

2012

Annual patterns of movement and distribution in the arctic breeding snow bunting (*Plectrophenax nivalis*)

Christie Macdonald

Follow this and additional works at: <https://scholar.uwindsor.ca/etd>

Recommended Citation

Macdonald, Christie, "Annual patterns of movement and distribution in the arctic breeding snow bunting (*Plectrophenax nivalis*) " (2012). *Electronic Theses and Dissertations*. 4798.
<https://scholar.uwindsor.ca/etd/4798>

This online database contains the full-text of PhD dissertations and Masters' theses of University of Windsor students from 1954 forward. These documents are made available for personal study and research purposes only, in accordance with the Canadian Copyright Act and the Creative Commons license—CC BY-NC-ND (Attribution, Non-Commercial, No Derivative Works). Under this license, works must always be attributed to the copyright holder (original author), cannot be used for any commercial purposes, and may not be altered. Any other use would require the permission of the copyright holder. Students may inquire about withdrawing their dissertation and/or thesis from this database. For additional inquiries, please contact the repository administrator via email (scholarship@uwindsor.ca) or by telephone at 519-253-3000ext. 3208.

**ANNUAL PATTERNS OF MOVEMENT AND DISTRIBUTION IN THE ARCTIC BREEDING SNOW
BUNTING (*PLECTROPHENAX NIVALIS*)**

By

CHRISTIE A. MACDONALD

A Thesis
Submitted to the Faculty of Graduate Studies
through **the Department of Biological Sciences**
in Partial Fulfillment of the Requirements for
the Degree of **Master of Science**
at the University of Windsor

Windsor, Ontario, Canada

2012

© 2012 Christie A. Macdonald

**Annual patterns of movement and distribution in the arctic breeding snow bunting
(*Plectrophenax nivalis*)**

by

Christie A. Macdonald

APPROVED BY:

Dr. Daniel D. Heath, Internal Examiner
Department of Biological Sciences

Dr. Aaron T. Fisk, External Examiner
Great Lakes Institute for Environmental Research

Dr. Kevin C. Fraser, Additional Examiner
Department of Biology, York University

Dr. Oliver P. Love, Advisor
Department of Biological Sciences

Dr. Dennis Higgs, Chair of Defense
Department of Biological Sciences

19 September 2012

I. DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is the result of joint research. My data chapters are co-authored with my supervisor, Dr. Oliver Love, as well as our collaborators Dr. Kevin C. Fraser, Dr. H. Grant Gilchrist and Dr. T. Kurt Kyser. While the primary contributions to these chapters have been by the author, my supervisor and our collaborators all provided important feedback in designing the project and statistical analyses. Drs. Love and Fraser provided valuable input during the writing of this manuscript. Additionally, Drs. Gilchrist and Kyser also contributed through provision of logistics and equipment needed to complete this project. Chapters 2 and 3 are prepared as manuscripts in review at *Animal Migration* and to be submitted to the *Auk*, respectively. I am the sole author of Chapters 1 and 4.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above materials in my thesis. I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work, completed during my registration as a M.Sc. candidate at the University of Windsor.

II. DECLARATION OF PREVIOUS PUBLICATION

This thesis includes [1] original paper that has been previously submitted for publication in peer reviewed journals, as follows:

Thesis Chapter	Publication Title	Publication Status
<i>Chapter 2</i>	<i>Macdonald C.A., Fraser, K.C., Gilchrist, H.G., Kyser, T.K., Fox, J.W. and O.P. Love. 2012. Combining techniques to reveal patterns of migratory connectivity in a declining arctic-breeding passerine. Animal Migration.</i>	<i>Submitted</i>

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone's copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owners to include such materials in my thesis.

I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution.

ABSTRACT

Arctic-nesting birds are declining and at risk due to predicted ecological effects of climate change at high latitudes. Tracking the migration of these small migratory birds can provide insight into the factors driving their spatial and behavioural patterns, but is a challenge due to their small body size, long-distance migrations and remote breeding locations. We integrated spatial and behavioural information from multiple concurrent sources (banding, stable isotopes and geolocators) from the sexually dimorphic snow bunting (*Plectrophenax nivalis*) and found strong evidence for an east-west parallel migratory system in North America. Our results also suggest that observed wintering sex-segregation is driven by the improved cold tolerance of larger males, and by selection for early arrival of males to the breeding grounds. These results improve the abilities of population models to predict and respond to declining population trends, and identifies the different selective forces that may constraint individuals in their response to future environmental challenges.

ACKNOWLEDGEMENTS

Firstly, I would like to thank my advisor, Oliver Love, for giving me the freedom to explore my own research interests, for his unquestioning confidence in my abilities, and for providing me with endless support and encouragement both as a student, and in my ongoing career in wildlife conservation science. I thank Kevin Fraser for his willingness to teach, for giving me confidence in my methods and valuable perspective when interpreting my results. I also thank Grant Gilchrist for sharing his incredible enthusiasm, funding and logistical support as well as his wealth of experience and perspectives on the issues surrounding arctic birds and ecosystems in Canada.

I am extremely grateful to all the field crews at East Bay who have not only contributed to the collection of the data presented in this thesis, but also for teaching me about the arctic, helping to keep an eye out for polar bears, and for laughing and dancing around in the kitchen tent even at 2am. The Canadian Wildlife Service, the Nunavut Research Institute and Kenn Borek Air in Iqaluit have generously provided equipment and logistical support. I would also like to thank Kim Goodyear, for being my longstanding example of how to have fun while working hard in the field.

I thank Kurt Kyser for providing important technical equipment and advice, and for promoting detailed understanding and careful consideration of stable isotope methods. This thesis has also benefitted greatly by the comments from my advisory committee, Aaron Fisk and Daniel Heath. I thank Amie Black and April Vuletich for their logistical support and guidance. Thanks to all the members of the Canadian Snow Bunting Network for their dedicated efforts in supporting the ongoing research of temperate wintering

birds. Thanks also to my lab mates Sarah Baldo, Sarah Guindre-Parker, Chris Harris, Holly Hennin and Christine Madliger for continuing to set the bar high and for all the fun we have had over the past few years.

I would like to thank Mike Janssen for his thoughts and support from all over the world, throughout the entire duration of my degree. Your patience and courage continue to support and inspire me in all aspects of life.

Finally, I would like to thank my parents, John and Heather Macdonald, for always encouraging me to make my own decisions and for never being surprised when I tell them what I will be doing next. Knowing I have your constant support and encouragement has enabled me to do a lot of very intimidating things.

TABLE OF CONTENTS

I. DECLARATION OF CO-AUTHORSHIP	III
II. DECLARATION OF PREVIOUS PUBLICATION.....	III
ACKNOWLEDGEMENTS	VI
LIST OF TABLES	X
LIST OF FIGURES.....	XI
LIST OF ABBREVIATIONS/SYMBOLS	XIII
GLOSSARY	XIV
CHAPTER 1 - GENERAL INTRODUCTION	1
THE IMPORTANCE OF STUDYING ANIMAL MOVEMENT	1
MIGRATORY CONNECTIVITY	3
METHODS FOR TRACKING MOVEMENT	4
THE STATUS OF ARCTIC BIRDS IN CANADA	6
FILLING THE KNOWLEDGE GAP.....	10
FIGURES	11
CHAPTER 2 – COMBINING TECHNIQUES TO REVEAL PATTERNS OF MIGRATORY CONNECTIVITY IN A DECLINING ARCTIC BREEDING PASSERINE.....	17
INTRODUCTION	17
METHODS.....	20
RESULTS	24
DISCUSSION	27
CONCLUSIONS.....	31
FIGURES	33
CHAPTER 3 – FACTORS DRIVING PATTERNS OF GEOGRAPHIC SEX-SEGREGATION IN WINTERING SNOW BUNTINGS.....	37
INTRODUCTION	37
METHODS.....	42
RESULTS	46
DISCUSSION	50

CONCLUSIONS.....	55
FIGURES	59
TABLES	67
CHAPTER 4 - GENERAL DISCUSSION	68
CONCLUSION.....	71
REFERENCES	72
VITA AUCTORIS	81

LIST OF TABLES

Table 3.1 Summary of relative support for the cold tolerance, early arrival and social dominance hypotheses for driving geographic sex-segregation of wintering snow bunting populations in eastern North America.

LIST OF FIGURES

Figure 1.1 Geographic range of the greenish warbler and variation in song structure of populations around the Tibetan Plateau (from Irwin et al. 2001)

Figure 1.2 Theoretical examples of (a) strong and (b) weak patterns of migratory connectivity for a hypothetical migratory species across geographically distinct sub-ranges (from Webster et al. 2002)

Figure 1.3 Patterns of migratory connectivity in American redstarts (*Setophaga ruticilla*) in North America, estimated using stable isotope analysis of feathers collected at wintering sites (black dots) (from Martin et al. 2007)

Figure 1.4 Population trend data of arctic-breeding birds in Canada (from NABCI Canada 2012, The State of Canada's Birds)

Figure 1.5 Annual distribution of snow buntings in North America (from Montgomerie and Lyon 2011)

Figure 1.6 East Bay Island (Mitivik Island) research site. This island is part of the East Bay Migratory Bird Sanctuary located on Southampton Island, in Nunavut, Canada (from Mallory and Fontaine 2004)

Figure 2.1 Band encounters of snow buntings from (a) North American and (b) Greenland banding sites showing geographic linkages of individual between wintering (black), spring migration (green), breeding (red) and fall migration (orange) periods. Lines link encounter sites with original banding sites, but do not represent the actual path travelled by individuals recovered.

Figure 2.2 Annual distribution of snow buntings tracked with geolocators from East Bay Island between in 2010-2011 (n=6) and 2011-2012 (n=7) combined. Maps represent 90, 75 and 50% kernel density of combined daily location points of all 13 tracked individuals. Star = mean wintering location for each individual (i.e. mean of all daily point locations obtained for the wintering period).

Figure 2.3 Results of probability-based assignment tests used to assign stable-hydrogen isotope values claws to estimated wintering origin of snow buntings from a breeding location on East Bay Island.

Figure 2.4 Suggested continental patterns of migratory connectivity of North American wintering snow buntings revealed using band recoveries, stable- isotope analysis, citizen-science data and geolocators.

Figure 3.1 Mean body size and percent males of snow bunting populations compared with total winter HDD using regression analyses with $\alpha=0.05$. Body size increases linearly with decreasing winter temperatures both across (a) and within sexes (c; significant only in males). Percent males increases (second degree polynomial) with decreasing winter temperatures (b).

Figure 3.2 No relationship was found between predicted wintering site food accessibility ($PC1_{climate}$) and population mean fat score (sexes combined), illustrating that population fat scores do not increase at sites with limited predicted winter food accessibility.

Figure 3.3 Proportion of males and females (separated by age) banded with respect to predicted winter food accessibility metric $PC1_{climate}$.

Figure 3.4 Fall migration phenology of birds arriving to wintering grounds at Thunder Cape Bird Observatory, near Thunder Bay, Ontario, Canada (a). Standardized arrival dates represent annual fall migration (October 6-31). Mean arrival dates compared between groups using a two-tailed t-test with $\alpha=0.05$ (b).

Figure 3.5 Overwinter change in the proportion of males in relation to total winter snowfall (cm). Positive values for $m_{\Delta males}$ represent an overwinter increase and negative values represent an overwinter decrease in the proportion of males.

Figure 3.6 Female snow bunting fat scores do not vary significantly with the proportion of males banded in wintering populations in eastern North America.

Figure 3.7 Spring migration phenology of snow buntings banded during early (Rivière - au-Tonnerre, QC; a, b) and late spring stopovers (East Bay Island, NU; c, d). Mean arrival dates compared between groups using one-way ANOVA (Tukey-Kramer HSD) (b) and one-tailed t-test (d) with $\alpha=0.05$.

Figure 3.8 Spring migration behaviour of breeding snow buntings from East Bay Island, NU, measured using i) geolocators (a-c) and ii) spring banding data (d). Estimated means of (a) straight-line migration distance, (b) wintering departure date, (c) spring migration rate and (d) arrival date of breeding males and females were compared using one-tailed t-tests with $\alpha=0.05$.

LIST OF ABBREVIATIONS/SYMBOLS

AHY – After Hatching Year

ASY – After Second Year

BAS – British Antarctic Survey

BBO – Bird Banding Office

CBC – Christmas Bird Count

CSBN – Canadian Snow Bunting Network

HDD – Heating Degree Day

HY – Hatching Year

OIPC – Online Isotopes in Precipitation Calculator

PCA – Principle Components Analysis

SY – Second Year

GLOSSARY

After hatching year – a bird captured between breeding and December 31st, known to have hatched >1 full year prior to the date of capture.

After second year - a bird captured between January 1st and breeding, known to have hatched >1 full year prior to the date of capture.

Atlantic Canada – geographic region in eastern Canada comprised of the provinces of New Brunswick, Newfoundland, Prince Edward Island and Nova Scotia.

Band Encounter – the record of a recovered bird band, either through re-sighting or recapturing a live bird or, alternatively, finding a broken/lost band or a dead banded bird.

Band number – numeric code engraved on the ring (usually metal) carried by a bird on their tarsus.

Banding – the process of attaching a ring (usually metal) on a bird's tarsus which is engraved with a unique numeric code (i.e. band number) used for identifying re-sighted or recaptured individuals.

Bird Banding Office (BBO) – organization administering Canadian banding programs (e.g. issuing banding permits, distributing bands and storing banding records).

Breeding Bird Survey (BBS) - Annual survey along pre-defined routes to provide continent-wide estimates of changes to breeding bird populations in North America.

Christmas Bird Count (CBC) – annual census performed by volunteers between December 14 and January 5 (in Canada) to count and record the abundance of bird species within pre-defined “count circles”.

Differential Migration – pattern whereby some groups of individuals (ages or sexes) differ in their migration behaviour, distance or timing.

Fat reserves – fat stored by birds in order to survive periods of fasting or fuel periods of intense muscular endurance (i.e. migration)

Fat score – system used to record the fat reserves of birds based on a scale from 0 (=zero fat) to 7 (=very fat).

Geolocator – archival (non-transmitting) tracking device that measures and records light-levels with respect to time.

Hatching year – a bird captured between breeding and December 31st, known to have hatched <1 year prior to the date of capture.

Heating degree days (HDD) – for a given day, the number of Celsius degrees that the mean daily temperature is below 18°C. For example, if the mean daily temperature is above or equal to 18°C, then the number will be zero.

High Arctic – loose term used to refer to areas in the Arctic at high latitudes.

Long-distance migration – loosely applied term referring to the regular seasonal movement of individuals across thousands of kilometres or between >1 continent.

Low Arctic - loose term used to refer to areas in the Arctic at lower latitudes

Migratory Divide – imaginary geographic line whereby populations on each side migrate in different directions.

Moult/molt – regular intended replacement of feathers (usually annually, or bi-annually), not including the unexpected replacement of lost feathers.

m_{Δmales} – slope of statistically significant regression lines ($\alpha < 0.05$) of percent males versus winter ordinal date.

Non-breeding period – the portion of the annual cycle occurring between breeding periods. Include both wintering as well as spring and fall migration.

Passerine – refers to species from the largest order of birds (Passeriformes); also often referred to as the perching birds or songbirds.

PC1_{body size} – resulting variable from principle components analysis of wing chord (mm) and body mass (g).

PC1_{climate} – resulting variable from principle components analysis of total winter heating degree days, total winter snowfall (cm) and average winter snow depth (cm)

Second year - a bird captured between January 1st and breeding, known to have hatched <1 year prior to the date of capture.

Stopover – a geographical and temporal pause in migration; commonly used to acquire fuel or fat reserves for migration.

Wing chord – anatomical measurement of a birds wing representing the distance between the tip of the wrist (when bent at 90 degrees) to the tip of the longest primary flight feather.

Wintering – another term for used to refer to non-breeding.

CHAPTER 1 - GENERAL INTRODUCTION

THE IMPORTANCE OF STUDYING ANIMAL MOVEMENT

Determining the factors that drive the distribution and abundance of organisms is essential for effective conservation and management of free-living animal populations. Just as rates of dispersal, immigration or survival between breeding populations can influence meta-population dynamics (Hanski 1991), the level of interaction between different wintering and breeding populations across migration (migratory connectivity) has the potential to influence the dynamics of entire species (Martin et al. 2007). Regions occupied by migratory birds during various stages of their annual cycle are often separated by large geographic and temporal spans, and patterns of habitat occupancy, behavioural interactions or weather events can have significant consequences for the survival and reproduction of individuals during subsequent stages (e.g. Sillett and Holmes 2002, Norris et al. 2004). While small-bodied long distance migrants may be difficult to track, understanding these movement patterns can provide insight into their evolutionary history and are fundamental for the effective design and implementation of conservation efforts for migratory species (Martin et al. 2007).

Evolutionary Significance

Differences in distributional patterns and migratory behaviour have been shown to correspond with intra-specific variation in morphological or behavioural traits. For example, in their study on greenish warblers (*Phylloscopus trochiloides*) in Siberia, Irwin et al. (2000) found that variation in sexually selected traits (i.e. male song) around a

migration barrier (the Tibetan Plateau) caused reproductive isolation between eastern and western-migrating sub-forms, where the two come into contact in central Siberia (Fig. 1.1). Thus, migration behaviour and geographic barriers to migration can play an important role in speciation (Irwin and Irwin 2005).

Furthermore, because migrating species occupy highly disparate geographic areas and ecosystems throughout their annual migratory cycle, they may be subject to different selective pressures during each stage (i.e.: migration, breeding and wintering). For example, explanations of sexual size dimorphism in American redstarts (*Setophaga ruticilla*) (males larger than females) have suggested that energetic constraints on females during reproduction (i.e. incubating and parental care) select for smaller body size (Downhower 1976). However, further studies on American redstarts on the wintering grounds, where larger body size has been linked with an individual's ability to obtain territories in high quality wintering habitats, suggest that selection should favour large size in females (Marra 2000). Thus, examining selective forces throughout the full life cycle will provide a more complete explanation of sexual size dimorphism in this, and other migratory species.

Applied Significance

Identifying the mechanisms that drive migratory distributional or behavioural patterns can also provide insight into their influence on population dynamics through their potential consequences to subsequent life history stages. For example, Norris et al. (2004) found that wintering habitat quality in American redstarts had significant consequences

for subsequent reproductive success. Similarly, patterns of non-breeding habitat occupancy can also influence annual adult survival rates (e.g. Sillett and Holmes 2002). Thus, carry-over effects of migratory decisions and strategies can significantly impact populations, especially where they exhibit spatial sex- or age-segregation during the non-breeding period (e.g. Ketterson and Nolan 1976, Marra and Holmes 2001). Additionally, plasticity in migration behaviour is expected to influence a species' ability to adapt to climate change. For example, warming climates in many systems are now causing seasonal advances in food abundance (Visser and Both 2005). Species exhibiting constrained migratory phenology such as the wood thrush (*Hylocichla mustelina*) (Stanley et al. 2012), may be unable to adapt to these changes through similar advancement in their migration schedules, and may suffer population-wide consequences as the timing of movement becomes mismatched with the seasonal abundance of important food resources. Thus, identifying constraints in both the spatial and behavioural components of a species' annual distributional patterns will improve our ability to determine the mechanisms for declining population trends and effectively respond.

MIGRATORY CONNECTIVITY

Migratory connectivity is a concept used to consider the geographic relationships among individuals within a population across the breeding and non-breeding periods. Strong connectivity occurs when individuals from one breeding population also share a common wintering area, whereas common breeding individuals dispersed throughout the species wintering range indicates weak connectivity; Fig. 1.2). This concept is useful in applied

studies of migratory behaviour because it allows scientists to consider the health and status of a widespread species within smaller, biologically relevant geographic units, allowing for both the development of population response models to habitat loss or applied management actions (Webster and Marra 2005, Martin et al. 2007), as well as furthering our understanding of patterns of wildlife disease transmission (e.g. Iverson et al. 2011). Unfortunately, this type of detailed information is not available for many migratory species (Bowlin et al. 2010) largely due to an inability to effectively track individuals throughout the full annual cycle (Robinson et al. 2010).

METHODS FOR TRACKING MOVEMENT

Methods available to determine the migratory connectivity in small long-distance migrants include both direct and indirect techniques (e.g. Robinson et al. 2010). Large-scale tagging or banding efforts in small organisms including anadromous fishes and migratory songbirds have provided important insight into long-distance migratory movements (e.g. Robichaud and Rose 2004, Norris et al. 2006). However, recovery rates often remain low even among the most commonly marked species (Wassenaar and Hobson 2001, Boulet and Norris 2005). Additionally, it is often impossible to determine if capture locations represent true migration start or endpoints to evaluate the migratory connectivity of multiple populations. Nonetheless, banding is often accessible to large numbers of researchers and citizen scientists, and remains a fundamental and inexpensive method for tracking animals, especially when combined with other techniques (e.g. Norris et al. 2006, Ryder et al. 2011).

Other direct methods include the application of tracking tags, including satellite, radio-telemetry or acoustic tracking, which can pinpoint individuals to within <1m. However, high costs associated with accessing the data, short transmission distances required by receivers and often bulky size and weight of the units themselves have limited their utility for tracking small long-distance migrants and as such are more commonly used to track local movements of larger-bodied animals such as ungulates, elasmobranchs or waterfowl (Robinson et al. 2010). Fortunately, recent advances in the size and weight of light-level geolocation tracking tags (hereafter, geolocators) have allowed for the global tracking of even small passerines (Stutchbury et al. 2009, Bairlein et al. 2012).

Geolocators record light levels with reference to time and provide daily location estimates using the timing of sunset and sunrise as well as day length (longitude and latitude, respectively). Given limitations in their size for use on small birds, these archival devices do not contain transmitters, and therefore must be retrieved to download location data, often resulting in low sample sizes (n=3 in Bairlein et al. 2012, n=3.5 in Seavy et al. 2012, n=9 in Tøttrup et al. 2012). Despite these constraints, applications of this technology to philopatric populations have provided important insights into migration phenology and individual migration routes of small birds, which were previously impossible using conventional techniques (e.g. band recoveries or indirect methods).

Indirect methods of studying animal movement patterns involve the molecular structure (e.g. DNA, stable isotope ratios) of tissues (e.g. blood, feathers or claws) to assign individuals to a genetically or biochemically distinct region of origin. Stable-hydrogen isotope analysis of feathers and claws has been widely used to detect broad

patterns of migratory connectivity in small passerines (e.g. Hobson and Wassenaar 2008; Fraser et al. 2008; Bearhop et al. 2003). This technique exploits naturally occurring patterns of variation in stable-hydrogen isotope ratios from precipitation (Bowen et al. 2005a), which are integrated into animal tissues and can be used as a biological marker to determine the geographic origin of tissue synthesis (Hobson and Wassenaar 1997) and assign populations to regions of probable origin (e.g. Fig. 1.3, from Martin et al. 2007). Unlike band recoveries, this technique requires only a single capture of an individual to potentially determine its migratory origin, allowing for larger sample sizes of tracked individuals. However, greater uncertainty is associated with this technique since geographic assignment can be influenced by the relative abundance and inter-annual variation in hydrogen isotopes in precipitation (Royle and Rubenstein 2004, Van Wilgenburg et al. 2012). Ideally, researchers should integrate multiple tracking techniques to advance our understanding of animal migration (e.g. Mazerolle et al. 2005, Ryder et al. 2011).

THE STATUS OF ARCTIC BIRDS IN CANADA

Arctic-breeding birds represent a particularly poorly studied group of North American avifauna (NABCI Canada 2012). Low human population density combined with remote and challenging landscapes in the Arctic have resulted in poor coverage by annual surveys such as the Christmas Bird Count (CBC) or the Breeding Bird Survey (BBS). While funding resources are often directed towards species with high socio-economic value (i.e. harvested eider ducks, *Somateria spp.*) or immediate conservation concern (i.e. threatened Ivory Gull, *Pagophila eburnean*), many other arctic-nesting species are

thought to be experiencing widespread populations declines (e.g. shorebirds and landbirds, NABCI 2012) (Fig. 1.4). Unfortunately, very few breeding populations of these species are accessible for long-term monitoring or research into important demographic parameters, and most data collected to evaluate the health and status of these populations occurs along migration routes and on wintering grounds. Resulting trend estimates may therefore be imprecise given the influence of shifting distributions and migration behaviour (NABCI Canada 2012). This gap in our knowledge is a particular conservation concern for these species, considering projected expansion of natural resource development and broad-scale habitat changes predicted for high latitudes (Cox 2010, NACBI Canada 2012).

Snow Buntings

The snow bunting is a circumpolar arctic-breeding passerine that is thought to have experienced recent widespread population declines in North America (64% over 40 years, Butcher and Niven 2007). Nonetheless, the snow bunting is also a common and globally abundant species (est. 40 million adults, Birdlife International 2012), which can be frequently observed in large numbers (>1000 individuals) throughout their open grassland and agricultural wintering areas in the central latitudes of North America (Fig. 1.5). These large flocks are often accompanied by smaller numbers of other temperate wintering arctic-breeders (e.g. Lapland longspur *Calcarius lapponicus*, horned lark *Eremophila alpestris*). Snow buntings are the earliest arriving spring migrant to the arctic, with some individuals arriving at breeding latitudes in Greenland by early April (Meltote 1968) and at some High Arctic sites in Canada as early as mid-April (Black et

al. 2012). Additionally, the timing of spring migration is linked with the timing of snowmelt as individuals feed on emerging seeds and insects along the margins of snow-free areas (Montgomerie and Lyon 2011). Since snow buntings are relatively common, conspicuous throughout the annual cycle, accessible in large numbers in the winter and their annual migration behaviour is linked with climate they are ideal for serving as an important indicator species for monitoring ongoing changes in abundance of arctic avifauna and health of arctic ecosystems.

Research Opportunities for Snow Buntings

Banding Records

During the wintering period snow buntings can be captured and banded in high numbers (>200 birds/day or >6000/year at some sites) using baited ground in snow-covered areas. Since 1930, more than 53,000 snow bunting banding records have been collected in North America (Canadian Bird Banding Office, BBO). Recent increases in effort and the number of measurements collected by winter banding programs have led to an increased number of band encounter records (recaptured and recovered bands) and provided new insights into the timing of migration as well as migration routes and fattening rates (Canadian Snow Bunting Network, *unpubl. data*). Banding data has also revealed patterns of geographical and temporal sex-stratification of wintering and migrating populations in eastern North America. While readily available (provided by the Canadian BBO, free of cost), this data has never before been used to examine questions regarding snow bunting migration biology or distributional patterns.

East Bay Island, Nunavut

A philopatric breeding population of snow buntings at East Bay Island (64°01'N, 81°47'W), located within the East Bay migratory bird sanctuary, offers a particularly tractable opportunity to study migration behavior in this species. This 24ha island, located at the center of a long (40 km), shallow bay on the eastern shore of Southampton Island (Fig. 1.6), is dominated by granite rocks with numerous small, highly productive ephemeral ponds owing to the nitrogen input from a large colony (3000-8000 pairs/year) of breeding common eiders (*Somateria mollissima*) and king eiders (*S. spectabilis*). Spring migrant passerines are thought to pass through East Bay Island moving north during May and early June. Since 2007, more than 1,300 arctic passerines have been banded at this site during the spring migration period; including 830 snow buntings. Access to migratory arrival individuals to the island for stable-hydrogen isotope analysis on tissues (i.e. claws) has the potential to provide estimates of wintering locations following only a single capture. Additionally, breeding individuals show high philopatry to this site and high inter-annual return rates (25-45%; O. Love, *unpubl. data*), which is important for the retrieval of archival geolocators deployed on adult breeding birds. Combining these additional techniques (stable isotopes and geolocators) with banding data can therefore provide novel insight into patterns of migratory movement and non-breeding distribution, which would be otherwise unattainable for a large number of individuals.

FILLING THE KNOWLEDGE GAP

To effectively monitor and manage snow bunting populations, detailed knowledge of their annual distributional patterns is required. By applying the techniques outlined above, this thesis focuses on two aspects of snow bunting distributional patterns, 1) migratory connectivity and 2) geographic variation in sex ratios of wintering populations. By integrating spatial information from multiple concurrent sources (banding, stable isotopes and geolocators) our goals are to first compile spatial data from all available sources to describe continental patterns of migratory connectivity in North American snow bunting populations, in order to improve the strength of future population models designed to predict the response of populations to limiting factors occurring during multiple stages of the annual cycle. Secondly, we will integrate data from banding (morphometrics, capture dates), weather stations and geolocators to test longstanding hypotheses surrounding the patterns of geographic sex-segregation to identify how selective forces acting independently on males and females may limit the ability of individuals to respond to future environmental challenges. Taken together, this research aims to provide novel and important insight into snow bunting migration and distributional patterns, which will guide future conservation efforts for arctic-breeding passerines.

FIGURES

Figure 1.1 Geographic range of the greenish warbler and variation in song structure of populations around the Tibetan Plateau. Hatching represents region where eastern and western sub-forms do not hybridize (from Irwin et al. 2001).

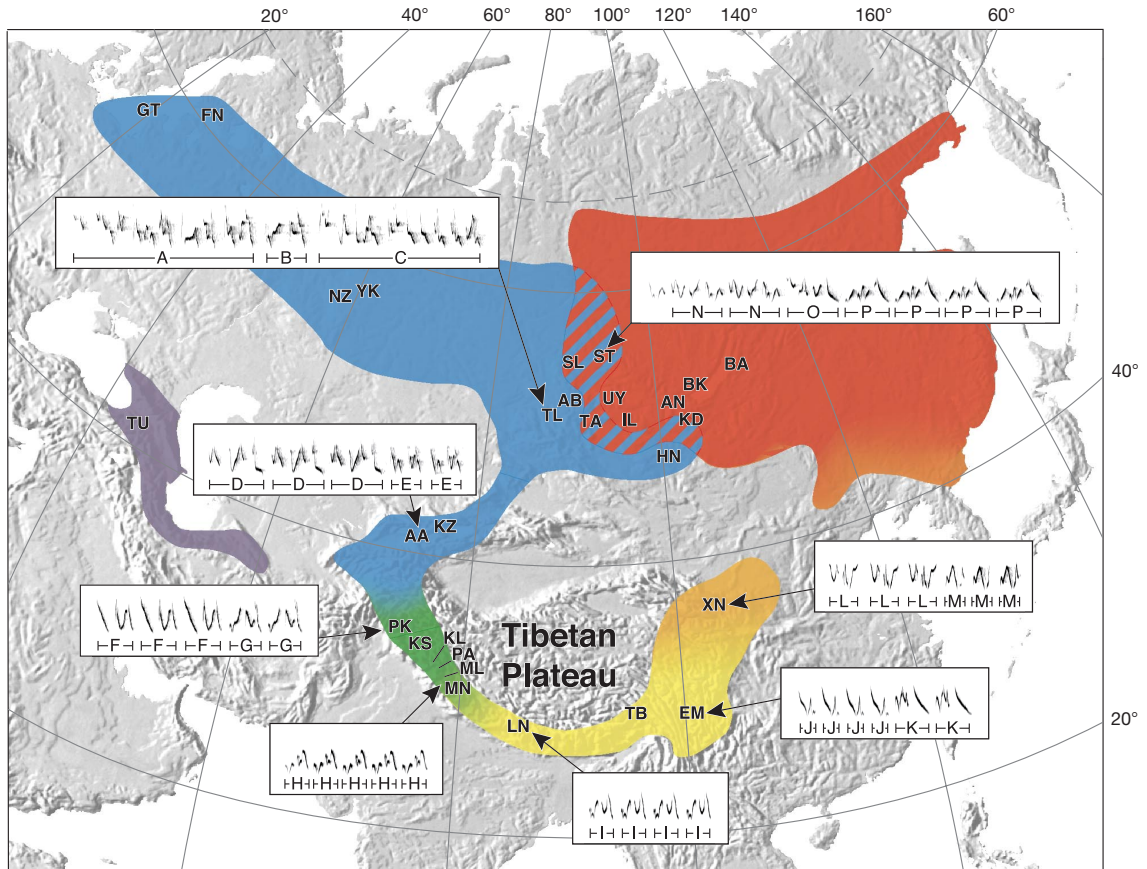


Figure 1.2 Theoretical examples of (a) strong and (b) weak patterns of migratory connectivity for a hypothetical migratory species across geographically distinct subranges (from Webster et al. 2002).

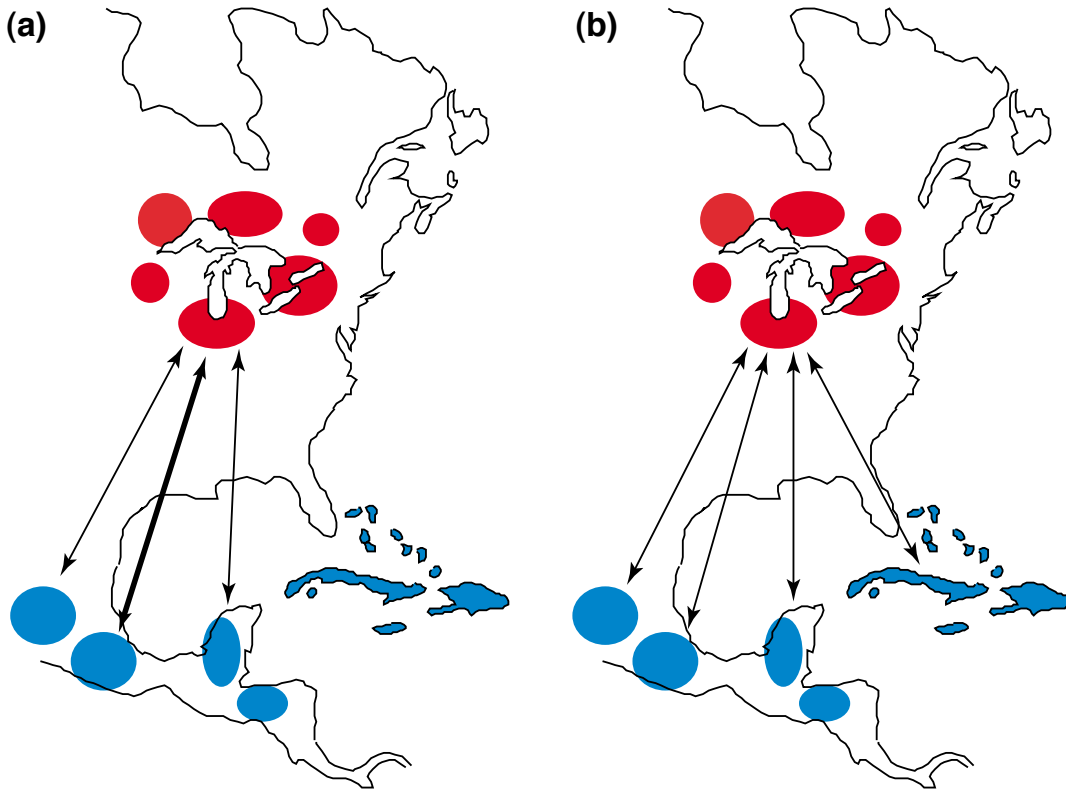


Figure 1.3 Patterns of migratory connectivity in American redstarts (*Setophaga ruticilla*) in North America, estimated using stable isotope analysis of feathers collected at wintering sites (black dots) (from Martin et al. 2007).

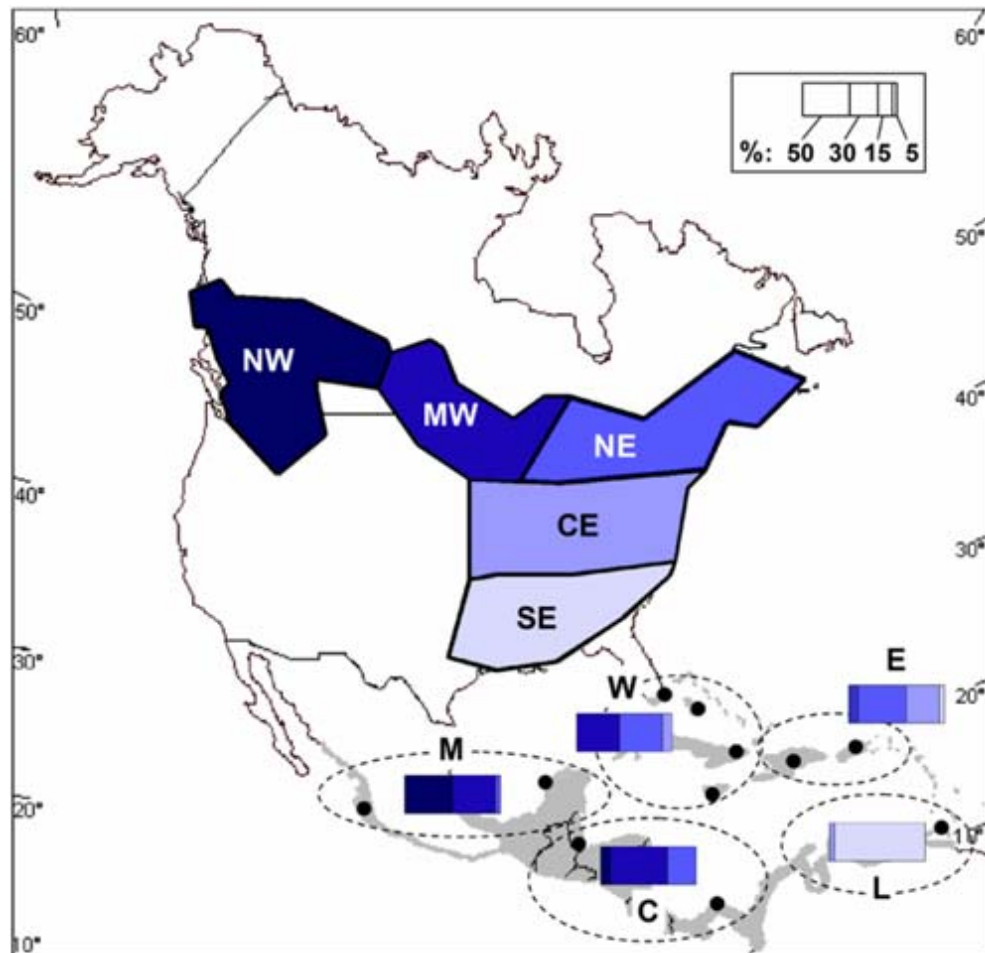


Figure 1.4 Population trend data of arctic-breeding birds in Canada (from NABCI Canada 2012, The State of Canada's Birds).

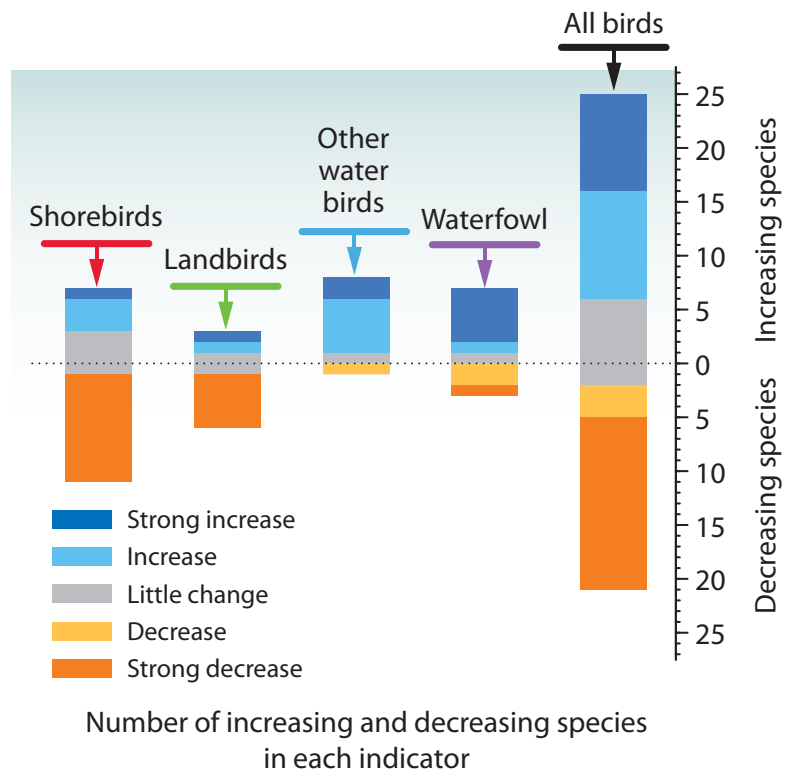
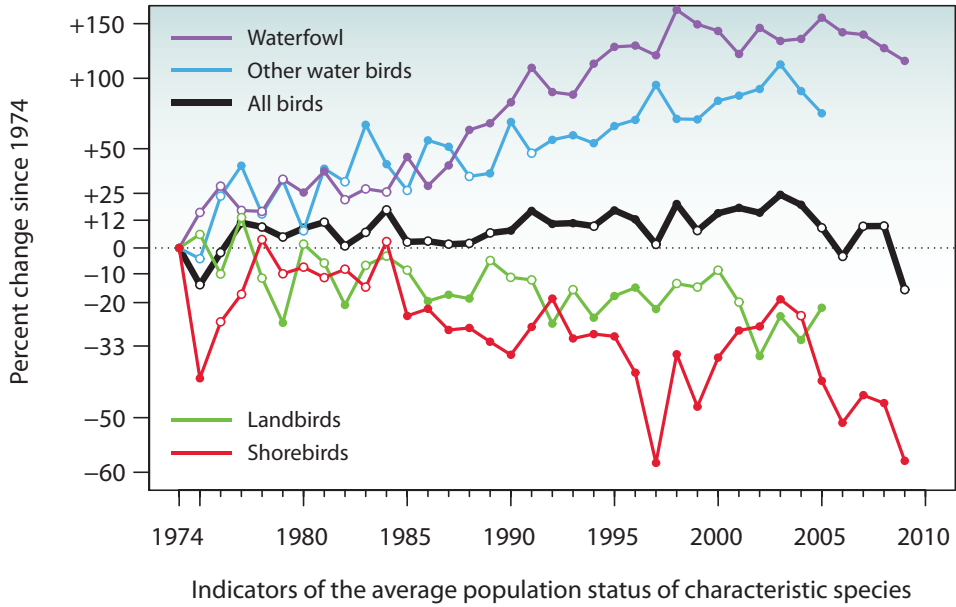
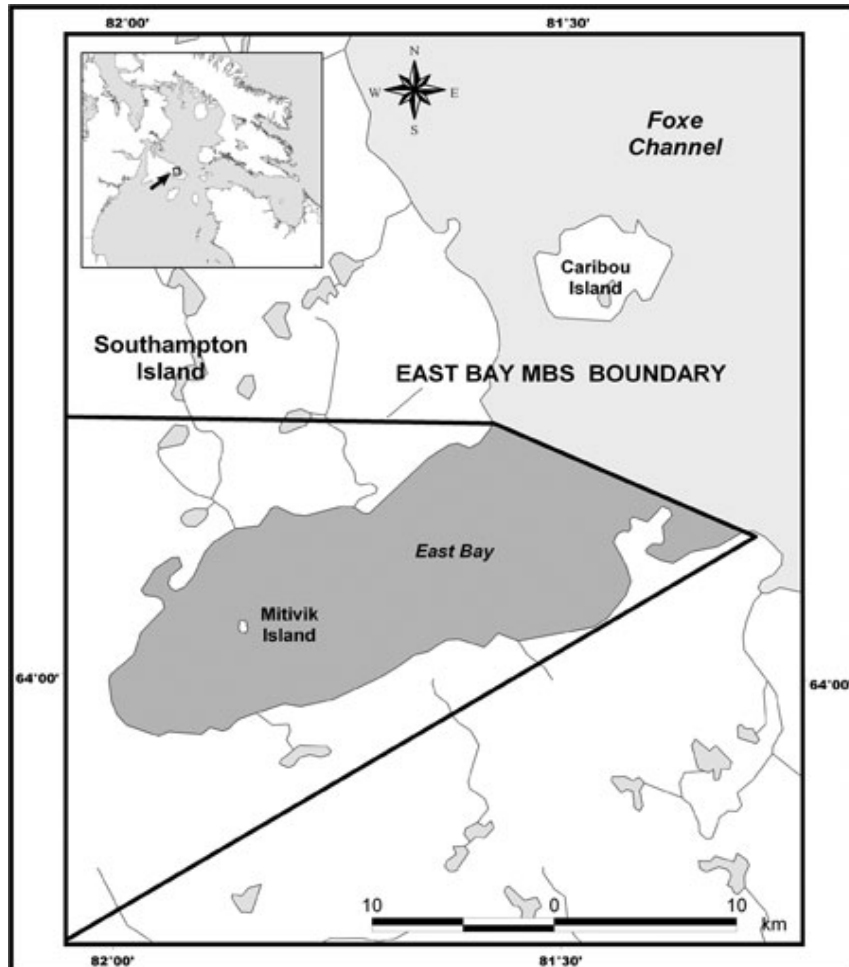


Figure 1.5 Annual distribution of snow buntings in North America (from Montgomerie and Lyon 2011).



Figure 1.6 East Bay Island (Mitivik Island) research site. This island is part of the East Bay Migratory Bird Sanctuary located on Southampton Island, in Nunavut, Canada (from Mallory and Fontaine 2004)



CHAPTER 2 – COMBINING TECHNIQUES TO REVEAL PATTERNS OF MIGRATORY CONNECTIVITY IN A DECLINING ARCTIC BREEDING PASSERINE

INTRODUCTION

Determining links between populations of migratory animals across the various stages of the annual cycle is necessary for understanding population dynamics and for effective wildlife conservation and management (Martin et al. 2007). Long-distance migratory songbirds pose particular challenges as breeding and non-breeding areas may be thousands of kilometers apart, migratory connectivity (Webster et al. 2002) has been determined for few species, and small body size has limited direct tracking using devices such as satellite transmitters (Faaborg et al 2010). Arctic-breeding migratory passerines may be the most difficult to study because their polar breeding distribution represents a challenging environment that is relatively inaccessible to researchers. Additionally, winter movements may be unpredictable and cover great distances (Grubb and Greenwald 1982, Brown and Long 2007) making it difficult to define population boundaries or monitor population trends. As a result, migratory connectivity of many arctic-breeding passerines has never been assessed. These challenges have led to a poor understanding of population trends, and the spatiotemporal extent of factors limiting the health and status of arctic-breeding passerine populations. The latter is of particular concern considering broad-scale habitat changes predicted for high latitudes (Cox 2010).

The snow bunting (*Plectrophenax nivalis*) is a small (<50g) circumpolar arctic-breeding passerine, which, in North America, overwinters throughout southern Canada and the northern United States. While a common and globally abundant species (est. 40 million adults) (Birdlife International 2012), recent evidence from a long-term North

American winter census (the Christmas Bird Count - CBC) suggests that this species has undergone a range-wide population decline of 64% over 40 years (Butcher and Niven 2007). However, while broad-scale citizen science driven surveys (i.e., CBC) and regional observations (i.e., databases such as eBird) can provide valuable information for detecting general changes in the distribution and abundance of many passerines, we remain limited in our understanding of how limiting factors are spatially linked with population trends across more than one life history or migratory stage.

Like many other passerines, banding effort in snow buntings has had a recovery rate of less than 0.5% (estimated <2% across all passerines) (Wassenaar and Hobson 2001). However, with >70,000 snow buntings banded since 1930, these data are still useful for suggesting broad movement patterns since recoveries span the breeding and non-breeding (wintering) stages. Stable-hydrogen isotope analysis has been widely applied to supplement banding data in studies of migratory connectivity in small passerines (Hobson and Wassenaar 2008). This indirect tracking technique exploits naturally occurring patterns of variation in stable-hydrogen isotope ratios from precipitation (Bowen et al. 2005a), which are integrated into animal tissues and can be used as a biological marker to determine the geographic origin of tissue synthesis (Hobson and Wassenaar 1997). This method has become fundamental to understanding range-wide movement patterns, especially where band recoveries are sparse.

Additionally, the recent application of archival light-level loggers (geolocators) to track small passerines has provided novel insight into the specific migratory routes and timing for tagged individuals (Stutchbury et al 2009, Ryder et al. 2011, Tøttrup et al. 2011, Stanley et al. 2012). However, while these archival units provide a direct tracking

method, they require the recapture of tagged individuals for data retrieval, and recent studies have resulted in relatively low sample sizes of tracked individuals (Stutchbury et al 2009, Ryder et al. 2011, Tøttrup et al. 2011, Bairlein et al. 2012). Ideally, studies should take advantage of integrating multiple techniques to examine the movement patterns and the spatiotemporal distribution of rarely encountered arctic species to identify the possible mechanisms of population decline.

In this study we combine multiple tracking techniques to reveal patterns of migratory connectivity of snow bunting populations across the North American wintering range. Historically, banding effort and reported recoveries have been restricted to the eastern part of this range; yet provide no geographical linkages to individuals breeding in the Canadian arctic. Here, we used stable-hydrogen isotope analysis of claws and light-level geolocators to test whether this eastern band recovery bias is due to the presence of an alternative western migration flyway (parallel migration) or a lack of eastern-derived band recoveries in the west. Additionally, data derived from this study can be used to better understand spatial and temporal vulnerabilities faced by different populations in light of current and future anthropogenic influences (i.e., climate change, human activity). This research is the first to follow an arctic-breeding migratory passerine throughout its entire North American migratory cycle, and can provide a model for understanding movement and its influence on population dynamics for this, and other arctic-breeding passerines.

METHODS

Field methods

We captured birds at Mitivik Island (East Bay Island) in the East Bay Migratory Bird Sanctuary, Nunavut, Canada (64°01'N, 81°47'W) (Fig. 1.6). In 2010 and 2011 we collected a 2mm sample from the left hind claw tip during the spring migration and breeding arrival period (May 25-June 15) from both stopover migrants and individuals that remained to breed, and stored samples in paper envelopes until laboratory analysis. We deployed ninety light-level geolocators (British Antarctic Survey, BAS; model MK12S in 2010 and MK20AS in 2011) on post-breeding adults (29 males and 29 females) and fledged juveniles (19 males and 13 females) during the post-breeding period between July 15-30th using a leg-loop harness technique (Rappole and Tipton 1991) and 2.5mm Teflon ribbon (Stutchbury et al. 2009). Total mass of the attachment (1.1g, geocator plus harness) represented $3.01\% \pm 0.25$ (SD, n=310) and $3.23\% \pm 0.32$ (SD, n=213) of male and female body weight, respectively, for birds captured at East Bay Island during the breeding season (May-July); this represents <5% recommended limit of body weight (Caccamise and Hedin 1985). Geolocators were retrieved in June 2011 and 2012.

Mark-recapture data

We obtained mark-recapture data from the Canadian Bird Banding Office and the Copenhagen Bird Ringing Centre for snow buntings either banded or recaptured in North America from 1930 to present (n = 347). We filtered data to remove encounters that

represented movements of less than 200km (following Reichlin et al. 2009). We grouped banding and encounter locations to represent the annual stages of breeding (June-July), fall migration (September-October), wintering (November-March) and spring migration (April-May) (following Lyngs 2003), and then filtered data again to remove records where banding and encounters occurred within the same stage. We mapped a total of 69 band encounters (26 originating from Greenland and 43 from North America; Fig. 2.1a and b, respectively), 14 of which represent connections between breeding and migration, 6 between breeding and winter, and 49 between winter and migration. Maps were generated using ArcMap (version 10.0, ESRI).

Light data analysis

Geolocators measure ambient light levels every 60s and record maximum light intensity for every 120s interval. Transitions were visually displayed and ranked for confidence using the software TransEdit (version 19.0, BAS). Transitions indicating sunset and sunrise events were defined using a light threshold of 5, which is an arbitrary unit representing light intensity on a scale from 1-64. Because transition times are ultimately used to calculate local noon and midnight times, arbitrary threshold values do not affect location estimates, but rather can be chosen to limit the number of false transitions when editing light data. We determined the average sun elevation that corresponded with this light threshold at the breeding site for each geocator model (-4.15 for MK12S and -4.02 for MK20AS) using the software LocatorAid (BAS) for a portion of the pre-migration period where clear sunrise and sunset periods were observed (July 15-30th). Because light-levels can be obscured by cloudy weather or shading events on the light sensor, and

such errors can be converted to errors in estimates of longitude and latitude, we included only locations calculated from high-confidence transitions (i.e.: confidence ≥ 6 ; see Stutchbury et al. 2009: supplementary material). We excluded latitude estimates for 15 days surrounding the fall and spring equinoxes (Sept. 7-Oct. 7 and March 5-April 5) because day length is equal at all latitudes during these periods, and relied on longitude estimates during this period to determine directional changes.

We present the mean wintering locations for all 13 individuals successfully tracked (Fig. 2.2). To calculate the wintering locations, we considered all daily locations with high confidence rankings for the period between the end of fall migration to the start of spring migration for each bird. Longitude estimates are unaffected by the equinoxes and therefore provide a robust method for determining position throughout the year. We defined a stop in movement as the date at which the directional change in longitude consistent with migration is followed by a stationary period (10-day mean longitude has a standard deviation < 1). We defined start of movement as directional change in > 5 degrees longitude over a 24-hour period resulting in a new location that is > 2 degrees different from the previous 10-day mean. We present annual range estimates for the East Bay Island breeding population during the fall migration, wintering and spring migration periods (Fig. 2.2). For this analysis we combined daily point locations from all 13 tracked individuals (both high and low confidence) and weighted the contribution of each point by its confidence ranking (see above). Maps were generated using the spatial analyst tool in program ArcMap (v.10.0, ESRI) by estimating the 50, 75 and 90% maximum kernel densities of point locations (following Ryder et al. 2011 and Bächler et al. 2010).

Stable-hydrogen isotope analysis

We washed claws to remove particles and lipids using a 2:1 chloroform:methanol solution. We standardized lab analysis of claw material using a precise mass (0.14-0.18mg) trimmed from the claw tip and placed these sub-samples in silver capsules. The samples were placed in a drying oven at 100°C for 24h to remove surface moisture, which can contribute greater than 7% of the measured signal in keratin (Bowen et al. 2005b). Capsules were then crushed, loaded into a zero blank autosampler connected to a Finnigan TC/EA reduction furnace (1450°C) and then passed online to a Finnigan MAT Delta Plus XL isotope ratio mass spectrometer. To account for the effects of exchangeable organic hydrogen we used a comparative equilibration technique (Wassenaar and Hobson 2003) using calibrated keratin standards; THS (-38‰), EC2 (-54‰), Spectrum KP (-122‰) and EC1 (-197‰). Standards were weighed to the same target weight, allowed to equilibrate with local atmosphere alongside samples for at least 72 hours before analysis, and analyzed concurrently. After analysis we adjusted our raw sample values based upon known values of keratin standards (Wassenaar and Hobson 2003). All values are reported in permil (‰), relative to the standard Vienna standard mean ocean water (VSMOW) according to the formula: $\delta^2\text{H} = \left[\left(\frac{^2\text{H}/^1\text{H}_{\text{sample}}}{^2\text{H}/^1\text{H}_{\text{standard}}} \right) - 1 \right] \times 1000$. Because claw tissue reflects a period of continuous growth along their length (2-5 months within 1-2mm, or 3-7weeks within 0.08 to 0.22mg of the claw tip) (Bearhop et al 2003, Fraser et al 2008), claws sampled at arrival are expected to represent winter growth. Replicate samples were repeatable to 6‰ ±4 (SD; n=9). We used likelihood-based assignment tests to assign the $\delta^2\text{H}$ values of arrival claws to one of four wintering regions (mountains - M, northwest - NW, northeast - NE and southeast - SE) selected

following known patterns of isotopic variation in precipitation (Bowen et al 2005a) and encompassing the known wintering range of snow buntings (Montgomerie and Lyon 2011) (Fig. 2.3). We obtained mean annual precipitation $\delta^2\text{H}$ values for 30-50 randomly selected locations within each of the 4 regions using the Online Isotopes in Precipitation Calculator (OIPC) (Bowen 2012) and extracted mean \pm SD for each region and applied a discrimination factor of -25‰ (Bowen et al. 2005a) to account for the fractionation of $\delta^2\text{H}$ between keratin and precipitation. We also calculated the relative abundance of snow buntings in each of the four wintering regions using observational data from the eBird reference dataset (eBird 2012). Arrival claws were assigned a probability of origin based on a standard likelihood function incorporating mean and standard deviation of $\delta^2\text{H}$ values, and relative abundance for each region (Royle and Rubenstein 2004, Norris et al. 2004). We only considered individuals with resulting assignment probabilities of 50% or higher.

RESULTS

Band Recovery Data

Of the 71,277 snow buntings banded in North America and Greenland between 1930 and 2010, 69 were encountered at a distance of >200km from their original banding site and during a different stage from the original banding encounter (CWS BBO, *unpubl. data*) (Fig. 2.1). Of these, 67 recoveries show linkages between wintering sites in eastern North America (from 41°45' to 52°03'N and 98°45' to -53°25'W), migration routes throughout the Gulf of St. Lawrence, Newfoundland and Labrador, and breeding sites in western

Greenland (Fig. 2.1). In total 95.6% (66 of 69) of band recoveries span regions east of -86°W degrees and none link to breeding populations in the Canadian Arctic.

Geolocators

Migration Timing

Individuals departed from the breeding grounds at East Bay between Sept. 23-Oct. 6 in 2010 and from Oct. 8-10 in 2011. Fall migration spanned 25 ± 5 (SD, n=6) days in 2010; and 18 ± 5 (SD, n=7) days in 2011. Arrival to the wintering grounds was between Oct. 20-28 in 2010; and Oct. 22-Nov. 4 in 2011. The wintering period was similar between years and spanned an average of 192 ± 7 days (SD, n=11), representing 50-54% of the annual cycle. Spring migration was initiated between Apr. 28-May 8 in 2011 and Apr. 28-May 12 in 2012, representing a period of 40 ± 4 (mean \pm SD, n=4) days in 2011 and 31 ± 5 (mean \pm SD, n=7) days in 2012 between wintering departure and arrival to the breeding site.

Annual Distribution

All thirteen birds migrated to the western part of the species North American wintering range. Mean wintering locations for individuals spanned 5.5° latitude and 11.3° longitude, including one U.S. state (North Dakota) and three Canadian provinces (Manitoba, Saskatchewan and Alberta) (Fig. 2.2b). Batteries in four of the thirteen geolocators failed at various dates (December 4, 2010, and January 25, May 19 and May 29, 2011) prior to retrieval at the breeding site (June 2011). Thus, for two individuals

tracked between 2010-2011 (#92378 and 92440), mean wintering locations were calculated using daily point locations for only a partial wintering period and did not contribute point locations for spring migration. Estimated population distribution of 90% kernel densities for fall migration period represented a span of almost 20° latitude (Fig. 2.2a) over a period of 22±6 days, with individuals initiating fall migration as early as Sept. 23 (2010) and completing no later than Nov. 4 (2011). Distribution of 90% kernel density for spring migration represented a narrower latitudinal span of ~7° (Fig. 2.2b) over an average of 34±6 days.

Stable-hydrogen Isotope Analysis

Our results indicate that snow buntings breeding and migrating through East Bay Island preferentially overwinter in the Great Plains and prairies of southern Canada and the northern United States (Fig. 2.3). A total of 67 individuals were assigned to wintering regions: 87% to NW, 12% to NE, 1% to SE and 0% to M,. Incorporating relative abundance for each of the four regions (NW=61.6%, M=12.6%, NE=16.1% and SE=9.7%) changed 68% of original assignment tests that did not account for relative abundance. Overall, the assignment of 87% of individuals (58 of 67) to the NW region was higher than expected if wintering origin had been estimated using only relative abundance (i.e.: not incorporating isotope assignments) ($\chi^2 = 26.11$, $df = 3$, $P < 0.0001$) There was no sex-bias in the assignment probability among individuals to each wintering region, with males representing 50% of assignments in NE (4 of 8), 50% in NW (29 of 58) and the only individual in SE (1 of 1). For the stopover migrants, 100% (23 of 23) of

were assigned to NW, whereas 80% (35 of 44) of breeders were assigned to NW, 18% (8 of 44) to NE and 2% (1 of 44) to SE.

DISCUSSION

Using a novel combination of tracking methods and citizen science data, our results reveal that snow buntings breeding in the Canadian Low Arctic have a high degree of migratory connectivity with the western North American wintering range. Furthermore, 95.6% of band recovery data linked the eastern wintering populations with migration routes and breeding sites in eastern North America and Greenland east of -86°W . This range-wide pattern of connectivity suggests a parallel migration pattern with Hudson's Bay acting as a migratory divide between eastern and western wintering populations. This result is surprising, considering that another broadly distributed arctic-breeding passerine showed relatively weak connectivity, with tracked individuals sharing a broad wintering region in equatorial Africa (Bairlein et al. 2012). We also found that the wintering period makes up more than half the annual migratory cycle and individuals may spend more time at spring migratory stopover sites than necessary to refuel energy reserves for migration (Newton 2008), suggesting some additional function of these sites.

Band Recoveries

The route that eastern wintering populations take along the Gulf of St. Lawrence to breeding sites in western Greenland represents a much greater annual migration distance when compared to a more direct line path (adding up to 2000 km per year when travelling

between southern Ontario and Greenland). These data suggest that either large areas of boreal forest in Ontario and Quebec act as a barrier to migration, that this species relies on southern coastal habitats during spring migration, or both. Snow buntings follow the advancing snowmelt during spring migration, migrating along the margin of snow-free areas where they forage on emerging berries, seeds and insects (Montgomerie and Lyon 2011). Coastal areas, with a more moderate annual climate regime, may provide some of the most northern snow-free areas in relation to Greenland breeding sites when compared to a more direct continental route (through interior Quebec), or an alternative coastal route (migrating north along the eastern shores of Hudson Bay and the Ungava Peninsula). These coastal routes may allow snow buntings, especially early-arriving males (Montgomerie and Lyon 2011), to migrate northwards earlier than expected based on snow cover in interior regions.

Geolocators

We used geolocators to track snow buntings through their annual migration between the Canadian Low-Arctic and their wintering grounds in southwestern Canada and the northwestern United States. Location estimates from geolocators suggest that snow buntings may arrive on their wintering grounds by late October (precluding winter snow cover), completing migration no later than November 4th. Birds then remain at these sites for more than 50% of the annual cycle. Observational citizen science reports from eBird (eBird 2012) indicate that snow buntings are rarely sighted north of the wintering range boundary (see Montgomerie and Lyon 2011) later than October 30th, suggesting birds that breed across the eastern Low-Arctic have completed migration by this date. While

anticipated effects of climate change predict that many species will experience a northward range expansion caused by increasing temperatures, the snow bunting may be limited in its ability to respond because of the distribution of the boreal forest as a physical barrier. Additionally, due to the challenges of studying multiple breeding populations in the arctic, the wintering range is where human populations may have the greatest capacity for monitoring and management of arctic passerines. Thus, these range limitations combined with the large proportion of the annual cycle spent on the wintering grounds indicates that wintering habitat may be of particular importance when searching for potential mechanisms of population decline, or considering future management actions.

Data from geolocators suggest that spring migration in snow buntings takes on average 12 days longer to complete than fall migration. This result is unique amongst songbirds, as spring migration is generally shorter (Stutchbury et al. 2009, Bairlein et al. 2012, Newton 2008). However, while fall migration is shorter in total duration, it occurs over a much larger geographic area compared to distribution during spring migration. This concentration over a much smaller area during the spring migration period indicates that snow buntings use a more restricted geographic area for migratory stopover in the spring, suggesting the presence of important resources or favorable climatic conditions in these areas. Alternatively, because snow buntings are one of the earliest spring migrants to arrive at arctic latitudes, they constitute an important part of the diet for early arriving predators such as peregrine falcons (*Falco peregrinus*), before many terrestrial mammals or other avian prey species are available (Alastair Franke *unpubl. data*). Thus, these spring migration stopovers may serve as “muster” points where snow buntings form large

flocks to forage sufficiently while remaining vigilant against potential predators during migration (Beauchamp 2008). Future geolocator analysis or deployment from other breeding populations could reveal additional important migratory stopover sites, patterns of sex-specific migration strategies, or individual plasticity in timing and route selection for migration (Stanley et al. 2012).

Stable-hydrogen Isotope Analysis

We assessed the proportion of individuals assigned to each of four wintering regions using $\delta^2\text{H}$ values of claws collected during the migration and arrival period of individuals to an established breeding site in the Canadian low arctic. Given the estimated length of the wintering and spring migration periods using geolocator data (approx. 6 months and 1 month, respectively), and assuming the widest range of claw growth rates reported in claw turnover studies (Bearhop et al. 2003, Fraser et al. 2008), we estimate that the standardized claw samples analyzed in our study reflect integration of $\delta^2\text{H}$ within a period of 1-7 months and, thus, represent $\delta^2\text{H}$ values of the wintering area. Our study shows that a large proportion (87%) of individuals from a breeding and migration stopover site in the eastern Canadian low arctic over-wintered in the Great Plains and Prairie regions of western central North America.

Furthermore, assignments of claws from stable-isotope analyses provided similar geographic estimates as direct tracking methods (geolocators, band recoveries).

Although a greater degree of uncertainty is associated with indirect tracking methods (Faaborg et al. 2010) to estimate *individual* origin, stable isotope analysis allows us to

incorporate origin estimates for a greater number of individuals compared to direct tracking methods alone. Thus, assignment of $\delta^2\text{H}$ values to wintering regions allows for *population* level estimates of origin, which can be easily obtained over a single season of sampling. The claw samples analyzed from individuals returning with geolocators generally confirmed the utility of this assignment technique in snow buntings since claw $\delta^2\text{H}$ values from wintering regions matched mean wintering locations (for 3 of 4 individuals tracked). As such, stable isotope analysis could be used to supplement data from direct-tracking methods of small birds by providing a secondary estimate of population origin when the sample size of returning tagged individuals is low.

Data collected by citizen scientists is proving increasingly important for assessing the population health of migratory species (Hurlbert and Liang 2012) and was useful for incorporating a measure of abundance in our assignment tests that was not available by any other means. Incorporating relative abundance changed 68.4% of assignments when compared to tests based on equal abundance. This effect is high compared to other studies (i.e.: 5.9%) (Norris et al. 2004), which illustrates the importance of incorporating abundance into assignment tests for species such as snow buntings with high inter-region variation in abundance.

CONCLUSIONS

This study provides novel insights into the migratory patterns of snow bunting populations throughout their North American breeding and wintering range and represents the first time a breeding population has been tracked throughout the annual

cycle. Our results provide strong evidence of east-west patterns of migratory connectivity and migration distance. Evidence that some populations may exist entirely within the boundaries of one or two countries suggests that North American nations, especially Canada, hold a significant global responsibility for the successful conservation and management of this species. By integrating spatial information from multiple concurrent sources, researchers can improve the strength of future population models that attempt to predict the response of populations to limiting factors occurring during portions of the annual cycle for the effective conservation and management of migratory species (Martin et al. 2007). Polar and high altitude environments are currently experiencing some of the most profound impacts of climate change (IPCC 2007), affecting the quality of breeding habitat available for snow buntings. As forecasted impacts of climate change continue to affect these areas, the ability to detect the mechanistic drivers of population change in breeding populations using more accessible wintering populations could provide management opportunities if snow bunting populations continue to decline across North America in the future.

FIGURES

Figure 2.1 Band encounters of snow buntings from (a) North American and (b) Greenland banding sites showing geographic linkages of individual between wintering (black), spring migration (green), breeding (red) and fall migration (orange) periods. Lines link encounter sites with original banding sites, but do not represent the actual path travelled by individuals recovered.

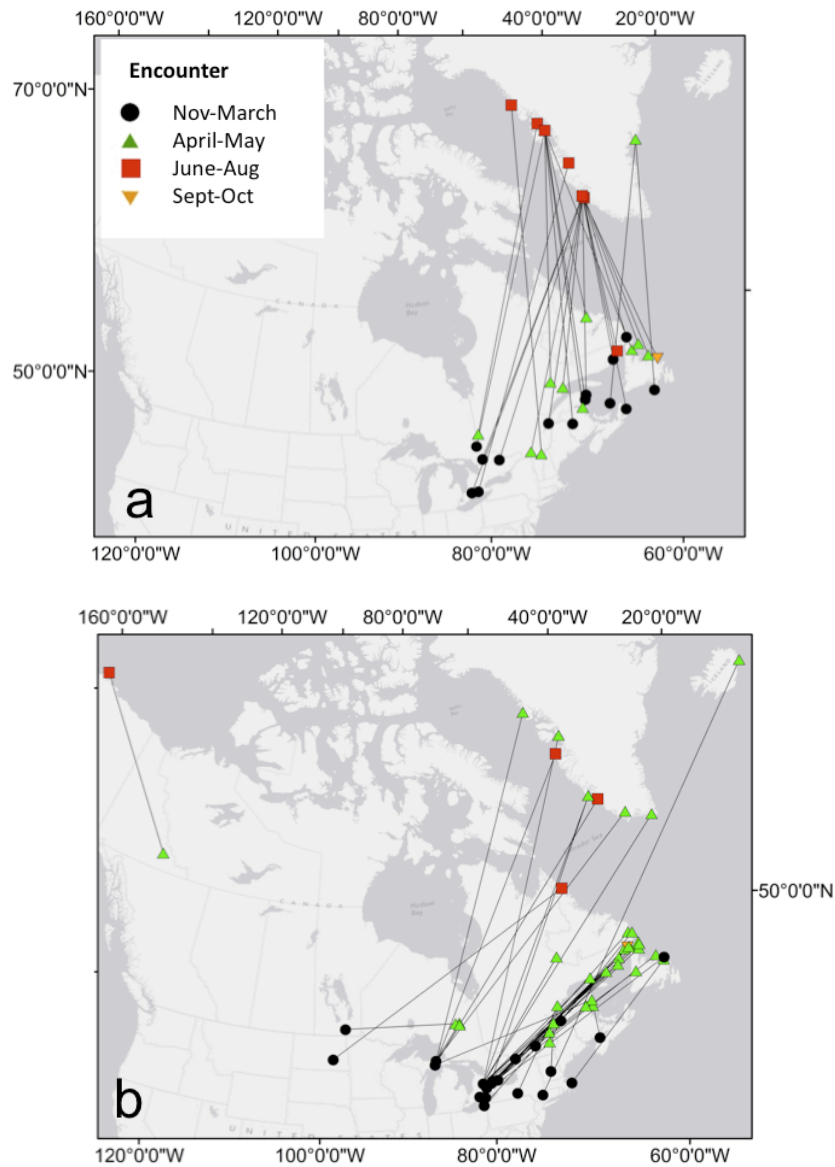


Figure 2.2 Annual distribution of snow buntings tracked with geolocators from East Bay Island between in 2010-2011 (n=6) and 2011-2012 (n=7) combined. Maps represent 90, 75 and 50% kernel density of combined daily location points of all 13 tracked individuals. Star = mean wintering location for each individual (i.e. mean of all daily point locations obtained for the wintering period).

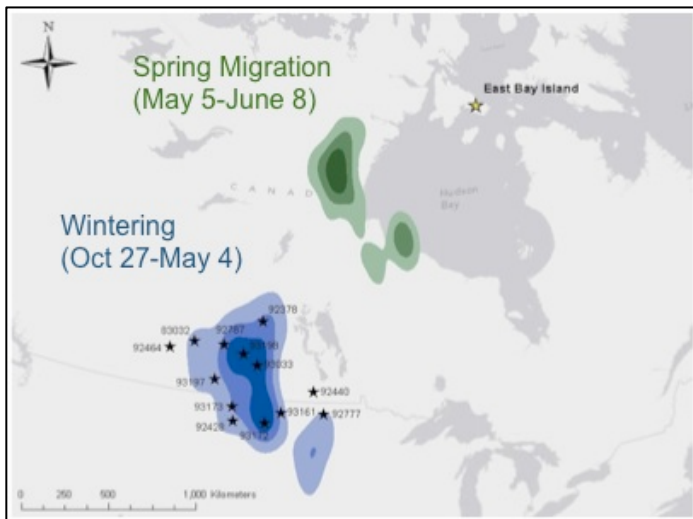
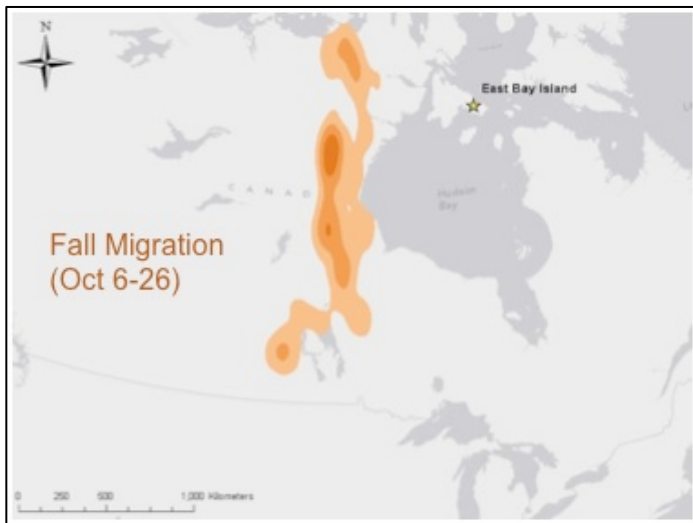


Figure 2.3 Results of probability-based assignment tests used to assign stable-hydrogen isotope values claws to estimated wintering origin of snow buntings from a breeding location on East Bay Island.

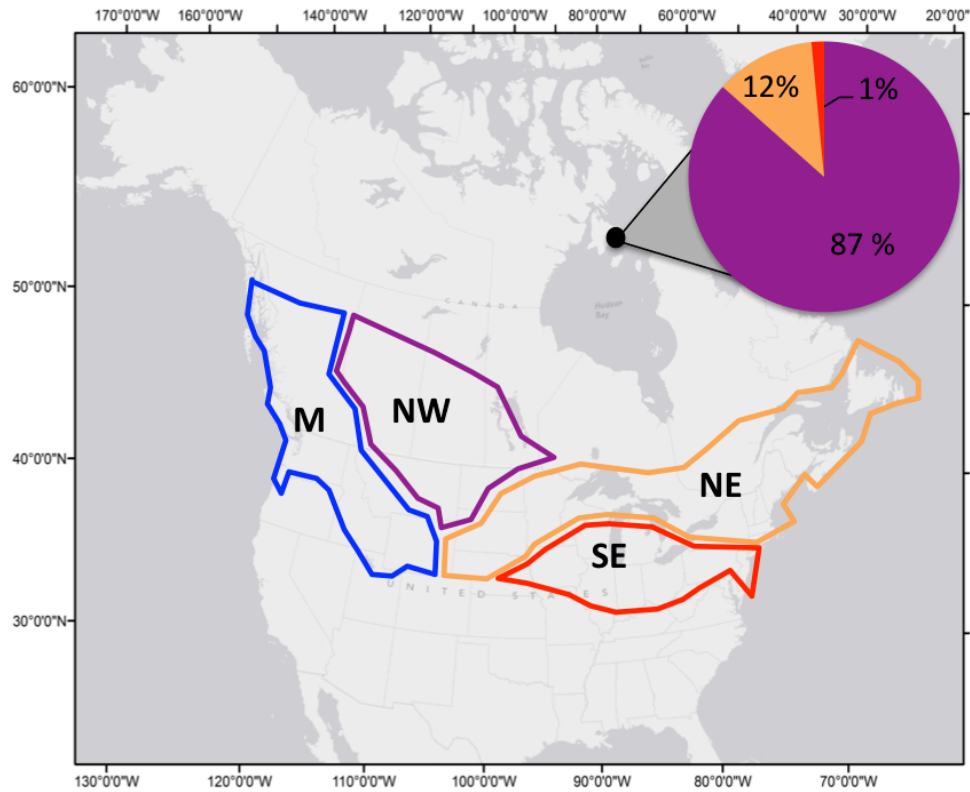
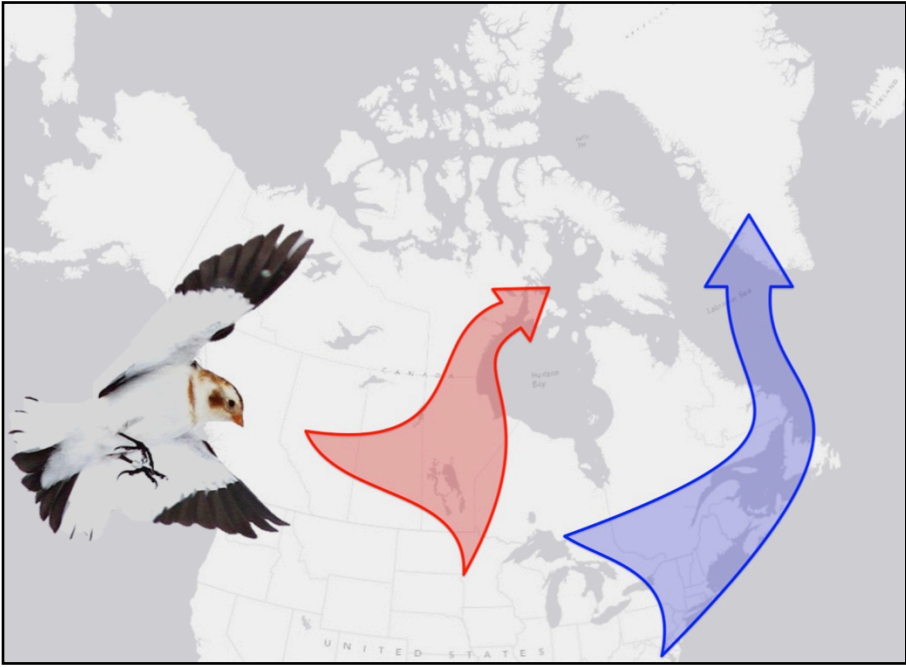


Figure 2.4 Suggested continental patterns of migratory connectivity of North American wintering snow buntings revealed using band recoveries, stable- isotope analysis, citizen-science data and geolocators.



CHAPTER 3 – FACTORS DRIVING PATTERNS OF GEOGRAPHIC SEX-SEGREGATION IN WINTERING SNOW BUNTINGS

INTRODUCTION

Geographic patterns of sex segregation during the non-breeding period are a widespread phenomenon that exists across multiple migratory taxa (Stewart 1997, Marra 2000, Phillips et al. 2004). These patterns appear especially prevalent in species showing sexual size dimorphism or sexual variation in life history strategies (e.g. Myers 1981, Bai and Schmidt 2012). Examining the mechanisms that drive this segregation is valuable for understanding the evolution of migratory strategies since these various strategies are expected to impose sex-specific selective pressures. Sex segregation often corresponds with variation in wintering habitat quality (Marra et al. 1998, Holberton and Able 2000) and has important consequences for survival, both within a season and for subsequent seasons (i.e.: carry-over effects; Norris et al 2004).

Several longstanding hypotheses have been proposed to explain geographic sex-segregation (e.g. Myers 1981, Ketterson and Nolan 1983) and include: 1) *body size hypothesis*, whereby the larger sex (usually older males) winter in colder areas with greater snow cover since body mass positively influences basal metabolic rate as well as fasting endurance (Scholander 1950, Kendeigh 1969, Ketterson and King 1977); 2) *social dominance hypothesis*, whereby the dominant individuals (often males or older birds) exclude subordinates (often females or younger birds) from preferred wintering habitats (e.g. Gauthreaux 1978); and 3) *arrival time hypothesis*, whereby the territorial sex (often males) gain reproductive benefits from early arrival to the breeding grounds and therefore attempt to overwinter closer to the breeding grounds (Ketterson and Nolan 1976, Cristol

et al. 1999). These hypotheses need not be mutually exclusive and observed distributional patterns may be the result of multiple interacting forces (Ketterson and Nolan 1979).

The snow bunting (*Plectrophenax nivalis*) is a temperate-wintering migratory passerine common to open coastal and agricultural habitats of the central latitudes of North America. Banding data from the eastern North American wintering range demonstrates that geographic sex-stratification occurs with some populations consisting of >95% males across the entire wintering period (November-March). Snow buntings are sexually dimorphic in plumage and body size, with males averaging larger than females in both structural size and mass (Lyon and Montgomerie 2011). This species also exhibits sexual variation in spring migration phenology with males arriving to the arctic-breeding regions prior to females (Lyon and Montgomerie 2011). As such, this species appears ideal for field-testing hypotheses of geographic patterns of sex segregation. Moreover, while a globally abundant species (est. 48 million adults; BirdLife International 2012), recent evidence from annual Christmas Bird Count surveys suggests continental declines in North American snow bunting populations (64% over 40 years; Butcher and Niven 2007). This declining trend, combined with risks associated with forecasted climate change, demonstrate the need to identify the factors limiting distribution and influencing population dynamics of this poorly studied species.

The goal of this study was to test the three main sex segregation hypotheses to explain the patterns of sex-specific spatial distribution commonly reported in wintering snow bunting populations. To examine these questions, we used metrics of body size from historic and current banding data from an eastern North American wintering population, and combined these with data on local weather as well as data on migratory

phenology via 1) capturing birds at arrival through migratory stopover and breeding sites, and 2) using geolocation technology to track annual migratory location and timing of individuals from a breeding population in the Canadian Low-Arctic.

Body Size Hypothesis

Bergmann's rule states that larger body sizes are associated with colder parts of a species' range since body mass directly drives variation in basal metabolic rate (Scholander 1950, Daan et al. 1989). This body mass, metabolic-rate relationship therefore suggests that sexual segregation during the non-breeding winter period is the result of variation in body size caused by sexual size-dimorphism. In support of this hypothesis, Ketterson and Nolan (1979) found that climate had a greater influence than latitude (i.e. distance to breeding sites) on sex ratios of Dark-eyed Junco (*Junco h. hyemalis*) populations wintering in eastern North America, with larger males wintering in colder climates. Thus, we would expect that if cold tolerance drives the geographic variation in sex ratios among wintering snow bunting populations, we expect 1) birds captured at banding sites with colder winter temperatures would have larger mean body size than those captured at warmer sites, and 2) this relationship should be found both within *and* across sexes (Table 3.1).

Social Dominance Hypothesis

Behavioural studies on wintering snow buntings have indicated that larger, more experienced males may have an advantage foraging in large flocks, and that subordinate

and inexperienced females will either delay feeding, or forage in smaller flocks, to avoid this competition (Smith and Metcalfe 1997a). Moreover, energy reserves were found to increase in habitats with poor food availability (in this case, colder temperature and more wind and snow associated with high altitudes) attributed to increased starvation risk in these habitats (Smith and Metcalfe 1997b). Therefore, if geographic variation in sex ratios is driven by social dominance interactions, and larger males exclude subordinate females from preferred habitats, we would predict that 1) in contrast to predictions for Bergmann's rule, larger and more dominant older males should be less common in sites with limited resource availability (i.e., colder temperatures and greater snow cover) whereas fat reserves should be higher in these more ephemeral feeding environments (Table 3.1). We would also expect that 2) fat reserves would be higher in areas with colder temperatures and more snow cover. Furthermore, we predict that 3) males would arrive on wintering grounds ahead of females, or 4) if females arrive first, the number of females banded would decrease at "good quality" sites and increase at "poor quality" sites across the winter banding period as subordinate females should be gradually excluded by dominant males from preferred habitats (Table 3.1). Finally, because birds often store fat to buffer against starvation in regions with unpredictable food availability, we predict that 5) female body fat reserves would be lower in male-biased populations indicating males preferentially occupy more reliable feeding environments (Table 3.1).

Arrival Time Hypothesis

Patterns of spring protandry (males arrive to breeding grounds ahead of females) are common in migratory taxa (reviewed by Morbey and Ydenberg 2001) and are particularly well known among many short and long-distance migratory birds (Francis and Cooke 1986) including snow buntings (Montgomerie and Lyon 2011). Benefits of early arrival for males include improved access to high quality breeding territories and potential for multiple successful broods within the same breeding season; ultimately increasing reproductive success (Newton 2008). Previous studies on snow buntings have indicated that males can arrive at breeding latitudes more than 3 weeks earlier than females (Meltofte 1968, Montgomerie and Lyon 2011). If selection for earlier arrival of males to breeding sites drives the geographic variation of wintering male and female snow buntings, we would predict that: 1) males arrive before females at migratory stopover sites both early and late in migration. Furthermore, constraints on timing and speed of migration require males to winter closer to breeding sites in order to achieve earlier arrival, thus, we predict that 2) males and females fly at the same speed and depart at the same time for spring migration, and 3) migration distances between breeding and wintering sites of individually tracked males should be shorter than in females (Table 3.1).

METHODS

Body Size and Social Dominance Hypotheses

We obtained historical bird banding data (Band number, sex, age, banding location, date) from the Canadian Bird Banding Office (BBO) for 1975-2012. Additional body size metrics (body mass, wing chord and fat score) were collected by bird banders participating in the Canadian Snow Bunting Network (<http://web2.uwindsor.ca/biology/olove/CSBN>) from 2009 onwards. In both cases, birds were trapped using baited ground traps in open habitats (coastal and agricultural areas) commonly used by wintering snow buntings. Sex was determined using Pyle (1997) and aged according to Hussell (*unpubl. data*). We measured mass to the nearest 0.1 g and unflattened wing chord to 1 mm. Body fat reserves were scored on a scale from 0-7 according to Kaiser (1993).

Wintering period was defined for populations within central eastern North America as November 1-March 15, modified from Lyngs 2003 (Nov-March) based on 1) the departure of birds from winter banding areas before March 15th, 2) reported pre-migration behavioural changes beginning in mid-March (Vincent and Bédard 1976), and 3) arrival to migratory stopover sites before the end of March (Fig. 3.7) among populations within the eastern migratory sub-population (Fig. 2.4). We filtered BBO data to remove any records from outside this period. We observed no change in sex ratios across the winter. For 53 of 69 site-year combinations the daily percent of males banded showed no significant correlation with ordinal date ($\alpha=0.05$) and as such, we used annual sex-ratios representing the total number of birds banded at each site between November 1 and March 15 each year.

Historical weather data for the wintering period was obtained from the Environment Canada Weather Office online (www.weatheroffice.gc.ca) using the weather station closest to each banding site (12.75 ± 0.78 km, mean \pm SE, range = 3.17-30.25 km). We extracted daily *total snow* (i.e. snowfall) (cm) and *total heating degree days* (HDD), as well as monthly *snow on ground* (i.e. snow depth) (cm) for each site. Total winter HDD is defined as [$18^{\circ}\text{C} - (\text{mean daily temperature})$] summed for every day across the defined wintering period. Weather data was only collected at sites where ≥ 50 birds were banded/site/year as sites with < 50 birds banded annually were excluded from further analyses to prevent erroneous results caused by low sample sizes.

Snow buntings are a ground foraging species that feeds on various weed and grass seeds (including spilled corn) throughout the winter (Lyon and Montgomerie 2011). Snow depth has been shown to decrease the abundance of temperate wintering, granivorous birds (Best et al. 1998). Since snow cover limits access to these food resources and because the probability of precipitation falling as snow or becoming ice increases with colder winter temperatures, we used climate-driven access to food as a proxy for wintering habitat quality, where lower winter temperatures (higher total winter HDD) and greater snow cover (total winter snowfall and average winter snow depth) represent poor quality habitats for snow buntings.

Previous studies have found dominance interactions to be affected by age as well as size (Smith and Metcalfe 1997a, 1997c). Therefore, for predictions relating to the dominance interactions hypothesis, we chose to examine populations by age in addition to sex. To simplify age classifications for the wintering period, we merged the two commonly used age categories 1) for birds less than one year old (i.e.: hatching-year or

“HY” and second year or “SY” representing those banded from hatching until December 31st and those banded from January 1st and onwards, respectively), hereafter simply “second-year” or “SY”, and 2) for birds aged greater than one year old (i.e.: after hatching year or “AHY” and after second year or “ASY” representing those banded from breeding to December 31st and from January 1st and onwards, respectively), hereafter, simply “after second-year” or “ASY”.

To test whether males arrival to wintering grounds occurs prior to females, we used fall migration banding data collected at Thunder Cape Bird Observatory (48°15'N 88°55'W) near Thunder Bay, Ontario, Canada, in years when ≥ 50 snow buntings were banded (1999, 2002, 2003 and 2010). This was the only fall banding site where more than 50 birds have been banded annually. We used a standardized arrival date, where day 0 represented the first day a snow bunting was banded each fall and compared the phenology of arriving males and females (separated by age).

Arrival Time Hypothesis

We collected banding data near Rivière-au-Tonnerre, Quebec (50°16'N 64°47'W) (n=2110 birds) during early spring migration (March 28-April 28, 2012) and at East Bay Island (n=501 birds) during late spring migration (May 25-June 15 in 2008, 2009 and 2011) to compare spring migration phenology of individuals (by age and sex). We used a standardized arrival date for the multi-annual East Bay data, where day 0 each year was the first day of banding each year. Migration phenology results are presented as cumulative total number of individuals banded for each site/year (Fig. 3.7 a and c).

We also used light-level geolocators (hereafter, geolocators) to compare migration behaviour of males and females, controlling for breeding site. Geolocators were deployed in 2010 and 2011 on post-breeding individuals using a breeding population at East Bay Island in Nunavut, Canada (64°01'N, 81°47'W). We used a leg-loop harness technique (Rappole and Tipton 1991) and 2.5mm Teflon ribbon (Stutchbury et al. 2009). Total mass of the attachment (1.1g, geocator plus harness) represented 3.01%±0.25 (SD, n=310) and 3.23%±0.32 (SD, n=213) of male and female body weight, respectively, for birds captured at East Bay Island during the breeding season (May-July); this represents <5% recommended limit of body weight (Caccamise and Hedin 1985). We retrieved 6 units in June 2011 (4 males, 2 females) and 7 units in June 2012 (3 males, 4 females).

We downloaded, decompressed and visually ranked quality of light-level data using BASTrak software (British Antarctic Survey, version 19.0). Because light-levels can be obscured by cloudy weather or shading events on the light sensor, and such errors can be converted to errors in estimates of longitude and latitude, we included only locations calculated from high-confidence transitions (i.e.: confidence ≥ 6 ; see Stutchbury et al. 2009, supplementary material). We excluded latitude estimates for 15 days surrounding the fall and spring equinoxes (Sept. 7-Oct. 7, and March 5-April 5) because day length is equal at all latitudes during these periods, and relied on longitude estimates during this period to determine directional changes. We used daily point location estimates with high confidence transition rankings to calculate mean wintering site for each individual, which was then used to determine 1) one way, straight-line migration distance from breeding site. We used directional changes to determine 2) date of departure from wintering sites and then also calculated 3) spring migration rates of

individual males and females by dividing one way migration distance by the number of days between winter departure date and date of recovery at East Bay Island. Two geolocators retrieved in 2011 (both from males) experienced battery failure prior to departure from the wintering grounds. Thus, for these two males, the mean wintering locations were calculated using a reduced number of daily point locations and spring migration rate could not be determined.

RESULTS

Body Size Hypothesis

Analysis of winter banding data indicates that male snow buntings are on average 4.2g heavier than females ($t=1.96$, $p<0.0001$) (mass: $37.8\pm 2.5\text{g}$ and $33.5\pm 2.3\text{g}$, mean \pm SD, $n=5479$ and $n=2295$, respectively) and have an average 6.6mm longer wings ($t=1.96$, $p<0.0001$) (wing chord: $108.4\pm 3.0\text{mm}$ and 101.8 ± 2.8 , mean \pm SD, $n=5575$ and $n=2397$, respectively). To examine the relationship between mean body size for a wintering population (banded birds/site/year) and cold tolerance, we first performed a principle components analysis to reduce two metrics of body size (mass and wing chord) into one simplified variable ($\text{PC1}_{\text{body size}}$) (sexes combined). Second, we performed a linear regression comparing the resulting $\text{PC1}_{\text{body size}}$ with the total winter HDD (Fig. 3.1a) over the defined wintering period for each site where morphometric and weather data were available.

Both the mean $\text{PC1}_{\text{body size}}$ and the proportion of males increased with total winter HDD for populations banded each site/year combinations ($r^2=0.52$, $p<0.01$, $n=12$;

$r^2=0.36$, $p<0.0001$, $n=69$; Fig. 3.1 a, b, respectively). However, since the proportion of males was higher in sites with higher total winter HDD (Fig. 3.1 b) and given the size dimorphism, we performed linear regressions on each sex independently (Fig. 1c). Male $PC1_{\text{body size}}$ increased significantly with total winter HDD ($r^2=0.34$, $p<0.05$; Fig. 3.1 c) and we also found a positive, but non-significant relationship among females ($r^2=0.22$, $p=0.149$; Fig. 3.1 c).

Social Dominance Hypothesis

We performed a principle components analysis (PCA) to reduce three climate variables that reduce food accessibility for ground foraging species (total winter HDD, total winter snowfall and average winter snow depth) into one simplified variable for food accessibility as a proxy for wintering habitat quality ($PC1_{\text{climate}}$). We then compared $PC1_{\text{climate}}$ with the mean fat score and the percent of each sex and age category banded for each wintering population (sexes combined) using a second-degree polynomial regression, because fat score and percent males are not continuous variables (i.e.: cannot increase indefinitely). Fat score was not related with reduced access to food ($r^2=0.29$, $p=0.2753$; Fig. 3.2). The proportion of males banded increased with decreasing food accessibility in older but not younger males ($r^2=0.30$, $p<0.005$, $r^2=0.07$, $p=0.135$ for ASY and SY males, respectively; Fig. 3.3), whereas the proportion females decreased ($r^2=0.21$, $p<0.005$, $r^2=0.42$, $p<0.0001$ for ASY and SY females, respectively; Fig. 3.3).

We performed an analysis of covariance (ANCOVA) on arrival date with age, sex and age*sex interaction as the dependent variables ($\alpha=0.05$) and found that sex was the only significant predictor of arrival date ($F_{3,611}=3.79$, $p=0.0029$). Based on this analysis,

we then performed a two-tailed t-test ($\alpha=0.05$) and found that females arrived 1.1 ± 0.4 days earlier than males ($t=2.51$, $df=602$, $p=0.0062$).

Across all wintering populations, only 16 of 69 showed significant trends in percent males banded vs. wintering ordinal date, indicating that winter sex ratios do not appear to change significantly over the wintering period. To test whether increasing proportions of males occurred at sites with predicted high food accessibility, we tested for a relationship between the slope of these regressions ($m_{\Delta\text{males}}$ = overwinter change in percent males) and total winter snowfall using a ANOVA with $\alpha=0.05$. We used total winter snowfall rather than $PC1_{\text{climate}}$ since one contributing variable (average winter snow depth) to $PC1_{\text{climate}}$ was only available for 5 of the 16 sites and total winter snowfall corresponds positively with $PC1_{\text{climate}}$. There was no relationship between the overwinter change in the proportion of males and total winter snowfall, indicating that snow cover (as a proxy for habitat quality) does not appear to significantly contribute to the overwinter change in the proportion of males banded ($F_{1,11}=0.5387$, $p=0.1116$; Fig. 3.5).

Finally, we used a second-degree polynomial regression to determine if females in male biased populations had lower fat scores than those at female-biased sites, where low fat scores indicate more reliable food availability. We found no relationship between female fat scores and the percent males banded across sampled wintering populations ($r^2=0.26$, $p=0.1447$) (Fig. 3.6).

Arrival Time Hypothesis

As for analysis of fall migration phenology, we performed an ANCOVA on arrival date with age, sex and age*sex interaction as the dependent variables for each of the two spring migration banding sites ($\alpha=0.05$). All predictors were significant contributors to variation in arrival date ($F_{3,2106}=224.57$, $p<0.0001$) at Rivière-au-Tonnerre. We therefore performed a one-way ANOVA (Tukey-Kramer HSD) for the Rivière-au-Tonnerre site comparing the means of each age-sex combination ($\alpha=0.05$), and found that ASY males arrived 6.9 ± 0.4 days (mean \pm SE) before SY males, 10 ± 0.05 days before SY females and 10.9 ± 0.5 days before ASY females ($p<0.0001$ for each comparison; Fig. 3.7 b). Second year males also arrived significantly earlier than both ASY and SY females ($p<0.0001$ for both; Fig. 3.7 b). There was no significant difference in arrival times between ASY and SY females ($p=0.4031$). At East Bay Island, only sex contributed significantly to variation in arrival date ($F_{3,445}=5.28$, $p=0.0014$) with males arriving 1.3 ± 0.5 days earlier than females ($t=2.625$, $df=499$, $p=0.0002$; Fig. 3.7 d).

Daily point location estimates from geolocators were used to calculate 1) mean wintering locations and 2) spring migration rates for each tracked individual. Total migration time was defined as the number of days between departure from wintering grounds and date captured at the breeding site, including days spent at stopover sites. Migration distance was calculated as the distance between the mean wintering location and the known breeding site (East Bay Island). Because of small sample sizes (males $n=7$; females $n=6$), we were unable to examine the effect of age on migration rate estimated from geolocators data. Therefore, we compared migration distance, departure date and spring migration rate of males and females using one-tailed t-tests. Our results

indicate that males migrate 170 ± 82 km (mean \pm SD) less than females ($t=2.076$, $df=11$, $p<0.05$) (Fig. 3.8 a) although standardized departure date and spring migration rates did not differ between sexes ($t=0.4206$, $df=9$, $p=0.3419$; Figure 3.8 b, and $t=0.7818$, $df=8$, $p=0.2284$; Fig. 3.8 c, respectively).

DISCUSSION

Based on our predictions, results from our analysis of geolocator, banding and weather data provide support for body size and arrival time hypotheses, but not social dominance, as mechanisms explaining the geographic variation in sex-ratios of wintering snow buntings in eastern North America (Table 3.1). We used geolocators to determine timing of spring migration, migration distance and spring migration rates for 13 individual snow buntings from a breeding population in Nunavut, Canada, and compare these results with the North American banding data set. Larger body size is associated with colder wintering locations, suggesting that cold tolerance plays a role in the geographic patterns of sex-ratios observed at wintering banding sites in eastern North America. Snow buntings show constrained migration flight speeds and timing of departure from the wintering grounds. Thus, males winter closer to the breeding site in order to achieve early arrival. The consequences of wintering in colder, more northern locations may be a contributing factor to sexual size dimorphism in snow buntings. This study highlights the importance of examining selective forces throughout the full life cycle to test longstanding evolutionary hypotheses and to consider sex-specific constraints and their impact on population dynamics as a potential mechanism of population decline. This

study represents the first time migration data from direct tracking methods (geolocators) were used to test these longstanding hypotheses in an arctic-breeding passerine.

Body Size Hypothesis

Body size among wintering populations of snow buntings increased with decreasing winter temperatures (i.e., increasing total winter HDD) providing support for the cold tolerance hypothesis (Table 3.1). Given the larger body size of males, this suggests that climatic conditions influence the geographic patterns of sex-stratification observed in wintering snow buntings. When considering each sex independently, relationships between $PC1_{\text{bodysize}}$ and total winter HDD are weaker and non-significant in females, possibly owing to a possible outlier population of females with a high $PC1_{\text{bodysize}}$ score (Fig. 3.1 c). Although this could be the result of low sample size ($n=4$), this sample represents individuals from the eastern-most winter banding population ($46^{\circ}13'N$, $66^{\circ}53'W$) where males ($n=95$) have the highest $PC1_{\text{bodysize}}$ score of any population and yet this site does not experience correspondingly cold winter temperatures. Additional unmeasured climate variables, such as wind speed, which are known to contribute to reduced cold tolerance (Swanson and Liknes 2006) may account for the proportionately larger body size of individuals banded at this site. Furthermore, several snow bunting band recoveries from wintering populations in Atlantic Canada were recovered in eastern Greenland (Fig. 2.1). Since geographic patterns of variation in morphometric traits are common in widespread species (e.g. Irwin et al. 2009), individuals banded at this site may in fact be more representative of a completely different migratory sub-population experiencing stronger selection for larger body size.

If geographic patterns of sex-ratios in wintering populations are driven by cold tolerance, we would expect that inter-annual mean body size would vary to inter-annual variation in climate conditions within a population. Unfortunately, measurements of body size were only available from more recently established banding sites (2009-2012). As such, we encourage all banders to record morphometric variables so that as these data continue to be collected across multiple years, such that we can begin to examine population responses to inter-annual variation in winter climate. These types of questions will also improve our understanding of the evolution of inter and intra-specific variation in migratory strategies.

Dominance Interactions Hypothesis

We found no support for social dominance interactions driving the observed geographic sex-ratio patterns using multiple datasets (Table 3.1). Although inter-individual dominance interactions likely occur, the result of these interactions may influence the intra-flock distribution of individuals rather than across a broad geographic area. Smith and Metcalfe (1997) found that larger experienced (ASY) males were more commonly found foraging in the spatial centre of a flock than females and younger (SY) males which may account for the overall male-bias in our winter-banded snow buntings. Of the 53,297 records of snow buntings banded in North America between 1930 and 2010, 67% were male and 20% were female (13% sex unknown). This could represent an overall male-bias in North American populations suggesting higher annual survival of males. Additionally, dominance interactions where males exclude subordinates from baited ground traps (often located at the centre of the foraging flock) could also lead to this

relationship. If so, we would expect the proportion of males banded at a given site to increase with increasing intensity of competition for food (as a result of increasing amounts of snow cover and colder temperatures). Unfortunately, because our study could not include behavioural observations to measure these interactions directly we are currently unable to directly test this hypothesis. However, daily observations from banders suggest that sex-bias is apparent among un-trapped as well as captured individuals. Additionally, banders often use an array of ground traps, which diffuses the spatial “centre” of large foraging flocks, thus, reducing the potential affect of trapping bias influencing the observed distributional patterns further limiting support for a dominance-related mechanism.

A general lack of intra-winter changes in the proportion of males and females further limited support for the dominance hypothesis. Fifty-three of 69 banding populations showed no relationship between the proportion of males and ordinal date, suggesting that males are not gradually excluding females from preferred wintering sites. However, snow buntings are first reported to arrive to southern Ontario and Quebec by late October (eBird 2012) and winter banding does not typically begin until mid-late December because of poor trapping success until the onset of snowfall. As such, we cannot rule out the possibility that increasing proportions of males early in the wintering period from dominance interactions occur given the current banding dataset. Alternative banding techniques (e.g. mist netting) early in wintering (i.e. November) could potentially serve to fill this temporal absence of winter banding data.

Finally, fall migration phenology data did not support the dominance interactions hypothesis. Regardless of whether climatic variable or proximity to breeding site are

important wintering site selection criteria, we found no support for males migrating prior to females in the fall to defend preferred wintering areas (Fig. 3.4). Also, the overwinter change in the proportion of males did not increase with either food accessibility (proxy for habitat preference) or wintering latitude (proxy for migration distance) (Fig. 3.5). Thus, we found no evidence suggesting that dominant males excluding subordinate females drives the geographic variation in sex-ratios.

Arrival Time Hypothesis

Analysis of spring migration phenology from banding and geolocator data provide support for the early arrival hypothesis (Table 3.1). Males arrive earlier than females to both the early in spring migration (Rivière-au-Tonnerre) and on migration at breeding latitudes (East Bay Island). The discrepancy between male and female arrival dates was greater at the southern migration site (representing populations earlier in migration) than the northern migration site (representing populations later in migration). This could mean that females “catch up” to the males by migrating at faster rates. However, our geolocator data indicates that both sexes undergo spring migration at the same rate, and the relatively earlier arrival of males at Rivière-au-Tonnerre compared to East Bay Island, might be a function of these two banding sites representing different migratory sub-populations (see Chapter 2), where the geographic segregation of males and females may be less pronounced across western wintering populations resulting in smaller differences between male and female arrival dates. Expanding winter banding programs across the western snow bunting wintering range would provide additional insight into the potential differences in distribution and phenology of these two migratory sub-populations.

Geolocator data provided no evidence of advanced departure dates or faster rates of spring migration among males. Early arrival to East Bay Island seems to be a function of wintering location, where shorter one-way migration distances in males resulted in earlier arrival dates. Male snow buntings did not depart from the wintering grounds earlier than females or migrate faster, and while only geolocator data could be used to compare straight-line migration distances in this study, these observed patterns (behavioural and distributional) may represent alternative life history strategies for tropical and temperate-wintering male songbirds to achieve earlier arrival to the breeding grounds. For example, recent geolocator data from wood thrush (*Hylocichla mustelina*) wintering in Central America indicate that males achieve earlier arrival on breeding grounds by migrating shorter distances (E. McKinnon, *unpubl. data*). However, unlike snow buntings, wood thrushes are territorial and found in equal proportions throughout the wintering range (Evans et al. 2011, E. McKinnon, *unpubl. data*). As such, male wood thrushes achieve earlier arrival through earlier departure and by following more direct-line spring migration paths to the breeding site (E. McKinnon, *unpubl. data*), possibly since males occupy higher quality wintering territories and achieving sufficient pre-migratory fattening earlier (e.g. Marra and Holmes 2001).

CONCLUSIONS

Non-significant or contrasting relationships of fat score (Fig 3.5) and percent of individuals banded (Fig 3.6) with $PC1_{\text{climate}}$ could be the result of 1) climate variables considered in this study are not significant contributors to habitat preference by wintering snow buntings, or that 2) the energetic benefits of body temperature regulation might

outweigh the costs of foraging in colder and often more snow-covered environments (Kendeigh 1969). As an arctic-breeding passerine and early spring migrant, snow buntings are highly cold tolerant relative to other similarly-sized passerines. For example, Scholander (1950) found that snow buntings had a “lower critical temperature” (lower limit of thermo-neutral zone, i.e.: temperature below which energy must be consumed for thermoregulation) of 10°C, compared to >20°C for tropical birds. Previous studies have found that body size is positively correlated with basal metabolic rate (Scholander 1950, Kendeigh 1969, Ketterson and King 1977). Thus, potential physiological advantages for larger males overwintering in colder locations (compared to smaller females) could outweigh the costs of increased foraging or reduced access to food associated with these wintering sites. Additionally, habitat features such as proximity to road disturbance or cover for predator avoidance, as well as microhabitat effects on snow cover such as exposure to sun or wind that were not considered here, may contribute more significantly to winter habitat preference.

Additionally, differences in support for these hypotheses may also provide insight into the relative contributions, or interaction of both natural and sexual selection as drivers of body size. For example, reproductive benefits gained by males through early arrival to the breeding grounds, may be achieved through wintering in more northern, and therefore colder, locations. Thus, larger body size in males may be the result of sexual selection for early arrival and natural selection for improved cold tolerance. Future studies on snow buntings could look at how body size with wintering location and reproductive success of tracked individuals to test whether reproductive success is a carry-over effect of physiological habitat matching in the winter. Furthermore, examining

how physiological cold and heat tolerance varies with body size could provide additional support for the evolution of large body size in males through improved cold tolerance allowing for more northern wintering sites.

Overall, our results provide evidence for cold tolerance and early arrival, but not social dominance, as hypotheses explaining the geographic variation in sex ratios of a wintering arctic-breeding passerine in eastern North America (Table 3.1). Body size tended to increase among wintering snow bunting populations experiencing colder winter temperatures, despite larger males contributing to a greater proportion of banding populations in these colder climates. Furthermore, males migrated shorter distances between wintering and breeding sites, arrived ahead of females on both spring migration and to breeding sites. Similarities in spring migration rate between males and females suggest that males (and females) are constrained in their ability to increase migration rate, and instead select wintering sites that are closer to their breeding site in order to achieve earlier spring arrival. However, larger and potentially more dominant males did not arrive on wintering grounds ahead of females and were not more common than females at sites with improved access to winter food resources, suggesting that either female-mediated dominance interactions or additional variables not measured in this study are more important contributors to winter habitat preferences. Although often difficult to distinguish between these non-mutually exclusive hypotheses, these results provide new insight into the factors limiting the distribution of wintering snow buntings populations in eastern North America and enable greater predictive capacity when estimating population responses to future anthropogenic habitat alteration and climate change. Additionally, combined applications of traditional and modern tracking techniques provide a new

ability to test longstanding hypotheses to further our understanding of the evolution of these distributional patterns and migratory strategies of small migratory songbirds.

FIGURES

Figure 3.1 Mean body size and percent males of snow bunting populations compared with total winter HDD using regression analyses with $\alpha=0.05$. Body size increases linearly with decreasing winter temperatures both across (a) and within sexes (c; significant only in males). Percent males increases (second degree polynomial) with decreasing winter temperatures (b).

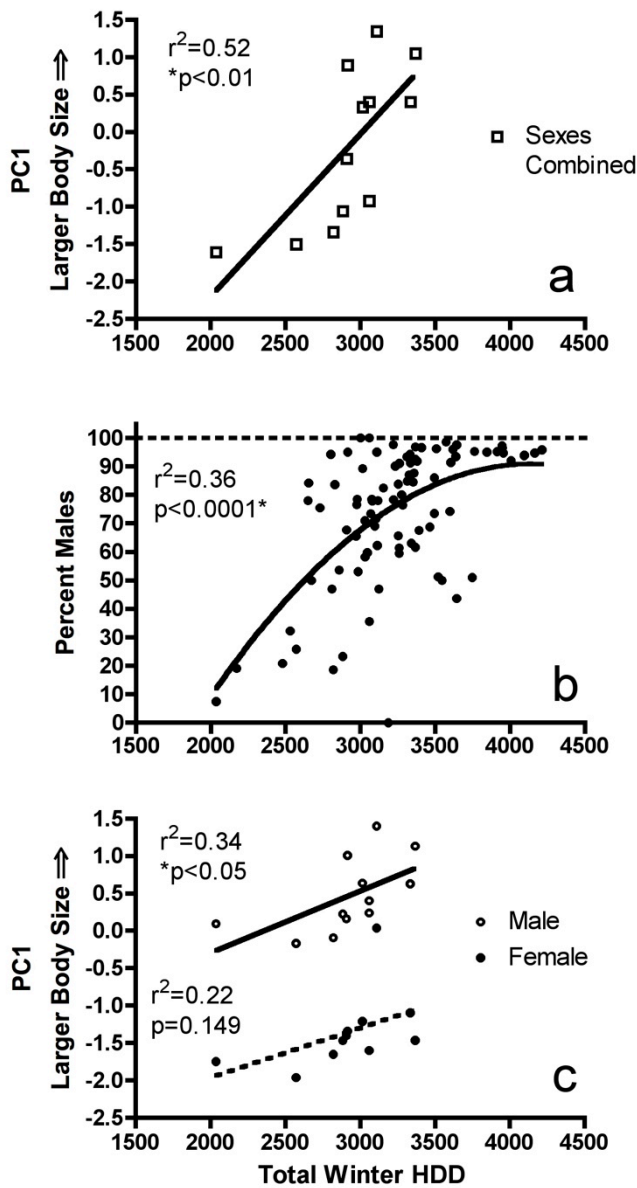


Figure 3.2 No relationship was found between predicted wintering site food accessibility ($PC1_{climate}$) and population mean fat score (sexes combined), illustrating that population fat scores do not increase at sites with limited predicted winter food accessibility.

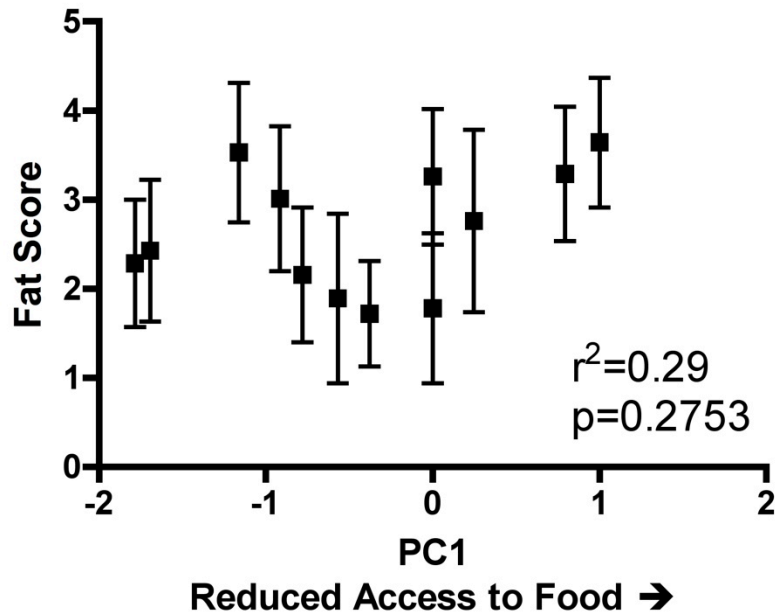


Figure 3.3 The proportion of male and female snow buntings (separated by age) banded with respect to predicted winter food accessibility metric $PC1_{climate}$ at winter banding sites in eastern North America.

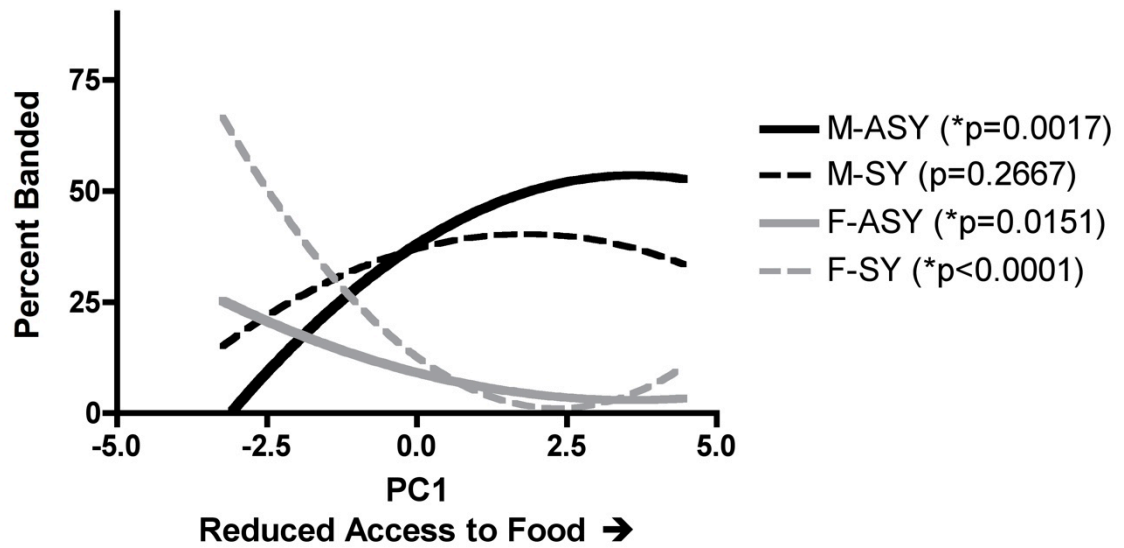


Figure 3.4 Fall migration phenology of birds arriving to wintering grounds at Thunder Cape Bird Observatory, near Thunder Bay, Ontario, Canada (a). Standardized arrival dates represent annual fall migration (October 6-31). Mean arrival dates compared between groups using a two-tailed t-test with $\alpha=0.05$ (b).

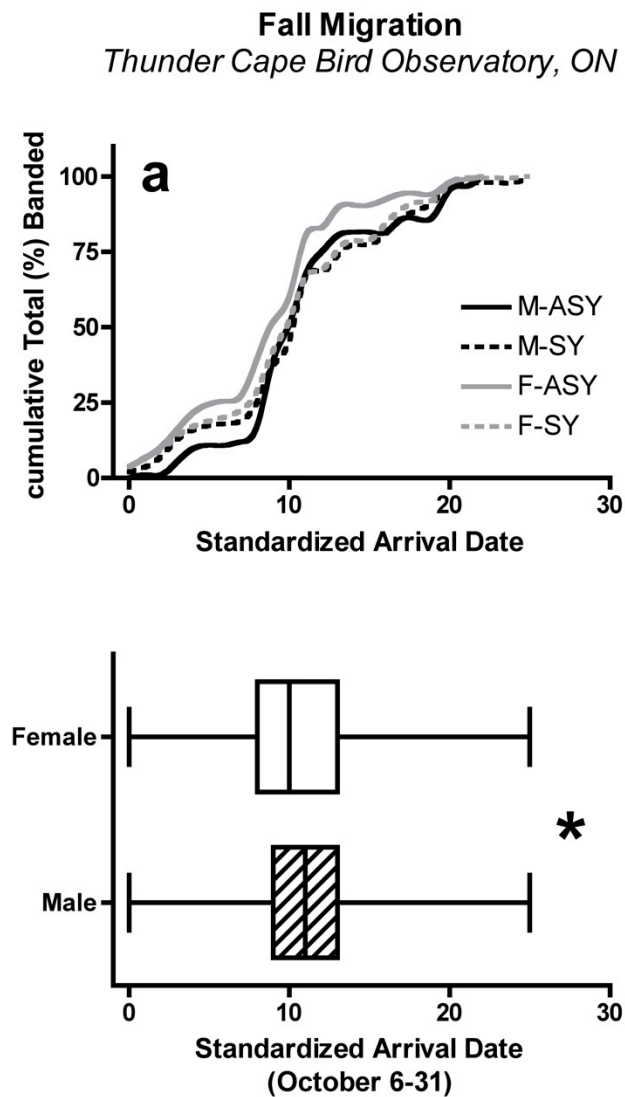


Figure 3.5 Overwinter change in the proportion of males in relation to total winter snowfall (cm). Positive values for $m_{\Delta\text{males}}$ represent an overwinter increase and negative values represent an overwinter decrease in the proportion of males.

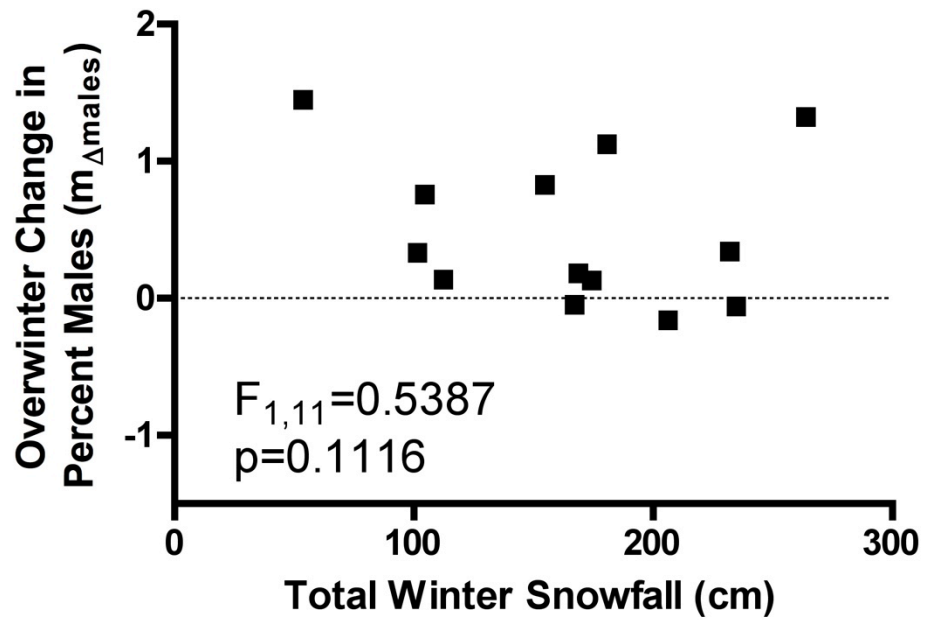


Figure 3.6 Female snow bunting fat scores do not vary significantly with the proportion of males banded in wintering populations in eastern North America.

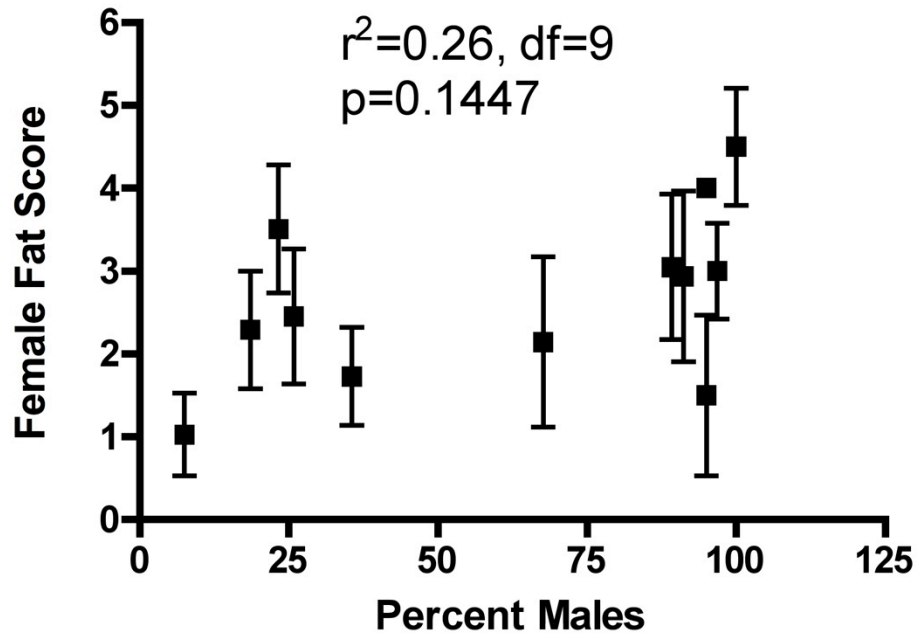


Figure 3.7 Spring migration phenology of snow buntings banded during early (Rivière - au-Tonnerre, QC; a, b) and late spring stopovers (East Bay Island, NU; c, d). Mean arrival dates compared between groups using one-way ANOVA (Tukey-Kramer HSD) (b) and one-tailed t-test (d) with $\alpha=0.05$.

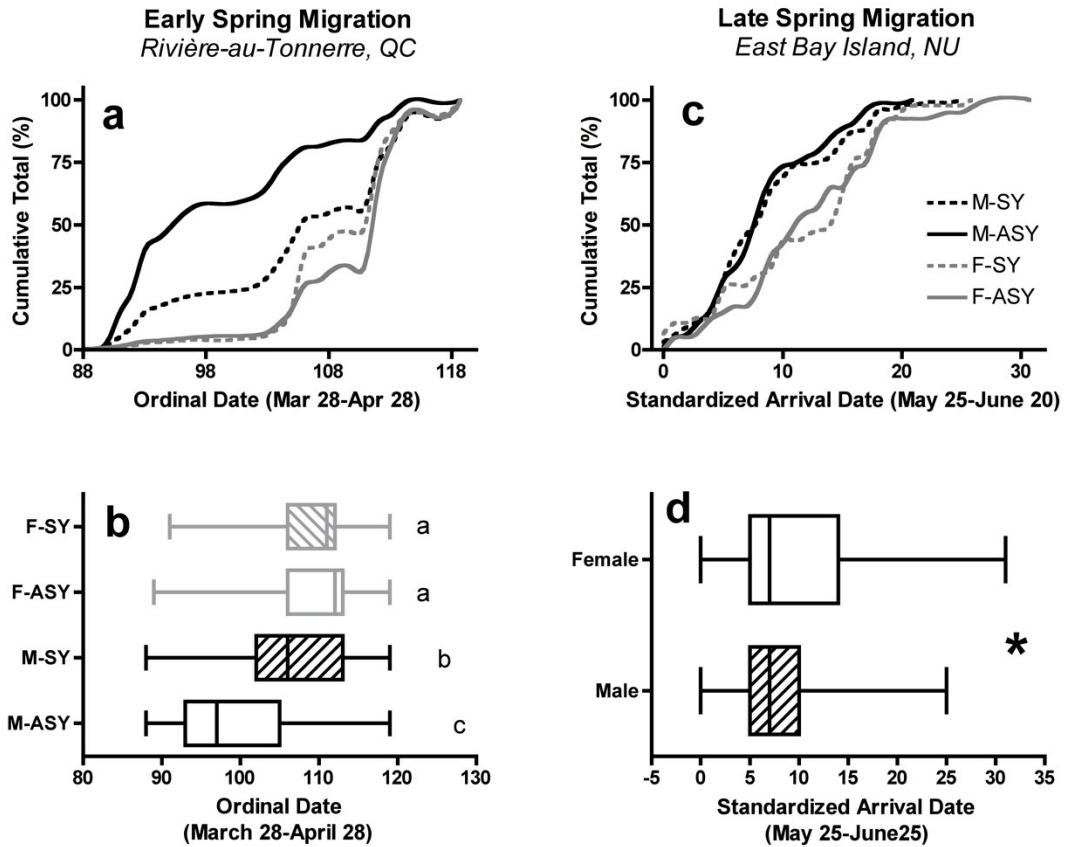
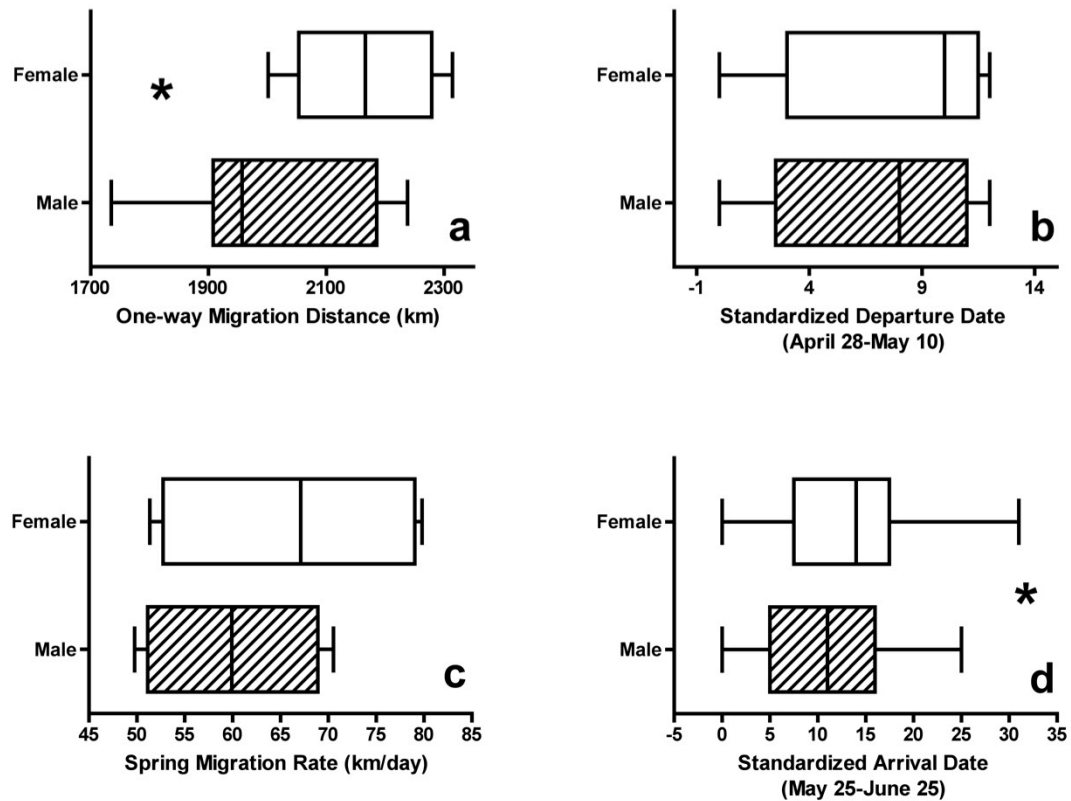


Figure 3.8 Spring migration behaviour of breeding snow buntings from East Bay Island, NU, measured using i) geolocators (a-c) and ii) spring banding data (d). Estimated means of (a) straight-line migration distance, (b) wintering departure date, (c) spring migration rate and (d) arrival date of breeding males and females were compared using one-tailed t-tests with $\alpha=0.05$.



TABLES

Table 3.1 Summary of relative support for the body size, social dominance and arrival time hypotheses for driving sex-ratio segregation in wintering snow bunting populations.

Hypothesis	Prediction	Result	Figure
1) Cold Tolerance	Body size increases with total winter HDD both i) independent of sex, <i>and</i>	yes	3.1 a
	ii) within each sex	yes, but only significant in males	3.1 c
2) Social Dominance	i) larger and more dominant older males are less common in sites with limited resource availability (i.e.: colder temperatures and greater snow cover)	no	3.2
	ii) fat reserves higher at locations with colder temperatures and more snow	no	3.3
	iii) males arrive to wintering grounds ahead of females <i>or</i>	no, females arrive first	3.4
	iv) the proportion of males banded at “good quality” sites increases over the winter as they out compete females	no	3.5
	v) lower female fat reserves in male-biased populations	no	3.6
3) Early Arrival	i) males arrive earlier on both migration routes and to breeding grounds	yes	3.7, 3.8 d
	ii) both sexes migrate at the same rate and depart on a similar date during spring migration	yes	3.8 b,c
	iii) males have shorter migration distances	yes	3.8 a

CHAPTER 4 - GENERAL DISCUSSION

Examining the spatial and temporal distribution of free-living animal populations is necessary for identifying the factors limiting this distribution and the capacity for populations to respond to changing environmental or climate conditions. This study highlights the importance of combining multiple tracking techniques in migratory studies involving small passerines. Over more than 80 years of banding and more than 50,000 band records for snow buntings (BBO *unpubl. data*), only 69 band encounter records showed geographic linkages of individual movements between the breeding and wintering range. This type of data provides two distinct points, which do not necessarily represent migration endpoints or precise departure or arrival times for migration. However, given the remote breeding range of arctic-nesting species, winter banding programs offer an invaluable opportunity to study the spatial, behavioural and morphological distributions of these species during the non-breeding period.

Opportunistic studies of breeding populations have great potential to quickly increase our knowledge of migration patterns and are especially important for populations or arctic regions that remain poorly studied. At East Bay Island, we were able to collect hundreds of tissue samples, which could be used for stable isotope analysis or genetic studies to improve our knowledge of the degree of migratory connectivity within this population. Estimates of migratory origin via these techniques require only a single capture, and thus, can be collected opportunistically with little previous knowledge of the breeding populations being sampled. Additionally, snow buntings will readily build nests in artificial structures and rock piles, and will commonly breed in towns because of the increased availability of nesting sites provided by these structures (Montgomerie and

Lyon 2011). Because access to remote breeding populations may be low, we encourage researchers to take advantage of rare sampling opportunities and maximizing the use of these samples by collaborating with other researchers or programs.

Geolocators enable relatively short-term studies to gain novel information about migratory distributions and behaviour. At East Bay Island, we were able to track 13 individuals throughout their entire annual cycle after only two years of geocator deployment. Combining our results with analysis of band recoveries and stable isotopes indicate limited exchange of individuals between eastern and western wintering populations. Such strong patterns of migratory connectivity could lead to genetic differentiation or reproductive isolation as sub-populations experience different selective pressures (e.g. Irwin et al 2001). Additionally, knowledge of migratory connectivity allows scientists to predict the response of populations to both localized and widespread threats. Thus, geolocators and stable isotope analysis can provide a wider sampling distribution of populations to determine wintering locations, which may otherwise remain undetected through band recoveries.

Geolocators have also improved our ability to track birds throughout large geographic as well as temporal spans. Geocator data from snow buntings suggests that individuals depart from the wintering grounds up to one month before arrival to the breeding grounds and yet the majority of this time is not spent migrating, but at a single stopover site. Based on previously measured fattening rates of birds at stopover sites, this period is much longer than necessary to acquire sufficient fat reserves to fuel the remaining migration (Stutchbury et al. 2009, Newton 2008). Therefore, further studies of snow buntings on migration routes may suggest additional functions of these sites or

potential reasons for such lengthy stopovers. These studies may shed light on how the early arrival of males to breeding sites might be mediated through intra or interspecific interactions at the stopover sites (i.e. social dominance, or predator avoidance), or how conditions from wintering and migration affect arrival condition and reproductive success measured through physiological variables including energetic metabolites (Lyons et al. 2008). By continuing to deploy geolocators we can determine the level of plasticity in migration behaviour in relation to naturally occurring variation in climate and predicted changes to the phenology of important seasonal resources (i.e. seed crops, emergence of insects). The quality and quantity of this type of spatial data is unprecedented by previously available tracking techniques and can be used as a valuable tool in the conservation of migratory species.

Additionally, for the first time, direct tracking methods were used to test three longstanding hypotheses to explain differential wintering distributions and migration movements of males and females. Previous studies have used banding or museum specimens to test these hypotheses (Ketterson and Nolan 1976, 1979), thus, provide known locations of an individual for only a single day. Geolocators provide daily location estimates, which can be used to compare with an individual's body size and overwintering climate conditions. These relationships will ultimately improve our ability to identify the mechanisms driving their distribution, both within and across seasons.

CONCLUSION

To effectively monitor and manage snow bunting populations, detailed knowledge of their annual distributional patterns is required. The results presented here show that eastern and western wintering populations of snow buntings are also geographically distinct breeding populations. Although these findings should be considered with some caution until wider sampling of Canadian breeding populations can be conducted, these results provide important evidence of population differentiation with respect to migration behaviour. Our findings also suggest that sexual variation in climate tolerance and life history strategies drive the distributional patterns of sex-segregation during the non-breeding period. These different selective pressures may cause male and females to be differentially affected by predicted climate change or habitat alteration, and therefore, considering the distribution of individuals both within and across populations need to be considered for future conservation and management of this species. The methods and results here can be incorporated into future studies on the factors affecting the distribution and abundance of arctic-breeding passerines.

REFERENCES

- Arnold, T. W. 1991. Geographic variation in sex ratios of wintering American Kestrels *Falco sparverius*. *Ornis Scandinavica* 22(1):20-26.
- Bächler, E., Hahn S., Schaub M., Arlettaz R., Jenni L., Fox J. W., V. Afanasyev, and F. Leichti. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS ONE* 5:e9566.
- Bai, M-. L. and D. Schmidt. 2012. Differential migration by age and sex in central European Ospreys *Pandion haliaetus*. *Journal of Ornithology*. 153:75-84.
- Bairlein, F., D. R. Norris, R. Nagel, M. Bulte, C. Voigt, J. W. Fox, D. J. T. Hussell, and H. Schmaljohan. 2012. Cross-hemisphere migration of a 25g songbird. *Biology Letters* 8(4):505-507.
- Bearhop, S., R. W. Furness, G. M. Hilton, S. C. Votier, and S. Waldron. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Functional Ecology* 17(2):270-275.
- Beauchamp, G. 2008. What is the magnitude of the group-size effect on vigilance? *Behavioral Ecology* 19(6):1361-1368.
- Best, L. B., H. Campa III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P Weeks, Jr., and S. R. Winterstein. 1998. Avian abundance in CRP and crop fields during winter in the Midwest. *American Midland Naturalist* 139(2):311-324.
- Birdlife International, IUCN Red List for Birds, 2012, <http://www.birdlife.org> on 20/04/2012.
- Black, A. L. H. G. Gilchrist, K. A. Allard and M. L. Mallory. 2012. Incidental observations of birds in the vicinity of Hell Gate Polynya, Nunavut: Species, timing, and diversity. *Arctic* 65(2):145-154.

- Bowen, G. J., The Online Isotopes in Precipitation Calculator, version 2.2, 2012:
<http://www.waterisotopes.org>
- Bowen, G. J., L. I. Wassenaar, and K. A. Hobson. 2005a Application of stable hydrogen and oxygen isotopes to wildlife forensic investigations at global scales. *Oecologia* 143:337–348.
- Bowen, G. J., L. Chesson, K. Nielson, T. E. Cerling, and J. R. Ehleringer. 2005b. Treatment methods for the determination of delta H-2 and delta O-18 of hair keratin by continuous-flow isotope-ratio mass spectrometry. *Rapid Communications in Mass Spectrometry* 19:2371–2378.
- Brown, D. R., and J. A. Long. 2007. What is a winter floater? Causes, consequences, and implications for habitat selection. *Condor* 109: 548-565.
- Butcher, G. S. and D. K. Niven. 2007. Combining data from the Christmas Bird Count and the Breeding Bird Survey to determine the continental status and trends of North American Birds, <http://stateofthebirds.audubon.org/cbid/report.php>
- Caccamise, D. F. and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 97:306-318.
- Cox, G. 2010. Bird migration and global change. Island Press, Washington.
- Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: Latitudinal segregation by age and sex class. *Current Ornithology* 15:33–88.
- Daan, S. A. Masman, A. Strijkstra and S. Verhulst. 1989. Intraspecific allometry of basal metabolic rate: relations with body size, temperature, body composition and circadian phase in Kestrel *Falco tinnunculus*. *Journal of Biological Rhythms* 4:267-284.
- Downhower, J. F. 1976. Darwin's finches and the evolution of sexual dimorphism in body size. *Nature* 263:558-563.

- eBird: an online database of bird distribution and abundance [web application], Version 2, eBird, Ithaca, New York, 2012. Available <http://www.ebird.org>.
- Evans, M., E. Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (*Hylocichla mustelina*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/246>
- Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K.M. Dugger, S. A. Gauthreaux, Jr, P. Heglund, K. A. Hobson, A. E. Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, P. P. Marra, C. L. Merkord, E. Nol, S. I. Rothstein, T. W. Sherry, T. S. Sillett, F. R. Thompson III, and N. Warnock. 2010. Recent advances in understanding migration systems of New World land birds. *Ecological Monographs* 80(1):3-48.
- Francis, C. M and F. Cooke. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103(3):548-556.
- Fraser, K. C., T. K. Kyser, R. J. Robertson and L. M. Ratcliffe. 2008. Seasonal patterns in hydrogen isotopes of claws from breeding wood-warblers (Parulidae): utility for estimating migratory origins. *Avian Conservation and Ecology* 3(1):2.
- Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioural dominance. Pages 17-54 *In Perspectives in Ethology* (P. P. G. Bateson and P. H. Kopfer, Ed.). Plenum Press, New York.
- Grubb, T. C. and L. Greenwald. 1982. Sparrows and a bushpile: foraging responses to different combinations of predation risk and energy cost. *Animal Behaviour* 30: 637-640.
- Hanski, I. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3-16.
- Hobson, K. A. and L. I. Wassenaar (Eds.). 2008. Tracking Animal Migration with Stable Isotopes. *Handbook of Terrestrial Ecology Series*. Academic Press, London.

- Hobson, K. A. and L. I. Wassenaar. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers, *Oecologia* 109:142–148.
- Holberton, R. L. and K. P. Able. 2000. Differential migration and an endocrine response to stress in wintering dark-eyed juncos (*Junco hyemalis*). *Proceedings of the Royal Society of London* 267:1889-1896.
- Humple, D. L., N. Nur, G. R. Geupel and M. P. Lynes. 2001. Female-biased sex ratio in a wintering population of Ruby-crowned Kinglets. *Wilson Bulletin* 113(4):419-424.
- Hurlbert, A. H. and Z. Liang. 2012. Spatiotemporal variation in avian migration phenology: citizen science reveals effect of climate change. *PLoS ONE* 7(2): e31662.
- Intergovernmental Panel on Climate Change, Fourth assessment report (AR4) of the IPCC on climate change part I - the physical science basis. IPCC, Geneva, Switzerland, 2007.
- Irwin, D. E. 2000. Song variation in avian ring species. *Evolution* 54:998-1010.
- Irwin, D. E., S. Bensch, and T. D. Price. 2001. Speciation in a ring. *Nature* 409:333-337.
- Irwin, D. E., A. Brelsford, D. P. L. Toews, C. Macdonald and M. Phinney. 2009. Extensive hybridization in a contact zone between MacGillivray's warblers *Oporornis tolmiei* and mourning warblers *O. philadelphia* detected using molecular and morphological analyses. *Journal of Avian Biology* 40: 539-522.
- Kaiser, A. 1993. A new multi-category classification of subcutaneous fat deposits of songbirds. *Journal of Field Ornithology* 64(2):246-255.
- Kendeigh, S. C. 1969. Tolerance of cold and Bergmann's rule. *The Auk* 86(1):13-25.
- Ketterson, E.D., and V. Nolan, Jr. 1976. Geographic variation and its climate correlates in the sex ratio of eastern-wintering dark-eyed juncos (*Junco hyemalis hyemalis*). *Ecology* 57(4):679-693.

- Ketterson, E.D. and J. R. King. 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Physiological Zoology* 50:115-129.
- Ketterson, E. D. and V. Nolan, Jr. 1983. The evolution of differential bird migration. Pages 357-402. *In* Current Ornithology, Vol. I (R.F. Johnston,Ed.). Plenum Press, New York.
- Lynch, J. F., E. S. Morton and M. E. Van der Voort. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). *Auk* 102:714-721.
- Lyngs, P., 2003. Migration and wintering ranges of birds in Greenland: An analysis of ringing recoveries. *Dansk Ornithologisk Forenings Tidsskrift* 97(1):1-167.
- Mallory, M. L. and A. Fontaine. 2004. Key marine habitat sites for migratory birds in Nunavut and the Northwest Territories. CWS, Occasional Paper No. 109, ISBN 0-662-34046-9.
- Marra, P. P. 2001. The role of behavioural dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioural Ecology* 11(3):299-308.
- Marra, P. P., T. W. Sherry and R. T. Holmes. 1993. Territorial exclusion by a Neotropical migrant warbler in Jamaica: A removal experiment with American Redstarts (*Setophaga ruticilla*). *Auk* 110:565-572.
- Marra, P. P., and R. L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116(1-2):284-292.
- Marra, P. P. and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the non-breeding season. *The Auk* 118 (1):92-104.

- Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham and D. R. Norris. 2007. Optimal conservation of migratory species. PLoS ONE 2:751.
- Montgomerie, R. and B. Lyon. 2011. Snow Bunting (*Plectrophenax nivalis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/198>
- Morbey, Y. E. and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663-673.
- Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Canadian Journal of Zoology 59:1527-1534.
- Newton, I. The Migration Ecology of Birds. Academic Press, London, 2008.
- Nolan Jr., V. and E. D. Ketterson. 1983. An analysis of body mass, wing length, and visible fat deposits of Dark-eyed Juncos wintering at different latitudes. Wilson Bulletin 95(4):603-620.
- Norris, D. R., P. P. Marra, T. K. Kyser, T. W. Sherry and L. M. Ratcliffe. 2004. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird, Proceedings of the Royal Society of London, Series B 271:59– 64.
- Phillips, R. A., J. R. D. Silk, B. Phalan, P. Catry and J. P. Croxall. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? Proceedings of the Royal Society of London, Series B 271(1545):1283-1291.
- Prescott, D. R. C. 1994. Intraspecific and geographic trends in body size of a differential migrant, the Evening grosbeak. Auk 111(3):963-702.
- Prescott, D. R. C., and A. L. A. Middleton. 1990. Age and sex differences in winter distribution of American Goldfinches in eastern North America. Ornis Scandinavica, 21(2):99-104.

- Pyle, P. 1997. Identification Guide to North American Birds. Part 1. Slate Creek Press: Bolinas.
- Rappole, J. H., and A.R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- Reichlin, T. S., M. Schaub, M. H. M. Menz, M. Mermod, P. Portner, R. Arlettaz, and L. Jenni. 2009. Migration patterns of Hoopoe *Upupa epops* and Wryneck *Jynx torquilla*: an analysis of European ring recoveries, *Journal of Ornithology* 150:393–400.
- Royle, J. A., and Rubenstein D. R. 2004. The role of species abundance in determining the breeding origins of migratory birds using stable isotopes. *Ecological Applications* 14:1780–1788.
- Ryder, T. B., J. W. Fox, and P. P. Marra. 2011. Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark-recapture data. *Auk* 128:448–453.
- Scholander, P. F., R. Hock, V. Walters, F. Johnson, and L. Irving. 1950. Heat regulation in some arctic and tropical mammals and birds. *Biology Bulletin* 99:237-258.
- Sillett, T. S. and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71(2):296-308.
- Smith, R. D., and N. B. Metcalfe. 1997a. Where and when to feed: sex and experience affect access to food in wintering snow buntings. *Behaviour* 134(1-2):143-160.
- Smith, R. D., and N. B. Metcalfe. 1997b. Diurnal, seasonal and altitudinal variation in energy reserves of wintering snow buntings. *Journal of Avian Biology* 28(3):216-222.
- Smith, R. D., and N. B. Metcalfe. 1997c. Why does dominance decline with age in wintering snow buntings. *Animal Behaviour* 53:313-322.
- Stanley, C. Q., M. MacPherson, K. C. Fraser, E. A. McKinnon, B. J. M. Stutchbury. 2012. Repeat Tracking of Individual Songbirds Reveals Consistent Migration Timing but Flexibility in Route. *PLoS ONE* 7(7): e40688.

- Stewart, B. S. 1997. Ontogeny of differential migration and sexual segregation in Northern Elephant Seals. *Journal of Mammology* 78(4):1101-1116.
- Stutchbury, B. J. M., S. A. Tarof, T. Done, E. Gow, P. M. Kramer, J. Tautin, J. W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323: 896.
- 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.
- Swanson, D. L., and E. T. Liknes. 2006. A comparative analysis of thermogenic capacity and cold tolerance in small birds. *Journal of Experimental Biology* 209:466-474.
- Tøttrup, A., R. Klaassen R., R. Strandberg R., K. Thorup K., M. Kristensen M., P. S. Jørgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam. 2011. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society of London, Series B* 279: 1008-1016.
- Vincent, J., and J. Bédard. 1976. Fat reserves in snow buntings. *Canadian Journal of Zoology* 54:1051-1063.
- Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London, Series B* 272(1581):2561-2569.
- Wassenaar, L. I., and K. A. Hobson. 2001. A stable-isotope approach to delineate geographic catchment areas of avian migration monitoring stations in North America, *Environmental Science and Technology* 35: 1845-1850.
- Wassenaar, L. I., and K. A. Hobson. 2003. Comparative equilibrium and online technique for determination of non-exchangeable hydrogen for keratins for use in animal migration studies. *Isotopes in Environmental and Health Studies* 39(3): 211–217.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76–83.

VITA AUCTORIS

NAME: Christine Alayne Macdonald

PLACE OF BIRTH: Toronto, ON

YEAR OF BIRTH: 1984

EDUCATION: Markham District High School, Markham ON,
2003

University of British Columbia, B.Sc.,
Vancouver, BC, 2008

University of Windsor, M.Sc., Windsor, ON,
2012