

**ECOLOGY OF MIGRATORY TIMING BY SOUTHBOUND
MALE AND FEMALE WESTERN SANDPIPERS (*Calidris mauri*)**

by

Amanda Christine Niehaus

B.Sc. (Hons) Biological Sciences, University of Iowa, 1999

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

In the Department

of

Biological Sciences

© Amanda C. Niehaus 2003

SIMON FRASER UNIVERSITY

October 2003

All rights reserved. This work may not be
reproduced in whole or in part, by photocopy
or other means, without permission of the author.

APPROVAL

Name: Amanda Christine Niehaus

Degree: Master of Science

Title of Thesis:

Ecology of migratory timing by southbound male and female Western Sandpipers (*Calidris mauri*)

Examining Committee:

Chair: Dr. Elizabeth Elle

~~Dr. R. Ydenberg, Professor, Senior Supervisor~~
Department of Biological Sciences, S.F.U.

Dr. D. Lank, Research Associate and Adjunct Professor
Department of Biological Sciences, S.F.U.

Dr. T. Williams, Professor
Department of Biological Sciences, S.F.U.

Dr. J. Brown, Professor
Department of Biological Sciences,
University of Illinois at Chicago
Public Examiner

3 October 2003
Date Approved

PARTIAL COPYRIGHT LICENCE

I hereby grant to Simon Fraser University the right to lend my thesis, project or extended essay (the title of which is shown below) to users of the Simon Fraser University Library, and to make partial or single copies only for such users or in response to a request from the library of any other university, or other educational institution, on its own behalf or for one of its users. I further agree that permission for multiple copying of this work for scholarly purposes may be granted by me or the Dean of Graduate Studies. It is understood that copying or publication of this work for financial gain shall not be allowed without my written permission.

Title of Thesis/Project/Extended Essay

Ecology of migratory timing by southbound male and female Western Sandpipers (*Calidris mauri*)

Author:

(signature)

(name)

10-27-03

(date)

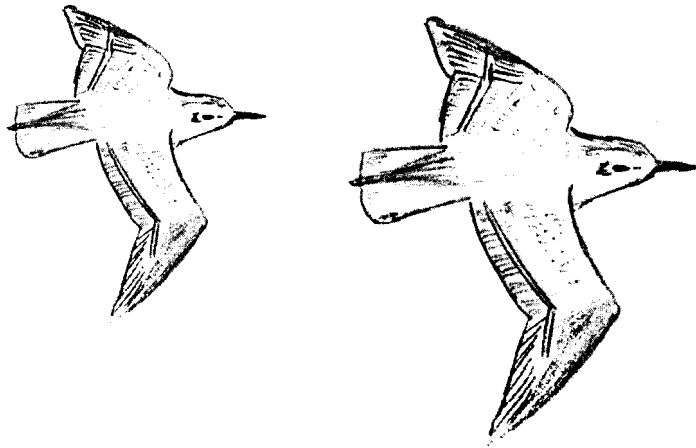
ABSTRACT

Western Sandpipers (*Calidris mauri*) show the pattern typical of long-distance migrants of the family Scolopacidae, with male-biased parental care, female-first southward migration, and independent migration of age classes. I investigated the migratory timing of southbound Western Sandpipers, focusing on the period between departure from breeding sites and the first major stopover. A simulation model based on published breeding parameters predicted that females should precede males to post-breeding sites by 1.1-5.3 d, which agreed well with data (2.3-8.3 d). At the first major stopover, the mean difference was only 1.2 days, but varied over 14 years from -7.8 days (females-first) to +2.3 days (males-first). Juvenile females preceded males by on average 0.5 d (-5.1 to +1.1 d, n=19).

To examine this interannual variation, I compiled data on snowmelt, breeding phenology, and the migration of an important predator, the Peregrine Falcon (*Falco peregrinus*). Snowmelt and falcon migratory timing varied greatly year-to-year, and were strongly correlated. These events bracketed sandpiper breeding and migration, which in contrast varied relatively little. Sandpipers migrated later relative to falcons in years with early snowmelt, which I infer makes the journey more dangerous.

I compared predictions of five hypotheses about sandpiper migratory timing (Breeding Recovery, Migration Distance, Molt Deadline, Escape Performance, Territoriality) to data. I found strongest support for the hypothesis that migration timing results from a trade-off between benefits (more time for parental care or development) and costs (greater exposure to falcons) of delayed migration. Females weigh costs more heavily due to their poorer escape performance.

To those who have encouraged me to spread my wings



ACKNOWLEDGMENTS

My deepest gratitude goes to my entire supervisory committee, Ron Ydenberg, Dov Lank and Tony Williams, for helpful criticism during design of my studies and on various drafts of my thesis, and for encouraging my growth as a scientist. My thanks to my senior supervisor, Ron Ydenberg, for teaching me independence in research and scientific writing, and for daring to think outside the box. Thanks to Dov Lank for sharing with me his knowledge of shorebirds and statistics, and for many interesting conversations and ideas. I am grateful to Tony Williams for his perspective on my thesis work and inspiration to keep running.

Thank you to Joel Brown, for acting as a most enthusiastic and supportive public examiner and for valuable comments on my thesis. I thank Elizabeth Elle for many interesting discussions about science and life, and for being an incredible mentor to young women in science.

To my friends and peers of the Centre for Wildlife Ecology, the Behavioural Ecology Research Group and Peepers, I couldn't have done this without you all—you have inspired me, challenged me, and supported me these past three years.

To Brian McCaffery, Dan Ruthrauff and the Yukon Delta National Wildlife Refuge, I offer deep thanks for the experience of a lifetime—giving me the opportunity to study breeding Western Sandpipers and fall in love with Alaska.

My research and degree were funded by a National Science Foundation Graduate Fellowship and the Centre for Wildlife Ecology at Simon Fraser University.

And finally, thank you to my friends and family, for reminding me of my other priorities in life.

TABLE OF CONTENTS

Approval	ii
Abstract.....	iii
Acknowledgments	v
Table of Contents.....	vi
List of Figures.....	ix
List of Tables	x
PROLOGUE	1
Literature Cited	3
CHAPTER I: DIFFERENTIAL TIMING OF SOUTHWARD-MIGRATING WESTERN SANDPIPERS	4
Abstract.....	5
Introduction	6
Methods	8
Study species	8
Simulation model	9
Assessment of migratory timing.....	15
Results	20
Simulation model	20
Post-breeding and staging	23
Southward migration.....	26
Discussion.....	33
Literature Cited	38

CHAPTER II: SOUTHWARD MIGRATORY TIMING OF WESTERN SANDPIPERS IN RELATION TO SNOWMELT, BREEDING AND PREDATORS.....	41
Abstract.....	42
Introduction	43
Methods	46
Study species	46
Snowmelt	47
Timing of breeding.....	47
Sandpiper migratory timing	48
Falcon migratory timing.....	49
Statistical analyses.....	50
Results	50
Snowmelt and timing of breeding.....	50
Adult sandpiper migratory timing	51
Juvenile sandpiper migratory timing.....	54
Falcon migratory timing.....	57
Discussion.....	61
Acknowledgments.....	69
Literature Cited	70

CHAPTER III: EVALUATING HYPOTHESES TO EXPLAIN THE MIGRATORY TIMING OF SOUTHBOUND MALE AND FEMALE WESTERN SANDPIPERS.....	74
Abstract.....	75
Introduction	76
Patterns of adult sandpipers	79
Females provide shorter brood care than males.....	79
Investment in parental care declines seasonally for both sexes	80

Migratory timing shows catch-up features	82
Difference in timing decreases when mean hatch is later	83
Hypotheses	84
Breeding Recovery	84
Territoriality	88
Migration Distance	90
Molt Deadline	92
Escape Performance	95
Synthesis for adults	98
Patterns for juvenile sandpipers	101
Juvenile females precede juvenile males on the southward migration	101
Difference in timing of juveniles decreases when mean hatch is later	102
Hypotheses	103
Breeding Recovery and Territoriality	103
Molt Deadline	103
Migration Distance	104
Escape Performance	104
Synthesis for juveniles	105
Synthesis for Western Sandpipers	108
Patterns of Pacific Dunlin	108
Predictions for Pacific Dunlin	110
Discussion	113
Acknowledgments	115
Literature Cited	116
EPILOGUE	122
Literature Cited	127

LIST OF FIGURES

Figure I-1. Simulation model of the breeding season for Western Sandpipers.	10
Figure I-2. Patterns of parental care for males and females for the base model and sensitivity analyses.....	13
Figure I-3. Capture sites for post-breeding, staging, and southward-migrating Western Sandpipers.	16
Figure I-4. Predicted cumulative distribution of departure of adult Western Sandpipers from breeding sites.	21
Figure I-5. Migratory timing by sex class of adult and juvenile Western Sandpipers in Alaska and British Columbia.	25
Figure I-6. Differential timing of adult Western Sandpipers in British Columbia.	27
Figure I-7. Differential migratory timing for juvenile Western Sandpipers.	29
Figure I-8. Relationship between differential timing of adults and juveniles....	30
Figure I-9. Summary of timing of males and females from breeding to migration.....	32
Figure II-1. Mean hatch date in relation to snowmelt.	52
Figure II-2. Interannual variation in migratory timing of adult Western Sandpipers in the Strait of Georgia, BC.	53
Figure II-3. Difference in the southward passage of adult male and female sandpipers in relation to mean hatch date.....	55
Figure II-4. Mean passage of juvenile sandpipers in relation to snowmelt and hatch timing.	56
Figure II-5. Interannual variation in migratory timing of juvenile males and females in the Strait of Georgia, BC.	58
Figure II-6. Difference in the southward passage of juvenile male and female Western Sandpipers in relation to mean hatch date.	59
Figure II-7. Timing of falcon arrival at the Strait of Georgia, BC, in relation to snowmelt.....	60
Figure II-8. Synthesis of snowmelt, breeding, and migratory timing of sandpipers and falcons.	62

PROLOGUE

Shorebirds (Scolopacidae and Charadriidae) have proved a useful group for examining the evolution of parental care and migratory systems of birds, with species differing widely in migratory distance, parental care patterns, and mating systems (Myers 1981, Székely and Reynolds 1995). An additional level of variation occurs between males and females, and between adults and juveniles of many species. The sexes differ in breeding and migratory strategies, and appear to consider the whole of the annual cycle in decision-making and trade off the costs of breeding and migration in efforts to live and reproduce one more year (Nebel and Lank 2003).

The most common of sandpipers migrating along this Pacific coast of North America, the Western Sandpiper (*Calidris mauri*), displays fascinating patterns of parental care and migratory timing. At tundra breeding sites in Alaska, females desert broods earlier than their mates, who often persist with the young until they can fly (Holmes 1972). Females then migrate first (Butler et al. 1987), ahead of the males, to wintering sites along temperate and tropical coasts (Wilson 1994).

In my thesis, I explore the relationship between these breeding and migratory events for Western Sandpipers, focusing on the time period between departure from breeding sites and early southbound stopovers. I describe the patterns of migration (Chapter I), attempt to relate the timing of migration to events at breeding sites and migratory stopovers

(Chapter II), and finally consider why Western Sandpipers might exhibit male-biased parental care and female-first southward migration (Chapter III).

In Chapter I, I describe the differential migratory timing of males and females during breeding, post-breeding and migratory phases. I challenge the traditional thinking that differences in parental care translate directly into differences in migratory timing by showing how failed breeders influence empirical estimates of differential migratory timing measured at the population level. Because departing sandpipers have not been captured at breeding sites, I estimate departure timing of successful and failed breeders using a simulation model. I then compare these predictions to data on timing at post-breeding, pre-migratory staging and migratory stopover sites. Finally, I compare the migrations of male and female juveniles on southward migration, which has implications for several mechanistic and ultimate hypotheses proposed to explain patterns in adults.

In Chapter II, I examine possible sources of the variation in migratory timing that are observed among years (Chapter I). I relate the migratory timing of sandpipers to the timing of breeding in Alaska and the timing of arrival and subsequent persistence of predatory falcons at migratory stopover sites. In addition, I test the strength of the relationship between climate at breeding sites and the timing of breeding for sandpipers.

Finally, in Chapter III I examine why male and female sandpipers might utilize different strategies of parental care and migration. I dissociate these two events and review and test five hypotheses addressing the southward migratory timing of sandpipers. I then contrast the outcomes for adult Western Sandpipers with those for juveniles and Pacific Dunlin in an assessment of the general applicability of these hypotheses.

Literature Cited

- Butler, R.W., G.W. Kaiser, and G.E.J. Smith. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers, (*Calidris mauri*) on the south coast of British Columbia. *Journal of Field Ornithology* 58(2): 103-111.
- Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. *American Midland Naturalist* 87(2): 472-491.
- Myers, JP. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behavioral Ecology and Sociobiology*, 8:195-202.
- Nebel, S. and D.B. Lank. 2003. Cross-seasonal and cross-disciplinary interactions: synergy from studying the year-round physiology, behaviour, and population biology of migratory shorebirds. *Wader Study Group Bulletin* 100: 118-121.
- Székely, T. and J.D. Reynolds. 1995. Evolutionary transitions in parental care in shorebirds. *Proceedings of the Royal Society of London, Series B* 262: 57-64.
- Wilson, W.H. 1994. Western Sandpiper in *The Birds of North America* (eds. A. Poole and F. Gill). The Academy of Natural Sciences of Philadelphia, Pennsylvania. Vol. 90, pp 1-19.

CHAPTER I

DIFFERENTIAL TIMING OF SOUTHWARD-MIGRATING WESTERN SANDPIPERS

Amanda C. Niehaus, David B. Lank, Robert E. Gill, Jr., Colleen M. Handel, and Brett K. Sandercock

Abstract

Western Sandpipers (*Calidris mauri*) show the pattern typical of long-distance migrants of the family Scolopacidae, with male-biased parental care and female-first southward migration. We study the relationship between male-biased parental care and female-first migration by comparing the predicted timing of adult male and female Western Sandpipers as they disperse from tundra breeding sites, with the timing of sandpipers captured at coastal post-breeding sites in Alaska and at a southbound stopover site in British Columbia. We contrast these findings with the timing of sex classes of juvenile Western Sandpipers on the southward migration.

The breeding simulation model predicts that females should precede males in departure from breeding sites (by 3.3 d), varies with changes in survival of nests or fledglings, and is particularly sensitive to changes in male or female parental care. Females precede males in timing at a coastal post-breeding site (by 2.3 d) as well as a staging site (by 8.3 d). At the stopover to the south, adult females precede adult males by 1.2 days, and differential timing differs widely among years. Surprisingly, juvenile females also significantly precede juvenile males, by 0.5 days over all years. Again, differential timing is highly variable, although to a lesser magnitude than for adults. In particular, these results highlight the need for further studies of post-breeding and staging patterns of adult and juvenile Western Sandpipers in Alaska.

Introduction

Differential timing by sex class is common among North American migratory birds (Ketterson and Nolan 1983) and is typically attributed to the distinct breeding ecologies or wintering distributions of males and females (Myers 1981, Ketterson and Nolan 1983, Butler et al. 1987, Chandler and Mulvihill 1990, Swanson et al. 1999). Western Sandpipers (*Calidris mauri*) show the pattern typical of long-distance migrants of the family Scolopacidae, with male-biased parental care and female-first southward migration. Generally, other *Calidris* sandpipers adhere to the same pattern, with males preceding females northward, and females preceding males southward (Butler et al. 1987, Jehl et al. 1989, Gratto-Trevor 1992, Butler and Kaiser 1995).

Female-first migration in the *Calidris* sandpipers has historically been linked to the 'male-biased' parental care common in this group (Pitelka et al. 1974, Myers 1981, Butler et al. 1987, Neville 2002). Typically, females remain with broods for a shorter time than their mates, and are thought to initiate southward migration after departing the breeding grounds. Adult female Western Sandpipers, for example, also winter farther south than males, on average (Nebel et al. 2002). The migratory timing of sex classes is known in some cases to reflect differential wintering distributions, with those classes wintering farthest from the breeding grounds migrating first (Fairfield and Shirokoff 1978,

Ketterson and Nolan 1983, Chandler and Mulvihill 1990, Swanson et al. 1999).

Therefore, we expect adult female Western Sandpipers to precede males on the southward migration, based on our understanding of parental care and wintering patterns. However, do females precede males on migration by the same amount of time as males care for chicks alone? Although female brood desertion occurs up to two weeks earlier than that of males (Neville 2002), these estimates of timing include only the successful breeders. In contrast, failed breeders of both sexes typically depart the breeding grounds simultaneously. Thus, the timing of both failed and successful breeders influence the overall timing of Western Sandpipers through post-breeding, staging, and stopover sites.

In contrast to adults, little work has been done on the migratory timing of juvenile sandpipers. A recent study of Western Sandpipers shows that not only do adult females winter farther south than adult males, but juvenile females also winter farther south than juvenile males. In fact, among all age and sex classes, juvenile females appear to migrate farthest south and juvenile males farthest north, in general (Nebel et al. 2002). Therefore, we expect that juvenile females might precede males southward as well.

We simulate the Western Sandpipers' breeding season using a simple numerical model, which allows us to estimate the overall differences between males and females as they depart breeding sites.

Both failed and successful breeders are thus accounted for. We then examine data from two post-breeding sites in Alaska, where birds spend time between breeding and initiation of southward migration. Finally, we examine data from a site in British Columbia where southbound sandpipers stop over soon after departing Alaska. We compare the timing of male and female adults between these three phases, and also present male-female differences for juveniles at the stopover site.

Methods

Study species

The monogamous Western Sandpiper breeds predominantly in the upland tundra of western Alaska (Wilson 1994). Following departure from breeding sites, Western Sandpipers move along tidal rivers to coastal mudflats, where they fatten prior to the southward migration (Holmes 1972). Although little is known about post-breeding movements of male and female Western Sandpipers, in general these birds move southward through Alaska (Gill 1979) before eventually departing on over-water flights to southwestern British Columbia (Butler et al. 1996).

After this initial stopover, they progress southward along the Pacific coast to non-breeding sites in Pacific or Caribbean coastal regions of southern North America, Central America and northern South America (Wilson 1994), with some taking an inland route (Senner and Martinez 1982). Juveniles arrive at coastal sites in Alaska when most adults have

moved on (Gill 1979) and are about a month behind adults when they pass through southwestern British Columbia (Butler et al. 1987).

Simulation model

Because there are no capture data for Western Sandpipers as they depart breeding sites, we constructed a simple simulation model based on published breeding parameters to estimate departure timing of adult Western Sandpipers. The numerical procedure is represented graphically in Figure I-1, and shows how birds move through a breeding season beginning with nest initiation and ending with departure from breeding sites. Parameters are described below.

The entire breeding season was limited to 40 days, and pairs of Western Sandpipers initiated nests between days 1 and 19. In this case, nest initiation refers to the beginning of incubation of a full clutch. In the model, the distribution of first initiations was left-skewed to reflect the relative synchrony of arrival and egg-laying described by Sandercock et al. (1999).

On each successive day after nest initiation, a proportion of nests fail, while the remaining nests survive until the next day. Nest failure of Western Sandpipers increases seasonally (Sandercock 1997, Ruthrauff 2002), and this is represented in the base model, as 1% of nests fail on days 1 to 8 of the season and 3% fail on days 9 to 15. We examined how

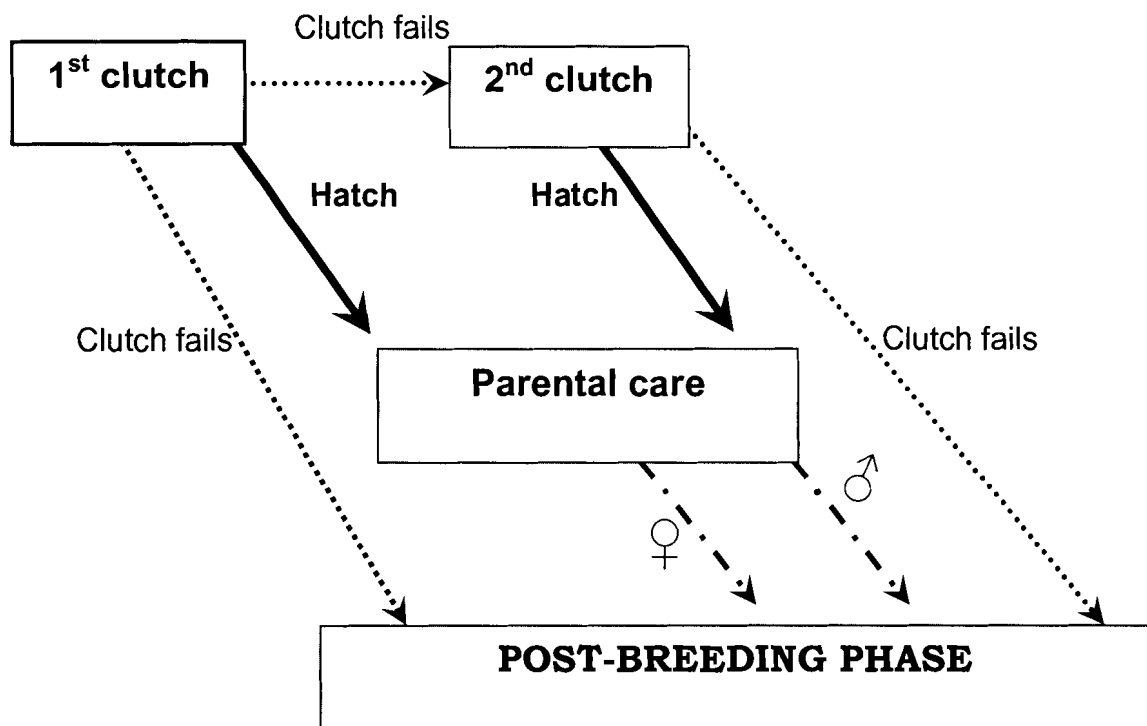


Figure I-1. Simulation model of the breeding season for Western Sandpipers.

Nests proceed day-by-day through the breeding season, beginning with the first clutch initiated. This clutch can fail, in which case the nest moves to second clutch or the parents depart the nest area and begin the post-breeding phase, or hatch, whereby the male and female parents give some parental care before departing for the post-breeding phase. Second nests follow the same chain of events, although failed parents do not have the option of re-nesting again.

deviations from these base rates of nest failure influenced differential departure timing of males and females by varying estimates within the natural range for Western Sandpipers, between 0% and 5% (Niehaus et al., in press), while holding all other parameters constant.

If a pair's first nest failed early in the season, the pair either re-nested or departed the breeding area. Re-nesting is common for Western Sandpipers, but pairs are less likely to try again after a nest failure in late stages of incubation (BKS, pers. obs) or late in the season (Holmes 1972). Pairs do not re-nest after eggs hatch. We attempted to simulate the seasonal decline in re-nesting probability in our base model. If a pair lost their nest on days 1 to 8 in the season, they had a 75% probability of re-nesting. On days 9 to 15, this probability declined to 50%, and after day 15 in the season they did not re-nest.

We tested the effect re-nesting on differential departure timing of males and females by varying re-nesting rates from our base model, while holding all other parameters constant. In these tests, re-nesting probabilities early in the season varied between 50% and 10%.

Re-nests were initiated on the fifth day after failure of the first nest, as this time is required for fertilization and re-laying of the new clutch. These second nests also experienced identical rates of daily nest failure to first nests, but pairs were not allowed to re-nest multiple times. Instead, pairs with failed re-nest attempts departed the breeding site. Overall, 0.6% of nests in the base model were re-nests, compared with a

recent estimate of 1.7% for Western Sandpipers breeding in Alaska (Sandercock 1997).

Pairs with nests that survived the 21-day incubation period (Holmes 1972, Tomkovitch and Morozov 1983, Sandercock 1997), whether this was a first or re-nest attempt, began parental care of the chicks. At this time, pairs were divided considered as individual parents, because male and female Western Sandpipers are known to give differing amounts of parental care (Neville 2002, Ruthrauff 2002). In general, female Western Sandpipers spend less time with the chicks than do their mates, spending 6 to 8 days in brood care early in the season and only 2 to 3 days late in the season (Neville 2002, Ruthrauff 2002). Males also show a seasonal decline in parental care, ranging from about 14 to 4 days from early to late in the season (Neville 2002, Ruthrauff 2002).

In the base model, parental care declined according to a step function, depending on the date in the season when the chicks hatched (Figure I-2). Each step in this decline is intended to represent the average parental care by a male or female during that part of the season, although in reality parental care differs greatly among individuals. To evaluate the effect that parental care has on differential departure timing, we manipulated the duration of parental care by males and females, while holding all other parameters in the base model constant. The various step functions associated with these manipulations are

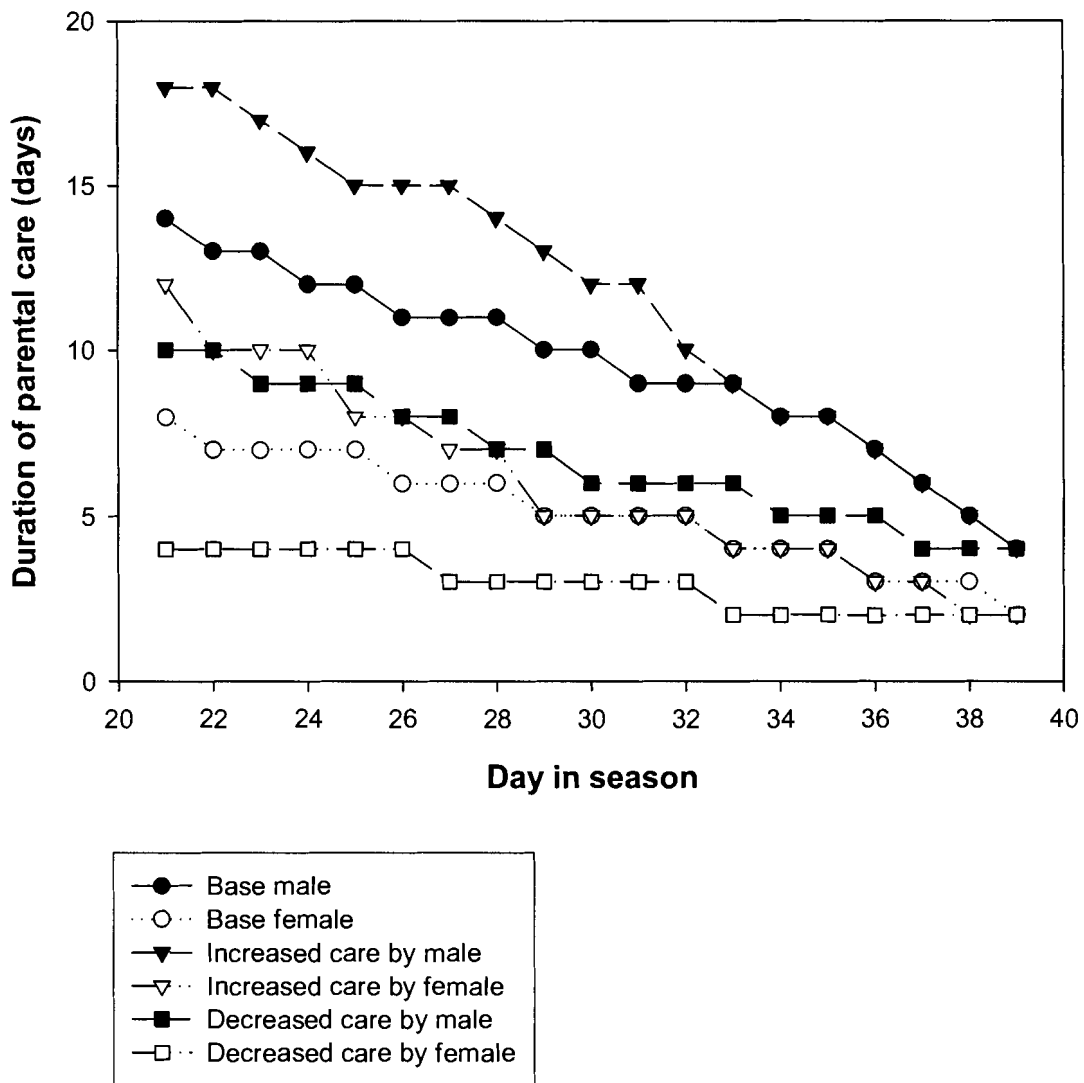


Figure I-2. Patterns of parental care for males and females for the base model and sensitivity analyses.

The maximum durations of parental care by males and females are manipulated in the simulation model. In the model, females always remain with broods for a minimum of two days at the end of the season, but the maximum parental care ranges between 4 to 12 days early in the season. Males give a minimum of four days of parental care at the end of the season, but can stay up to 10 to 18 days early on.

shown in Figure I-2. In each case, the minimum time a female or male can remain with the brood is two or four days, respectively.

Just as nests are lost to predators throughout the incubation period, so can chicks be lost at any time during this period of parental care. In the model, broods either fledged or were predated as a whole unit. The rate by which broods were predated (daily brood failure) was calculated as proportion of broods surviving the season/age at which the chick is fledged. The number of broods failing each day was therefore the number of broods * this daily brood failure rate. For young Western Sandpipers, which leave the nest within 24 hrs of hatching (Holmes 1972), fledging occurs when the young can fly, between 2.5 to 3 weeks (Holmes 1972). In the base model, broods fledged at 18 days, and we allowed 100% of broods to survive until this stage. We later manipulated daily brood failure rates between 2 to 4 % to evaluate the effect on differential departure timing of adult sandpipers.

Adult Western Sandpipers departed breeding sites for a number of reasons. During the nesting phase, adults could depart together after failure of a first nest (if they chose not to re-nest) and always departed together after failure of a re-nest attempt. During the parental care phase, adults could depart together after brood failure or separately after giving parental care to a successful brood. The differential departure timing was therefore included sandpipers that failed (or were successful) at various stages of the breeding season. The proportions of departing

males and females were cumulated over the season, and the distributions were compared using Morbey's method (Morbey 2000), described further below.

Assessment of migratory timing

We analyzed differential timing of Western Sandpipers using capture records of post-breeding adults in Alaska and southward-migrating adult and juveniles in southwestern British Columbia (Figure I-3). Post-breeding adult Western Sandpipers were captured in mist nets while foraging on coastal mudflats at Safety Sound, Alaska (64°29'N, 164°46'W), between 30 June and 11 July in 1993, following peak hatch at a nearby study site, and with rocket nets at Nelson Lagoon, Alaska (56° 00'N, 161° 10'W) between 28 June and 8 August in 1977 (Gill 1979).

Safety Sound is adjacent to Western Sandpiper breeding areas and is used by post-breeding adults for short periods. In contrast, land near Nelson Lagoon is not used by Western Sandpipers for breeding, but is exploited by a number of shorebird species, including Western Sandpipers, over a potentially-longer period (Gill 1979).

In British Columbia (49°05'N, 123°00'W and 48°40'N, 123°20'W), southward-migrating adults were captured in 1978 to 1983, 1985, 1990, and 1995 to 2000, and juveniles were captured in 1978 to 1983, 1985, and 1989 to 2000. Years with fewer than 20 captures were excluded from analyses. Capture efforts were initiated in British Columbia when



Figure I-3. Capture sites for post-breeding, staging, and southward-migrating Western Sandpipers.

Adult Western Sandpipers were captured in mist-nets at post-breeding sites near Safety Sound, Alaska (black), and in rocket nets at Nelson Lagoon, Alaska (black). Adult and juvenile Western Sandpipers were captured in mist nets at the first major stopover on the southward migration, in the Strait of Georgia, British Columbia (white).

appreciable numbers of migratory sandpipers appeared in the area, typically within the first week of July, and continued throughout the adult and juvenile migrations, in July and August, respectively. Total numbers of captures for each site in each year are summarized in Table I-2.

Males and females were assigned to a sex based on culmen length: <24.3mm were classified as males; >24.7mm as females (Page and Fearis 1971, Prater et al. 1977). Those with intermediate bill lengths were classified as unknown and excluded from analyses. As culmens of some juvenile Western Sandpipers were still growing at Alaskan sites, we could not assign sex to juveniles with certainty until their arrival at the first migratory stopover.

Captured sandpipers were assigned to age classes (adult or juvenile) based on plumage (Prater et al. 1977). In British Columbia, sandpipers were assigned to age classes in the field after 1983. Because the southward migrations of adults and juveniles are temporally distinct (Butler et al. 1987, Wilson 1994), we retrospectively classified birds captured prior to 1983 using known migration timing of age classes as described by Butler et al. (1987).

In this manner, Western Sandpipers captured between 29 June and 29 July were considered as adults, and those captured after 2 August were considered as juveniles. In later years, when age classes

Years	Adult numbers	Adult Julian dates	Juvenile numbers	Juvenile Julian dates
1978	118	179-211	372	219-268
1979	487	177-211	699	219-260
1980	1221	189-213	626	219-255
1981	310	190-213	524	217-241
1982	762	185-205	1734	217-245
1983	686	187-210	1297	217-250
1984	0	X	X	X
1985	217	185-206	91	227-242
1986	0	X	X	X
1987	0	X	X	X
1988	0	X	X	X
1989	17	191-207	57	223-232
1990	103	191-213	129	215-236
1991	0	X	X	X
1992	14	202-223	38	204-232
1993	18	195-232	138	211-243
1994	8	215	93	215-238
1995	36	189-229	142	205-242
1996	113	192-236	415	211-242
1997	124	191-221	228	204-240
1998	38	193-208	97	208-237
1999	23	184-195	55	215-232
2000	179	186-221	174	186-240

Table I-1. Timing and numbers of captures at Strait of Georgia, British Columbia.

In some years (X), no birds were captured in British Columbia. Adult captures prior to Julian date 179 or juvenile captures after date 268 were excluded from analyses. Also excluded were data from years with fewer than 20 captures. Age classes were considered independently.

were defined in the field, up to 5% of juveniles migrated during the early, “adult” time period, and less than 1% of adults migrated during the late “juvenile” time period. Therefore, misclassification errors appear minimal.

We applied a method developed by Morbey (2000) to calculate the difference in migratory timing of the sexes. Morbey’s method estimates the difference in timing of males and females based on the area (in units of days) between the cumulative percent distribution of male and female captures. Mean or median passage date is often used to examine differential migratory timing by age or sex classes (DeLong and Hoffman 1999, Swanson et al. 1999). Morbey’s method may, however, be superior for examination of timing differences because it smoothes the episodic capture distributions.

This is similar, but not identical, to the Kolmogorov-Smirnov (K-S) test, a non-parametric test to determine whether two samples come from the same distribution. The K-S test is based on the maximum difference at any point in the two distributions, when the data are ordinaly ranked. Here, the data are ranked from earliest to latest captures, and differences between the distributions are measured horizontally, so that the resultant value is in units of days.

To calculate the statistical significance of the differential migratory timing, we developed a null distribution by randomly assigning sex for each individual in proportion to those observed, over all observed capture

dates. We performed 1000 iterations of this sex-randomization. Differential timing was significant if the observed difference between males and females was greater than 95% of the null distribution.

Results

Simulation model

The simulation model predicted that adult females should precede adult males in departure from breeding sites by 3.3 days ($p < 0.0001$) (Figure I-4). However, the pattern of differential departure of males and females was not consistent across the season. Because we assumed that failed breeders departed the breeding grounds together, there was no difference in departure timing of males and females early in our modeled breeding season (Figure I-4a). When successful breeders began to depart breeding sites mid-season (Figure I-4b), females preceded males by up to six days, but as the breeding season came to an end (Figure I-4c), females preceded males by only a few days.

Model estimates of differential departure timing varied between 2.1 to 4.9 days (Table I-2) when parameters were individually manipulated. In each case, however, females preceded males by more than 2 days. Manipulations of daily nest failure rates had the largest influence on the differential departure timing for Western Sandpipers. Greater rates of nest failure were associated with smaller differences in overall departure between males and females (Table I-2). Manipulation of fledging success had a similar, though less powerful, effect on differential departure

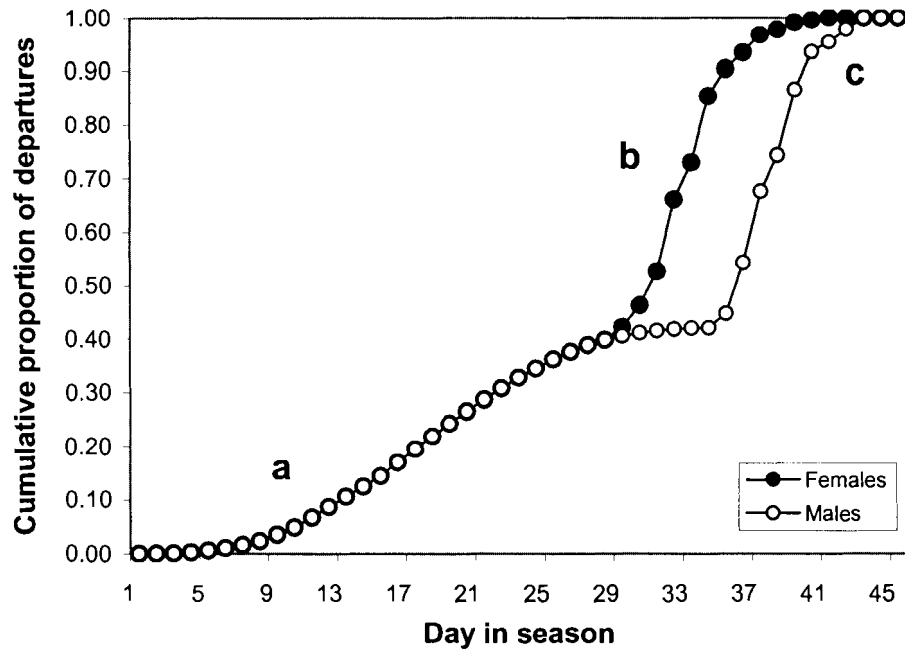


Figure I-4. Predicted cumulative distribution of departure of adult Western Sandpipers from breeding sites.

Early in the season (a), male and female timing is identical as failed breeders leave breeding sites together. Later (b), females precede males by up to six days, although near the end of the season (c), this difference decreases as males decrease the duration of parental care at a faster rate than do females.

Parameter	Value	Females first (days)
Daily nest failure	0%	4.91
	1%	4.17
	1%, 3%	3.31
	5%	2.09
Re-nest rate	75%, 50%, 0%	3.31
	50%, 25%, 0%	3.26
	25%, 10%, 0%	3.22
	10%, 0%	3.19
Daily brood failure	0%	3.31
	2%	2.77
	4%	2.43

Table I-2. Variation in differential departure estimates with changes in breeding parameters.

Values included in base model are in bold. All differential timing estimates were significant to $p < 0.0001$. Of these parameters, changes in daily nest failure rates appear to have the greatest influence on differential departure estimates for males and females.

compared with nest failure rates. Higher rates of daily brood failure resulted in lower estimates of differential departure, as failed males and females left the breeding grounds simultaneously. Finally, manipulation in re-nesting rates did not produce large effects on differential departure (Table I-2).

Manipulation of the maximum average duration of parental care for males or females strongly affected the differential timing of departure (Table I-3). The difference in departure appeared to decrease when males provided less parental care than the base model, or females provided more parental care than the base model.

Post-breeding and staging

Adult females preceded males at both Alaskan post-breeding sites (Figure I-5a,b). Though data from post-breeding areas in Alaska were limited to single and different years, we found intriguing differences in the timing of adult males and females between Safety Sound and Nelson Lagoon. Safety Sound and Nelson Lagoon significantly differed in timing for adults ($F=115.4$, $p<0.0001$). Mean capture at Safety Sound (\pm st dev) was on 2 July \pm 2.8 days, and mean capture at Nelson Lagoon (\pm st dev) was on 19 July \pm 8.9 days.

At the sight adjacent to breeding grounds (Safety Sound) females preceded males by 2.3 days ($p<0.0001$). This closely matched the departure timing estimated by the simulation model. However, at the

Max. duration male care (d)	Max duration female care (d)	Females first (d)
14	8	3.31
18	8	5.32
10	8	1.13
14	12	2.4
14	4	4.98

Table I-3. Variation in differential departure estimates with changes in maximum average duration of parental care.

Durations in bold represent those for the base model. In each case, the minimum average parental care was four days for males and two days for females, and parental care declined seasonally. All female-first estimates were significant to $p < 0.0001$. The differential timing varied widely depending on the duration of parental care, even more so than with changes in daily nest or brood failure or reneating rates (Table 1).

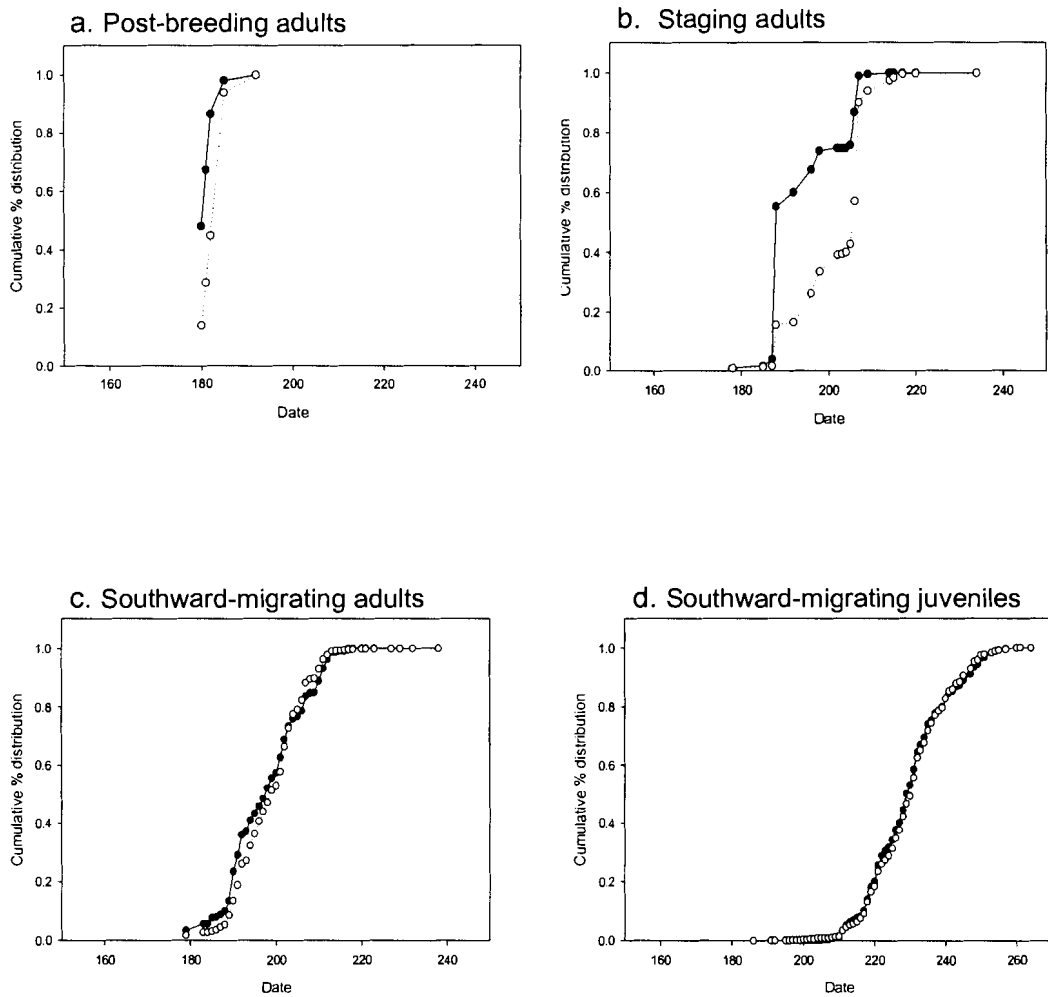


Figure I-5. Migratory timing by sex class of adult and juvenile Western Sandpipers in Alaska and British Columbia.

Females (filled circles) precede males (clear circles) on the southward migration in both adult (a) and juvenile (b) age classes, by 1.2 days and 0.5 days ($p < 0.0001$ for both). Females also appear to precede males to coastal post-breeding sites at Safety Sound, Alaska (c) and Nelson Lagoon, Alaska (d). These differences are 2.3 and 8.3 days, respectively, and both differences are significant ($p < 0.0001$).

site farther to the south (Nelson Lagoon), females were 8.3 days ($p < 0.0001$) ahead of males.

Cumulative proportions of males and females captured at Safety Sound (Figure I-5a) were more gradual than at Nelson Lagoon (Figure I-5b), which was characterized by sharp increases in females at 7 July (Julian date 188) and sharp increases in males at 26 July (Julian date 207).

Southward migration

Mean migratory migration (\pm st dev) of adult Western Sandpipers was around 17 July \pm 5.6 days. Females were generally ahead of males on the southward migration (Figure I-5c), by 1.2 days ($p < 0.0001$) over all years combined.

This composite estimate, however, masks the marked variation in differential timing among years. Individual years differed slightly in the overall timing and patterns of southward migration. Adult females preceded males by up to 7.8 days, but in most years they were only ahead by 1 to 2 days (Figure I-6). In contrast to differential timing estimates from breeding, post-breeding and staging areas, males preceded females by more than a day in three years. In only 3 of 13 years, adult females *significantly* preceded males at the stopover site (4/13 if marginal significance is included) (Figure I-6).

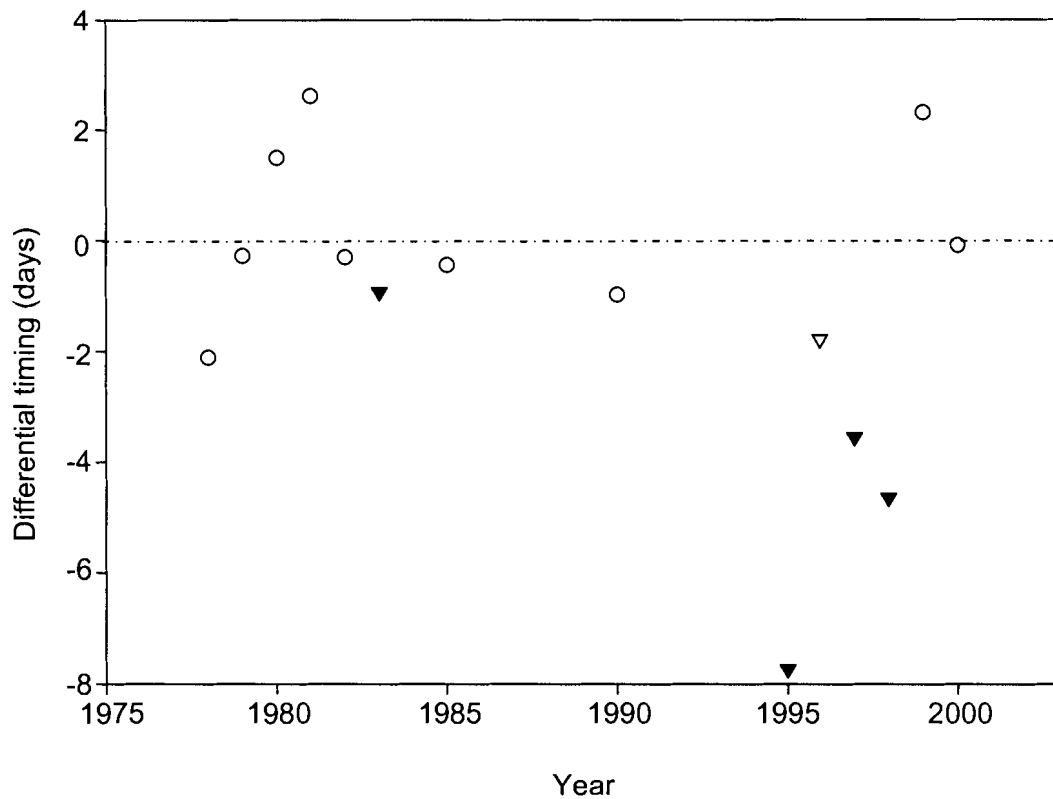


Figure I-6. Differential timing of adult Western Sandpipers in British Columbia.

The difference in timing between males and females varied from year-to-year. In most years, females were ahead of males, as shown by negative values of differential timing (under the dotted line). In a few years, males preceded females southward, as shown by the positive numbers (above the dotted line). Overall, females preceded males by 1.2 days ($p < 0.001$). Filled triangles are significant ($p < 0.05$), open triangles are marginally significant ($p < 0.11$), and open circles are not significant ($p > 0.11$).

Mean juvenile migration (\pm st dev) occurred on about 17 August \pm 4.8 days. Unexpectedly, juvenile females significantly preceded juvenile males on the southward migration, by 0.5 days ($p=0.02$) overall (Figure I-5d).

As with adults, differential timing of juveniles was highly variable among years, although to a slightly lesser magnitude. In most years, females preceded males by at least 1 to 2 days, though were ahead by up to five days in some years (Figure I-7). In two years, males preceded females southward by about one day. Interestingly, females were *significantly* ahead of males in a higher proportion of years for juveniles than for adults. In 5 of 18 years, juvenile females were significantly ahead of males, and in another 3 years the significance was marginal (Figure I-7).

The differential timing for adults and juveniles was not significantly related among years ($r=0.38$, $p>0.1$) (Figure I-8), although this result was strongly affected by data from two years, 1998 and 1999. In 1998, adult females were nearly five days ahead of adult males, while juvenile males were about one day ahead of juvenile females. In 1999, the pattern was opposite: adult males preceded females by more than two days, and juvenile females were ahead of males by three days. Possibly, relatively low sample sizes for adults (<50 captures) influenced the estimated differential timing in these years. When they are excluded, the differential timing of adults and juveniles are strongly correlated

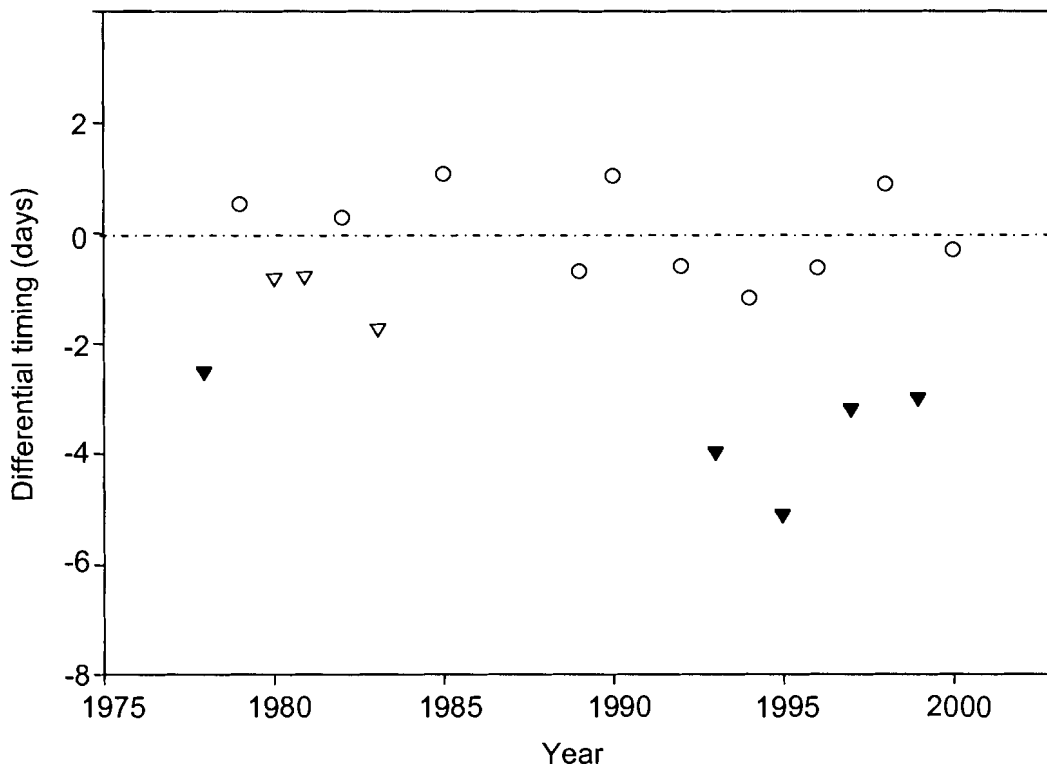


Figure I-7. Differential migratory timing for juvenile Western Sandpipers.

The difference in timing between juvenile males and females varied from year-to-year. In most years, females were ahead of males, as shown by negative values of differential timing (under the dotted line). In a few years, males preceded females southward, as shown by the positive numbers (above the dotted line). Overall, females preceded males by 0.5 days ($p=0.02$). Filled triangles are significant ($p<0.05$), open triangles are marginally significant ($p<0.11$), and open circles are not significant ($p>0.11$).

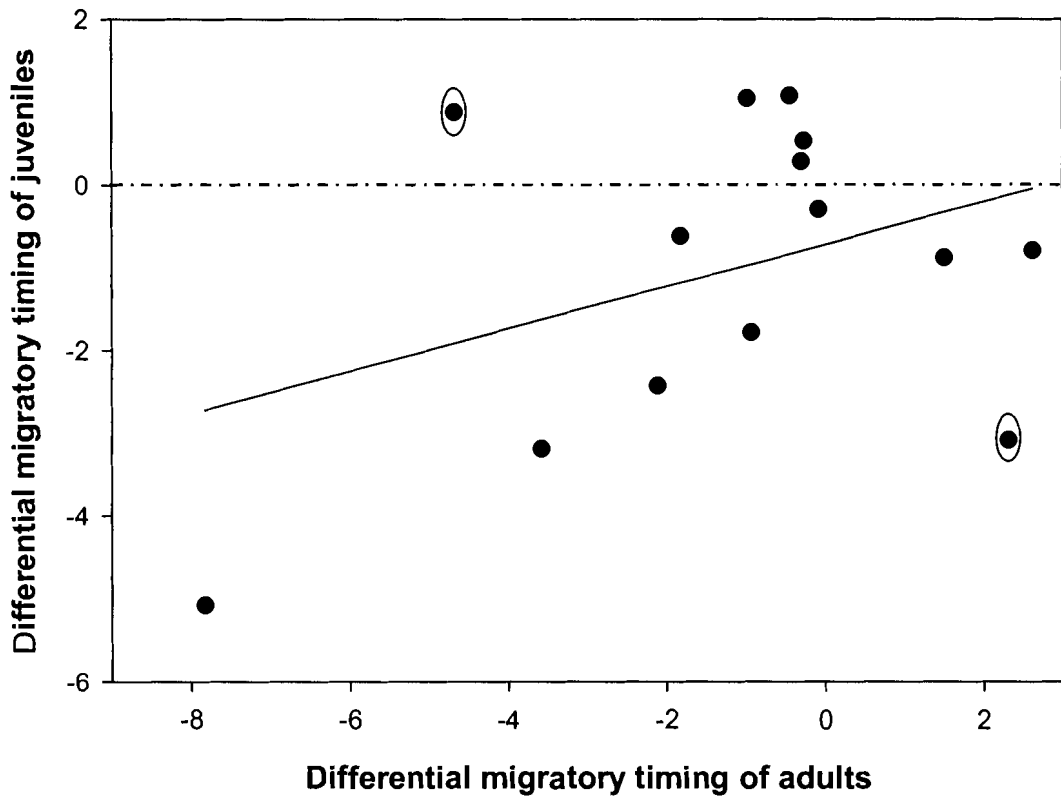


Figure I-8. Relationship between differential timing of adults and juveniles.

The differential timing of adults and juveniles was not significantly related ($p > 0.1$) unless data from 1998 and 1999 were excluded (marked with circles). Then, the amount by which females preceded males was related between age classes ($p = 0.006$).

among years ($r=0.74$, $p=0.006$).

Overall, females appeared to precede males (Figure I-9). The simulation model based on published breeding parameters predicted that females should precede males to post-breeding sites by 1.1-5.3 d, which agreed well with data (2.3-8.3 d). At the first major stopover, the mean difference was only 1.2 days, but varied over 14 years from -7.8 days (females-first) to +2.3 days (males-first). Juvenile females preceded males at the stopover by on average 0.5 d (-5.1 to +1.1 d, $n=19$).

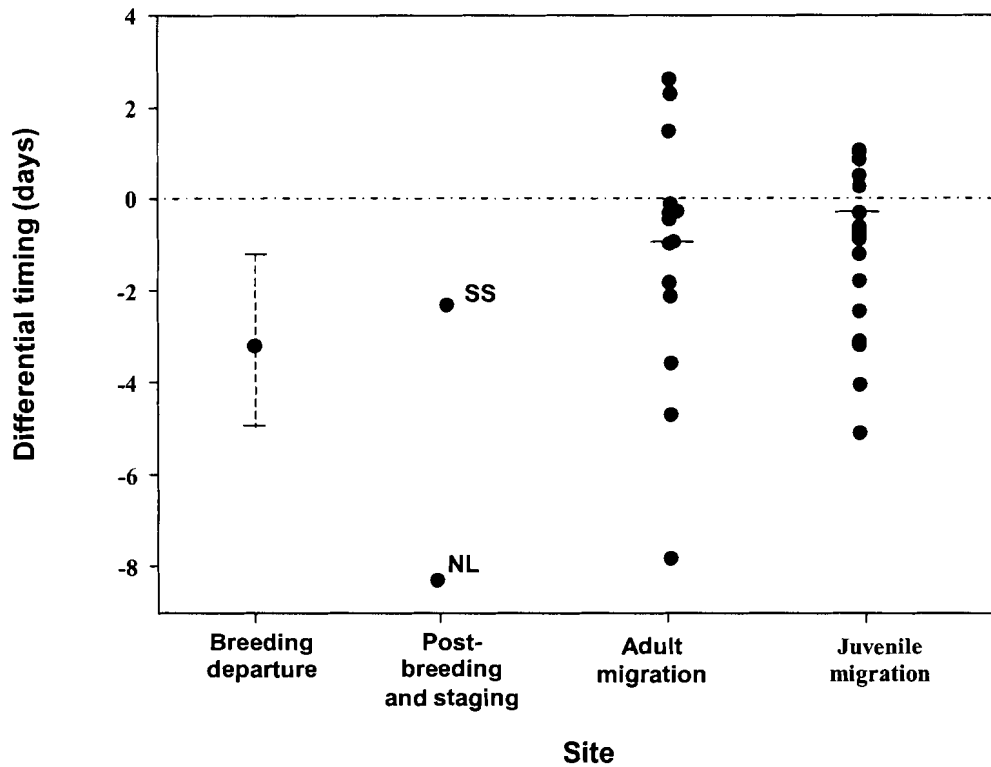


Figure I-9. Summary of timing of males and females from breeding to migration.

Estimates of differential timing from the breeding simulation model and from captures at post-breeding and migratory stopover sites. Negative numbers represent females first. The range of differential timing estimates from breeding was determined via sensitivity analyses on a simulation model, the range of which is indicated by a dashed line. The base result of the model (-3.3 days), prior to these analyses, is indicated by a point on the dashed line. Data from Safety Sound (SS; 1993) were used to estimate post-breeding timing and data from Nelson Lagoon (NL; 1977) were used to estimate staging timing. Migration timing of adults and juveniles in British Columbia was from 14 or 19 years respectively, between 1978 and 2000. Points represent mean differential timing for individual years. The mean difference over all years is indicated by a black line through each set of points.

Discussion

Female Western Sandpipers provide less parental care to broods than do males, and as a result can be expected to precede males on the southward migration. However, we show that in many years adult females are not significantly first when they arrive at the early southbound stopovers in British Columbia. The overall mean is 1.2 days, which is less than predicted by the simulation model, or observed at either post breeding site in Alaska, and differential timing varies a lot among years.

Juvenile Western Sandpipers also exhibit interesting patterns in southward migratory timing. Previously, male and female juvenile sandpipers have not been known to migrate separately, but here we show that in most years, females are first upon arrival in British Columbia. As with adults, this varies a lot among years, but surprisingly, juvenile females are significantly ahead in more years than adults.

What can cause such variability among years? Capture effort appears to be consistent, varying only with the earliest arrival of good-sized flocks. In most years, capture was continuous between adults and juveniles, so no early juveniles would have been missed.

Other work shows that the male-female differences for both age classes are associated with the earliness of breeding (Chapter II) and indirectly, the timing of predators at stopovers sites (Chapter II). Females, with lower escape performance than males (Chapter III), may

attempt to migrate southward early, during a time when fewer falcons are present at stopover sites or wintering areas (Chapter II).

Captures of Western Sandpipers at breeding, post-breeding and migratory sites in the *same* years will be necessary to further elucidate the connectivity of migratory timing among these phases. However, on average, the male-female difference in timing appears to decrease between breeding and British Columbia. We suggest that this shrinking difference between adult males and females results from males making an effort to catch up to females. If early migrants encounter fewer Peregrine Falcons (Lank et al. 2003, Chapter II), a principal predator of shorebirds, then both males and females might benefit by migrating as early as possible.

Early migration is thought to increase a female's probability of surviving to the next breeding event (Gratto-Trevor 1991). This may be through additional opportunity for foraging (Ashkenazie and Safriel 1979), better food resources (Schneider and Harrington 1981), or lower numbers of predators at stopover sites (Lank et al. 2003). Each of these hypotheses were proposed based on female-first patterns for adults, as this trend was previously unreported for juvenile sandpipers.

The timing of predators has the potential to exert a strong influence on the migratory timing of adult and juvenile Western Sandpipers (Lank et al. 2003). Females, in particular, may be more vulnerable to predation as a result of their larger size and potentially

poorer escape performance (Chapter III). As a result, early migrants of either sex will be safer, but that this window of safety is more critical for female sandpipers than males. Having traded-off early migration in favor of extended parental care, male sandpipers may then attempt to catch up to females by spending shorter amounts of time preparing for southward migration. A comparison of the duration of stays at postbreeding sites and of body condition of males and females would address this issue.

Alternatively, the small differential timing observed in many years could result in imperfect filtering of failed breeders of both sexes with successful females early in the season. If failed breeders migrate at the same time as successful females, this could decrease the perceived differential timing measured at British Columbia overall. However, it is unclear why failed breeders would wait, as they have an opportunity to migrate early, when predation danger is lower (Lank et al. 2003, Chapter II).

Contrary to our expectations, we did not observe mixed flocks of failed males and females early in the adult southward migration. It seems unlikely that the failed breeders were missed as a result of capture effort. In Alaska, birds were captured over more than a month at Nelson Lagoon and an even longer period in British Columbia. Possibly, failed breeders migrate in small, scattered groups, use alternative routes, or wait at northern sites and filter in with successful breeders to head south. At this time, we are unable to describe the migration patterns of

failed breeders, but early southward migration is safer (Lank et al. 2003, Chapter II), so failed breeders could benefit by moving southward as soon as possible.

As well as varying among years at British Columbia, differential timing varied between the two Alaskan sites. However, Safety Sound and Nelson Lagoon differed in a number of respects besides year, including timing, methods and use by shorebirds. Safety Sound is directly adjacent to breeding areas, and appears to be used on a short-term basis by birds immediately after departure from nest or natal areas. In contrast, Nelson Lagoon is a pre-migratory staging site for a number of long-distance migrants, including Bar-tailed Godwits, which spend longer periods preparing for a trans-oceanic flight (Gill 1979). Western Sandpipers may use this area to prepare for migration in a similar manner.

Unfortunately, surprisingly little is known about the post-breeding and pre-migratory patterns of Western Sandpipers. In general, sandpipers are thought to move south and east through Alaska before movement southward to British Columbia (Gill 1979). Southbound Western Sandpipers do not appear to use the same large stopovers as they do on the northward migration, such as Copper River Delta and the Stikine River Delta.

In fact, large numbers of southbound sandpipers have not been recorded in southeastern Alaska at all, only near breeding areas on the

Yukon-Kuskokwim Delta and at the staging site at Nelson Lagoon. This has led to speculation that the sandpipers bulk up at staging sites such as Nelson Lagoon and then use the wind produced by storm systems to power their flight across the Gulf of Alaska to stopovers in coastal British Columbia (Butler and Kaiser 1995). However, masses of Western Sandpipers at these sites appear insufficient for such a long flight (Gill pers. obs.). Where do the sandpipers go during this time period? Their absence from major stopovers makes it seem unlikely that they hop down the coast as they do on the northward migration, but perhaps they move to lesser-known staging sites in eastern Alaska to fuel before making the cross-water jump. Surveys and radio-tracking studies are necessary to examine site use by adults and juveniles between the time of their departure from breeding or natal sites and their arrival at coasts of British Columbia.

Literature Cited

- Ashkenazie, S. and U.N. Safriel. 1979. Time-energy budget of the Semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. Ecology 60: 783-799.
- Butler, R. and G. Kaiser. 1995. Migration chronology, sex ratio, and body mass of Least Sandpipers in British Columbia. Wilson Bulletin 107(3): 413-422.
- Butler, R.W., F.S. Delgado, H. de la Cueva, V. Pulido, and B.K. Sandercock. 1996. Migration routes of the Western Sandpiper. Wilson Bulletin 108(4): 662-672.
- Butler, R.W., G.W. Kaiser, and G.E.J. Smith. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers, (*Calidris mauri*) on the south coast of British Columbia. Journal of Field Ornithology 58(2): 103-111.
- Chandler, C.R. and R.S. Mulvihill. 1990. Interpreting differential timing of capture of sex classes during spring migration. Journal of Field Ornithology 61: 85-89.
- DeLong, J and SW Hoffman. 1999. Differential autumn migration of Sharp-shinned and Cooper's Hawks in western North America. Condor 101: 674-678.
- Gauthreaux, S.A., Jr. 1982. The ecology and evolution of avian migration systems. In: Avian Biology, Vol 6 (eds. D.S. Farner and J.R. King) Academic Press, New York. pp 93-167.
- Gill, R.E., Jr. 1979. Shorebird studies in western Alaska, 1976-1978. Wader Study Group Bulletin 125: 37-40.
- Gill, R.E., Jr. and P.D. Jorgenson. 1979. A preliminary assessment of timing and migration of shorebirds along the northcentral Alaska Peninsula. Studies in Avian Biology 2: 113-123.
- Gratto-Trevor, C.L. 1991. Parental care in Semipalmated Sandpipers *Calidris pusilla*: brood desertion by females. Ibis 133: 394-399.
- Gratto-Trevor, C.L. 1992. Semipalmated Sandpiper In The Birds of North America, Vol. 6 (eds. A. Poole, P. Stettenheim, and F. Gill). The Academy of Natural Sciences of Philadelphia, Pennsylvania. pp1-20

- Holmes, R.T. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). *Oecologia* (Berlin) 7: 191-208.
- Holmes, RT. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. *American Midland Naturalist* 87(2): 472-491.
- Iverson, G.C., S.E. Warnock, R.W. Butler, M.A. Bishop, and N. Warnock. 1996. Spring migration of Western Sandpipers (*Calidris mauri*) along the Pacific coast of North America: a telemetry study. *Condor* 98: 10-22.
- Jehl, J.R., Jr. 1979. The autumnal migration of Baird's Sandpiper, in *Studies in Avian Biology* No. 2 (F.A. Pitelka, ed.), pp. 55-68, Cooper Ornithological Society, Allen Press, Lawrence, Kansas
- Ketterson, E.D. and V. Nolan, Jr. 1983. The evolution of differential migration. *Current Ornithology* 1: 357-402.
- Lank, D.B. R.W. Butler, J. Ireland, and R.C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303-319.
- Morbey, Y.E. 2000. Protandry in Pacific salmon. *Canadian Journal of Fisheries and Aquatics Science* 57: 1252-1257.
- Myers, JP. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behavioral Ecology and Sociobiology*, 8:195-202.
- Nebel, S., D.B. Lank, P.D. O'Hara, G. Fernández, B. Haase, F. Delgado, F.A. Estela, L.J. Evans Ogden, B. Harrington, B.E. Kus, J.E. Lyons, F. Mercier, B. Ortego, J.Y. Takekawa, N. Warnock, and S.E. Warnock. 2002. Western Sandpipers (*Calidris mauri*) during the non-breeding season: spatial segregation on a hemispheric scale. *Auk* 119: 922-928.
- Neville, J.A. 2002. Division of parental roles in the monogamous Western Sandpiper, *Calidris mauri*. Unpubl. M.Sc. thesis, University of Alaska, Fairbanks, AK.
- Niehaus, A.C. 2003. Ecology of migratory timing for southbound male and female Western Sandpipers (*Calidris mauri*). Unpubl. M.Sc. thesis, Simon Fraser University, Burnaby, BC.

- Niehaus, A.C., D.R. Ruthrauff, and B.J. McCaffery. In press. Response of predators to Western Sandpiper nest exclosures. *Waterbirds* XX:XX
- Page, G. and B. Fearis. 1971. Sexing Western Sandpipers by bill length. *Bird-Banding* 42: 297-298.
- Prater, A.J., J.H. Marchant, and J. Vuorinen. 1977. Guide to the identification and aging of Holarctic waders. British Trust Ornithological Guide No. 15.
- Ruthrauff, D.R. 2002. Seasonal and age-related trends in the reproductive output of Western Sandpipers (*Calidris mauri*) at Kanaryaraq, Alaska. MSc thesis, Humboldt State University, Arcata, CA.
- Sandercock, B.K. 1997. Factors affecting the breeding demography of Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*Calidris pusilla*) at Nome, Alaska. Unpubl. Ph.D. thesis, Simon Fraser University, Burnaby, BC
- Sandercock, B.K., D.B. Lank, and F. Cooke. 1999. Seasonal declines in the fecundity of arctic-breeding sandpipers: different tactics in two species with invariant clutch size. *Journal of Avian Biology* 30(4): 460-468.
- Schneider, D.C. and B.A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98: 801-811.
- Senner, S.E. and E.F. Martinez. 1982. A review of Western Sandpiper migration in interior North America. *The Southwestern Naturalist* 27: 149-159
- Swanson, D.L., E.T. Liknes, and K.L. Dean. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant Ruby-crowned Kinglets. *Wilson Bulletin* 111(1): 61-69.
- Tomkovitch, P.S. and V.V. Morozov. 1983. Biological characteristics of the Western Sandpiper on the Chukchi Peninsula. Translated from the Russian. *Bulletin of the Moscow Nature Society* 88: 38-50.
- Wilson, W.H. 1994. Western Sandpiper in *The Birds of North America* (eds. A. Poole and F. Gill). The Academy of Natural Sciences of Philadelphia, Pennsylvania. Vol. 90, pp 1-19.

CHAPTER II

SOUTHWARD MIGRATORY TIMING OF WESTERN SANDPIPERS IN RELATION TO SNOWMELT, BREEDING AND PREDATORS

Amanda C. Niehaus and Ronald C. Ydenberg

Submitted for publication, September 2003

Abstract

Several recent reports highlight long-term trends toward earlier or later passage dates of migratory birds. Climate change is suspected to be the cause, but few studies have investigated the mechanisms underlying variation in migratory timing, and it is not yet understood how or even whether climate change could cause such changes. We examine relationships between snowmelt, the timing of breeding, and the timing of southward migration of Western Sandpipers (*Calidris mauri*).

We also consider the migratory timing of an important predator, the Peregrine Falcon (*Falco peregrinus*). We find that Sandpiper breeding and migratory timing vary less than snowmelt. Though the mean hatch date of sandpipers is earlier in years with earlier snowmelt, hatch usually occurs much later than snowmelt, and is on average delayed by only 0.26 days for each day that snowmelt is later. Western Sandpipers seem to time their arrival at breeding sites to correspond with average date of snowmelt, rather than earliest possible snowmelt, so that snowmelt can affect breeding only in late years.

We could detect no correlation between snowmelt and the southward migratory timing of sandpipers. In contrast, we found that snowmelt and the migratory timing of falcons were strongly associated, with each days' delay in snowmelt delaying falcon migration by 1.09 days. The result of these relationships is that sandpiper migration occurs later relative to falcon migration in years with early snowmelt, which we surmise makes migration more dangerous. We suggest that sandpipers may be able to use environmental conditions to judge whether the year is early or late, and adjust migratory patterns and behaviors accordingly.

Introduction

Recent reports highlight long term changes in the timing of breeding attributed to climate change (Crick et al. 1997, Brown et al. 1999), however few studies have evaluated the effects of climate on other parts of the annual routine, such as southward migration (Jenni and Kéry 2003 and references therein). On a long-term scale, some migrants appear to have altered migratory timing with changes in climate (Jenni and Kéry 2003), although it is unclear whether or how climate could elicit such responses in migratory patterns on an inter-annual basis.

In the arctic, for example, climate and weather are widely believed to drive the timing of migratory birds breeding during the short summer. Snow on the tundra can influence nest site availability as well as food resources, and weather is favorable and food abundant for a relatively limited period. However, few studies have directly addressed the relationship between northern climates and inter-annual variation in the timing of breeding or migration.

Babcock et al. (2002) found a correlation between snowmelt at a breeding site and arrival and initiation of breeding for Tundra Swans (*Cygnus columbianus*) in sub-arctic Alaska. However, many reports are anecdotal. For example, Young et al. (1995) discuss but do not test the possibility of a relationship between timing of breeding and climate for Golden Eagles (*Aquila chrysaetos*), and Holmes (1972) simply states that Western Sandpipers (*Calidris mauri*) "...begin to arrive on their breeding

areas with the first appearance of snow-free tundra” and “gradually disperse onto the newly exposed tundra”.

The timing of breeding has been linked to northward migratory timing for some birds (Both and Visser 2001), but southward passage may also be affected by the timing of events at breeding sites. The migratory timing of southbound Western Sandpipers varies widely among years, and this variation extends even to the differences in timing between males and females (Chapter 1). These inter-annual differences could result from variation in the initiation of the breeding season as determined by snowmelt, or could reflect events immediately following breeding, such as the imminent decline of conditions at breeding sites or on migration (Jenni and Kéry 2003).

Local conditions at breeding or post-breeding sites do not appear to force the migratory timing of adult Western Sandpipers (Holmes 1972). Juveniles continue to use northern mudflats for a month or more after adults have departed (Gill and Handel 1990). In fact, over 90% of the birds using these areas through early October are “small shorebirds”, including Western Sandpipers, Dunlin (*C. alpina*), Rock Sandpipers (*C. ptilocnemis*) and Semipalmated Sandpipers (*C. pusilla*) (Gill and Handel 1990). Post-breeding Dunlin and Rock Sandpipers molt at these sites before departing for wintering areas (Gill and Handel 1990). Therefore, it seems that factors other than climate and weather conditions at post-

breeding sites are responsible for the early migratory departure of adult Western Sandpipers.

Western Sandpipers may adjust their timing to coincide with favorable conditions at stopover sites (Lank et al, in press). In some studies, shorebird food resources were found to be abundant earlier during the period of southward migration (Schneider and Harrington 1981, Boates and Smith 1989), however, results from recent studies contrast with these findings (Wolf 2001; Lank et al. 2003), casting doubt on this as a general explanatory factor. Alternatively, inter-annual changes in the seasonal abundance of avian predators, predominantly the Peregrine Falcon (*Falco peregrinus*) could affect migratory timing of Western Sandpipers (Lank et al. 2003). Many of the falcons that hunt sandpipers at stopovers and wintering sites are migratory and return to these areas only after completing their own breeding cycles. Predation danger influences many facets of the migration of Western Sandpipers (Ydenberg et al. 2002, Lank et al. 2003, Butler et al., in press, Lank and Ydenberg, pers. comm.), so adjustment of timing in relation to predation danger seems plausible.

The aims of this study are to examine the relationships among climate, the timing of breeding, and the timing of migration. Annual variation in the timing of hatch and the migration of adult and juvenile Western Sandpipers is reported, and the associations of these events with snowmelt and falcon migratory timing are explored. We discuss

these findings in the context of migratory strategies of adult and juvenile Western Sandpipers.

Methods

Study Species

Western Sandpipers breed predominantly in western Alaska and to a lesser extent in northern Alaska and eastern Siberia (Wilson 1994), and exhibit biparental care during incubation (Holmes 1972, Neville 2002). Typically, males care for the chicks for an average of six to eight days longer than females (Neville 2002, Ruthrauff 2002), and the duration of parental care declines seasonally for both sexes (Neville 2002, Ruthrauff 2002). Following cessation of parental care, birds move to post-breeding and pre-migratory staging sites before departing southward (Holmes 1972). As a result of seasonal trends in parental care, adult females precede adult males in departure from breeding sites by about 12 days early in the season to five days late in the season (Neville 2002), by more than two days at post-breeding sites in coastal Alaska (Chapter 1) and by more than one day at the first stopover on the southward migration, in southwestern British Columbia (Butler et al. 1987, Chapter 1). Juvenile females also significantly precede juvenile males on the southward migration in British Columbia. The difference in migratory timing between males and females of both age classes varies substantially among years (Chapter 1). Western Sandpipers spend the nonbreeding

period at sites along the Pacific and Atlantic coasts of southern North America, Central America and northern South America (Wilson 1994).

Snowmelt

The date of snowmelt was estimated from daily snow depth data at three sites nearest the high-density breeding areas of Western Sandpipers in Alaska (see Holmes 1972): Bethel (60°47.0'N, 161°50.0'W), Emmonak (62°47.0'N, 164°29.0'W), and Nome (64°30.0'N, 165° 25.8'W) (National Data Centers, National Oceanic and Atmospheric Administration 2000). In most years, data were available for two or three of these sites, and snowmelt dates were averaged across sites for an annual regional estimate. At each site, the snowmelt date was defined as the last day on which greater than 1.25 cm of snow was registered.

Timing of breeding

Mean hatch dates for Western Sandpipers were estimated from breeding bird surveys conducted on the Yukon-Kuskokwim Delta in western Alaska in 1982 and 1985-2000, and are reported by Bowman et al. (2001). In that study, surveys were conducted during the peak period of incubation, and hatch dates for all avian species breeding in this region, including 'small shorebirds', were estimated by egg floatation. The mean number of nests (\pm 95% CI) used to calculate mean hatch dates was 9.4 (\pm 3.7) nests. 'Small shorebirds' are primarily sandpipers (Scolopacidae), including Western Sandpipers and other Calidridine species (e.g. *C. pusilla*, *C. alpina*, *C. ptilocnemis*), phalaropes (*Phalaropus*

spp.), and turnstones (*Arenaria* spp.). Small shorebirds breeding in the same geographical location exhibit similar temporal patterns of breeding (Sandercock 1997, A.C.N. pers.obs.), and so the dates reported are assumed to be representative of Western Sandpipers. Also, the range of annual mean hatch estimates for small shorebirds provided by Bowman et al. (2001) is similar to estimates provided by breeding studies of Western Sandpipers (Holmes 1972, Sandercock 1997, Neville 2002, Ruthrauff 2002).

Sandpiper migratory timing

The migratory timing of Western Sandpipers was estimated using data collected in a multi-year collaborative effort by the Canadian Wildlife Service and the Centre of Wildlife Ecology at Simon Fraser University. Adult and juvenile Western Sandpipers were captured in mist nets at their first major stopover on the southward migration (Butler and Kaiser 1995), in the Strait of Georgia, British Columbia (49° 05'N, 123° 00'W or 48° 40'N, 123° 20'W). Analyses were restricted to years in which more than 20 Western Sandpipers were captured over at least a 15-day time period. This includes 1978-1983, 1985, 1990, and 1996-2000 for adults; and 1978-1983, 1985, and 1989-2000 for juveniles. In general, mist-netting effort began when adult sandpipers were observed foraging in appreciable numbers on the coastal mudflats, and efforts continued until late in the juvenile migration. Females and males were gender-assigned based on culmen length (Page and Fearis 1971, Prater et al.

1977), and aged using plumage characteristics (Prater et al. 1977). Age classes were assigned in the field after 1983, and age classes were retrospectively assigned for Western Sandpipers captured in 1978-1983 by classifying captures before 30 July as adults, based on known migratory timing of age classes (Butler et al. 1987).

The mean passage date within each year was used as a measure of the migratory timing. To examine the difference in migratory timing between females and males in each year, we used a method developed by Morbey (2000) that estimates the difference in timing of females and males based on the area (in units of days) between the cumulative percent distribution of female and male captures. This procedure is superior for examination of the difference in timing because it smoothes the episodic capture distributions. The result can be interpreted as the expected number of days by which a randomly-selected female preceded a randomly-selected male on the southward migration, with females-first expressed as negative values.

Falcon migratory timing

The annual migratory timing of Peregrine Falcons was measured using near-daily surveys conducted since 1986 at the Reifel Island Migratory Bird Sanctuary on the Fraser Estuary (Lank et al. 2003). Falcons are absent at this site during June and July, but numbers rise sharply during August, and plateau in October (Lank et al. 2003). Peak falcon abundance was estimated as the average number of sightings

during three-day increments for the month of October. The first three-day period during which the count reached 50% of the annual peak level was used as an index of the timing of falcon arrival.

Statistical analyses

We used simple correlation coefficients (r) to examine relationships between variables. Slopes were compared using two-tailed small sample tests t -tests for parallelism (Kleinbaum and Kupper 1978).

Results

Snowmelt and timing of breeding

Among years, the timing of snowmelt varied by more than 40 days, and as expected, the hatch of small shorebirds took place earlier in years with earlier snowmelt ($r=0.60$, $P=0.01$, $n=17$) (Figure 1). Western Sandpipers require about nine days for courtship and egg-laying, and 21 days for incubation (Sandercock 1997), so hatch could have occurred no earlier than 30 days after snowmelt. The mean ($\pm 95\%$ CI) time between snowmelt and mean hatch was 53.2 ± 4.9 days, and in the years with the earliest snowmelt, hatch occurred more than two months after snow melted. In years of late snowmelt, the time between snowmelt and mean hatch was between 41 to 49 days. Overall, mean hatch advanced by 0.26 days for each day that snow melted earlier, significantly less than expected if shorebirds began to breed as soon as snowmelt exposes nest sites ($t_{36}=9.2$, $P<0.001$, $n=17$).

Adult sandpiper migratory timing

Mean passage of adult Western Sandpipers through the first stopover on the southward migration ($\pm 95\%$ CI) occurred 25.7 ± 6.5 days after mean hatch and did not vary with snowmelt ($P > 0.5$) or hatch timing ($P > 0.5$). Generally, mean migratory passage of adults varied less among years than snowmelt or hatch timing, differing by only 19 days among years. The migratory timing of adult males and females was strongly correlated ($r = 0.88$, $P < 0.001$, $n = 14$) (Figure 2), with females on average preceding males southward (Chapter 1).

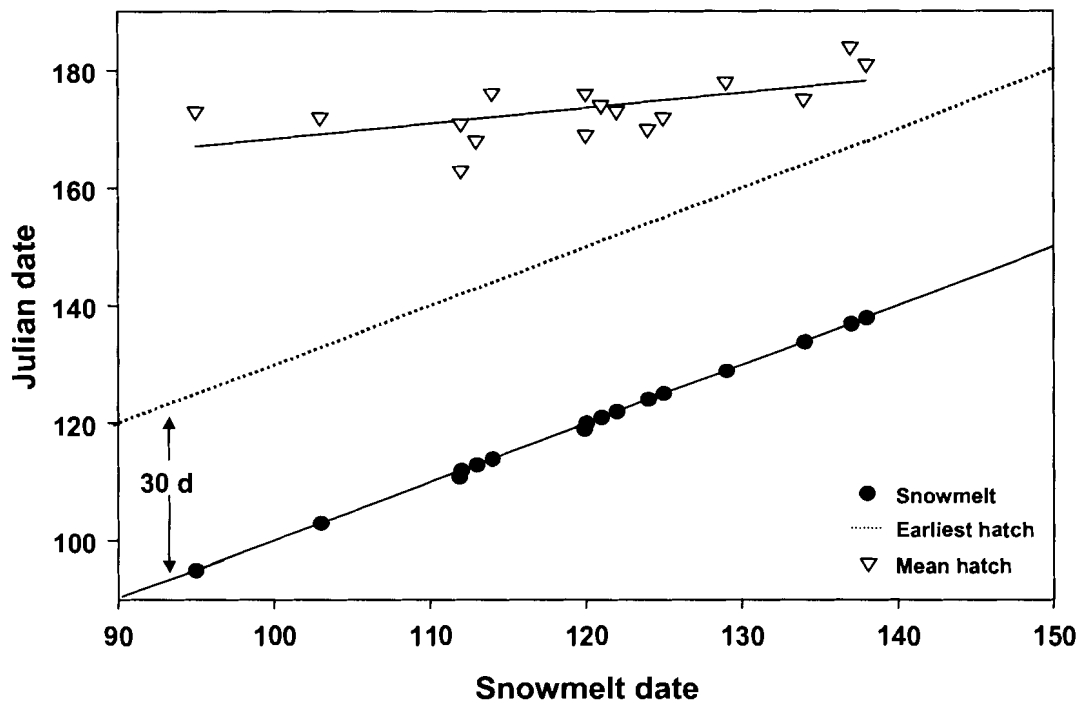


Figure II-1. Mean hatch date in relation to snowmelt.

Dots on the bottom line show snowmelt data, with points jittered to reveal overlapping data. The middle, dotted line is an estimate of the earliest mean hatch, given the timing of snowmelt and sandpiper breeding biology. The top line shows that snowmelt and hatch timing are positively correlated, indicating that years of late snowmelt are associated with years of later mean hatch ($r=0.6$, $P=0.01$, $n=17$). The slope of the change in hatch timing differs significantly from that of snowmelt, when snowmelt is plotted with a slope of 1, as seen here ($t_{36}=9.2$, $P<0.001$, $n=17$). The earliest possible hatch for each year is indicated by the dashed line, and occurs about 30 days after snowmelt.

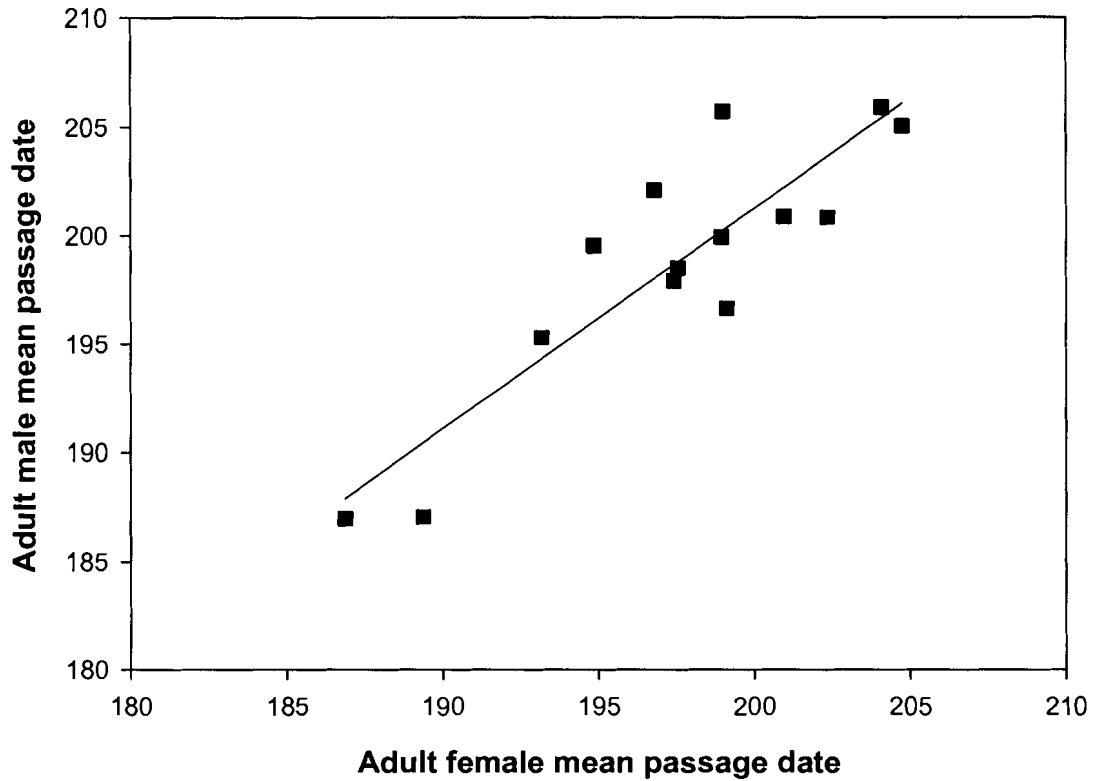


Figure II-2. Interannual variation in migratory timing of adult Western Sandpipers in the Strait of Georgia, BC.

The best fit is indicated as a solid line, and a 1:1 reference is a dashed line. The migratory timing of adult males and females is strongly correlated ($r=0.88$, $P<0.001$, $n=14$). Most points are above the reference line, indicating that on average adult males are later than females in their passage southward.

The difference between males and females varied by more than ten days among years: females were up to 7.8 days ahead of males, and in two years males were up to 2.6 days ahead of females (this study, Niehaus 2003). The difference between males and females was positively, though not significantly, correlated with hatch timing ($r=0.55$, $P=0.13$, $n=9$) (Figure 3), suggesting that when hatch took place earlier, females preceded males by a greater extent on the southward migration.

Juvenile sandpiper migratory timing

The timing of juvenile migratory passage did not change with either snowmelt ($P>0.5$) or timing of breeding ($P>0.5$). Juvenile Western Sandpipers passed through the first stopover on the southward migration ($\pm 95\%$ CI) an average of 54.3 ± 3.6 days after mean hatch (Figure 4). Young Western Sandpipers attain flight by about 21 days of age (Wilson 1994), leaving about 32 days to move from natal sites to coastal pre-migratory staging areas, fatten, and initiate southward migration before they are observed in British Columbia. This is almost a week longer than the 25.7 days adults require to make the same journey.

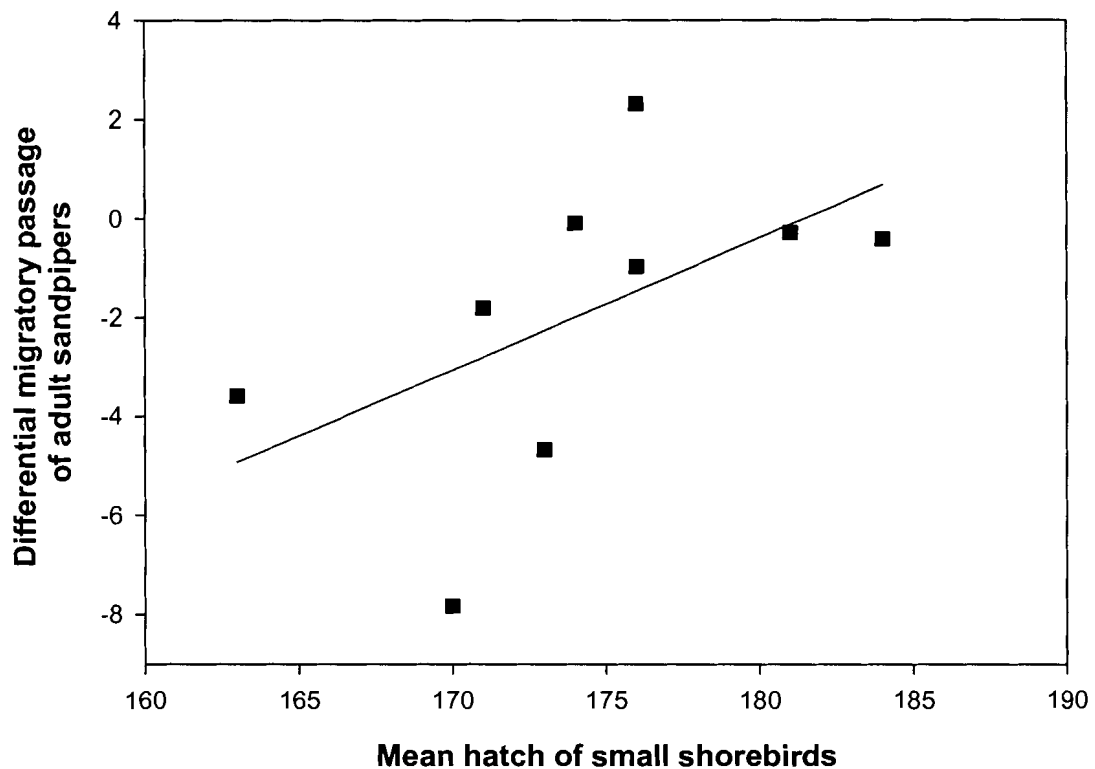


Figure II-3. Difference in the southward passage of adult male and female sandpipers in relation to mean hatch date.

Female-first differential migratory patterns are characterized by negative numbers and male-first patterns by positive numbers. Females appear to precede males by a greater extent on the southward migration when mean hatch of small shorebirds is earlier, although this relationship is not significant ($P=0.13$).

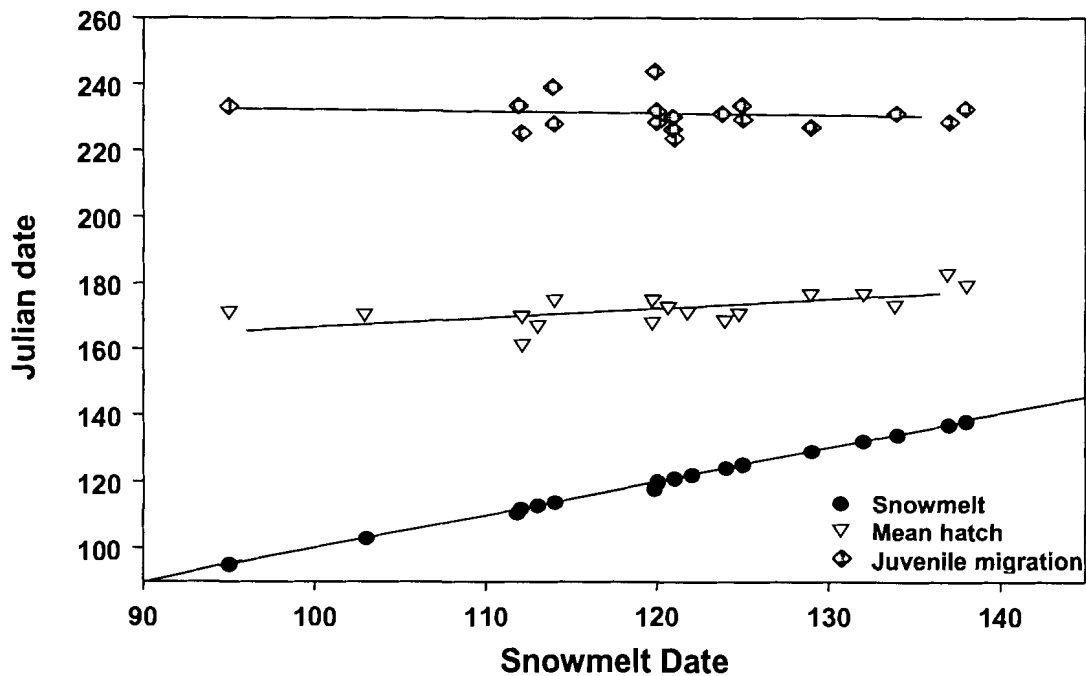


Figure II-4. Mean passage of juvenile sandpipers in relation to snowmelt and hatch timing.

Here, snowmelt is plotted as a 1:1 reference line. In general, mean juvenile migration was between Julian days 220 and 240. Migratory timing was unrelated to snowmelt ($P>0.5$) or hatch timing ($P>0.5$).

The migratory timing of juvenile males and females was even more strongly correlated than for adults ($r=0.94$, $P<0.001$, $n=17$) (Figure 5). Mean migratory passage of juveniles varied similarly to that of adults, differing by 20 days among years. Overall, juvenile females preceded males on the southward migration (this study, Chapter 1).

Migratory timing of males and females differed by only six days among years. Females preceded males by up to five days, and in a few years males preceded females by up to one day (Figure 6). The difference between males and females was positively correlated with hatch timing ($r=0.58$, $P=0.04$, $n=13$).

Falcon migratory timing

The timing of Peregrine Falcon migration in southwestern British Columbia ($\pm 95\%$ CI) was 100.2 ± 5.3 days after snowmelt. The relationship between snowmelt and falcon timing was among the strongest detected ($r=0.81$, $P<0.001$, $n=13$) (Figure 7), and years of early snowmelt corresponded with years when falcons arrived early in the Strait of Georgia, British Columbia. Falcon timing advanced 1.09 days for each day that snowmelt was earlier, which is not significantly different from the slope of 1.0 expected on the basis of snowmelt ($t_{32}=-0.6$, $P>0.5$, $n=13$).

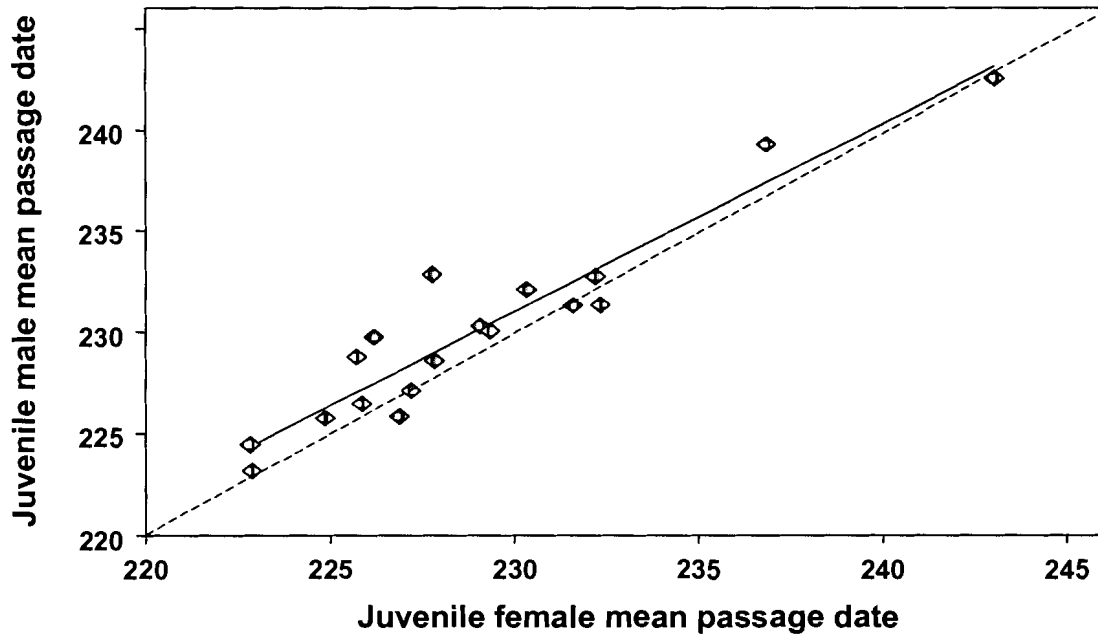


Figure II-5. Interannual variation in migratory timing of juvenile males and females in the Strait of Georgia, BC.

The best fit is indicated as a solid line, and a 1:1 reference is a dashed line. The migratory timing of juvenile males and females was strongly correlated ($r=0.94$, $P<0.001$, $n=17$). As with adults, most points are above the reference line, indicating that on average juvenile males are later than females in their passage southward.

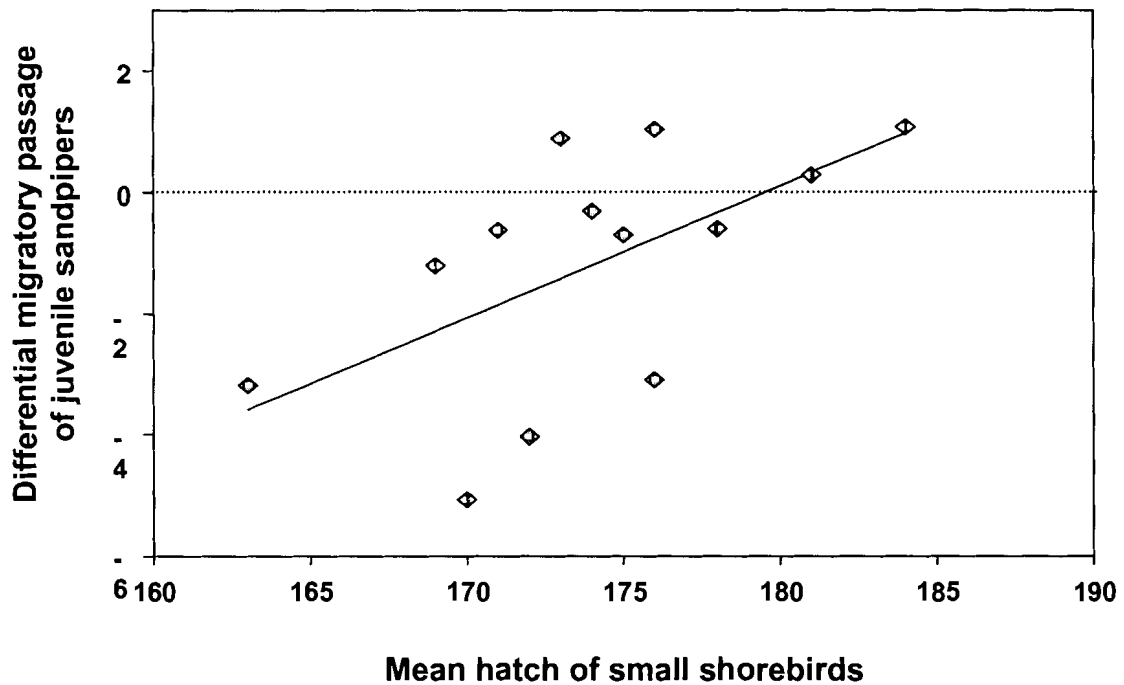


Figure II-6. Difference in the southward passage of juvenile male and female Western Sandpipers in relation to mean hatch date.

Female-first patterns are characterized by negative numbers and male-first patterns by positive numbers. As for adults, females significantly precede males by a greater extent on the southward migration when mean hatch of small shorebirds is earlier ($P=0.04$).

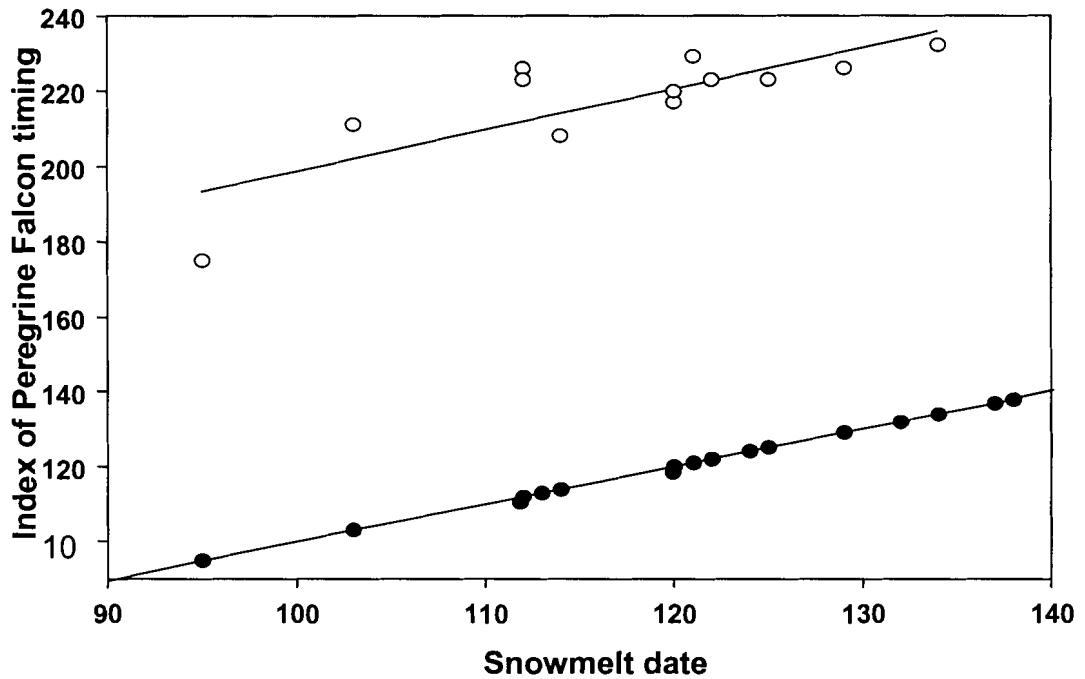


Figure II-7. Timing of falcon arrival at the Strait of Georgia, BC, in relation to snowmelt.

Falcon migratory timing was closely related to snowmelt, with years of late snowmelt corresponding very closely with years of later mean hatch ($r= 0.81, P<0.001, n=13$). The slope of the change in falcon migration does not differ from that of snowmelt, when snowmelt is plotted with a slope of 1, as seen here ($t_{32}= -0.6, P>0.5, n=13$).

Discussion

Results of this study are summarized in Figure 8, which plots all the relationships together, using the date of snowmelt for reference. The data show that the timing of Western Sandpiper migration from northern breeding and natal sites does not vary as much between years as do the major ecological events that bound its occurrence, namely snowmelt on the tundra in spring, and the reappearance of Peregrine Falcons (and perhaps other raptors) at southbound stopover sites in the summer. The timing of these events is so strongly correlated that Western Sandpiper breeding and migration in each year can be classified as 'early' or 'late' relative to them. In contrast, the mean passage dates of adults and juvenile Western Sandpipers at their first major southbound stopover indicate no relationship with snowmelt among years.

This result is somewhat of a surprise, as other studies report, at least anecdotally, a strong effect of snowmelt on the timing of breeding (e.g. Holmes 1972, Young et al. 1995, Babcock et al. 2002). Can these results be reconciled with the weak relationship reported here? One possibility is that we used a regional while most other studies use a local measure of snowmelt. The regional measure gives a composite measure of conditions across the relatively small breeding range of Western Sandpipers, but it may be that the onset of breeding at specific locales varies somewhat according to circumstances in the immediate area.

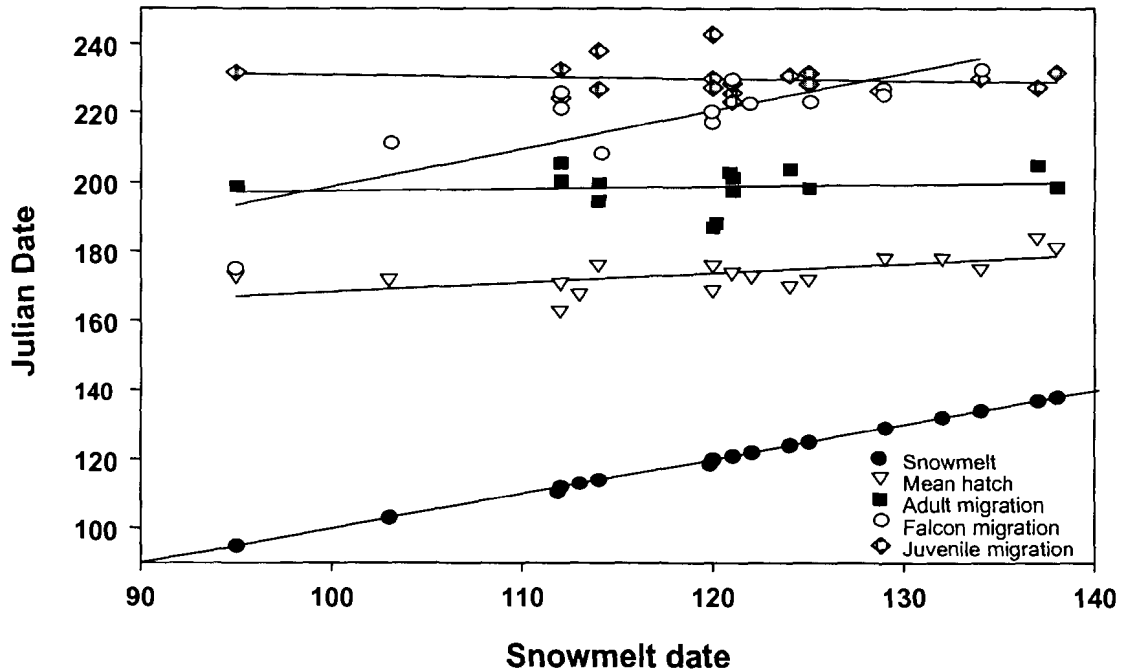


Figure II-8. Synthesis of snowmelt, breeding, and migratory timing of sandpipers and falcons.

When all data are plotted against snowmelt date, the only meaningful relationship is that between snowmelt and falcon timing. Because of this strong relationship, years of early or late snowmelt mean different conditions for southward-migrating adult sandpipers. When snowmelt is early, the southward migration is more dangerous for adult Western Sandpipers, in contrast to years of late snowmelt, when adults always precede falcons to the Strait of Georgia, BC. For juveniles, the southward migration is always dangerous.

To investigate the difference between snowmelt on a regional versus local scale, our regional estimates of snowmelt were compared with those reported by Babcock et al. (2002) for a particular site on the Yukon-Kuskokwim Delta. The regional and local measures differed substantially in only one of 17 years (1998; local Julian day 94 vs. regional Julian day 140). The 1998 regional estimate had to be based on data from the Bethel site only, as data from the other sites were not available; hence the “regional” estimate might not be indicative of range-wide snowmelt as are other years. With 1998 excluded, there is a strong relationship between Babcock’s local estimates and the regional estimates reported here ($r=0.70$, $P=0.02$, $n=16$). Also, using Babcock’s data, the relationships between snowmelt and hatch timing ($r=0.70$, $P<0.01$, $n=16$) and between snowmelt and falcon migratory timing ($r=0.67$, $P=0.02$, $n=12$) remain strong and significant.

An alternative possibility to explain the unexpected discrepancy between snowmelt and hatch timing is that the re-nesting that may occur following nest failure of small shorebirds (Ruthrauff 2002) biases the measure of hatch timing. If a higher proportion of re-nesting attempts occurs in early than in late years, the estimated hatch estimate would be later than the true hatch date. The survey methodology used by Bowman et al. (2001) does not discriminate among nesting attempts, so there is no direct way to evaluate this possibility. A rank correlation test shows that years of early hatch timing of small shorebirds

correspond closely with the overall hatch timing for all other species recorded by Bowman et al. (2001) on the Yukon-Kuskokwim Delta, including geese, ducks, Tundra Swans (*Cignus columbianus*), Sandhill Cranes (*Grus canadensis*), loons, gulls and terns ($r_s=0.84$, $P<0.001$, $n=17$). Snowmelt is positively related to the timing of breeding of all species ($r=0.50$, $P=0.02$, $n=20$), but as with small shorebirds, the combined mean hatch of all species advanced by only 0.20 days for each day that snowmelt was earlier. It seems unlikely that the effect would register so consistently across species if it were due to re-nesting behavior, as these species are rather diverse in re-nesting habits.

We conclude that the direct effect of snowmelt does not seem able to explain interannual variation in the timing of breeding and migratory timing. Nevertheless, snowmelt may exert an indirect effect. It appears that Western Sandpipers time their arrival at breeding sites to correspond with average date of snowmelt, rather than the earliest possible snowmelt, so that consequently snowmelt exerts no direct effect, except in late years. The northbound migration of Western Sandpipers peaks in southwestern British Columbia in the last days of April and the first days of May (~ Julian day 120) (Butler et al. 1987), and the arrival of Western Sandpipers at breeding sites may occur around day 130 (Lank et al. in press). The mean snowmelt date ($\pm 95\%$ CI) in the years reported here is Julian day 120.0 (± 4.4 days), so on a regional level, snowmelt takes place just before the arrival sandpipers. Therefore, the timing of

breeding can be set by arrival timing, except in years when snowmelt does not take place until after arrival. For Western Sandpipers, the possibility of earlier breeding may be opposed by the ecology of northward migration, which is in turn affected by factors at the wintering sites or migratory stopovers, rather than at the breeding site (Both and Visser 2001).

The weak relationship between sandpiper breeding and snowmelt contrasts with the strong relationship between snowmelt and the timing of falcon migration, which advanced by 1.09 days for each day that snowmelt was earlier. In the spring, migratory subspecies of Peregrine Falcons (*F.p. anatum* and *F.p. tundrius*) move northward to breeding sites in temperate and arctic Canada and Alaska. Peregrine Falcons breeding in arctic and sub-arctic North America lay eggs over a very short period of time (e.g. 12-30 days) compared with other parts of the species' range (Bradley et al. 1997 and references therein), and the timing of snowmelt may influence the timing of breeding for high-latitude breeding raptors by affecting their ability to locate and capture food or find nesting sites (Young et al. 1995). After completion of breeding, these falcons migrate southward along coastlines, many passing through coastal British Columbia in late summer and autumn (Lank et al. 2003).

Peregrines are important predators of sandpipers, and like their prey many migrate to nonbreeding sites in Central and South America. The contrasting relationships with snowmelt timing between sandpipers

and falcons combine to create interannual differences in the danger experienced on migration for southbound sandpipers, because the timing of sandpiper migration relative to that of falcons changes. Years with early snowmelt advance the breeding of falcons much more than that of sandpipers, which increases the exposure of sandpipers to falcons on the southbound migration. In contrast, adult Western Sandpipers are able to migrate ahead of migratory falcons in years with late snowmelt (Figure 9), though juvenile sandpipers are not able to initiate southward migration until about three weeks later than their parents (Butler et al. 1987, Gill and Handel 1990), and as a consequence experience more dangerous migrations. We believe that years with early snowmelt are more dangerous for both age classes of Western Sandpipers in terms of exposure to falcons during the southward migration. Sandpipers may be able to use environmental conditions to judge whether the year is early or late, and adjust migratory patterns and behaviors accordingly.

The female-first migration and male-biased parental care system of Western Sandpipers and other *Calidris* sandpipers have been explained by the need for post-breeding recuperation (Ashkenazie and Safriel 1979, Myers 1981) and the longer migration distance of females (Myers 1981, Butler et al. 1987). Our data show that females precede males on southward migration among both adults and juveniles (Niehaus 2003). In addition, the difference between males and females is greater in years of earlier hatch, such that females are on average further ahead of males.

This relationship is similar for both age classes (Fig. 3 and 6), and the slope seems absolutely greater for adults (though not quite statistically significant, perhaps due to smaller sample size). The recuperation and migration distance hypotheses do not seem able to explain these and other aspects of the migratory departure of sandpipers. We suggest instead that the data indicate that adults experience a trade-off between parental care and migration, and that the evaluation of the trade-off differs between the sexes, and between early and late years. We hypothesize that, due to their larger size, females have higher wingloading and thus poorer escape performance than males (Burns and Ydenberg 2002). Consequently, females are selected to weigh the dangers posed by predators such as falcons more heavily, and so contribute less to parental care and migrate earlier than males. The situation is affected by seasonal timing because early years are more dangerous, so the increased difference in southward migratory timing in years of early hatch may result from females reducing parental care in early years, by males extending parental care to compensate, or a combination of these behaviors. These hypotheses have yet to be tested.

Several recent studies have evaluated trends in the timing of breeding and migratory timing with respect to changing climates (e.g. Crick et al. 1997, Stevenson and Bryant 2000, Both and Visser 2001, Jenni and Kéry 2003), but the relationship may not be as direct as implied. Here, we have shown that the relationship between snowmelt

and the timing of breeding and southward migration of Western Sandpipers is weak or non-existent. In contrast, Peregrine Falcon migratory timing shows a strong relationship with snowmelt, which make years of early snowmelt relatively dangerous for migrating sandpipers. Our data suggest that sandpipers may have some ability to adjust their migratory behavior in early and late years.

Long-term management programs have restored populations of raptors across North America and Europe. As a result of these changes in predator abundance, prey species such as sandpipers may alter aspects of their migratory behavior, such as length of stay or the selection of stopover sites (Ydenberg et al., submitted). Increases in the numbers of falcons and other raptors over the past few decades, concurrent with but unrelated to global warming trends, may also cause responses in the patterns of migratory birds, indirectly associating these changes with climate change. Future work should assess the effects of climate change on the timing of predators as well as the effects of raptor recovery programs in studies of climate change and prey.

Acknowledgments

We thank the various associates of the Canadian Wildlife Service and the Centre for Wildlife Ecology at Simon Fraser University who helped collect data on sandpiper migration. Thank you to Tim Bowman providing us with his report on the breeding of birds in western Alaska and to Gary Kaiser for making his falcon sighting data available. David Lank, Tony Williams and anonymous reviewers provided valuable comments on this study or manuscript. Research was funded by a graduate fellowship from the National Science Foundation (to ACN), the Canadian Wildlife Service, and the National Science and Engineering Research Council of Canada.

Literature Cited

- Ashkenazie, S. and U. N. Safriel. 1979. Time-energy budget of the Semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* 60: 783-799.
- Babcock, C. A., A. C. Fowler, and C. R. Ely. 2002. Nesting ecology of Tundra Swans on the coastal Yukon-Kuskokwim Delta, Alaska. *Waterbirds* 25(SP1): 236-240.
- Boates, J. S. and P.C. Smith. 1989. Crawling behavior of the amphipod *Corophium volutator* and foraging by Semipalmated Sandpipers, *Calidris pusilla*. *Canadian Journal of Zoology* 67:457-462.
- Both, C. and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296-298.
- Bowman, T., R. Stehn, and G. Walters. 2001. Population size and production of geese and eiders nesting on the Yukon-Kuskokwim Delta, Alaska, in 2001. U.S. Fish and Wildlife Service, Anchorage, AK. Field report.
- Bradley, M., R. Johnstone, G. Court, and T. Duncan. 1997. Influence of weather on breeding success of Peregrine Falcons in the arctic. *Auk* 114(4): 786-791.
- Brown, J. L., S. Li, and N. Bhagabati. 1999. Long-term trend toward earlier breeding in an American bird: A response to global warming? *Proceedings of the National Academy of Science USA*. 96: 5565-5569.
- Burns, J. G. 2001. The ecological consequences of fuel storage in migrating *Calidris* sandpipers. M.Sc. dissertation, Simon Fraser University, Burnaby, BC.
- Burns, J. G., and R. C. Ydenberg. 2002. The effects of wing loading and gender on the escape flights of Least Sandpipers (*Calidris minutilla*) and Western Sandpipers (*Calidris mauri*) *Behavioural Ecology and Sociobiology* 52: 128-136.
- Butler, R. and G. Kaiser. 1995. Migration chronology, sex ratio, and body mass of Least Sandpipers in British Columbia. *Wilson Bulletin* 107(3): 413-422.

- Butler, R. W., F. S. Delgado, H. de la Cueva, V. Pulido, and B. K. Sandercock. 1996. Migration routes of the Western Sandpiper. *Wilson Bulletin* 108(4): 662-672.
- Butler, R. W., G. W. Kaiser, and G. E. J. Smith. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers, (*Calidris mauri*) on the south coast of British Columbia. *Journal of Field Ornithology* 58(2): 103-111.
- Butler, R. W., T. D. Williams, N. Warnock, and M. Bishop. 1997. Wind assistance: a requirement for migration of shorebirds? *Auk* 114(3): 456-466.
- Crick, H. Q. P. and T. H. Sparks. 1999. Climate change related to egg-laying trends. *Nature* 399: 423-424.
- Crick, H. Q. P., C. Dudley, D. E. Glue, and D. L. Thompson. 1997. UK birds are laying eggs earlier. *Nature* 411: 296-298.
- Gauthreaux, S. A., Jr. 1982. The ecology and evolution of avian migration systems. P 93-167. In D. S. Farner and J. R. King [eds.] *Avian Biology*, Vol 6. Academic Press, New York.
- Gill, R. E., Jr., and C. M. Handel. 1990. The importance of subarctic intertidal habitats to shorebirds: a study of the central Yukon-Kuskokwim Delta, Alaska. *Condor* 92:709-725.
- Holmes, R.T. 1966a. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. *Condor* 68: 3-46.
- Holmes, RT. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. *American Midland Naturalist* 87(2): 472-491.
- Jenni, L., and M. Kéry. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London Series B*. online.
- Kleinbaum, D. G., and L. L. Kupper. 1978. *Applied regression analysis and other multivariate methods*. Duxbury Press North Scituate, Massachusetts

- Lank, D. B. R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303-319
- Morbey, Y. E. 2000. Protandry in Pacific salmon. *Canadian Journal of Fisheries and Aquatics Science* 57: 1252-1257.
- Morrison, R. I. G. 1984. Migration systems of some new world shorebirds, p. 125-202. In J. Burger and B. L. Olla [eds.], *Shorebirds: migration and foraging behavior*. (eds). Plenum Publishing Co., New York.
- Myers, JP. 1981. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behavioral Ecology and Sociobiology* 8:195-202.
- Nebel, S., D. B. Lank, P. D. O'Hara, G. Fernández, B. Haase, F. Delgado, F. A. Estela, L. J. Evans Ogden, B. Harrington, B. E. Kus, J. E. Lyons, F. Mercier, B. Ortego, J. Y. Takekawa, N. Warnock, and S. E. Warnock. 2002. Western Sandpipers (*Calidris mauri*) during the non-breeding season: spatial segregation on a hemispheric scale. *Auk* 119: 922-928.
- Neville, J. A. 2002. Division of parental roles in the monogamous Western Sandpiper, *Calidris mauri*. M.Sc. dissertation, University of Alaska, Fairbanks, AK.
- Niehaus, A.C. 2003. Ecology of migratory timing for southbound male and female Western Sandpipers (*Calidris mauri*). Unpubl. M.Sc. thesis, Simon Fraser University, Burnaby, British Columbia.
- Page, G. and B. Fearis. 1971. Sexing Western Sandpipers by bill length. *Bird-Banding* 42:297-298.
- Ruthrauff, D. R. 2002. Seasonal and age-related trends in the reproductive output of Western Sandpipers (*Calidris mauri*) at Kanaryaraq, Alaska. M.Sc. dissertation, Humboldt State University, Arcata, CA.
- Sandercock, B. K. 1997. Factors affecting the breeding demography of Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*Calidris pusilla*) at Nome, Alaska. Ph.D. dissertation, Simon Fraser University, Burnaby, BC.
- Schneider, D. C. and B. A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98:801-811.

- Stevenson, I. R., and D. M. Bryant. 2000. Climate change and constraints on breeding. *Nature*. 406: 366-367.
- Wilson, W.H. 1994. The Western Sandpiper, p. 1-19. In A. Poole and F. Gill [eds.] *The Birds of North America*. The Academy of Natural Sciences of Philadelphia, Pennsylvania. Vol. 90.
- Wolf, N. 2001. Foraging ecology and site selection in Western Sandpipers during their fall migration through southwestern British Columbia. M.Sc. dissertation, Simon Fraser University, Burnaby, BC.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, C. G. Guglielmo, M. Lemon, and N. Wolf. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. *Journal of Avian Biology* 33: 47-55.
- Young, D. D., Jr., C. L. McIntyre, P. J. Bente, T. R. McCabe, and R. E. Ambrose. 1995. Nesting by Golden Eagles on the north slope of the Brooks Range in northeastern Alaska. *Journal of Field Ornithology* 66(3): 373-379.

CHAPTER III

EVALUATING HYPOTHESES TO EXPLAIN THE MIGRATORY TIMING OF SOUTHBOUND MALE AND FEMALE WESTERN SANDPIPERS

Amanda C. Niehaus

Submitted for publication October 2003

Abstract

Males and females of the sandpiper genus *Calidris* often differ in both duration of parental care and the timing of migration to and from breeding sites. Here, I review hypotheses proposed to explain the female-first southward migration of Western Sandpipers (*Calidris mauri*), and test the predictions made for adults. To dissociate patterns of parental care from migratory timing, I also evaluate the predictions made for juvenile Western Sandpipers and a near relative, the Pacific Dunlin (*C. alpina pacifica*). Juvenile females migrate ahead of juvenile males, but this migration is not associated with parental care. For Pacific Dunlin, parental care and migration are separated by molt near breeding grounds.

Of the five hypotheses examined (Breeding Recovery, Territoriality, Migration Distance, Molt Deadline and Escape Performance), the Escape Performance hypothesis appears to best explain why female Western Sandpipers migrate first in both adult and juvenile age classes. I present a series of predictions for Pacific Dunlin, and suggest work to further test the Escape Performance hypothesis. These results correspond with a general shift in thinking about avian migratory strategies, from migrants as predators to migrants as prey, and highlight the importance of predation danger to migratory birds.

Introduction

Shorebirds are among the best-known migrants and are exceptionally diverse in migration strategies (Myers 1981, Morrison 1984), mating systems (Pitelka et al. 1974, Myers 1981, Szekely et al. 2000), and parental care strategies (Myers 1981, Jonsson and Alerstam 1990, Szekely and Reynolds 1995, Reynolds and Szekely 1997). The most abundant shorebirds migrating along the western coast of North America are the ‘typical sandpipers’ (Scolopacidae, Calidridinae; Butler and Kaiser 1995, Morrison 2001), including the Dunlin (*Calidris alpina*), Least Sandpiper (*C. minutilla*), Western Sandpiper (*C. mauri*), and Semipalmated Sandpiper (*C. pusilla*).

In general, sex classes of adult *Calidris* sandpipers migrate at different times. During northward migration, males precede females, and during southward migration, females precede males, on average (Butler et al. 1987, Jehl et al. 1989, Gratto-Trevor 1992, Butler and Kaiser 1995; Chapter I). Western Sandpipers exhibit biparental care during incubation (Holmes 1972, Neville 2002), although males typically care for the chicks for about a week longer than females (Neville 2002, Ruthrauff 2002).

The sandpipers begin their southbound movement by departing breeding sites in western or northern Alaska or far-eastern Siberia (Wilson 1994), then moving to coastal mudflats (Holmes 1972, Gill and Handel 1990) before flying directly to an initial stopover in southwestern

British Columbia (Butler et al. 1996). Peak migration of adults at this stopover occurs in July, and juveniles follow adults by about three to four weeks (Butler et al. 1987, Chapter I). Southbound departure from Alaska occurs long before conditions deteriorate at these sites, which are used by several species of small shorebirds for staging and molt through October (Gill and Handel 1990). Western Sandpipers progress southward to wintering sites along the Pacific or Caribbean coasts of North America, Central America and northern South America (Senner and Martinez 1982, Wilson 1994), with males settling north of females, on average (Nebel et al. 2002).

For birds, earlier termination of parental care allows the parent to either reproduce again or initiate preparation for earlier migration, and whatever costs the parent incurs are outweighed by the benefits of departure. The costs and benefits of brood desertion by shorebirds have been assessed theoretically and empirically (e.g. Erckmann 1981, Székely and Williams 1995, Székely and Cuthill 2000), and the timing of southward migration by Western Sandpipers can be considered within this framework, as a trade-off between increasing reproductive fitness (by extending parental care) and increasing survival (by extending preparation for southward migration or by migrating early). Parents likely do not make independent decisions about desertion timing, but assess the decisions of their mate as well as their own condition when deciding how long to provide parental care (McNamara et al. 2002). In

fact, males and females appear to trade off parental duties on an evolutionary scale (Reynolds and Székely 1997).

When brood desertion is not related to re-mating potential, a potential benefit is increased survival on migration (Reynolds and Székely 1997). Differential migratory timing by classes is common among avian species (Ketterson and Nolan 1983), but hypotheses to explain southward timing have not been described or tested to the same extent as those for northward migration (Ketterson and Nolan 1983).

Typically, sandpiper studies have linked female-first migration with the male-biased system of parental care. In fact, previous knowledge of these patterns has centered around the idea that female Western Sandpipers give less parental care than males (Sandercock 1997, Neville 2002, Ruthrauff 2002) and then precede them on the southward migration through British Columbia (Butler et al. 1987).

Recent work, however, has expanded our understanding of these events. Parental care is not constant but declines seasonally for both male and female Western Sandpipers (Neville 2002). Although females do appear to precede males in departure from breeding sites, during preparation for southward migration and at a southbound stopover, the difference between males and females appears to diminish by the time the sandpipers reach British Columbia (Chapter I). In many years, there is almost no difference in timing at this early stage of the southward migration, despite the differential parental care given by the sexes

(Chapter I). Also, migrating females appear to be more ahead of males in years when hatch timing is earlier (Chapter II). Therefore, it seems necessary to tease apart parental care from migratory timing when considering why female sandpipers migrate first.

Here, I review hypotheses that have been suggested or implied relating to the southward migratory timing of birds and form specific hypothesis statements for testing against patterns of parental care and migratory timing for adult Western Sandpipers. These hypotheses may make similar predictions for close relatives of Western Sandpipers, and similar patterns are described for other sandpiper species.

To test the general applicability of these hypotheses, and to isolate migratory timing from parental care, I also consider what the hypotheses predict for southward-migrating juvenile Western Sandpipers. Juveniles have no parental care, yet females migrate first (Chapter I) and are more ahead of males in years of earlier hatch (Chapter II). Finally, I use these hypotheses to propose patterns of parental care and migration for Pacific Dunlin (*C. alpina pacifica*), in which these two events are separated by molt.

Patterns of adult sandpipers

Females provide shorter brood care than males

Although historically Western Sandpipers were considered to have biparental care (Myers 1981), recent work has shown the contribution of females to care of the offspring declines over the course of incubation

and brood-rearing (Neville 2002, Ruthrauff 2002). If females remain with broods at all (Tomkovitch and Morozov 1983), it is for only an average of five to seven days, in contrast with males, which typically provide about 13 days of parental care (Neville 2002, Ruthrauff 2002). Deserting females do not remain at breeding sites and are thus free to initiate migration southward.

Male-biased parental care is the most typical pattern among the *Calidris* sandpipers, including Least Sandpipers (*C. minutilla*; Miller 1985), Semipalmated Sandpipers (*C. pusilla*; Gratto-Trevor 1991), Baird's Sandpipers (*C. bairdii*; Jehl et al. 1989), Purple Sandpipers (*C. maritima*; Reynolds and Székely 1997), Red Knots (*C. canutus*; Reynolds and Székely 1997), and some European subspecies of Dunlin (*C. alpina* spp.; Soikkeli 1967).

Investment in parental care declines seasonally for both sexes

Not only do female Western Sandpipers give less parental care than males, but the length of time spent with the brood declines for both sexes as the season progresses (Neville 2002, Ruthrauff 2002). Early in the season, or for broods hatching prior to median hatch date, males spend an average 14 to 15 days with chicks, whereas late in the season this declines by about 55% to 7 to 9 days. Similarly, females remain with broods an average of 9 days early in the season, declining by about 72% to 2 to 3 days late in the season. This trend holds even at remote portions of the Western Sandpipers' breeding range. At the Chutchki

Peninsula in eastern Siberia, broods were cared for by both parents only early in the season, while later only males remained with broods (Tomkovitch and Morozov 1982).

A seasonal decline in parental care has been suggested for other *Calidris* sandpipers, including Semipalmated Sandpipers breeding in northern Manitoba (Gratto-Trevor 1991) and northern Alaska (Ashkenazie and Safriel 1979), as well as for Least Sandpipers at various sites in Canada (Miller 1985) and the schinzii race of Dunlin in Finland (Soikkeli 1967).

A multitude of seasonal effects influence the breeding of shorebirds. In general, weather becomes more consistent as the season progresses (Székely and Cuthill 2000; ACN pers. obs.). Although food may decline at breeding sites (Holmes 1972), food abundances are great enough to support the still-growing juveniles, which remain near breeding sites for three to four weeks after adults depart (Holmes 1972, Gill and Handel 1990). Presumably, adult Western Sandpipers could also remain longer at breeding or staging sites before migrating southward. In addition, Pacific Dunlin remain near tundra breeding sites to molt later in the season (Holmes 1966). Parent Western Sandpipers choosing to extend parental care would not have to compete with many other adults, or even young, as the space available for feeding is generally larger than that utilized (Gratto-Trevor 1991).

Food availability does not seem to be a limiting factor at breeding sites while young are growing, and chick mortality tends to result from predation rather than starvation (Gratto-Trevor 1991, Székely and Cuthill 2000). Western Sandpiper chicks from earlier nests are more likely to hatch and fledge, corresponding with seasonal increases in predation pressure (Ruthrauff 2002), seeming to suggest that brood guarding may become more important later in the season, rather than less important.

In contrast to the seasonal decline in parental care exhibited by many *Calidris* sandpipers, female Kentish Plovers (*Charadrius alexandrinus*) remain longer with broods hatching later in the season (Székely and Cuthill 2000). The authors suggest that this might be related to seasonal increases in predation at their site, so that later broods require more protection than earlier broods. Why do the trends differ among shorebirds experiencing similar predation trends? Perhaps female sandpipers weigh more heavily the costs of continued parental care than the female plovers, and depart even though continued care might increase the chances of offspring survival.

Migratory timing shows catch-up features

Female Western Sandpipers that are successful in hatching chicks will in most cases precede males in departure from breeding sites (Sandercock 1997, Neville 2002, Ruthrauff 2002). Even when unsuccessful breeders are considered, over the whole breeding season

females are estimated to be ahead of males by three days (Chapter I). However, by the time they arrive at stopover sites in southwestern British Columbia, males have nearly caught up to females in most years, and in some years even precede females through this site. On average, the difference in migratory timing between males and females at this location is only one day (Chapter I). Manipulation of duration of parental care in a simulation model shows that changes in male care have an effect of greater magnitude on estimated departure timing from breeding sites (Chapter I). On the whole, male Western Sandpipers appear to catch up to females somewhat on the southward migration. As this type of assessment has not been done for other *Calidris* species, it is not known if these changes in male-female differential timing between breeding and migration are common among sandpipers.

Difference in timing decreases when mean hatch is later

The difference in timing between male and female Western Sandpipers on their southward migration appears to be positively related to the timing of breeding. Generally, in years when the mean hatch of small shorebirds (including Western Sandpipers) is later, males are less behind females on the southward migration (Chapter II). Although this trend was not significant, the pattern is strikingly similar to the significant trend found for juveniles. The relationship between the timing of breeding events and the timing of males and females on the

southward migration has not been studied for other *Calidris* sandpipers, so we do not know whether this pattern holds across the group.

Hypotheses

Breeding Recovery

Egg-laying is widely recognized as a costly period for female birds, affecting parental effort and future reproduction (Erckmann 1981, Monaghan et al. 1998, Nager et al. 2001, Visser and Lessells 2001). For many shorebirds, the combined mass of a clutch of 4 eggs is 75% the entire mass of the female (Rahn et al. 1975). For obvious reasons, then, many researchers have linked early female departure from breeding to the need to recuperate lost reserves. If investment in egg production has a persistent effect on the condition of females (Erckmann 1981), then energetically taxed females might increase their survival on the southward migration by deserting the brood early (Ashkenazie and Safriel 1979).

Studies of Semipalmated Sandpipers suggest that females, having greater daily energy needs than males, accumulate a negative energy balance during egg production and incubation (Ashkenazie and Safriel 1979), though likely not to the extreme levels proposed (Erckmann 1981). Recent experimental work on European Starlings (*Sturnis vulgaris*) shows that metabolic rates of egg-producing females do not increase to the extent predicted by models (Vezina and Williams 2002). However, female Western Sandpipers were less able to support the costs

of incubation when mates were absent, losing weight at faster rates than males and abandoning nests earlier (Erckmann 1981). Although unpaired males aggressively defending territories or courting females expend energy in the pre-incubation period, the daily energy expenditure of females is estimated to be at least 27% greater than that of either unpaired or paired males (Erckmann 1981).

Some evidence suggests that female departure is not directly associated with an energy deficit. For example, masses of male and female Kentish Plovers (*Charadrius alexandrius*) do not decline during breeding, and parental condition is not related to the duration of parental care given in this species (Amat et al. 2000). Western Sandpiper females appear to increase their contribution to incubation later in the incubation period (Neville 2002), and there is no direct relationship between mass of female Western Sandpipers and the duration of parental care (Neville 2002).

If female condition more depleted than the males', then females might depart breeding sites to seek out foraging areas with less competition (Pitelka et al. 1974) or better food availability (Gratto-Trevor 1991). Early migrants reduce competition with offspring for food on breeding sites (Holmes and Pitelka 1968) but will likely experience intra-specific competition at staging sites, as failed breeders have already moved to these coastal areas. Possibly, early-deserting females are able

to take advantage of peak food abundances at post-breeding, staging or migratory stopover sites, in addition to obtaining extra foraging time.

Evidence for declining food abundances at stopovers is equivocal. Studies on southward migratory stopovers in eastern North America have shown that food availability declines over the period of the southward migration for some shorebirds (Schneider and Harrington 1981, Boates and Smith 1989). In contrast, a study in British Columbia found a seasonal increase in food abundance for southward-migrating Western Sandpipers (Wolf 2001). Moreover, juveniles migrate southward later than adults (Butler et al. 1987, Chapter I), and appear to find sufficient resources.

I define the **Breeding Recovery (BR) hypothesis** as follows: The energy and nutrient requirements of egg production and incubation deplete female condition, so females desert earlier and precede males on the southward migration to take advantage of additional time for foraging and/or more plentiful food resources.

The Breeding Recovery hypothesis is consistent with the pattern of male-biased parental care, since females emancipated from parental duties can spend additional time foraging at coastal sites prior to southward migration. Females giving on average six to eight days less parental care than their mates can spend a few extra days preparing for southbound flight and still precede males to migratory stopovers in British Columbia.

Although the Breeding Recovery hypothesis predicts that female participation in parental care should decline seasonally, due to accumulation of energy deficit, this hypothesis makes no prediction about parental care patterns of males. The duration of parental care by males would not be predicted to decline seasonally as a result of female breeding condition, and in fact, if males progressively evaluate female condition and behavior (McNamara et al. 2002), they might increase parental effort to compensate for recuperating females.

According to the Breeding Recovery hypothesis, successfully-breeding female Western Sandpipers will desert broods in order to spend additional time foraging prior to southward migration or take advantage of better conditions on the southward migration. During this time, while females recuperate reserves, males guard offspring at breeding sites. Therefore, we do not expect males to necessarily catch up to females on the southward migration, as they do not need to make up as large an energy deficit and could increase reproductive success by spending that additional time with chicks. The Breeding Recovery hypothesis does not predict this change in timing.

The Breeding Recovery hypothesis does not address changes in timing related to seasonal timing. According to this hypothesis, egg-laying females would always require time for recuperation, regardless of the lateness of breeding, so we do not expect the relative timing of males and females to change much among years.

Territoriality

In many migrant species, individuals seek to improve nest sites for future reproductive event, and “prospect” while on breeding grounds, typically at the end of the breeding season (Reed et al. 1999). Both failed and successful breeders could gain advantage by examining future nest sites (Reed et al. 1999), and perhaps by exhibiting territorial behaviors to demarcate these sites. Transient Spotted Sandpipers (*Actitus macularia*) appeared to move through breeding sites about a week prior to the initiation of southward migration (Reed and Oring 1992), and small flocks of Western Sandpipers are often seen at breeding areas late in the season (Holmes 1972), potentially evaluating nesting areas as they make their way to coastal post-breeding sites. Both failed and successful males may thus remain later at breeding sites to improve their breeding territories in the subsequent year, exhibiting territoriality as these transients pass through and prospecting local nest sites themselves.

Field studies suggest that male Western Sandpipers may not exhibit such territoriality during the brood rearing period as suggested by the Territoriality hypothesis. Holmes (1972) reports that territorial behaviors of Western Sandpipers decrease over the course of incubation, and after hatch, parents typically lead broods to feeding areas away from the nest site. This reduction in territorial behavior corresponds with a decrease in plasma testosterone for male Western Sandpipers during the

incubation and post-hatch periods, during which male testosterone levels are not different from those of females (O'Reilly 1995).

I define the **Territoriality (T) hypothesis** as follows: Male Western Sandpipers remain in the vicinity of the breeding territory longer than do females in order to improve territory possession in the following year. As a result, they follow females on migration.

Finally, if males remain at breeding sites to investigate or defend territories (Territoriality hypothesis), then females could potentially participate in parental care for as long as the male, if the additional benefit of care (brooding or guarding), increases the survival of the offspring. However, chicks reach thermoregulatory independence during their first week of life, and one parent may be able to successfully guard the chicks after this stage is reached (Erckmann 1981). If males and females monitor each other's behavior when making decisions about duration of parental care (McNamara et al. 2002), then females might observe the male tendency to remain longer at breeding sites and take the opportunity to depart earlier, because two parents are unnecessary for brood rearing after the first week.

The Territoriality hypothesis makes no predictions about changes in relative migratory timing of males and females and cannot explain why males might try to catch up to females. Males choosing to remain at breeding sites to improve territory possession have no reason to rush the migration southward.

The Territoriality hypothesis also makes no predictions about interannual variation in southward migratory timing. Males will always stay longer than females at breeding sites, and there is no reason to expect the difference between them to change in early versus late years.

Migration Distance

Based predominantly on descriptive evidence, differential migratory timing by age or sex classes has long been associated with migration distance. For several passerine species, the class that winters the farthest from breeding sites appears to migrate southward first (Fairfield and Shirokoff 1978, Ketterson and Nolan 1983, Chandler and Mulvihill 1990, Swanson et al. 1999). Within the calidrine sandpipers, long-distance migration is associated with reduced parental care (Myers 1981, Reynolds and Székely 1997). Female Western Sandpipers winter farther south than males, on average (Nebel et al. 2002, and references therein), and female-first southward migration in this species has long been attributed to the longer migration females must undertake (Butler et al. 1987).

Despite its prevalence in the literature, migratory distance on its own is generally an unsatisfactory explanation for breeding and migratory patterns. As Lank et al. (2003) suggest, “why might not parents leave at the same time, and the longer distance migrant simply arrive farther south at a later date?” If the parent migrating farther leaves the breeding grounds first, then there must be some advantage to

earlier arrival on wintering sites or early passage through migratory stopovers. This advantage, however, is not part of the general, empirical Migration Distance hypothesis.

I define the **Migration Distance (MD) hypothesis** as follows: The timing of brood desertion is related to migration distance. Individuals that must migrate farther desert earlier. Because females on average migrate farther, they desert earlier and precede males on migration.

The Migration Distance hypothesis is consistent with early female desertion at breeding sites. Because adult female Western Sandpipers generally migrate farther than males (Nebel et al. and references therein), they might give up some brood care in order to migrate this longer distance.

The Migration Distance hypothesis is unable to explain the seasonal decline in parental care by either sex. If males and females have no deadline by which to arrive at wintering sites, they could provide the same amount of parental care to late broods as to early, and then make a later southward migration.

The Migration Distance hypothesis also does not predict that males should catch up to females on the southward migration. Males in general migrate shorter distances, so do not need to depart breeding sites as early as females. Males do not take advantage of the possible additional time at high latitudes, as there are almost three weeks between the southward movements of adults and juveniles that adult

males could use to extend parental care or forage. Instead, they appear to reduce the amount of time spent preparing for the southward migration in order to catch up to females. Migration Distance is an inadequate explanation, as males would never need to catch up to females, or precede females on the southward migration. Because they winter farther north, they would not need to 'hurry-up' southward.

Similarly, Migration Distance is unable to account for interannual changes in timing, as females always migrate farther than males. Females would be expected to precede males in an amount proportional to distance, which would not change much among years, particularly in relation to a temporal variable such as the timing of breeding.

Molt Deadline

Differences in the timing of molt among age or sex classes have been implicated in the differential migratory timing of some passerine species (Chandler and Mulvihill 1990), and it is possible that the urgency of molt plays a role in the differential timing of male and female Western Sandpipers. Adult Western Sandpipers, like most Calidridines, begin pre-basic molt during migration but most do not molt flight feathers until they arrive at wintering sites (O'Hara et al. 2002, but see Senner and Martinez 1982). In some cases, flight abilities are severely compromised during molting (Watts 2001).

Peregrine Falcon subspecies (*F. p. anatum* and *F. p. tundrius*) migrate between inland, northern breeding sites and coastal wintering

sites in Central and South America, similar to the wintering distribution of Western Sandpipers. Falcons are fast, highly-maneuverable predators that prey heavily on migrating and wintering shorebirds. The timing of southward migration may allow adult Western Sandpipers to molt flight feathers prior to the influx of migratory Peregrine Falcons (*Falco peregrinus*) to wintering sites in Central and South America (McGrady et al. 2002, O'Hara 2002, Lank et al. 2003). In fact, in most years adult Western Sandpipers will precede the large numbers of falcons on the southward migration (Lank et al. 2003; Chapter II), settling on wintering sites in both the northern and southern parts of the range with some time to spare for a quick molt. Sandpipers that arrive at wintering sites and complete molt before the migratory falcons appear may increase their probability of survival during this time, and those Western Sandpipers wintering farther south (females) may migrate first in order to get to these sites and complete molt.

Essentially, this hypothesis is based on the Migration Distance hypothesis, but includes an advantage to early migration.

I define the **Molt Deadline (MDL) hypothesis** as follows: Adults must arrive at non-breeding destinations by a deadline in order to complete a molt. Adults migrating farther must depart sooner in order to achieve this. Because females on average migrate farther, they desert earlier and precede males on migration. Juveniles do not molt in their first winter and so do not face a molt deadline.

Similarly, if females must migrate farther by a deadline (Molt Deadline hypothesis), then they may desert breeding sites early to make this longer migration.

In contrast, if sandpipers truncate parental care in order to meet a deadline (MDL hypothesis), then the duration of care might decrease as the season progresses. Parents with broods earlier in the season would have a greater amount of time to spend with broods before leaving to meet the deadline, and those with broods later in the season would have less time.

In contrast, the Molt Deadline hypothesis and the Escape Performance hypothesis offer possible explanations for the hurry-up features of southbound Western Sandpipers. In these cases, earlier migrations mean safer molt at wintering sites or safer migratory stopovers, for both males and females. So, males can increase reproductive fitness by extending parental care, but then they must hurry-up to make it south prior to the wave of migratory falcons. In addition, according to the Escape Performance hypothesis, catching up to females might increase the males' chances of survival by dilution effect as well as better flight performance relative to the larger, heavier females.

Both the Molt Deadline and Escape Performance hypotheses, however, incorporate temporal components on which changing hatch timing could have an effect. Earlier migration (EP) and earlier molt at wintering sites (MDL) are safer for both sexes of Western Sandpipers, and

the need to remain longer on breeding grounds when mean hatch is later may influence the timing of the migration southward, as the sandpipers attempt to outpace the falcons southward. In years of earlier breeding, female Western Sandpipers precede males by a greater extent on the southward migration—an apparent contradiction, as it appears that females would have more, not less, time to spend with the brood in these early years. However, earlier timing at breeding sites also corresponds with earlier return of the falcons to the important sandpiper stopover site in southwestern British Columbia (Chapter II). In these years, then, it is perhaps most important for females to migrate southward early.

Escape performance

The return of migratory falcons to coastal regions not only influences the survival ability of Western Sandpipers at wintering sites, but that during migration (Butler et al. 2003). Lank et al. (2003) suggested that “southbound sandpiper migrants are able to gain a safety advantage by migrating ahead of the wave of falcon migration”. At the Fraser River Delta in southwestern British Columbia, the first major stopover of the sandpipers’ southward migration (Butler and Kaiser 1996), falcons are largely absent during the early summer, but then begin to reappear in late July with numbers peaking late in October (Lank et al. 2003). Recent work has shown that early-migrating sandpipers will precede the falcons southward in most years (Chapter II). However, the southward migratory timing of adult and juvenile Western

Sandpipers coincides with a period of continuously increasing predation danger.

Avian predators prefer larger individuals and are capable of distinguishing among size classes in migratory flocks (W. Cresswell, pers. comm.). Western Sandpiper females are larger than males and have higher wing loading (or mass/wing area) due to this larger size (R. Ydenberg, pers. comm.). Wing loading is closely associated with escape performance, as heavier birds are less capable of avoiding capture by predators (Kullberg et al. 1996, Lind et al. 1999). Peregrine Falcons often combine their speed with an element of surprise in attacks on flocks (Warnock and Gill 1996), and are more successful in attacks on shorebirds when the shorebirds on the ground, and less so in the air (Page and Whitacre 1975). Thus, lighter birds have an advantage in take off speed or maneuverability, allowing them to get into the air faster, where they are less catchable (Page and Whitacre 1975, Cresswell 1993). Larger or heavier shorebirds (in this case, females) may therefore migrate earlier to more completely avoid the return of avian predators to the coast (Lank et al. 2003).

I define the **Escape Performance (EP) hypothesis** as follows: The danger level for Western Sandpipers rises seasonally at migratory stopovers due to falcon migration. Therefore, extending parental care necessarily increases the danger during migration. Because females have poorer escape performance than males, they evaluate this trade-off

differently and are more strongly selected to reduce parental investment in order to advance migration.

Because numbers of falcons rise sharply at stopover sites late in the migration of adult Western Sandpipers (Lank et al. 2003), females could gain a head start by reducing their parental care to initiate southward migration. Therefore, the Escape Performance hypothesis is also consistent with the observed pattern of parental care.

The Escape Performance hypothesis also includes a temporal component, with earlier migration being safer for both males and females, but particularly for females. Longer delays at breeding sites, due to extended parental care, mean that more predatory falcons are likely to be present at southbound stopover sites when the sandpipers arrive there. As with the Migration Distance hypothesis, parents with broods that hatch earlier in the season have more time to spend with these broods before they must consider the reappearance of falcons on the migratory route, and parents with broods later in the season might have to desert the broods earlier to beat the falcons to British Columbia.

In contrast, the Molt Deadline hypothesis and the Escape Performance hypothesis offer possible explanations for the hurry-up features of southbound Western Sandpipers. In these cases, earlier migrations mean safer molt at wintering sites or safer migratory stopovers, for both males and females. So, males can increase reproductive fitness by extending parental care, but then they must

hurry-up to make it south prior to the wave of migratory falcons. In addition, according to the Escape Performance hypothesis, catching up to females might increase the males' chances of survival by dilution effect as well as better flight performance relative to the larger, heavier females.

Both the Molt Deadline and Escape Performance hypotheses, however, incorporate temporal components on which changing hatch timing could have an effect. Earlier migration (EP) and earlier molt at wintering sites (MDL) are safer for both sexes of Western Sandpipers, and the need to remain longer on breeding grounds when mean hatch is later may influence the timing of the migration southward, as the sandpipers attempt to outpace the falcons southward. In years of earlier breeding, female Western Sandpipers precede males by a greater extent on the southward migration—an apparent contradiction, as it appears that females would have more, not less, time to spend with the brood in these early years. However, earlier timing at breeding sites also corresponds with earlier return of the falcons to the important sandpiper stopover site in southwestern British Columbia (Chapter II). In these years, then, it is perhaps most important for females to migrate southward early.

Synthesis for adults

The Molt Deadline and Escape Performance hypotheses best predicted the parental care and migratory patterns of adult Western Sandpipers (Table III-1). These hypotheses fit well with the breeding and

migratory phenomena observed, whereas other hypotheses contradicted or were unable to make predictions about some aspects of the patterns. In particular, seasonal and inter-annual differences in the amount of parental care or differences in migratory timing between males and females could not be explained by Breeding Recovery, Migration Distance or Territoriality, because these hypotheses lacked a temporal component or were incapable of explaining differences in male parental care or migratory timing.

In contrast, the Molt Deadline and Escape Performance hypotheses were based on seasonal predator patterns at stopover and wintering sites, so males and females would have to trade-off parental care for relative safety during migration or molt. In theory, these hypotheses are more relevant in describing years with early timing on breeding sites, as in later years the timing of falcons is also delayed (Chapter II), and adult sandpipers, male and female, should have more time to migrate southward ahead of predators.

All of the hypotheses predicted that females should give shorter brood care than males, however the hypotheses differ in why females should reduce parental care. The Breeding Recovery hypothesis presumes that females use this time to make up lost reserves, and the Territoriality hypothesis allows females to depart because they can, whereas the remaining hypotheses suggest that females instead depart on southward migration.

Hypotheses	Females give less brood care than males	Duration of brood care declines seasonally for both sexes	Difference in timing decreases from breeding to BC	Difference in timing decreases when mean hatch is later
Breeding Recovery	Y	N	N	NA
Migration Distance	Y	N	N	N
Molt Deadline	Y	Y	Y	Y
Escape Performance	Y	Y	Y	Y
Territoriality	?	N	N	N

Table III-1. Predictions matrix for adult Western Sandpipers.

'Y' means that the hypothesis predicts the observed pattern, 'N' means that the hypothesis does not support the observed pattern, 'NA' means that the hypothesis makes no prediction, and '?' means that the predictions made by the hypothesis are unclear with respect to the observed pattern.

Breeding Recovery and Migration Distance were unable to account for why the duration of parental care declines seasonally, and why the difference in migratory timing between males and females changes between the breeding grounds, coastal stopover sites, and British Columbia, or among years with different hatch timing. The Molt Deadline and Escape Performance hypotheses fit all of the observed phenomena, and could not be differentiated for adult Western Sandpipers.

Patterns for juvenile sandpipers

One possible way to test the general applicability of these hypotheses is to evaluate the whether they accurately predict the migratory patterns observed for juvenile Western Sandpipers. Juveniles follow adults southward by about three to four weeks (Holmes 1972, Butler et al. 1987, Chapter I) and are unconstrained by the necessity of parental care at breeding sites or molt at wintering sites. Migratory patterns of other juvenile sandpipers are largely unknown or unpublished, so it is uncertain whether the predictions made by these hypotheses can be generalized to close relatives of Western Sandpipers.

Juvenile females precede juvenile males on the southward migration

Recently, we found that among juvenile Western Sandpipers, females precede males in most years, by as many as five days. In most years, however, this difference ranges from less than one to two days, so

the overall estimate is only 0.5 days ($p=0.02$) (Chapter I). Though adults of many sandpiper species are known to migrate at different times, the finding that females are also significantly ahead in the juvenile age class was unexpected (but see Butler et. al 1987) and warrants further attention in other *Calidris* species.

Although juvenile females precede males by fewer days than observed for adults (0.5 versus 1.2 days; Chapter I), they are significantly ahead of males in more years than adult females precede adult males (Chapter I). This differential timing for juveniles is in fact more biologically interesting than that of adults, as adult females begin southward movement ahead of males (through differences in duration of parental care and departure from breeding sites), whereas there is no evidence that female juveniles are earlier than males in departure from breeding sites. This would require seasonal changes in sex ratios at hatch, a trend not yet tested for many *Calidris* sandpipers. However, Schamel (2000) found no seasonal trends in sex ratios of hatching red-necked phalaropes (*Phalaropus lobatus*), and growth rates of young male and female sandpipers do not differ until they approach adult size (Holmes 1966).

Difference in timing of juveniles decreases when mean hatch is later

As with adults, female juveniles precede males to a greater extent when mean hatch timing is earlier, and the difference in timing between males and females decreases when mean hatch timing of small

shorebirds (including Western Sandpipers) is later (Chapter II). This relationship is striking in its similarity to that of adults, although in this case the correlation was statistically significant.

Hypotheses

Breeding Recovery and Territoriality

Because the Breeding Recovery and Territoriality hypotheses specifically address the needs of females to recuperate reserves following reproduction or the territorial behaviors of breeding males, they make no predictions about the migratory timing of juveniles.

Possibly, male juveniles benefit by remaining longer at natal areas, scouting future breeding territories. Many young birds at wintering sites in Panama, do not migrate northward in their first year (O'Hara 2002), and these may be predominantly females (Nebel et al., 2002). Therefore, juvenile males may have more to gain by delaying southward migration to scout future breeding territories, particularly because fidelity of Western Sandpipers to natal areas (3%) is high given the high mortality rates of young shorebirds in their first year (Holmes 1971). However, young sandpipers do not typically remain in natal areas for long after they attain flight (ACN, pers. obs.), and quickly move along tidal rivers to the coast (Holmes 1972).

Molt Deadline

Similarly, the Molt Deadline hypothesis refers directly to the molt schedule of adult Western Sandpipers. Juveniles do not molt upon

arrival at wintering sites, and many will make a roundtrip journey back to the breeding grounds before molting in the following winter (O'Hara 2002).

Migration Distance

Recently, Nebel et al. (2002) established that across the wintering distribution of Western Sandpipers, higher proportions of juvenile females winter the farthest south, even farther south than adult females. In contrast, juvenile males winter the farthest north, or closest to the breeding grounds. This means that the difference in migratory distance among male and female juveniles is even greater than that for adults. The Migration Distance hypothesis accurately predicts that we would expect female juveniles to precede males on the southward migration, and could even account for why females precede males in more years for juveniles than for adults.

Because the Migration Distance hypothesis does not incorporate a temporal component by which to account for interannual variation in migratory timing, it cannot predict the observed variation. Because female juveniles would always, in general, winter farther south than males (Nebel et al., 2002), then we expect females to always precede males southward, regardless of the timing of hatch.

Escape Performance

The Escape Performance hypothesis also presents a reason for female juveniles to migrate first. Whereas early-migrating adults can

miss the largest abundances of falcons at stopover sites, southbound juveniles never have that option—increasing numbers of falcons are present during their migration (Lank et al. 2003). However, because falcon abundances are continuously increasing, early-migrating juveniles can also reduce the danger of predation relative to late-migrating juveniles. In this case, the larger, heavier females exhibit poorer escape performance and may migrate early, when falcon predation pressure is less.

The Escape Performance hypothesis, however, predicts this pattern for juveniles, similar to the explanation for the previous migratory pattern. Females, with poorer escape performance, are expected to migrate as early as possible, because falcon numbers continue to rise during the juveniles' southward movement (Lank et al. 2003).

Synthesis for juveniles

The Escape Performance hypothesis was the best of the five hypotheses evaluated for juvenile Western Sandpipers (Table III-2). This hypothesis fit best with the migratory phenomena observed, whereas other hypotheses contradicted at least one of the observed patterns. The Breeding Recovery, Molt Deadline and Territoriality hypotheses could not make predictions about the juvenile migration, because juveniles have not reproduced and do not molt in their first year. In contrast, the Migration Distance and Escape Performance hypotheses could account

for the general female-first pattern of migration for juveniles, and the Escape Performance hypothesis predicted the observed changes in differential timing as a result of hatch timing.

Hypotheses	Females precede males on southward migration	Difference in timing decreases when mean hatch is later
Breeding Recovery	N	NA
Migration Distance	Y	N
Molt Deadline	N*	N*
Escape Performance	Y	Y
Territoriality	NA	NA

Table III-2. Predictions matrix for juvenile Western Sandpipers.

'Y' means that the hypothesis predicts the observed pattern, 'N' means that the hypothesis does not support the observed pattern, 'NA' means that the hypothesis makes no prediction. The Molt Deadline hypothesis by definition cannot apply to juvenile migration, but possibly juveniles experience an alternative deadline (*).

Synthesis for Western Sandpipers

It appears that for both adult and juvenile Western Sandpipers, a temporal threshold exists that influences the migratory decisions of males and females and, ultimately, the differential migratory timing that is observed. For adults, the timing of migration or arrival at wintering sites may be important enough to influence even parental care patterns. For juveniles, it appears that the timing of migration is of greater importance than arrival at wintering sites, as juveniles do not molt in their first winter, however it is also possible juveniles experience a different deadline that makes earlier arrival at wintering sites better. Wintering habitats are varied in quality (G. Fernandez, pers. comm.), and early-arriving juveniles could possibly settle in sites with better food or lower predation danger. Little is known about the period of arrival of adult or juvenile Western Sandpipers at wintering sites, and whether such competition may actually occur.

Patterns of Pacific Dunlin

In their discussion of migratory strategies of *Calidris* sandpipers, Lank et. al (2003) contrast the annual routine of Semipalmated and Western Sandpipers with that of the Pacific Dunlin (*C. alpina pacifica*), which breeds sympatrically with these species in western Alaska. Pacific Dunlin exhibits an alternative life history strategy, molting at breeding sites or coastal post-breeding areas prior to migrating southward.

Another Alaskan-breeding Dunlin (*C. alpina arctica*), breeding farther to the north, employs a similar breeding-molt schedule before migrating to wintering sites in Asia. How does this alternative strategy compare with the migratory timing and parental care patterns of Western Sandpipers?

Studies of the parental care patterns of Alaskan races of Dunlin are lacking, and only a few casual observations have been reported. In Europe, male and female Dunlin are known to give differing amounts of parental care (Soikkeli 1967), however there are contradicting anecdotal reports pertaining to North American Dunlin. Holmes (1966) refers to the formation of post-breeding flocks in western Alaska (likely *C. a. pacifica*) consisting of “the first adults, usually females, to leave their mates and broods”, though Ashkenazie and Safriel (1979) suggest that for Dunlin breeding at Barrow, Alaska, (likely *C. a. arctica*) “both parents stay with the brood”. Possibly *C.a. arctica* and *C.a. pacifica* differ in their patterns of parental care, with Pacific Dunlin more closely resembling the patterns of the other shorebirds breeding in the same region, including Western and Semipalmated Sandpipers. However, both *C.a. pacifica* and *C.a. arctica* molt prior to migration (Holmes 1966), so differing parental care strategies could reflect interesting trade-offs between reproduction and survival between these races.

The migratory timing of Alaskan-breeding Dunlin is also relatively unknown. In 1978, Pacific Dunlin were captured at the Fraser Estuary, a southbound stopover site and wintering area (Shepherd et al. 2001). I

used these data for a preliminary estimation of the southward migratory timing of Dunlin. I separated migratory Dunlin from winter residents by only considering birds captured prior to 21 November (G. Kaiser, unpubl. data), and then evaluated the migratory timing of 158 southbound juveniles and 154 southbound adults. The mean passage of juvenile Dunlin occurred on Julian day 312.2 and the mean passage of adults on Julian day 317.3. This five-day difference between age classes was significant ($F=24.4$, $p<0.0001$), so analyses of sex differences in timing were conducted separately for age classes. Males and females did not differ in southward timing in either adult ($F=0.07$, $p=0.92$) or juvenile ($F=0.28$, $p=0.76$) age classes.

Predictions for Pacific Dunlin

Of the five hypotheses examined here, four make predictions about the patterns of parental care and southward migratory timing of Pacific Dunlin (Table III-3), as adults do not encounter a post-migratory Molt Deadline. Because the Pacific race of Dunlin molts at northern latitudes prior to migrating south, any necessary recuperation by females or territorial behaviors by males should influence parental care but not southward migratory timing. Therefore, both the Breeding Recovery and Territoriality hypotheses predict early female desertion of broods but simultaneous southward migration by males and females. Possibly, females winter farther south than males (Shepherd et al. 2001), but further study of the latitudinal segregation of sexes is necessary to

elucidate this. If females do migrate farther, then we might expect them to depart Alaska prior to males, however, because both sexes molt near breeding grounds prior to migrating, females do not necessarily need to desert broods early. Thus, the Migration Distance hypothesis predicts biparental care and female-first southward migration. Finally, the Escape Performance hypothesis predicts that the larger, heavier females should migrate during the period of least predation danger. In this case, because Pacific Dunlin remain north until October or November (Gill and Handel 1990, Lank et al, in press), they follow the migratory falcons southward. Late-migrating females may be safer, so we predict either no difference in migratory timing or a male-first pattern. Again, because the Dunlin molt prior to migration, this hypothesis predicts equal parental care between males and females.

There was no sex-class difference in migratory timing, so the Migration Distance hypothesis is not appropriate for describing the patterns observed for Pacific Dunlin. Unfortunately, data on parental care patterns are unclear, and further study will be necessary to determine whether Breeding Recovery, Escape Performance or Territoriality best explains the patterns of adult Pacific Dunlin. As with Western Sandpipers, migratory patterns were conserved between age classes, and of the three remaining hypotheses, only the Escape Performance hypothesis can be applied to both adults and juveniles.

Hypotheses	Pattern of parental care predicted	Pattern of southward migratory timing predicted
Breeding Recovery	Early female departure	Females and males together
Migration Distance	Totally biparental care	Females first
Molt Deadline	NA	NA
Escape Performance	Totally biparental care	Females and males together or males first
Territoriality	Early female departure	Females and males together

Table III-3. Predictions matrix for parental care and migratory timing of Pacific Dunlin.

Pacific Dunlin exhibit an alternative life history strategy from Western Sandpipers and other *Calidris* sandpipers, remaining near breeding grounds to molt before migrating to wintering sites. The predicted pattern of parental care or southward migratory timing differs among these hypotheses, and further study of this system is warranted to elucidate if the same hypothesis that best explains Western Sandpiper migratory patterns (Escape Performance) also influences the patterns of Dunlin.

Interestingly, there was a suggestive (though not significant) difference in migratory timing of male and female juveniles, with females migrating southward about a day behind males. As juveniles migrate earlier than adults, they may encounter a higher number of Peregrine Falcons on their southward movement, and female juveniles may delay southward movement as an anti-predator behavior. If a real pattern, this is consistent with the predictions made by the Escape Performance hypothesis, but greater sample sizes in additional years will be necessary to address this question.

Discussion

Parental care by monogamous shorebirds is closely linked with southward migration (Myers 1981), and many hypotheses related to timing do not differentiate between these two events (but see Chapter I). The contrasting life histories of adult and juvenile Western Sandpipers and Pacific Dunlin illustrate how predictions of these hypotheses can vary when parental care is isolated from migratory timing or eliminated altogether. In all three cases, however, migratory timing appears related to the return of predatory falcons to migratory stopovers and/or wintering sites.

These results correspond with a general shift in thinking about avian migratory strategies, from migrants as predators to migrants as prey. Historically, hypotheses to evaluate parental care or migratory

timing focused on energetics or resource abundance, either at breeding sites (Holmes and Pitelka 1968, Holmes 1972, Pitelka et al. 1974, Ashkenazie and Safriel 1979, Erckmann 1981) or migratory stopovers (Schneider and Harrington 1981, Boates and Smith 1989). Food-based theories are prevalent for both northward and southward migration, although in general the relationships are unclear (Lank et al. 2003). Recently, the influence of predators on avian behavior has been extended from local to hemispheric-scale phenomena, such as migratory patterns (Woodrey and Moore 1997, Clark and Butler 1999, Ydenberg et al. 2002, Butler et al. 2003, Lank et al. 2003), and provides an alternative explanation for the patterns observed. In particular, as populations of raptors recover from declines during the 20th century (Hoffman and Smith 2003), the effects of predators should be considered in study of avian migratory strategies.

In this evaluation of migratory and parental care patterns of the Western Sandpipers, the most plausible hypotheses are those relating to the timing of migration or the timing of arrival at wintering sites, with respect to the timing of predators in these areas. Even Pacific Dunlins, which exhibit an alternative life history strategy to Western Sandpipers, may migrate southward at a time when predator pressure is reduced (this study; Lank et al. 2003). However, as Ketterson and Nolan (1983) discovered, it is often a combination of hypotheses that best describes avian migratory or wintering patterns. Here, I have attempted to isolate

these hypotheses to evaluate what each predicts individually about migratory timing of Western Sandpipers and *Calidris* allies. In fact, the relative importance of breeding recovery, territoriality and danger from predators on the migration and at wintering sites likely varies at the individual level, depending on factors such as condition and experience.

Acknowledgments

I thank R.C. Ydenberg, D.B. Lank, T.D. Williams, and J.S. Brown for helpful comments on the development of this paper. Members of the Ydenberg lab and the Peepers group also contributed to the ideas presented here. Funding was provided to ACN by a National Science Foundation Graduate Fellowship.

Literature Cited

- Amat, J.A., G.H. Visser, A. Pérez-Hurtado, and G.M. Arroyo. 2000. Brood desertion by female shorebirds: a test of the differential parental capacity hypothesis on Kentish Plovers. *Proc. Roy. Soc. London, Ser. B.* 267: 2171-2176.
- Ashkenazie, S. and U.N. Safriel. 1979. Time-energy budget of the Semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* 60: 783-799.
- Boates, J.S. and P.C. Smith. 1989. Crawling behavior of the amphipod *Corophium volutator* and foraging by Semipalmated Sandpipers, *Calidris pusilla*. *Can. J. Zool.* 67:457-462.
- Burns, J.G., and R.C. Ydenberg. 2002. The effects of wing loading and gender on the escape flights of Least Sandpipers (*Calidris minutilla*) and Western Sandpipers (*Calidris mauri*) *Behav. Ecol. Sociobiol.* 52: 128-136.
- Butler, R. and G. Kaiser. 1995. Migration chronology, sex ratio, and body mass of Least Sandpipers in British Columbia. *Wils. Bull.* 107: 413-422.
- Butler, R.W., G.W. Kaiser, and G.E.J. Smith. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers, (*Calidris mauri*) on the south coast of British Columbia. *J. Field Ornith.* 58: 103-111.
- Butler, R.W., F.S. Delgado, H. de la Cueva, V. Pulido, and B.K. Sandercock. 1996. Migration routes of the Western Sandpiper. *Wils. Bull.* 108: 662-672.
- Butler, R. W., R. C. Ydenberg, and D. B. Lank. 2003. Wader migration on the changing predator landscape. *Wader Stud. Grp. Bull.* 99: 100-103.
- Chandler, C.R. and R.S. Mulvihill. 1990b. Interpreting differential timing of capture of sex classes during spring migration. *J. Field Ornith.* 61: 85-89.
- Clark, C.W. and R.W. Butler. 1999. Fitness components of avian migration: a dynamic model of Western Sandpiper migration. *Evol. Ecol. Res.* 1: 443-457.

- Erckmann, W.J. 1981. The evolution of sex-role reversal and monogamy in shorebirds. Unpublished Ph.D. thesis. University of Washington, Seattle, Washington.
- Fairfield, D.M. and P.A. Shirokoff. 1978. Migratory patterns and winter distribution in the Ruby-crowned Kinglet (*Regulus calendula*). Blue Bill 25:22-25
- Gill, R.E., Jr., and C.M. Handel. 1990. The importance of subarctic intertidal habitats to shorebirds: a study of the central Yukon-Kuskokwim Delta, Alaska. Condor 92:709-725.
- Gratto-Trevor, C.L. 1991. Parental care in Semipalmated Sandpipers *Calidris pusilla*: brood desertion by females. Ibis 133: 394-399.
- Hoffman, S.W. and J.P. Smith. 2003. Population trends of migratory raptors in western North America, 1977-2001. Condor 105: 397-419.
- Holmes, R.T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68: 3-46.
- Holmes, R.T. 1971. Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). Oecologia 7: 191-208.
- Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. Am. Midl. Nat. 87: 472-491.
- Holmes, R.T. and F.A. Pitelka. 1968. Food overlap among co-existing sandpipers on northern Alaskan tundra. Syst. Zool. 17:305-318.
- Jehl, J.R., Jr. 1979. The autumnal migration of Baird's Sandpiper, in Studies in Avian Biology No. 2 (F.A. Pitelka, ed.), pp. 55-68, Cooper Ornithological Society, Allen Press, Lawrence, Kansas
- Jonsson, P.E. and T. Alerstam. 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. Biol. J. Linn. Soc. 41: 301-314.
- Ketterson, E.D. and V. Nolan, Jr. 1983. The evolution of differential migration. Curr. Ornith. 1: 357-402.

- Lank, D.B. R.W. Butler, J. Ireland, and R.C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303-319.
- Lindstrom, A. 1990. The role of predation risk in stopover habitat selection in migrating Bramblings, *Fringilla montifringilla*. *Behav. Ecol.* 1: 102-106.
- McGrady, M.J., T.L. Maechtle, J.J. Vargas, W.S. Seegar, and M.C.P. Pena. 2002. Migration and ranging of Peregrine Falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. *Condor* 104: 39-48
- McNamara, J.M., A.I. Houston, T. Székely, and J.N. Webb. 2002. Do parents make independent decisions about desertion? *Anim. Behav.* 64: 147-149.
- Miller, E.H. 1985. Parental behavior in the Least Sandpiper (*Calidris minutilla*). *Can. J. Zool.* 63:1593-1601.
- Monaghan, P., R.G. Nager, and D.C. Houston. 1998. The price of eggs: Increased investment in egg production reduces the offspring rearing capacity of parents. *Proc. Roy. Soc. Lond., Series B* 265: 1731-1735.
- Morrison, R.I.G. 1984. Migration systems of some new world shorebirds. In *Shorebirds: migration and foraging behavior.* (eds. J. Burger and B.L. Olla). Plenum Publishing Co., New York. pp. 125-202.
- Myers, JP. 1981a. Cross-seasonal interactions in the evolution of sandpiper social systems. *Behav. Ecol. Sociobiol.* 8:195-202.
- Nager, R.G., P. Monaghan, and D.C. Houston. 2001. The cost of egg production: increased egg production reduces future fitness in gulls. *J. Avian Biol.* 32: 159-166.
- Nebel, S., D.B. Lank, P.D. O'Hara, G. Fernández, B.Haase, F. Delgado, F.A. Estela, L.J. Evans Ogden, B. Harrington, B.E. Kus, J.E. Lyons, F. Mercier, B. Ortego, J.Y. Takekawa, N. Warnock, and S.E. Warnock. 2002. Western Sandpipers (*Calidris mauri*) during the non-breeding season: spatial segregation on a hemispheric scale. *Auk* 119: 922-928.
- Neville, J.A. 2002. Division of parental roles in the monogamous Western Sandpiper, *Calidris mauri*. Unpublished M.Sc. thesis, University of Alaska, Fairbanks, AK.

- Niehaus, A.C. 2003. Ecology of migratory timing by southbound male and female Western Sandpipers (*Calidris mauri*). Unpublished M.Sc. thesis, Simon Fraser University, Burnaby, BC.
- O'Hara, P.D. 2002. The role of feather wear in alternative life history strategies of a long-distance migratory shorebird, the Western Sandpiper (*Calidris mauri*). Unpublished Ph.D. thesis, Simon Fraser University, Burnaby, BC.
- O'Hara, P.D., D.B. Lank, and F.S. Delgado. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of Western Sandpipers (*Calidris mauri*) in Panamá. *Ardea* 90:61-70.
- O'Reilly, K.M. 1995. Ecological basis of endocrine phenomena: Field studies of Scolopacidae as model systems. Unpublished Ph.D. thesis, University of Washington, Seattle, WA.
- Pitelka, F.A., R.T. Holmes and S.F. Maclean, Jr. 1974. Ecology and evolution of social organization in Arctic sandpipers. *Am. Zool.* 14:185-204.
- Rahn, H., C.V. Paganelli, and A. Ar. 1975. Relation of avian egg weight to body weight. *Auk* 92: 750-762.
- Reed, J.M. and L.W. Oring. 1992. Reconnaissance for future breeding sites by Spotted Sandpipers. *Behav. Ecol.* 3: 310-317.
- Reed, J.M., T. Boulinier, E. Danchin, and L.W. Oring. 1999. Informed dispersal: prospecting by birds for breeding sites. *Curr. Ornith.* 15:189-259
- Reynolds, J.D. and T. Szekely. 1997. The evolution of parental care in shorebirds: life histories, ecology, and sexual selection. *Behav. Ecol.* 8: 126-134.
- Ruthrauff, D.R. 2002. Seasonal and age-related trends in the reproductive output of Western Sandpipers (*Calidris mauri*) at Kanaryaraq, Alaska. Unpublished M.Sc. thesis, Humboldt State University, Arcata, California.
- Sandercock, B.K. 1997. Factors affecting the breeding demography of Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*Calidris pusilla*) at Nome, Alaska. Unpublished Ph.D. thesis, Simon Fraser University, Burnaby, BC.

- Schamel, D.L. 2000. Male and female reproductive strategies in the red-necked phalarope, a polyandrous shorebird. Unpublished Ph.D. thesis, Simon Fraser University, Burnaby, BC.
- Schneider, D.C. and B.A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98:801-811.
- Senner, S.E. and E.F. Martinez. 1982. A review of Western Sandpiper migration in interior North America. *Southwest. Nat.* 27:149-159
- Shepherd, P.C.F., D.B. Lank, B.D. Smith, N. Warnock, G.W. Kaiser, and T.D. Williams. 2001. Sex ratios of Dunlin wintering at two latitudes on the Pacific coast. *Condor* 103:352-360.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in the Dunlin (*Calidris alpina*). *Ann. Zool. Fenn.* 4:158-198.
- Swanson, D.L., E.T. Liknes, and K.L. Dean. 1999. Differences in migratory timing and energetic condition among sex/age classes in migrant Ruby-crowned Kinglets. *Wils. Bull.* 111: 61-69.
- Székely, T. and J.D. Reynolds. 1995. Evolutionary transitions in parental care in shorebirds. *Proc. Roy. Soc. Lond., Series B* 262: 57-64.
- Székely, T. and T.D. Williams. 1995. Costs and benefits of brood desertion in female Kentish Plovers, *Charadrius alexandrinus*. *Behav. Ecol. Sociobiol.* 37: 155-161.
- Székely, T. and I.C. Cuthill. 2000. Trade-off between mating opportunities and parental care: brood desertion by female Kentish Plovers. *Proc. Roy. Soc. Lond., Ser. B.* 267: 2087-2092.
- Székely, T., J.D. Reynolds and J. Figuerola. 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* 54: 1404-1413.
- Tomkovitch, P.S. and V.V. Morozov. 1983. Biological characteristics of the Western Sandpiper on the Chukchi Peninsula. Translated from the Russian. *Bull. Moscow Nat. Soc.* 88: 38-50.
- Vezina, F. and T.D. Williams. 2002. Metabolic costs of egg production in the European Starling (*Sturnus vulgaris*). *Physiol. Biochem. Zool.* 75: 377-385.

- Visser, M.E. and C.M. Lessells. 2001. The costs of egg production and incubation in Great Tits (*Parus major*). Proc. Roy. Soc. Lond., Ser. B 268: 1271-1277.
- Warnock, N.D. and R.E. Gill. 1996. Dunlin. *In* The Birds of North America (eds. A. Poole and F. Gill). The Academy of Natural Sciences of Philadelphia, Pennsylvania. Vol. 203, pp. 1-24.
- Wilson, W.H. 1994. Western Sandpiper in The Birds of North America. *Edited by* A. Poole and F. Gill. The Academy of Natural Sciences of Philadelphia, Pennsylvania. Vol. 90, pp. 1-19.
- Wolf, N. 2001. Foraging ecology and site selection in Western Sandpipers during their fall migration through southwestern British Columbia. Unpublished M.Sc. thesis, Simon Fraser University, Burnaby, BC.

EPILOGUE

This work highlights the need to consider in more detail the relationships between the timing of parental care and migration as components of the annual cycle of Western Sandpipers, and other shorebirds. In Chapter I, I found that females significantly preceded males, within both adult and juvenile age classes. Differential timing was highly variable among years, but in most years females preceded males. In some years, however, males actually preceded females southward, contrary to the male-biased pattern of parental care observed in this species. In addition, the magnitude of differential migratory timing was less than expected if only successful breeders were considered, because failed breeders reduced the overall difference between males and females.

In my simulation model, changes in parental care had the strongest influence on differential migratory timing from breeding sites, followed by changes in nest failure rates. Although the breeding model and post-breeding data provided similar estimates of differential timing, females preceded males to a much greater extent at a staging site farther to the south.

Temporal patterns of migration by males and females changed between breeding sites and migratory stopovers. Unfortunately, we know little about the time period between departure from breeding sites and arrival at stopovers in British Columbia to address this issue.

Mistnetting and telemetry work focusing in coastal Alaska may elucidate which sites the sandpipers use to refuel and prepare for migration during this time, how long they use them, and how they move among sites prior to initiating migration. Do female Western Sandpipers really precede males by more than eight days in coastal southern Alaska, and if so, why do we not see differences of that magnitude farther south, at stopovers? Field data from breeding, post-breeding or pre-migration and stopover sites in the *same* years will help us learn more about the temporal changes in migratory patterns of male and female Western Sandpipers.

In Chapter II I found, contrary to expectations, that the timing of snowmelt was not a strong predictor of hatch timing. This discrepancy results from the northward migratory ecology of Western Sandpipers, which appear to time arrival at breeding sites to correspond with mean snowmelt, rather than the earliest possible snowmelt. The southbound timing of sandpipers was not related to events at breeding sites (snowmelt or hatch), but the difference between males and females did differ among years with earlier or later hatch timing. In years of early hatch, females preceded males to a greater extent. This pattern was nearly identical between adults and juveniles.

Interestingly, the timing of falcon arrival at stopovers correlated strongly with snowmelt. As a result, years of early snowmelt, and subsequently, early falcons, produced more dangerous southward passage for Western Sandpipers of both age classes. However, Western

Sandpipers may be able to use snowmelt as a cue for falcon timing and adjust migration accordingly.

From phenology alone, one might have expected females to stay longer when breeding was earlier, since they would have more time prior to some seasonal deadline. I found the opposite -- females were farther ahead of males in these early years, perhaps reflecting the relatively greater importance of survival on migration to females.

These results further highlight the partial independence of parental care and migration patterns. They suggest that climate change at breeding sites may not have a direct effect on avian breeding patterns, if arrival at these areas is determined by northward migratory timing, in turn determined by events at wintering sites or stopovers (Both and Visser 2001). Finally, it appears that the effects of raptor population growth and timing should be considered in studies of the timing of breeding and migration of prey species, such as Western Sandpipers (Lank et al, in press).

In Chapter III, I tested five hypotheses to explain patterns associated with the male-biased parental care and female-first migration of Western Sandpipers and some near relatives. I found that some hypotheses (Breeding Recovery, Migration Distance, and Territoriality) were generally unsatisfactory in logic, and did not clearly predict the patterns observed for Western Sandpipers. Two hypotheses (Molt

Deadline and Escape Performance) were adequate predictors of patterns for adult Western Sandpipers.

All of these hypotheses are defined and discussed in the literature with reference only to adult age classes. However, when I examined the predictions they made for migratory patterns of juvenile Western Sandpipers, as well, I found that the Molt Deadline hypothesis could be eliminated. The Escape Performance hypothesis is best overall for Western Sandpipers.

The alternate molting and migration strategy of Pacific Dunlin is often contrasted with that of Western Sandpipers (Butler et al. 2003, Lank et al. 2003). Here, I present predictions for parental care and timing for each hypothesis considered, eliminating the Migration Distance and Molt Deadline hypotheses. Further study of parental care and migratory timing by sex class is necessary to discriminate among the remaining hypotheses.

This study continues the development of ideas about migratory and parental care strategies of sandpipers, starting with consideration of sandpipers as predators (food-based theories) and more recently incorporating sandpipers as prey (predation danger based theories). The influence of predators is increasingly recognized on the hemispheric level of avian migration (Ydenberg et al. 2002, Butler et al. 2003, Lank et al. 2003). Here, I show that most plausible of hypotheses tested here are those that include predator timing.

Field tests of these hypotheses are necessary to substantiate the predictions made here. For example, relatively little is known about the breeding or migratory patterns of the Alaskan races of Dunlin, compared with other *Calidris* sandpipers common in North America. The Escape Performance hypothesis, most strongly supported by evidence presented here, should be tested experimentally by further examination of take-off performance and aerial maneuverability.

Though the annual cycle of Western Sandpipers has been well-studied over recent decades, this small shorebird remains a fascinating model of avian breeding, migratory and wintering patterns. In all of these studies, we have found that the decisions made by individuals during one phase of this cycle, whether on the scale of the nest, the mudflat, or the wintering distribution, resonate throughout the life history of the bird. Our understanding of Western Sandpiper ecology will therefore continue to develop as we extend the communication and collaboration of researchers during all stages of this bird's life history.

Literature Cited

- Both, C. and M.E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296-298.
- Butler, R.W., R.C. Ydenberg and D.B. Lank. 2003. Wader migration on the changing predator landscape. *Wader Study Group Bulletin* 100: 130-133.
- Lank, D.B., R.W. Butler, J. Ireland, and R.C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 133: 303-319.
- Ydenberg, R.C., R.W. Butler, D.B. Lank, C.G. Guglielmo, M. Lemon, and N. Wolf. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. *Journal of Avian Biology* 33: 47-55.