within these habitats to a varying degree. The activity with the most impact is cattle raising. The grassland-shrubland and swampy lowlands are used intensively to maintain large herds of sheep, goats, cattle and donkeys. The swampy lowlands are the only areas that are green all year round and contribute greatly to the hydraulic balance of certain important wetlands (e.g. Vilama, Blanca and Leandro lakes). The underbrush is cleared to make up for shortfalls in energy and is used by Puna settlers almost exclusively for fuel. New areas, such as those adjacent to Lake de los Pozuelos and Lake Larga-Lagunilla, are cleared to grow forage grasses. This means more livestock entering natural areas shortly, given the rapid impoverishment of crop areas. These practices eventually favour the introduction of pockets of sand and, consequently, sand dunes, which are already common in Puna. In addition, there are the effects of major earth moving, done for incomplete mining projects. Mining is now done on a small scale only, and the bigger mines are not in operation. Some of them, such as the Pan de Azucar Mine, are flooded, and the waters of the Cincel River continue to leach toxic materials into Lake de los Pozuelos.

Not all human activities in Puna have adverse effects. In 1990, a group of technicians was able to have named as a MAB-UNESCO (Man and the Biosphere Programme of the United Nations Educational, Scientific and Cultural Organization) World Biosphere Reserve the watershed where Lake de los Pozuelos is located (Arabella 1991). Others continue to work from public sector institutions to create the Vilama Binational Andean Wildlife Reserve (the exact area yet to be determined), which will include large portions of the Rinconada department in Argentina and the Sub-Lipez department in Bolivia.

Although the data referred to here are discontinuous and rather dispersed, certain preliminary conclusions can be drawn. In view of logistic and methodological constraints, particularly regarding the censuses, the data reported here are considered to illustrate certain aspects of interest in connection with the shorebirds in this part of the Argentine Puna.

- (1) The species of migrant shorebirds that occur in the wetlands visited can be divided into three groups according to numeric importance, permanence and use of available resources. A tentative decreasing model of the three aspects indicated could coincide with the following model: *Pluvialis tricolor* and *Calidris bairdii* (abundant); *Calidris melanotos*, *Pluvialis dominica*, *Tringa melanoleuca* and *Tringa flavipes* (fairly common); *Limosa haemastica*, *Calidris himantopus* and *Tryngites subruficollis* (scarce).
- (2) Three wetlands can be highlighted as significant for migratory species as staging sites and wintering grounds. In view of the foregoing point, they could be (i) Lake de los Pozuelos, (ii) the complex made up of Lake Vilama, Lake Pululos and the extensive adjacent system of temporary ponds and (iii) Lake Guayatayoc.
- (3) The censuses of September 1991 appear to indicate a significant migratory peak, at least for three species: *Phalaropus tricolor*, *Calidris bairdii* and *Calidris melanotos*.
- (4) With respect to the resident species, the wetlands studied offer favourable conditions for populations of *Vanellus resplendens*, *Charadrius alticola*, *Himantopus himantopus* and *Recurvirostra andina*. Meanwhile, populations of the scarcer species, *Oreopholus ruficollis*, *Phegornis mitchellii*, *Gallinago andina*, *Thinocorus orbignyianus*, *Thinocorus rumicivorus* and *Attagis gayi*, could be threatened by increasing losses of their breeding grounds and activity sites.

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Part III

Shorebird foraging ecology and energetics

Nocturnal foraging in shorebirds

Raymond McNeil & José Ramón Rodríguez S.

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Members of seven families of shorebirds forage both by day and by night in tropical and temperate latitudes. In some species, foraging takes place principally at dusk and at night. Some species appear to use their daytime territory at night. Some visually guided peckers and some long-billed tactile probers forage by the same preferred method both during the day and during the night. However, some long-billed species change from visual to tactile foraging between day and night. The roles of moonlight and bioluminescence in prey detection are discussed. Two main hypotheses can explain why shorebirds forage at night: (1) night feeding occurs only when the daytime feeding has been inadequate to meet the birds' energetic requirements; this is called the 'supplementary hypothesis'; and (2) birds prefer to feed at night because it provides the most profitable (most available prey), or safest, feeding opportunities. Day and night habitat segregation has been reported for wintering shorebirds.

Miembros de unas siete familias de chorlos y playeros, tanto de regiones tropicales como templadas, se alimentan de noche y de día. En ciertas especies, el forrajeo ocurre principalmente al atardecer y de noche. Unas especies parecen usar de noche sus territorios de alimentación diurna. Ciertos cazadores visuales y ciertos cazadores táctiles de pico largo se alimentan de la misma manera de noche como de día. Sin embargo, otras especies de pico largo, cazadores visuales de día, cambian su estrategia y se alimentan táctilmente de noche. Se discute el papel jugado por las mareas, el alumbrado lunar y la bioluminescencia. Dos hipótesis principales permiten explicar porque las aves limícolas se alimentan de noche: (1) la alimentación nocturna ocurre únicamente cuando, al alimentarse solo de día, el ave no logra satisfacer sus exigencias energéticas, y así necesita de una alimentación suplementaria de noche; (2) la noche presenta las condiciones alimenticias más provechosas (mayor disponibilidad o actividad de presas) y más seguras y así las aves se alimentan de noche por preferencia. En lugares de invernada en región tropical, ciertas especies parecen alimentarse de noche en lugares diferentes de los que frecuentan de día.

Les membres de quelque sept familles d'oiseaux de rivage, tant des régions tropicales que tempérées, s'alimentent de nuit et de jour. Chez certaines espèces, la chasse de proies se fait surtout au crépuscule et la nuit. Quelques espèces semblent utiliser de nuit les territoires d'alimentation qu'ils exploitent de jour. Certains chasseurs visuels et quelques chasseurs tactiles à long bec s'alimentent de nuit de la même façon que durant le jour. Cependant, d'autres espèces à long bec, chasseurs visuels de jour, changent leur stratégie et s'alimentent tactilement de nuit. Le cycle de la marée, l'éclairage lunaire et la bioluminescence jouent un certain rôle. Deux hypothèses principales permettent d'expliquer pourquoi les oiseaux de rivage s'alimentent de nuit: (1) l'alimentation nocturne a lieu uniquement quand, à s'alimenter seulement de jour, l'oiseau ne réussit pas à satisfaire ses besoins énergétiques, et ainsi a besoin d'une alimentation supplémentaire de nuit; (2) la nuit offre des conditions plus avantageuses (plus grande disponibilité ou activité des proies) et plus sécuritaires et ainsi les oiseaux s'alimentent de nuit par préférence. Sur les aires d'hivernage en régions tropicales, certaines espèces semblent utiliser de nuit des sites différents de ceux qu'ils fréquentent de jour.

R. McNeil, Département de sciences biologiques, Université de Montréal, CP 6128, Succ. 'A', Montréal, Québec H3C 3J7, Canada.

J.R. Rodríguez S., Departamento de Biología, Universidad de Oriente, Cumaná, Sucre, Venezuela.

Introduction

The habit of being active during darkness has been viewed as characteristic of a minority of bird species, with most considered entirely diurnal. Primary examples of activity in minimal light conditions are found in the Apterygiformes, Strigiformes, Caprimulgiformes and Apodiformes (Martin 1990). In shorebirds of the order

Charadriiformes, members of seven families forage regularly or mainly at night.

The behaviour of shorebirds during darkness is largely unknown. Night activities in shorebirds have been documented by direct observation only on rare occasions (Wood 1986; McNeil & Robert 1988; Robert & McNeil 1989; Robert, McNeil & Leduc 1989; Burger & Gochfeld 1991). This is due particularly to the difficulty of making observations

during darkness; however, with the recent development of night-vision light intensifiers, nocturnal observation of animals has become possible (see McNeil & Robert 1988; Robert & McNeil 1989; Robert, McNeil & Leduc 1989).

Because the main nocturnal activity reported to occur regularly in shorebirds is foraging, the important questions are: why forage at night? and what are the causes of selection for night activity in shorebirds? This paper overviews published information on (1) the occurrence of nocturnal foraging in shorebirds, (2) the special adaptations favouring such habits and (3) the suspected benefits these birds may get from foraging at night.

Nocturnal foraging activity

Who forages at night?

There are no reports that any shorebird forages exclusively at night. Yet there are many reports of species regularly foraging both during the day and during the night (Table 1). Such species include oystercatchers (*Haematopus*), plovers (*Pluvialis*, *Charadrius*), many *Calidris* species and most other Scolopacidae, the major family of shorebirds, and stilts (*Himantopus*). Other shorebird species are less likely to forage in full daylight but restrict their activity to twilight and night-time (Table 1). Such species include Painted Snipe *Rostratula benghalensis*, Crab Plover *Dromas ardeola*, Burhinidae (*Esacus*, *Burhinus*), coursers (*Rhinoptilus*), a few lapwing species (*Vanellus*), Inland Dotterel *Peltohyas australis*, woodcocks (*Scolopax*), a few snipe species (*Lymnocyptes*, *Gallinago*, *Coenocorypha*) and Ruff *Philomachus pugnax*. Pratincoles (*Glareola*) and the Australian Courser *Stiltia isabella* are active mainly at dawn and dusk; the latter and the Common Pratincole *Glareola pratincola* continue foraging at night under moonlight conditions (Ali & Ripley 1981; Cramp & Simmons 1983). Shorebird mist-netting done on staging or wintering areas with better profit at night-time is another indication that some species are very active at night.

Night-time foraging territories

During the non-breeding season, many species of shorebirds defend foraging territories (Myers, Connors & Pitelka 1979). Wood (1986) has shown that some Grey Plovers *Pluvialis squatarola* continue to use their feeding territories at night. Furthermore, there are indications that territories defended by Eurasian Curlews *Numenius arquata*, Willets *Catoptrophorus semipalmatus* and Whimbrels *Numenius phaeopus* during daylight were occupied by individuals of the same species during darkness (Cramp & Simmons 1983; R. McNeil, unpubl. data).

Latitude and seasons

Except for the Painted Snipe, Crab Plover, Burhinidae, Glareolidae, lapwings and other species that reside year-round in the tropics, nocturnal activities in shorebirds have been reported almost exclusively for birds staging or wintering in coastal and estuarine habitats in temperate latitudes. Recent studies in Venezuela and Mauritania have shown that some Neotropical residents and Holarctic winter migrants feed at night in tropical environments (McNeil & Robert 1988; Robert & McNeil 1989; Robert, McNeil & Leduc 1989; Zwarts & Dirksen 1990; Zwarts, Blomert & Hupkes 1990; Morrier & McNeil 1991). There seem to be only a few exceptions, and sometimes there are regional variations. For example, the Curlew Sandpiper *Calidris ferruginea* forages at night in Australia (Dann 1981) but not in South Africa (Puttick 1979).

Most accounts of nocturnal feeding in northern Europe report that it is most intense during winter and less intense or absent in the early autumn and the spring (Goss-Custard 1969; Heppleston 1971; Pienkowski 1981a, 1982; Puttick 1984). In southern Portugal, Batty (1991) found that nocturnal feeding is the norm during the migration periods but much less common from November to March. In addition, the woodcocks are known to switch from their winter pattern of feeding at night to feeding only during the day in summer (Dunford & Owen 1973; Hirons 1988).

Almost nothing is known about the occurrence of nocturnal foraging in breeding shorebirds. However, in the tropics, Two-banded Coursers *Rhinoptilus africanus* are known to feed chicks mainly at night (MacLean 1967). In the northern latitudes, breeding Eurasian Dotterels *Charadrius morinellus* and Piping Plovers *Charadrius melodus* forage both during darkness and during daylight (Kalas 1986; K.J. Staine & J. Burger, pers. commun.).

Foraging behaviour

Shorebirds use two basic types of foraging techniques (Table 1): visual searching (e.g. plovers) for prey items, or indications of their presence, on or near the surface; and probing (e.g. Short-billed Dowitcher *Limnodromus griseus*) with the bill for buried prey, which are detected by tactile and taste cues. While some species may feed exclusively with one of these techniques (e.g. visual searching by most plovers, or tactile probing by Short-billed Dowitchers), other species (e.g. Semipalmated Sandpipers *Calidris pusilla*) use both techniques, being visual in some conditions and tactile in others, according to food items and feeding habitats (see Goss-Custard 1970; Evans 1979; Schneider 1983). Pratincoles are a special group; they feed extensively by aerial hawking for flying insects (Brosset 1979; Hayman, Marchant & Prater 1986).

Table 1. Daytime and night-time foraging habits and strategies of shorebirds. DIU = diurnal; CRE = crepuscular; NOC = nocturnal; VIS = visual; TAC = tactile; (+) partly; (++) largely; (-) occasionally. Sequence of genera and nomenclature follow Hayman, Marchant & Prater (1986).

Families & genera	Foraging pattern				Foraging strategy				
	DIU	CRE	NOC	Principal references ^a	Day		Night		Principal references ^a
					VIS	TAC	VIS	TAC	
ROSTRATULIDAE									
<i>Rostratula</i>	-	++	+	1,2,3,4		+		+	1,4
DROMADIDAE									
<i>Dromas</i>	-	++	++	2,3	+		?		5
HAEMATOPODIDAE									
<i>Haematopus</i>	+	+	+	4,5,6,7,8,9	+			+	7,8,9
RECURVIROSTRIDAE									
<i>Himantopus</i>	+	+	+	2,10,11,12	++	+	+	+	10,11,13
<i>Recurvirostra</i>	+	+	+	2,4,13,14	+	+			13
BURHINIDAE									
<i>Burhinus</i>	+	++	++	1,2,3,4,15,16					
<i>Esacus</i>	+	++	++	1,2,16,17	++	-			17
GLAREOLIDAE									
<i>Rhinoptilus</i>	-	+	++	3,4,18			+		3,18
<i>Stiltia</i>	-	++	+	3,16					
<i>Glareola</i>	+	++		2,3,4,16,19				(text)	
CHARADRIIDAE									
<i>Vanellus</i>	+	+	+	1,2,3,4,20,21					
<i>Pluvialis</i>	+	+	+	2,4,22,23,24,25	++		++		26,27
<i>Charadrius</i>	+	+	+	10,11,12,26,28	++		++		1,26,27,28
<i>Thinornis</i>	+	+	+	3,29					
<i>Peltohyas</i>	+	+	++	3,30,31					
<i>Eudromias</i>	+	+	+	4,32,33					
SCOLOPACIDAE									
<i>Limosa</i>	+	+	+	2,22,26		++		++	26
<i>Nuneniuss</i>	+	+	+	2,22,26,34,35	++		++		35
<i>Tringa</i>	+	+	+	2,10,11,12,36,37	++			++	
<i>Catoptrophorus</i>	+	+	+	12,38	++	+	+	+	38,46
<i>Actitis</i>	+	+	+	2					
<i>Arenaria</i>	+	+	?	22,39,40					
<i>Scolopax</i>	+	++	++	2,41,42,43					
<i>Coenocorypha</i>	-	++	++	3,44					
<i>Gallinago</i>	-	++	++	1,2,4,45					
<i>Lymnocyptes</i>	+	++	++	2					
<i>Limnodromus</i>	+	+	+	12,13		++		++	12,13
<i>Calidris</i>	+	+	+	2,12,22,26,40,47	+	+	+	++	26,38
<i>Micropalama</i>	+	+	+	12		++		++	38
<i>Philomachus</i>	+	+	++	1,2,4					

^a 1, Ali & Ripley (1980–1981); 2, Cramp & Simmons (1983); 3, Hayman, Marchant & Prater (1986); 4, Urban, Fry & Keith (1986); 5, Swennen *et al.* (1987); 6, Heppleston (1971); 7, Hulscher (1976); 8, Sutherland (1982); 9, Goss-Custard (1983); 10, McNeil & Robert (1988); 11, Robert & McNeil (1989); 12, Robert, McNeil & Leduc (1989); 13, Hamilton (1975); 14, Gibson (1978); 15, Glue & Morgan (1974); 16, Pringle (1987); 17, Woodall & Woodall (1989); 18, MacLean (1967); 19, Brosset (1979); 20, Spencer (1953); 21, Milson (1984); 22, Evans (1976); 23, Dugan (1981); 24, Pienkowski (1981a); 25, Wood (1983); 26, Pienkowski (1982); 27, Pienkowski (1983a); 28, Pienkowski (1983b); 29, Phillips (1977); 30, MacLean (1976); 31, McNamara (1980); 32, Kalas (1986); 33, Nethersole-Thompson (1973); 34, Hale (1980); 35, Zwarts (1990); 36, Goss-Custard (1969); 37, Goss-Custard (1970); 38, R. McNeil, unpubl. data; 39, Schneider (1985); 40, Zwarts, Blomert & Hupkes (1990); 41, Hirons & Bickford-Smith (1983); 42, Sheldon (1961); 43, Hirons (1988); 44, Miskelly (1990); 45, Grisser (1988); 46, McNeil & Rodríguez S. (1990); 47, Manseau & Ferron (1991).

Some shorebirds may modify their foraging techniques between night and day. Thus, oyster-catchers (Hulscher 1976) and *Tringa* species (Goss-Custard 1970; McNeil & Robert 1988; Robert & McNeil 1989) are normally sight feeders during

daylight but switch to tactile foraging at night. During daylight and on bright moonlit nights, Black-winged Stilts *Himantopus himantopus* are usually visual peckers, but they use scythe-like sweeps of the bill (a tactile technique) on moonless

nights or under lower moonlight conditions (McNeil & Robert 1988; Robert & McNeil 1989).

Foraging success

Compared with visual 'plover strategists', shorebirds that feed by touch both by day and by night should be relatively unaffected by darkness (Dugan 1981; Pienkowski 1981b; Goss-Custard 1983). It is very difficult to find out the proportion of attempts to capture prey that are successful at night. Some, but not all, authors have observed or assumed that the rate of prey intake is less at night than by day. For example, Heppleston (1971) and Goss-Custard & Durell (1987) found oystercatchers to be feeding less during darkness, but Hulscher (1976), Swennen, Leopold & De Bruijn (1989) and Swennen (1990) found no difference in average food consumption between hours of daylight and darkness. The case of some plover-like species is surprising. For example, Wood (1984) measured the time budget of a Grey Plover on its territory by day and by night and found no significant difference in the total time spent foraging and in the bird's peck rate in these two periods. Ingestion rates of Northern Lapwings *Vanellus vanellus* at night can be double those achieved during the day (McLennan 1979).

Sensory adaptations, moonlight and bioluminescence

Shorebirds have visual or tactile adaptations that may enhance foraging at night. According to Dugan (1981) and Pienkowski (1983a, 1983b), the large eye in relation to head size of plovers, compared with that of sandpipers, is assumed to be an advantage for low light intensity. The Crab Plover, Burhinidae, coursers (*Rhinoptilus*) and woodcocks also have large eyes. In addition, the actual visual receptors of birds, as in other vertebrates, are rods and cones. Nocturnal birds have a great preponderance of rods in their retinae (Tansley & Erichsen 1985). The Grey Plover, a diurnal and nocturnal sight feeder, has more rods, a greater rod/cone ratio and longer rod outer segments than the Greater Yellowlegs *Tringa melanoleuca*, a daylight sight feeder that most of the time switches to tactile foraging at night (Rojas de Azuaje 1991). The Short-billed Dowitcher, a tactile forager during both day and night, is intermediate.

The presence of many touch-sensitive nerve endings (e.g. Herbst's corpuscles) in the bill tip favours touch feeding by many scolopacid species (*Limnodromus*, *Gallinago*, *Calidris*, etc.) (Bolze 1968; Schwartzkopff 1973, 1985). In addition, taste or chemoreception (presence of taste buds in the tip of the beak) may play a role in locating areas rich in prey (Gerritsen, Heezik & Swennen 1983; Heezik, Gerritsen & Swennen 1983). Finally, it has been

suggested that plovers may also use acoustic cues to locate prey (Fallet 1962).

Pienkowski (1982, 1983a) concluded that plovers use sight as the main means of prey detection, even on dark nights, and showed that, compared with daylight, Grey Plovers have lower pecking rates on dark moonless nights but not on moonlit nights. In addition, Double-banded Plovers *Charadrius bicinctus* in Australia roost for longer periods (and thus feed for shorter periods) during days that follow moonlit nights, suggesting that their energy intakes were greater on the moonlit nights (Dann 1981). Although the moon seems to influence nocturnal foraging activity for some species, it does not appear that moonlight *per se* is the proximate factor. Thus, for most of the lunar month, Northern Lapwings and Eurasian Curlews forage by day and roost at night. For a few days around the full moon period, the situation is reversed, even if the moon is not visible (Spencer 1953; Hale 1980). The significance of this is not known, but it may reflect an increased activity of prey items influenced by the lunar cycle.

Pienkowski (1983a, 1983b) suggested that shorebirds might take advantage of luminescent organisms at night. In a coastal lagoon of northern Venezuela, no relationship was found between the presence or absence of bioluminescence and the types of nocturnal foraging methods of shorebirds (McNeil & Robert 1988; Robert & McNeil 1989). The relationship could be indirect, if it were shown that prey (e.g. fishes) on which *Tringa* and *Himantopus* species feed at night (Robert & McNeil 1989) are attracted by luminescent organisms.

Why forage at night?

There are two main hypotheses: (1) the 'supplementary hypothesis', suggesting that night feeding occurs only when the daytime feeding has been inadequate to meet the birds' energy requirements; and (2) the 'preference hypothesis', suggesting that birds prefer to feed at night because it provides the most profitable, or safest, feeding opportunities.

Supplementary hypothesis

Tides may limit access to feeding sites regardless of prey abundance (Burger 1984), and thus shorebirds might be limited in their diurnal feeding time and need to feed at night to satisfy their energetic needs. However, even species not affected by tides may sometimes feed at night. For example, shorebirds feeding in coastal lagoons in northern Venezuela can feed all of the time, even during most high tides, yet many species feed by both night and day.

Activity patterns of birds are related to energetic needs, which vary during the annual cycle, and nocturnal feeding in temperate zones was first interpreted as a strategy to 'top up' an inadequate daytime energy intake. In temperate latitudes, energy requirements are generally higher during winter, and most accounts of nocturnal feeding by shorebirds in northern Europe report that it is most intense during winter and less intense or absent in early autumn and spring (Goss-Custard 1969; Heppleston 1971; Goss-Custard *et al.* 1977; Pienkowski 1981a, 1982; Puttick 1984). In winter, there is less daylight time available to search for food, and prey availability may decrease because intertidal invertebrates move deeper within the sediment (and sometimes are less active) as temperature falls (Goss-Custard *et al.* 1977; Pienkowski 1982). In the tropics, these factors do not apply, yet several shorebirds feed regularly at night (Robert & McNeil 1989). In some tropical situations, *e.g.* mudflats in Mauritania, daytime prey abundance is low, and feeding in daylight alone is sometimes insufficient for shorebirds to achieve their daily energetic needs (Engelmoer *et al.* 1984).

Finally, we suspect that, even in the tropics, the occurrence of nocturnal feeding may be greater when migratory species have higher energetic demands (Myers & McCaffery 1984) — for instance, during the time of pre-migratory fattening, when refuelling at a stop-over place or when landing after a long oversea flight. The higher incidence of nocturnal feeding during pre-migratory or migration periods in southern Portugal (Batty 1991), Mauritania (Zwarts, Blomert & Hupkes 1990) and northern South America (Morrier & McNeil 1991) provides support to the supplementary hypothesis.

Preference hypothesis

Some species may take advantage of increased availability and activity of prey at night (Dugan 1981; Pienkowski 1983a, 1983b; Townshend, Dugan & Pienkowski 1984; Evans 1987; Robert & McNeil 1989). It may even be advantageous for shorebirds to feed at night at sites and on prey that are not used during the day (Evans & Dugan 1984; Townshend, Dugan & Pienkowski 1984; Robert & McNeil 1989; Robert, McNeil & Leduc 1989). At some sites, the abundance or activity of prey is higher at night than during daylight (Evans 1987; Robert & McNeil 1989). Black-winged Stilts and *Tringa* species use such sites principally at night and seem to feed then on food items (fishes, Pelecypoda and Hemiptera) at least partly different from those they foraged for during daylight (Robert & McNeil 1989). The use of different day and night habitats might be a fundamental requirement for wintering shorebirds, at least in some regions.

Nocturnal activities in shorebirds may be related to the avoidance of diurnal predators or other kinds of diurnal disturbance. Although the effect of human disturbance has been little studied, Sanderlings *Calidris alba* avoid disturbance by people on Florida beaches, and thus increase the time they feed at low tide, by feeding at night (Burger & Gochfeld 1991). In the Chacopata Lagoon (Venezuela), small bays surrounded by mangrove woodlands are used for feeding by shorebirds much less frequently by day than by night. This is in spite of the fact that they are very rich in prey at all times. During the day, the birds congregate on vast, open mudflats, apparently to avoid predation by Peregrine Falcons *Falco peregrinus* (Robert, McNeil & Leduc 1989). Also in the same lagoon, Wilson's Plovers *Charadrius wilsonia*, in spite of the *Uca* crab abundance, forage very little during daytime; daylight prey intake alone is insufficient to balance their energy budget, and the fact that they forage mainly at night appears related to predator avoidance during daylight (Morrier & McNeil 1991). In north-eastern Africa, Painted Snipes feed at times during the day if the area is undisturbed by humans and other mammals, although only where cover is plentiful (A.J. Tree, *vide* Cramp & Simmons 1983).

During the winter in northern latitudes, Common Snipes *Gallinago gallinago* (Grisser 1988) and woodcocks (Dunford & Owen 1973; Hirons 1988) roost in woodland in daytime but feed on pastures at night. The switch to night feeding in the open habitats may reflect increased vulnerability to predators in these situations during the day. According to Cramp & Simmons (1983), Pintail Snipes *Gallinago stenura* feed mainly at night but may feed during daytime, if undisturbed.

Conclusions

Nocturnal foraging in shorebirds may be considered as a behaviour that evolved in different groups of species for different reasons and whose occurrence is governed by a variety of factors. For the more terrestrial species, nocturnal foraging occurs regularly and seems to be preferred to feeding by day. For the majority of species and populations, however, foraging at night seems less preferred and probably less efficient than foraging by day. However, the use of open habitats by these species, and their ability to locate prey by tactile cues, have given them the option of feeding at night should energetic demands not be satisfied by daytime feeding. Thus, these birds have a flexibility in foraging strategy that few other avian groups possess. Nocturnal feeding is important for the successful completion of the annual cycle in many populations of shorebirds and so should be taken into account in any conservation measures. The indication that some shorebirds feed nocturnally at sites and on prey that are not used

during the day could demand the protection of some wintering habitats less densely populated by shorebirds during the day but more intensively used at night. Many authors have dealt with time-activity or energy budgets of shorebirds. However, nobody seems to have taken nocturnal activities into account. Most information on the time and energy budgets of shorebirds needs to be revised, bearing in mind their nocturnal activities.

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Energetic constraints on the non-breeding distribution of coastal shorebirds

Theunis Piersma

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The chain of coastal wetlands along the East Atlantic Flyway, spanning northern Europe to tropical Africa, harbours a 'wintering' population of approximately 7.5 million shorebirds, consisting of about 25 species. Notwithstanding the overall similarity in habitat (open mud- and sandflats containing shellfish, polychaete worms and crustaceans as food), individual shorebirds wintering at varying latitudes face very different environmental conditions. Latitudinal differences in day-length, temperature, wind, solar radiation and humidity define the variable climate space that they face during the non-breeding season. The distances to the breeding areas vary ten-fold between species and affect the required migratory performance in spring and fall. Latitudinal variations in the harvestable biomass of the benthic prey species affect foraging performance. I begin this paper by exploring the methodology used to measure environmental variability encountered by shorebirds along the East Atlantic Flyway. Emphasis is laid on variations in the thermodynamic costs of shorebirds of different size. I follow this with an analysis of latitudinal trends in body mass of coastal shorebirds along the East Atlantic Flyway and along the coasts of South America. There were no relationships between body mass and migration distance when all species of the East Atlantic Flyway were combined. Along both flyways, small species 'wintered' closer to the equator than large species, suggesting that the smaller energetic scope for thermoregulation in small shorebirds limits their non-breeding distribution. Along the East Atlantic Flyway, plovers wintered closer to the equator than sandpipers, which in turn suggests that feeding opportunities are an important factor influencing non-breeding latitude. An energy-based conceptual framework as presented here allows energy intake and expenditure studies to be integrated quite easily. I have summarized possible research topics for shorebird ecologists based on the amount of time and technical support available. There is something for everyone to contribute in order to further the understanding of the (energetics of the) distribution and abundance of shorebirds.

La cadena de humedales costeros a lo largo de la Ruta Migratoria del Atlántico Oriental, que se extiende del norte de Europa al África tropical, alberga una población 'invernal' de unos 7,5 millones de aves costeras, que incluyen unas 25 especies. A pesar de la similitud general del hábitat (tierras bajas inundadas con la marea alta y playas abiertas que contienen como alimento mariscos, poliquetos y crustáceos), las aves costeras que pasan el invierno en diferentes latitudes enfrentan condiciones ambientales muy diferentes. Las diferencias latitudinales relativas a duración del día, temperatura, viento, radiación solar y humedad definen el espacio climático variable que deben enfrentar durante el período en que no se reproducen. Las variaciones en la distancia a los criaderos observadas entre especies pueden llegar a un factor de 10, viéndose afectada la capacidad migratoria requerida en la primavera y el otoño. Las variaciones latitudinales en la biomasa cosechable de las especies de los organismos que viven en las profundidades de las aguas afectan la capacidad de búsqueda de alimento. En este artículo se explora primeramente la metodología empleada para medir la variabilidad ambiental que encuentran las aves costeras a lo largo de la Ruta Migratoria del Atlántico Oriental. Se hace hincapié en las variaciones en el costo termostático de las aves costeras de diferente talla. A continuación, se hace un análisis de las tendencias latitudinales en la masa corporal de las aves costeras a lo largo de esa ruta migratoria y a lo largo de las costas de Sudamérica. No se observaron relaciones entre masa corporal y distancia de migración cuando se combinaron todas las especies que emplean la Ruta Migratoria del Atlántico Oriental. A lo largo de ambas rutas migratorias, las especies pequeñas 'invernaron' más cerca del Ecuador que las especies de mayor tamaño, lo que parece indicar que los límites más reducidos de la termoregulación de las aves costeras de menor tamaño limita su distribución durante el período internupcial. A lo largo de la Ruta Migratoria del Atlántico Oriental, los chorlitos pasaron el invierno más cerca del Ecuador que los playeros lo que, a su vez, parece indicar que las oportunidades para encontrar alimento son un factor importante que influye sobre la latitud durante el período internupcial. Un marco conceptual basado en la energía, tal como el presentado en este artículo, permite integrar fácilmente los estudios sobre aporte y gasto de energía. Se sugieren posibles temas de investigación para los ecólogos especializados en aves costeras atendiendo al tiempo y al apoyo técnico disponible. Todos podemos hacer una contribución para llegar a comprender mejor los factores energéticos que inciden en la distribución y abundancia de las aves costeras.

L'ensemble des milieux humides côtiers qui borde la voie migratoire de l'Atlantique-est, et qui s'étend de l'Europe septentrionale à l'Afrique tropicale, abrite une population «hivernante» d'environ 7,5 millions d'oiseaux de rivage répartis en quelque 25 espèces. Même si, globalement, l'habitat est semblable (estran sableux et vaseux exposé abritant des crustacés, des coquillages et des vers polychètes dont se nourrissent les oiseaux de rivage), les conditions environnementales sont très différentes selon les latitudes. Ainsi, l'espace climatique dans lequel les oiseaux de rivage vivent durant la saison internuptiale est caractérisé par les différences latitudinales de durée du jour, de température, de vent, de rayonnement solaire et d'humidité. Les distances que ces oiseaux ont à parcourir varient d'un ordre de grandeur; on comprend qu'elles aient un effet sur la performance migratoire au printemps et en automne. Les variations latitudinales de la biomasse récoltable des proies benthiques exercent un effet sur la performance alimentaire. L'auteur commence par examiner la méthodologie utilisée pour mesurer la variabilité de l'environnement que rencontrent les oiseaux de rivage le long de la voie migratoire de l'Atlantique-est. L'accent est mis sur les coûts thermostatiques des oiseaux de rivage de diverses tailles. Suit une analyse des tendances latitudinales de masse corporelle des oiseaux de rivage que empruntent cette voie migratoire et de ceux qui se trouvent le long des côtes d'Amérique du Sud. On n'a pas observé de rapport entre la masse corporelle et la distance de migration pour toutes les espèces qui empruntent cette voie. Les espèces de petite taille «hivernent» plus près de l'équateur que les espèces de plus grande taille dans les deux cas, ce qui semble indiquer que la plus faible capacité de thermorégulation des premières limite leur répartition durant la période internuptiale. Ainsi, le long de la voie migratoire de l'Atlantique-est, les pluviers passent l'hiver plus près de l'équateur que les Scolopacidae, ce qui pourrait indiquer que les possibilités d'alimentation constituent un facteur important du choix des latitudes d'hivernage. Une structure conceptuelle fondée sur les échanges énergétiques, comme celle utilisée ici, permet d'intégrer facilement les études sur les apports et sur les dépenses d'énergie. Nous avons résumé les thèmes de recherche sur lesquels les écologistes spécialisés dans l'étude des oiseaux de rivage pourraient vouloir se pencher, en fonction du temps et du soutien technique dont ils disposent. Tous peuvent contribuer à une meilleure compréhension de la dynamique énergétique de la répartition et de l'abondance des oiseaux de rivage.

Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, and Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands.

Introduction

On the basis of general habitat preferences, coastal shorebirds usually occur in open and exposed areas, whether during the breeding season or the non-breeding season. Their occurrence in two-dimensional habitats makes shorebirds amenable to observational study, and the availability of their prey can often be evaluated with relative ease as well. This makes the group of shorebirds, or waders (Charadrii), an excellent choice for detailed ecological and ethological research.

The same characteristics make shorebirds more exposed to the vagaries of weather than are most other groups of birds. A mudflat or open arctic tundra gives little protection to wind and cold, precipitation and solar heat. In addition, most coastal shorebird species are unwilling to hide from the elements even when they have the opportunity. Hiding behind a discarded beer can on a beach or sitting in a tight flock of conspecifics or in an open patch between the mangroves is usually as far as they want to go. Clearly, their adventure is not to seek the energetic rewards of crevices and thickets but to use the world at large, by flying great distances from their temperate-to-arctic breeding grounds to temperate-and-tropical wetlands and even to the southern shores beyond.

This contribution examines the energetics behind the non-breeding distribution of shorebirds. It

builds on the same assumptions made by Evans (1976) in an earlier review, which stated that many of the behavioural decisions taken by animals are somehow (evolutionarily or ontogenetically) motivated by energetic considerations; within certain time frames, each animal simply has to balance its budget. The time within which the budget sheets are balanced depends on the size of the animal (almost a year in the great whales, but less than a day in shrews). Accounting in shorebirds is probably a matter of weeks or months.

Energetic considerations affect virtually all aspects of the biology of a species. As in any study, this one has its biases. I will concentrate on the repercussions of using different wintering latitudes on the day-to-day energy balance, especially as they pertain to the cost of living in different climatic environments. I will briefly examine the concomitant costs of travelling between the breeding and non-breeding areas. Allometric scaling of energetics-related phenomena on body size (provisionally approximated by mass) provides a means by which to examine the shorebird community as a whole. By comparing species across flyways, I hope to show which steps can be made towards understanding the wintering patterns of coastal shorebirds with the help of energetics (see Hockey *et al.* 1992 for a completely different attempt).

Application of the energetics approach

Budgeting over different lengths of time

Three basic ingredients make up a treasurer's balance sheet (see *Wader Study Group Bull.* 62: 5-6): the receipts, the expenses and the accumulated fund. These can be translated in biological terminology as energy intake, energy expenditure and bodily energy stores, respectively.

Two variants of energy budgeting studies will be distinguished here, based on whether or not the energy store enters the balance equation. For shorebirds, there is no need for energy intake and expenditure to be exactly in balance on a daily basis, as they have the possibility of storing energy-rich nutrients such as fat when in positive balance so as to keep them going for a couple of days or weeks when in negative balance. It is therefore possible to use the daily energy budget as a basic unit from which to build seasonal energy budgets. In the latter type of budget, not only intake and expenditure are accounted for, but also the build-up and use of energy stores, and here the resulting balance has to equal zero. The daily energy budget with its intake and expenditure sides is illustrated in Figure 1, whereas Figure 2 tries to visualize the seasonal (in this case annual) energy budget of a typical wader (and see Owen, Wells & Black 1992 for an empirical attempt to make a seasonal budget for geese).

The daily energy budget thus consists of an intake side (Figure 1 left) and an expenditure side (Figure 1 right), each of which can be dissected into several components. Only part of the gross energy intake (the energy equivalent of all the ingested food) can be retrieved during digestion. The remainder is voided as regurgitates or faeces. The metabolizable energy that remains can be used for productive purposes. Energy expenditure consists of four cost components: basal metabolic rate, cost of thermoregulation, activity and the heat increment of feeding. The basal metabolic rate (commonly abbreviated as BMR) is the lowest possible rate of energy expenditure of a living bird; it is the amount of energy consumed when a bird is not digesting, not busy with any activities and not shivering because of the cold. When temperatures are not high enough to prevent shivering, birds additionally expend energy on thermoregulation. The sum of BMR and cost of thermoregulation (the energy expenditure of inactive and not-digesting warm-blooded animals under all environmental conditions) is called the thermostatic cost. The heat increment of feeding is the energy used in the digestive and assimilation processes. It is either lost as excess heat or used for thermoregulatory purposes (e.g. Masman, Daan & Dietz 1989; Meienberger & Dauberschmidt 1992; Sedinger,

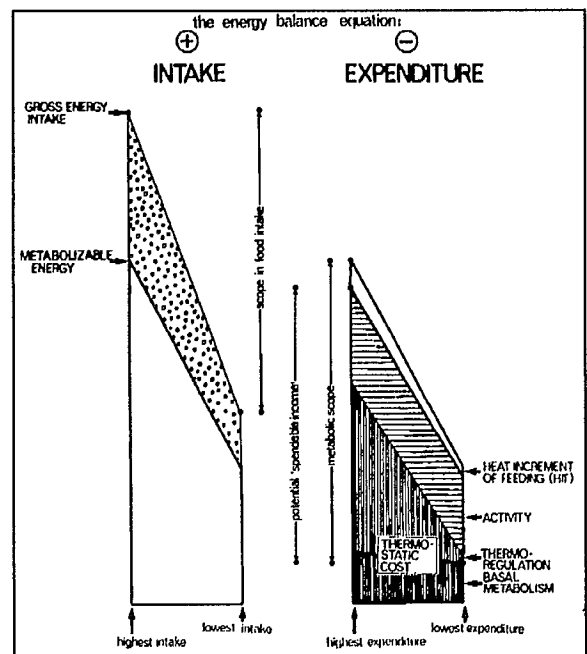


Figure 1. The energy balance equation illustrated. The left stacked bar represents the intake side of life, the right bar the expenditure side. The left and right sides of each bar are indicative of the highest and lowest weekly average intake or expenditure rates, respectively. Different kinds of shading indicate the breakdown in different yield and cost components, as explained in the text. The difference between energy intake and expenditure over a certain time interval will be expressed as storage (positive balance) or nutrient loss (negative balance).

White & Hauer 1992). Any surplus energy of intake over expenditure can be stored. A negative balance leads to a reduction in the energy content (and, thus, body mass) of a bird. For strategic reasons (e.g. before midwinter and migration), shorebirds have to store energy regularly.

The total variation in energy intake and energy expenditure in the medium term (*i.e.* weekly) is indicated by the difference between the left and right sides of the stacked bars in Figure 1. The variation in gross energy intake gives the scope in food intake rates (over a period of about a week). Not all 'income' is 'spendable' according to an animal's free choice, as, in order to stay alive, it has to keep up its core temperature and basic body functions (the obligatory cost factor called BMR). The range in total expenditure relative to BMR is called the metabolic scope (Bartholomew 1977; Peterson, Nagy & Diamond 1990).

The daily energy balance figures can be summed or averaged over a monthly period. The differences between total intake and expenditure have to be balanced by energetically equivalent changes in the energy content of a shorebird. During episodes of pre-migratory fattening, the balance will be (must be) positive; during the long-distance flights, the

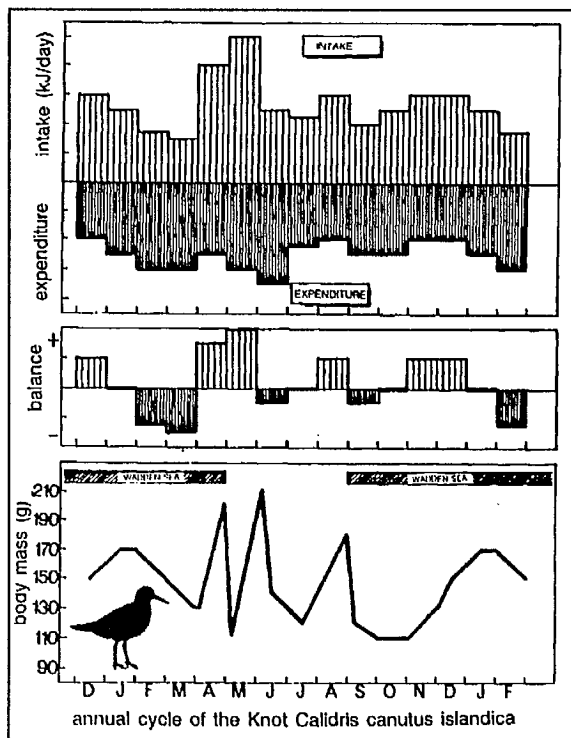


Figure 2. Seasonal changes in the relative intake and expenditure rates (top panel) and the resulting energy balance figure (middle panel) in relation to changes in the amount of stored energy in the birds' bodies as indicated by body mass (lower panel). The annual cycle characteristics of *islandica* knots (see Piersma & Davidson 1992) were used as an example.

balances are strongly negative for a few days (high activity costs and no intake at all) (e.g. Piersma & Jukema 1990). After a midwinter mass peak, the intake rate does not (have to) equal the expenditure rate, and body mass (stored energy) is lost (Pienkowski, Lloyd & Minton 1979; Davidson 1981; Johnson 1985).

Estimating the various cost factors

How does one go about measuring or estimating the various cost factors listed in Figure 1? The complete story is, of course, a long one, but what follows is a brief listing of the most common approaches (see Gessaman 1987 for a more comprehensive review).

BMR is measured by placing a shorebird in a 'metabolic chamber', usually an airtight dark-walled Plexiglas box through which air is sucked or blown at a specified rate (Figure 3 at right). By measuring the differences in oxygen concentration between the incoming and outgoing air, the oxygen consumption of the bird in the box can be calculated. Usually the birds are measured in a noise-free, dark and temperature-controlled room, and most shorebirds tend to go to sleep readily. As was pointed out, the energy equivalent of the oxygen consumption per unit time of a sleeping

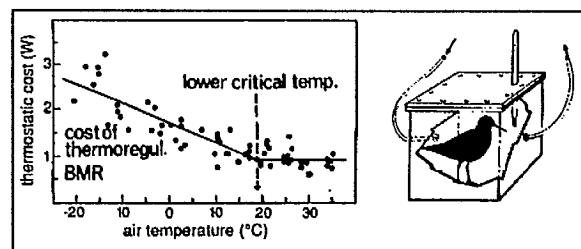


Figure 3. Relationship between energy expenditure of Red Knots sleeping in a darkened metabolic chamber (depicted at right) in relation to the air temperature in the box. The heavy line (giving the total thermostatic costs) is fitted according to the Scholander model (Scholander *et al.* 1950; McNab 1980) for a core temperature of 41 °C. The shaded part of the diagram indicates the BMR of 0.95 W; the open area between this level and the heavy line indicates the cost of thermoregulation. The lower critical temperature above which energy is constant and equal to BMR is also indicated. This figure is adapted from Piersma, Drent & Wiersma (1991).

bird not digesting food at a congenial temperature (above the lower critical temperature; see McNab 1980; Wiersma, Bruinzeel & Piersma *in press*) is called BMR (see Castro 1987; Kersten & Piersma 1987; Mathiu *et al.* 1989; Piersma, Drent & Wiersma 1991; and Figure 3 for measurements of a shorebird species).

BMR, cost of thermoregulation and, thus, thermostatic cost are easy to measure in the set-up described above (*i.e.* just vary the air temperature; see the pioneering studies by Scholander *et al.* 1950 and Figure 3). The slope of the sum of BMR and the cost of thermoregulation on air temperature below the temperature interval at which thermostatic costs are constant and equal to BMR (below the lower critical temperature; Figure 3) is called conductance. Conductance of birds (of the same size) is a measure of the insulative properties of a bird's plumage: the higher the conductance, the lower the insulation and the larger the heat loss.

The oxygen measurements of birds in boxes do not necessarily describe the thermostatic cost levels of free-living birds adequately, as a sleeping bird in a box feels no wind and no radiation. Both are important factors that interact with temperature in the real world (Figure 4). Instead of trying to quantify all the avenues of physical heat losses and gains in different environments (Figure 4), we can take a short cut by using bird models to give us an integrated value for thermostatic costs in different habitats (Bakken *et al.* 1981; Bakken, Erskine & Santze 1983). Taxidermic mounts (hollow copper models covered by a real skin) are kept heated to a bird's normal internal temperature (approx. 41 °C in Red Knots *Calidris canutus*; T. Piersma, unpubl. data) by a subcutaneous heating wire. A datalogger registers the electric power required to do so (see Figure 5 right). Measurements with copper

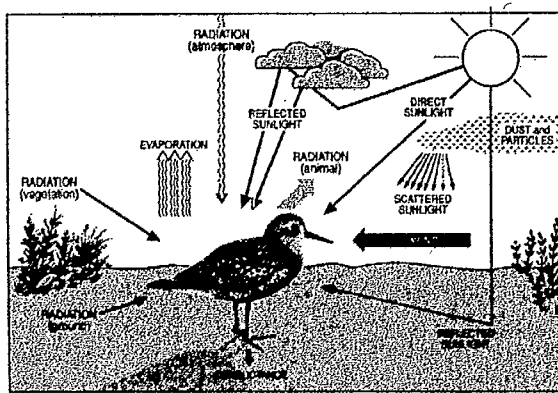


Figure 4. Summary diagram giving all the physical avenues of energy losses and gains affecting shorebirds owing to variations in climatic circumstances. This figure is adapted from the 'horse figure' in Porter & Gates (1969).

models in different habitats under a variety of weather conditions and calibrations under laboratory conditions to living birds yield habitat-specific equations relating thermostatic costs to climatic variables such as air temperature, wind speed and solar radiation (Piersma, Drent & Wiersma 1991; P. Wiersma & T. Piersma, unpubl. data). By subtracting BMR (independent of climatic variables by definition) from the thermostatic cost, the cost of thermoregulation is obtained.

Recent studies have shown that the thermostatic cost weighs heavily in the energy budgets of medium-sized shorebirds (Piersma, Drent & Wiersma 1991). On the basis of the measurements by heated taxidermic mounts (the 'copper knots') and the relevant climatic data, Piersma, Drent & Wiersma (1991) estimated the thermostatic costs of Red Knots on their arctic breeding grounds and in the temperate and tropical non-breeding areas (Figure 5). Thermostatic costs amount to about 3 W during both the arctic summer and the temperate winter (as in the Dutch Wadden Sea), but only half this value in the tropical winter (as on the Banc d'Arguin in Mauritania). The high thermostatic costs in summer and the northern winter give them only little leeway (between the thermostatic cost level and the estimated maximum metabolizable energy level, ME_{max}) for other cost factors. The study on latitudinal variation in the energetics of non-breeding Sanderlings *Calidris alba* by Castro, Myers & Ricklefs (1992) has confirmed that coastal environments that are costly in thermostatic terms are indeed accompanied by high field metabolic rates.

Finally, we have to consider the costs of various activities. Walking, feeding and preening, roosting and flying are the most common activities of shorebirds in the non-breeding season, and very little published work is available to estimate the magnitude of their costs (Pienkowski *et al.* 1984).

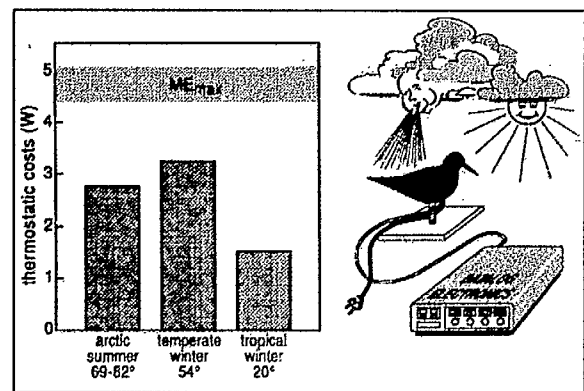


Figure 5. The thermostatic costs incurred by Red Knots with a BMR of 0.95 W (see Figure 3) under the average meteorological conditions in the breeding season in the Canadian Arctic, in the temperate winter in the Dutch Wadden Sea and in the tropical winter on the Banc d'Arguin, Mauritania (from Piersma, Drent & Wiersma 1991). Latitudes of the three areas are indicated in °N. The figure to the right gives an impression of the 'copper knot' set-up used to derive the predictive equation to relate thermostatic costs to the three climatic variables — temperature, wind speed and global solar radiation.

The cost of flight in birds has been repeatedly considered in very general terms (Masman & Klaassen 1987; Castro & Myers 1988; Pennycuik 1989; Rayner 1990), and the estimates obtained are reasonable on this basis (Piersma & Jukema 1990). Roosting and resting probably add little to the thermostatic cost as estimated by the heated taxidermic mount approach. The cost of activities such as walking and feeding can be studied by varying the work level of birds under controlled circumstances and measuring their total energy expenditure with the doubly labelled water technique and by having birds walking on treadmills while simultaneously measuring their oxygen consumption (see, *e.g.*, Fedak, Pinshow & Schmidt-Nielsen 1974; Paladino & King 1984; Zerba & Walsberg 1992). Both approaches are currently being employed on Red Knots at our laboratory (M. Poot, L. Bruinzeel & T. Piersma, unpubl. data).

Estimating the potential nutrient yields of feeding habitats

The rate at which animals can extract food from their environment obviously depends on the size and density of available food items. The generalized form of such relationships (the functional response equation) was first described by Holling (1959). In principle, it should be possible to derive the relationships between food abundance and intake rates for all types of prey and predators (Holling 1965); however, even when we are concerned with one type of predator, there are a couple of difficulties to be resolved. For example, not all prey of a species are equally suitable for a predatory shorebird (Figure 6). Some may be too

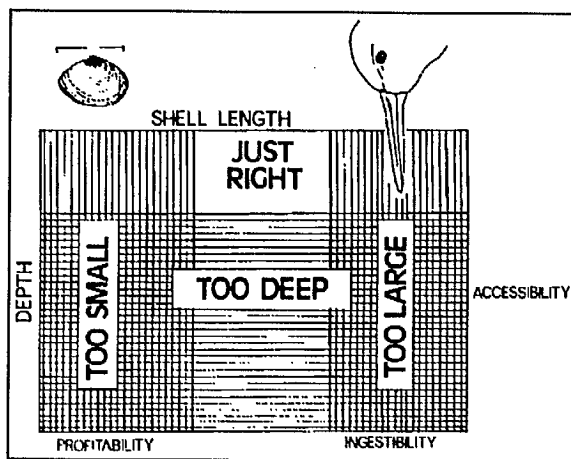


Figure 6. 'Ecological cage' of a mollusc-eating shorebird predator with the 'predation window' from which the examined can eat. Some molluscs are too small to be profitable or are too large to be ingestible, and all size categories can be too deeply buried to be within reach of the bill. The fraction that is 'just right' is called 'harvestable'.

small to be worth the energy invested in searching, catching and ingesting them (*i.e.* they are not profitable), whereas others may be too large to be swallowed (*i.e.* they are not ingestible), and still others may occur too deep in the sediment (or the water column), beyond the reach of the bill (*i.e.* they are not accessible). Only prey that fall in the 'predatory window' of the particular shorebird species determine the potential food intake rate; we call this the harvestable fraction (Zwarts, Blomert & Wanink 1992). Studies by Myers, Williams & Pitelka (1980), Hulscher (1982), Wanink & Zwarts (1985), Zwarts & Blomert (1992) and Zwarts, Blomert & Wanink (1992) and our own work on Red Knots have shown that in probe-feeding waders, especially those feeding on slow-moving bivalve prey, it is possible to quantify the harvestable biomass and, in some cases, to relate it to intake rate by a type-2 functional response equation (Figure 7; see Holling 1959, 1965). Indeed, we have now been able to verify these results for Red Knots for a variety of prey types under standardized laboratory conditions simulating intertidal mudflats (T. Piersma, J. van Gils & P. de Goeij, unpubl. data).

Obviously, differences in the types of prey (in relation to their mass, size, behaviour and depth of extraction from the sediment) will influence the form of the functional response equation. For this reason, comparisons between equations for different prey types can be used to explain diet selection in shorebirds (Wanink & Zwarts 1985). In order to compare feeding areas on the basis of their potential nutrient yields, we would require the functional response equations for all kinds of prey encountered as well as accurate data on the size and depth distributions of these prey at the sites to be

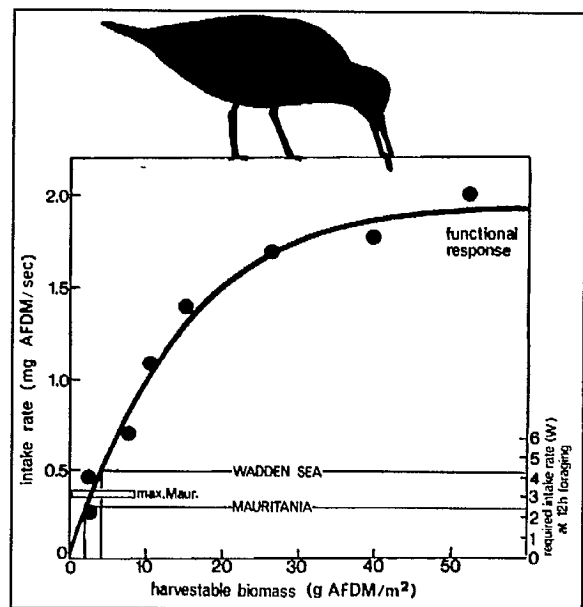


Figure 7. Generalizing the relationship between the harvestable biomass of a benthic prey species and the intake rate of a predator: the approximate functional response curve of Red Knots feeding on *Macoma balthica*. The data points are from small-scale laboratory experiments as well as from field observations (T. Piersma, unpubl. data); see Zwarts & Blomert (1992) for further information on this predator-prey relationship.

compared. This is an ambitious programme, which has yet to be carried out.

A very rough attempt to illustrate this approach can, however, be made on the basis of the generalized functional response curve relating measured intake rates of Red Knots to the harvestable biomass of Baltic Tellins *Macoma balthica* in the Dutch Wadden Sea (Figure 7). To achieve energy balance in the cold and windy Dutch Wadden Sea in winter, given that they forage for the entire low-water periods throughout day and night (about 12 hours), Red Knots would require an intake rate of about 0.5 mg ash-free dry mass (AFDM) per second. This would require a harvestable biomass of 3–5 g AFDM/m² (Zwarts, Blomert & Wanink 1992: Figure 11). Harvestable biomasses of bivalves on the Banc d'Arguin in Mauritania, the stronghold of Red Knots and many other shorebirds wintering in West Africa (see below and Ens *et al.* 1990), are much lower (Figure 7). Indeed, the data in Zwarts, Blomert & Hupkes (1990) suggest that during migratory fattening on the Banc d'Arguin, a period of peak demand when Red Knots feed for all available time, day and night, intake rates are limited to 0.37 mg AFDM/s. If this situation is typical for the entire winter period spent on the Banc d'Arguin, Red Knots would not be able to balance their budget there if the climate were as demanding as in the Dutch Wadden Sea (*cf.* Figure 5). It is likely that

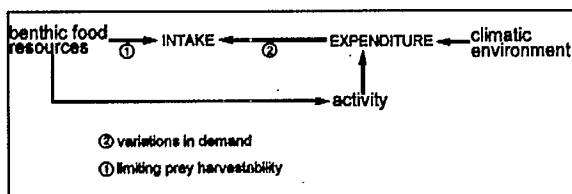


Figure 8. A crude interactive model to outline how the expenditure and intake sides of the energy balance equation (Figure 1) are causally interconnected. Variations in demand as well as prey availability can delimit the occurrence of a specified shorebird predator. See Piersma (1987) for a much more comprehensive scheme of relationships between benthic biomass production and shorebird foraging.

Red Knots are able to use the Banc d'Arguin only as a wintering area (one that is relatively poor in food), in view of the low local thermostatic costs (Piersma, Drent & Wiersma 1991).

Interactions between the intake and expenditure sides of individual energy budgets

The interactions between intake and expenditure can be summarized in the simplified scheme of Figure 8. For a shorebird in energy balance, higher levels of energy expenditure require a higher daily food intake. This is achieved by higher intake rates per unit feeding time or longer feeding periods, or both. Longer feeding periods are necessary if the benthic food resources on the foraging grounds limit intake rate. If this is indeed the case, then the period during which a relatively costly activity like feeding increases may in turn result in increased expenditures (Figure 8).

Generalizing the energetics approach: scaling on size

To enable a comparison of shorebird 'communities' along the gradients provided by the major flyways, it is necessary to extract from nature some generalities about the levels of intake and expenditure and their components. The allometric scaling of energy-related phenomena on body size has provided a powerful tool to extrapolate detailed knowledge, based on studies of a limited array of species, to the remaining unstudied species or to communities (Calder 1974, 1984; Kendeigh, Dolnik & Gavrilov 1977; Schmidt-Nielsen 1984). Although size and mass are distinct variables (see Piersma & Davidson 1991), body mass (which may include a size-independent storage component) is commonly used as an approximation of body size, and I will continue this practice here. Important examples of allometric scaling are the log-log regressions of BMR on body mass (Lasiewski & Dawson 1967; Aschoff & Pohl 1970) and of field metabolic rates on body mass (Nagy 1987). By allometrically scaling BMR on body mass, Kersten & Piersma (1987) were

able to show that shorebirds in general have high metabolic rates compared with other non-passerine birds, which implies that a common explanation has to be sought for the group as a whole. Zwarts *et al.* (1990a: Figure 7) give an example of the allometric scaling of food intake rate and individual prey mass on body mass of shorebirds on the Banc d'Arguin, Mauritania.

As much more is known about the scaling of expenditure-related processes on body mass than of intake-related phenomena, and as the components of energy expenditure and the external factors (*e.g.* climate) influencing them are relatively well understood, I will limit further discussion of the energetics of shorebirds in relation to their distribution along the flyways to the expenditure side of the balance sheet. This is like telling only half the story, but, in the absence of relevant information on latitudinal trends in food and feeding opportunities in relation to the size and mass of shorebirds, there is no other way. Let us concentrate on two aspects of energy expenditure that may vary with shorebird size and with latitude: the costs to cover the distances between breeding and non-breeding areas in flight and the thermostatic costs.

Little is clear about the dependence of migratory flight performance on body size. If it would be more costly or take longer for shorebirds of a certain size to migrate, then we would predict them to cover shorter migratory distances than heavier or lighter birds, everything else being equal. For such an analysis, we would need to know the relative energy requirements to cover the same distance in migratory flight in shorebirds of different body sizes. The empirical models that are available today disagree about the size/mass effects on flight range in shorebirds (McNeil & Cadieux 1972; Summers & Waltner 1978; Davidson 1984; Castro & Myers 1989), for reasons that are unclear.

We also need to know how long it would take shorebirds of different body size/mass to deposit the required energy stores to cover a certain distance (Zwarts *et al.* 1990b). Lindström (1991) showed that larger bird species have relatively lower rates of fat deposition and suggested that larger species may have lower speeds of migration. As all species, whether large or small, have the same time limitations, we would predict that those with the lower speeds of migration would migrate the shortest distances. However, in view of all these uncertainties, it may be more insightful to look at the empirical patterns of flight distances shown by shorebirds of different body mass along the East Atlantic Flyway (Figure 9). Although migration distances vary ten-fold between shorebird species (Figure 9), there are no clear trends in migration distances (or in the average breeding latitude) in relation to body mass, except

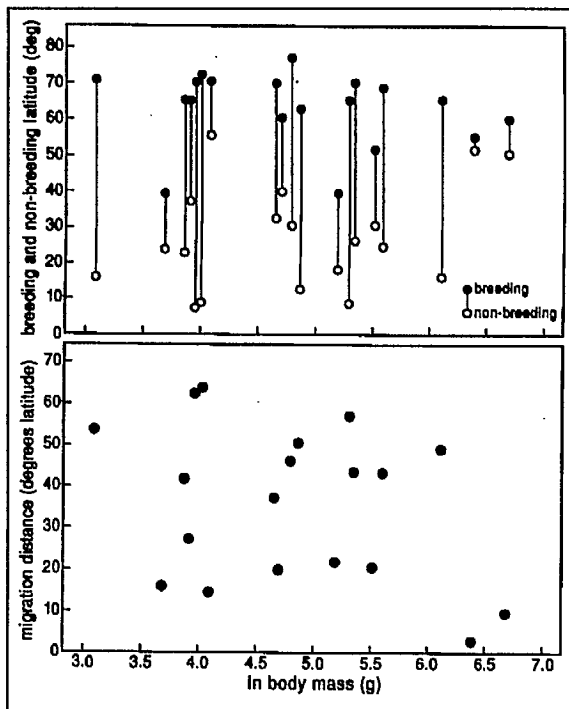


Figure 9. Allometry of breeding and wintering latitude and migration distance in the shorebird species of the East Atlantic Flyway. The average breeding latitude is from Piersma *et al.* (1990: Table 1), and the average non-breeding latitude is computed from Smit & Piersma (1989: Tables 3 & 5).

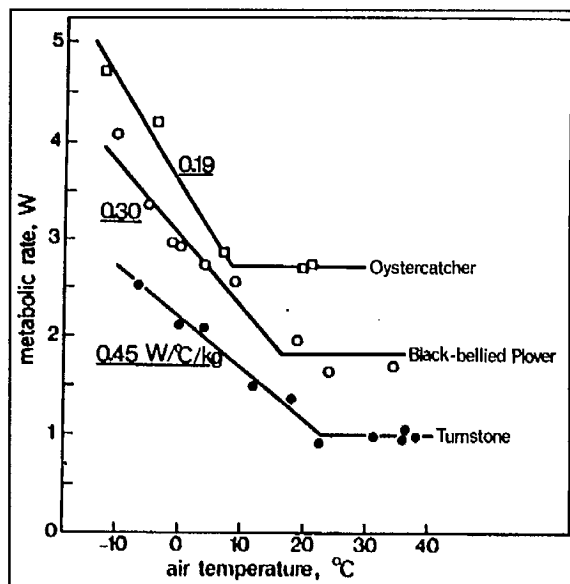


Figure 10. The metabolic rates of Eurasian Oystercatcher *Haematopus ostralegus*, Black-bellied Plover *Pluvialis squatarola* and Ruddy Turnstone *Arenaria interpres* measured by conductance. Heavier shorebirds have higher absolute conductance values but lower relative conductance values. In combination with their lower critical temperatures, the relative thermostatic costs decrease with increasing body mass. The values for Eurasian Oystercatcher, Black-bellied Plover and Ruddy Turnstone presented here are from Kersten & Piersma (1987).

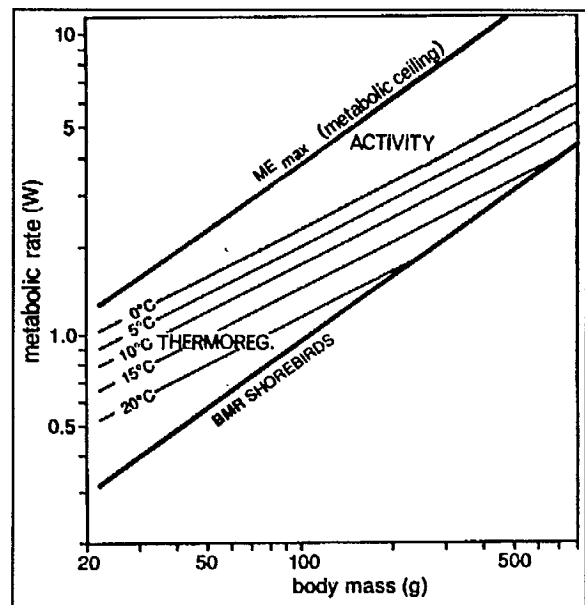


Figure 11. Scope for expending energy on thermoregulation and activity by shorebirds of increasing body mass (adapted from Visser 1991, p. 159). The scope is constrained by the absolute minimum expenditure (BMR, according to the equation of Kersten & Piersma 1987) and the maximum metabolizable energy (ME_{max} , according to the equation of Kirkwood 1983, on the basis of daily energy intake rates of maximally performing individuals such as lactating mammalian mothers and brood-provisioning avian parents).

that the two largest species (Eurasian Oystercatcher *Haematopus ostralegus* and Eurasian Curlew *Numenius arquata*) show the shortest migration distances. This is not due to these species being unable to cover long migration distances, as some Eurasian Oystercatchers and Eurasian Curlews winter as far south as Guinea-Bissau (9°N) and represent the northernmost breeders and farthest migrants amongst their species (Zwarts 1988).

An important variable that influences the level of thermostatic costs in shorebirds of different size is their conductance. Although larger birds have higher conductances (Figure 10), this is not so on a mass-specific basis (Aschoff 1981). Larger and heavier shorebirds devote relatively less energy to thermoregulation and have therefore, within the constraints of their metabolic physiology, more energy available to cover the remaining expenditure — that is, mainly the cost of activity (Figure 11). Figure 11 also shows that the range of air temperatures over which shorebirds do not have to expend energy on thermoregulation is much smaller in small than in large species. An 800-g Eurasian Curlew can spend all its energy on BMR and activity even if air temperatures are as low as 10 °C, but a 20-g Little Stint *Calidris minuta* has to spend quite a bit of its energy on thermoregulation even if it is 20 °C. On the basis of Figure 11, we predict that the smaller species occur in relatively

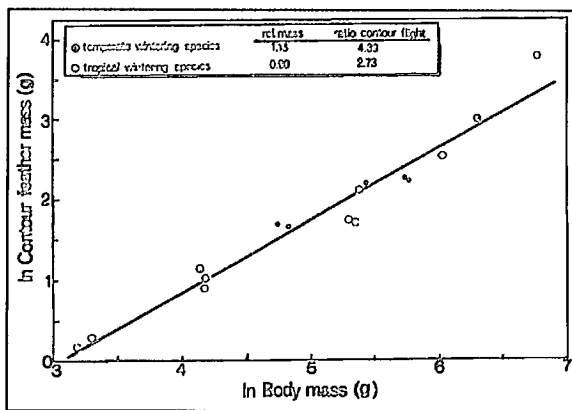


Figure 12. The dry mass of contour feathers (a parameter of the quality of the main insulative layer) in relation to body mass in a series of wader species that are assignable (or not: small symbols) to different wintering latitudes. Species averages (based on 1–85 individuals) are given. The linear regression line across the species averages is indicated and given by the equation: $Y = 0.0657X^{0.892}$ ($n = 16$, $r^2 = 0.96$).

benign climates (high temperatures, low wind speeds) and that only the large species spend the non-breeding season in the cold and windy north.

Before examining the mass-related distribution of shorebirds along the East Atlantic Flyway, I wish to point out a further interesting complication. Tropical- and temperate-wintering shorebirds of the same species and/or mass may differ with respect to their conductance or with respect to their rate of energy expenditure under warm climatic conditions. Piersma, Drent & Wiersma (1991) suggest that tropical-wintering Red Knots have a lower mass-specific BMR than conspecifics wintering in north-western Europe, which implies subspecific differences in physiology. An allometric analysis of the dry mass of contour feathers of shorebirds from different wintering areas (Figure 12) suggests that temperate-wintering species have a relatively heavy plumage and that tropical-wintering species have a relatively light plumage, whether expressed relative to the predicted average for all species or relative to the mass of the flight feathers (the latter serving only a minor role in the insulation of the body). If the dry mass of contour feathers is a good (inverse) measure of conductance, tropical-wintering shorebird species may have relatively higher conductances than temperate-wintering ones. The fact that the two smallest shorebird species, both of which are wintering in the tropics, nevertheless have higher than average contour feather masses (Figure 12) may indicate that what we consider as tropical (and hotter than average) conditions still requires a larger than average investment in an insulative layer for the smallest birds. This provides an added argument for predicting that small species should winter in the warmest climates.

Size-dependent shorebird distribution along the East Atlantic Flyway

The chain of coastal wetlands along the East Atlantic Flyway, spanning northern Europe to tropical Africa, harbours a 'wintering' population of approximately 7.5 million shorebirds, consisting of about 25 species (Smit & Piersma 1989). An analysis of body size and taxon/feeding style in relation to the average numbers and distribution of coastal waders along the East Atlantic Flyway (Smit & Piersma 1989) is presented in Figure 13. I have differentiated between plovers and sandpipers in view of their distinct phylogenies and feeding methods: plovers usually feed by sight, sandpipers usually by touch (Pienkowski 1981a). The sandpipers were split into a group of small species (weighing less than 148 g) and a group of large species (heavier than 148 g). Plovers and small sandpipers winter predominantly in the tropics, with the average plover being encountered at even more southerly latitudes (25°N) than the average small sandpiper (30°N). Most of the large sandpipers and Eurasian Oystercatchers winter at temperate latitudes around 38°N. Although this type of data does not allow statistical testing, the hypothesis still maintains that smaller shorebirds winter at more southerly latitudes (which, along the East Atlantic Flyway, correlates with lower thermostatic requirements; Drent & Piersma 1990; Piersma, Drent & Wiersma 1991) in view of their relatively high energetic requirements for thermoregulation (Figure 11). The fact that plovers show an even more southerly distribution than the small sandpipers is in line with the arguments put forward by Pienkowski (1981a, 1981b, 1983). As the visual prey detection by plovers is particularly susceptible to the adverse effects of wind and low temperature (interfering either with the detection itself or with prey activity), plovers in general should select warmer climates than shorebirds with a probing, and less easily affected, style of feeding.

Testing the trends: latitudinal distribution patterns on the South American continent

Morrison & Ross (1989) counted coastal shorebirds along the entire shoreline of the South American continent from the air. This provides a particularly nice and uniform data set to test if the trends in body size of shorebirds in relation to latitude found along the East Atlantic Flyway are true for other areas as well. This is because the climatic gradient along the South American shores is exactly the opposite of the one found along the shores of Europe and West Africa. The more southerly and farther from the breeding areas one goes, the colder and windier the environment. A comparison

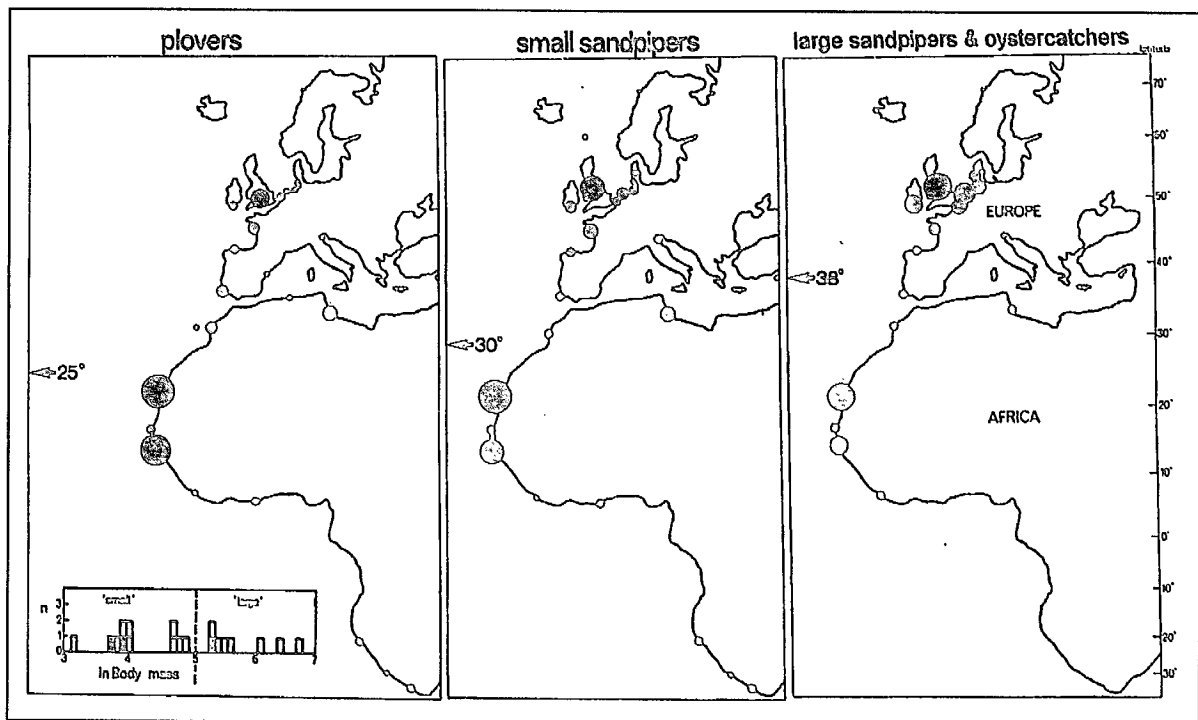


Figure 13. Relative distribution pattern of plovers (Charadriidae) and small and large sandpipers and oystercatchers (Scolopacidae and Haematopodidae) along the East Atlantic Flyway (based on Tables 3 & 5 in Smit & Piersma 1989). The inset gives the boundary mass between 'small' and 'large' sandpipers/oystercatchers at $\ln(\text{mass}) = 5$ (i.e. body mass = 148 g); open histograms are sandpipers/oystercatchers, and the three closed squares represent the three plovers. The 'small sandpiper' group is composed of *Calidris minuta*, *C. alpina*, *C. alba*, *C. ferruginea*, *C. maritima*, *C. canutus*, *Actitis hypoleucos*, *Arenaria interpres*, *Tringa totanus* and *T. erythropus*. The 'large sandpiper' group is composed of *Himantopus himantopus*, *T. nebularia*, *Recurvirostra avosetta*, *Limosa lapponica*, *L. limosa*, *Numenius phaeopus*, *N. arquata* and *Haematopus ostralegus*.

between size-related shorebird distribution along the South American and European/West Africa coasts would thus control for migration distance, as the climatic trends in relation to distance are reversed. The distribution of coastal shorebirds of different sizes over the entire South American continent is presented in Figure 14. The data are summarized and compared with the pattern of the East Atlantic Flyway in Figure 15. Clearly, the trends are the same. Along both the European/African coastline and the South American coasts, the average body mass of shorebirds is smallest close to the equator (although species of all sizes occur at all latitudes). This suggests that, with respect to body size and mass, climate (and therefore thermostatic costs) is likely to be a more important factor determining non-breeding area than the distance that has to be covered to get there from the breeding grounds and to get back.

Scope for future work

The present analysis of the distribution of coastal shorebirds in relation to latitude and likely thermostatic costs is just one example of the use of energetics in the analysis of distribution and abundance. Thermostatic costs, as incurred by shorebirds of varying body size and mass, could be

an important selective factor in the determination of non-breeding latitude. The differences between plovers and sandpipers at non-breeding latitudes along the East Atlantic Flyway further suggest that it is the thermostatic requirements, relative to the quality of the feeding grounds (the potential nutrient yields in different areas), that count most. I was surprised that such a coarse-grained analysis (with so many interfering variables not taken into account) yielded such clear patterns. At the same time, the described latitudinal trends, although giving good hints, have little predictive power and do not really show the energetic constraints faced by individual shorebirds of different species. Perhaps intraspecific comparisons would turn out to be even more insightful than the present comparison between species.

In order to obtain such information, we need much more work on (1) the definition of microclimatic conditions for different types of shorebirds, (2) metabolic adaptations to climate within and between species, (3) the energetics of migratory flights and the use of migratory corridors with favourable winds (cf. Piersma & de Sant 1992) and (4) the use of stop-over sites in relation to the distances between them, their quality and the time constraints of the birds, building on the theoretical work of Alerstam & Lindström (1990). We also

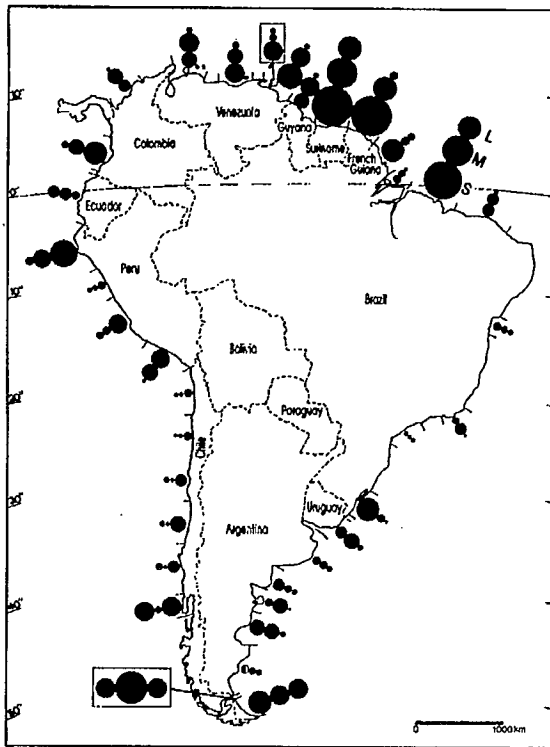


Figure 14. Distribution patterns of variously sized shorebird species around the South American continent according to the results of aerial counts presented by Morrison & Ross (1989) and summarized by Morrison & Myers (1989) in their Figure 2 (on which this figure is based). S = small shorebirds (from Least Sandpiper *Calidris minutilla* to Buff-breasted Sandpiper *Tryngites subruficollis*), M = medium-sized shorebirds (from Stilt Sandpiper *Calidris himantopus* to Greater Yellowlegs *Tringa melanoleuca*) and L = large shorebirds (comprising Willet *Catoptrophorus semipalmatus*, Whimbrel *Numenius phaeopus* and Hudsonian Godwit *Limosa haemastica*) (see Table 2.2 in Morrison & Ross 1989). The surface of the dots is proportional to the numbers found along the indicated stretch of coastline, the biggest dot representing 100,000-300,000 birds.

badly need (5) more comparative descriptive work on the quality of feeding habitats by careful empirical studies on food selection and prey harvestability. Along the shores of South America, precious little work has hitherto been carried out, although important studies are now in progress at several locations.

If this paper is read as a guide to the technically advanced and suggests near-impossible field and laboratory studies, I have failed. I hope that everyone sees that the framework of energetics offers the possibility of integrating the results of research efforts of very different intensity and character. Table 1 lists possible research activities for people with different means to carry out their studies. Only by combining the results of the research efforts of workers from a wide geographical range, studying a wide range of topics

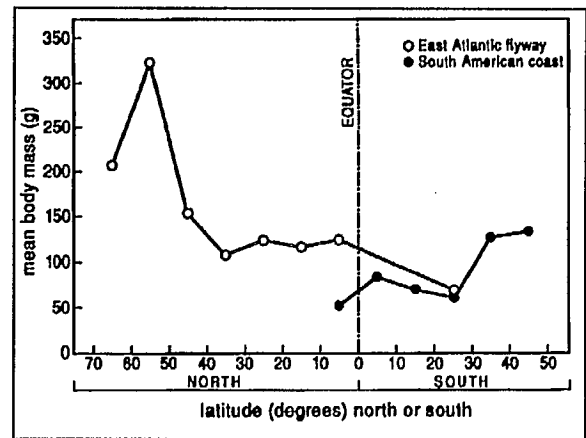


Figure 15. Latitudinal trends in the average mass of shorebirds spending the non-breeding season along the coasts of the East Atlantic Flyway (computed from Tables 3 & 5 in Smit & Piersma 1989) or along the shores of South America (computed from Table 3.2 in Morrison & Ross 1989).

and a large number of species, can the conceptual richness of shorebird biology be harvested.

If, as shorebird ecologists, we are to advise governments and conservation bodies about the function and critical importance of the wetlands under their responsibility, we need to know much more than the numbers and species composition of shorebirds frequenting these areas. We need to know how and why a species uses a site and whether there are alternatives. Studies on the energetics of shorebirds, whether focusing on the intake, the expenditure or the storage part of the balance sheet, are (because of their relative conceptual simplicity) likely to contribute importantly to our understanding of the limitations on the distribution and sizes of shorebird populations. Many more empirical studies, whether on a small or a large scale, and the appropriate integration of their results (*e.g.* in thematic workshops) are urgently called for.

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Table 1. Summary of the possible research activities for students of shorebird biology with different levels of research time and technical support.

Time	Technical facilities	Distribution of shorebirds	Energy intake	Energy expenditure
Short	Limited	- Point counts - Catching (weights, measurements, moult)	- Diet study (visual observations, pellets, droppings) - Use of feeding habitats - Harvestable biomass (benthic sampling of selected species)	- Activity budgets - Microhabitat selection during feeding and roosting
Long	Limited	- Counts (seasonal occurrence) - Catching (seasonal mass changes, biometry, moult)	- Food choice re season and weather - Harvestable biomass re season in a range of species - Measurement of intake rates	- Activity budgets re season and weather - Seasonal changes in the use of microhabitats
Long	Large	- Radio-tracking (tidal and seasonal movements of individual shorebirds)	- Experiments to measure functional response curves of different prey - Field experiments on causation of variation in prey abundance and harvestability	- Respirometry to measure BMR, cost thermo-regulation and cost of activity - Effects of weather and microhabitat on thermo-static costs

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Migration and mass change of *Calidris fuscicollis* in North and South America¹

Brian A. Harrington, F.J. Leeuwenburg, S. Lara Resende, R. McNeil, B.T. Thomas, J.S. Grear & E.F. Martinez

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B.A. Harrington, Manomet Bird Observatory, PO Box 1770, Manomet, Massachusetts 02345, USA.

F.T. Leeuwenburg & S. Lara Resende, MSPW Q18-Cj.4-Casa 01, Brasília, D.F. 71.700 Brazil.

R. McNeil, Département de sciences biologiques, Université de Montréal, CP 6128, Succ. 'A', Montréal, Québec, Canada H3C 3J7.

B.T. Thomas, Waterfield, Route 1, Box 212c, Castleton, Virginia 22716, USA.

J.S. Grear, Department of Wildlife and Range Science, University of Florida, Gainesville, Florida 32611, USA.

E.F. Martinez, PO Box 1333, Great Bend, Kansas 67530, USA.

White-rumped Sandpipers *Calidris fuscicollis* migrate between Canadian breeding areas and wintering areas in Patagonia, one of the longest animal migrations in the Western Hemisphere. Migrating *C. fuscicollis* employ both long-distance, non-stop and short-distance, multiple-stop flights. Southbound migrants fly over the ocean after fattening at Atlantic coast staging areas in eastern Canada, mostly located north of 46°N. Landfall is in north-eastern South America, with principal locations along the coasts of the Guianas. The migrants then move gradually south-east along the coasts of the Guianas and north-eastern Brazil before turning inland on a multiple-flight, trans-Amazonian course, where frequent stops are evidently made on sand-bars and river banks that are available owing to seasonally low water levels. There is no evidence of fattening prior to these flights. The subsequent route once again takes advantage of coastal habitats between southern Brazil (Rio Grande do Sul) and Argentina, where peak numbers occur between late October and early February.

Northward migration routes from Patagonia are evidently similar to the southward routes but, instead of being accomplished in a series of short flights with stops on river banks and sand-bars, are accomplished in rapid, non-stop flights following pre-migratory fattening periods at southern Atlantic staging areas. Because the rivers tend to be high at this season, little habitat is available in the interior. Major staging areas are unknown during northward migration in northern South America, the Caribbean Basin or the North American Atlantic and Gulf coasts. A major staging area is identified in the Great Plains of the United States, where birds fatten before their last remaining flight to Nearctic breeding zones. Similar staging sites probably exist in the southern prairies of Saskatchewan.

The information on the routes used and the extreme dependence of high proportions of the species' population on pre-migratory fattening at strategic sites indicate that *C. fuscicollis* is a species whose well-being is closely linked to the well-being of its migration sites.

¹ This abstract is based on a more complete paper published in December 1991 in *Wilson Bull.* 103(4): 621-636.



The International Wader Study Group (WSG) is a voluntary association of amateur and professional researchers on all aspects of the biology of waders (shorebirds). The Group has rapid access to experienced people throughout the international field of wader research. Founded in Britain in 1970, the Group now has a worldwide membership. The WSG acts as the Wader Specialist Group of Wetlands International (WI).

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Shorebird ecology and
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The world of migrant shorebirds in the Western Hemisphere consists of staging areas and geographical bottlenecks along a chain of migration all the way from the arctic tundra to the shores of Tierra del Fuego. Shorebird biologists in the northern and southern portions of the Western Hemisphere have long known that certain sites across this vast geography are of critical importance to shorebirds. Biologists and conservationists in North America meet regularly to discuss the importance and conservation of these sites; many South American biologists also meet to discuss the same issues in their countries. But rarely do scientists in both portions of the hemisphere have the opportunity to get together to discuss questions of mutual interest and concern. The IV Neotropical Ornithology Congress held in Quito, Ecuador, went a long way toward establishing closer links between North and South.

The 21 papers and expanded abstracts collected in this volume are based on the papers presented at the 'Quito Symposium'. They bring together information that in many cases has been available only locally. Now, researchers throughout the Western Hemisphere can benefit from the wider dissemination of data on species of concern in both the North and the South. Information from field research conducted in Alaska, California, Minnesota, Mexico, Costa Rica, Colombia, Peru, Brazil, Chile, Argentina and Patagonia is arranged in three parts:

- i. Populations, habitat use and breeding biology of shorebirds in North America.
- ii. Ecology of migrant and resident shorebird populations in Central and South America.
- iii. Shorebird foraging ecology and energetics.

This volume will be of interest to shorebird biologists, conservationists and anyone who wants to preserve the splendour of shorebirds' annual migrations. Its aim is to benefit the long-distance wanderers that we all wish to better understand and protect.

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