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Migration and moult strategy of the Curlew Sandpiper

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BSc. ZOOLOGY, MSc. CONSERVATION BIOLOGY

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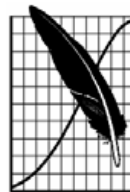
THESIS PRESENTED FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN THE DEPARTMENT OF ZOOLOGY

UNIVERSITY OF CAPE TOWN

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Declaration

I hereby declare that all of the work presented in this thesis, titled "Migration and moult strategy of the Curlew Sandpiper, is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed in Cape Town in February 2011,

Signed by candidate

Date of graduation: December 2010

University of Cape Town

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ABSTRACT

Breeding, migration and moult are the three most energy demanding activities in the annual cycle of migratory species. Because these traits are inter-connected, any change in the timing of one may induce a change in the timing of the other traits. The aim of this research is to describe the migration and moult strategies of the Curlew Sandpiper in relation to the different migratory routes and non-breeding areas of the species, focusing on the carry-over effects which conditions at the breeding grounds have on the timing of post-breeding migration and, subsequently, on the timing of moult at the non-breeding areas. Part of the study also describes the adaptive feature of moult in relation to migratory distance and environmental conditions at the non-breeding areas. Warm temperatures in June on the Arctic breeding grounds favoured early initiation of breeding and early migration of males because they do not partake in parental care. Low predation on clutches and warm temperatures during chick development in July favoured the late migration of females. Migration of juveniles was earlier in good breeding years compared with poor breeding years. Variation in the timing of autumn migration appeared to affect the timing of moult at the southernmost limit of the non-breeding areas in South Africa and Australia. Moult started late in years when predation pressure on the Arctic breeding areas was low and July temperatures were high compared to years when predation pressure was high. At more northerly non-breeding regions in Kenya and India, the onset and duration of moult appeared to be timed to coincide with rainfall periods, thus high food abundance, in these regions. In light of changing global climate and its effect on the annual cycle of organisms, the challenge is to define the extent to which carry-over effects influence future fitness and survival of individuals and, consequently, influence population dynamics.

Layout of thesis and contribution of co-authors

There are eight chapters in this thesis. The first and eighth chapters are the introduction and synthesis, respectively, while the other six chapters are the results of the analysed data on migration and moult. Each chapter is written as self contained paper, with its own introduction, methods, results, discussion, and list of references. Tables, figures follow the text of each chapter. I was responsible for the data analysis and writing of all chapters. The following people contributed data, helped with data analysis, and reviewed parts of the thesis. Professor Leslie G. Underhill provided moult data of Curlew Sandpipers in South Africa (Chapters 4, 5, 7) and reviewed all chapters. The mathematical models of Underhill and Zucchini (1988) of the statistical department, University of Cape Town, were used for the analysis of all moult data (chapters 4–7). Professor Anders Hedenström contributed the migration data of the Curlew Sandpiper through Sweden which was collected at the Ottenby Bird Observatory (Chapter 2), analysed part of the data and commented on this chapter. Professor Włodzimierz Meissner, as head of the Polish Waterbirds Research Group KULING, contributed the migration data of the Curlew Sandpiper through Poland (Chapter 3) and commented on the chapter. Dr. Clive D. T. Minton contributed the moult data of the Curlew Sandpiper in north-western and south-eastern Australia (Chapters 4, 5, 7), and commented on these chapters. Dr. Pavel Tomkovich provided insight into Arctic breeding conditions and reviewed chapters 2, 4, and 7. Birgit Erni wrote an extension of the Underhill and Zucchini (1988) moult models in R, which allowed the in-cooperation of covariates (chapters 4 and 5). Magdalena Remisiewicz analysed part of Chapter 4 and commented on chapters 2, 4 and 7.

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University of Cape Town

CHAPTER 1

INTRODUCTION

University of Cape Town

INTRODUCTION

1.1 Waders

Waders, also called shorebirds, belong to the diverse avian order Charadriiformes, suborder Charadrii. The subdivisions of waders following recent molecular evidence (Ericson *et al.* 2003, Paton *et al.* 2003; Thomas *et al.* 2004, van Tuinen *et al.* 2004, Paton & Baker 2006) are Scolopacidae (snipe, sandpipers, phalaropes), Jacanidae (jacanas), Rostratulidae (painted snipe), Thinocoridae (seed snipe), Pedionomidae (Plains Wanderer), Laridae (Gulls), Sternidae (Terns), Rhynchopidae (Skimmers), Stercorariidae (skuas), Alcidae (Auks), Glareolidae (pratincoles and coursers), Dromadidae (Crab Plover), Turnicidae (Buttonquail), Charadriidae (plovers and lapwings), Recurvirostridae (avocets and stilts), Haematopodidae (oystercatchers), Burhinidae (thick-knees), Chionididae (sheathbills), and Pluvianellidae (Magellanic Plover) (Fig. 1).

Waders spend much of their time in wetland habitats and derive their name from the fact that they are often found along the shores of oceans, lakes, and other wet or marshy areas. Most waders forage in shallow water inland or at the shore, although some species such as Upland Sandpiper *Bartramia longicauda*, and woodcocks *Scolopax* spp. forage in upland sites (Hayman *et al.* 1986, Bowen & Kruse 2009) while others such as the phalaropes forage in deeper water by swimming (Mercier & Gaskin 1985). The diet of waders mostly consists of insects, aquatic invertebrates, molluscs and small fish (Baker 1977, Puttick 1979, Pienkowski 1981, Boros *et al.* 2006). Each species seeks its preferred foods by using distinct feeding methods, which helps reduce direct competition among species for food. Beaks come in a

variety of shapes and sizes, and each is designed for a specific foraging method and substrate (Burton 1974, Zweers 1991).

Waders occupy a wide range of environments including coastal, saline, and freshwater wetlands, flooded agricultural fields, interior grasslands, and arctic tundra (Cramp & Simmons 1983, del Hoyo *et al.* 1996). Most species of waders, especially the sandpipers and allied species, breed in the Arctic or sub-Arctic, some species breed in the boreal, or northern coniferous, forest and temperate areas of North America, Europe and Asia (Arctic Breeding Birds Survey data), a few more breed southward through the tropical zone to the southern ends of South America, Africa and Australasia (Sinclair & Ryan 2003, Hockey *et al.* 2005, Tomkovich & Weston 2007). Many species of Arctic and temperate regions are migratory (e.g. Little Stint *Calidris minuta*, Ruff *Philomachus pugnax*, Ruddy Turnstone *Arenaria interpres*) spending the non-breeding season in the southern hemisphere. Tropical species such as Kittlitz's Plover *Charadrius pecuarius* are often resident, or move in response to rainfall patterns (Brown *et al.* 1982, Hockey *et al.* 2005).

The modes of reproduction in the charadriiforms are varied. Most members of the Scolopacidae (the snipes, sandpipers and woodcocks) construct nests on the ground, usually a scrape or hollow with scant lining which are well camouflaged (Cramp & Simmons 1983, Del Hoyo *et al.* 1996, Hockey *et al.* 2005, Tomkovich & Weston 2007). Some species such as the Crab Plovers *Dromas ardeola* nest in crevices or burrows (De Marchi *et al.* 2008), the Egyptian plover *Pluvianus aegyptius* buries its egg in sand by day and incubates at night (Johnsgard 1981, Hayman *et al.* 1986), and a few such as the Wood Sandpiper *Tringa*

glareola nest in trees (Johnsgard 1981, Hayman *et al.* 1986). While some form single family unit, some species, such as the plovers and pratincoles, are colonial.

The majority of species adopt the breeding strategies outlined below (Pitelka *et al.* 1974, Székely & Reynolds 1995):

(a) Monogamy— with both the male and female being responsible at least partly for parental duties, is the typical mating system of shorebirds.

(b) Polygyny— the breeding system here a male mates with several females within a very short period of time (simultaneous polygyny) or one after another over a long period of time (successive polygyny) and the male leaves all parental duties to the female. Ruff, Pectoral Sandpiper *Calidris melanotos*, Sharp-tailed Sandpiper *C. acuminata*, and Curlew Sandpiper *C. ferruginea* are polygynous.

(c) Polyandry — females compete for males and attempt to mate with several in succession. The male incubates the eggs and rears the young either without or with limited assistance from the female. The phalaropes, Comb-crested Jacana *Irediparra gallinacea* and plain-wanderer *Pedionomus torquatus* practice this system. The females are usually more brightly coloured than the male.

(d) double-clutch breeding system (or rapid multi-clutch polygamy), a combination of polygyny and polyandry, in which a female lays two clutches of eggs in quick succession and the first clutch is incubated by the male and the second clutch is incubated by the female. This can be found in the Temminck's Stint *Calidris temminckii*, Little Stint *C. minuta* and Sanderling *C. alba*.

Adaptations for feeding

The shape of the bill varies greatly within the order in accordance with special feeding methods. The hooked tip in gulls and jaegers facilitates grasping and tearing of food (Harrison 1988). Some species such as the Atlantic Puffin *Fratercula arctica*, Rhinoceros Auklet *Cerorhinca monocerata*, and Fairy Tern are able to carry several fish crosswise in the bill while capturing still more. They do this by holding the fish against the roof of the upper jaw with the spiny tongue (Harrison 1988, Alsop 2001). The bills of sandpipers are usually long and slender, and straight or curved up or down, the bill of plovers it is somewhat stouter and less flexible, often slightly swollen at the tip (Cramp & Simmons 1983; Fig. 2).

Feathers and moult

Moult is the periodic replacement of feathers. Feathers wear out from exposure to sun, rain, and abrasion, and need to be replaced. Moult in birds is a cyclical process. When and where a bird moults is inter-related to other aspects of its life history, in particular breeding, and when relevant, migration. Most species have a complete or near complete moult once a year. Most Charadriiformes have two moults between breeding periods; a partial body moult generally precedes breeding, and a complete moult following breeding. In some species such as populations of Dunlins *Calidris alpina* in northern Alaska, flight feathers of the wing and tail are moulted before the post-breeding migration (Holmes 1966). In other species (e.g Curlew Sandpiper, Little Stint) moult takes place on the non-breeding grounds (Thomas & Dartnall 1971, Pearson 1974, Tree 1974, Elliott *et al.* 1976, Waltner 1976, Dean 1977). Still other species (e.g Wood Sandpiper and Dunlin population which breed east of

the Ural Mountain) stop along the migration route to moult (Greenwood 1983, Remisiewicz *et al.* 2009).

The Sandpipers

Sandpipers belong to the family Scolopacidae, which are small to middle-sized birds, about 15 to 30 cm long. The group includes the shorebirds classified as *Calidris*, and some also known as dunlin, knot, and sanderling. Sandpipers can have short or long bills, usually slender, straight (e.g Marsh Sandpiper *Tringa stagnatilis*), decurved (e.g Curlew Sandpiper) or recurved (e.g Terek Sandpiper *Xenus cinereus*), long, narrow and pointed wings, and medium to short tails. Their colouring often consists of a complicated “dead-grass” pattern of browns, buffs, and blacks on the upperparts, with white or cream colouring below. They are frequently paler in the non-breeding than in the breeding season. Sandpipers formally divided among the genera *Erolia*, *Ereunetes*, and *Crocethia* are now placed in the broad genus *Calidris* (Cramp & Simmons 1983, Hayman *et al.* 1986, del Hoyo *et al.* 1996, Hockey *et al.* 2005, *Encyclopædia Britannica* 2011). Most sandpipers inhabit open areas and are strong fliers, some performing extensive migrations that cover long distances. A Ruddy Turnstone *Arenaria interpres* banded by the Victorian Wader Study Group, Australia, in 2009 completed a 27,000 km round trip migration twice in 2009 and 2010 (C.D.T. Minton pers. Comm.). Many sandpipers nest in the Arctic and sub-Arctic regions. They lay four spotted eggs, from which hatch active, downy young.

1.2 Life-history of the Curlew Sandpiper *Calidris ferruginea*

The Curlew Sandpiper breeds in the Central Siberian Arctic of northern Russia from 71°40' E on eastern Yamal Peninsula to 156°40'W near Barrow, Alaska, and from 67°05'N in the south in Chukotsky Peninsula to 77°23'N in the north at Taimyr (Holmes & Pitelka 1964, Lappo & Tomkovich 2006; Fig. 3). Outside the breeding season, the Curlew Sandpiper has a wide distribution from the coastlines of sub-Saharan Africa to Australasia (Cramp & Simmons 1983). The ratio of the non-breeding area to breeding area is one of the greatest for any calidrid sandpiper (Underhill 1995).

The Curlew Sandpiper shows no geographic variation or sub-populations based on mitochondrial DNA and microsatellite analysis (Wennerberg & Burke 2001). Ringing recoveries show no migratory divide between birds migrating from the breeding ground to Africa and those migrating to Southern Asia or Australasia (Underhill 1995, Minton *et al.* 2006b). The species exhibits sexual dimorphism; the female is usually larger than the male (Thomas & Dartnall 1970, Elliott *et al.* 1976). Bill length has proven to be a reliable criterion for sexing the species, females usually having longer bills (39–41 mm) than males (36–38 mm) (Elliott *et al.* 1976, Puttick 1981, Cramp & Simmons 1983). Adult birds can be sexed using the discriminant function equation of (Wymenga *et al.* 1990): $D = 0.07815 * W + 0.47962 * B - 28.7302$; $D = \text{discriminant score where } D < 0 = \text{males, } D > 0 = \text{females, } W = \text{wing length (mm) and } B = \text{bill length (mm)}$.

Breeding

The median arrival date on the breeding ground is 10 June although this varies from one year to the next due to varying snow and weather conditions at arrival time (Syroechkovski & Lappo 1994, Tomkovich *et al.* 1994). Peak egg-laying period is between 15–20 June (Tomkovich & Soloviev 2006). Egg-laying normally occurs over three days, and incubation lasts for 20.4 days on average (Tomkovich *et al.* 1994, Tulp *et al.* 1997). Curlew Sandpipers have a polygynous breeding system; the males leave all parental duties, including incubation and care of chicks from hatching to fledging to the female. The peak hatching period is 5–12 July, and chicks are completely independent about two weeks afterwards (Schekkerman *et al.* 1998, Tomkovich & Soloviev 2006).

Predation is generally considered to be the most important factor influencing the reproductive success of the Curlew Sandpiper (Underhill 1987, Soloviev *et al.* 2006). Usually, Arctic predators such as the Arctic fox *Alopex lagopus* and Long-tailed Skua *Stercorarius longicaudalis* have a preference for lemmings (*Lemmus spp.* and *Dicrostonyx spp.*) and in years when lemmings are abundant, birds breed unmolested by predators. When lemming numbers collapse and there are large numbers of predators, a large proportion of breeding attempts are lost to predation (Summers & Underhill 1987, Underhill *et al.* 1993). The lemming populations fluctuate cyclically, with a 3-4 year periodicity and in the Taymyr Peninsula and the breeding productivity of the Curlew Sandpiper also produces a cyclical pattern, coinciding with the lemming cycles (Underhill 1987, Summers *et al.* 1998).

Temperatures also mediate breeding productivity during the hatching period, which is in mid-July (Schekkermann *et al.* 1998, Soloviev *et al.* 2006). Warm temperatures during this period leads to a productive breeding season, whereas spells of freezing weather during the hatching period can result in breeding failure even in the absence of predators (Arctic Breeding Birds Survey, Schekkermann *et al.* 1998).

Migration and moult

Migration from the breeding grounds begins as soon as breeding is completed. The passage of adults through Europe is from late July through August and migration of juveniles is between August and September (Tulp & Schekkerman 2001, Meissner 2006). In low predation years, the passage of adults is bimodal; the passage of males produces the earlier peak and the females the later peak (Tulp & Schekkerman 2001). In high predation years passage is more synchronized between the sexes; females that fail to breed may start their post-breeding migration together with males resulting in a single peak. The Arrival of adults at the southern limit of the non-breeding range in Africa and Australia is between August and October; the general sequence of arrival being adult males, adult females and juveniles (Elliott *et al.* 1976, Waltner 1976, Minton *et al.* 2006a).

Primary moult in the Curlew Sandpiper typically takes place at the non-breeding areas. In Kenya, moult of adult birds usually begins by the end of August (Pearson 1974) and ends in February of the following year, in southern Africa moult starts by September and ends in February (Elliott *et al.* 1976, Dean 1977), in Australia and Tasmania moult begins between September and October and ends between February and March (Thomas & Dartnall 1971,

Minton *et al.* 2006a). The juvenile birds carry out a partial moult of flight feathers, 60–80% of birds replace the outer three to five feathers (Cramp & Simmons 1983, Tree 1974, Elliott *et al.* 1976, Waltner 1976). This moult takes place between February and May of the year following their arrival at the non-breeding areas when the primary feathers begin to show signs of wear. This thesis focuses on refining our knowledge of primary moult and the factors influencing the initiation of moult.

Adult Curlew Sandpipers leave on northward migration from the non-breeding grounds from the second half of April through early May (Elliott *et al.* 1976, Minton *et al.* 2006a). Immature birds do not breed in the first breeding season after they hatched; instead, they remain in the non-breeding areas, and migrate to the breeding areas in the second breeding season after they hatched. From egg-laying to adulthood the “life spiral” of the Curlew Sandpiper takes about 20 months (Underhill 2006; Fig.4).

1.3 This study

Rationale and aim of this thesis

The annual cycle of the Curlew Sandpiper consist of life-history stages such as breeding, migration and moult, the timing of which is largely under genetic (endogenous) control (Berthold & Querner 1982, Berthold 1996). However, biotic and abiotic variables of the environment such as temperature, rainfall, competition, and predation may invoke some adjustment in the timing of these life-history stages. For instance, when predation on eggs and chicks of the Curlew Sandpiper is high, the timing of migration is earlier than in the years when predation is low (Underhill 1987, Summers *et al.* 1998, Meissner 2006).

It is now clear that changing global climate is causing a phenological shift in life-history traits, such as spring migration and breeding, of Palearctic bird species (Gordo 2007, Pulido 2007, Rubolini *et al.* 2007). These studies raise questions about the consequences of these trends on other parts of the annual cycle and on population processes. To begin with, that there is unequal response to climate change across trophic levels (Lehikoinen *et al.* 2004, Both *et al.* 2009). Some populations of European migrants that did not advance their spring migration have declined, presumably due to a mismatch between the timing of breeding and the period of peak insect abundance (Møller *et al.* 2008). Their study demonstrates that species with declining populations may not have advanced their timing of breeding sufficiently to match the advancement in the optimal timing of reproduction, characterized by peak insect abundance.

The aforementioned studies focus mainly on spring migration and breeding phenology in European migrants. How conditions during the breeding season affect post-breeding (autumn) migration and subsequent events within the annual cycle on the non-breeding (e.g. moult and survival) deserve equal attention.

The aim of this research is to describe the migration and moult strategies of the Curlew Sandpiper in relation to the different migratory routes and non-breeding areas of the species. Part of the study examines the carry-over effects conditions at the breeding grounds have on the timing of post-breeding migration and, subsequently, the timing of moult at the non-breeding areas. The other part of the study examines the adaptive feature

of moult at the non-breeding grounds in relation to migratory distance and environmental conditions at the non-breeding areas.

Study sites and data analysis

The data used in this thesis were collected from six different sites (Fig. 4). Data on migration was obtained from the Ottenby Bird Observatory in Sweden and the Waterbird Ringing and Research Unit (KULING) in Poland. Primary moult data were obtained from Kenya, India, South Africa, north-eastern Australia, and south-eastern Australia. The moult data from Kenya was extracted from the South African Ringing Unit (SAFRING) and David Pearson provided more records from the Rift Valley region of Kenya ($00^{\circ}22'N - 3^{\circ}20'S$, $35^{\circ}2' - 39^{\circ}58'E$). Moult data from India were collected at Mandapam ($9^{\circ}17'N$, $79^{\circ}8'E$) and at the Great Vedaranyam Swamp ($10^{\circ}18'N$, $79^{\circ}51'E$), in south-eastern India as part of the Bombay Natural History Society's Bird Migration Project between 1980 and 1992. Moult data from South Africa were from the ringing activities of the Western Cape Wader Study Group at Langebaan Lagoon ($33^{\circ}05'S$, $18^{\circ}02'E$) and Rietvlei ($33^{\circ}50'S$, $18^{\circ}30'E$). Moult data from north-western Australia were of Curlew Sandpipers caught at Roebuck Bay and Eighty Mile Beach in Broome ($18^{\circ}07'S$, $122^{\circ}16'E$) by the Australasian wader study group, and data from south-eastern Australia ($38^{\circ}-39^{\circ}N$, $144^{\circ}-147^{\circ}E$) were provided by the Victorian Wader Study Group. Description of study sites, catching methods, and sample sizes are provided in the individual chapters.

The recording and analysis of moult

In the Curlew Sandpiper, as in most species of waders, primary flight feathers are shed in sequence from the innermost primary (P1) outwards to the 10th primary (P10). Primary moult scores were recorded using the British Trust for Ornithology technique (Ginn & Melville 1983) as follows: 0 = not dropped, 1 = missing or in pin, 2 = "brush" stage to one-third grown, 3 = one-third to two-thirds grown, 4 = two-thirds to full-grown but with waxy sheath remaining, 5 = completely regrown. The sum of these scores produced a single score reflecting the stage of moult in the individual concerned (Ashmole 1962, Evans 1966, Newton 1966). Species with 10 primaries had a moult score of 0 when all the primaries are old and 50 at the completion of moult.

In earlier studies, the mean start date and duration of moult of the population were estimated by regressing moult scores of all birds against the date (Evans 1966, Newton 1966, Ginn & Melville 1983). This method was unsatisfactory for two reasons. First, the regression line tends to run diagonally across the long axis of the parallelogram enclosing the scatter of points (Summers *et al* 1983). It was actually an estimate of the start and end dates for the population as a whole, rather than of the average bird. Regression methods underestimated the mean start date and overestimated the mean duration (Pimm 1976, Summers *et al.* 1983). The second problem with using regression methods was that the rate of increase in moult score was not linear throughout moult. This arises because primary feathers vary greatly in length, with long outer ones taking more than twice as long to grow as short inner ones (Underhill 2003, Remisiewicz *et al.* 2009, Chapter 4 & 6) but the growth stage of all feathers are scored equally (Ashmole 1962, Summers *et al.* 1983).

Underhill & Zucchini (1988) developed a number of models which made use of non-moulting as well as moulting birds, fitting the model using the method of maximum likelihood. In this study, the Underhill-Zucchini model type two, in which moult scores of birds in the categories moult not started, in moult and moult finished are used, and model type four in which only scores of birds in moult and birds that have completed moult are used. To apply any of these models the moult scores were converted into proportion of feather mass grown using the relative masses of primary feathers (Underhill & Joubert 1995, Underhill & Summers 1993), a process which accounts for the varying lengths of the primary feathers. This conversion essentially “straightens” the progress of moult (Summers *et al* 1983).

Layout of the thesis

The data used for this thesis were obtained from Kenya, India, South Africa, north-western Australia and south-eastern Australia (Fig. 5).

Chapter 1: Introduction

Chapter 2 and 3: Migration within the annual cycle.

These chapters examine the mechanism by which predation pressure (quantified by lemming and predator abundance) and temperature during the breeding season (in June and July) influence the timing of migration of adult, both males and females, and juvenile Curlew Sandpipers. The effect of changing climate on the timing of migration over the years is also examined. These chapters draw from the findings of a number of studies: Summers

et al. (1998) and Underhill *et al.* (1993) who demonstrated the link between lemming abundance and predator numbers on breeding success, Byrkjedal (1980), Schekkerman *et al.* (1998) and Meltofte (2007) who demonstrated the influence of weather condition during breeding on egg-laying dates and breeding success, Figuerola (2006) and Meissner (2006) who found a link between the timing of migration of adult birds with the proportion of juveniles.

Research questions are:

1. What conditions at the breeding grounds affect the timing of migration of adults and juveniles and by what mechanism is this achieved?
2. Is the migration of males and females affected differentially by conditions at the breeding grounds?
3. Has the timing of migration of the Curlew Sandpiper changed over the years and what has caused this change?

Chapter 4: Comparative study of the moult pattern of Adult Curlew Sandpipers at the southernmost limit of the non-breeding areas in South Africa, north-western Australia and south-eastern Australia. The purpose is to find out if the timing and speed of moult is governed by the migration distance, hence latitude, and how the speed of moult is regulated in different populations. Estimates of the population start date and duration of moult of adult Curlew Sandpipers were obtained and the growth pattern of individual primary feather growth was described. The moult parameters were estimated using the type two models of Underhill & Zuchinni (1988) which use moult scores of birds not started moult, in moult, and moult finished.

Chapter 5: Estimates of the annual moult parameters (start date, duration, and standard deviation of parameters) are obtained of adults as a whole and of the sexes in South Africa. north-western Australia and south-eastern Australia. The purpose is to examine whether the timing of moult differs between males and females, and if moult is adjusted in relation to breeding success and/or migration.

Chapter 6: A comparative study of the moult strategy of the Curlew Sandpiper on the non-breeding grounds closer to the equator in Kenya and India. The timing of moult is examined in light of the migration distance and environmental conditions in Kenya and India.

Chapter 7: Moult strategies and pattern of the immature Curlew Sandpipers in South Africa. north-western Australia and south-eastern Australia. The pattern and strategy of moult are explained in context of the annual cycle of the species and the environment in the non-breeding areas.

Chapter 8: Conclusion. Migration and moult within the annual cycle, in relation to migratory distance and how it is modified by conditions at both the breeding and non-breeding areas.

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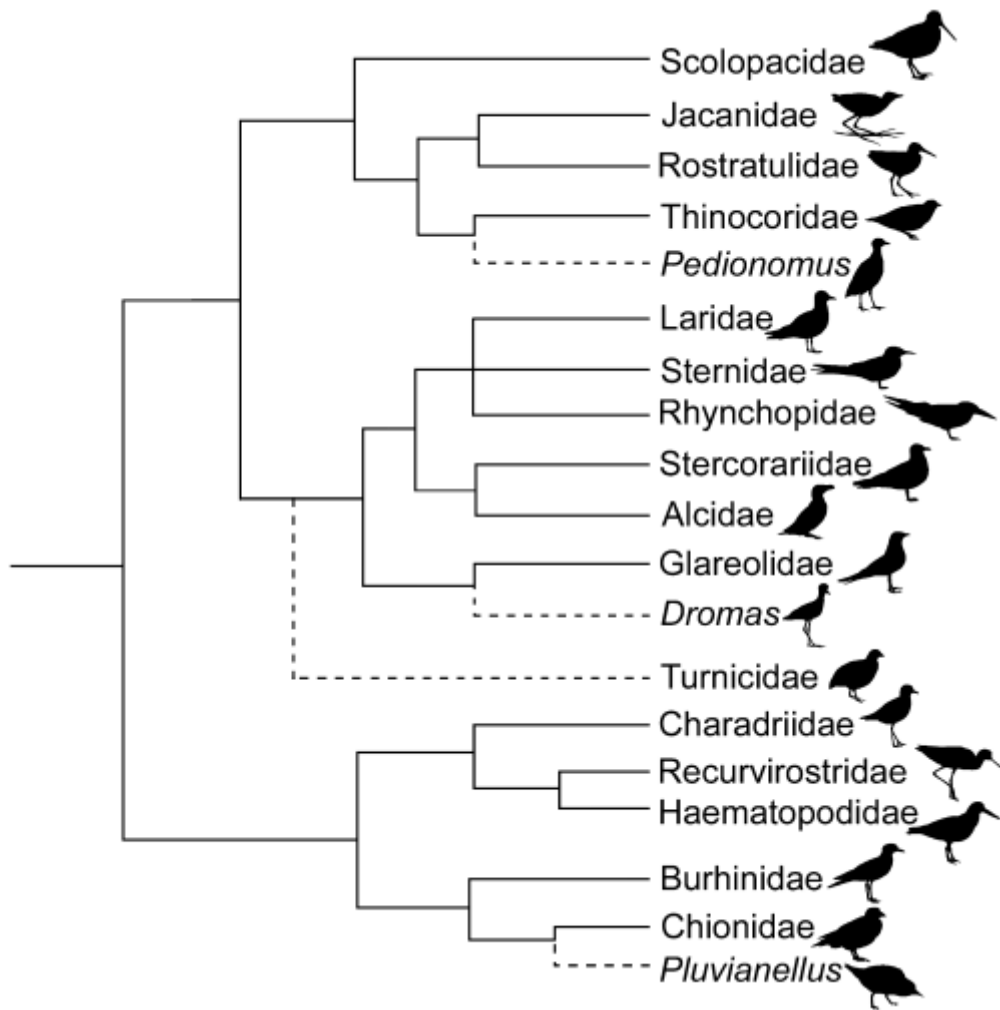


Fig.1. Phylogeny of modern shorebird (Charadriiformes) relationships according to new molecular data (adapted from van Tuinen *et al.* 2004).

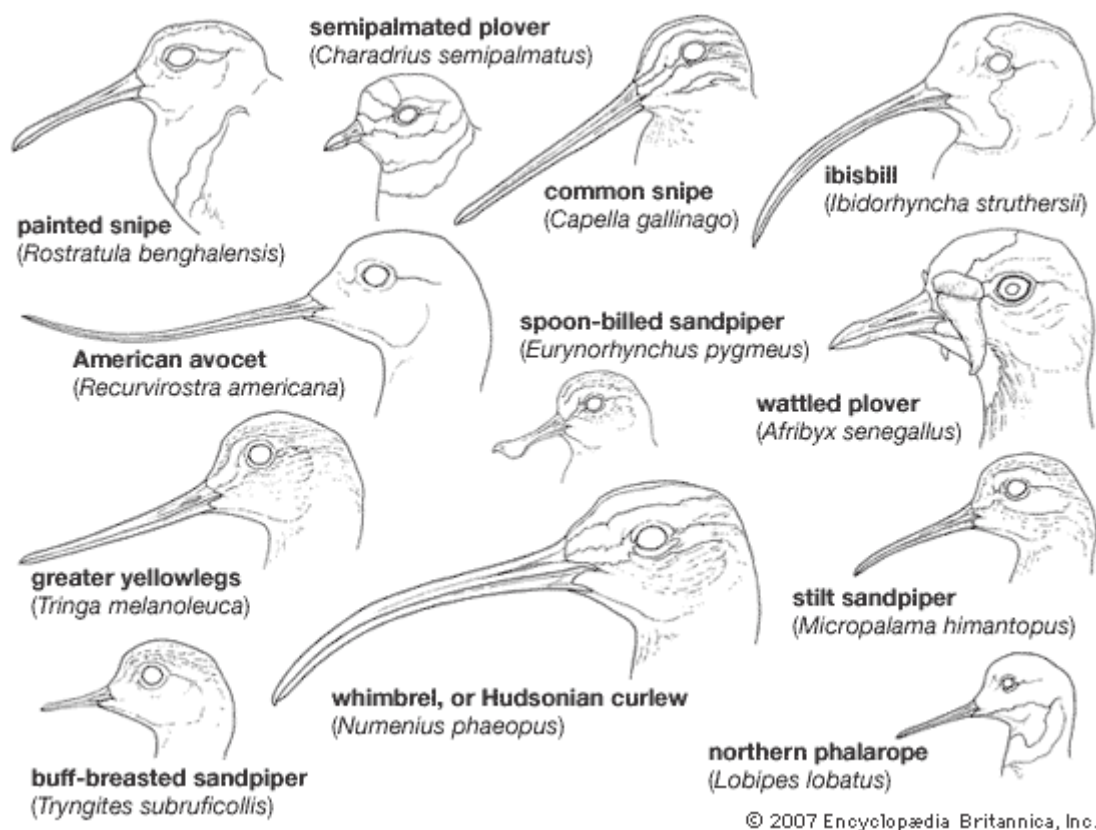


Fig. 2 Variations in the bills of shorebirds (order Charadriiformes) adapted from the Encyclopædia Britannica 2011.

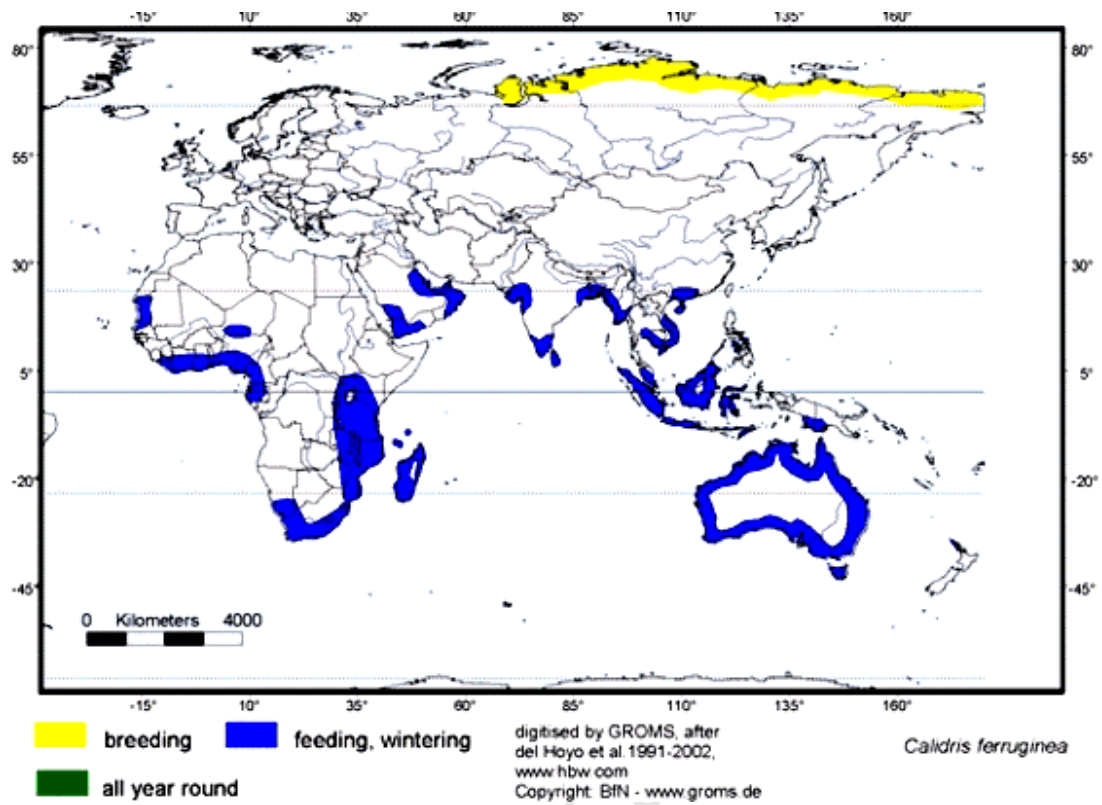


Fig. 3 Global distribution range of the Curlew Sandpiper *Calidris ferruginea* (adapted from del Hoyo *et al.* 1991)

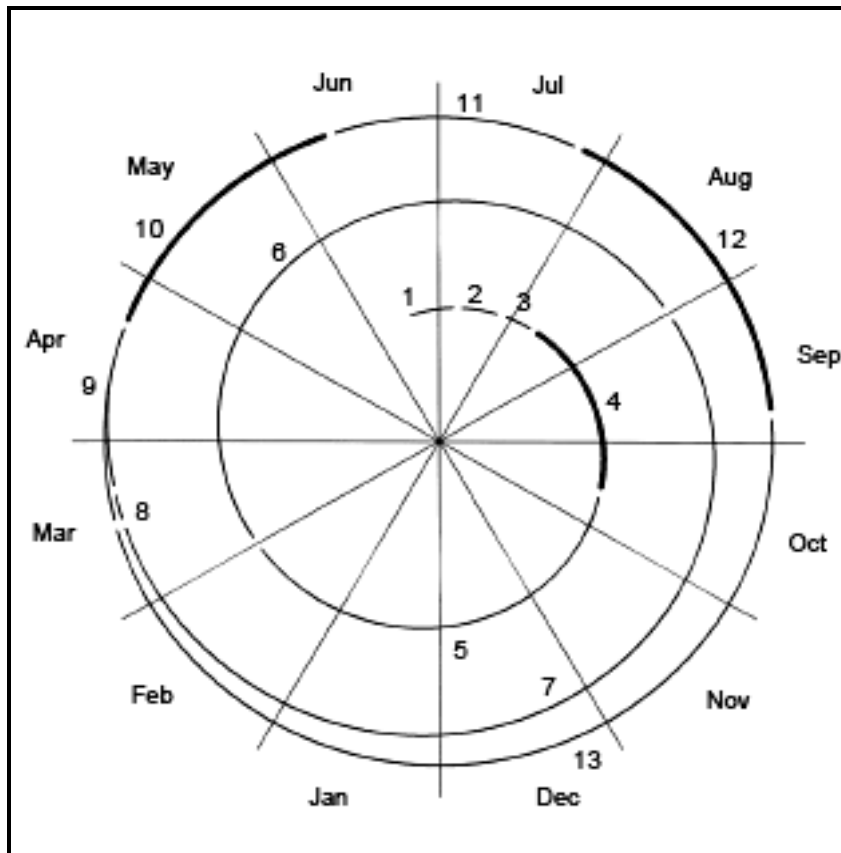


Fig. 4 The life spiral of Curlew Sandpipers migrating between the Taimyr Peninsula, Siberia, and the Western Cape, South Africa (adapted from Underhill 2006).

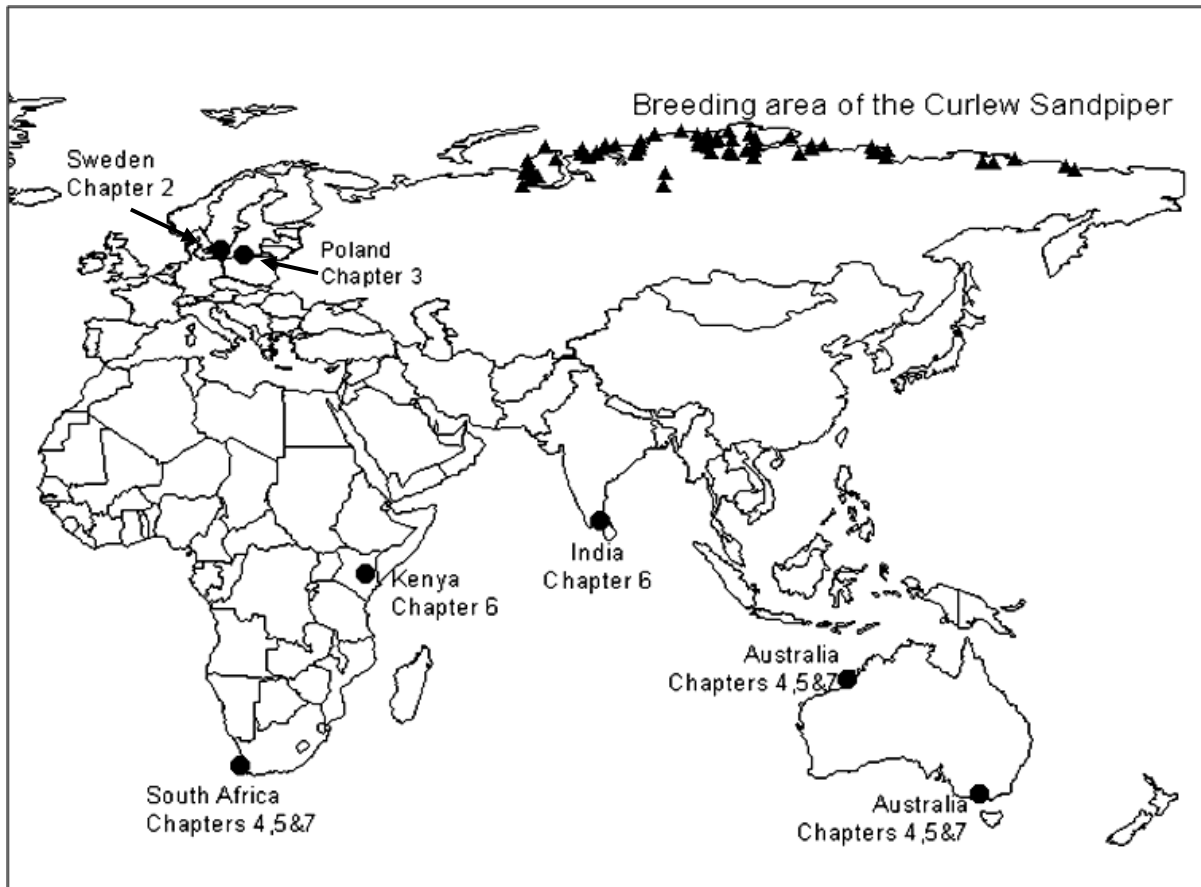


Fig. 5 Location of the sites where data for this thesis were collected in Kenya, India, South Africa, north-western Australia and south-eastern Australia in relation to the breeding area in northern Siberia (breeding range adapted from Lappo & Tomkovich 2006).

CHAPTER 2

IMPACT OF CLIMATE AND PREDATION ON AUTUMN MIGRATION OF THE CURLEW SANDPIPER THROUGH SWEDEN

University of Cape Town

IMPACT OF CLIMATE AND PREDATION ON AUTUMN MIGRATION OF THE CURLEW SANDPIPER THROUGH SWEDEN

ABSTRACT

Recent shifts in the timing of spring migration and breeding in some migratory birds has been attributed to recent climate change. However, the divergent patterns in the timing of migration among different bird species suggest that changes in the timing of autumn migration cannot be attributed solely to climate change. Using data of constant-effort catches, the causes for the annual variation in the timing of migration of Curlew Sandpipers *Calidris ferruginea* migrating through Sweden are investigated, as well as the trend in the timing of migration from 1946–2005. Variation in the timing of autumn migration of the adult and juvenile Curlew Sandpipers was influenced by breeding success, which is connected to predation pressure on the Arctic breeding grounds. Median migration date of adult birds was significantly later in good breeding years compared with poor breeding years while the migration of juveniles was earlier in good breeding years compared with poor breeding years. Also, adults migrated earlier when the average temperature in June was warmer. Median migration dates of adults have advanced by 23 days from 1946–2005, but the migration dates of juveniles have remained unchanged. This suggests that the advance in the departure of the adult Curlew Sandpipers from the breeding grounds was not due to earlier breeding. Increasing predation on the clutch might have resulted in this observed early departure of adults from the breeding grounds. One possible consequence of earlier migration is a mismatch between the timing of migration and seasonal peaks of food abundance on migration routes and at the wintering grounds, leading to a decline in adult and juvenile survival and the population.

INTRODUCTION

Migration is a critical event in the annual cycle of birds and must be timed carefully to coincide with periods of food abundance (Thomas 1979, Fransson *et al.* 2008, Newton 2008). A mismatch between the migration period and the period of peak food abundance will reduce a migrant's prospects of survival (Both *et al.* 2006, Møller *et al.* 2008, Reif *et al.* 2008). A shift in the timing of the post-breeding migration can also affect the subsequent events in the bird's life cycle. For instance, many waders (shorebirds) moult their flight feathers only after arriving at the non-breeding ("wintering") area (Ginn & Melville 1983, Hayman *et al.* 1986, Underhill 2003), which suggests that the timing of moult could shift in response to the timing of migration.

Climate change has already led to changes in the phenology of migration in many bird species (e.g. Mason 1995, Sparks 1999, Jenkins & Watson 2000, Hüppop & Hüppop 2003, Both *et al.* 2005). Earlier spring migration and arrival at the breeding grounds, enabled by milder winters, has resulted in many species breeding earlier in Europe and North America (e.g. Crick *et al.* 1997, Forchhammer *et al.* 1998, Brown *et al.* 1999, Crick & Sparks 1999). Earlier breeding should then also result in the birds leaving the breeding grounds earlier.

Among the waders, however, earlier, later or unchanged migration trends have been described. For instance, the timing of the southwards migration through Europe has advanced in Wood Sandpiper *Tringa glareola*, Common Sandpiper *Actitis hypoleucos* and Dunlin *Calidris alpina*, has been delayed in the Ruff *Philomachus pugnax*, Snipe *Gallinago gallinago*, and Little Ringed Plover *Charadrius dubius*, and has remained unchanged in the Little Stint *C. minuta* and Green Sandpiper *T. ochropus* (Anthes 2004, Adamik & Pietruszkova 2009). These divergent patterns suggest that changes in the timing of autumn migration cannot be attributed solely to climate change.

In waders, the timing of autumn migration depends largely on the end of the reproductive season. Adults can depart from the breeding grounds after they have completed breeding or if they lose their broods (Tomkovich & Soloviev 2006). Environmental conditions can thus affect the time when breeding starts and the success of nesting attempts of waders, and thus the time when post-breeding migration starts. Snow cover on the ground when birds arrive can delay egg-laying (Green *et al.* 1977, Summers & Underhill 1996), low temperatures can reduce the abundance of the insects on which they feed thus delaying egg-laying (Moltofte *et al.* 2006), and wind chill can interfere with mating and the incubation of eggs (Tomkovich 1995). Heavy snowfalls, storms, floods, or the trampling of nests by reindeer during the breeding season can cause the complete loss of clutches (Arctic Birds Breeding Survey). In waders such as Curlew Sandpiper *Calidris ferruginea*, Sanderling *C. alba*, and Turnstone *Arenaria interpres* predation also influences breeding success (Summers & Underhill 1987, Underhill *et al.* 1989).

The Curlew Sandpiper, as a migratory species of wader which breeds in the Arctic, is ideal for examining how a combination of different environmental conditions at the breeding grounds can affect the timing of autumn migration. The wide distribution range of the species during the non-breeding season provides the opportunity to compare the variation in the timing of migration between populations under different environmental conditions. Curlew Sandpipers breed in the high Arctic tundra between 71°40'E–156°40'W and 67°05'–77°23'N (Holmes & Pitelka 1964, Lappo & Tomkovich 2006). The species arrives in the Taimyr Peninsula in June (Syroechkovski & Lappo 1994) and egg-laying starts between 15–22 June (Tomkovich & Soloviev 2006). Only the females incubate. Males leave their territories soon after the females begin incubating and start migrating southwards by early July while the females migrate after the young have fledged or when breeding fails (Holmes & Pitelka 1964, Tomkovich 1988). The migration phenology of adults is

therefore observed at stopover sites in two waves; the first formed mainly of males and the second mainly of females (Diadicheva & Khomenko 2006, Meissner 2006, Morozov 2006).

Blomqvist *et al.* (2002) and Figuerola (2006) showed that the timing of adult migration was linked to predation in the arctic and the proportion of juveniles in the total number of birds observed respectively. In the Curlew Sandpiper, reproductive success (measured as the proportion of juveniles) is related to predation in the Arctic (Summers *et al.* 1998, Underhill *et al.* 1993, Blomqvist *et al.* 2002). Predators such as the Arctic Fox *Alopex lagopus* and other predators that prey primarily on lemmings (*Lemmus sibiricus* and *Dicrostonyx torquatus*) switch their diet to the eggs and chicks of waders in years of low rodent abundance (Summers *et al.* 1998, Underhill *et al.* 1993). Schekkerman *et al.* (1998) have also described a relationship between the breeding productivity of the Curlew Sandpiper and the temperature in the Arctic. Low temperature in the Arctic during the breeding season resulted in low breeding success.

Whether the temperature in the Arctic affects the timing of waders' southwards migration – and what the mechanism might be – has not yet been explored. Temperature could directly affect the timing of breeding, and thus of departure, or indirectly influence breeding success. Males and females differ in their involvement in parental care, and the juveniles are only ready to leave the breeding grounds after adults, so temperature and breeding success could act differently on the migration timing of each of these sex and age groups. This study aims to test the direct and indirect effects of weather and predation during the breeding season on the timing of migration for the adult males and females as well as for the juveniles. The mechanism by which climate change might affect trends in the timing of migration for these Arctic-breeding waders over the past 60 years is examined.

The hypotheses are that: 1) temperature and predation affect the timing of migration for adults and juveniles, 2) these conditions on the breeding grounds will affect males and females differently because of this species' system of parental care, 3) climate change will affect long-term trends in the timing of Curlew Sandpiper migration.

METHODS

Ringed data on Curlew Sandpipers were obtained from Ottenby Bird Observatory (56°12' N, 16°24' E, Fig. 1) on the island of Öland in the Baltic Sea at the southern tip of Sweden, where annual observations and ringing have been carried out since 1946 (Edelstam 1972, Hedenström 2004). Birds were captured from early July to late October/early November, the entire autumn migration period of the Curlew Sandpiper (for details see Hedenstrom 2004, Helseth *et al.* 2005, Stervander *et al.* 2005). Walk-in funnel traps (Bub 1991) were set in combinations on rotting seaweed at the shoreline of the southern point of Öland. The traps were checked and emptied every hour, from about an hour before dawn to about an hour after dusk.

Curlew Sandpipers have been aged since 1946 based on differences in plumage between adults and juveniles (Prater *et al.* 1977). Trapped birds were banded with numbered metal bands. From 1990 onwards, the following measurements were made: the maximum wing length (Svensson 1992) to the nearest 1 mm, total head length from the bill tip to the back of the skull (Green 1980) to the nearest 1 mm, and body mass to the nearest 0.1 g.

Data analysis

Adult birds were sexed using the discriminant function equation $D = 0.07815 * W + 0.47962 * B -$

28.7302: D = discriminant score where $D < 0$ = males, $D > 0$ = females, W = wing length, and B = bill

length (Wymenga *et al.* 1990). The histogram of bill lengths of sexed birds shows two clearly separated modes, confirming there was little misclassification of males and females. The bill lengths of the sexes overlapped between 37–39 mm, so birds within this range were excluded from analyses of the migration timing of the sexes.

The annual median dates of migration were computed separately for adults and juveniles. Also, median migration dates were computed for both sexes separately. The percentage of juvenile birds in the total annual catch was used as a measure of breeding success, a method widely used as an indicator of breeding performance especially in species that use well defined migration route and/or wintering areas (Scheckerman *et al.* 1998, Boyd & Piersma 2001, Meltofte 2001, Minton *et al.* 2005, Beal *et al.* 2006). Because breeding success in the Curlew Sandpiper usually exhibits a “boom-or-bust” pattern (Summers *et al.* 1998), years when juveniles constituted more than 20 % of the total catch were classified as good breeding years and years when juveniles constituted 13 % or less of the catch were classified as poor breeding years (Summers & Underhill 1987, Scheckerman *et al.* 1998).

How the timing of migration was affected by temperatures and predation in the Arctic was examined using general linear models (GLM). The annual median migration date was the dependent variable, with breeding success (good or poor) as fixed factor, and annual June average temperature and the predation index as covariates; the model included second-order interactions of the variables. Data on average June temperature in the Arctic (Polyakov *et al.* 2002) was used as a proxy for weather conditions on the breeding grounds during the egg-laying period since most Curlew Sandpiper clutches are completed during 15–22 June (Tomkovich & Soloviev 2006). The index of predation pressure provided by Blomqvist *et al.* (2002) was used to analyze the effects of

predation on migration. The index of predation is the likelihood that wader nests and chicks will be depredated, with scores from 0 (low predation pressure) to 3 (high predation pressure).

The overall migration pattern, derived from daily catches, was compared between poor and good breeding years separately for males and females. We combined the data from all years classified as good breeding years and did the same for poor years, and used the Kolmogorov-Smirnov test to reveal if the “waves” of migration of the different sexes differ in good and poor breeding years.

The trend of median migration dates of adult and juvenile birds over the past 60 years was examined using general regression models. The annual median migration dates was the dependent variable, the index of predation and the average June temperature in the Arctic were covariates, and the model included second-order interactions of the variables. The model with the lowest Akaike Information Criterion (AIC) was selected as the final best-fitted model. The slope “*b*” provided the measure of the magnitude and the direction of the trend. Statistica 9.0 (Statsoft Inc. 2010) was used for all statistical analyses.

RESULTS

In 1946–2005 the Ottenby station banded 5,854 Curlew Sandpipers, with annual totals ranging from one (1968 and 2002) to 623 (1999) (Fig. 2). There was no significant trend in the yearly number of birds banded at Ottenby over the past 60 years (linear regression: $b = 0.37$, $P = 0.62$, $n = 60$). Forty-one years were classified as good breeding years and 18 as poor breeding years. In the period 1946–1975 there were six years classified as poor breeding years, in 1976–2005 there were 11.

Migration pattern of adults in relation to ecological factors

The median migration date of adult birds in good breeding years was 4 August (inter-quartile range: 26 July–13 August), significantly later than the median migration date of 25 July in poor breeding years (inter-quartile range: 20 July–2 August, GLM: $F_{1,57} = 9.20$, $P < 0.01$). Median migration dates occurred earlier in years of high predation than in years of low predation ($F_{1,34} = 6.18$, $P = 0.01$, $b = -2.66$; Fig. 3). Also, birds migrated significantly earlier when the average temperature in June was warmer than colder years, on average 2.8 days earlier for every 1°C rise in temperature ($F_{1,57} = 4.97$, $P = 0.03$, $b = -2.76$; Fig. 4). The interaction of breeding success and June temperature was not significant ($F_{1,57} = 0.05$, $P = 0.81$), but the interaction of breeding success and the predation index was ($F_{1,37} = 2.16$, $P = 0.01$), indicating that as predation pressure increased the difference between the timing of migration in good and poor breeding years becomes more pronounced.

The median migration date of males in good breeding years was 19 July (inter-quartile range: 17 July–6 August), which was not significantly different ($F_{1,57} = 0.10$, $P < 0.901$) from the median migration date in poor breeding years on 21 July (inter-quartile range: 18 July–25 July). However, the males' pattern of migration differed significantly between good and poor breeding years (Kolmogorov-Smirnov test: $D_{1,447} = 0.25$, $P = 0.02$). The date of the maximum difference in the cumulative percentage of birds that had migrated through Ottenby in good and poor years was 31 July. In good breeding years 66% of the observed birds would have migrated by this date, but in poor years 88% of the birds would have migrated (Fig. 5). The median migration date for females in good breeding years was 10 August (inter-quartile range: 3 August–15 September) which was significantly later ($F_{1,57} = 7.61$, $P = 0.02$) than the median migration date in poor breeding years on 23 July (inter-quartile range: 20 July–29 July). There was also a significant difference in the

females' pattern of migration in good and poor breeding years (Kolmogorov-Smirnov test: $D_{1,468} = 0.61$, $P < 0.01$, Fig. 5). The date of the maximum difference in the cumulative percentage of birds recorded on migration in good and poor breeding years was 1 August. By this date, 19% of females recorded in good breeding years had migrated but 86% of females had migrated in poor breeding years.

Between 1946–1995 median migration dates advanced by an average of 23 days, a significant trend ($F_{1,78} = 16.72$, $P < 0.01$, $b = -0.39$, Fig. 6). Both the average June temperature ($F_{1,78} = 18.56$, $P < 0.01$, $b = -3.33$) and the predation index ($F_{1,78} = 7.83$, $P = 0.01$, $b = -2.26$) were significant predictors of this trend.

Migration timing of juveniles in relation to ecological factors

The median migration date of juvenile birds in good breeding years was 31 August (inter-quartile range: 27 August–7 September), significantly earlier than the median migration date of 10 September in poor breeding years (inter-quartile range: 2 September–17 September; $F_{1,54} = 14.31$, $P < 0.01$). Juvenile birds migrated significantly earlier in years with a low predation index compared with years with a high predation index ($F_{1,39} = 8.66$, $P = 0.01$, $b = 4.46$; Fig. 7). Their migration timing was not affected by average June temperature in the Arctic ($F_{1,39} = 0.25$, $P = 0.62$, $b = 0.58$). There was no significant trend in the median migration dates of juvenile birds over the years ($F_{1,32} = 0.38$, $P = 0.53$, $b = -0.07$).

DISCUSSION

The autumn passage of adult Curlew Sandpipers through their stopover sites in Europe usually has a bimodal pattern, with the males observed about 10–15 days ahead of females (Diadicheva & Khomenko 2006, Meissner 2006, Morozov 2006). The results of this study also showed an earlier passage of males through Ottenby compared to females, but the difference in the median migration dates of the sexes was smaller in poor breeding years (three days) than in good breeding years (20 days). The reason could be that in years of poor breeding success when many clutches are lost due to high predation, the females leave the breeding grounds soon after the males since most males leave the breeding ground soon after the eggs have been laid.

The reasons for the early departure of males is unknown but theoretical models proposed to understand the mechanism and patterns of migration in birds by, for instance, Alerstam and Lindström (1990) suggest that the optimal strategy for birds is to initiate migration as soon as free from parental duties. Because of this early departure of males, in high predation years, many females have no opportunity to lay a replacement clutch when the first one has been depredated. But in years with low predation and good breeding success, the females stay with their chicks and thus depart from the nesting grounds later than in years with high predation (Figuerola 2006).

The significant interaction of breeding success and the predation index shows that predation pressure is the main factor determining the difference in the timing of adult birds' migration (both sexes combined) between good and poor breeding years. This finding accords with the results of Summers *et al.* (1998), Blomqvist *et al.* (2002) and Figuerola (2006). However, the study also shows that the average June temperature in the Arctic contributes to the inter-annual variation in the timing of migration and that adults migrate earlier in warmer years. The variation in migration

dates could be an effect of a delay in breeding caused by cold weather at the breeding grounds. Although waders are “income breeders” they still depend on the food available at the breeding grounds to provide the nutrients they need for egg formation (Klaassen *et al.* 2001, Morrison & Hobson 2004). Egg-laying is delayed if cold weather limits the abundance of surface arthropods when the birds arrive at their breeding areas (Meltofte *et al.* 2006) or if the ground is still covered by snow (Green *et al.* 1977, Summers & Underhill 1996). The delay would therefore also delay the post-breeding migration.

The lack of a relationship between June temperatures and breeding success does not mean that weather plays no part in waders’ breeding success. The volcanic eruption of Mount Pinatubo in the Philippines in 1991 that caused low spring temperatures in the Arctic in 1992 (Ganter & Boyd 2000) and reports of the Arctic Birds Breeding Conditions Survey show that extreme weather can cause adults to abandon their nests or lead to the death of chicks. But these events might not occur frequently enough to produce a detectable trend.

The median migration date of juvenile birds occurred 11 days earlier in good breeding years than in poor years, and this difference was related to the predation index. The explanation could be that, based on predator functional response to prey abundance (Solomon 1949 Lack 1954), in years with high predation, and thus poor breeding success, more clutches laid early in the season are depredated, but the later clutches might have a higher chance of survival. As a result juvenile migration would occur later, than in years of low predation.

The results showed that both the average temperature in June and predation pressure in the Arctic contributed significantly to the trend towards earlier migration in adult Curlew Sandpipers,

particularly the males. Waders such as Wood Sandpiper, Common Sandpiper and Dunlin show a similar trend towards earlier autumn migration in response to global warming (Adamik & Pietruszkova 2009, Anthes 2004), which has been attributed to the advancement of the breeding season (Zack & Liebezeit 2008). But the relationship between the migration timing of the Curlew Sandpiper and the June temperature might not be caused by advancing breeding seasons for two reasons. Firstly, the early migration of both adults and juveniles is a pattern that would be seen in years of early breeding (Sokolov *et al.* 1998). However, no trend was found in the timing of migration of juvenile birds, only adults had advanced their timing of migration. Secondly, studies of breeding phenology in the Arctic have reported no trends in the first arrival dates of waders in the Taimyr Peninsula or in the Yukon-Kuskokwim Delta, despite a significant spring warming trend (Meltøfte *et al.* 2007).

Thus we might consider an alternative scenario suggested by Ims and Fuglei (2005) and Kausrud *et al.* (2008) that climate change has led to fewer lemming outbreaks in the tundra. Fewer lemmings would cause predators such as the Arctic Fox *Alopex lagopus* and other predators to prey more on the eggs and chicks of waders, which would decrease their breeding productivity. The results showed six poor breeding years from 1946–1975 but from 1976–2005 the number of poor breeding years increased to 11. Other studies also inferred more evidence of the increasing predation pressure on the Curlew Sandpiper and declining breeding productivity in the species. The index of predation calculated from the abundance of lemmings in the Arctic (Blomqvist *et al.* 2002) indicates an apparent increase in predation pressure on Arctic breeding birds. The number of juvenile Curlew Sandpipers observed at non-breeding grounds in Australia (Minton *et al.* 2005, Gosbell & Clemens 2006) and South Africa (Harebottle & Underhill 2006) has also declined over the years. Based on the result which indicated that adult Curlew Sandpipers migrated earlier in

poor breeding years, it is probable that the trend towards earlier migration from 1946 to 2005 was due to poor reproductive success. However, without further research, it would be difficult to pinpoint one major cause for the poor breeding success of the Curlew Sandpiper. The reasons could be varied, from a miss-match between the timing of breeding and period of peak insect abundance (Visser *et al.* 2004, Tulp & Schekkerman 2008) to an alteration of the breeding habitat resulting from climate change (Zöckler *et al.* 2003, Meltofte 2007).

The consequences of the earlier southwards migration on the population of the Curlew Sandpiper are difficult to predict but asymmetric climate change at temperate and tropical latitudes could result in a mistiming of the migration and the peak food abundance on route or at the non-breeding grounds (Houghton *et al.* 1995, IPCC 2007). This would lead to higher mortality of migrants after they leave the breeding grounds. Combined with low breeding success, this could considerably reduce the population size. Jones and Cresswell (2010) examined the population trends of 134 species of migratory birds and showed that populations that experience a greater rate of warming at their breeding grounds than at their wintering grounds are more likely to be in decline.

In conclusion, the results suggest that the more frequent poor breeding years in 1976–2005 than during the preceding 30 years, caused by the increased predation on waders clutches due to less frequent lemming outbreaks have led to earlier southwards migration from the breeding ground by Curlew Sandpipers. The link between climate change, the decreasing abundance of lemmings and increased predation on waders' clutches needs to be tested on other species whose breeding success is also affected by predation. The potential conservational implication is that the Curlew Sandpiper and probably other Arctic-breeding migrant waders could be facing a serious decline

due to the long-term effects of climate change on their reproductive output. This could be ameliorated by the preservation and management of their stopover and wintering sites to increase the migrants' survival rates outside their breeding grounds.

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Table 1 The number, percentage and median migration dates of adult and juvenile Curlew Sandpiper ringed at Ottenby, Sweden. Predation index (PI) estimates were obtained from Blomqvist *et al.* (2002) and Underhill (1987).

Year	PI	Adults			Juveniles		
		Percent	Number ringed	Median migration date	Percent	Number ringed	Median migration date
1946	1.5	0	0		100	97	7.Sep
1947	0.5	100	11	2.Aug	0	0	
1948	3	46	11	6.Aug	54	13	31.Aug
1949	0	80	135	4.Aug	20	33	25.Aug
1950	2	68	36	3.Aug	32	17	20.Sep
1951		53	25	22.Jul	47	22	4.Sep
1952		81	29	27.Jul	19	7	31.Aug
1953		29	94	30.Jul	71	235	1.Sep
1954		40	71	22.Jul	60	107	20.Aug
1955		0	0		100	3	24.Aug
1956		30	24	31.Jul	70	55	22.Aug
1957		85	11	27.Aug	15	2	18.Aug
1958		92	23	30.Jul	8	2	19.Aug
1959		19	9	18.Jul	81	38	31.Aug
1960		9	6	25.Jul	91	59	24.Aug
1961	1.5	85	33	16.Aug	15	6	4.Sep
1962	2.5	93	37	4.Aug	8	3	6.Sep
1963	0	20	38	13.Aug	80	151	19.Aug
1964	2	24	17	23.Jul	76	53	12.Sep
1965	2	69	41	10.Aug	31	18	9.Sep

Table 1 continued

Year	PI	Adults			Juveniles		
		Percent	Number ringed	Median migration date	Percent	Number ringed	Median migration date
1966	1	33	13	12.Aug	67	26	14.Sep
1967	1	11	7	13.Aug	89	54	7.Sep
1968	3	100	1	4.Aug	0	0	
1969	0.5	3	7	19.Jul	97	257	27.Aug
1970	1	7	5	4.Aug	93	63	30.Aug
1971	2.5	95	71	25.Jul	5	4	17.Aug
1972	2	3	6	15.Aug	97	197	28.Aug
1973	0	33	5	24.Jul	67	10	4.Sep
1974	2.5	100	63	30.Jul	0%	0	
1975	1.5	38	35	26.Jul	62	56	28.Aug
1976	0.5	8	4	30.Jul	92	46	6.Sep
1977	2.5	94	58	24.Jul	6	4	10.Sep
1978	1	23	66	20.Jul	77	223	27.Aug
1979	1	19	15	24.Jul	81	63	2.Sep
1980	2.5	67	72	22.Jul	33	36	29.Aug
1981	2	56	41	24.Jul	44	32	20.Aug
1982	0	64	34	19.Aug	36	19	20.Aug
1983	3	95	58	22.Jul	5	3	17.Sep
1984	1	93	37	25.Jul	8	3	13.Sep
1985	0.5	22	8	27.Jul	78	28	30.Aug
1986	2.5	76	34	20.Jul	24	11	24.Aug
1987	2	44	21	4.Aug	56	27	7.Sep
1988	0	8	14	7.Aug	92	151	25.Aug
1989	3	97	38	22.Jul	3	1	29.Sep
1990	1	30	57	19.Jul	70	135	31.Aug

Table 1 continued

Year	PI	Adults			Juveniles		
		Percent	Number ringed	Median migration date	Percent	Number ringed	Median migration date
1991	0.5	72	33	17.Jul	28	13	25.Aug
1992	2.5	86	74	3.Aug	14	12	3.Sep
1993	1.5	90	148	26.Jul	10	17	17.Aug
1994	1	13	14	20.Jul	87	90	4.Sep
1995	2	67	18	18.Jul	33	9	3.Sep
1996		100	66	21.Jul	0	0	
1997		38	13	3.Aug	62	21	1.Sep
1998		90	73	29.Jul	10	8	25.Aug
1999		3	19	17.Aug	97	604	20.Aug
2000		100	146	19.Jul	0	0	
2001		92	12	29.Jul	8	1	10.Sep
2002		100	1	19.Jul	0	0	
2003		8	2	8.Aug	92	22	30.Aug
2004		100	175	21.Jul	0	0	
2005		77	108	11.Aug	23	32	20.Aug

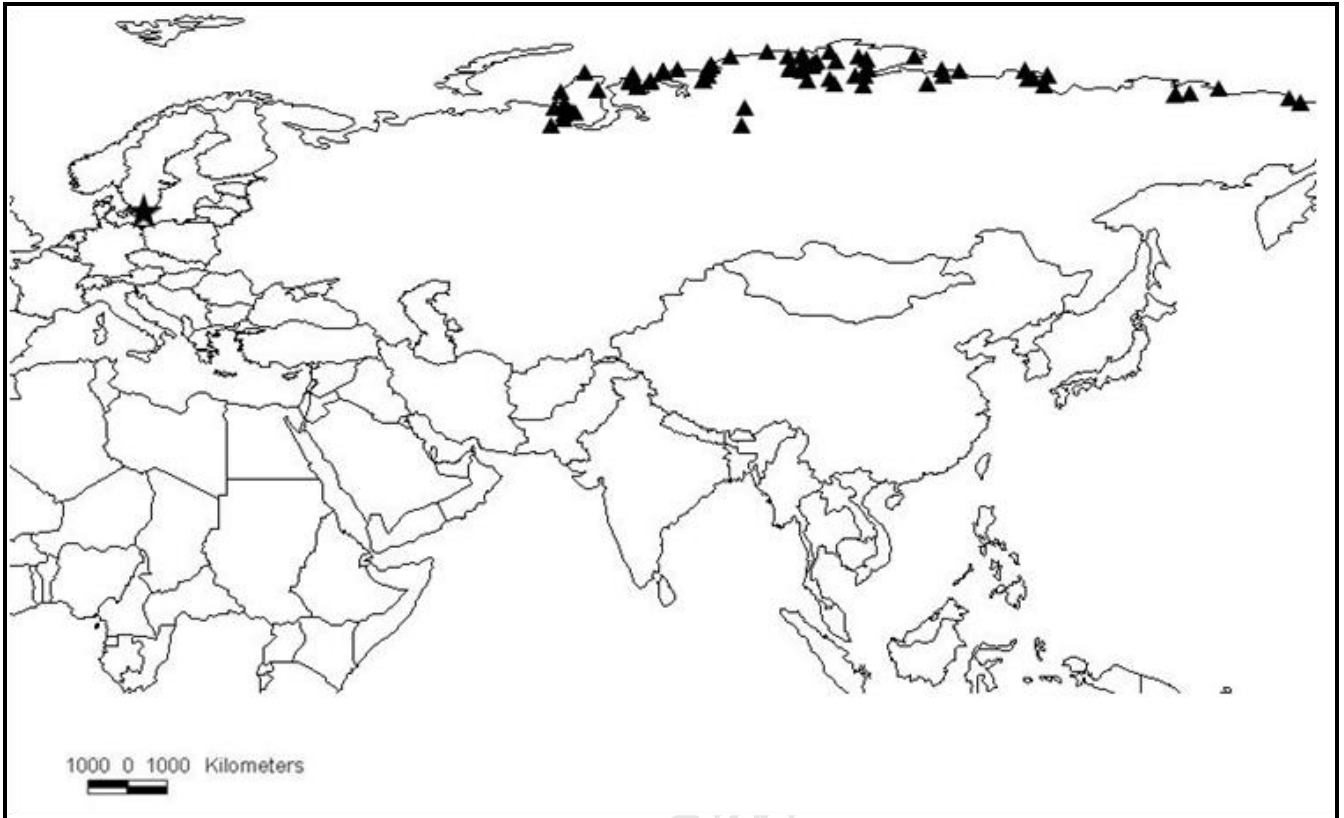


Fig. 1 Ottenby Bird Observatory, Sweden (solid black star) in relation to the breeding range (solid triangles) of the Curlew Sandpiper (breeding range adapted from Lappo & Tomkovich 2006).

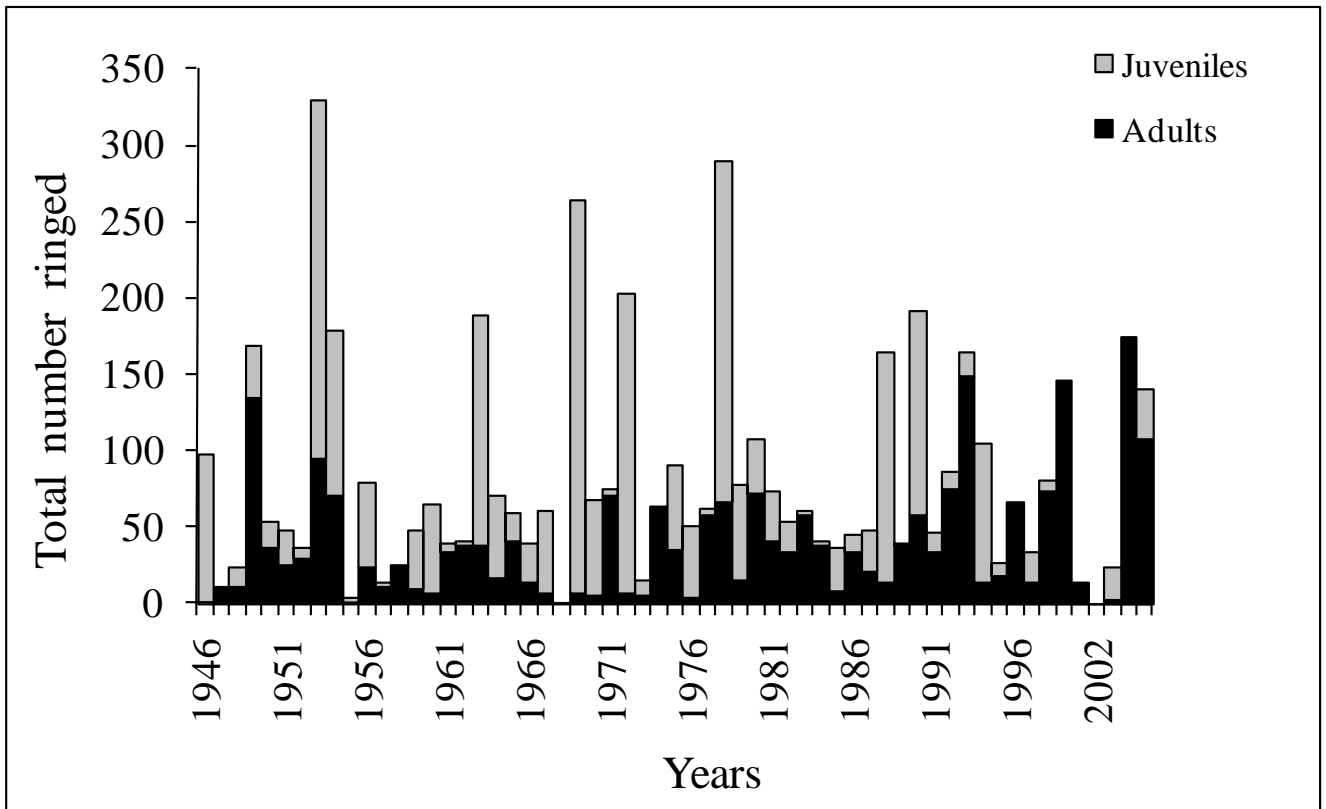


Fig. 2 Total number of Curlew Sandpipers ringed annually between 1946 and 2005 at Ottenby Bird Observatory, Sweden. Black bars represent adult birds and grey bars are the juvenile birds.

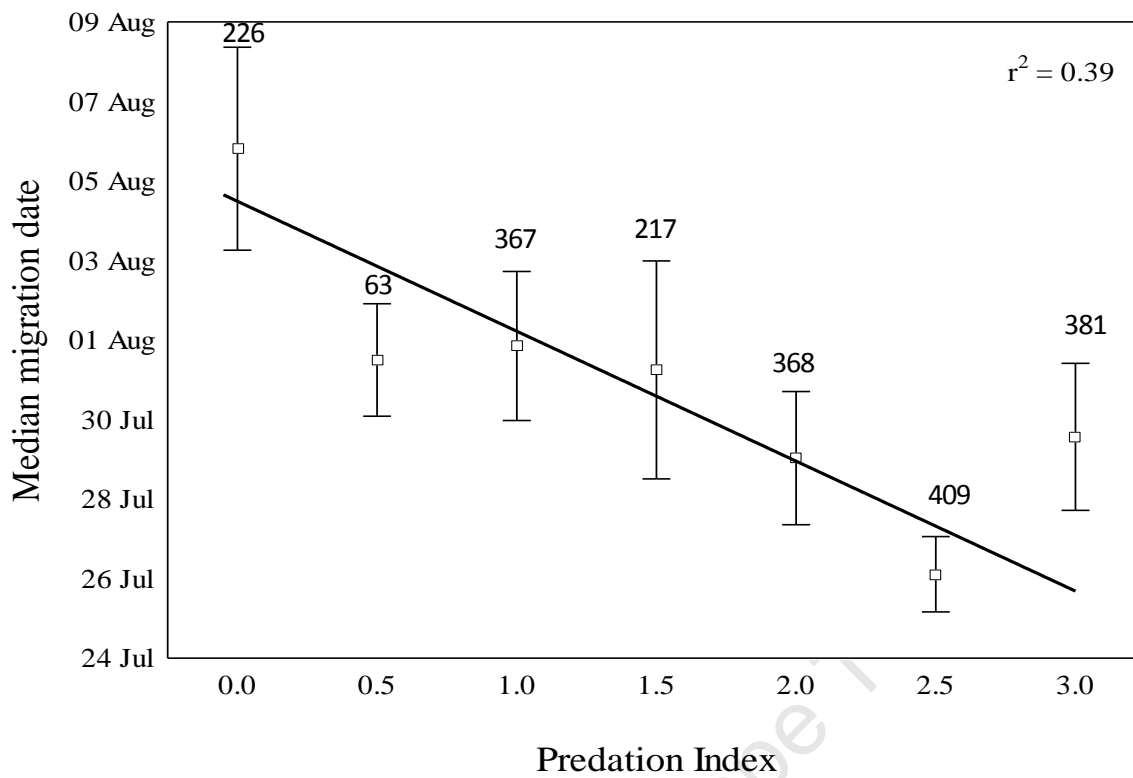


Fig. 3 Relationship between the median migration date of adult Curlew Sandpipers passing through Ottenby, Sweden and index of predation in the Arctic ($P < 0.01$, $b = -2.66$). White square is the mean migration date with given predation index, whiskers represent 95% confidence intervals, and the solid black line is the regression line. Numbers on top of error bars refer to sample size per PI

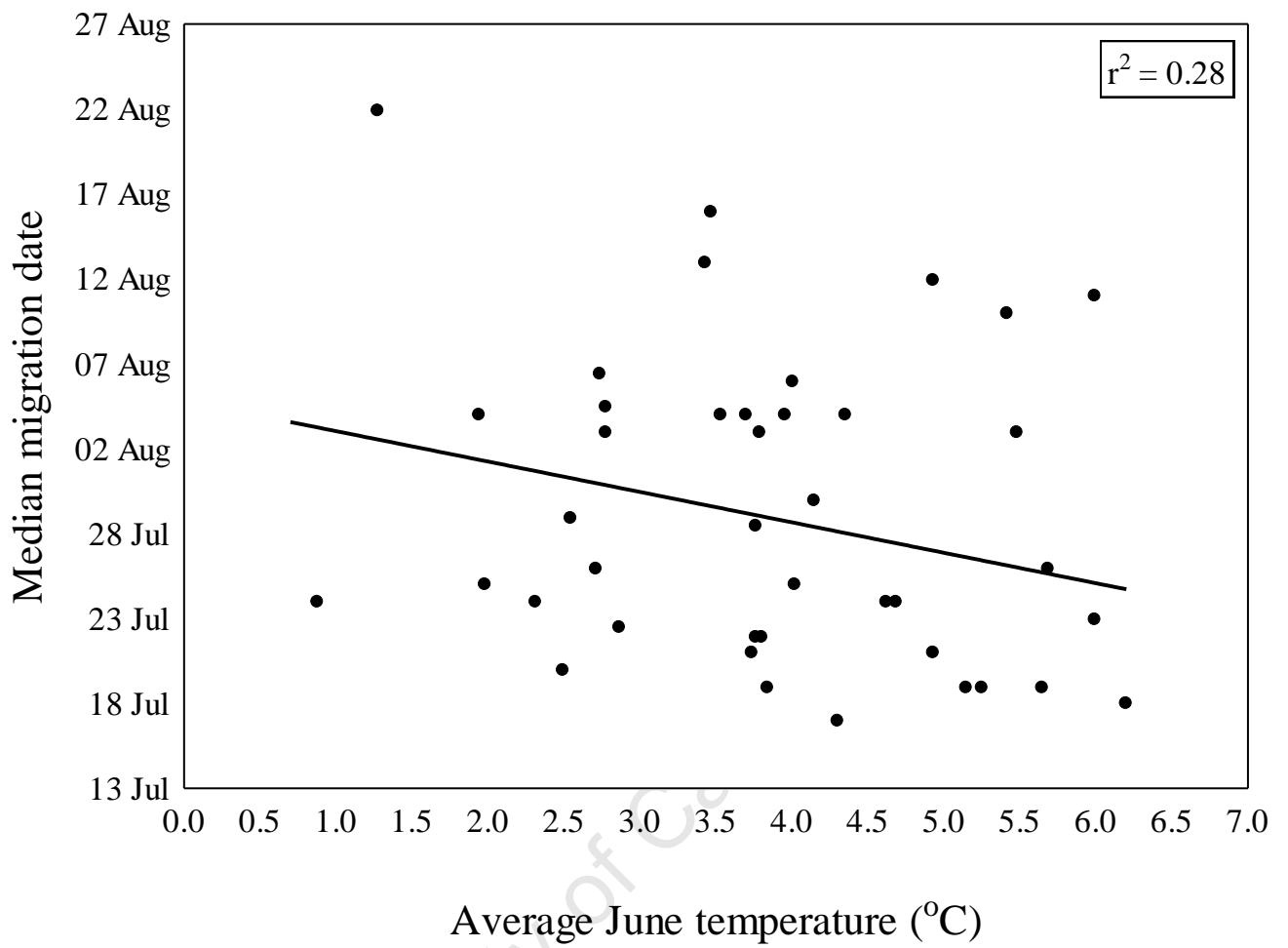


Fig. 4 The relationship between the median date of migration of adult Curlew Sandpipers through Ottenby, Sweden with the average June temperature in the Arctic ($P < 0.01$, $b = -2.76$)

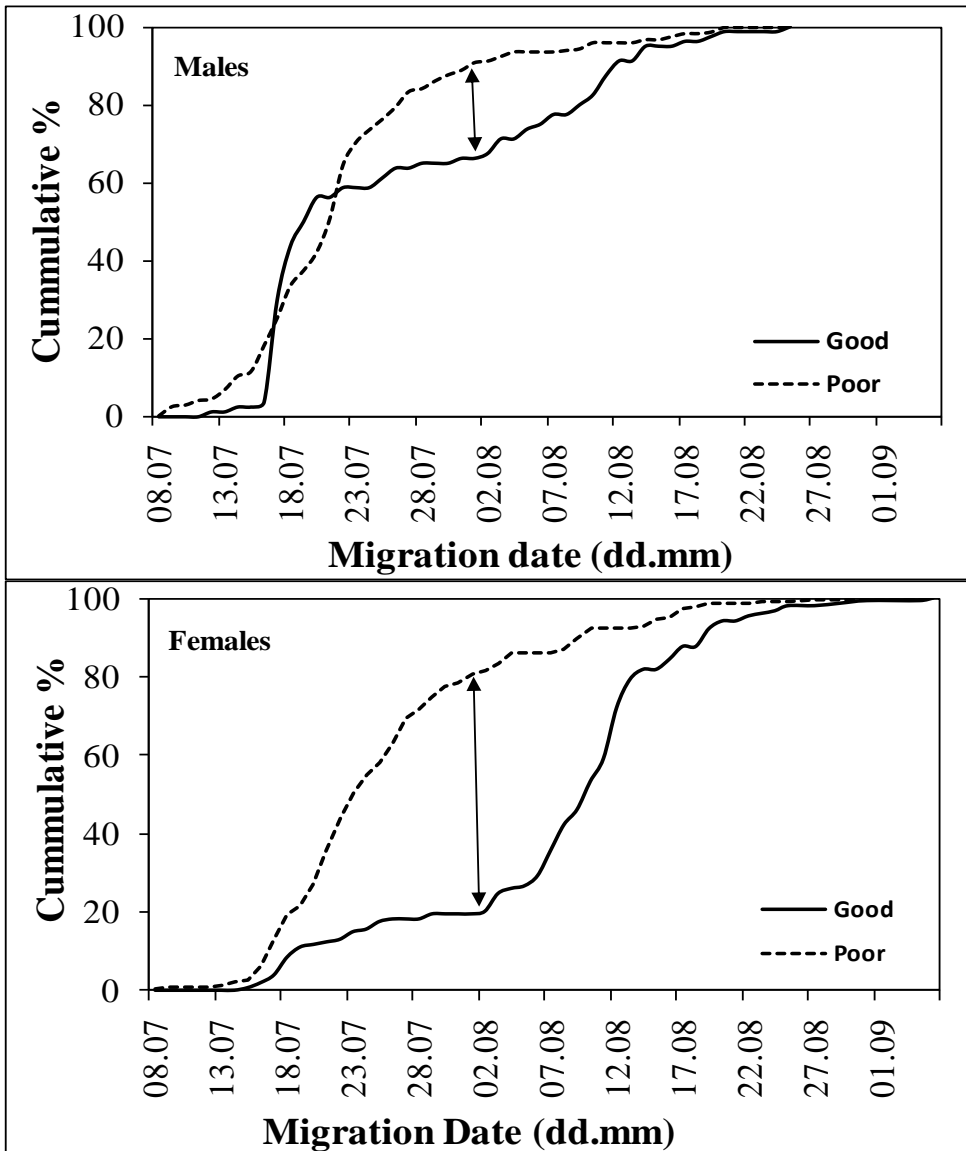


Fig. 5 The cumulative curve of the daily proportion of numbers of male (upper figure) and female (lower figure) Curlew Sandpipers passing through Ottenby, Sweden, illustrating the difference in the phenology of migration in good (—) and poor (...) breeding years. Arrow shows the date when maximum difference in the phenology occurs.

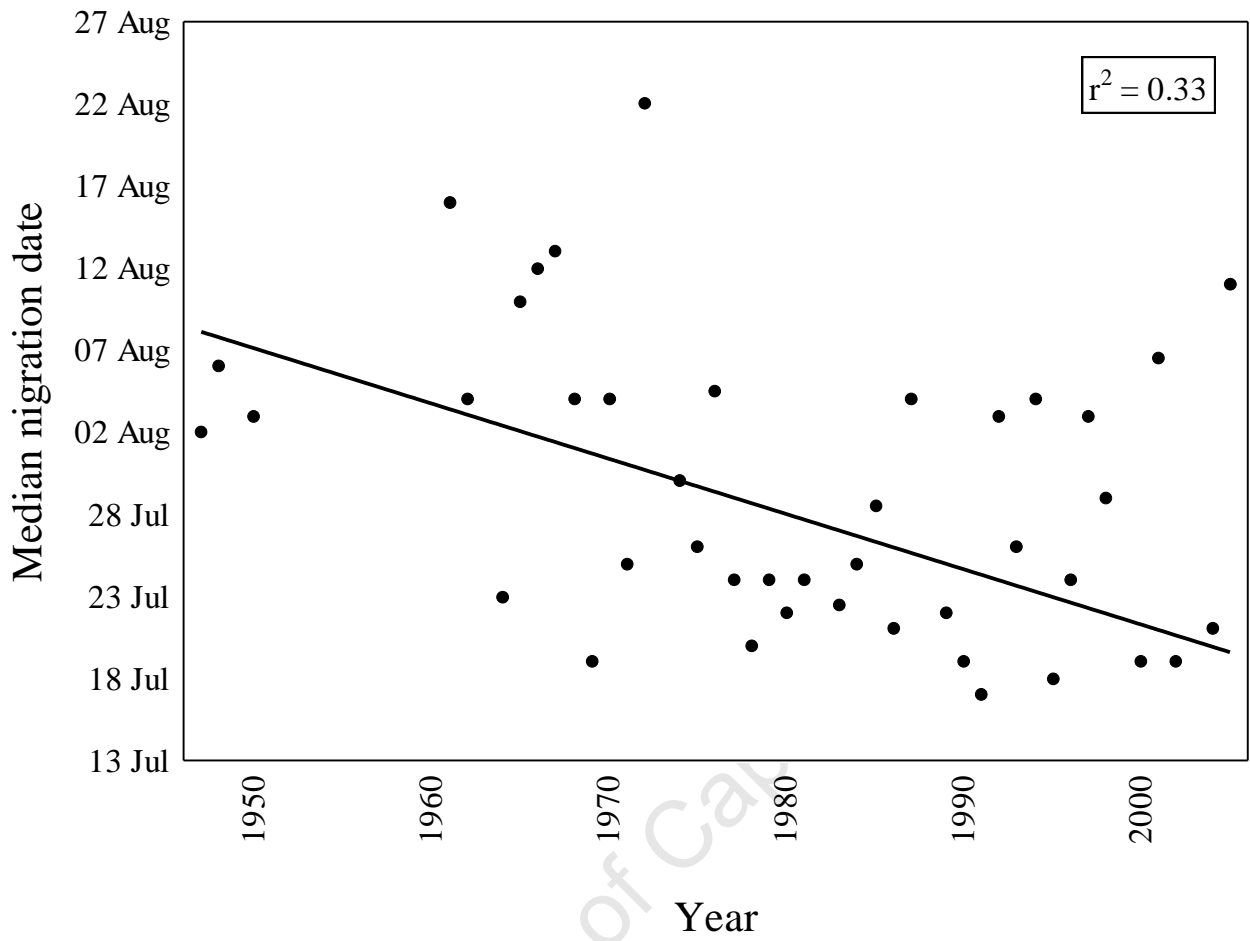


Fig. 6 Trend in the median migration dates of Curlew Sandpipers migrating through Ottenby, Sweden (1946 – 2005) on autumn migration after correction for predation index and June temperature.

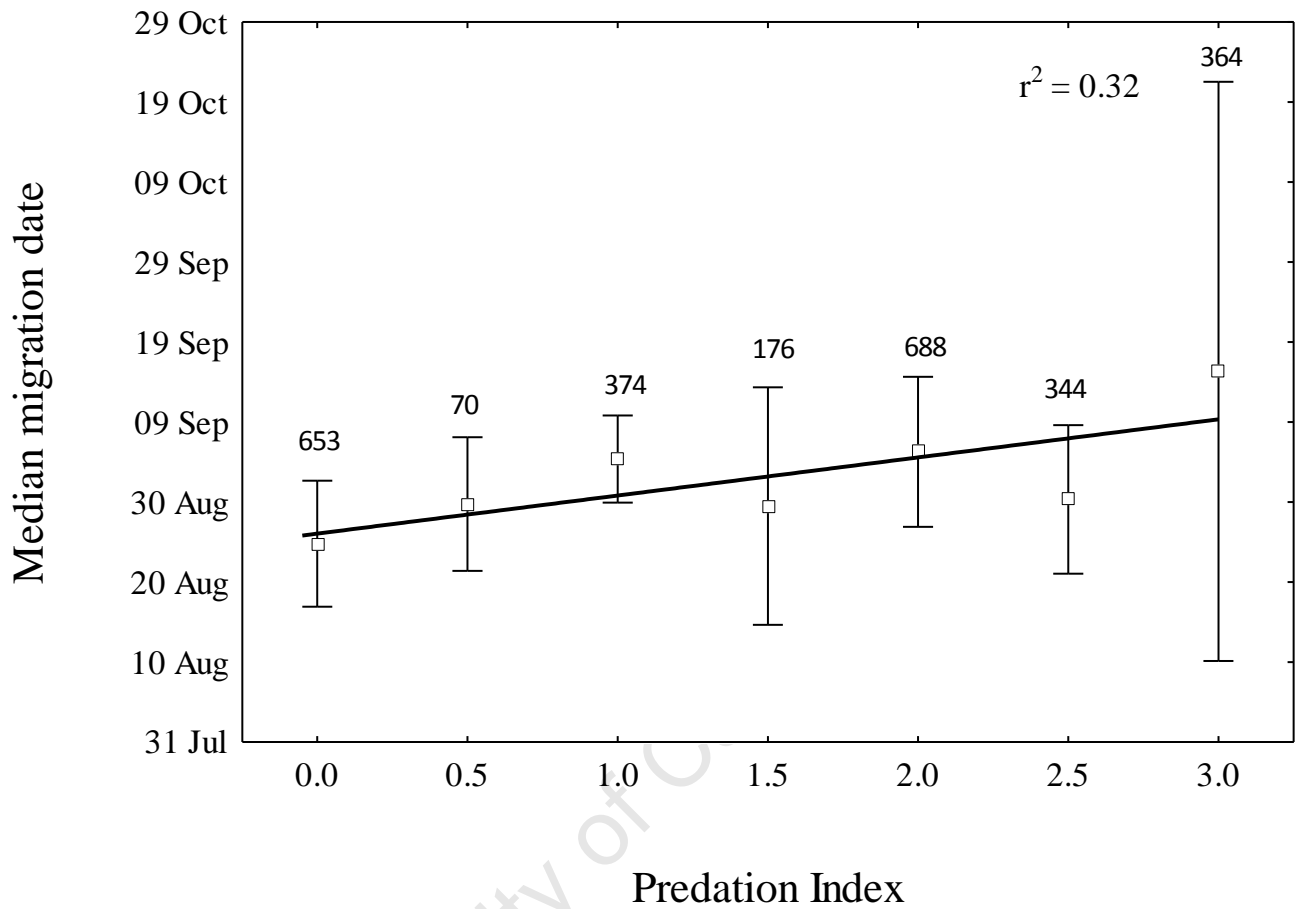


Fig. 7 Relationship between the median migration date of juvenile Curlew Sandpipers passing through Ottenby, Sweden, and index of predation in the Arctic ($P < 0.01$, $b = 4.46$). White square – mean, whiskers - 95% confidence intervals, dashed line – regression line. Numbers on top of error bars refer to sample size per PI

CHAPTER 3

**TIMING OF MIGRATION OF THE CURLEW SANDPIPER THROUGH POLAND IS RELATION TO
ARCTIC BREEDING CONDITIONS**

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TIMING OF MIGRATION OF THE CURLEW SANDPIPER THROUGH POLAND IS RELATION TO ARCTIC BREEDING CONDITIONS

ABSTRACT

Variation in the timing of autumn migration of the adult and juvenile Curlew Sandpipers *Calidris ferruginea* appears to be influenced by breeding success, which is connected to predation pressure and June and July temperature on breeding grounds. Median date of passage of adult birds was significantly later in good breeding years compared to poor breeding years. Migration date of adults was also related to the average June temperature in the arctic; the migration of adult birds was earlier by 2.3 days for every 1°C increase in average June temperature. Median migration date of juvenile birds was also correlated positively with predation index and negatively with June temperature. The median migration dates of adult birds has advanced by a factor of -0.59 days/year which translates into 10 days from 1984–2000. The results of this study illustrate that conditions on the breeding grounds could affect the schedule of subsequent life-history traits within the annual cycle. There is also circumstantial evidence that climate change might have intensified the level of predation on chicks and young of Curlew Sandpipers, increasing the frequency of poor breeding years and modifying the timing of autumn migration in the species.

INTRODUCTION

In many migratory Arctic breeding waders, autumn (post-breeding) migration begins as soon as parental responsibilities are completed (Tomkovich & Soloviev 2006). Therefore, factors which affect the onset and duration of the breeding season might influence the timing of autumn migration. Weather conditions in the Arctic prior to and during the breeding season can directly or indirectly influence the starting dates of breeding and ultimately the breeding success (Green *et al.* 1977, Schekkerman *et al.* 1998, Tomkovich & Soloviev 2001, Meissner 2005, Beal *et al.* 2006). For instance, the onset of egg-laying can be delayed when the ground is still covered by snow when birds arrive on the breeding ground (Summers & Underhill 1996, Meltofte *et al.* 2007), low temperatures can reduce the abundance of insects thereby delaying the initiation of egg-laying (Meltofte *et al.* 2006), and wind chill can interfere with mating and incubation of eggs (Tomkovich 1995).

In species such as the Curlew Sandpiper *Calidris ferruginea* and Red Knot *Calidris canutus*, the timing and intensity (i.e number of individuals passing through per day) of autumn migration is influenced by the level of predation on the eggs and chicks of these species (Blomqvist *et al.* 2002, Meissner 2005, Figuerola 2006, Tomkovich & Soloviev 2006).

Predators such as the Arctic Fox *Alopex lagopus* switch from a diet of lemmings, *Lemmus spp* and *Dicrostonyx spp*, to the eggs and young of Arctic breeding birds after a decrease in lemming abundance (Summers & Underhill 1987, Underhill 1987, Underhill *et al.* 1993, Summers *et al.* 1998) thereby ending the breeding season prematurely. Consequently, the timing of migration in these species was found to be correlated with lemming abundance

and predation pressure in the Arctic (Blomqvist *et al.* 2002, Figuerola 2006, Meissner 2006, Chapter 2).

Current knowledge of birds' migration indicates that changes in spring arrival dates for many species breeding in the northern hemisphere has advanced during the second half of the 20th century in response to warming climate trends (reviews by Gordo 2007, Rubolini *et al.* 2007). Changes in the timing of autumn migration, however, are more variable, and the observations cannot be explained simply by climatic changes. For instance, there is an advancement of autumn migration in some long-distance migrants and a delay in short-distance migrants (Jenni & Kéry 2003). Species which lay a single clutch have advanced their autumn migration while species with a double clutch system have delayed their migration (Jenni & Kéry 2003). Autumn migration dates of the Greenshank *Tringa nebularia*, Spotted Redshank *T. erythropus* and Wood Sandpiper *T. glareola* have advanced (Anthes 2004), while the timing of migration of Ruff *Philomachus pugnax* has been delayed (Adamík & Pietruszková 2008), presumably in response to climate change.

Recently, studies have considered the role which climate change plays in altering trophic level interactions, eventually leading to a change in the demography and life-history traits of the interacting organisms (Harrington *et al.* 1999, Ims & Fuglei 2005). Some studies have demonstrated that climate change has caused a decline in the regularly occurring large-scale lemming peaks (Kausrud *et al.* 2008, Hörnfeldt *et al.* 2005, P.A. Tomkovich & M.Y. Soloviev unpubl.data). These studies predict that the scarcity of lemmings will push predators such as foxes to increasingly prey on other species, including waders. The predicted consequence of

increasing predation on breeding Curlew Sandpipers is that the timing of autumn migration in this species should become earlier over the years. This predicted relationship between the timing of migration of the Curlew Sandpiper and conditions on the breeding ground is explored in this study.

Waders (shorebirds) migrating along the East Atlantic flyway often use the southern coast of the Baltic Sea, near Gdańsk, Poland, as a resting place (Gromadzka 1987) and one of the more numerous species caught here for study purposes is the Curlew Sandpiper (Meissner *et al.* 2009). This species breeds in the Arctic tundra north of 65°N in central Siberia, and migrates to the non-breeding (wintering) areas in Africa, southern Asia and Australasia. The aim of this study is to identify and quantify the effect temperature and predation on the Arctic breeding grounds have on the annual timing of migration of Curlew Sandpipers passing through Poland, and to quantify the trend in the timing of migration in the period 1983–2000 in relation to changing temperature and possibly predation.

METHODS

The data used in this study were from the ringing activities of the Polish Waterbird Research Group KULING from 1983–2000. Birds were caught on the Puck Bay coast at three sites on the inner coast of the Gulf of Gdańsk, Poland: Jastarnia (54°42'N, 18°40'E), Rewa (54°37'N, 18°39'E), and at the Reda River mouth (54°37'N, 18°47'E) (Fig. 1). At the three sites, Curlew Sandpipers were caught in walk-in traps (Meissner 1998). Birds were aged according to features described in, for instance, Prater *et al.* (1977). Wing length (maximum chord; Evans 1986), total head length (Green 1980), bill and nail length (Prater *et al.* 1977), and tarsus

length (Svensson 1992) were measured using the appropriate instruments. Measurements of total head, bill, tarsus and tarsus lengths were taken to the nearest 0.1 mm and weight was to the nearest 1 g. Ringers were checked every year with respect to comparability of measuring accuracy, according to the procedure described by Busse (1994). In addition to ringing activity,

three counts a day were conducted in Jastarnia and Rewa, while in Reda river mouth waders were counted only once a day about midday (Meissner *et al.* 2009). At Jastarnia and Rewa where three counts were conducted in a day only the count with maximum number of birds were taken into account (Meissner 2006, Meissner *et al.* 2009).

Statistica 9[®] for windows (Stasoft 2010) was used for data analyses. To correct for differences in sample size at the three different sites, the number of birds counted per day was converted into a proportion of the total number of birds recorded that year. Annual median migration dates were computed separately for adult and juveniles, and for adult males and females. This was done for each site separately. From the ringing data, adult birds were separated into sex classes using the discriminant function equation developed by Wymenga *et al.* (1990): The discriminant score (D) was computed from wing length (W mm) and Bill length (B mm) as $D = 0.07815 * W + 0.47962 * B - 28.7302$; for males $D < 0$ and for females, $D > 0 =$ females. Results of Meissner (2006) indicated that the proportion of birds in the count data is comparable to that in the ringing data, therefore it is likely that pattern of the migration of males and females from ringing data reflects the overall pattern of migration. Because the timing of fieldwork differed between years a standardized period

during which ringing and count activities were operated at all sites was determined (Busse & Kania 1970). This was fixed as 19 July–27 September every year.

General linear models were used to compare migration dates in good and poor breeding years, examine the effects which temperature and predation on the Arctic breeding grounds have on the timing of migration of adults and juveniles, and on adult males and females. The median migration date of each year was the dependent variable, sex and breeding success as fixed factors, and the average temperature in June and July, and the predation index included in the model as covariates. Proportion of juvenile birds in the total annual catch was used as a measure of breeding success (Schekkerman *et al.* 1998, Boyd & Piersma 2001, Meltofte 2001, Minton *et al.* 2005, Beal *et al.* 2006). Because breeding success in the Curlew Sandpiper usually exhibits a “boom-or-bust” pattern (Summers *et al.* 1998), years when the proportion of juveniles was more than 0.20 were classified as good breeding years and years when juveniles were 0.13 or less were classified as poor breeding years (Summers & Underhill 1987, Schekkerman *et al.* 1998).

Data on the average temperature in June and July were used as a proxy for weather condition in the Arctic during the breeding period (Tomkovich & Soloviev 2006).

Temperature data for the Arctic were obtained from the National Oceanic and Atmospheric Administration (NOAA). The index of predation pressure was obtained from Blomqvist *et al.* (2002). Their index of predation represents their assessment of the likelihood that wader nests and chicks will be depredated based on the abundance of lemmings; the index goes from 0 (low predation pressure) to 3 (high predation pressure).

RESULTS

The number of birds recorded at each site differed but the overall phenology of migration (proportion of birds caught per day) were similar (Kolmogorov-Smirnov test: $D = 1.10$, $P = 0.58$). Therefore, for the analysis on phenology of migration, data from all three sites were combined. Combining the data from the three sites, 15,344 birds (6,938 adults and 8,406 juveniles) were counted between 1984 and 2000. Additionally, 1,077 adults and 1,054 juveniles were caught and measured from 1983–2000. The annual numbers of adult birds counted varied between 109 in 1991 to 709 in 1984, and juveniles from 39 in 1989 to 1,743 in 1985 (Table 1). Controlling for observation differences at the three sites, there was no significant trend in the number of adults observed on migration from the period 1983–2000 ($r = -0.058$, $P = 0.131$, $df = 701$), but there was a significant decline in the number of juveniles observed ($r = -0.614$, $P < 0.001$, $df = 520$).

Autumn migration of adults

The median migration date of adult Curlew Sandpipers in good breeding years was 4 August, eight days later than the median migration date in poor breeding years on 27 July ($F_{1, 632} = 6.80$, $P = 0.026$). Birds migrated about 2.6 days earlier for every unit increase in the index of predation ($F_{1, 632} = 7.62$, $P = 0.010$, $b = -2.57$). Also, birds migrated 2.3 days earlier for every 1°C raise in average June temperature ($F_{1, 632} = 10.32$, $P = 0.014$, $b = -2.32$). There was no significant effect of the average temperature in July on the timing of migration of adult birds ($F_{1, 632} = 0.30$, $P = 0.594$, $b = -1.10$). The interaction of breeding success and the predation index was significant ($F_{1, 632} = 5.91$, $P = 0.035$, $b = -6.29$), indicating that as predation

pressure increased, the difference between the timing of migration in good and poor breeding years became further pronounced.

Autumn migration of juveniles

The median migration date of juveniles in good breeding years was 29 August, seven days earlier than the median migration date in poor breeding years on 5 September. The difference in the timing of migration between good and poor breeding years was not statistically significant ($F_{1, 523} = 0.41, P = 0.525$). The median migration dates of juveniles was affected significantly by the average Arctic temperature in June ($F_{1, 523} = 12.99, P = 0.003, b = -2.85$) and the index of predation pressure ($F_{1, 523} = 4.29, P = 0.038, b = 1.91$) but not by July temperature ($F_{1, 523} = 1.89, P = 0.168, b = -0.48$).

Migration of the sex in relation to breeding success

The overall median migration date of males was 23 July, significantly earlier than the median migration date of females on 4 August ($F_{1, 998} = 8.81, P = 0.003, b = -7.94$). The median migration date of males in good breeding years was 28 July and in poor breeding years it was 23 July ($F_{1, 607} = 1.48, P = 0.264$; Fig. 2). Median migration date of females in good breeding years was 6 August, significantly later ($F_{1, 468} = 7.10, P = 0.013$; Fig. 2) than the median migration in poor breeding years on 23 July (Fig. 3).

The migration dates of males were significantly affected by the average June temperature ($F_{1, 607} = 3.85, P = 0.0041, b = -1.01$) but not affected by either the average July temperature ($F_{1, 607} = 0.31, P = 0.586, b = -0.91$), or the index of predation pressure ($F_{1, 607} = 0.78, P = 0.784, b = 0.54$). The migration dates of females were significantly related to the index of

predation pressure ($F_{1,468} = 5.341$, $P = 0.021$, $b = -2.65$) and July temperature ($F_{1,468} = 19.08$, $P < 0.001$, $b = 1.69$) but not with the average Arctic temperature in June ($F_{1,468} = 0.19$, $P = 0.672$, $b = 0.79$).

Trend in migration dates

Controlling for the annual variability in predation pressure and average June temperature in the Arctic, there was a significant negative trend in the median migration dates of adults ($F_{16,686} = 7.68$, $P = 0.001$, $b = -0.59$; Fig. 3) from 1984–2000. Both predation index ($F_{1,678} = 4.77$, $P = 0.005$, $b = -1.16$) and the average June temperature ($F_{1,678} = 14.64$, $P = 0.002$, $b = 1.25$) were significant predictors of this trend, but not July temperature ($F_{1,678} = 2.02$, $P = 0.184$, $b = -0.99$). There was also a significant interaction between predation index and the average June temperature ($F_{1,674} = 6.13$, $P = 0.02$, $b = -2.98$).

There was no significant trend in the median migration dates of males ($F_{1,606} = 2.72$, $P = 0.099$, $b = -0.145$) but there was a significant negative trend in the median migration dates of females ($F_{1,468} = 8.461$, $P = 0.003$, $b = -0.28$) from 1983–2000. There was no significant trend in the median migration dates of juvenile birds over the period 1983–2000 ($F_{1,332} = 0.38$, $P = 0.53$, $b = -0.07$).

DISCUSSION

The relationship between the timing of migration of adult birds with predation and temperature in the Arctic is consistent with the observations of Figuerola (2006), Meissner (2005, 2006) and Soloviev & Tomkovich (2006). Generally, adult Curlew Sandpipers migrated

earlier in years when predation was higher (thus low breeding success) and June temperatures were colder than in years otherwise. The significant interaction of breeding success and predation index indicates that only in years of high predation pressure was there a noticeable difference in the timing of migration of adults between good and poor breeding years. This means that breeding success is not always determined by predation on the eggs and chicks of the Curlew Sandpiper. Heavy snow storms, floods and other extreme weather conditions can result in heavy mortality of chicks (Arctic Birds Breeding Conditions Survey 1984–2008). However, only poor breeding success resulting from high predation pressure had any significant impact on the timing of migration of adult birds.

Juvenile birds migrated later in years of high predation compared to years when predation was low. These late migrating juveniles might be late broods from re-nesting attempts. Observations in the tundra suggest that in high predation years, when nests in the southern parts of the breeding grounds were depredated, some birds moved northward where the late snowmelt allowed them to set up new territories (Tomkovich & Soloviev 2006). A similar situation was found in Sanderling *Calidris alba* on the High Arctic northern Taimyr. A third of the population may attempt to produce second clutches (under the double clutch breeding system) if breeding starts early, but in late breeding seasons or in years when clutches are predated upon late in the season, virtually no second clutches were laid (Tomkovich & Soloviev 2001).

The timing of migration of adult females occurred about 12 days later than males. This interval is less than the estimated 20 days incubation period (Schekkerman *et al.* 1998) so it

is possible that some males remain behind to offer protection to the females during the incubation period as reported by Lappo and Tomkovich (2006). However, when breeding failed females did migrate at an earlier date (Figuerola 2006) compared to successful breeding years. A similar pattern has been described in other waders such as Wilson's Phalarope *Phalaropus tricolor* (Jehl 1987) and Wood Sandpiper *Tringa glareola* (Remisiewicz & Wennerberg 2006) in all of which males migrate earlier than females.

The migration of males and females is affected differently by different factors on the breeding ground. The temperature in June was the main factor determining the timing of migration of males whereas in females it was predation pressure and the average temperature in July (Chapter 2). Males are not involved in parental care, so the timing of their migration would be determined by how early or late breeding starts. Warm weather in June decreases snow cover and increases food availability (Summers & Underhill 1996, Meltofte *et al.* 2006), facilitating early egg-laying and, therefore, early departure of the males from the breeding grounds. On the other hand, the migration of females will depend mostly on the success of the breeding attempt and by the time taken for the young to be independent. July temperature affects the rate of chick development and predation affects breeding success (Underhill *et al.* 1989, Schekkerman *et al.* 1998, Soloviev *et al.* 2006). Therefore these two factors affect the timing of migration of the females.

The overall timing of migration of adult birds had become earlier over the years by a factor of -0.59 days/year. This translates into an average advancement of the median migration date by 10 days from 1983–2000. This trend has also been observed in the adult Curlew

Sandpipers migration through Sweden (Chapter 2). Advancement in the timing of autumn migration is sometimes due to the advancement in breeding season (Zack & Liebezeit 2008, Sokolov *et al.* 1998). However, the non-directional trend in median migration dates of juveniles suggests that the start of breeding in this species and the duration of juveniles' development have remained unchanged. The second possibility is that the breeding season of the Curlew Sandpiper is being cut short due to increasing frequency of failed breeding attempts, causing the adults to leave the breeding grounds earlier than usual. The results of this study and other studies support the possibility of increasing predation on the eggs and young of the Curlew Sandpiper. Firstly, there was a significant negative trend in the number of juveniles observed on migration in Poland. Secondly, the results show that both predation pressure and the temperature in June were significant factors determining the trend in the median migration dates of adult birds. The significant interaction between predation pressure and June temperature also suggests that increasing temperature may have amplified the effect of predation on the trend of migration. Thirdly, studies by Kausrud *et al.* (2008) showed that the warming trends in the climate may have disrupted the lemming cycles, resulting in fewer lemming outbreaks in the tundra. In accordance with the lemming-bird hypothesis (Roselaar 1979, Summers 1986, Summers & Underhill 1987), this decline in lemming abundance will result in predators which usually feed on lemmings to increasingly prey on the eggs and young of shorebirds. The result would be an earlier departure of adult birds from the breeding grounds.

The main conclusion of this study is that climate change may have intensified the predator-prey interaction between Arctic breeding shorebirds and their predators and the

advancement of migration date of adult Curlew Sandpipers may be as a result of increased predation on eggs and chicks, causing birds to leave the breeding grounds earlier than in the past. For migratory species, it is important that the timing of migration coincide with periods of food availability on the migration route and non-breeding grounds. The change in the timing of migration could lead to a miss-timing between the timing of migration and periods of food abundance resulting in lowered survival of individuals. This study also adds support to the idea that the timing of migration can be used to infer conditions on the breeding ground, at least in migratory Arctic breeding birds.

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Table 1 Annual total counts and median migration dates of adult and juvenile Curlew Sandpipers passing through Poland (1984–2000)

Year	Adults		Juveniles		Median migration dates	
	N	%	N	%	Adults	Juveniles
1984	709	62.7	421	37.3	11 Aug	04 Sep
1985	637	26.8	1743	73.2	07 Aug	07 Sep
1986	460	42.2	629	57.8	11 Aug	05 Sep
1987	710	89.2	86	10.8	05 Aug	28 Aug
1988	710	89.2	86	10.8	05 Aug	28 Aug
1989	180	82.2	39	17.8	04 Aug	03 Sep
1990	514	67.7	245	32.3	30 Jul	29 Aug
1991	109	49.3	112	50.7	29 Jul	02 Sep
1992	170	72.6	64	27.4	29 Jul	11 Sep
1993	546	55.3	442	44.7	06 Aug	30 Aug
1994	260	69.7	113	30.3	24 Jul	28 Aug
1995	524	87.2	77	12.8	26 Jul	21 Aug
1996	533	60.2	352	39.8	05 Aug	09 Sep
1997	405	37.7	670	62.3	30 Jul	30 Aug
1998	689	73.1	253	26.9	02 Aug	05 Sep
1999	400	37.8	658	62.2	01 Aug	06 Sep
2000	321	71.8	126	28.2	31 Jul	06 Sep

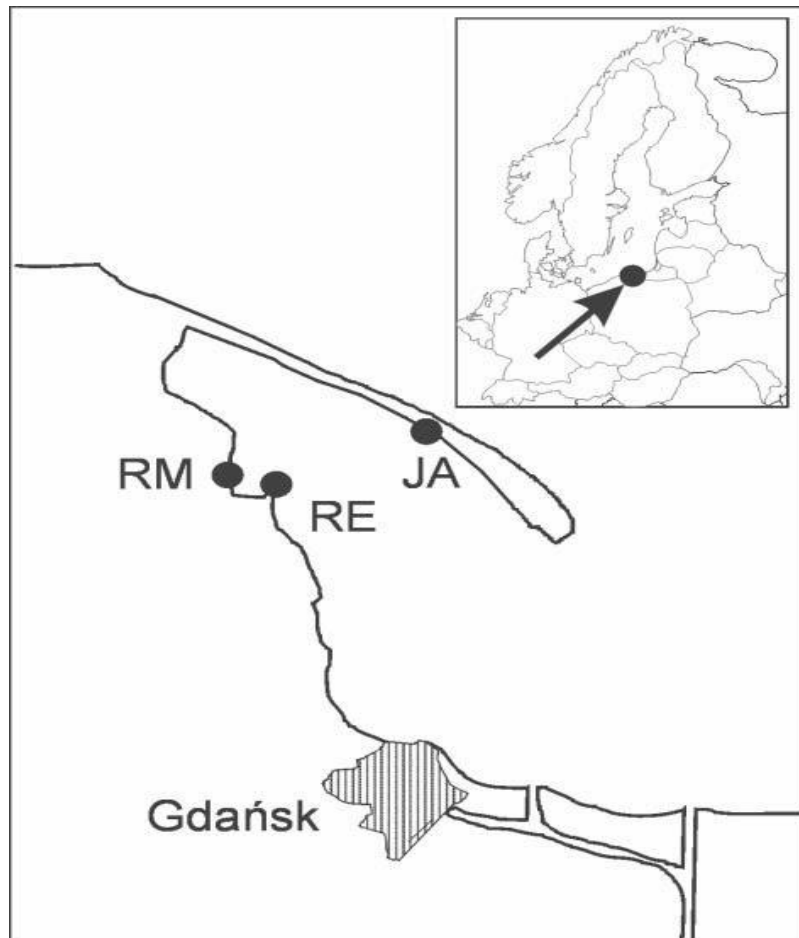


Fig. 1 Study area on the Baltic Sea coast of northern Poland. RM: Reda mouth; JA: Jastarnia; RE: Rewa. Adapted from Meissner (2006)

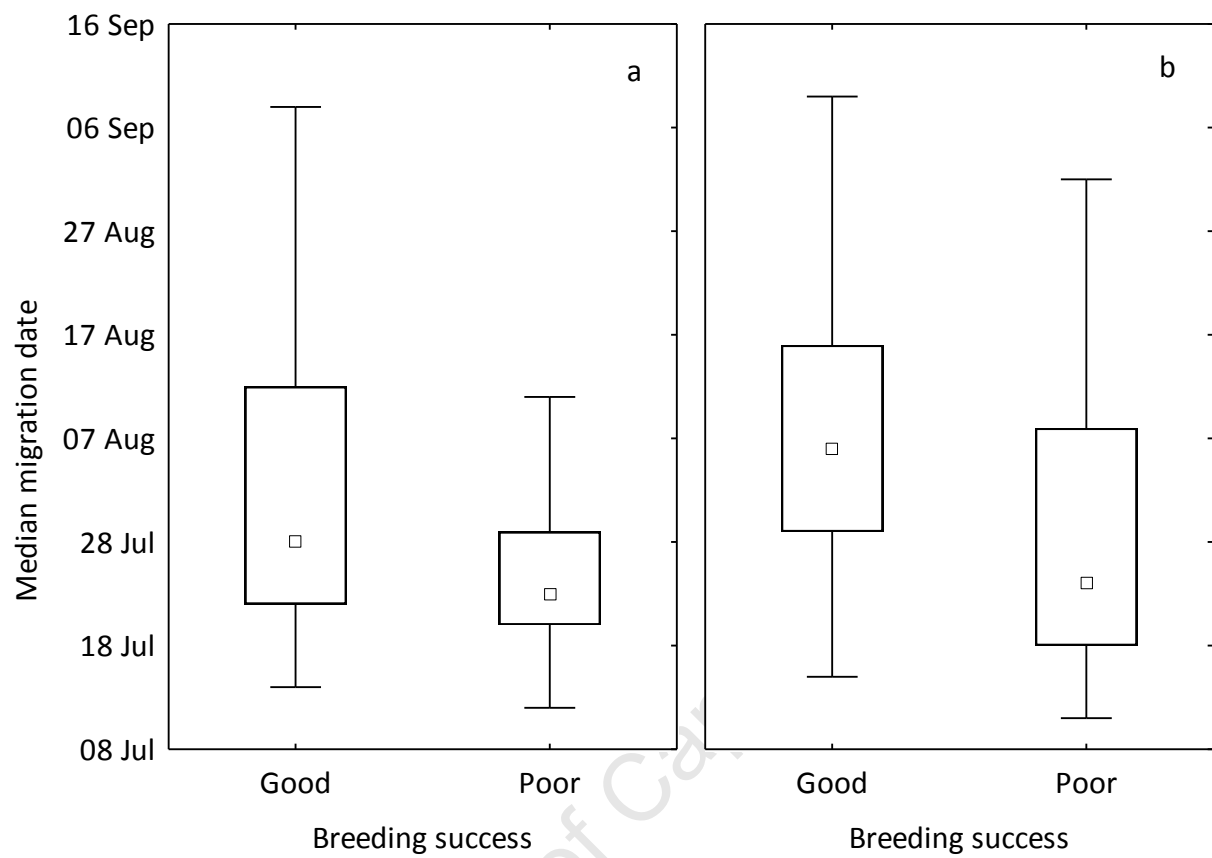


Fig. 2 Median migration dates of the passage of adult male (a) and female (b) Curlew Sandpipers in good and poor breeding years through northern Poland. Estimates are from ringed birds (1984–2000)

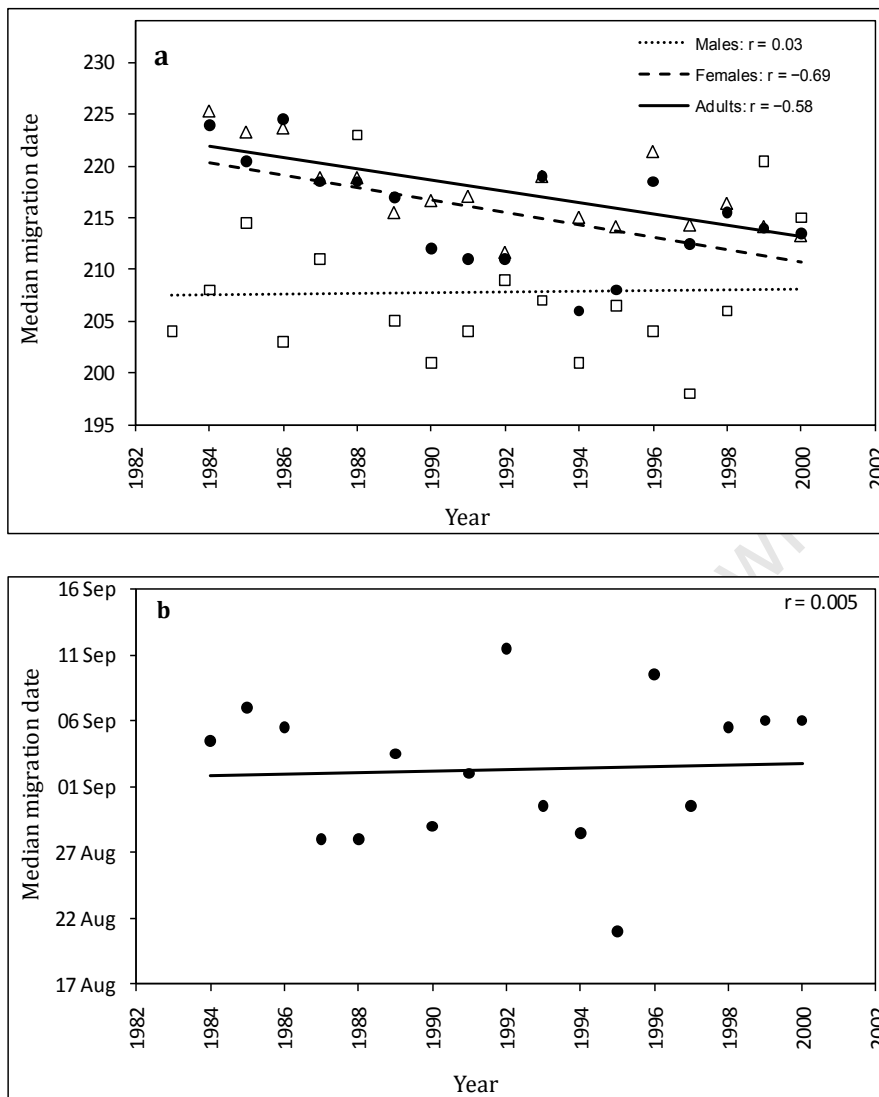


Fig. 3 Trend in the median migration dates of adult (a) and juvenile (a) Curlew Sandpipers passing through northern Poland (1983–2000). In (a) solid black circles=adults, open triangles=females, open squares=males

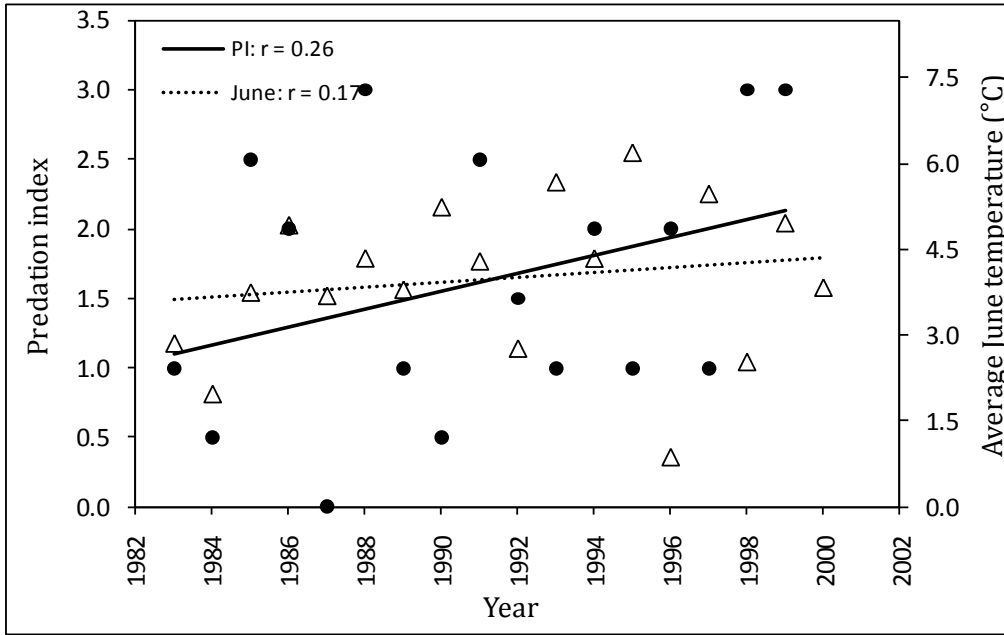


Fig. 4 Trend in predation index (PI) and average June temperature (June) in the Taimyr Peninsula in the Siberian Arctic (1983–2000). Predation index taken from Blomqvist *et al.* (2002), data on June temperature in the Arctic from the National Oceanic and Atmospheric Administration (NOAA)

CHAPTER 4

**FLEXIBILITY IN MOULT STRATEGY OF THE CURLEW SANDPIPER ON THE NON-
BREEDING AREAS IN RELATION TO DISTANCE TO BREEDING AREAS - A
COMPARISON OF THREE POPULATIONS WINTERING IN THE SOUTHERN
HEMISPHERE**

FLEXIBILITY IN MOULT STRATEGY OF THE CURLEW SANDPIPER ON THE NON-BREEDING AREAS IN RELATION TO DISTANCE TO BREEDING AREAS – A COMPARISON OF THREE POPULATIONS WINTERING IN THE SOUTHERN HEMISPHERE

ABSTRACT

This study examines the differences in moult strategies of adult Curlew Sandpipers, *Calidris ferruginea*, on their non-breeding areas in South Africa, north-western Australia and south-eastern Australia. The estimates of population moult parameters (start date and duration of moult) as well as the pattern of moult of individual primary feathers are described in relation to the distance between moulting and breeding areas. The onset of moult was earliest at the northernmost area in north-western Australia (18 September), then South Africa (4 October) and latest in south-eastern Australia (15 October). The duration of moult was 129 days in South Africa, 129 days in north-western Australia and 121 days in south-eastern Australia. Based on the number of primaries growing simultaneously, the pattern of moult in the three areas was similar. The rate of feather growth, expressed as the average proportion of feather mass growth, was highest in south-eastern Australia at 0.82%/day, then South Africa at 0.78%/day, and lowest in north-western Australia at 0.77%/day. The later and slightly more condensed moult of Curlew Sandpipers in south-eastern Australia may have been a result of later arrival on the non-breeding and the need for earlier spring departure to the breeding area. The moult strategy of Curlew Sandpipers in Australia and South Africa is compared with that of other wader species from comparable studies.

INTRODUCTION

Moult is one of the indispensable aspects of the annual cycle of birds and the maintenance of feathers in an “airworthy” condition is critical to their flight performance (Barrowclough & Sibley 1980). The timing and duration of moult varies between geographical locations (Holmes 1971, Prater 1981, Serra 2000, Underhill 2003, Summers *et al.* 2010) and it has been suggested that this is related to the migration distance of the wintering areas from the breeding areas and to the seasonality of food supply (Prater 1981, Underhill 2003). For instance, the population of the sub-species of Red Knot *C. canutus islandica* in northern Europe starts the moult of flight feathers on average 77 days earlier than the subspecies *C. canutus canutus* in southern Africa (Summers *et al.* 2010). The average duration of moult of the *islandica* sub-species is 18 days shorter than the *canutus* subspecies, a difference which has been linked to the need for the northern sub-species to complete moult before winter when food supply becomes limited (Summers *et al.* 2010). Limited food supply during the winter months increases conflict between energy allocated to moulting and to survival and thermoregulation (Barta *et al.* 2008).

Also, moult studies of Curlew Sandpiper *Calidris ferruginea* in Africa indicate that moult starts about a month earlier in Mauritania and three weeks earlier in Kenya compared to southern Africa (Pearson 1974, Elliott *et al.* 1976, Pienkowski *et al.* 1976) which indicates there may be differences in moult of different populations in relation to the distance between moulting and breeding area.

It has been difficult to discuss the differences in moult strategies between species and populations especially in relation to their different moulting areas and latitudes because of unstandardized methods used in estimating moult parameters (Prater 1981, Summers *et al.* 1983, Underhill & Zucchini 1988). However, in the studies of moult in shorebirds, an emerging pattern is that populations which winter and moult their flight feathers at tropical or southern temperate latitudes tend to start moult later and take much longer than those which moult in north temperate wintering areas (Serra 2000, Holmgren *et al.* 2001, Underhill 2003, Summers *et al.* 2004, Summers *et al.* 2010).

To better separate the effects of seasonality of food supply vs. migratory distance on moult strategies, we studied the moult pattern of the Curlew Sandpiper wintering in South Africa and Australia. The Curlew Sandpiper is a long-distance migratory wader (shorebird) which breeds in the high Arctic tundra between 71°40' E on eastern Yamal Peninsula to 156°40'W near Barrow, Alaska (Holmes & Pitelka 1964, Lappo & Tomkovich 2006). The species winters in the southern hemisphere which spans from Africa to New Zealand (Cramp & Simmons 1983). The birds reach their wintering grounds between August and November or December (Thomas 1970, Thomas & Dartnall 1971, Pringle & Cooper 1975, Elliot *et al.* 1976), where moult is then carried out (Thomas & Dartnall 1971, Elliot *et al.* 1976, Dean 1977, Cramp & Simmons 1983).

The aim of this study is to describe the moult of the Curlew Sandpiper at the southernmost limits of its non-breeding areas in South Africa and Australia using the moult models of Underhill & Zucchini (1988). The pattern and rate of growth of the individual primaries is

examined and compared between these regions with the purpose of finding out if the assumption of uniform primary growth is met. Results will be discussed in relation to the annual cycle and ecology of the species.

METHODS

The data used for this study were from Curlew Sandpipers caught in South Africa (SA) by the Western Cape Wader Study Group at Langebaan Lagoon (33°5'S, 18°2'E) and Rietvlei (32°37'S, 18°31'E), in north-western Australia (NWA) by the Australasian wader study group on the shores of Roebuck Bay and Eighty Mile Beach in Broome (18°7'S, 122°16'E), and in Victoria (38°–39°N, 144°–147°E) by the Victorian Wader Study Group in south-eastern Australia (SEA) (Fig. 1). Birds were aged based on wing condition (Prater *et al.* 1979, Rogers *et al.* 1990, Higgins & Davies 1996) and can be allocated to one of three age categories: birds in their first year of life (juveniles), birds known to be in their second year, and birds past their second year or older, defined to be adults. In this study, we consider only the moult of adult birds.

Moult estimation

Primaries were numbered P1 for the innermost primary to P10 for the outermost feather. Primary moult scores were recorded using the British Trust for Ornithology technique (Ginn & Melville 1983); old feathers were scored 0, new feathers 5, and growing feathers 1-5 depending on their stage of growth. Primary moult scores were transformed into moult indices following the relationship given by Underhill & Zucchini (1988); moult score 0 = 0, 1 =

0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875, and 5 = 1. All moult estimates were obtained using the software described in Brandão (1998), and Underhill *et al.* (2006).

The parameters of moult (start date, duration and standard duration) were estimated based on PFMG of the tract of 10 primary feathers combined, and from the growth of individual primary feathers. Moulting indices of the tract of 10 primary feathers were converted into Proportion Feather Mass Grown (PFMG) using the relative masses of primary feathers (Underhill & Joubert 1995; Table 1); a process demonstrated by Summers (1980) and Underhill and Summers (1993) to produce a moult index that increases approximately linearly with time. This approach was applied to estimate the parameters of moult for the entire population for all years combined. The data were assumed to be Type 2 of Underhill & Zucchini (1988) which uses observation of birds that have not yet started moult, birds in moult, and those that have completed moult.

The null hypothesis that the duration of primary moult is similar at all three sites was tested using the likelihood ratio test (Burnham & Anderson 1998). The Log likelihood of the models which assumed varying duration of moult was compared with the Log likelihood when data from all three sites were pooled, allowing for different start dates but common duration of moult, a method demonstrated in Remisiewicz *et al.* (2009).

The start date, duration and standard deviation of moult of each primary feather was estimated using the moult indices, an approach described in Underhill (2003), Serra and Underhill (2006) and Remisiewicz *et al.* (2009). This allowed for the estimate of the feather

material grown per day for each primary. To do this, the relative mass of each primary feather (Underhill & Joubert 1995) was divided by its corresponding duration of growth. This was summed for all feathers growing simultaneously on any given day and thus the daily rate of feather material production was modelled, a method described by Remisiewicz *et al.* (2009). Results are presented as the cumulative feather material produced on a given day. The size of the gap in the wing during moult was also estimated calculating Proportion of Feather Mass Missing (PFMM) for each individual (Remisiewicz *et al.* 2009, 2010, Ward *et al.* in press). This is an extension of the raggedness score (Haukioja 1971, Bensch & Grahn 1993) but this method takes into account the relative sizes of the primary feathers. Feathers that had moult scores 1, 2, 3 and 4 were estimated to be missing 0.875, 0.625, 0.375 and 0.125 respectively of the relative mass of the feathers.

RESULTS

For the tract of 10 primary feathers combined, the estimated start date of primary moult of the average bird in South Africa, based on PFMG, was 4 October (SD: 0.8); 95% of birds were estimated to start moult between 23 August and 30 December (Fig. 2). The mean duration of moult was 129 days (1.4), the end date 10 February (0.9), and the standard deviation parameter of the model was 21.5 days (0.9). In NWA, the estimated start date of moult was 18 September (SD: 0.4), mean duration 129 days (1.1), end date 25 January (0.8), and the standard deviation parameter of the model was 13.5 days (0.2; Fig. 2). 95% of adult birds were estimated to start moult between 21 August and 15 October. In SEA, the estimated mean start date of moult was 26 October (SD: 0.5), 95% of adult birds started moult between 17 September and 26 October (Fig. 2). The duration of moult was estimated to be

105 days (0.8), end date 8 February (0.8), and the standard deviation parameter of the model was 19.4 days (0.2).

Primaries were shed sequentially from innermost (P1) to the outermost (P10) primary (Fig 3). The moult duration of the primaries was correlated to their size (SA: $r = 0.78$, $P < 0.001$; NWA: $r = 0.91$, $P < 0.001$; SEA: $r = 0.91$, $P < 0.001$). The start date and duration of moult in SA estimated from the start moult date of P1 and end moult date of P10 was 30 September and 130 days respectively (Fig. 3, Table 2). In NWA, the start date of moult of P1 was 17 September and the end date of moult of P10 was 23 January (Fig. 3, Table 3), giving a moult duration of 128 days. In SEA, the start date and duration of moult estimated from the start moult date of P1 and end moult date of P10 was 15 October and 121 days respectively (Fig. 3, Table 4). In SA, the interval between shedding of successive primaries increased from 3 days (P1–P2) to a maximum of 19 days (P7 and P8), then reduced to 12 days (between P9 and P10). In NWA, the inter-primary shedding interval increased from an average of 2 days (P1–P2) to 16 days (P9–P10). In SEA, the interval between the moult of P1 and P2 was 2 days which increased to 12 days between P9 and P10.

In SA and NWA, estimate of the start date and duration of moult based on PFMG of the tract of 10 primary feathers combined were comparable to the estimated moult start date of P1 and moult end date of P10 (Table 2 & 3). In SEA, the moult start date based on PFMG of the tract of 10 primary feathers combined was 11 days earlier than the start date of P1. The duration of moult based on PFMG was 16 days longer than the estimate based on individual primaries growth (Table 4). The temporal distribution of the moult scores in SEA indicated

that the progress of moult was faster towards the end of moult than at the beginning (Fig. 2). The assumption of the Underhill-Zucchini model that feather material is deposited at a uniform rate was not met, hence the discrepancy in the estimates from the two methods. To achieve linearity of the PFMG, a power transformation (Box & Cox 1964) of the PFMG was applied as demonstrated in Summers *et al.* (1983) and Underhill *et al.* (1990). The transformation parameter was 0.89; this is the exponent to which the PFMG needs to be raised to become approximately linear with time. The new estimate of moult based on the transformed PFMG was comparable to the estimates of start and end dates of moult based on individual primaries growth (Table 4).

Based on the durations of 129 days in SA, 129 days in NWA and 121 days in SEA, the likelihood ratio test showed that the duration of moult was similar at all three sites ($\chi^2_2 = 5.22$; $P < 0.071$).

Rate of feather material growth

Variation in the masses of individual primaries resulted in a steady increase of relative feather masses from P1 to P10 (Table 1). The slopes of the growth lines of the primaries showed that the rate of feather material produced for the outer primaries was more rapid than for the inner primaries (Fig. 3, Table 2-4). However, at all three sites, the cumulative curve of PFMG/day showed that primary feather material was deposited at a fairly uniform rate over the entire moult period resulting in an almost linear curve (Fig. 4). The uniform rate of feather material growth was possible because of the overlap in the moult of the

smaller inner primaries (thus several feathers grew simultaneously) while there was little overlap in the moult of the larger outer primaries (Fig. 3 & 5).

The amount of feather material grown in a day expressed as average PFMG/day was estimated at 0.77% in South Africa, 0.78% in NWA, and 0.82% in SEA (Table 2-4). The average rate of feather material grown did not differ significantly between SA and NWA (Kolmogorov-Smirnov test: $D = 0.11$, $P = 0.27$), but differed significantly between SA and SEA ($D = 0.22$, $P = 0.01$) and between NWA and SEA ($D = 0.18$, $P = 0.03$; Fig 3). This difference in the amount of feather material deposited over the entire moult period in the three sites is shown by the difference in the slope of the cumulative frequency curves (Fig. 4). In NWA, the 25th percentile of primary feather mass production was achieved in 33 days, 50th in 66 days and 75th percentile in 98 days. In SA, the 25th percentile of primary feather mass production was achieved after 36 days, 50th in 74 days and 75th percentile in 104 days. Feather material was deposited at the average rate in the first 34 days of the moult period but dropped below the average afterwards. This resulted in the longer duration it took to reach the median and 75th percentile growth range compared to NWA. In SEA, the 25th quartile of primary feather mass production was achieved after 31 days, Median in 72 days and 75th percentile in 95 days. Primary feather material in the first 71 days was deposited at a rate of between 0.7 – 0.8%/day, and then feather material growth increased to an average of 0.9 – 1.3%/day during the latter part of moult.

Proportion of feather mass missing

The average proportion of feather missing (PFMM)/ day in SA was estimated at 0.051, the average of the daily minima was 0.01 and the average of the daily maxima was 0.11 (Fig. 6). This means that, on average, 5.1% of the mass of primary feathers was missing at any one time during moult. In NWA, the average PFMM/ day was estimated at 0.046, the average of the daily minima was 0.021 and the average of the daily maxima was 0.132. The average PFMM/day in SEA was estimated at 0.051, the average of the daily minima was 0.011 and the average of the daily maxima was 0.133.

DISCUSSION

The start of moult in SA, NWA, and SEA appear to begin a few days after arrival of birds at these wintering areas (Thomas & Dartnall 1971, Pringle & Cooper 1975, Elliot *et al.* 1976). Moult started the earliest in NWA (18 September) at 18°S, then in SA (33°S) 16 days later (4 October), and latest in SEA (15 October) at 39°S, 38 days after the commencement of moult in NWA. These results are within limits of earlier moult estimates given for Curlew Sandpipers in Australia on 17 September (Minton *et al.* 2006), between 8 August and 6 November in Tasmania (Thomas & Dartnall 1971), and September (exact dates not given) in South Africa (Elliott *et al.* 1976, Dean 1977). However, except for Minton *et al.* (2006), the technique used to estimate the start date and duration of moult in these earlier studies was to regress date (dependent variable) on moult score (independent variable) of captured individuals.

The pattern of latitudinal difference in the start of moult was also observed in the Grey plover *Pluvialis squatarola* (Serra 2000), Ruddy Turnstone *Arenaria interpres* (Summers *et al.* 1989, Underhill 2003), Purple Sandpiper *Calidris maritima* (Summers *et al.* 2004) and Red Knot (Summers *et al.* 2010). Moult generally started earlier in the populations wintering at northern latitudes compared to the populations wintering in southern latitudes. The duration of moult is also shorter in the northern latitudes wintering populations. The early start date and shorter duration of moult at the northern latitudes is linked to the need for these populations to complete moult before the onset of harsh winter weather when food becomes scarce.

The rate of feather material growth was highest in SEA at an average rate of 0.87%/day compared to 0.78% /day in SA and 0.77%/day in NWA. Curlew Sandpipers in SEA travel an extra ca. 3000 km to and from the breeding grounds compared to the population that remains in NWA (Minton *et al.* 2006b). The extra distance resulted in moult starting later in SEA compared to the other two population. In order to complete moult in time for breeding migration, birds in SEA increase the rate of feather growth. The rate of feather growth can be increased in two ways: either by manipulating the number of feathers growing simultaneously or by increasing the rate of growth of individual feathers (Prater 1981, Serra 2000). The former is the strategy employed by Turnstones (Underhill 2003) and Grey Plovers (Serra & Underhill 2006) wintering in northern temperate regions to shorten the duration of moult, while the latter appears to be the strategy adopted by the Curlew Sandpiper as is evident in the similar pattern of feather moult in the three areas and the shorter duration of moult of individual feather in SEA (Fig. 3, tables 1-3).

One probable explanation for the difference in the pattern of primary feather moult used by different wader species to manipulate the rate of feather material grown is that it is an adaptation to moulting in particular habitat types. For instance, Ruddy Turnstones inhabit mainly rocky shores (Cramp & Simmons 1983) where they are camouflaged and can escape predators by hiding in the rock crevices. Waders such as the Curlew Sandpipers which live in open habitats such as estuaries and mudflats might be at a higher risk to predator attack during the moult period because gaps in the wing reduce flight efficiency (Tucker 1991, Swaddle & Witter 1997, Hedenström & Sunada 1999, Bridge 2003). A comparable study by Remisewicz *et al.* (2010) on the Wood Sandpiper also shows that the wing gap in this wader, which also inhabits open inland water bodies, is between 0.21% and 0.51%. This was interpreted as an adaptive strategy to minimize wing gaps during moult.

The small number of birds with suspended moult (five in SA, eight in NWA, and one in SEA) probably indicates that there is little movement between sites during the moult period. Curlew Sandpipers have adapted to living in such open habitats by minimizing the number of concurrently moulted feathers and increasing the inter-shedding interval progressively from P1–P10, thereby minimizing the wing gap and reducing the loss of flight efficiency during the moult period. The phenomenon of suspended moult has been noted in Kenya (Pearson 1974) but these were birds suspected to have started moult further north then moved southwards. Generally, birds will suspend moult if they need to move to another location some distance away.

The attempt to minimize wing gap is reflected in the proportion of feather material missing during moult with average values of 5.1% in SA, 4.6% in NWA and 5.1% in SEA. These values are smaller than the PFMM reported for adult and sub-adult Wood Sandpipers at 10% and 11%, respectively (Remisiewicz *et al.* 2009, 2010).

Finally, this study shows that the assumption of uniform production of feather material is not always met, even within the same species. In SEA, the rate of feather growth was faster toward the end of moult compared to the beginning. This non-uniform rate of feather growth has been pointed out in a number of studies (Summers *et al.* 1983, Serra & Underhill 2006). Caution should, therefore, be exercised about reading too much into small differences in results obtained from the combined moult scores of P1-10 especially in situations where any of the moult parameters (length of moult or start dates) are estimated based on the assumption of constant feather growth.

Based on our results, the following conclusions can be drawn from this study. First, the distance between the breeding grounds and the wintering areas determines the moult strategy adopted by the Curlew Sandpipers wintering in the southern hemisphere; the farther south the wintering area, the later the commencement of moult. Secondly, the sequence of moult and number of concurrently growing primaries is similar at all three locations. The pattern of moult is probably an adaptation by species found in open habitats to minimizing vulnerability to predation during the moulting period. Moult is accelerated by increasing the growth rate of individual feathers rather than altering the number of

simultaneously growing primaries. This minimizes wing gap to about 5% of the total primary feather mass, keeping the loss of flight efficiency to a minimum during the moult period.

This study re-emphasize that the avian moult is capable of much variation and modification. It also the first study to demonstrate rate of feather material growth in the Curlew Sandpiper (now included in page). This description of the pattern of moult was necessary for further comparison with other species.

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Table 1 Relative masses of the primary wing feathers of the Curlew Sandpiper (Underhill & Joubert 1995).

Primary	Percentage feather mass
1	4.0
2	4.8
3	5.7
4	7.0
5	8.6
6	10.4
7	12.0
8	13.9
9	15.6
10	18.0

Table 2 Estimates of moult parameters of each primary and of all 10 primaries pooled and their growth rate (expressed as percent Proportion Feather Mass Grown (PFMG) per day), for adult Curlew Sandpipers that perform continuous complete primary moult in South Africa

Primaries	Moult parameters				Sample sizes			
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	not in moult	in moult	moult complete	%PFMG/day
P1	30 Sep (1.1)	19.5 (1.2)	21.4 (0.8)	19 Oct (1.0)	283	214	2021	0.21
P2	2 Oct (1.1)	19.1 (1.2)	20.3 (0.8)	22 Oct (1.0)	204	214	2100	0.25
P3	9 Oct (0.9)	17.8 (1.1)	19.6 (0.7)	26 Oct (0.9)	376	200	2042	0.32
P4	17 Oct (0.9)	17.8 (1.1)	20.1 (0.7)	4 Nov (0.9)	473	193	1952	0.39
P5	27 Oct (0.9)	18.9 (1.0)	19.9 (0.6)	15 Nov (0.9)	583	211	1824	0.46
P6	10.Nov (1.0)	16.8 (1.0)	20.5 (0.7)	27 Nov (0.9)	729	228	1663	0.62
P7	24 Nov (0.9)	22.3 (1.1)	22.2 (0.7)	16 Dec (0.9)	921	343	1354	0.54
P8	13 Dec (0.9)	24.2 (1.2)	22.3 (0.7)	6 Jan (1.0)	1200	346	1072	0.57
P9	30 Dec (0.9)	21.5 (1.1)	22.9 (0.7)	21 Jan (1.1)	1474	245	899	0.73
P10	11 Jan (0.9)	26.6 (1.3)	23.4 (0.7)	7 Feb (1.1)	1614	259	745	0.68
PFMG combined	4 Oct (0.8)	129.2 (1.4)	21.5 (0.9)	7 Feb (0.9)	282	1592	744	0.77

Table 3 Estimates of moult parameters of each primary and of all 10 primaries pooled and their growth rate (expressed as percent Proportion Feather Mass Grown (PFMG) per day), for adult Curlew Sandpipers that perform continuous complete primary moult in North-west Australia

Primary	Moult parameters				Sample sizes			% PFMG /day
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	not in moult	in moult	moult complete	
P1	17 Sep (0.5)	16.5 (0.6)	13.7 (0.3)	4 Oct (0.5)	1210	443	4032	0.24
P2	19 Sep (0.5)	16.7 (0.6)	13.7 (0.3)	5 Oct (0.5)	1260	442	3983	0.29
P3	24 Sep (0.5)	17.0 (0.6)	13.4 (0.3)	11 Oct (0.5)	1401	434	3850	0.34
P4	1 Oct (0.5)	18.9 (0.6)	13.9 (0.3)	20 Oct (0.5)	1600	471	3614	0.37
P5	11 Oct (0.5)	19.4 (0.7)	14.1 (0.4)	30 Oct (0.5)	1820	520	3345	0.44
P6	24 Oct (0.5)	17.7 (0.7)	13.4 (0.4)	11 Nov (0.6)	2185	478	3022	0.59
P7	8 Nov (0.5)	18.3 (0.8)	12.5 (0.4)	26 Nov (0.8)	2583	382	2720	0.66
P8	25 Nov (0.8)	23.0 (1.2)	14.8 (0.6)	17 Dec (1.2)	2909	226	2550	0.60
P9	10 Dec (1.1)	24.3 (1.6)	17.7 (0.7)	3 Jan (1.5)	3063	123	2499	0.64
P10	26 Dec (1.4)	28.0 (1.8)	21.2 (0.7)	23 Jan (1.8)	3151	124	2410	0.64
PFMG combined	18 Sep (0.4)	129 (1.0)	13.8 (0.2)	25 Jan (0.8)	1210	2068	2407	0.79

Table 4 Estimates of moult parameters of each primary and of all 10 primaries pooled and their growth rate (expressed as percent Proportion Feather Mass Grown (PFMG) per day), for adult Curlew Sandpipers that perform continuous complete primary moult in south-eastern Australia

Primary	Moult parameters				Sample sizes			% PFMG /day
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	not in moult	in moult	moult complete	
P1	15 Oct (0.6)	13.7 (0.6)	16.3 (0.5)	28 Oct (0.5)	812	351	6315	0.29
P2	17 Oct (0.6)	13.4 (0.7)	13.8 (0.5)	30 Oct (0.6)	875	339	6271	0.36
P3	22 Oct (0.5)	13.4 (0.6)	13.4 (0.4)	4 Nov (0.5)	984	344	6155	0.43
P4	30 Oct (0.6)	14.2 (0.6)	13.9 (0.5)	13 Nov (0.6)	1185	338	5972	0.49
P5	7 Nov (0.6)	14.9 (0.6)	14.2 (0.4)	22 Nov (0.6)	1393	361	5740	0.58
P6	21 Nov (0.6)	23.8 (0.7)	13.4 (0.3)	15 Dec (0.5)	1669	768	5053	0.44
P7	11 Dec (0.4)	19.2 (0.6)	12.5 (0.3)	30 Dec (0.5)	2334	776	4407	0.63
P8	25 Dec (0.6)	21.1 (0.5)	0.6 (0.4)	15 Jan (0.4)	2868	1064	3647	0.66
P9	7 Jan (0.4)	22.3 (0.5)	17.7 (0.3)	29 Jan (0.4)	3461	1050	3008	0.70
P10	16 Jan (0.4)	28.1 (0.5)	21.2 (0.2)	13 Feb (0.4)	3931	1287	2301	0.64
PFMG combined	26 Oct (0.5)	105.1 (0.8)	19.4 (0.2)	8 Feb (0.4)	1005	3666	2807	0.82
Transform-ed PFMG	15 Oct (0.4)	121.6 (0.3)	14.5 (0.2)	14 Feb (0.5)	1005	3666	2807	0.82

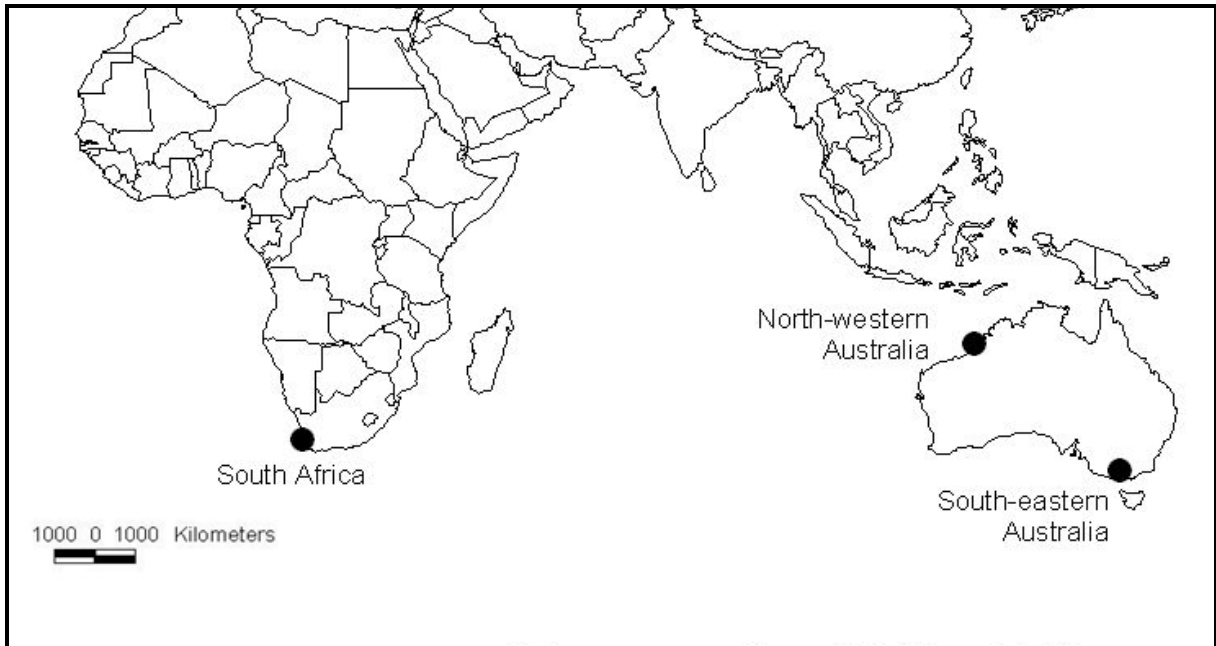


Fig. 1 Location of trapping sites of Curlew Sandpipers in South Africa, north-western Australia and south-eastern Australia.

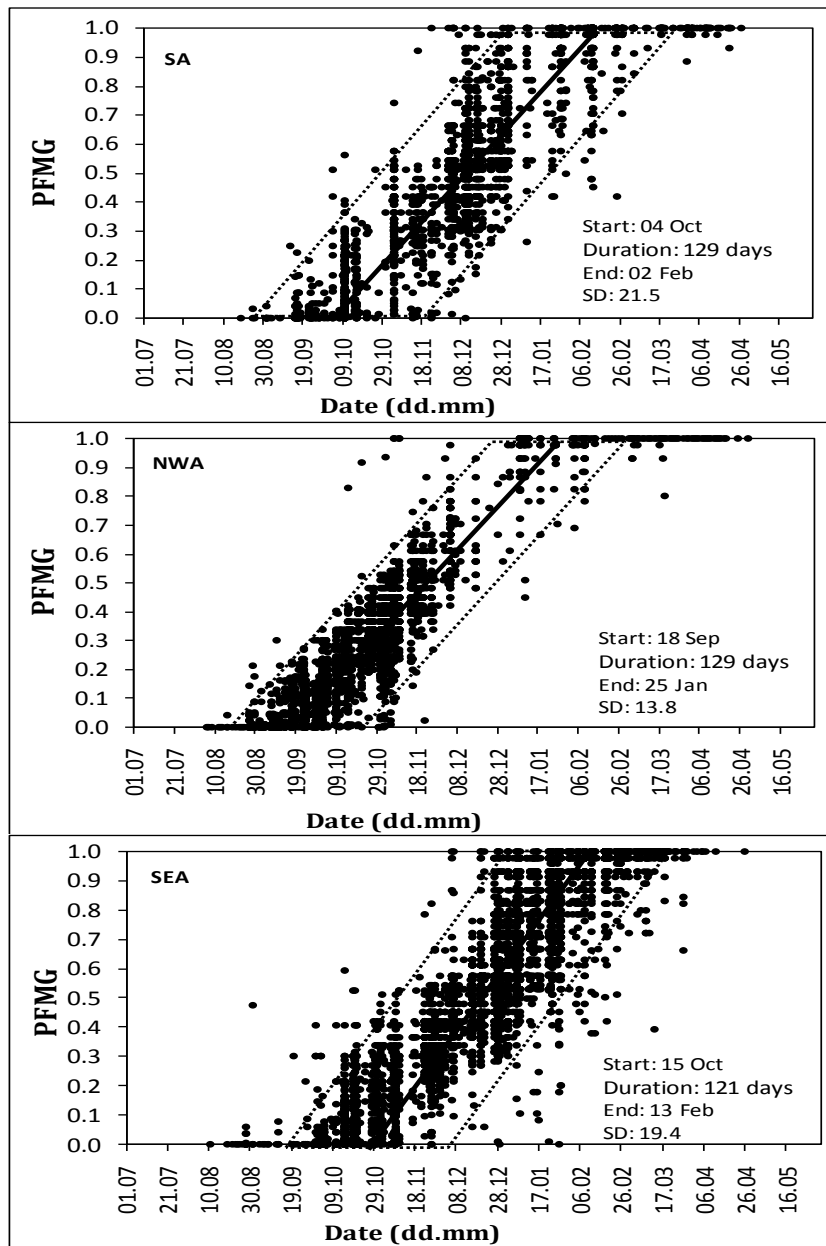


Fig. 2 Temporal distribution of the Proportion Feather Mass Grown (PFMG) of adult Curlew Sandpipers in South Africa (SA), north-western Australia (NWE) and south-eastern Australia (SEA). Continuous black line reflects the start and end dates; dotted lines indicate the 95% confidence intervals.

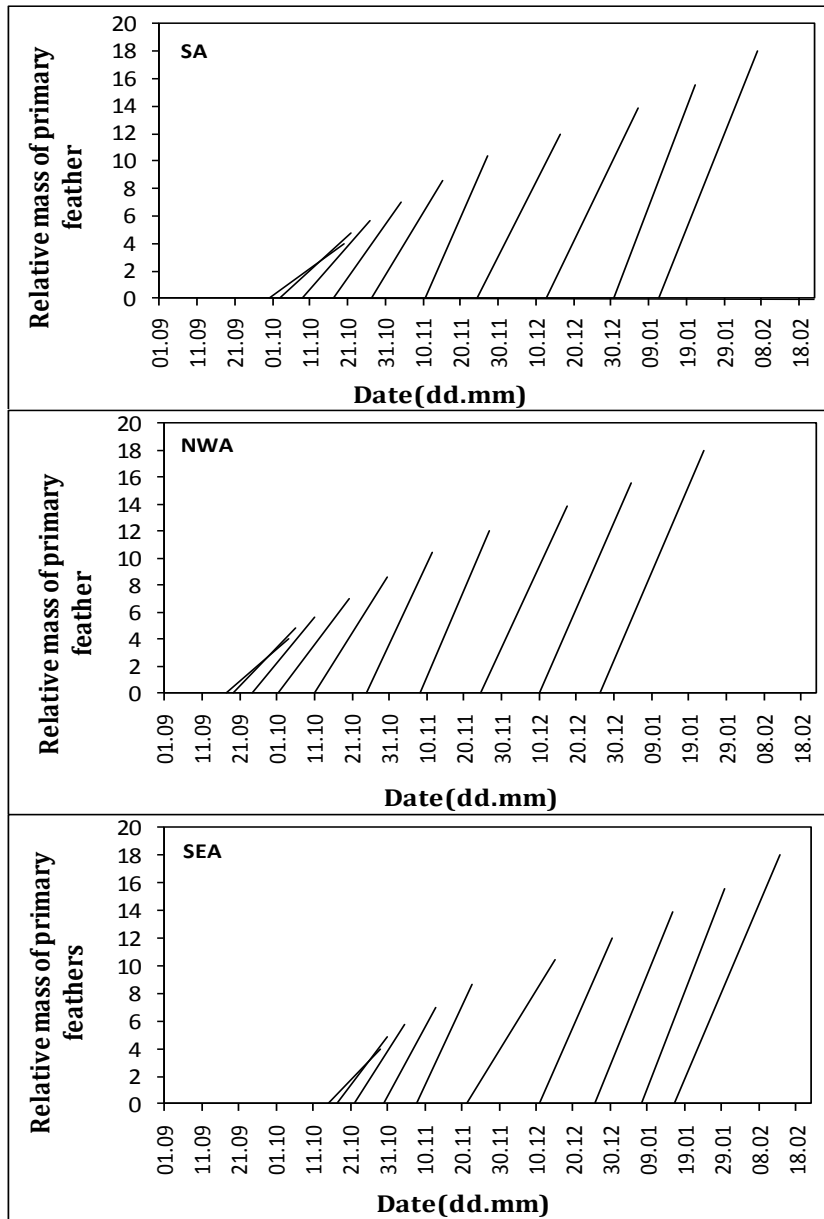


Fig. 3 Growth lines of primaries P1-P10 of Curlew Sandpipers in South Africa, north-western Australia and south-eastern Australia, showing the amount of the primary mass produced between start and end date of each primary development. Slopes of the lines reflect the growth rate of each primary.

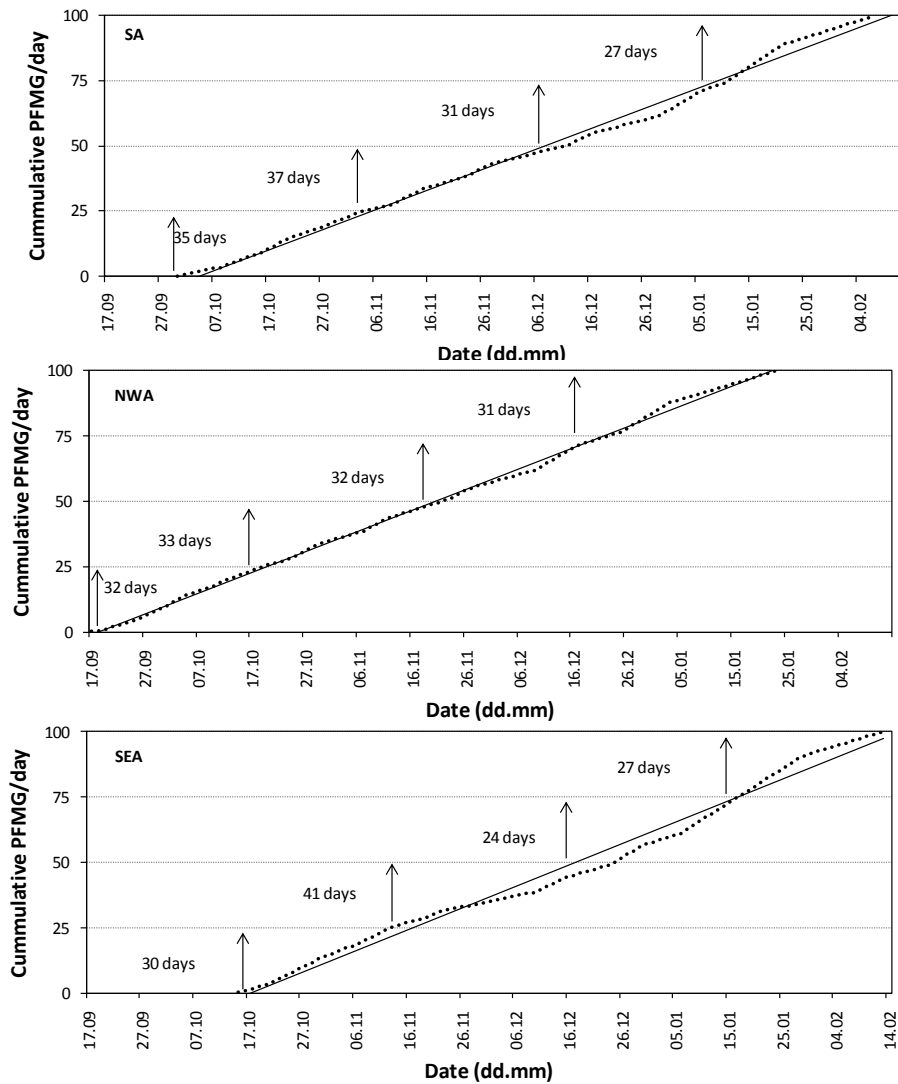


Fig. 4 Modelled cumulative rate of percentage feather mass grown (dotted lines) of Curlew Sandpipers in South Africa (SA), north-western Australia (NWE) and South-eastern Australia (SEA) estimated from daily values of the moult parameters of individual primary feathers (Tables 1–3). Thin lines are linear regression lines fitted through the cumulative daily values of proportion feather mass grown (PFMG); numbers refers to the number of days taken to reach each quartile.

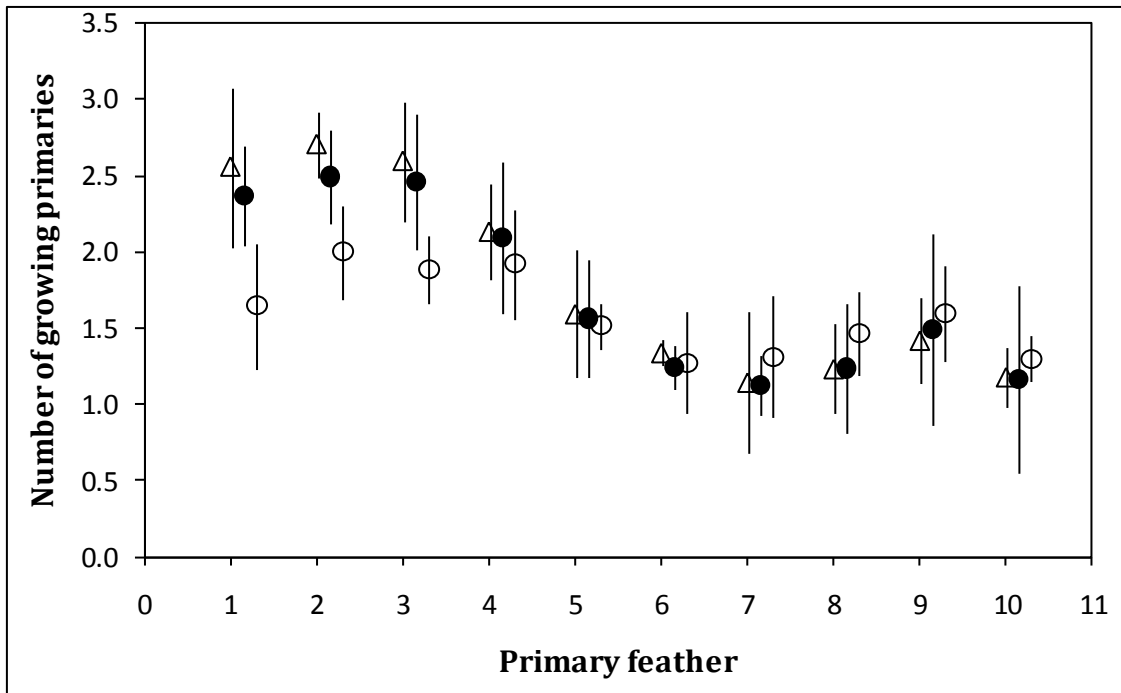


Fig. 5 Average number of Curlew Sandpiper primaries growing simultaneously during the moult of each primary in South Africa (SA), north-western Australia (NWE) and South-eastern Australia (SEA). Open triangles = South Africa, open circles = north-western Australia, Solid black circles = south-eastern Australia.

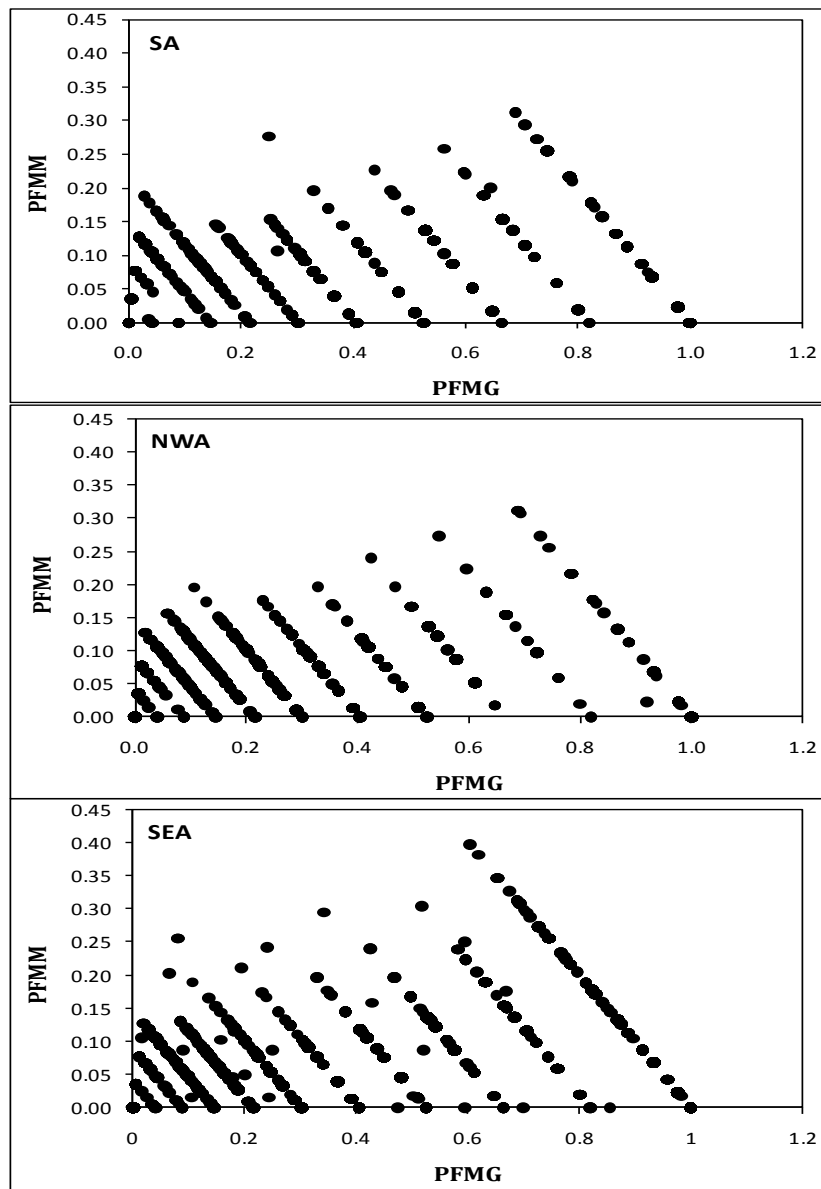


Fig. 6 The relationship between the size of the wing gap during moult expressed as a Proportion of Feather Mass Missing (PFMM) and Proportion of Feather Mass Grown (PFMG) for Curlew Sandpipers in South Africa (SA), north-western Australia (NWA) and south-eastern Australia (SEA). The pattern of parallel lines is a consequence of the recording of moult scores for individual feathers to integer values.

CHAPTER 5

VARIABILITY OF ANNUAL MOULT IN THE CURLEW SANDPIPER IS RELATED TO BREEDING SUCCESS

University of Cape Town

**VARIABILITY OF ANNUAL MOULT IN THE CURLEW SANDPIPER
IS RELATED TO BREEDING SUCCESS**

ABSTRACT

The carry-over effects of predation pressure and average June and July temperature in the Arctic on the timing of moult was studied in the Curlew Sandpiper *Calidris ferruginea* in South Africa (SA), north-western Australia (NWA), and south-eastern Australia (SEA). The start date of moult in good breeding years was later than the start date of moult in poor breeding years by five days in SA, 10 days in NWA and nine days in SEA. The estimated start dates of moult of adult birds (males and females combined) were earlier in years with a higher index of predation and higher temperature in June compared to years when predation was low or June temperatures were low. The effect of predation and temperature in the Arctic on the start of moult was sex-specific. The moult of males was negatively correlated with the average June temperature while the onset of moult in females was negatively correlated with predation index and positively with July temperature. These results demonstrate that the effect environmental variables on the Arctic breeding areas have on breeding productivity can affect the schedule of other life-history stages within the annual cycle, in this case moult on the non-breeding areas.

INTRODUCTION

The three most energy-demanding events in the annual cycles of birds are breeding, migration and moult (Newton 2008). In many species, these activities often occur at different seasons and at different places so energy demands are minimized by the separation of these activities. Those waders (Charadrii) which migrate long-distances have evolved a wide variety of moult strategies which allows them fit moult into their annual cycle (Ginn & Melville 1983). Species such as the Little Stint *Calidris minuta* and Red Knot *C. canutus* moult most body and flight feathers almost exclusively on the wintering ground (Middlemiss 1961, Pearson 1984, Summers *et al.* 2010). Some like the Dunlin *C. alpina* and Golden Plovers *Pluvialis apricaria* start moult on or near the breeding grounds (Holmes 1966, Byrkjedal 1978, Kania 1990). Others like the Wood Sandpiper *Tringa glareola* and Wilson's Phalarope *Phalaropus tricolor* start moult at some appropriate stop-over site during migration which is then suspended and continued on the wintering ground (Jehl 1987, Pinchuk *et al.* 2008, Remisiewicz *et al.* 2009).

The major ecological significance of moult in avian life-history lies in its timing in relation to other events within the annual cycle. Theoretical models have been used to illustrate how different factors such as migratory distance, energy reserves, breeding status, and environmental seasonality can affect moult schedules in birds (e.g Holmgren & Hedenström 1995, Barta *et al.* 2006). In species for which wing moult typically occurs after they have arrived at their non-breeding (wintering) areas there is the possibility that prior events such as breeding and migration can displace the timing of moult within the annual cycle. The relationship between the timing of breeding and migration on the schedule of moult has

been documented in bird species such as Greater Snow Geese *Anser caerulescens atlantica* (Reed *et al.* 2003), Lazuli Bunting *Passerina amoena* (Young 1991), Great Tit *Parus major* and Willow Tit *P. montanus* (Orell & Ojanen 1980), Yellow Warbler *Dendroica petechia* (Rimmer 1988), and White-crowned Sparrows *Zonotrichia leucophrys* (Morton & Morton 1990), but these are species that overlap moult with either breeding or migration.

In this study, the moult of adult Curlew Sandpipers *Calidris ferruginea* on their non-breeding grounds in South Africa and Australia is described. The clear separation of breeding, migration and moult in time and space makes this species an ideal candidate for the study of how the schedule of one annual event might affect the subsequent within the annual cycle.

Curlew Sandpipers breed between June and July in the Arctic Siberian tundra then migrate to spend the non-breeding season to Africa, the Indian sub-continent, and Australasia (Vaurie 1965, Cramp & Simmons 1983). The timing of post-breeding migration in this species has been linked to breeding productivity. In years of low reproductive success, the passage of birds on migration is earlier compared to years of high reproductive success (Blomqvist *et al.* 2002, Figuerola 2006, Meissner 2006, Chapters 2 and 3). Breeding productivity in the Curlew Sandpiper is negatively correlated with lemming abundance in the tundra. In years of peak lemming abundance, predators such as Arctic Foxes *Alopex lagopus* consume mainly lemmings and the birds breed successfully. When lemming densities decline, the predators switch diet to the eggs and chicks of the Arctic breeding birds (Underhill *et al.* 1993, Summers *et al.* 1998), causing the birds to leave their breeding ground early. Schekkerman *et al.* (1998) have also described a relationship between the

breeding productivity of the Curlew Sandpiper and the temperature in the Arctic. In years of low predation and low mean temperature in the Arctic during the breeding season resulted in low reproductive success.

Adult Curlew Sandpipers reach their non-breeding grounds between August and September, where they undergo a complete moult (Thomas 1970, Thomas & Dartnall 1971, Pringle & Cooper 1975, Elliott *et al.* 1976). This study examines whether the timing of moult is adjusted in relation to breeding success and/or migration. The hypothesis is that if the timing of moult is displaced by breeding and migration, then annual variation of the onset of moult will be related to some indicator of breeding success.

METHODS

The moult records of 2618 Curlew Sandpipers caught in South Africa (1970–1974) at Langebaan Lagoon and Rietvlei (33°S, 18°E), 5685 moult records (1981–2006) from north-western Australia (18°S, 122°E), and 7524 records (1978–2008) from south-eastern Australia (39°S, 147°E) were used in this study. Birds were aged based on feather appearance and wing condition (Prater *et al.* 1979, Rogers *et al.* 1990). Birds were allocated to one of three age categories: birds in their first year of life (juveniles), birds known to be in their second year, and birds past their second year or older, defined to be adults. In this study, only the moult of adult birds is considered. Adults were sexed using the discriminant function formula of Wymenga *et al.* (1990): $D = 0.07815 * W + 0.47962 * B - 28.7302$: D = Discriminant score where $D < 0$ = males, $D > 0$ = females; W = wing length; B = Bill length.

Primary feathers were numbered P1 for the innermost primary to P10 for the outermost feather. Primary moult scores were recorded using the British Trust for Ornithology technique (Ginn & Melville 1983) as follows: 0=not dropped, 1=missing or in pin, 2="brush" stage to one-third grown, 3=one-third to two-thirds grown, 4=two-thirds to full-grown but with waxy sheath remaining, 5=completely re-grown. To estimate the parameters of moult (start date, duration and standard duration) of the tract of 10 primary feathers combined, the moult scores were converted into Proportion Feather Mass Grown (PFMG) using the relative masses of primary feathers (Underhill & Joubert 1995, Underhill & Summers 1993), a process used in several studies (e.g. Summers *et al.* 1983, Underhill & Summers 1993, Remisiewicz *et al.* 2009). Estimates of annual moult parameters were obtained using an extension of the maximum likelihood model of Underhill & Zucchini (1988) which allows the inclusion of covariates in the model (B. Erni *in litt.*). The data were assumed to be Type 2 of Underhill & Zucchini (1988) which uses moult scores of birds that have not yet started moult, birds in moult, and those that have completed moult.

Annual estimates of moult for all adults as well as for both sexes were also obtained using the combined PFMG of all 10 primary feathers. Three separate models were considered for each data set. The model with the fewest parameters assumed a separate start date of moult for each year and a common duration of moult and standard deviation of start date. An intermediate model had a separate start date for each year and separate duration of moult for each year and a common standard deviation of start date. The model with the most parameters assumed a separate start date, duration and standard deviation of start

date for each year. The model with the smallest Akaike Information Criterion (AIC) was selected as the best fit.

The relationship between the mean start dates of moult on the wintering grounds with breeding success was explored. The proportion of juvenile birds in catch totals was used as an index of breeding success (Minton *et al.* 2005). A year was classed as a good breeding year when the proportion of juvenile birds was greater than 0.20 and a poor breeding year when less than 0.10. Both predation and temperature in the Arctic during June and July (the breeding season) were included as covariates in the model. Data on the average temperature in the Arctic in June and July were obtained from the National Oceanic and Atmospheric Administration (NOAA) and used as a proxy for weather conditions on the breeding grounds during the egg-laying and chick rearing period (Tomkovich & Soloviev 2006). Although other climate parameters such as precipitation and timing of snowmelt could also have been of major importance, air temperature was the only variable for which it was possible to obtain consistent, long-term data for the area of interest. The index of predation pressure, calculated from the abundance of lemmings on the Taimyr Peninsula, was obtained from Blomqvist *et al.* (2002). Scores of predation index go from 0 (low predation pressure) to 3 (high predation pressure).

RESULTS

Annual estimates of moult

The estimated start dates of moult (all years combined) differed significantly between South Africa (SA), north-western Australia (NWA) and south-eastern Australia (SEA) ($F_{1,15824} =$

16.95, $P < 0.001$). The moult start date in SA was 4 October, about 16 days later than the estimated start of moult in NWA on 18 September, and 11 days earlier than the estimated moult start in SEA on 15 October. Based on the value of the AIC, the model with the best fit for the estimation of annual starting dates was the one which assumed a separate start date, duration and standard deviation of start date for each year. The yearly estimates of the start date of moult in SA showed that the earliest start date of moult was 3 October and the latest was 13 October (Fig. 1, Table 1). In NWA, the start date of moult ranged from 31 August to 22 October (Fig. 2, Table 2), and in SEA, the start dates of moult ranged from 29 September to 12 November (Fig. 3, Table 3). There was a negative correlation between the start date and the duration of moult in SA (Pearson's correlation: $r = -0.80$, $P < 0.001$, $df = 9$), SEA ($r = -0.72$, $P < 0.001$, $df = 58$), but not in NWA ($r = -0.26$, $P = 0.062$, $df = 48$).

The pattern of yearly start dates of moult, especially in NWA and SEA, showed that prior to 1990 there was low between-year variation in the start dates of moult, but from 1991 onwards, there was increased variability in the annual start dates of moult (Fig. 2 & 3). F-test for equality of standard deviations was used to test the null hypothesis that the standard deviations of the two periods were equal. In NWA, the average start date of moult in the period 1981–1990 was 23 September (SD: 1.4) while the mean start date of moult in the period 1991–2006 was 22 September (SD: 2.8). Variability in the period 1991–2006 was significantly greater than the period 1981–1990 ($F_{14,8} = 4.0$, $P < 0.05$). In SEA, the mean start date of moult in the period 1978–1990 was 17 October (SD: 1.9) and the mean start date in the period 1991–2008 was 24 October. Variability in the period 1991–2008 was significantly greater than the period 1978–1990 ($F_{8,11} = 4.0$, $P < 0.05$).

On average, moult started later in good breeding years compared with poor breeding years but this difference varied between sites. In SA, the estimated start date of moult in good breeding years was 9 October (SD: 1.0) which was not significantly later ($F_{1,2617} = 0.32$, $P = 0.455$) than the estimated start date of moult in poor breeding years on 4 October (SD: 1.5). In NWA mean start date of moult in good breeding years was 25 September (SD: 0.4), significantly later ($F_{1,5299} = 10.01$, $P < 0.001$) than the estimated mean start date of moult in poor breeding years on 15 September (SD: 14.0). In SEA, the estimated moult start date in good breeding years was 28 October (SD: 0.6) which was significantly later ($F_{1,7489} = 19.40$, $P < 0.01$) than the estimated start date of moult in poor breeding years on 19 October (SD: 0.5).

Predation index and June temperature were also significant predictors of the onset of moult. For all adults (males and females combined), moult started relatively later in years with a low index of predation compared to years with a high index of predation (slope = -2.44 , $P = 0.007$). Also, moult started earlier in years when the average June temperature in the arctic was high compared to years when the temperature was low (slope = -2.63 , $P = 0.003$), but July temperature did not have a significant effect on the start date of moult (slope = -0.82 , $P = 0.348$).

Moult of the sexes

The annual moult estimates for each sex in SA were obtained with the model which assumed a separate start date, duration, and standard deviation of start date for each year while the estimates in NWA and SEA were obtained by fitting a model which assumed a

separate start date of moult for each year and a common annual duration of moult. In NWA and SEA, most years had insufficient moult record of each sex in each year to allow for reliable separate annual estimate of moult parameters. In SA, the annual estimates of the start dates of moult for males ranged from 12 September to 8 October (25 days) and for females it ranged from 16 September to 23 October (38 days) (Fig. 4, Table 4). In NWA, the earliest start date of moult in males was 28 August and the latest 14 October (46 days) while the earliest start date of moult in females was 3 September and the latest was 26 October (54 days) (Fig. 5, table 5). In SEA, the earliest start date of moult in males was 12 October and the latest 22 October (10 days) while the earliest start date of moult in females was 17 October and the latest was 31 October (14 days) (Fig.6, Table 6).

The mean start date of moult of males was significantly earlier than that of females at all three sites: SA ($F_{1, 2111} = 7.27, P = 0.045$), NWA ($F_{1, 2440} = 8.79, P = 0.001$), and SEA ($F_{1, 3742} = 9.01, P = 0.003$) (Table 7). The average difference in the start date of moult between males and females was 11 days in SA, 14 days in NWA, and nine days in SEA. In both sexes the start date of moult was earlier in poor breeding years compared with good breeding years (Table 7). However, at all three sites, the start date of moult in males in good breeding years did not differ significant with poor breeding years (SA: $F_{1, 930} = 0.09, P = 0.771$; NWA: $F_{1, 1156} = 2.02, P = 0.170$; SEA: $F_{1, 1897} = 0.07, P = 0.733$). In females, the difference in the start date of moult between good and poor breeding years was not significant in SA ($F_{1, 1080} = 1.44, P = 0.125$), but moult started significantly later in good breeding years compared to poor breeding years in NWA ($F_{1, 1282} = 13.60, P < 0.001$) and SEA ($F_{1, 3740} = 6.07, P = 0.031$) (Fig.7).

Controlling for the different starting dates at the three sites, the start of moult in males was significantly earlier in years with high June temperature (slope = -3.45 , $P = 0.03$) but was not affected by predation in the Arctic (slope = -0.31 , $P = 0.35$) or July temperature (slope = 0.56 , $P = 0.46$). The start of moult in females was significantly earlier in years of high predation pressure compared to years when predation was low (slope = -3.61 , $P < 0.01$), and high July temperature (slope = 2.47 , $P = 0.01$.) but not June temperature (slope = 0.20 , $P = 0.59$).

DISCUSSION

When the estimated moult start dates of all adults were considered, the onset of moult in the Curlew Sandpiper was found to be earlier when predation in the Arctic was high or average June temperature in the Arctic was high. June temperature and predation pressure affect the onset of breeding and breeding success, respectively (Underhill *et al.* 1993, Schekkerman *et al.* 1998, Summers *et al.* 1998), which in turn affects the timing of migration of adult birds (Blomqvist *et al.* 2002, Figuerola 2006, Meissner 2006). When migration is late, the arrival of adults on the non-breeding areas is also late, resulting in a late start of moult. A link between breeding success and the timing of moult has also been observed in species such as Greater Snow Goose (Reed *et al.* 2003), Great Tit and Willow Tit (Orell & Ojanen 1980), and White-crowned Sparrows (Morton & Morton 1990). However, in none of these species was it demonstrated that the timing of moult was affected by predation on the breeding areas. Also, these are species that overlap moult with either breeding or migration, unlike the Curlew Sandpiper where breeding, migration and moult are carried out separately.

The variability in the annual start dates of moult was largest in NWA, with 56 days' difference between the earliest start date of moult and the latest start date. In SEA, the difference between the earliest and latest start date of moult was 50 days, and in SA it was 10 days, although the latter was based on a short time series. This difference of almost two months is larger than the difference in the migration dates between good and poor breeding years, an estimated 11 days (Chapter 2). A likely explanation is that the interval between arrival of the birds on the non-breeding areas and the commencement of moult is longer in some years than in others. This could happen if small inter-annual variations in environmental conditions and habitat quality on the non-breeding grounds affect the commencement of moult, at least in the short term. Ashmole's (1962) account of the biology of the Noddy *Anous tenuirostris atlanticus* on Ascension Island indicates that variation in food abundance cause a variation in the annual timing of breeding, which carried over into variation in the timing of moult.

Results indicate that the variability in the start date of moult has increased over the years. The high variability of moult start dates after 1991, compared to the period prior to 1990, suggests that either temperature or predation has disrupted the regular pattern of breeding productivity of the Curlew Sandpiper, causing the birds to breed exceptionally later than normal or leave the breeding grounds exceptionally earlier than normal. Increasing occurrence of extreme climatic events as a result of climate change (Easterling *et al.* 2000) can be mirrored in the timing of moult. For instance Van De Pol *et al.* (2010) demonstrated that changes in the frequency, magnitude and timing of flooding events at coastal sites in Europe has reduced the reproductive output in at least one species, the Eurasian

Oystercatcher *Haematopus ostralegus*. There is also evidence that climate change has caused reduction in the frequency of lemming outbreaks (Kausrud *et al.* 2008). These studies suggest that the scarcity of lemmings means that predators such as foxes will increasingly prey on other species, including waders. If the cyclical pattern of breeding productivity of the Curlew Sandpiper is disrupted, it would be reflected in the timing of migration and moult.

Moult of the sexes

In general, the start date of moult in males was earlier than that of females. This difference in the moult schedule of the sexes can be linked to the parental care roles of the sexes. In Curlew Sandpipers, only the females partake in parental care (Tomkovich & Soloviev 2006). The timing of their migration and, consequently, moult will depend on the length of the breeding season. In years when predation on the eggs and chicks was low, the timing of post-breeding migration is later (Blomqvist *et al.* 2002, Figuerola 2006, Meissner 2006), resulting in an overall late onset of moult at the non-breeding grounds compared to years when predation pressure was high. Males, who play no part in parental care, leave the breeding grounds and begin migration to the non-breeding areas soon after the females start incubation of eggs (Holmes & Pitelka 1964, Tomkovich 1988). Consequently, males reach the non-breeding grounds and start moult earlier than females. A similar relationship between parental care roles of the sexes and the onset of moult has been found in Wilson's Phalarope (Jehl 1987), Purple Sandpiper *Calidris maritima* (Morrison 1976, Summers *et al.* 2004), and Dunlin (Greenwood 1981) where the sex least involved in parental care started moult ahead of the sex that cared for the young.

Related to the parental care role is the annual variability in the start date of moult. The little parental responsibilities of males imply that their annual timing of moult would be less variable than that of females. The difference between the earliest and the latest start date of moult in SA was 25 days, 46 days in NWA, and 10 days in SEA. In contrast, the moult of females showed a wider inter-annual variation compared to the males. The difference between the earliest start and latest start date of moult of females in SA was 38 days, 58 days in NWA, and 14 days in SEA.

The relationship between the onset of moult in the Curlew Sandpiper with predation pressure, June and July temperature on the breeding ground was sex-specific. The onset of moult in males was positively correlated with the June temperature while the moult of females was negatively correlated with predation pressure and positively with July temperature on the Arctic breeding ground. This is, again, related to the breeding system of the Curlew Sandpiper. Temperature in June affects the onset of breeding (Tomkovich & Soloviev 2006, Meltofte *et al.* 2007); the warmer the temperature is in June, the earlier the start and completion of egg-laying and the earlier the departure of males from the breeding areas. This would result in an early start of moult of males on the non-breeding grounds. On the other hand, the duration of breeding depends on predation pressure and the temperature in July on the Arctic breeding grounds. When predation on the eggs and chicks is low or the temperature when the chicks hatch in July is high, females will remain on the breeding grounds caring for the young until they fledge (Schekkerman *et al.* 1998, Summers *et al.* 1998, Soloviev *et al.* 2006). As such, their migration is much later in those years (Figuerola 2006), and consequently the onset of moult is later as well.

Potential consequence of moult schedule

The timing and duration of moult can affect the time available for birds to accumulate pre-migratory fat. The speed of moult can also affect feather quality. The timing of moult can also potentially affect migratory phenology through time constraint; the potential delay of departure until complete moult. Any of these factors can have negative consequences on the state of the individuals which could eventually affect population parameters such as lowered adult survival and reproductive output (Hemborg & Lundberg 1998, Hemborg & Merilä 1998)

The following conclusions can be derived from the above:

1. Prior events in the annual cycle can displace the timing of moult in the Curlew Sandpiper. In years when predation on the eggs and chicks of the Curlew Sandpiper was low (hence good breeding success), moult begins later compared to years of high predation. Also, the start of moult was earlier in years of warm temperature in June on the Arctic breeding grounds compared to years when June temperature was cold.
2. The link between moult and conditions on the breeding grounds are, however, sex specific. The moult of males is modified by June temperatures on the breeding grounds; males generally began moult earlier in years when temperature in June on the Arctic breeding grounds were high compared to cold years. The start date of moult in females was affected by predation and July temperature; moult in females is delayed in years of low predation pressure and/or warm July temperature *vice versa*.
3. In cases where a moult starts late its duration was commonly, but not always, correspondingly short. As the displacement of moult could potentially affect subsequent

events in the annual cycle such as the time available for building fat reserves for spring migration, variability in the start dates of moult necessitates flexibility in the duration of moult. A flexible moult schedule is perhaps an adaptive advantage in long-distance migratory birds to minimize metabolic stress.

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Table 1 Annual estimate of the moult parameters of adult Curlew Sandpipers in South Africa. Estimates are based on the proportion of feather mass grown (PFMG) of the tract of 10 primaries combined.

Year	Mean start date		Duration (days)		Mean end date		Standard deviation		Sample size		
	Mean	sd	D	sd	Mean	sd	S	sd	Not in moult	In moult	Moult complete d
1970	6 Oct	1.3	130.9	1.9	11 Feb	2.5	19.5	1.3	0	216	9
1971	4 Oct	1.5	123.2	1.2	9 Feb	3.7	19.1	0.2	72	438	86
1972	3 Oct	1.9	123.8	2.3	8 Feb	2.3	17.8	0.9	67	640	410
1973	5 Oct	1.3	129.2	2.1	10 Feb	2.5	17.8	0.6	142	266	200
1974	13 Oct	1.4	128.0	3.9	18 Feb	2.4	18.9	1.0	1	32	38

Table 2 Annual estimates of the moult parameters of adult Curlew Sandpipers in north-west Australia based on the proportion of feather mass grown (PFMG) of the tract of 10 primaries combined.

Year	Mean start date		Duration (days)		Mean end date		Standard deviation		Sample size		
	Mean	sd	D	sd	Mean	sd	S	sd	Not in moult	In moult	Moult complete
1981	16 Sep	2.6	123.8	3.1	17 Jan	4.1	15.3	0.5	67	8	0
1982	23 Sep	1.2	148.7	3.2	18 Feb	4.2	17.8	1.2	513	41	0
1983	22 Sep	0.7	107.0	3.2	6 Jan	2.0	16.1	1.5	2	539	4
1986	21 Sep	2.3	138.3	3.7	6 Feb	1.3	17.9	1.2	71	12	0
1988	14 Oct	2.3	104.0	2.5	26 Jan	1.6	18.4	1.0	0	21	713
1990	17 Sep	1.7	119.1	3.2	14 Jan	3.6	16.2	1.2	0	32	367
1992	18 Sep	1.6	126.5	2.7	22 Jan	4.0	18.1	1.0	125	385	0
1993	6 Oct	4.6	124.1	2.4	7 Feb	3.3	15.4	0.9	14	26	18
1994	23 Sep	2.1	140.8	2.5	10 Feb	2.0	17.6	0.3	53	18	376
1995	3 Oct	2.1	146.0	1.6	25 Feb	1.9	16.4	0.6	10	20	0
1996	8 Oct	3.8	173.1	2.4	30 Mar	2.9	19.5	1.3	0	35	343
1997	1 Sep	3.5	139.2	3.4	19 Jan	1.3	17.9	0.5	11	13	6
1998	17 Sep	1.7	130.2	1.9	25 Jan	1.7	16.5	0.5	312	253	6
1999	18 Oct	2.9	151.4	4.3	19 Mar	4.2	19.1	0.3	0	14	0
2000	22 Sep	2.9	143.9	1.3	12 Feb	1.9	16.1	0.5	5	23	21
2001	13 Sep	1.9	124.1	3.9	15 Jan	3.6	18.2	1.3	9	372	27
2002	23 Aug	3.8	119.8	2.3	20 Dec	1.4	19.4	0.2	0	147	0
2003	25 Sep	5.9	119.0	1.5	21 Jan	2.7	18.6	0.3	45	3	2
2004	29 Sep	2.2	129.6	2.7	5 Feb	2.1	17.9	1.4	2	49	37
2005	20 Sep	1.9	119.3	3.6	17 Jan	2.3	17.3	0.6	1	55	114
2006	15 Sep	1.5	122.9	2.5	15 Jan	3.5	17.8	0.9	0	107	2

Table 3 Annual estimates of the moult parameters of adult Curlew Sandpipers in south-east Australia based on the proportion of feather mass grown (PFMG) of the tract of 10 primaries combined.

Year	Mean moult start date		Duration (days)		Standard deviation		Moult end date		Sample size		
	Mean	sd	D	sd	S	sd	Mean	sd	Not in moult	In moult	Completed moult
1978	5 Oct	1.5	122.2	1.5	13.9	0.2	4 Feb	1.6	9	122	2
1979	17 Oct	0.8	112.3	1.2	16.3	0.3	7 Feb	0.9	13	234	561
1980	6 Oct	1.2	129.7	1.0	15.4	0.3	13 Feb	0.8	59	461	114
1981	4 Oct	1.2	131.5	1.4	21.1	0.1	12 Feb	1.4	18	137	190
1982	13 Oct	1.9	124.5	2.5	18.4	0.2	14 Feb	1.2	34	216	108
1983	29 Sep	1.7	138.3	1.6	16.4	0.3	14 Feb	1.0	17	143	240
1984									0	7	121
1985	11 Oct	2.0	120.9	1.6	24.8	0.3	9 Feb	2.0	99	46	0
1986	4 Oct	2.8	127.6	1.2	18.7	0.2	8 Feb	1.9	22	69	147
1987	10 Oct	2.5	124.1	1.2	16.1	0.2	11 Feb	1.9	35	84	0
1988	18 Oct	2.7	111.4	0.8	20.7	0.2	7 Feb	1.3	315	162	102
1989									1	1	0
1990	11 Oct	3.9	131.6	2.5	6.9	0.2	19 Feb	3.0	16	22	0
1991	17 Oct	3.4	119.9	2.5	12.2	0.2	14 Feb	2.9	7	26	1
1992	18 Oct	4.0	118.1	1.2	15.0	0.2	13 Feb	1.7	1	54	54
1993	23 Oct	1.7	115.9	1.1	18.1	0.6	16 Feb	1.1	32	172	47
1994	20 Oct	2.6	127.2	1.3	16.4	0.2	24 Feb	1.2	5	333	6
1995	7 Nov	4.1	99.3	2.2	28.5	0.3	15 Feb	1.9	0	44	22
1996	8 Oct	2.0	133.9	1.2	17.0	0.2	19 Feb	1.2	17	186	38
1997	15 Oct	2.9	122.1	2.1	19.7	0.2	14 Feb	1.8	2	54	37
1998	8 Oct	2.1	130.4	1.8	14.4	0.2	15 Feb	2.7	0	28	31
1999	4 Oct	2.8	132.4	1.2	15.8	0.3	13 Feb	1.7	105	142	150
2000	13 Oct	2.1	110.2	1.2	26.2	0.2	1 Feb	1.4	89	155	156

Table 3 continued

Year	Mean moult start date		Duration (days)		Standard deviation		Moult end date		Sample size		
	Mean	sd	D	sd	S	sd	Mean	sd	Not in moult	In moult	Completed moult
2001									0	56	163
2002	13 Oct	2.7	132.7	1.2	18.9	0.2	23 Feb	1.7	70	57	127
2003	13 Oct	2.9	121.9	1.2	20.9	0.2	12 Feb	1.0	1	245	97
2004	14 Oct	2.4	119.0	2.4	24.2	0.3	10 Feb	3.8	11	16	3
2005	12 Nov	3.2	83.6	1.2	33.7	0.2	3 Feb	2.0	7	51	100
2006	2 Oct	4.4	133.0	1.8	17.3	0.2	12 Feb	1.1	1	286	34
2007	22 Oct	3.3	102.1	2.2	14.9	0.2	1 Feb	3.0	20	25	3
2008	12 Oct	4.0	113.7	1.4	14.7	0.3	3 Feb	1.5	0	42	153

Table 4 Annual estimates of the moult parameters of adult male and female Curlew Sandpipers in South Africa based on the proportion of feather mass grown (PFMG) of the tract of 10 primaries combined.

Year	Males						Females					
	Moult start		Duration		Mean moult end		Mean moult start		duration		Mean moult end	
	Mean	sd	d	sd	Mean	sd	Mean	sd	d	Sd	Mean	sd
1970	12 Sep	8.2	158.8	0.4	18 Feb	2.7	16 Sep	2.1	151	2.1	14 Feb	3.6
1971	28 Sep	5.1	131.9	1.7	7 Feb	5	5 Oct	6.4	131.9	8.1	14 Feb	2.1
1972	25 Sep	4.5	133.4	1.7	5 Feb	6.4	6 Oct	4.1	124.4	2.5	8 Feb	3
1973	8 Oct	3.8	110.6	0.7	27 Jan	2.3	18 Oct	7.8	110.6	4.4	6 Feb	1.6
1974	2 Oct	9	126.9	2	6 Feb	5.6	23 Oct	3.4	129.2	2.6	29 Feb	1.5

Table 5 Annual estimates of the start date of moult of male and female Curlew Sandpipers in north-western Australia. Start dates of moult were estimated by assuming a common duration of moult and standard deviation of start date for either sex. Common duration of moult in males: 122.8, common SD: 15.1. Common duration of moult in females: 128.1, common SD: 14.6.

Year	Males				Females			
	Mean moult start		Moult end date		Mean moult start		Moult end date	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
1982	21 Sep	3.0	21 Jan	1.9	24 Sep	3.9	30 Jan	3.7
1983	22 Sep	3.7	22 Jan	7.5	22 Sep	3.5	28 Jan	3.0
1985	28 Aug	3.8	29 Dec	2.6	23 Oct	6.0	28 Feb	4.8
1986	18 Sep	9.0	19 Jan	3.1	27 Sep	8.0	3 Feb	3.8
1988	14 Oct	9.4	13 Feb	7.4	20 Oct	9.5	25 Feb	1.0
1990	9 Sep	6.3	10 Jan	7.8	21 Sep	3.2	27 Jan	9.4
1991	3 Oct	2.9	2 Feb	6.9	12 Oct	4.0	17 Feb	6.2
1992	18 Sep	2.7	19 Jan	2.1	22 Sep	2.9	28 Jan	2.9
1993	11 Oct	1.9	10 Feb	6.5	26 Oct	9.7	2 Mar	2.7
1994	5 Oct	5.0	4 Feb	1.1	12 Oct	6.8	17 Feb	1.9
1995	9 Sep	8.2	9 Jan	1.6	14 Sep	7.4	20 Jan	5.0
1996	4 Oct	5.7	4 Feb	1.0	14 Oct	5.1	19 Feb	2.6
1997	1 Sep	2.6	2 Jan	1.0	3 Sep	3.7	9 Jan	3.7
1998					15 Sep	8.9	21 Jan	4.0
1999	14 Sep	3.7	15 Jan	3.0	20 Sep	4.3	26 Jan	6.9
2000	3 Sep	4.0	3 Jan	3.2	16 Sep	4.6	22 Jan	5.1
2001	14 Sep	6.9	14 Jan	1.4	23 Sep	9.6	30 Jan	5.1
2002	15 Sep	5.1	15 Jan	1.3	20 Sep	5.8	26 Jan	4.4
2003	9 Aug	4.4	9 Dec	1.9	17 Oct	5.2	22 Feb	3.6
2004	27 Sep	3.7	27 Jan	1.4	07 Oct	4.6	12 Feb	3.1
2005	18 Sep	5.1	18 Jan	1.3	24.Sep	5.0	30 Jan	3.1
2006	15 Sep	6.8	16 Jan	3.1	17.Sep	2.6	23 Jan	3.2

Table 6 Annual estimates of the start date of moult of male and female Curlew Sandpipers in south-eastern Australia. Start dates of moult were estimated by assuming a common duration of moult and standard deviation of start date for either sex. Common duration of moult in males: 122.9, common SD: 19.3. Common duration of moult in females: 129.0, common SD: 14.4.

Year	Males				Females			
	Mean moult start		Moult end sate		Mean moult start		Moult end sate	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
1978	17 Oct	1.4	16 Feb	0.5	21 Oct	1.5	27 Feb	2.5
1979	16 Oct	1.1	16 Feb	0.1	21 Oct	1.5	27 Feb	2.3
1980	15 Oct	2.1	15 Feb	3.0	19 Oct	1.5	25 Feb	3.7
1981	18 Oct	1.5	18 Feb	1.0	22 Oct	1.5	28 Feb	4.6
1982	20 Oct	1.4	20 Feb	0.5	24 Oct	1.5	1 Mar	3.0
1983	12 Oct	1.5	12 Feb	2.5	17 Oct	1.5	23 Feb	2.8
1984	16 Oct	1.1	15 Feb	1.5	20 Oct	2.1	26 Feb	1.9
1985	20 Oct	1.5	20 Feb	1.0	24 Oct	1.5	1 Mar	3.7
1986	17 Oct	1.5	17 Feb	2.0	20 Oct	1.5	26 Feb	4.9
1987	16 Oct	1.6	16 Feb	1.0	20 Oct	2.0	26 Feb	3.6
1988	22 Oct	1.5	22 Feb	2.0	26 Oct	1.5	3 Mar	4.5
1989								
1990	21 Oct	1.5	21 Feb	1.0	25 Oct	1.5	2 Mar	5.2
1991	21 Oct	1.5	20 Feb	2.5	25 Oct	1.5	2 Mar	4.2
1992	13 Oct	1.9	13 Feb	4.9	18 Oct	1.9	24 Feb	4.2
1993	20 Oct	1.9	20 Feb	3.8	25 Oct	1.9	2 Mar	2.7
1994	20 Oct	1.4	19 Feb	2.7	24 Oct	1.4	1 Mar	5.6
1995	20 Oct	2.5	20 Feb	5.6	25 Oct	1.5	2 Mar	4.3

Table 6 continued

Year	Males				Females			
	Mean moult start		Moult end sate		Mean moult start		Moult end sate	
1996	14 Oct	2.3	14 Feb	4.1	19 Oct	2.3	25 Feb	6.0
1997	19 Oct	1.2	19 Feb	3.7	23 Oct	2.2	1 Mar	0.8
1998	17 Oct	1.0	16 Feb	5.9	21 Oct	1.0	27 Feb	5.4
1999	16 Oct	1.0	16 Feb	3.5	20 Oct	1.0	26 Feb	1.0
2000	14 Oct	1.1	14 Feb	7.9	18 Oct	2.5	24 Feb	1.0
2001	17 Oct	1.0	17 Feb	3.0	21 Oct	1.0	27 Feb	2.5
2002	20 Oct	2.0	20 Feb	3.0	25 Oct	2.5	2 Mar	2.0
2003	19 Oct	1.5	18 Feb	1.0	24 Oct	1.5	1 Mar	3.0
2004	16 Oct	1.5	16 Feb	1.0	21 Oct	1.5	27 Feb	1.0
2005	17 Oct	1.0	17 Feb	1.5	22 Oct	1.0	28 Feb	2.5
2006	13 Oct	3.8	13 Feb	1.1	31 Oct	5.4	8 Mar	2.5
2007	14 Oct	2.5	14 Feb	2.0	21 Oct	1.0	27 Feb	2.0
2008	16 Oct	3.4	16 Feb	3.4	23 Oct	1.0	29 Feb	3.0

Table 7 Summary of the start date and duration of moult (all years combined) of male and female Curlew Sandpipers in good and poor breeding years in South Africa (SA), north-western Australia (NWA) and south-eastern Australia (SEA).

Site		Males		Females		F	p
		Start (sd)	Duration (sd)	Start (sd)	Duration (days)		
SA	All	27 Sep (1.2)	131.5 (1.2)	08 Oct (1.1)	123.9 (2.2)	7.27	0.045
	good	05 Oct (2.1)	128.5 (2.7)	07 Oct (2.2)	123.4 (2.2)		
	poor	02 Oct (1.5)	139.2 (4.8)	29 Sep (1.9)	129.6 (4.6)		
NWA	All	16 Sep (0.8)	132.1 (0.7)	30 Sep (0.9)	130.0 (1.1)	8.79	0.001
	good	17 Sep (1.1)	121.5 (1.1)	28 Sep (1.4)	123.9 (2.5)		
	poor	13 Sep (0.9)	136.9 (1.0)	17 Sep (1.4)	125.6 (1.3)		
SEA	All	15 Oct (0.9)	124.0 (0.9)	24 Oct (0.8)	114.2 (1.0)	9.16	0.003
	good	16 Oct (1.2)	110.5 (1.2)	26 Oct (1.1)	110.5 (1.8)		
	poor	15 Oct (0.9)	131.1 (2.0)	14 Oct (0.6)	125.6 (1.3)		

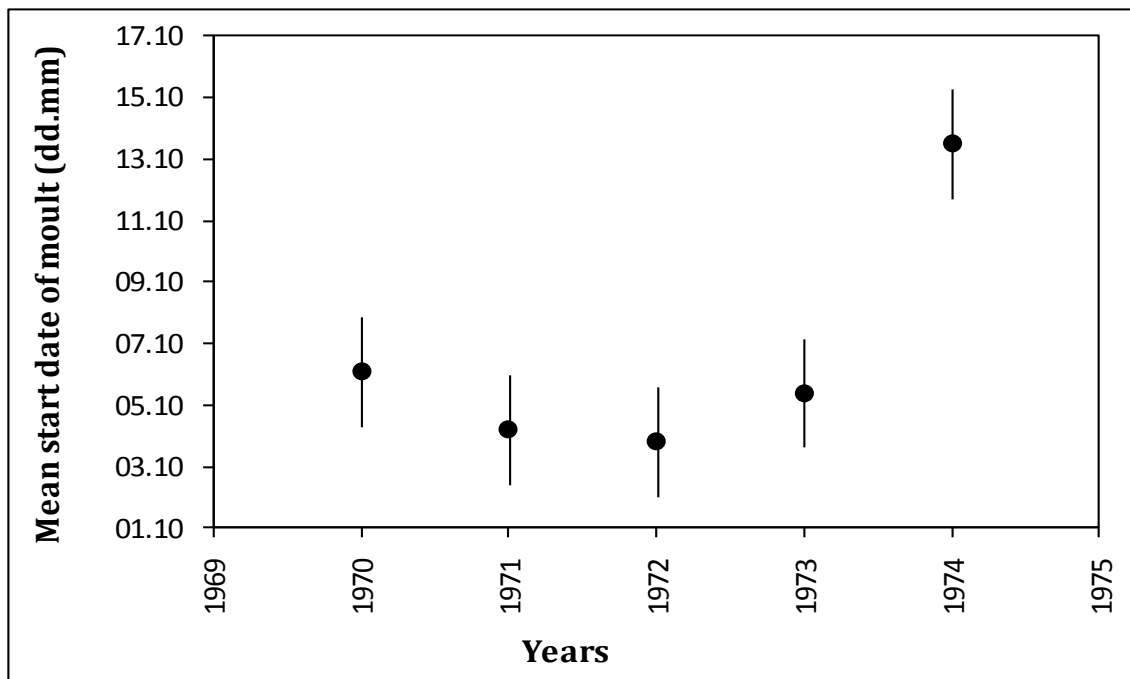


Fig. 1 Annual estimates of the moult start date of adult Curlew Sandpiper in South Africa (1970–1974) based on the proportion of feather mass grown of all primaries combined.

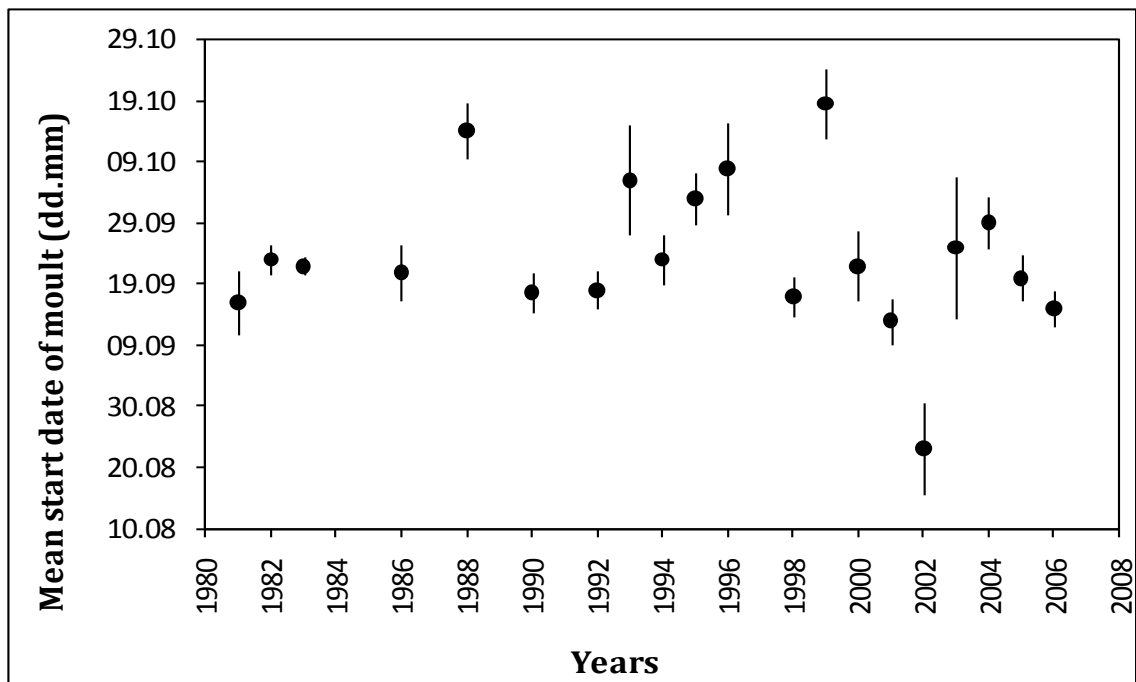


Fig. 2 Annual estimates of the moult start date of adult Curlew Sandpiper in north-western Australia (1983–2006) based on the proportion of feather mass grown of all primaries combined.

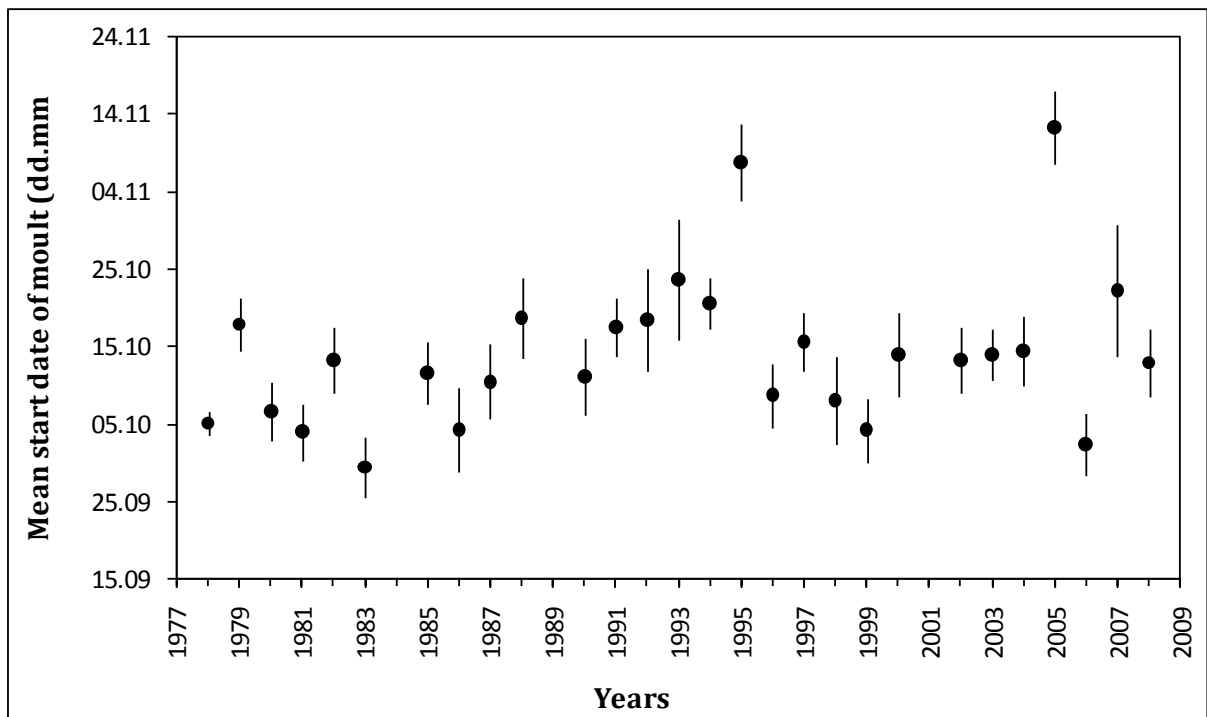


Fig. 3 Annual estimates of the moult start date of adult Curlew Sandpipers in south-eastern Australia (1978–2008) based on the proportion of feather mass grown of all primaries combined.

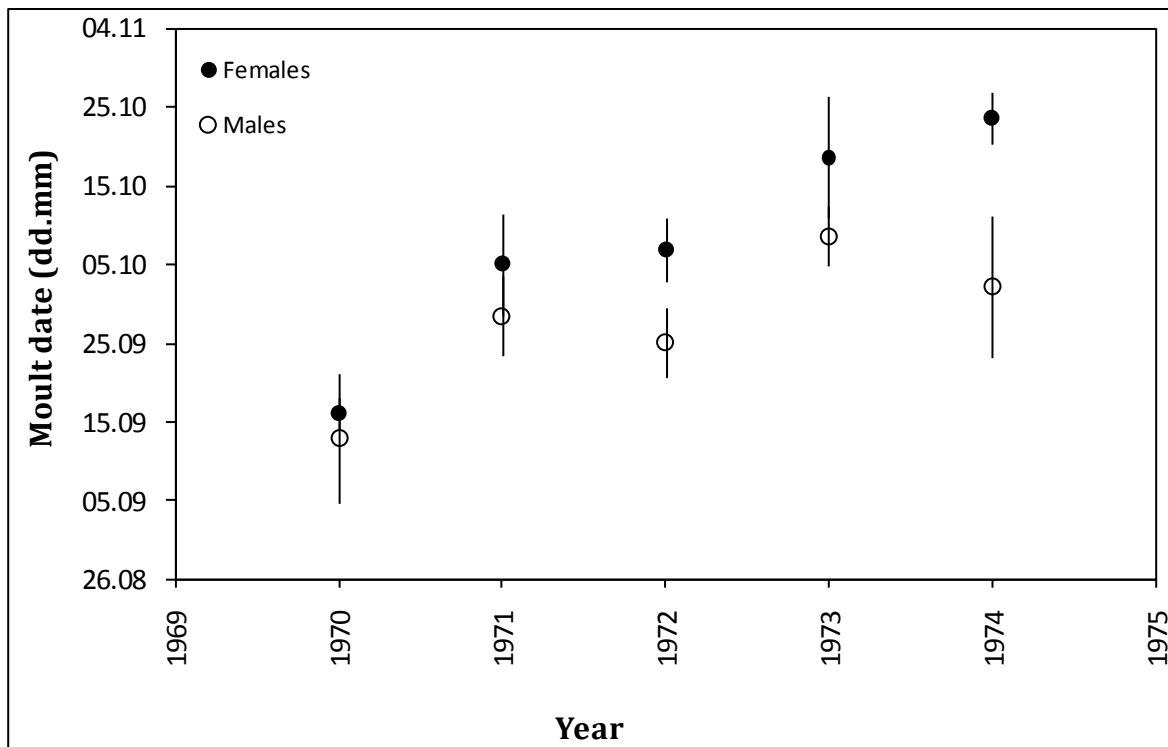


Fig. 4 Annual estimates of moult start date of adult male and female Curlew Sandpipers in South Africa based on the proportion of feather mass grown of all primaries combined.

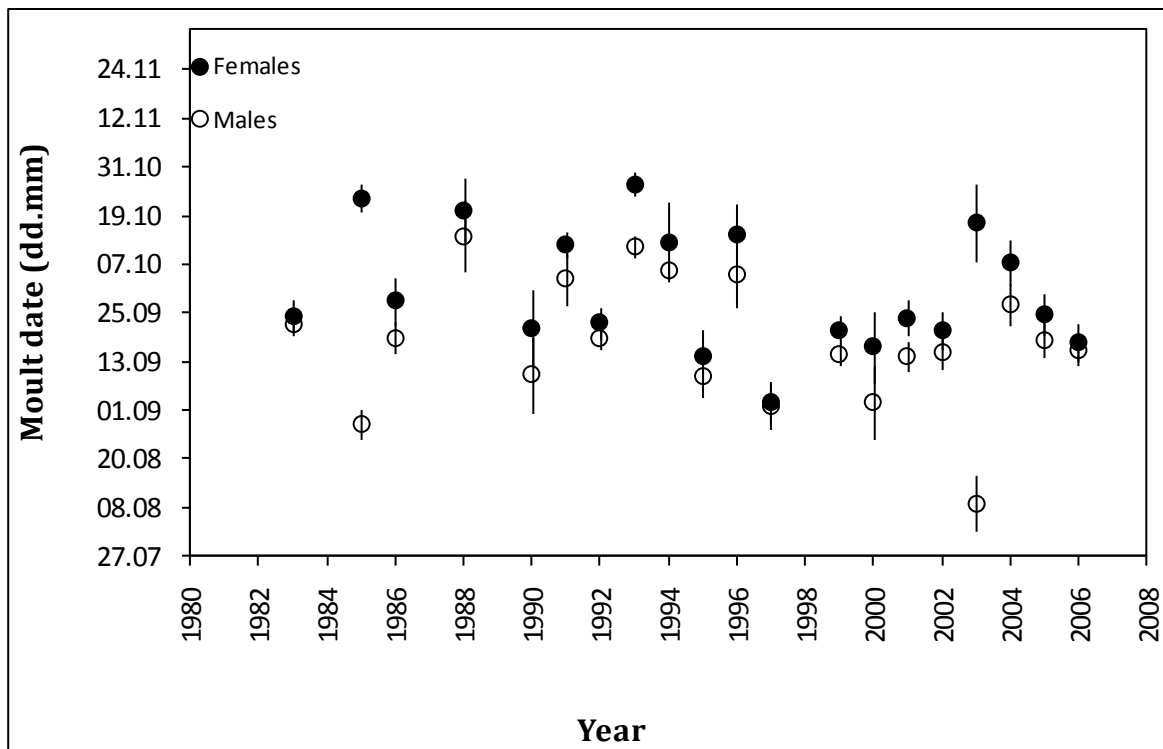


Fig. 5 Annual estimates of moult start date of adult male and female Curlew Sandpipers in north-western Australia based on the proportion of feather mass grown of all primaries combined.

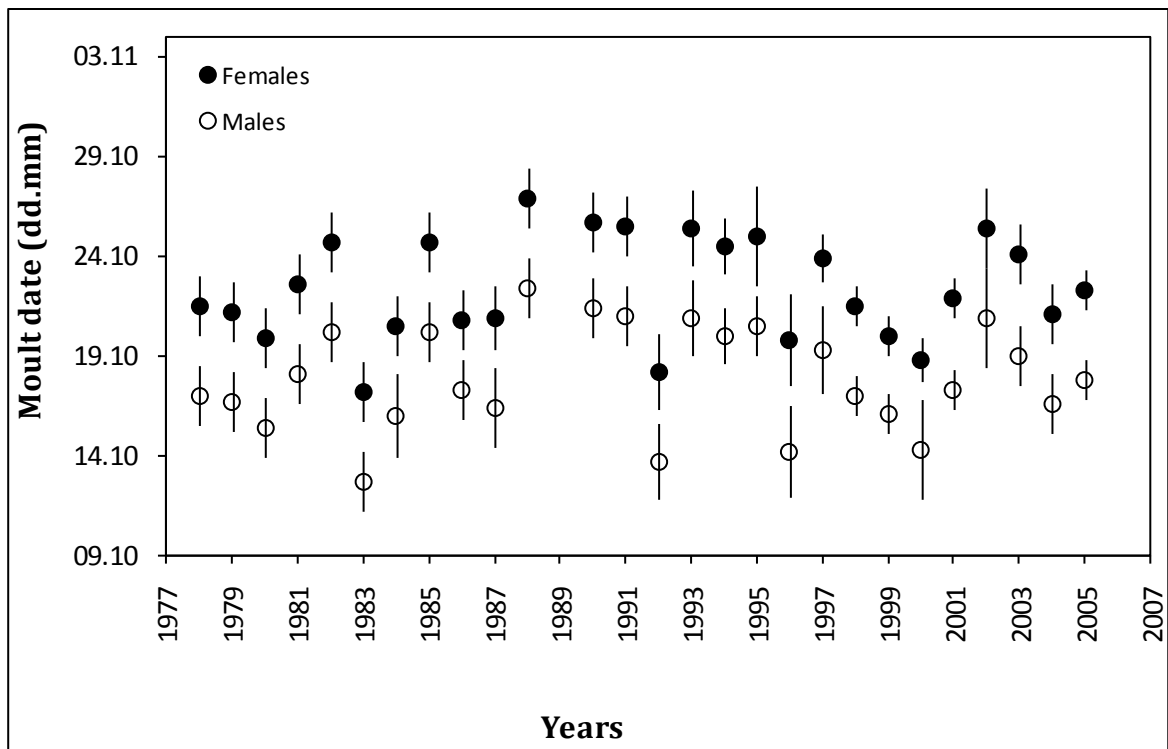


Fig. 6 Annual estimates of moult start date of adult male and female Curlew Sandpipers in south-eastern Australia based on the proportion of feather mass grown of all primaries combined.

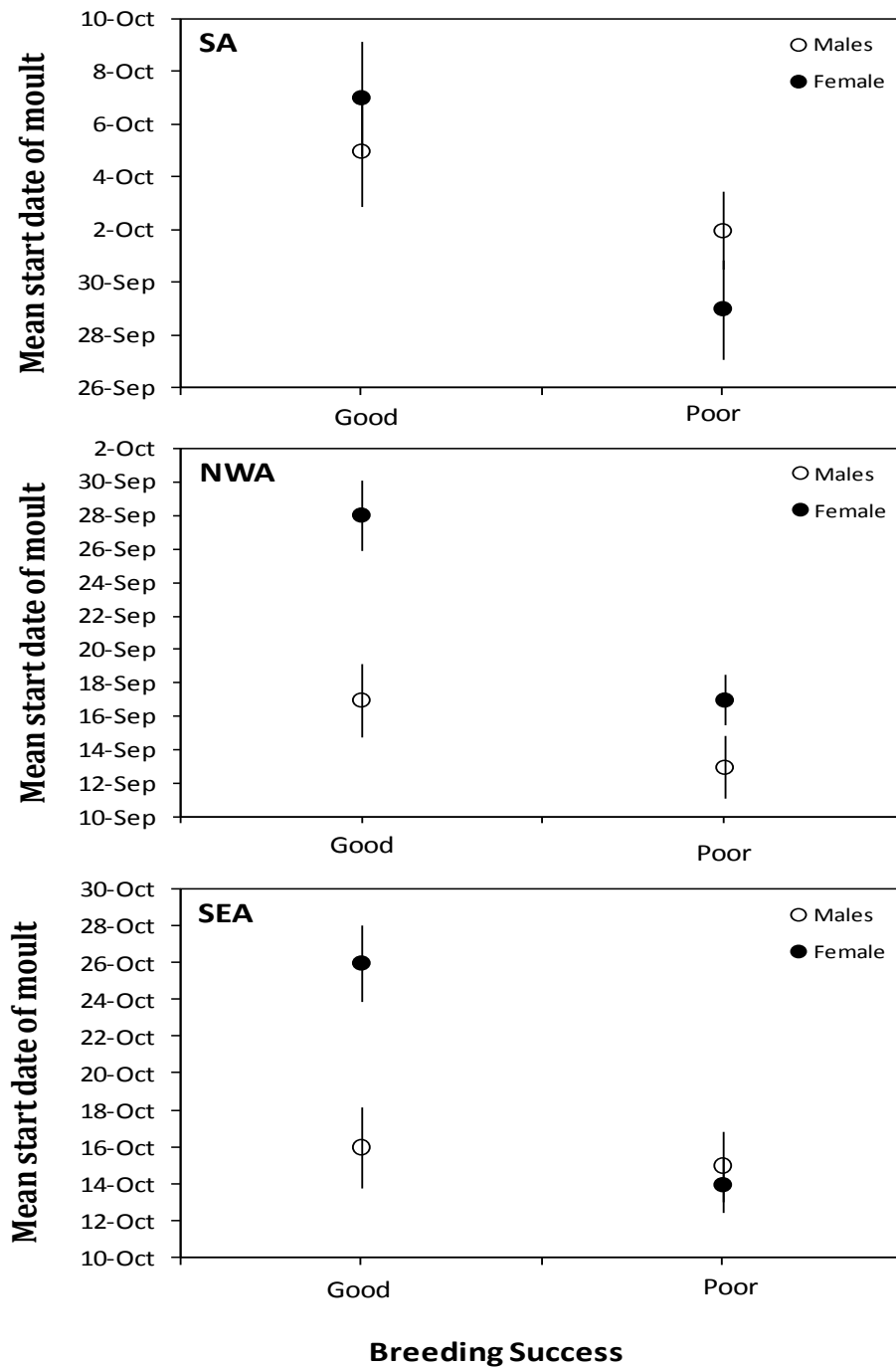


Fig. 7 Summary of the start date of moult of male (open circles) and female (solid black circles) Curlew Sandpipers in good and poor breeding years in South Africa (SA), north-western Australia (NWA) and south-eastern Australia (SEA).

CHAPTER 6

DIFFERENTIAL MOULT STRATEGIES OF ADULT CURLEW SANDPIPER IN KENYA AND INDIA IN RELATION TO CLIMATIC CONDITIONS

University of Cape Town

**DIFFERENTIAL MOULT STRATEGIES OF ADULT CURLEW SANDPIPER
IN KENYA AND INDIA**

ABSTRACT

Moult of adult Curlew Sandpiper *Calidris ferruginea* was studied at the non-breeding sites in Kenya and India. Parameters of moult (start date, duration and standard deviation) and the pattern of moult of individual primaries was estimated. The estimated start date of moult in Kenya was 2 October, duration 128 days and in India the estimated start date of moult was 15 August, duration 107 days. The estimated daily rate of feather material growth was 0.88%/day in Kenya; the rate of feather material grown was relatively uniform at the beginning and middle of moult but feather material growth accelerated towards the end of moult. In India, the estimated daily rate of feather material growth was 0.93%/day; the daily rate of feather material grown was relatively uniform at the beginning and middle of moult but moult progress slowed down towards the end of moult. Circumstantial evidence suggests that the rate of growth of the primaries is also affected by food supply. The onset and duration of moult in both Kenya and India appeared to have been timed to coincide with rainfall periods, an adaptation to carry out this energy demanding activity at a period of food abundance.

INTRODUCTION

The different moult strategies undertaken by long-distance migratory waders have been interpreted as adaptive responses to a variety of factors such as their geographical origin (Prater *et al.* 1977, Prater 1981, Ginn & Melville 1983), seasonal patterns of food abundance (Prater 1981), and the length of the migratory journey to the winter quarters (Morrison 1976). An emerging pattern in the primary moult characteristics of populations on their non-breeding areas at different latitude is that the start of moult is later and takes longer in populations at tropical or southern latitudes than those which moult in north temperate areas (Underhill 2003, Summers *et al.* 2004, Serra & Underhill 2006). Unpredictable food resources and feeding opportunities for shorebirds during the winter months have been cited as reasons for the early start and quick completion of moult observed in the populations moulting at temperate latitudes (Prater 1981, Underhill 2003, Summers *et al.* 2004, Summers *et al.* 2010).

For many populations of waders that migrate to the tropics, the distance between their breeding areas and non-breeding sites explains the variation in the onset of moult. In Africa, for instance, populations of species such as the Grey Plover *Pluvialis squatarola* (Serra 2000), Wood Sandpiper *Tringa glareola* (Remisiewicz *et al.* 2009), and Curlew Sandpiper *Calidris ferruginea* (Elliott *et al.* 1976, Pienkowski *et al.* 1976) at more northern latitudes of Africa start moult earlier than populations farther south. It has been shown that rainfall pattern within the tropics modify the schedule of moult in other groups of birds such as some *Euplectes* species and *Quelea quelea* (Oschadleus 2005, Oschadleus & Underhill 2006, Oschadleus & Underhill 2008), but it is not known if migrant waders that moult in tropical

areas modify their timing of moult according to weather patterns on their non-breeding areas. If rainfall patterns affect food abundance and food abundance in turn affects the timing and rate of moult, then the weather patterns in the tropics can potentially modify the schedule of moult. To explore the potential link between rainfall patterns on the non-breeding areas and the schedule of moult in long-distance migratory waders, we examine the moult pattern of populations of Curlew Sandpiper at similar latitudes in Kenya and India, two regions with contrasting weather patterns, especially in the timing of the wet season.

The Curlew Sandpiper is a migratory wader (shorebird) that breeds on the tundra of Arctic Siberia. It has a wide non-breeding (wintering) distribution spanning Africa, the Indian subcontinent, and Australasia (Cramp & Simmons 1988, del Hoyo *et al.* 1996). Primary moult is usually carried out on the non-breeding grounds (Cramp & Simmons 1988). There is little detailed account of the moult patterns of this species in these regions. Both regions occur at similar latitudes in tropical regions, but each area has different season and weather characteristics. The aim of this study is to describe primary moult pattern of Curlew Sandpipers in Kenya and India, with the purpose of explaining the moult strategies in relation to weather conditions at both areas. The study contributes information on how birds can modify the timing of their moult in relation to environmental conditions.

METHODS

The data from Kenya were collected at various sites around the coastal regions of the Rift Valley (00°22'N–03°20'S, 35°02'–39°58' E; Fig. 1) from 1978–1988. The data from India were collected at Mandapam (9°17'N, 79°8'E) and at the Great Vedaranyam Swamp (10°18'N,

79°51'E), in south-eastern India as part of the Bombay Natural History Society's Bird Migration Project between 1980 and 1992 (Balachandra *et al.* 2000; Fig. 1). Birds were aged based on feather appearance and wing condition as described in, for instance, Prater *et al.* (1979). The moult of birds aged as adults is explored in this study. Moulting scores of the primaries were recorded using the British Trust for Ornithology technique (Ginn & Melville 1983); old feathers were scored 0, new feathers 5, and growing feathers 1–4 depending on their stage of growth. Moulting scores were converted into moulting indices following the relationship: moulting score 0 = 0, 1 = 0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875, and 5 = 1.000 (Underhill & Summers 1993, Underhill & Joubert 1995), a process which aimed to achieve linearity through time of moulting progression (Summers 1980). Moulting indices were then transformed into the proportion of feather mass grown (PFMG) using the relative masses of primary feathers (Underhill & Joubert 1995).

The start date and duration of primary moulting of all years combined was estimated based on the methods of Underhill and Zucchini (1988) and Underhill *et al.* (1990). The samples of birds captured in each region were assumed to be part of a population that arrived with old feathers, moulted and remained in the region so that the data were taken as type 2 of the Underhill & Zucchini (1988) model. This method was also used to estimate yearly moulting parameters at both sites. Due to limited moulting records in Kenya, the yearly moulting estimates were obtained by fitting a model which assumed a separate start date of moulting for each year and a common duration of moulting and standard deviation. The start dates and duration of moulting for individual primaries were also estimated following Serra (2002), Underhill (2003) and Remisiewicz *et al.* (2009).

An estimate of the gap in the wing during moult was obtained for each individual from the proportion of feather mass missing (PFMM), an extension of the raggedness score (Haukioja 1971) but takes into account the relative sizes of the missing feathers (Remisiewicz *et al.* 2009, Ward *et al.* 2009). To calculate PFMM, the opposite approach to the calculation of PFMG was used. Feathers that had moult scores 1, 2, 3 and 4 were given a corresponding moult indices of 0.875, 0.625, 0.375 and 0.125 respectively to represent the relative mass for the missing feathers (Remisiewicz *et al.* 2009, Ward *et al.* 2009). Both old and fully grown new feathers were given a moult index of 0. PFMM of the 10 primaries were summed which gave a measure of the relative size of the wing gap for individual birds.

Moult in relation to weather pattern

To relate the onset and duration of moult in Kenya and India with weather patterns in the two countries, the monthly averages of rainfall and temperature were obtained from the National Oceanic and Atmospheric Administration (NOAA) stations in each of the two countries. The data from Kenya was from the NOAA station on the coast at Malindi (03°23'S, 40°12'E) where the rainfall data at the study sites was obtained. The data from India was from the station in Pamba (09°16'N, 79°18'E), c. 6 km east of the Mandapam study site.

RESULTS

The estimated start date of moult in Kenya using the PFMG of the tract of all primaries combined was 6 October, the duration was 137 days, and end date of moult was 20 February (Fig. 2). The estimated standard deviation of the start date of moult was 39.5 days; thus 95% of birds were estimated to start moult between 21 July and 23 December. In India,

the estimated start date of moult estimated from the PFMG of the tract of all primaries was 26 July, duration was 145 days, and moult end date was 18 December (Table 3, Fig. 2). The estimated standard deviation of start date was 31.5 days; 95% of birds were estimated to start moult between 18 May and 03 October. The annual estimates of the start date of moult in Kenya varied from 24 July to 21 October (Table 4). In India the annual estimate of the start date of moult ranged from 4 July to 26 September (Table 4).

In Kenya, estimated starting date of P1 and moult end date of P10 were 2 October and 7 February, respectively, suggesting an overall moult duration of 128 days (Table 1, Fig. 3). In India, these dates were 15 August and 30 November, suggesting a moult duration of 107 days (Table 2, Fig. 3). There was a difference in the estimated start date and duration of moult from the tract of 10 primaries combined and the estimates obtained when considering the moult of individual primary feathers. In Kenya, there was a two-day difference in the moult start date, nine-day difference in the moult duration, and a 13-day difference in the end date of moult between the two methods (Table 1). In India, there was a 21-day difference in the start date of moult, a 38-day difference in the moult duration, and a 16-day difference in the end date of moult from the two methods (Table 2). The temporal distribution of moult scores indicates that the progress of moult in Kenya was faster towards the end of moult compared to the beginning, whereas in India, the progress of moult was slower towards the end compared to the beginning. Both deviations from the assumed constant progress of moult assumption lead to an overestimation of the duration of moult. Therefore, in discussing the difference in the estimates of moult between Kenya and India, we will refer to estimates obtained from individual primaries.

In Kenya, the duration of moult of individual primaries increased from 10 days (P1) to 23 days (P10) (Table 1), while in India duration of moult of P1 was also 10 days increasing to 40 days for P10 (Table 2). In Kenya the interval between the shedding of neighbouring primaries increased from nine days between P1 and P2 to a maximum of 23 days between P8 and P9 while the interval between the shedding of neighbouring primaries in India ranged from one day between P1 and P2 to a maximum of 12 days between P9 and P10. The shorter interval between the moult of primaries coupled with the longer duration of moult of individual primaries in India compared to Kenya resulted in greater overlap in the growth of successive primaries (Table 3, Fig. 4). Consequently, the average number of primaries growing simultaneously in India was larger (average: 2.3, range: 1.4–3.2) than the average number in Kenya (average: 1.6; range: 1.1–2.4) and this difference was statistically significant (t -test: $t = -2.27$, $P = 0.03$, $df = 18$, Fig. 4).

Rate of moult

By dividing the relative mass of each primary by its moult duration, the PFMG/day of each primary was estimated (Table 1). By summing up the PFMG/day for all feathers growing simultaneously on any given day, the daily rate of feather material production for the entire moult period could be modelled, a method demonstrated by Remisiewicz *et al.* (2009). The daily rate of feather material growth in Kenya was estimated at an average of 0.88%/day (Table 1), less than the estimated rate of PFMG/day in India of 0.93%/day (Kolmogorov-Smirnov test: $D = 0.39$, $P = 0.019$). The daily rate of feather material grown was relatively uniform at the beginning and middle of moult in Kenya; this is demonstrated by the almost

linear cumulative curve of PFMG until a value of c. 76% is reached; thereafter, towards the end of moult in Kenya, rate of feather material growth accelerated (Fig. 5). In contrast, in India, the opposite pattern was observed; moult progress slowed down in India towards the end of moult (Fig. 5). Consequently, in Kenya the 25th percentile of primary feather mass production was achieved after 33 days (average 0.82 PFMG/day), 50th percentile in 41 days (average of 0.65 PFMG/day), 75th percentile in 33 days (average of 0.87 PFMG/day), and 100th percentile in 22 days (average of 1.10 PFMG/day). In India, the 25th percentile of primary feather mass production was achieved after 21 days (average 1.21 PFMG/day), 50th percentile in 28 days (average 0.97 PFMG/day), 75th percentile in 27 days (average 0.97 PFMG/day), and 100th percentile in 34 days (average 0.80 PFMG/day). These are close to the values obtained by assuming constant rate of feather material deposition despite the fluctuation of feather material growth above and below the overall average.

Proportion of feather mass missing

The average proportion of feather missing (PFMM) per day in Kenya was estimated at 0.028, the average of the daily minima was 0.01 and the average of the daily maxima was 0.05 (Fig. 6). This means that, on average, 2.8% of the mass of primary feathers was missing during moult at any one time. The average PFMM/day in India was 0.020 (average min–max range: 0.011–0.013); 2.0% of the mass of primary flight feathers was missing during moult at any one time. The PFMM was negatively correlated with PFMG in both Kenya ($r = -0.24$, $P = 0.01$) and India ($r = -0.54$, $P < 0.001$). PFMM in Kenya was not correlated with the average number of primaries in moult ($r = -0.12$, $P = 0.08$) whereas in India there was a negative

correlation between PFMM and the average number of primaries in moult ($r = -0.647$, $P < 0.001$).

Timing of moult in relation to rainfall and temperature pattern

The start dates of moult of the Curlew Sandpiper in Kenya and India corresponded well with rainfall seasons in these areas (Fig. 7). Most regions in Kenya experience two rainy seasons: the “long rains” extends roughly from March to June, and the “short rains” lasts from approximately October to December (Kenya Meteorological Department 2009). Adult Curlew Sandpipers arrive at the coast of Kenya in August (Pearson 1969) but moult is delayed until October to coincide with the onset of the short rain season. While there is no specific information about the timing of arrival of the Curlew Sandpiper in India, studies in other species like the Grey Plover indicate that waders reach India in July (Balachandran *et al.* 2000). Curlew Sandpipers in India thus commence moult about two weeks after arrival, coinciding with the Monsoon rains which extend from June through September (Guhathakurta & Rajeevan 2006).

DISCUSSION

Pattern of primary moult

Similar to the pattern of moult observed in Curlew Sandpipers moulting in southern Africa (Elliott *et al.* 1976, Chapter 3), north-western and south-eastern Australia (Minton *et al.* 2006, Chapter 3), Tasmania (Thomas & Dartnall 1971) and Morocco (Pienkowski 1976), Curlew Sandpipers moulting in Kenya and India moulted and grew their three inner primaries simultaneously at the beginning of moult, while only two or even one feather

were moulted at a time towards the end (Fig. 3). This pattern has also been observed in similar-sized waders such as Sanderling *Calidris alba* (Underhill 2003), and Wood Sandpiper *Tringa glareola* (Remisiewicz *et al.* 2009). It is likely to be an adaptation by these species to minimize the size of wing gap during moult because gaps in the wing compromise flight efficiency (Tucker 1991, Swaddle & Witter 1997, Hedenstrom & Sunada 1999).

Two contrasting moult strategies were employed by Curlew Sandpipers in Kenya and India: a rapid moult of a single feather at a time in Kenya vs. a slow moult of several feathers simultaneously in India. This difference in moult strategies between Kenya and India suggest that either different sub-species are involved or conditions on the non-breeding areas are influencing the moult patterns. Since no geographic variation or sub-species have been found in the Curlew Sandpiper (Wennerberg & Burke 2001), it is likely that the divergent nature of these strategies is an adaptation by different populations to climatic conditions at these two locales. Despite this difference, both strategies are aimed at maintaining a uniform rate of feather material growth and, possibly, minimizing wing gap during moult. In Kenya, for instance, the constant daily rate of feather material growth was possible because of the overlap in the growth of the smaller inner primaries and little overlap in the growth of the larger outer primaries. The seven days overlap in the growth of P1 and P2 resulted in a combined PFMG/day of 0.85, a value similar to the amount of feather material deposited per day during the moult of P9 and P10 (0.89). This value is also close to the overall average daily feather material deposition throughout the moult period (0.88%/day).

On the other hand, the larger number of primaries moulted simultaneously in India would

normally imply that the amount of feather material deposited daily would increase progressively during moult especially towards the end of moult when the larger primaries are growing simultaneously. But the lower daily rate of feather material grown during the replacement of the outer five primaries (compared to Kenya) ensured a fairly constant rate of daily feather material growth.

On average, the amount of feather material missing was estimated at 3% in Kenya and 2% in India. This is smaller than the PFMM reported for adult and sub-adult (10% and 11% respectively) Wood Sandpipers (Remisiewicz *et al.* 2009, 2010). The average number of primaries growing simultaneously in the Wood Sandpiper was estimated at 2.4 (Remisiewicz *et al.* 2009), similar to the 2.3 found in the Curlew Sandpiper in India, although larger than the number in Kenya, 1.6. The size of wing gap could either be due to the number of primaries moulted simultaneously and/or the wing area (Hedenström 1998). In this instance, the difference in the amount of feather material missing might be a result of the Wood Sandpiper having a longer wing span (40–42 cm) thus larger wing area compared to the Curlew Sandpiper (50–56 cm), despite both species being of similar size at 19–22 cm (Cramp & Simmons 1983).

Timing of moult

Based on the estimated start date of moult of P1, moult on average started about two months earlier in India (15 August) compared to Kenya (2 October). Our estimated start date of moult in Kenya was similar to the preliminary result presented by Pearson (1984) of adult Curlew Sandpipers at Lake Magadi. To the best of our knowledge, there are no prior

estimates of moult start dates for Curlew Sandpipers in India to which we can compare our results, but in relation to the estimate start date of moult in the Grey Plover on 1 September (Balachandran *et al.* 2000), Curlew Sandpipers started moult about two weeks earlier.

Also, based on the start date of moult of P1 and moult end date of P10, moult duration of 107 days in India was shorter than moult duration in Kenya of 128 days (Table. 1 & 2). In India, the short duration of moult was achieved by shortening the interval between shedding of individual primaries, resulting in the growth of several feathers simultaneously; a tactic used by Grey Plovers (Serra 2000, Serra & Underhill 2006) and Ruddy Turnstone *Arenaria interpres* (Underhill 2003) to increase the rate of feather material growth. Birds in Kenya compensate for the late start of moult by increasing the rate of feather material growth, achieved through the increased growth rate of individual feathers rather than the number of feathers moulted simultaneously (Table 1). Overall, birds in Kenya and India completed moult in February and December, respectively, giving them sufficient time to prepare for northward migration to the breeding grounds.

The cost of an early moult start, especially within the tropics, is that strong sunlight coupled with a highly saline or alkaline environment causes new flight feathers to wear out within a few weeks (Evans 1976). Birds moulting early will likely migrate to their breeding grounds with fairly worn feathers. For Curlew Sandpipers in India, the early moult start might incur negligible fitness cost because of the short migratory distance to the breeding grounds compared to the population in, say, Australia (Chapter 4). Also, the slow moult of individual primaries would result in the production of high quality feathers (Serra 2001). Conversely,

by delaying start of moult, Curlew Sandpipers in Kenya could potentially increase the likelihood of migrating to the breeding grounds with fairly new feathers but the rapid moult of individual primaries would result in lower quality of feathers (Serra 2001) than would be otherwise.

Timing of moult in relation to rainfall patterns

Contrasting rainfall patterns between Kenya and India may explain the differences in the onset of moult in these areas. Most regions in Kenya experience two rainy seasons: the “long rains” extends roughly from March to June, and the “short rains” from approximately October to December (Kenyan Meteorological Department 2010). Adult Curlew Sandpipers arrive in Kenya in August (Pearson 1974), during the dry period between the two rainy seasons. The late start of moult in October suggests that moult was deliberately delayed until the “short rains” started (Fig. 7).

In India, Curlew Sandpipers commenced moult in August, soon after arrival in July, to coincide with the monsoon (rainfall) season which extends from June through September (Indian Meteorological Department 2010). However, the later part of the moult extends into the post-monsoon (or "retreating" monsoon) season, a period characterized by the rapid decline in rain, high daily temperatures and dry northeast winds (Indian Meteorological Department 2010). This change in weather pattern could potentially result in a decline of available prey for the Curlew Sandpiper, consequently resulting in a slower rate of moult of the outer five primaries.

The diet of the Curlew Sandpiper consists mostly of the larvae and imagos of Coleoptera, *Brachicera* sp., *Daphnia* sp., and *Bolboschoenus* sp. (Puttick 1979, Barker & Vestjens 1989). Studies show that both high and low temperatures reduce the hatchability of eggs and slow the larval development of these insect species (Howe 1956, Lee & Denlinger 1991). High temperatures coupled with low precipitation results in high evapotranspiration which leads to the hardening of the substrate from which prey has to be extracted. A decline in food during the post-monsoon rain is the likely reason for the slow rate of moult of the outer primaries in India, compared to the rate observed in comparable primaries in Kenya.

Empirical findings have demonstrated that food shortage slows moult in certain species. Riddle (1908) found that the linear growth rate of the feathers of Ring Doves *Streptopelia risoria* became much slower after three days of starvation. Ashmole (1962) found that in a population of the Black Noddy *Anous tenuirostris* primary moult was slower when food was inferred to be scarce than when it was more plentiful. However, there is also the possibility that the slowing down of moult in India could be that an early moult start afforded the birds plenty of time to complete moult. Johnson and Minton (1980) found that Dunlins initiating moult relatively early, moulted at a slower rate such that moult was completed more or less simultaneously with birds that started at a later date.

In conclusion, moult in the Curlew Sandpiper at the non-breeding areas in Kenya and India appears to be related to rainfall patterns in these regions. There is circumstantial evidence to suggest that the rate of growth of the primaries is affected by food supply. If, indeed, the timing of moult is sensitive to rainfall patterns, it suggests that moult is a potential variable

at measuring the impacts of climate change on life-history traits within the annual cycle of migratory birds.

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Table 1 Primary moult estimates of individual primaries of the Curlew Sandpipers in Kenya

Primaries	Moult parameters				Sample sizes			% PFMG/day
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	not in moult	in moult	moult complete	
P1	2 Oct (2.5)	10.8 (4.3)	51.3 (5.6)	13 Oct (4.0)	115	20	366	0.37
P2	6 Oct (2.3)	10.1 (4.1)	50.0 (5.4)	16 Oct (3.9)	121	19	361	0.48
P3	10 Oct (2.3)	12.7 (3.8)	47.4 (4.9)	23 Oct (3.7)	134	19	348	0.45
P4	17 Oct (3.3)	16.2 (3.6)	45.2 (4.2)	2 Nov (3.8)	138	41	322	0.33
P5	28 Oct (2.8)	16.4 (3.4)	42.8 (3.9)	14 Nov (3.8)	163	32	306	0.52
P6	12 Nov (3.1)	17.3 (4.0)	49.9 (4.1)	29 Nov (4.4)	188	30	283	0.6
P7	26 Nov (3.5)	22.6 (3.9)	46.4 (3.4)	19 Dec (4.5)	217	35	249	0.53
P8	19 Dec (3.4)	18.4 (4.2)	46.3 (3.1)	7 Jan (4.7)	252	24	225	0.76
P9	5 Jan (3.6)	18.4 (4.4)	47.7 (3.0)	24 Jan (4.7)	275	22	204	0.85
P10	15 Jan (4.4)	23.4 (4.5)	47.8 (2.9)	7 Feb (4.7)	287	25	189	0.77
Combined PFMG	6 Oct (3.0)	137 (5.3)	39.5 (1.7)	20 Feb (4.0)	115	193	185	0.88

Table 2 Primary moult estimates of individual primaries of the Curlew Sandpipers in India

Primaries	Moult parameters				Sample sizes			% PFMG/day
	Mean start date (SD)	Duration (SD)	Standard deviation of start date (SD)	End date (SD)	not in moult	in moult	moult complete	
P1	15 Aug (2.8)	10.1 (5.6)	20.8 (3.8)	23 Aug (3.3)	15	10	1736	0.40
P2	16 Aug (3.0)	10.7 (5.9)	23.1 (4.0)	27 Aug (3.5)	17	11	1733	0.45
P3	18 Aug (5.2)	14.3 (3.5)	22.0 (2.2)	2 Sep (3.4)	18	20	1723	0.40
P4	22 Aug (4.2)	15.2 (3.1)	20.6 (2.8)	7 Sep (2.7)	22	25	1714	0.46
P5	30 Aug (2.9)	16.7 (2.7)	18.0 (2.0)	16 Sep (2.1)	38	35	1697	0.51
P6	4 Sep (2.8)	26.2 (2.7)	20.5 (1.7)	1 Oct (2.0)	51	54	1663	0.40
P7	14 Sep (3.6)	35.3 (3.4)	35.4 (2.0)	20 Oct (2.7)	82	70	1613	0.34
P8	28 Sep (3.6)	38.1 (3.1)	44.7 (1.9)	5 Nov (2.7)	133	105	1525	0.36
P9	10 Oct (3.5)	38.7 (2.9)	45.7 (1.9)	17 Nov (2.7)	161	110	1480	0.40
P10	22 Oct (3.2)	39.7 (2.8)	43.9 (1.7)	30 Nov (2.4)	196	129	1405	0.45
Combined PFMG	26 Jul (4.0)	145 (4.4)	31.8 (1.2)	18 Dec (3.7)	22	377	778	0.96

Table 3 The number of days the growth of each primary feather overlapped in moult with the growth of adjacent primaries during moult of adult Curlew Sandpipers in Kenya and India.

	Kenya										India									
	P2	P3	P4	P5	P6	P7	P8	P9	P10		P2	P3	P4	P5	P6	P7	P8	P9	P10	
P1	7.1	3.1									9.1	9.1	2.9							
P2		6.1										9.7	4.5							
P3			6.2										9.1	1.1						
P4				4.4										7.2	2.3					
P5					2.2										12.8	5.9				
P6						2.9										19.3	2.6			
P7							-0.8										18.6	6.8		
P8								1.4										26.3	14.3	
P9									9.2											26.7

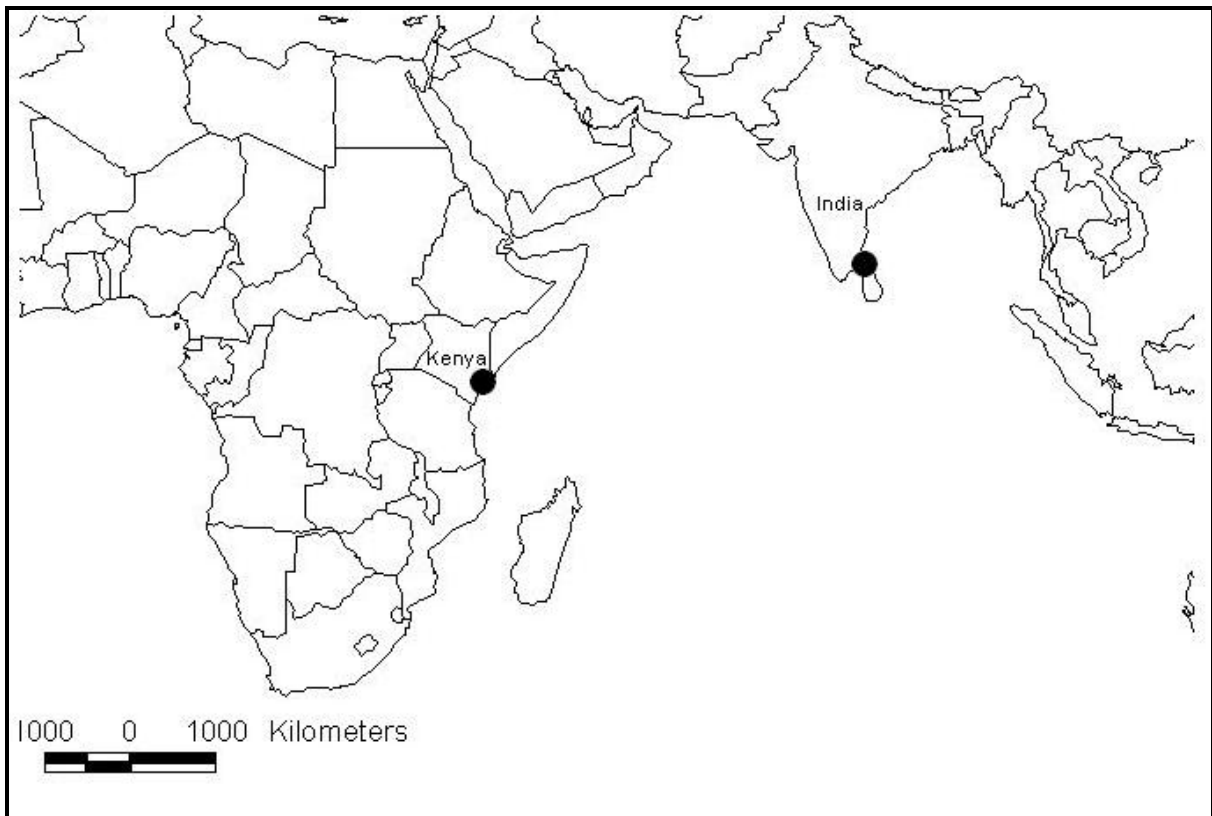


Fig. 1 Locations of the study sites in Kenya ($00^{\circ}22'N-03^{\circ}20'S$, $35^{\circ}22'-39^{\circ}58' E$) and India ($09^{\circ}17'-10^{\circ}18'N$, $79^{\circ}08'-79^{\circ}15'E$).

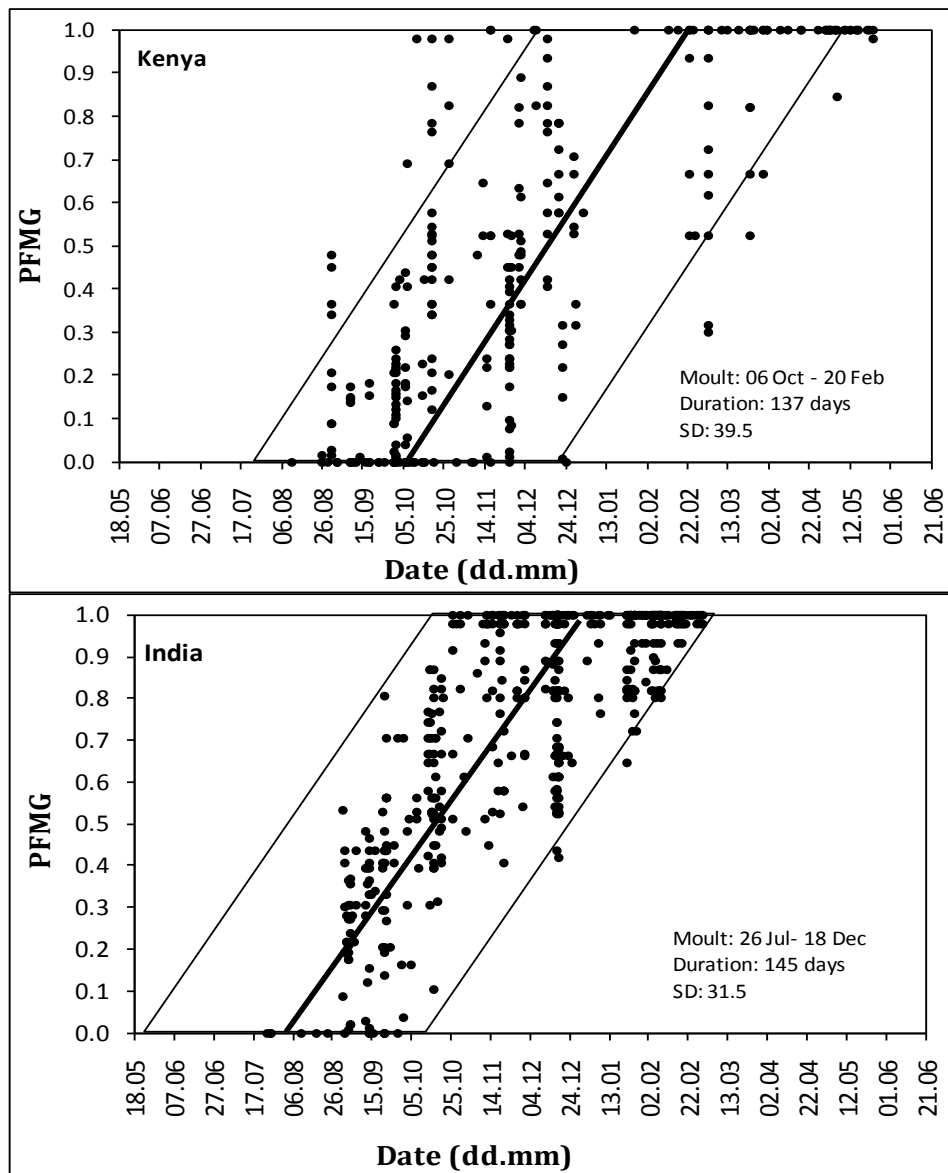


Fig. 2 Temporal distribution of the Proportion Feather Mass Grown (PFMG) of adult Curlew Sandpipers moulting in Kenya and India. Thick black line reflecting the course of moult from estimated start to end dates; thin lines—95% confidence intervals.

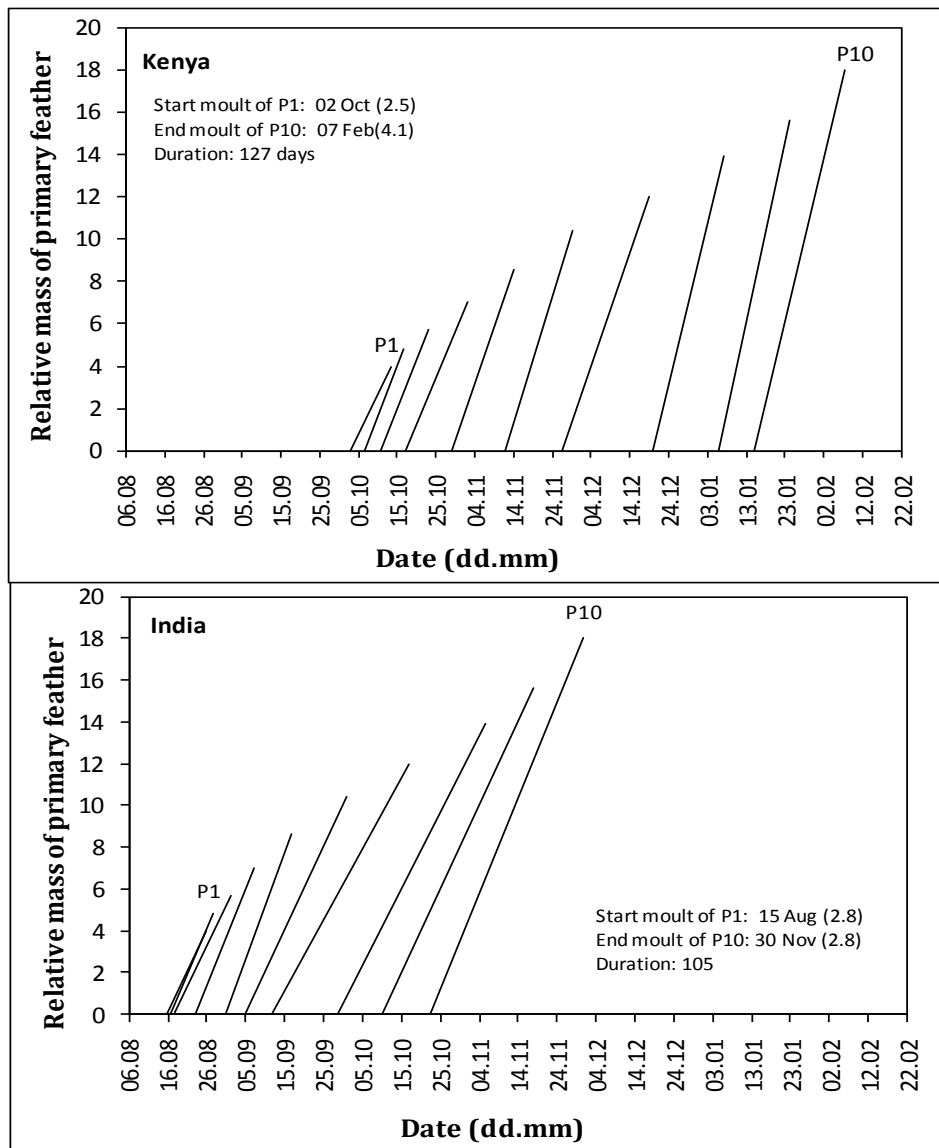


Fig. 3 Growth lines of primary feathers P1–P10 of Curlew Sandpipers in Kenya and India, showing the amount of the primary mass produced between start and end date of each primary development. Slopes of the lines reflect the growth rate of each primary.

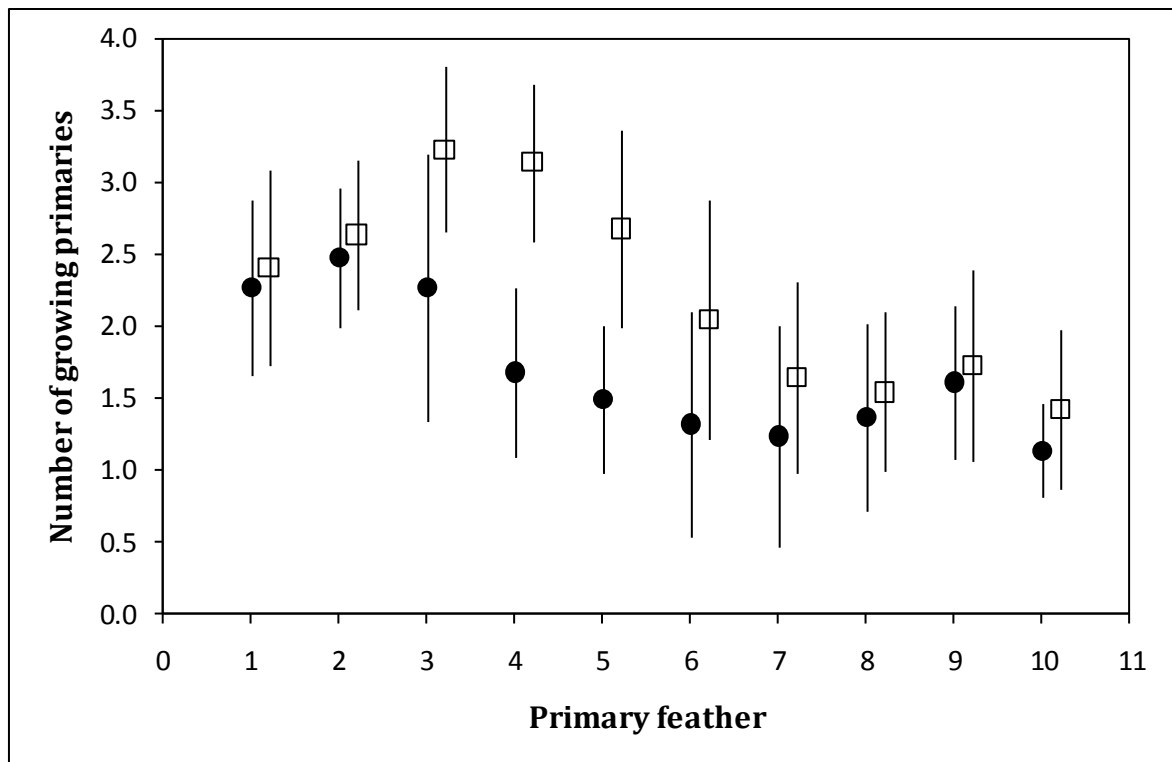


Fig. 4 Average number of primary feathers growing simultaneously during the moult of individual primaries (P1–P10). Solid circles = Kenya; open squares = India.

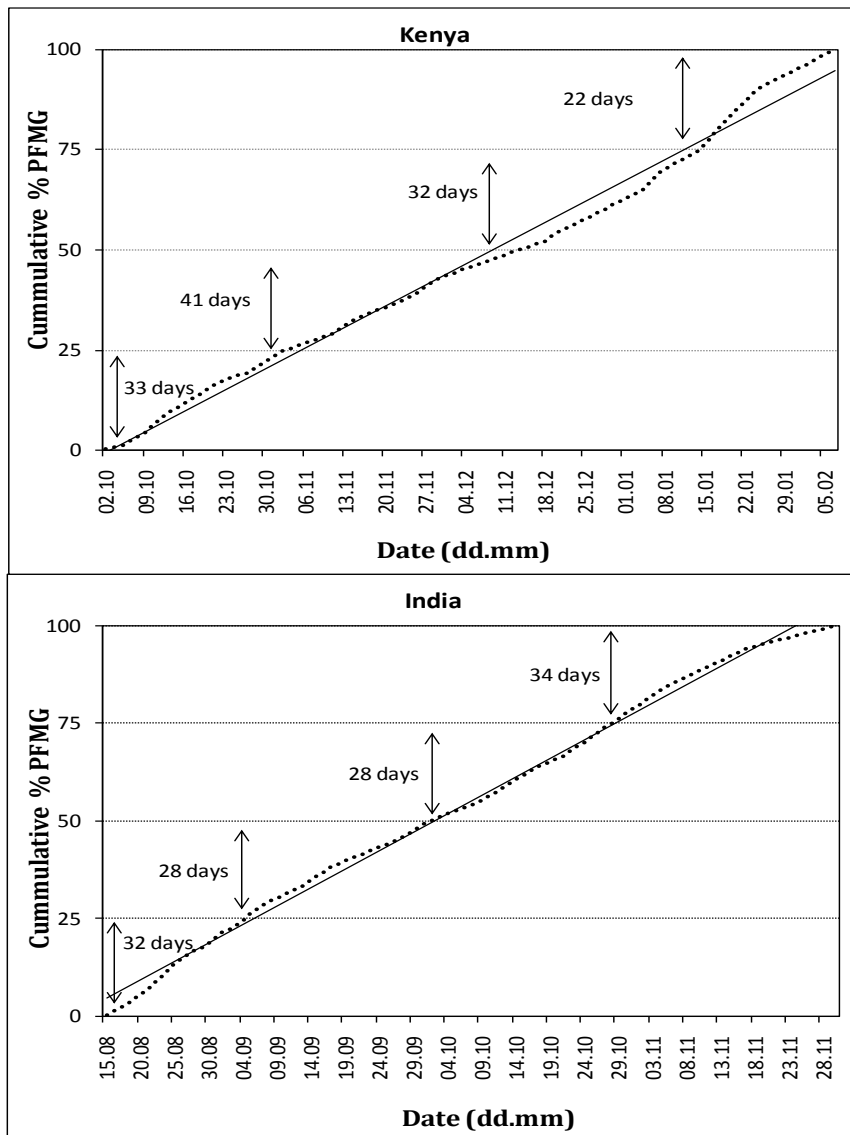


Fig. 5 Modelled cumulative rate of percentage feather mass grown (dotted lines) in Kenya and India estimated from daily values of the moult parameters of individual primary feathers (Tables 1 & 2). Thin lines are the linear regression lines fitted through the daily values of PFMG.

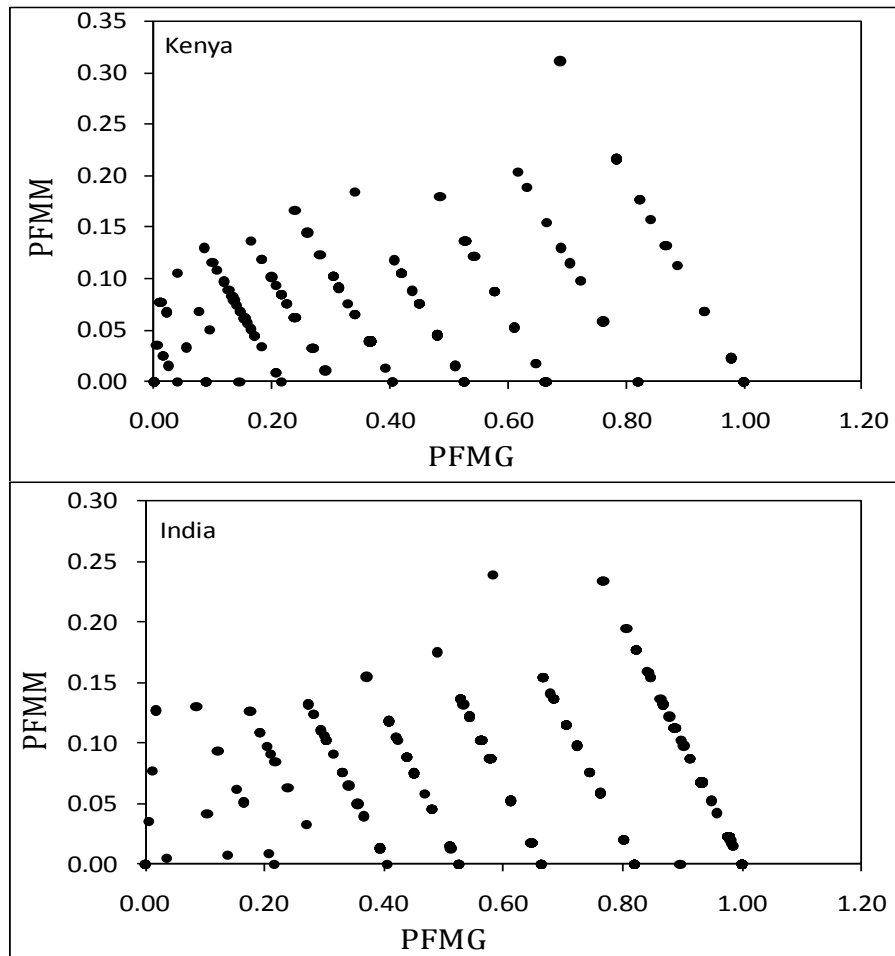


Fig. 6 The relationship between the size of the wing gap during moult expressed as a Proportion of Feather Mass Missing (PFMM) and Proportion of Feather Mass Grown (PFMG). The pattern of parallel lines is a consequence of the recording of moult scores for individual feathers to integer values.

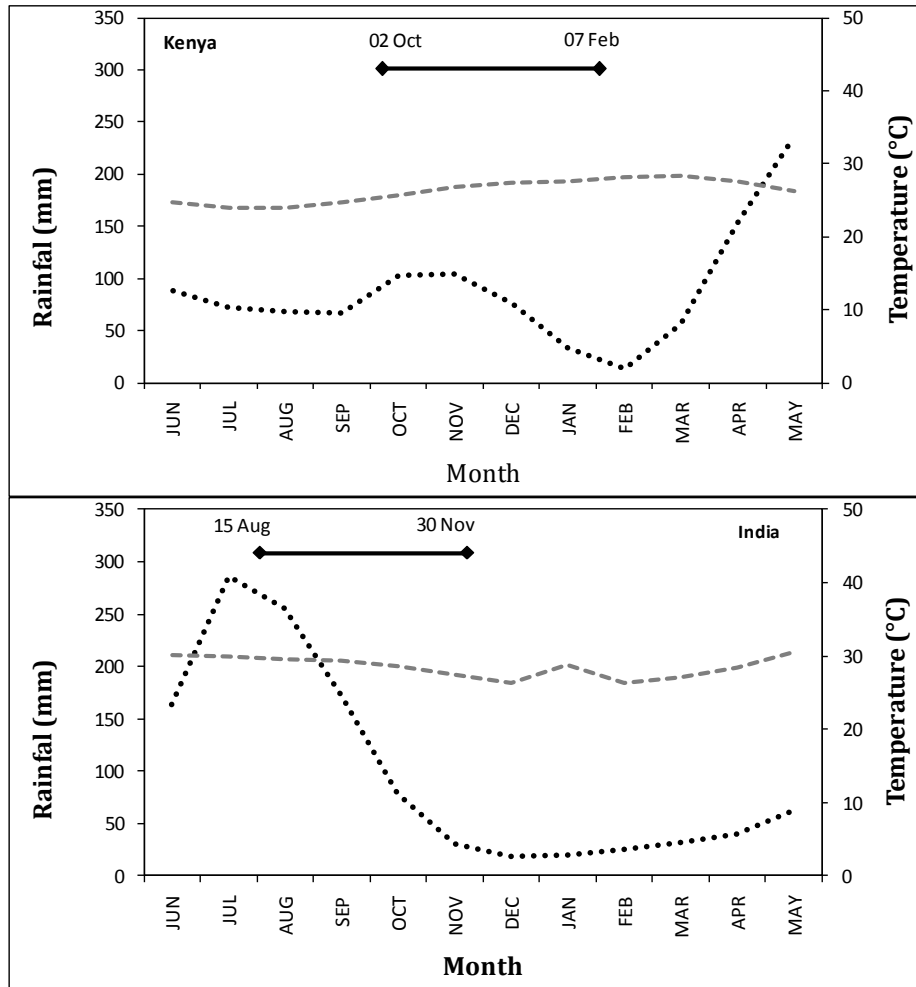


Fig. 7 Onset and duration of moult (solid black line) in relation to rainfall (dotted lines) and temperature (dashed grey lines) pattern in India and Kenya.

CHAPTER 7

PRIMARY MOULT STRATEGIES OF IMMATURE CURLEW SANDPIPERS

University of Cape Town

PRIMARY MOULT STRATEGIES OF IMMATURE CURLEW SANDPIPERS

ABSTRACT

Primary moult is described in immature Curlew Sandpipers *Calidris ferruginea* on their non-breeding areas in South Africa, north-western Australia and south-eastern Australia. Birds replaced between two and six outer primaries; a majority (79–84%) replacing between four and five outer primaries. At all three regions, moult started earliest in the group moulting the most number of primaries and got progressively later in groups moulting fewer primaries. The duration of moult was also longest in the group moulting the highest number of primary feathers and shortest in the group moulting the least number of primary feathers. In South Africa, moult started between 2 February and 30 April and lasted between 71 days and 133 days depending on the number of primaries moulted. In north-western Australia, moult started between 17 November and 13 February and lasted between 95 to 153 days. In south-eastern Australia, the estimated start date of moult ranged between 30 December and 5 March, and lasted between 121 days and 174 days. The geographic difference in the start dates and duration of moult of the different populations is probably an adaptation to the climatic conditions at the different non-breeding areas.

INTRODUCTION

Existing literature shows that the immature of many waders (shorebirds) exhibit several patterns of post-juvenile moult. Immature Western Sandpipers, *Calidris mauri*, on the non-breeding grounds in North America do not moult their wing feathers until summer or early autumn during their second year of life (age >22 months) just before their first breeding migration (O'Hara 2002, O'Hara *et al.* 2002). In species such as the Little Stint, *Calidris minuta*, all flight feathers are renewed (Pearson 1974). The young of species such as Whimbrel, *Numenius phaeopus*, Bar-tailed Godwit, *Limosa lapponica*, and Semi-palmated Sandpiper which spend their first year on the non-breeding areas undergo a partial or *preformative* (Howell *et al.* 2003) moult, usually replacing the outer three to five feathers (Gratto & Morrison 1981, Prater 1981, Cramp & Simmons 1983, Ginn & Melville 1983). Even within the same species, moult strategies can differ between geographical populations. For instance, a large proportion of juvenile Common Sandpiper *Actitis hypoleucos* in the southern hemisphere undergo a partial moult (Pearson 1974, Prater *et al.* 1977, Nicoll & Kemp 1983) during their first winter but some juveniles in Morocco undergo a complete primary moult (Pienkowski *et al.* 1976).

The reasons for these variations are not clear. It has been suggested that the young of species which migrate as far as the southern hemisphere are more likely to carry out a partial or complete moult of flight feathers during their first year of life while the young of species which over-winter at northern temperate latitudes will not likely moult in their first year of life (Spaans 1976, Hale 1980). Also Prater (1981) showed that larger waders tend to replace fewer primaries than do smaller species. In southern Africa, immature Greenshanks

Tringa nebularia, Marsh Sandpipers *T. stagnatilis*, Ruffs *Philomachus pugnax* and Curlew Sandpipers *Calidris ferruginea* moult varying numbers of outer primaries; in contrast the smaller waders such as Common Sandpipers *Actitis hypoleucos* and Little Stints *C. minuta* which usually replace all primaries (Tree 1974, Elliott et al. 1976, Schmitt & Whitehouse 1976)

This study describes the moult of immature (age 5–13 months) Curlew Sandpipers which migrate to South Africa and Australia. Curlew Sandpipers breed in the Arctic tundra (Vaurie 1965, Cramp & Simmons 1983) and migrate to Africa, India and Australasia to spend the non-breeding season (Thomas & Dartnall 1971, Pringle & Cooper 1975, Elliott *et al.* 1976). In South Africa and Australia, juveniles arrived in September and October, about two weeks after the first influx of adults (Elliott *et al.* 1976, Minton *et al.* 2006). Most juvenile Curlew Sandpipers do not migrate northward to their Arctic breeding grounds the following year but remain in the non-breeding areas (Elliott *et al.* 1976). Between February and May of the year following their arrival at the non-breeding areas, the primary feathers of juveniles begin to show signs of wear. About 60–80% carry out a partial moult at this time, replacing the outer three to five feathers (Tree 1974, Elliott *et al.* 1976, Waltner 1976).

In a study examining the partial moult of immature Wood Sandpipers *Tringa glareola* in southern Africa, Remisiewicz *et al.* (2010) demonstrated how the Underhill & Zucchini (1988) moult models, which have been widely used for estimating moult parameters of adult birds (e.g. Serra 2000, Underhill 2003, Summers *et al.* 2010), could be extended to study the partial moult of immature birds. The aim of this study is to describe the different

strategies used by first-year Curlew Sandpipers moulting varying number of primary feathers on their wintering grounds in South Africa and Australia, adopting the method described in Remisiewicz *et al.* (2010). The pattern and strategy of moult are explained in context of the annual cycle of the species and the environment in the non-breeding areas.

METHODS

The moult records used in this study were of immature Curlew Sandpipers banded at Langebaan Lagoon (33°05'S, 18°02'E) and Rietvlei (33°50'S, 18°30'E) in South Africa, Roebuck Bay and 80-Mile beach (18°07'S, 122°16'E) in north-western Australia, and Victoria (38°–39°N, 144°–147°E) in south-eastern Australia. Curlew Sandpipers can be aged based on plumage characteristics and feather wear (e.g. Prater *et al.* 1977, Rogers *et al.* 1990, Higgins & Davies 1996). Between September and December, juvenile birds have relatively new primaries which contrasted with the old worn feathers of the adults, and by January and February most of the juvenile primaries are worn and contrast with the now new primaries of the adults.

Moult scores were recorded following the standard approach of Ashmole (1962) and Ginn and Melville (1983). Old feathers were scored 0, new feathers 5, and growing feathers 1–4 depending on their stage of growth. Partial moult in immature birds usually begins with one of the inner primaries, usually the fifth, sixth or seventh primary, and proceeded outwards to the 10th (Thomas & Dartnall 1971, Elliott *et al.* 1976, Paton *et al.* 1982). Whether moult is just starting or it has been completed, the point at which moult started indicates the number of primaries moulted or to be moulted by the birds. Based on the number of

primaries moulted, immature birds were divided into four groups: birds that moulted three (3PP), four (4PP), five (5PP), or six (6PP) primaries. For each bird, the moult scores were transformed into a moult index following the relationship: 0 = 0, 1 = 0.125, 2 = 0.375, 3 = 0.625, 4 = 0.875, and 5 = 1 (Underhill & Zucchini 1988, Underhill & Summers 1993).

Moult parameters (start date, duration and standard deviation) were estimated for individual primary feathers using the moult indices, an approach which has been used by Serra (2000) Underhill (2001), Underhill (2003) to estimate moult parameters of adult birds, and used by Remisiewicz *et al.* (2010) on immature Wood Sandpipers. These moult estimates were obtained for each group of moulters separately. Moult parameters of the first primary moulted in each group were estimated using model type 4 of Underhill *et al.* (1990) which uses observations of birds in moult and those that have completed moult. Estimates for the remaining primaries were obtained using model type 2 of Underhill & Zucchini (1988) which uses observations of birds that have not yet started moult, birds in moult and those that have completed moult (Underhill *et al.* 1990).

Moult parameters were also estimated using the tract of all primary feathers combined. The moult indices were converted into the proportion feather mass grown (PFMG) using the relative feather masses of the primary feathers (Underhill & Summers 1993, Underhill & Joubert 1995), a value which goes from 0 (all old primaries) to 1 (all primaries replaced). Because immatures perform a partial moult replacing less than the 10 primary feathers, the maximum PFMG relative to the masses of the 10 primaries was less than 1. For instance a bird which replaced six primaries attained a maximum PFMG value of 0.77 when moult was

completed. Because the Underhill & Zucchini (1988) model requires that PFMG be in the range 0–1, the PFMG value of each bird was divided by the maximum PFMG at moult completion (Remisiewicz *et al.* 2010).

Only birds which had started or completed moult could be included in the analyses and birds that had not started moult (moult score 0) were excluded. This is because in birds that had not started moult, it was not possible to tell how many feathers they would replace or if they would moult at all. The data were assumed to be Type 4 of Underhill *et al.* (1990) which uses observations of birds in moult and those that have completed moult (Underhill *et al.* 1990). Moult parameters were estimated using the software described in Brandão (1998). In some groups, the sample sizes of individual primaries were too small for the algorithm to converge or the standard errors of the estimates were too large to be biologically meaningful. In such cases, only the result of the PFMG of all the moulting primaries combined was reported.

By dividing the relative mass of each primary by its moult duration obtained from moult model, the PFMG/day of each primary was estimated. By summing up the PFMG/day for all feathers growing simultaneously on any given day, the daily rate of feather material production for the entire moult period could be modelled, a method demonstrated by Remisiewicz *et al.* (2010).

In cases when the rate of moult was not uniform throughout the moult period, a power transformation (Box & Cox 1964) of the PFMG was applied as demonstrated in Summers *et al.* (1983) and Underhill *et al.* (1990). The transformed PFMG (tPFMG) = PFMG^x

Where the transformation parameter (x) is estimated as:

$$x = \frac{\ln(\text{expected PFMG at the 50th percentile date assuming a constant rate of feather growth})}{\ln(\text{observed PFMG on the 50th date percentile})}$$

The transformation parameter was estimated and applied separately to each group of moulters when it was necessary.

RESULTS

The moult records of 458 first year Curlew Sandpipers from South Africa (SA) (1970–1974), 1,317 from north-western Australia (NWA) (1982–2006) and 1,872 from south-eastern Australia (SEA) (1972–2008) were used in this study. Depending on the number of primaries moulted, or to be moulted, birds were divided into the group which moulted two (2PP), three (3PP), four (4PP) five (5PP) and six (6PP) primaries. A majority of birds moulted four (4PP) and five (5PP) primaries making up 79–84% of moulters (Table 1). Due to small sample size in the 2PP group, these were excluded from further analyses. The maximum PFMG – relative to the mass of all 10 primaries – at the completion of moult varied between 0.34 in birds moulting two primaries (2PP) to 0.79 in birds moulting six primaries (Table 1).

Moult estimates

In some groups, the estimated start dates and duration of moult from the PFMG of all the primaries combined differed from the estimates obtained from the start date of moult of the first primary moulted and the moult end date of the last moulted primary (Tables 2–5). This was because the rate of moult was not uniform throughout the moult period. For instance, plot of the daily amount of feather material grown per day in the group of birds which moulted three primaries in SEA indicated that moult was relatively slower at the

initial phase of moult compared to the end (Fig. 1). In this example the transformation parameter was estimated as 0.728. In the groups where PFMG were transformed, the estimates of moult parameters from the transformed PFMG were closer to the estimates obtained from the growth of individual primaries (Table 2-5).

South Africa

From the PFMG of all primaries moulted combined, the estimated start date of moult of immature Curlew Sandpipers that moulted three outer primaries (3PP) was 30 April and got progressively earlier in the 4PP (7 March), 5PP (6 March) and 6PP (2 February) groups (Table 2). 6PP start moult on average 32 days before 5PP, 33 days before 4PP, and 87 days before 3PP (Table 2, Fig. 2). The duration of moult varied between 73 days in the 3PP group to 96 days in the 6PP group (Table 2). In 3PP, the estimated moult start date of P8 was 29 April and moult end date of P10 was 12 July, making the duration of moult 73 days. In the 4PP group, the duration of moult estimated from the moult start date of P7 (06 April) and moult end date of P10 (24 June) was 79 days. In 5PP, the duration of moult estimated from the moult start date of P6 (10 March) and moult end date of P10 (14 June) was 96 days (Table 3). The moult records of birds that had not started moult, birds in moult and birds that had completed moult were insufficient to obtain moult estimates of single primaries for the 6PP group.

North-western Australia

The start date of moult estimated from the PFMG of all moulted primaries combined for the 3PP group was 13 February, for 4PP 21 January, 5PP 20 December and for 6PP 17 November

(Table 2). Group 6PP start moult on average 33 days before 5PP, 65 days before 4PP, and 88 days before 3PP (Table 2, Fig. 3). In the group which moulted three primaries (3PP), the estimated moult start date of P8 was 10 February and moult end date of P10 was 17 May, making the duration of moult 97 days. In the 4PP group, the duration of moult estimated from the moult start date of P7 (20 January) and moult end date of P10 (15 May) was 116 days (Table 4). In 5PP group, the start date of moult of P6 was 16 December and the end date of moult of P10 was 28 April, which gave the duration of moult 133 days (Table 4). Moulting records were insufficient to obtain moult estimates of single primaries for the 6PP group.

South-eastern Australia

The estimated start date of moult based on the PFMG of all the moulted primaries combined are 5 March for 3PP was 14 February for 4PP, 11 January for 5PP, and 30 December for 6PP (Table 2). 6PP started moult on average 12 days before 5PP, 45 days before 4PP, and 65 days before 3PP (Table 2, Fig. 4). The overall duration of moult increased from 121 days for birds that moulted three primaries to 174 days for birds that moulted six primaries (Table 2). In the 3PP group, the estimated start date and duration of moult estimated from the beginning of moult of P8 and end date of moult of P10 were 19 January and 119 days, respectively. In 4PP the estimated start date of moult of P7 was 11 February and moult end date of P10 was 29 June, making the moult duration 148 days. In 5PP, the starting date of moult of P6 was 13 January and moult duration was 167 days. In 6PP, the moult start date of P5 was 28 December and moult duration was 176 days (Table 5).

Rate of feather synthesis

The daily growth rate was estimated for groups 3PP, 4PP and 5 PP by summing up the values of PFMG/day all primaries growing simultaneously. In 6PP, where the moult estimates of individual primaries was not possible for SA and NWA, the summed relative masses of the primaries moulted for that group were divided by the estimated duration of moult from all primaries combined, and this provided an approximate estimate of the daily growth rate. Only the 3PP–5PP groups could be compared with statistical tests.

In SA, the average proportion of feather mass grown (PFMG)/day was 0.76 for group 3PP, 0.72 for group 4PP, 0.74 for group 5PP, and 0.59 for group 6PP (Fig. 5). The average daily growth rate of feather material did not differ significantly between the groups 3PP–5PP ($F_{2,251} = 0.23$, $P = 0.771$). In NWA, PFMG/day was 0.49 for group 3PP, 0.50 for group 4PP, 0.54 for group 5PP, and 0.51 for group 6PP (Fig. 5). This rate of the growth of the feather material did not significantly differ between the groups 3PP–5PP ($F_{2,341} = 2.05$, $P = 0.127$). The average PFMG/day in SEA was 0.39 for 3PP, 0.43 for 4PP, 0.42 for 5PP, and 0.45 for 6PP (Fig. 5). There was no significant difference in the average daily growth rate of feather material between these groups ($F_{2,430} = 2.77$, $P = 0.063$)

Comparisons between sites and groups

Among all groups of moulters that replaced the same number of primaries at different sites, moult started earliest in NWA and finished the earliest as well, while the start of moult was latest in SA but finished the latest in SEA in all groups but 3PP (Fig. 6). In all groups, the duration of moult was shortest in SA and longest in SEA (Table 2, Fig. 6). So, even though moult started earlier in SEA compared to SA, moult in SEA was completed at about the same

time as SA (Fig. 6). In all the group of moulters, the average PFMG/day was highest in SA and lowest in SEA (Fig. 5). This difference in PFMG/day between the sites was significant (3PP: $F_{2,290} = 80.91, P < 0.001$; 4PP: $F_{2,360} = 56.36, P < 0.001$; 5PP: $F_{2,396} = 66.77, P < 0.001$).

DISCUSSION

At all three sites, the predominant moult strategy adopted by up to 80% of birds was to moult the outer four or five primaries. Immatures of many Palearctic waders have similar partial moults of flight-feathers, e.g. Ruff *Philomachus pugnax*, Common Sandpiper, Marsh Sandpiper *T. stagnatilis*, Red-necked Stint *Calidris ruficollis* and Wood Sandpiper (Tree 1974, Pearson 1975, Paton & Wykes 1978). Because moult is energetically costly (Ginn & Melville 1983, Lindstöm *et al.* 1993, Klaassen 1995), replacing this number of primaries is likely to be a balance between reinforcing the most important flight feathers and the energetic costs associated with moult.

At all three sites, the estimated start dates of moult were widely varied depending on the number of primary feathers moulted but the end dates were more synchronous. The start date of moult in SA ranged from 2 February in 6PP to 30 April in 3PP (87 days), in NWA the start date of moult ranged from 17 November in 6PP to 13 February in 3PP (88 days), and in SEA, start date of moult ranged from 22 December in 6PP to 21 April in 3PP (65 days). In SA, the end date of moult ranged from 15 June in 6PP to 10 July in 3PP (25 days), 20 April in 6PP to 18 May in 3PP (28 days) in NWA, and in SEA, from 22 June in 6PP to 4 July in 3PP (12 days). Moult typically took between 71 and 174 days to complete depending on the number of primaries moulted. This duration does not necessarily indicate that the moult of

individual birds took this long, but that starting dates were widely varied between individuals.

The only other species for which analogous results exist is the Wood Sandpiper (Remisiewicz *et al.* 2010). Certain parallels and contrasts can be drawn between the moult patterns of these two species. In both the Curlew Sandpiper and the Wood Sandpiper, a majority of birds moulted four or five primaries, making up about 90% of moulters in the Wood Sandpiper and between 79–84% in the Curlew Sandpiper. In both species, moult started earliest in the group which moulted six primaries and got progressively later in the groups that moulted five, four, and three primaries. Start dates of moult of the different groups in the Wood Sandpiper were: 24 January for the group that moulted three primaries, 6 January in the group that moulted four primaries, 16 December in the group that moulted five primaries and 8 December in the group that moulted six primaries (Remisiewicz *et al.* 2010). The start dates of moult in both species were more varied than the end date, although this variation was much smaller in the Wood Sandpiper compared to the Curlew Sandpiper (Remisiewicz *et al.* 2010). The difference between the start date of moult of the earliest and the latest groups of moulters in the Curlew Sandpiper in South Africa was 88 days while the moult start date of the Wood Sandpiper ranged from 8 December to 24 January (47 days). The range of the moult end dates of Curlew Sandpiper in South Africa was 25 days while in the Wood Sandpiper the moult end dates ranged from 19 March to 28 March (9 days). Most Wood Sandpipers leave the non-breeding areas heading to the breeding grounds at the end of their first year of life. They therefore, need to complete moult in time for the northwards departure. Curlew Sandpipers, on the other hand, remain on the non-breeding

areas in their second year of life and only depart for their first breeding migration when they are about 17 months old. They therefore have enough time to replace their primaries at a slower pace compared to immatures of species that spend only a few months on the non-breeding grounds, such as the Wood Sandpiper.

Another difference in the moult patterns of the Curlew Sandpiper and the Wood Sandpiper is, in corresponding groups of moulters in southern Africa, the start date of moult in the Wood Sandpiper was earlier than the start date of moult of Curlew Sandpipers. Moulting in the Curlew Sandpiper was 96 days earlier than the Wood Sandpiper in the 3PP group, 60 days in the 4PP, 80 days in 5PP, and 56 days in 6PP. In southern Africa, the daily rate of feather mass production in the Wood Sandpiper was lowest in the group that moulted six primaries and became progressively higher in subsequent groups (6PP: 0.69%/day, 5PP: 0.69%/day, 4PP: 0.78%/day, 3PP: 0.82%/day). In the Curlew Sandpiper in South Africa, there was no trend in the daily rate of feather mass production (Table 2). In south-eastern Australia, however, the daily rate of feather mass production in the Curlew Sandpiper was highest in the group that moulted six primaries and became progressively lower in subsequent groups (Table 2), oppositely than in the Wood Sandpipers.

In conclusion, immature Curlew Sandpipers on their non breeding sites in SA, NWA and SEA have different strategies of partial moult. Immatures in SA started moult late but moulted fast in comparison to the other two regions, immatures in NWA started moult early and moult speed was intermediate in comparison to the other groups, while the immatures in SEA started moult at an intermediate period but rate of moult was slower than at SA and

NWA. The start dates and duration of moult of the different populations is probably an adaptation to the climatic conditions at their different non-breeding areas.

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Table 1 Numbers of non-moulting (0PP) and moulting immature Curlew Sandpipers replacing two (2PP), three (3PP), four (4PP), five (5PP) and six (6PP) outer primaries in South Africa (SA), north-western Australia (NWA) and south-eastern Australia (SEA).

Group	SA		NWA		SEA		PFMG at moult completion
	n	Percent	n	Percent	n	Percent	
0	86	15.8	65	4.7	15	0.8	
2PP	0	0	2	0.1	4	0.2	0.34
3PP	59	10.8	99	7.2	188	9.9	0.475
4PP	240	44.1	575	41.5	809	42.8	0.595
5PP	129	23.7	534	38.6	670	35.4	0.699
6PP	30	5.5	109	7.9	205	10.8	0.785

Table 2 Estimates of moult parameters for groups of immature Curlew Sandpipers replacing three to six outer primaries) in South Africa, north-western Australia and south-eastern Australia. Estimates are based on the proportion of feather mass grown (PFMG) of tract of primaries moulted combined and the new estimates of transformed PFMG.

Initial estimates						transformed				
Site	Group	Mean start (sd)	duration (sd)	mean end (sd)	Standard deviation (sd)	Transformation parameter			%PFMG/day	
SA	3PP	30 Apr (4.6)	71.4 (3.8)	10 Jul (1.2)	44.1 (2.4)					0.67
	4PP	7 Mar (7.4)	102.4 (9.4)	18 Jun (5.3)	45.7 (6.0)					0.58
	5PP	6 Mar (7.9)	101.8 (7.6)	16 Jun (5.2)	33.4 (4.4)					0.69
	6PP	2 Feb (5.1)	133.8 (5.1)	15 Jun (5.1)	37.8 (8.1)					0.59
NWA	3PP	13 Feb (7.6)	95 (6.1)	18 May (7.2)	37.4 (2.0)					0.51
	4PP	4 Feb (7.1)	102.4 (7.4)	17 May (2.2)	36.2 (3.1)	0.783	21 Jan	15 May	114	0.52
	5PP	31 Dec (9.6)	118.9 (9.7)	28 Apr (3.0)	30 (2.4)	0.661	20 Dec	28 Apr	129	0.54
	6PP	17 Nov (3.1)	153.8 (3.8)	20 Apr (8.1)	39.1 (6.4)					0.51
SEA	3PP	21 Apr (7.8)	121.7 (8.7)	8 Jul (4.8)	44.8 (4.9)	0.728	5 Mar	4 Jul	121	0.39
	4PP	25 Mar (6.9)	97.9 (7.4)	1 Jul (2.3)	41.3 (1.5)	0.831	14 Feb	29 Jun	135	0.44
	5PP	23 Jan (5.6)	161.8 (7.5)	3 Jul (1.7)	45.3 (3.2)	0.789	11 Jan	29 Jun	169	0.41
	6PP	22 Dec (7.5)	196.2 (11.3)	24 Jun (5.9)	37.7 (2.6)	1.070	30 Dec	22 Jun	174	0.45

Table 3 Estimates of moult parameters and daily growth rates (expressed as a proportion of feather mass grown per day) of individual primaries for three groups of immature Curlew Sandpipers replacing different numbers of primaries in southern Africa

Group	Primary	mean start	Duration	mean end	SD	%PFMG /day	Not in moult	In moult	Moult complete
3PP	P8	30 Apr	23.8	23 May	40.1	0.58	0	2	57
	P9	21 May	20.1	10 Jun	52.0	0.78	2	8	49
	P10	6-Jun	36.0	12 Jul	40.2	0.5	6	24	29
4PP	P7	6 Apr	21.1	27 Apr	25.9	0.57	0	6	233
	P8	21 Apr	19.8	10 May	21.3	0.73	5	6	226
	P9	5 May	29.1	3 Jun	30,0	0.54	11	22	206
	P10	27 May	28.3	24 Jun	28.7	0.64	23	40	175
5PP	P6	10 Mar	38.2	17 Apr	38	0.27	0	5	121
	P7	28 Mar	23.1	20 Apr	36	0.52	2	8	117
	P8	13 Apr	29.5	12 May	34	0.48	9	5	113
	P9	20 Apr	36.9	26 May	43	0.43	14	7	106
	P10	10 May	35.0	14 Jun	36	0.51	18	17	92

Table 4 Estimates of moult parameters and daily growth rates (expressed as a proportion of feather mass grown per day) of individual primaries for three groups of immature Curlew Sandpipers replacing different numbers of primaries in north-western Australia

Group	Primary	mean		mean	SD	%PFMG /day	Not in moult	In moult	Moult complete
		start	Duration	end					
3PP	P8	10 Feb	74.9	17 Mar	48	0.38	0	7	92
	P9	14 Mar	49.1	13-Apr	16.9	0.31	6	10	83
	P10	12 Apr	35.1	17-May	13.4	0.51	18	17	64
4PP	P7	20 Jan	47.9	19 Feb	49.2	0.39	0	19	554
	P8	16 Feb	30.6	16 Mar		0.47	18	35	517
	P9	17 Mar	29.3	15 Apr	34.7	0.54	63	61	451
	P10	13 Apr	28.6	15 May	39.1	0.55	117	98	360
5PP	P6	19 Dec	44.6	4 Feb	31.8	0.22	0	9	525
	P7	13 Jan	29.1	7 Feb	31.4	0.69	7	8	519
	P8	3 Feb	30.2	4 Mar	43.2	0.46	13	18	503
	P9	28 Feb	25.7	25 Mar	37.6	0.6	29	31	474
	P10	26 Mar	32.8	28 Apr	36.9	0.54	62	61	411

Table 5 Estimates of moult parameters and daily growth rates (expressed as a proportion of feather mass grown per day) of individual primaries for three groups of immature Curlew Sandpipers replacing different numbers of primaries in south-eastern Australia

Group	Primary	mean start	Duration	mean end	SD	%PFMG/ day	Not in moult	In moult	Moult complete
3PP	P8	5 Mar	41	15 Apr	51.2	0.23	0	34	152
	P9	8 Apr	44.2	22 May	66.2	0.35	40	29	118
	P10	28 May	34.9	2 Jul	55.3	0.52	72	31	84
4PP	P7	11 Feb	45.7	18 Mar	50.9	0.26	0	163	643
	P8	7 Mar	44.1	16 Apr	55.2	0.35	161	112	533
	P9	19 Apr	34.1	23 May	51.2	0.46	280	101	425
	P10	23 May	36.2	29 Jun	47.7	0.5	381	110	315
5PP	P6	13 Jan	57.6	31 Jan	45.8	0.27	0	82	585
	P7	25 Jan	49.6	15 Mar	48.1	0.24	58	116	493
	P8	8 Mar	37.7	14 Apr	51.1	0.36	182	106	379
	P9	22 Apr	32.4	25 May	51.3	0.48	310	79	278
	P10	24 May	35.2	28 Jun	48.4	0.51	388	78	201
6PP	P5	28 Dec	33.8	31 Jan	21.2	0.25	0	17	187
	P6	11 Jan	30.2	10 Feb	23.2	0.34	4	22	178
	P7	28 Jan	36.8	5 Mar	34.8	0.33	23	37	144
	P8	5 Mar	32.6	6 Apr	35.4	0.43	61	38	105
	P9	10 Apr	33.9	14 May	38.4	0.46	102	28	74
	P10	13 May	28.8	21 Jun	45.7	0.46	126	26	52

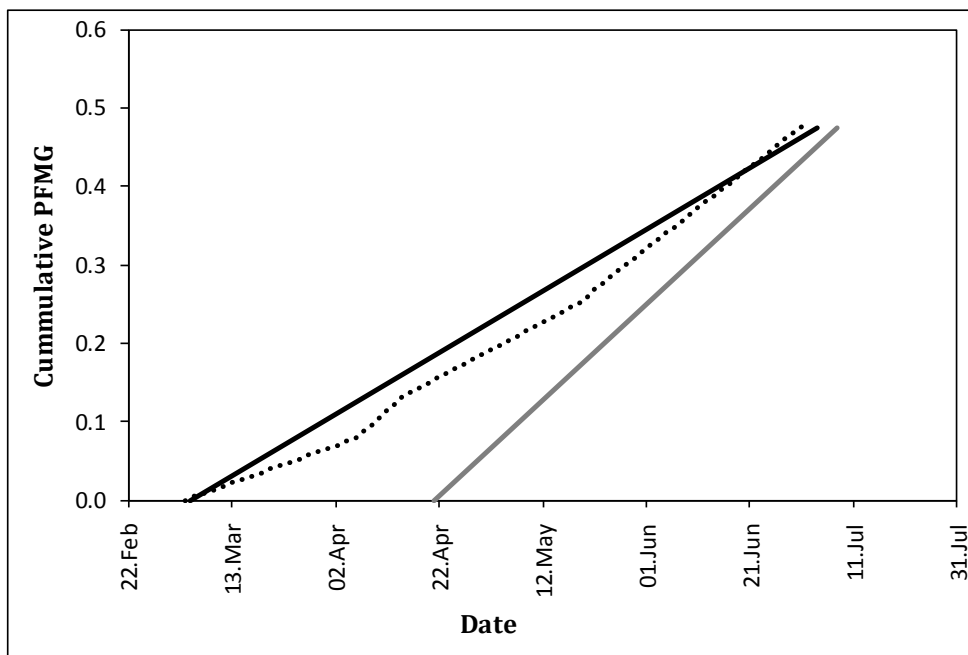


Fig. 1 The start and finish dates of moult of immature Curlew Sandpipers moulting three outer primaries in south-eastern Australia based on individual feather growth (dotted lines), PFMG of the moulted primaries combined (solid grey line) and transformed PFMG (solid black line)

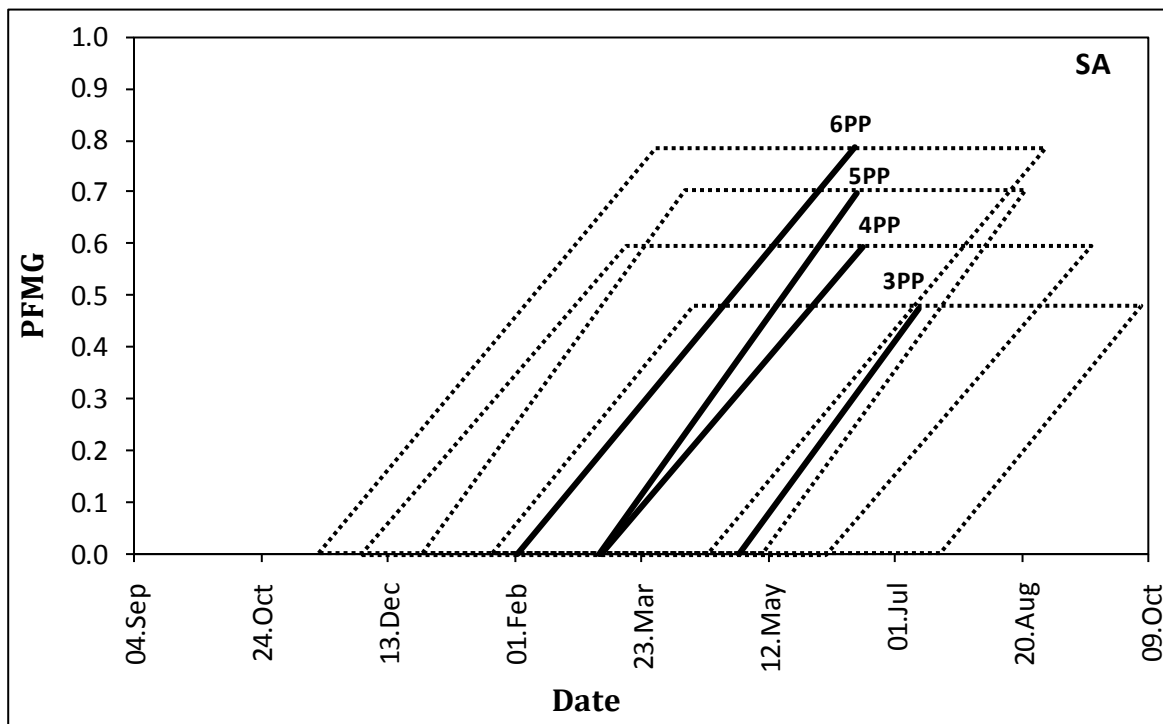


Fig. 2 The estimated timing of moult based on the proportion of feather mass grown (PFMG) of immature Curlew Sandpipers that moulted three (3PP), four (4PP) five (5PP) and six (6PP) outer primaries in South Africa. Thick lines show the timing of moult for an average bird of each group, thin lines show the estimated 95% confidence intervals

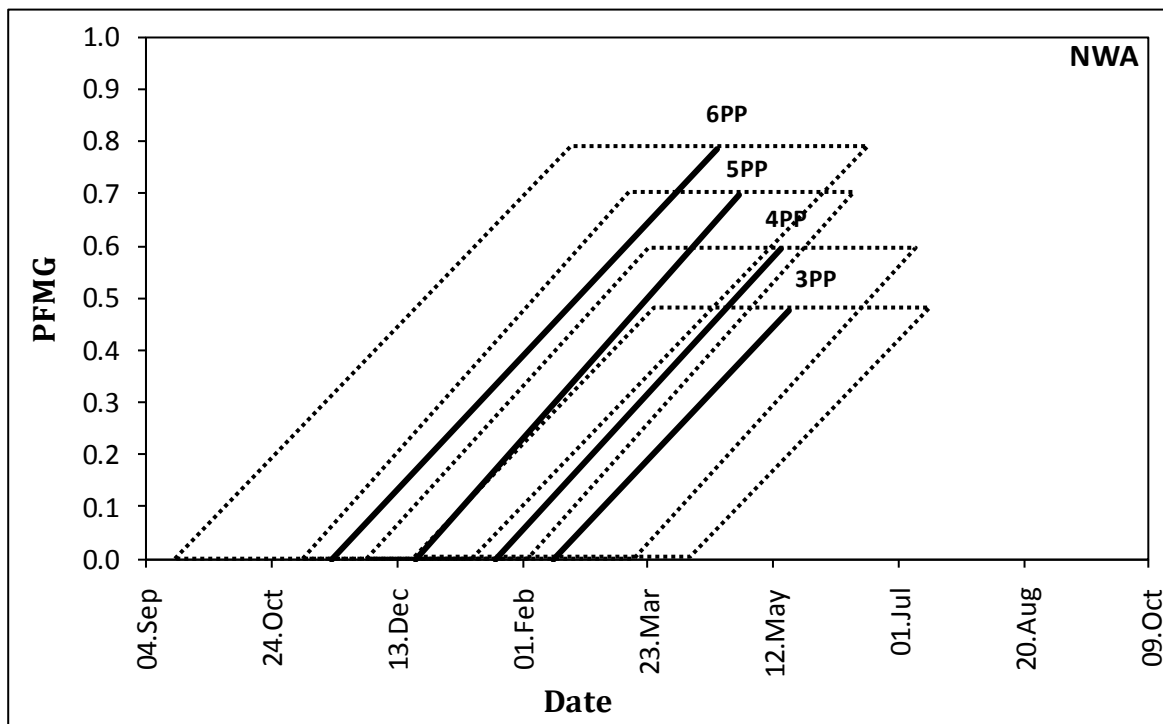


Fig. 3 Estimates of the timing of moult based on the proportion of feather mass grown (PFMG) of immature Curlew Sandpipers that moulted three (3PP), four (4PP) five (5PP) and six (6PP) outer primaries in north-western Australia. Thick lines show the timing of moult for an average bird of each group, thin lines show the estimated 95% confidence intervals

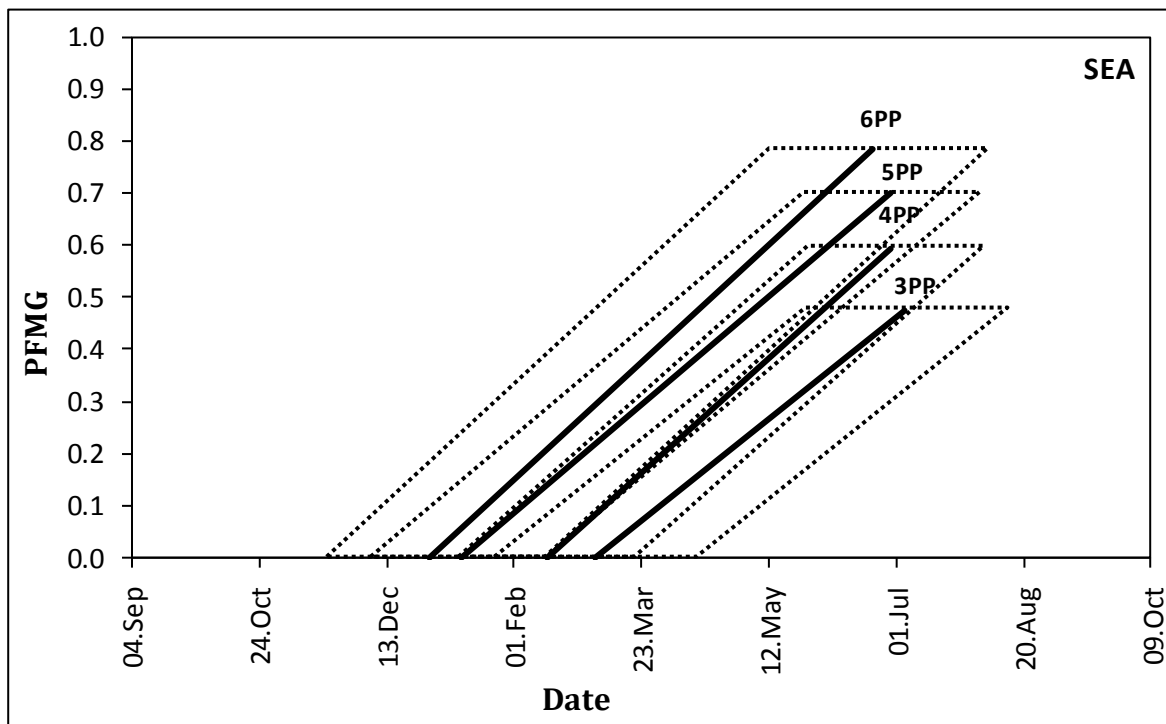


Fig. 4 The estimates timing of moult based on the proportion of feather mass grown (PFMG) of immature Curlew Sandpipers that moulted three (3PP), four (4PP) five (5PP) and six (6PP) outer primaries in south-eastern Australia. Thick lines show the timing of moult for an average bird of each group, thin lines show the estimated 95% confidence intervals

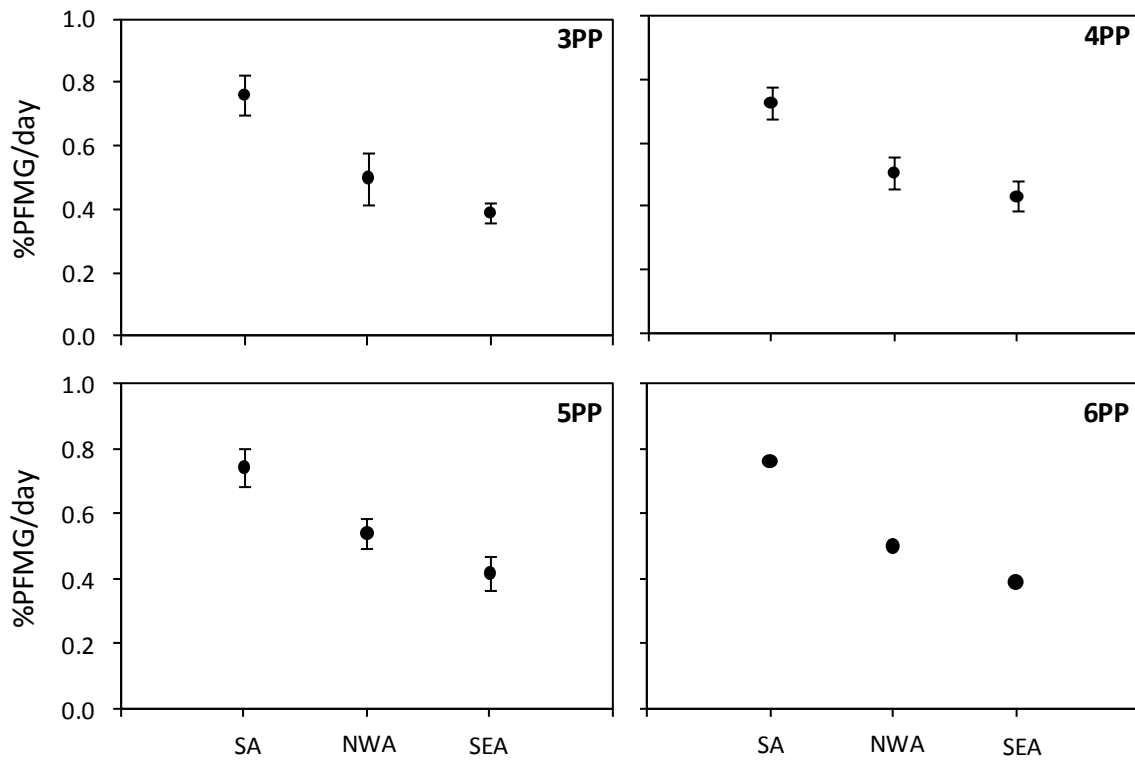


Fig. 5 Average proportions of feather mass grown (PFMG)/day for groups of immature Curlew Sandpipers in South Africa, north-western Australia, and south-eastern Australia replacing different numbers of primaries

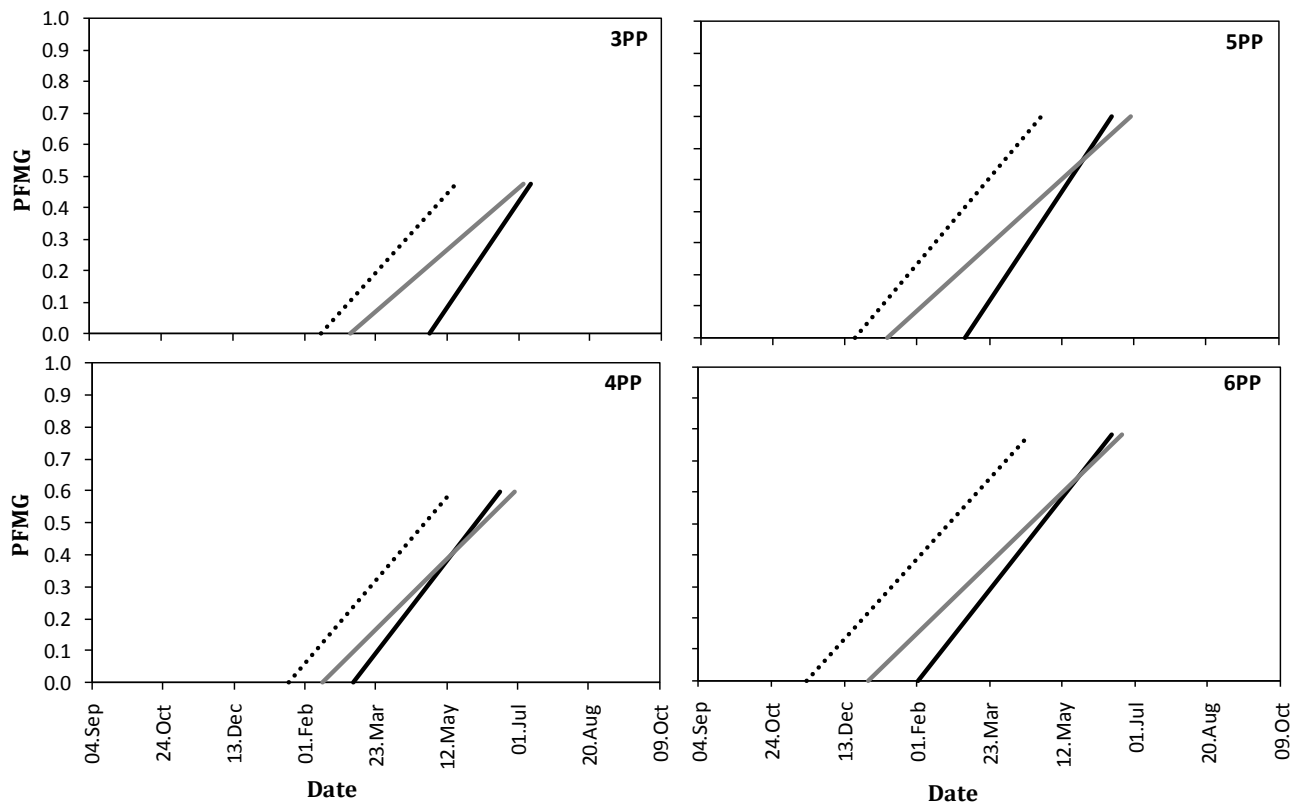


Fig. 6 Within-group comparison of estimates of the timing of moult on the proportion of feather mass grown (PFMG) of immature Curlew Sandpipers in South Africa (solid black lines), north-western Australia (dashed lines), and south-eastern Australia (solid grey lines)

CHAPTER 8

MIGRATION AND MOULT WITHIN THE ANNUAL CYCLE OF THE CURLEW

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MIGRATION AND MOULT WITHIN THE ANNUAL CYCLE OF THE CURLEW SANDPIPER

INTRODUCTION

One of the most measurable responses of organisms to their environment lies in observing the timing of their annual activities (Sparks *et al.* 2005). Ecological variables such as temperature, precipitation, predation and competition are some of the factors that can effect a change in the timing of annual activities (Meltofte *et al.* 2007). Studies in Europe and North America have revealed that the recent shift in the timing of biological activities such as breeding and migration of many bird species is due to warming global temperatures (Mason 1995, Crick & Sparks 1999, reviewed by Walther *et al.* 2002).

In long-distance migratory species, the life-history stages such as breeding, migration, and moult are delineated in time and space in order to minimize resource conflicts for these events (King 1974, Jenni & Winkler 1994, Ginn & Melville 1983). These traits are connected to some extent, and a shift in the timing of one activity in any direction will induce a corresponding shift in the timing of the next stage within the annual cycle. A shift in the timing of migration, for instance, can have consequences for reproductive success and or annual survival (Marra *et al.* 1998, Inger *et al.* 2010).

This thesis is essentially a study of the migration and moult strategies of the Curlew Sandpiper *Calidris ferruginea* in relation to environmental variables on both the breeding and non-breeding areas. The focus is on the carry-over effects which changing

environmental conditions have on subsequent life-history traits within the annual cycle, namely migration and moult. This chapter is a comparative overview of the preceding chapters and summarizes the main findings of this thesis.

MIGRATION

I found that the migration schedule of both adult and juvenile Curlew Sandpipers was modulated by the environmental conditions experienced on the breeding grounds (Chapters 2 & 3). In males, the average temperature in June, which corresponds to the egg-laying period, was the important climatic factor determining the timing of migration. In years with warm average June temperatures, the migration of males was earlier than in years when the average June temperature was cold. The migration of females, on the other hand was influenced more by predation pressure and July temperatures in the Arctic, the two factors that are correlated with breeding success and chick development (Underhill 1987, Schekkerman *et al.* 1998, Soloviev *et al.* 2006). Female birds generally migrated later in years when predation was low and/or July temperatures were warm.

The timing of migration of juvenile birds was affected by predation pressure; juveniles migrated earlier in years of low predation compared to years when predation was high. These late migrating juveniles are hypothesised to be broods of re-nesting attempts of failed females (Tomkovich & Soloviev 2006, P.S. Tomkovich pers. comm.). Although circumstantial, there are some evidences of re-nesting attempts in the Curlew Sandpiper. In cases of early nest predation in the Taimyr when some males are still around, some colour marked males and females were observed further north on new territories in areas of snow-free patches

(Tomkovich & Soloviev 2006). Also, the observation of females with active brood patches late in the breeding season (in late June and in July) suggests that these are birds that might have re-nested (Tomkovich & Soloviev 2006).

Comparison of migration pattern between Sweden and Poland

The estimated median migration date of adult Curlew Sandpipers in Sweden (all years pooled) was 27 July, about 7 days earlier than the estimated overall median migration date of adult in Poland on 3 August (Table 1, Chapter 2 & 3). The median migration dates of juveniles was similar in both Sweden (3 September) and Poland (2 September). At both sites, the median migration date of males was earlier than that of females. In Sweden, the estimated median migration date of males in good breeding years was 22 days earlier than that of females while in poor breeding years there was a difference of two days between the median migration dates of the sexes (Table 1). In Poland, the estimated median migration date of males in good breeding years was nine days earlier than that of females while the estimated median migration dates of the sexes was the same in poor breeding years (Table 1). The similarity in the overall pattern of migration of adult males and females in both Sweden and Poland suggest a geographically widespread effect of predation and temperature on the migration of the Curlew Sandpiper, at least on the population at the western component of the breeding range of the species.

MOULT

Geographic variation in adult moult

Generally, moult started earliest at the northernmost latitudes and got progressively later farther south (Fig. 1). Kenya, however, was an exception to the general pattern. The start of

moult in Kenya appeared to have been delayed to correspond with the onset of the rain season which starts in October (Chapter 6). The start dates of moult were almost significantly negatively correlated with the latitude (Pearson's correlation: $r = -0.753$, $P = 0.071$, $df = 3$, one-sided test). However, when the start date of moult in Kenya was excluded, the correlation between start date and latitude was highly significant ($r = -0.991$, $P = 0.002$, $df = 2$, one sided test). Thus adult birds commence moult at the earliest possible date after reaching their non-breeding areas. Because adults reach Kenya in August/September (Pearson 1974) and the distance to the breeding ground is shorter compared to that of the population in, say, South Africa, birds in Kenya can afford to delay the start of moult until a more convenient time. It also ensures that these birds can migrate to the breeding grounds with relatively fresh feathers.

The pattern of latitudinal gradient in the start date of moult was also found in the Grey Plovers *Pluvialis squatarola* (Serra 2002), Red Knot *Calidris canutus* (Summers *et al.* 2010) Purple Sandpiper *Calidris maritima* (Summers *et al.* 2004) and Ruddy Turnstone *Arenaria interpres* (Summers *et al.* 2004) at different geographic areas (Table 2). Generally, the populations in the more northerly temperate regions started moult earlier and moulted faster compared to the populations at the more southerly regions. This is presumably a need for the northern populations to complete moult before the onset of harsh winter months (Prater 1981).

In the Curlew Sandpiper, there was no correlation between duration of moult and start date of moult ($r = 0.74$, $P = 0.155$, $df = 3$) or latitude ($r = -0.51$, $P = 0.382$, $df = 3$). Moult duration

was shortest at the most northerly site in India at 107 days, followed by the most southerly location at south-eastern Australia (121 days), then Kenya at 128 days and NWA and SA at 129 days (table 2). In India, moult appeared to be accelerated so that it could be completed before the end of the monsoon season in September (Guhathakurta & Rajeevan 2006). The post-monsoon season is typically characterized by rapid decline in rains, high daily temperatures and dry northeast winds (Guhathakurta & Rajeevan 2006), the combined effect of which would be reduced prey abundance for the Curlew Sandpipers, resulting in more difficult feeding conditions. At the southernmost non-breeding site in south-eastern Australia where moult starts the latest, birds needed to hasten moult so as to complete it in time to prepare for northward migration to the breeding grounds.

Primary moult speed can be adjusted by varying the number of feathers growing simultaneously or by varying the growth rate of individual primaries (Pimm 1976, Serra 2000, Underhill *et al.* 2006). In the Curlew Sandpiper, both methods were employed. For instance, in India, moult duration was shortened by reducing the interval between shedding of individual primaries (Table 3), resulting in the growth of several feathers simultaneously (Fig. 2). In south-eastern Australia, moult duration was shortened by progressively increasing the rate of moult of individual primaries (Table 3) rather than adjusting the number of primaries growing simultaneously (Fig. 2).

Pattern of moult of adults

With the exception of India, there was little difference in the pattern of primary feather replacement within the species (Fig 3). In Kenya, South Africa, north-western Australia and

south-eastern Australia, the average number of primaries which overlapped in growth between the moult of P1 and P4 was 2.4 and between the moult of P5 and P10, the average number of primaries which overlap in growth was 1.4 (Fig. 2). The similarity in moult patterns suggests that this might be a habitat related adaptation rather than an adaptation to geographic region. Curlew Sandpipers live in open habitats such as the shore and open inland wetlands and there is a need to minimize the wing gap during moult in order to minimize loss of flight efficiency, thus vulnerability to predation during the moult period.

Moult of adults in relation to environmental factors

One of the major accomplishments of this thesis is the estimation of annual parameters of moult using the moult models of Underhill & Zucchini (1988). The extensions of the original moult model (Birgit Erni, Department of Statistical Sciences, UCT, *in litt.* and Erni in prep.) allowed the inclusion of covariates such as predation index and temperature, making it possible to explore the link between the start of moult with environmental variables. In the populations at the southernmost non-breeding areas in South Africa, north-western Australia and south-eastern Australia, the onset of moult in males was related to the average June temperatures while moult in females was related to the level of predation pressure and July temperatures on the Arctic breeding grounds. This demonstrates that the effect of predation and temperature on the breeding grounds on the timing of migration (chapter 2 and 3) is carried over to the timing of moult. For the populations at the more northerly sites in Kenya and India, the timing of onset of moult was found to be related to rainfall conditions at these sites.

Moult of immature birds

Irrespective of the number of primary feathers replaced, moult started earliest in north-western Australia, then south-eastern Australia and latest in South Africa. The duration of moult was longest in south-eastern Australia and shortest in South Africa. Consequently, moult started earliest and ended earliest in north-western Australia, started latest in South Africa but ended earlier than in south-eastern Australia, except in the group which moulted three primaries when moult in South Africa ended later than in south-eastern Australia. The start and duration of moult of immature Curlew Sandpipers probably reflects the adaptation of immature moult to the environment of their different moulting areas, although this was not demonstrated in this study. In other groups of birds, for example the Citril Finch *Serinus citronella*, the start and duration of moult was a reflection of habitat quality (Borras *et al.* 2004). It is possible that immature Curlew Sandpipers time their moult so it coincides with periods of peak food abundance on their non-breeding areas.

Impact of climate change on migration and moult

The ecological response of bird populations to climate variables has recently become the focus of many ecological investigations (Crick & Sparks 1999, Møller *et al.* 2007). One of the more visible impacts of climate change on the scheduling of annual events is in the change of migration date. The results on migration presented in this study show the advancement of autumn migration dates of adult Curlew Sandpipers by 23 days from 1946–2005 in Sweden and by 10 days from 1983–2000 in Poland, about half a day per year on average. This trend was correlated negatively with June temperature and with the index of predation on the breeding ground in Siberia.

It has been demonstrated already that the change in phenology of spring migration of many bird species is correlated with warming temperatures. The mechanism through which climate change affects autumn migration is still being debated. The present study combined with other recently published results lends support to the hypothesis that the dampening of lemming cycles as a result of climate change has led to increased predation on the eggs and young of arctic breeding birds (Kausrud *et al.* 2008). The consequence of this increased predation would be earlier departure of adult birds from the Arctic breeding grounds (Chapters 2 and 3). Some evidence of this increased predation is also seen in the decline in the proportion of juvenile birds recorded at the non-breeding areas in South Africa (Harebottle & Underhill 2006) and Australia (Minton *et al.* 2005).

Compared to the number of studies on spring migration and breeding of some migrant species in Europe, considerably less is known about how climate change has affected the timing of moult especially in species which migrate and moult in the southern hemisphere. Based on the results of this study, the effect of climate change on the schedule of moult is evident, not so much in the trend, as in the variability of start dates (Chapter 5). Increased variability over time of moult start dates suggests intensification of the processes which modulate the timing of migration and moult; in this particular case, the temperature and predation on the arctic breeding areas.

Conclusions and future prospects

The major findings of this thesis are:

1. Annual variability in the timing of migration of adult Curlew Sandpipers is negatively correlated with June temperature and predation on the Arctic breeding grounds. Warm temperatures during the breeding season in June and July are hypothesised to advance the egg-laying in the breeding season leading to an early conclusion of the breeding season thereby resulting in an early onset of autumn migration. High predation on clutches resulted in early departure of birds from the breeding areas. The effects of temperature and predation on the timing of migration were age and sex-specific. The timing of migration of males was negatively correlated with June temperature; in contrast the timing of migration of females was positively correlated with July temperature and negatively with predation pressure. The timing of migration of juveniles was positively correlated with predation pressure on the Arctic breeding grounds (Chapter 2 & 3).
2. Median migration dates of adult birds have advanced over the years. The trend in the timing of migration is a direct result of increased predation pressure on the Curlew Sandpiper. The decrease in the amplitude of the “boom or bust” cycle of lemmings coupled with long-term decline in the abundance of lemmings, an indirect consequence of climate change, has resulted in increased predation on the eggs and young of the Curlew Sandpiper, causing the birds to leave the breeding area earlier.
3. There was a pattern of geographic variation in the start of moult. With the exception of Kenya, where the unexpectedly late start to moult could be explained by weather conditions, moult started earliest at the northernmost region in India and got progressively later in the more southern areas (Chapter 4). There was no clear geographic pattern in the

duration of moult. The possible cost of differences in timings could be: quick feather wear in early moulters while late moulters might face a time constraint during spring migration.

4. The pattern of moult of individual primaries was similar at Kenya, South Africa, north-western Australia and south-eastern Australia but the overlap in number of primaries growing simultaneously was higher in India compared to the other regions. The rate of production of feather mass was different in the different regions. The speed of moult was regulated either by the number of primaries growing simultaneously or by the rate of moult of individual primaries (Chapter 4-7).

5. The annual start date of moult at the southernmost limit in South Africa, north-western Australia and south-east Australia was correlated with predation pressure and average temperature in June and July on the Arctic breeding areas (Chapter 5). Start dates of moult in Kenya and India was probably modulated by rainfall pattern at these regions (Chapter 6).

6. Males generally started moult earlier than females. In South Africa, males started moult 11 days earlier than females; in north-western Australia, males started moult 14 days earlier than females; and in south-eastern Australia, males started moult nine days earlier than females.

7. The start date of moult of both males and females was affected by breeding success, but the difference between moult start dates in good and poor breeding years was larger in females compared with males.

8. Increased variability in the start date of moult since 1990 suggests that either temperature or predation has disrupted the regular pattern of breeding productivity of the Curlew Sandpiper, causing the birds to breed exceptionally later than normal or leave the breeding grounds exceptionally earlier than normal.

Future prospects

The extended Underhill and Zucchini (1988) models offers novel opportunities to study the inter-annual variation in the timing of moult in relation to environmental as well as endogenous factors. The results of this kind of investigation might contribute to the understanding of the magnitude of species and populations response to changing environment. This can be applied to models used for assessing the ability of birds to adapt to global change.

Since climate change does not only involve a directional change in climatic variables but also the frequency and magnitude of extreme climatic events (Easterling *et al.* 2001), the study of the frequency of extreme events and their effect on avian life-history stages is worth investigating.

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Table 1 comparison of the migration dates of adult and juvenile Curlew Sandpipers observed in Sweden (1946–2005) and Poland (1983–2000).

Age	Sex	Breeding success	Sweden		Poland	
			Median migration date	Inter-quartile range (Q25–Q75)	Median migration date	Inter-quartile range (Q25–Q75)
Adults		Overall	27 Jul	21 Jul–5 Aug	3 Aug	23 Jul–17 Aug
		Good	4 Aug	26 Jul–13 Aug	4 Aug	31 Jul–6 Aug
		Poor	25 Jul	20 Jul–2 Jul	27 Jul	24 Jul–1 Aug
	Males	overall	21 Jul	16 Jul–24 Jul	23 Jul	19 Jul–2-Aug
		Good	19 Jul	17 Jul–6 Aug	28 Jul	29 Jun–27 Aug
		Poor	21 Jul	18 Jul–25 Jul	23 Jul	16 Jul–5 Aug
	Females	overall	29 Jul	26 Jul–4 Aug	2 Aug	23 Jul–14 Aug
		Good	10 Aug	3 Aug–15 Aug	6 Aug	21 Jul–14 Aug
		Poor	23 Jul	20 Jul–29 Jul	23 Jul	16 Jul–25 Aug
Juveniles	overall	3 Sep	19 Aug–10 Sep	2 Sep	23-Aug–12-Sep	
	Good	31 Aug	27 Aug–07 Sep	29 Aug	28 Aug–6 Sep	
	Poor	10 Sep	2 Sep–17 Sep	5 Sep	2 Sep–6 Sep	

Table 2 Estimated mean start dates of primary moult of wader species at different latitudes

Species	region	Latitude	Mean start	Duration (days)	References
Grey Plover <i>Pluvialis squatarola</i>	Britain	NA	19-Aug	90	Serra 2002
	Italy	44–45°N, 12°E	19-Aug	93	
	India	9–10°N, 79°E	1-Sep	127	
	Kenya	03°20'S, 29°55'E	13-Sep	130	
	South Africa	33°12'–45'S, 18–25°E	30-Sep	131	
	North-western Australia	18–20°N, 119–122°E	9-Oct	121	
South-eastern Australia	38–39°N, 144–147°E	5-Oct	128		
Red Knot <i>Canutus canutus islandica</i>	Britain	56–57°N, 02–4°W	20-Jul	77	Summers <i>et al.</i> 2010
<i>C.c. canutus</i>	South Africa	33–31°S, 18°E	25-Oct	95	
Turnstone <i>Arenaria interpres</i>	Scotland	NA	5-Aug	73.8	Summers <i>et al.</i> 2004
	South Africa	NA	9-Oct	119.4	
Purple Sandpiper <i>Calidris maritima</i>	Britain	54–57°N	21-Jul	61	Summers <i>et al.</i> 2004
	Iceland	64–65°N	22-Jul	51	
Curlew Sandpiper <i>Calidris ferruginea</i>	Norway	70°N	15-Sep	48	Chapter 4 Chapter 4 Chapter 4 Chapter 6 Chapter 6
	North-western Australia	18–20°N, 119–122°E	18-Sep	129	
	South-eastern Australia	38–39°N, 144–147°E	15-Oct	131	
	South Africa	33°12'S –45'S, 18–25°E	4-Oct	129	
	Kenya	00°22'N–03°20'S, 35°02'–58' E	6-Oct	133	
India	9–10°N, 79°8–51'E	26-Jul	145		

Table 3 Estimated moult start date and proportion of feather mass grown (PFMG) of individual primaries of the adult Curlew Sandpiper in Kenya, India, South Africa, north-western Australia and south-eastern Australia.

SA				NWA			SEA			Kenya			India		
Primary	Moult start	SD	PFMG/day	Moult start	SD	%PFMG/day	Moult start	sd	%PFMG/day	Moult start	SD	%PFM G/day	Moult start	SD	%PFMG/day
P1	30 Sep	1.1	0.21	17 Sep	0.5	0.24	15 Oct	0.6	0.29	2 Oct	2.5	0.37	25.Aug	3.0	0.40
P2	2 Oct	1.1	0.25	19 Sep	0.5	0.29	17 Oct	0.6	0.36	6 Oct	2.3	0.48	27.Aug	5.2	0.45
P3	9 Oct	0.9	0.32	24 Sep	0.5	0.34	22 Oct	0.5	0.43	10 Oct	2.3	0.45	01.Sep	4.2	0.40
P4	17 Oct	0.9	0.39	1 Oct	0.5	0.37	30 Oct	0.6	0.49	17 Oct	3.3	0.43	07.Sep	2.9	0.46
P5	27 Oct	0.9	0.46	11 Oct	0.5	0.44	7 Nov	0.6	0.58	28 Oct	2.8	0.52	17.Sep	2.8	0.49
P6	10 Nov	1	0.62	24 Oct	0.5	0.59	21 Nov	0.6	0.44	12 Nov	3.1	0.60	01.Oct	3.6	0.40
P7	24 Nov	0.9	0.54	08 Nov	0.5	0.66	11 Dec	0.4	0.63	26 Nov	3.5	0.53	17.Oct	3.6	0.34
P8	13 Dec	0.9	0.57	24 Nov	0.8	0.60	25 Dec	0.6	0.66	19 Dec	3.4	0.76	05.Nov	3.5	0.36
P9	30 Dec	0.9	0.73	10 Dec	1.1	0.64	7 Jan	0.4	0.70	5 Jan	3.6	0.85	17.Nov	3.2	0.40
P10	11 Jan	0.9	0.68	26 Dec	1.4	0.64	16 Jan	0.4	0.64	15 Jan	4.4	0.77	30.Nov	4.0	0.45

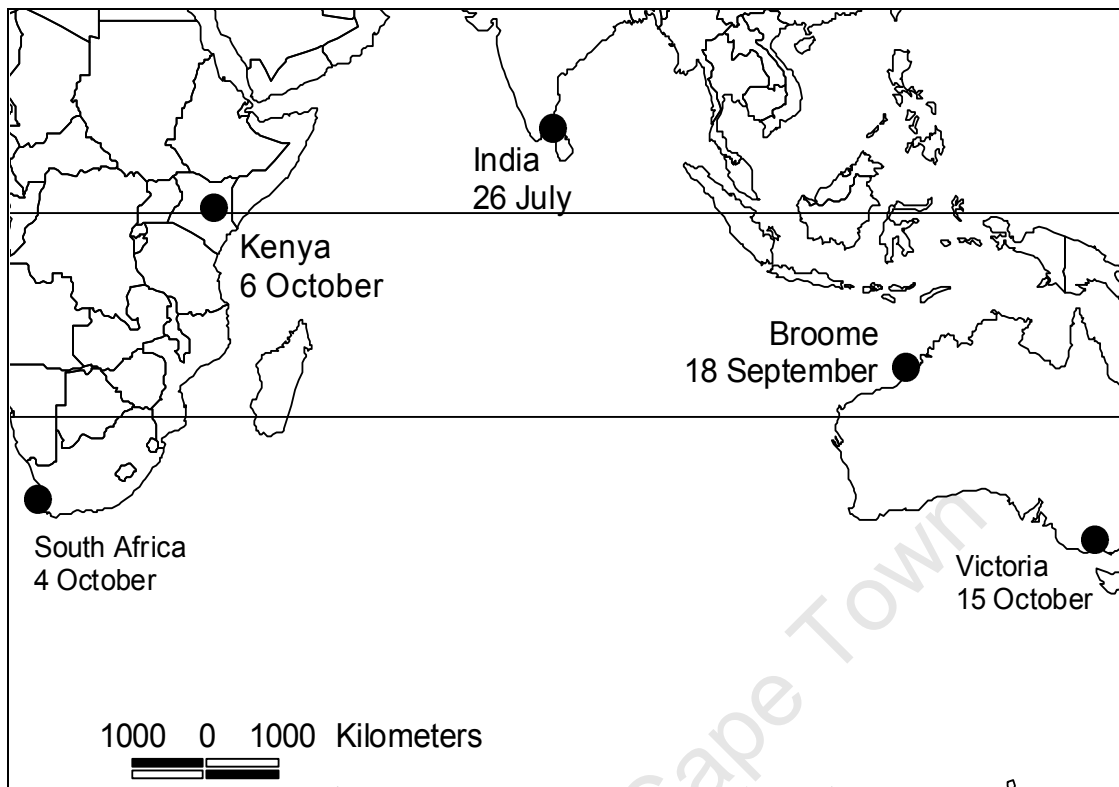


Fig. 1 Estimated mean start date of moult of adult Curlew Sandpipers at Kenya, India, South Africa, north-western Australia and south-eastern Australia.

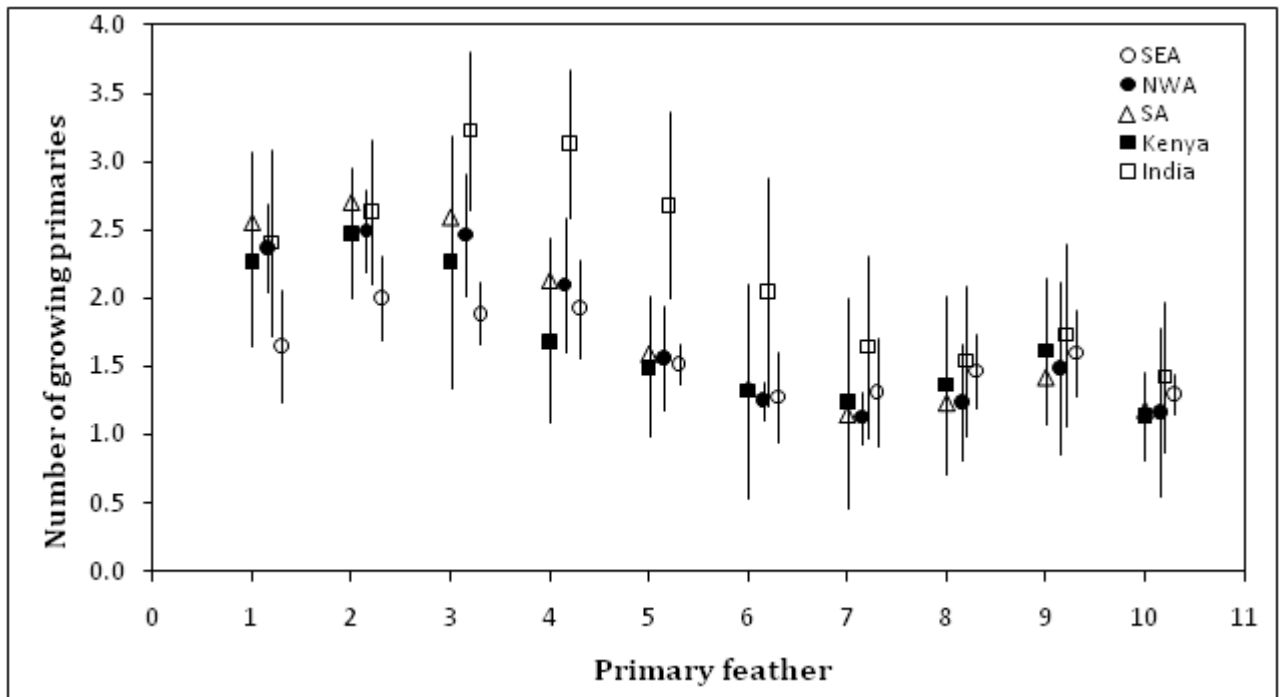


Fig. 2 Average number of primaries growing simultaneously during the moult of each primary in Kenya, India, South Africa, north-western Australia and south-eastern Australia.

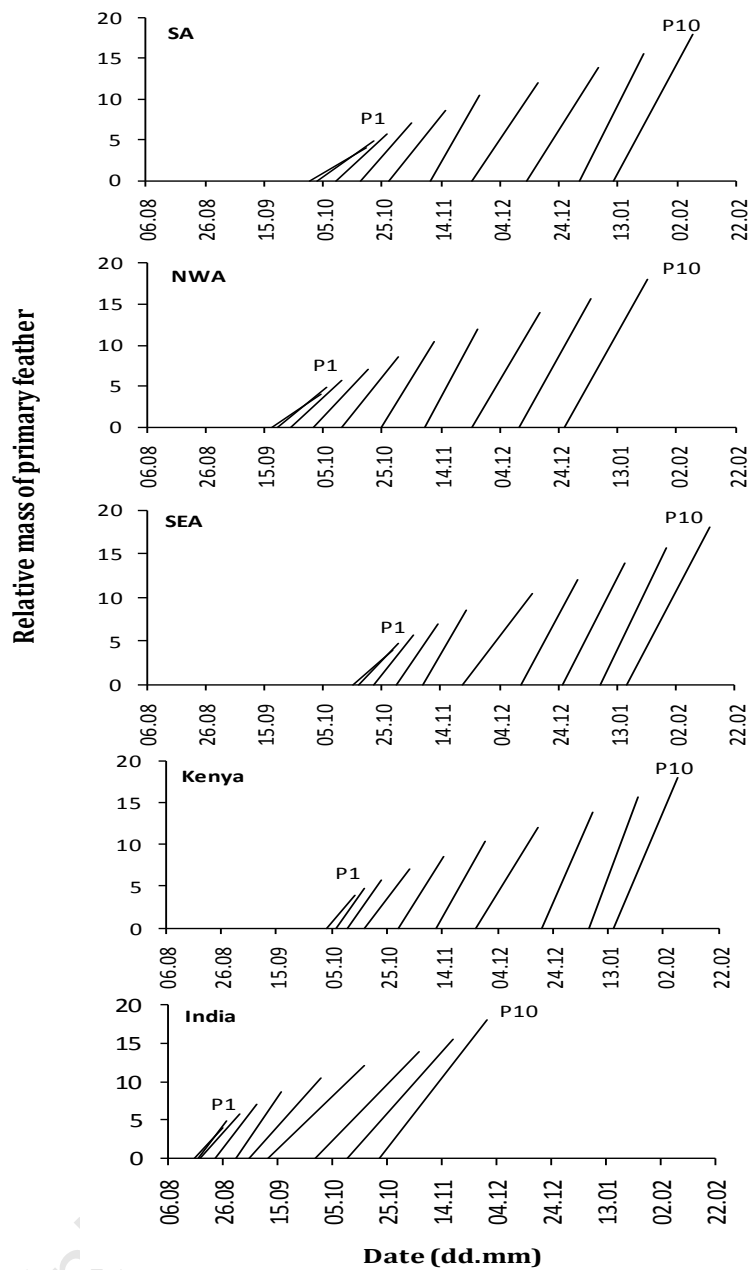


Fig. 3 Growth lines of primaries P1–P10, showing the amount of the primary mass produced between start and end date of each primary development. Slopes of the lines reflect the growth rate of each primary. Moulting locations: Kenya, India, South Africa, north-western Australia and south-eastern Australia.