MIGRATORY CONNECTIVITY IN WHITE-THROATED SPARROWS: INFERENCES FROM STABLE HYDROGEN ISOTOPE ANALYSES

A Thesis

Submitted to the College of Graduate Studies and Research in Partial Fulfillment of the Requirements for the Degree of Doctor Philosophy in the Department of Biology, University of Saskatchewan, Saskatoon.

By

Daniel F. Mazerolle

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ABSTRACT

Tracking migratory movements of birds between breeding and wintering areas is important for both theoretical and conservation purposes. In particular, information about linkages between stages of the annual cycle (i.e., migratory connectivity) is essential for identifying factors and processes limiting population sizes of birds. Further, this information is necessary for testing assumptions and hypotheses about the evolution of avian migratory patterns. Here, I used stable hydrogen isotope (δD) analyses of tissues representing different periods and geographic regions of the annual cycle of white-throated sparrows, *Zonotrichia albicollis*, to provide new information on spatial and temporal linkages between stages of the annual cycle of this species. To achieve this objective, I sampled white-throated sparrows during spring and fall migration of 2002 and 2003 at a key staging ground for North American migratory birds located at Delta Marsh, Manitoba.

Based on evaluations of the correspondence between δD values of feathers, claws, and cellular portions of blood of migrants, I determined that δD values of claws and blood cells were not suitable for estimating wintering origins of individuals captured *en route* to breeding areas. However, δD values of head feathers grown on wintering areas and tail feathers grown on breeding areas corresponded to values expected for feathers grown in broad areas within the wintering and breeding range of the species, respectively. The δD values of feathers showed no relationship between estimated breeding or natal and wintering latitudes of white-throated sparrows. However, band-

encounter analyses indicated a clear east–west segregation of populations across Canada, a finding that suggests that this species has a parallel migration system. Temporally, all components of the breeding populations migrated together during spring migration. However, as expected, white-throated sparrows exhibited sex-biased differential timing of spring arrival and latitude of wintering origin. Consistent with several other differential migrants, female white-throated sparrows arrived later and originated from more southern latitudes. There was also a negative relationship between wintering latitude and arrival dates of individuals during the second spring of the study. The existence of this relationship is a key assumption of differential migration hypotheses that had not been previously validated. Furthermore, since timing of arrival at breeding areas is critical to establishing high-quality territories and pair bonds, relationships between wintering latitude and arrival date of individuals could have important carry-over effects to reproduction. Based on standard body condition indices, white-throated sparrows migrating longer distances to reach breeding areas were not in poorer body condition than those migrating shorter distances. Thus, the cost of migrating longer distances does not appear to affect pre-breeding body condition, a parameter known to be linked with reproductive success.

ACKNOWLEDGMENTS

I thank Dr. Keith Hobson, my supervisor, for his insights, support and guidance, which have greatly improved this thesis and my abilities as a researcher. I also thank the members of my advisory committee, Drs. Robert Clark, Tracy Marchant, and Trent Bollinger for their advice and input, and Dr. Blair Wolf for acting as my external examiner. Funding for this project was provided by the Canadian Wildlife Service, University of Saskatchewan (Scholarships to DFM), Environment Canada's Science Horizons Youth Internship Program, American Ornithologists' Union (Research Award), and Society of Canadian Ornithologists (Taverner Award). I thank the staff and volunteers of the Delta Marsh Bird Observatory and am especially grateful to Heidi den Haan. I thank the University of Manitoba Field Station and the Bell family for allowing me access to their lands. Melanie Hosegood and Hollie Remenda provided excellent assistance in the field and laboratory and Patricia Healy helped with the preparation of samples for isotopic analyses. I greatly appreciate the office space and the enjoyable work environment provided by Saskatoon CWS and its staff. I thank Allan R. Smith for providing the drawing of the white-throated sparrow that appears in many of the figures in the thesis. I am also grateful to David Hussell for advice on the band returns of white-throated sparrows and to Louise Laurin of the Canadian Wildlife Service for providing me with a copy of those data. Dr. Charles Blem kindly provided the data analyzed in Appendix 2. Drs. Robert Clark, Tracy Marchant, Trent Bollinger, Leonard Wassenaar, Daniel Cristol, Kevin Dufour, and Keith Hobson provided helpful comments that greatly improved the thesis. Finally, I would like to thank my family for their love, support, and understanding. Most of all, I would like to thank Diana, my wife and best friend, for her love, support, and her patience.

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CHAPTER 1: GENERAL INTRODUCTION

1.1. INTRODUCTION

Concerns over population size declines in many species of migratory songbirds have prompted considerable interest and debate about factors limiting their population growth rates (Keast and Morton 1980; Askins et al. 1990; Hagan et al. 1992; Martin and Finch 1995; Newton 2004). However, these concerns, and our overall understanding of factors limiting migratory bird populations, have generally been based on scarce and geographically limited data sets (Donovan et al. 2002; Rich et al. 2004) that have been evaluated with approaches that do not directly consider events occurring throughout the annual cycle (Sillett and Holmes 2002; Norris et al. 2004). An increasing number of studies indicates that certain migratory birds are sensitive to changes in environmental conditions, including habitat loss and climate change, in all regions and during all periods of their annual cycle (Fig. 1.1; Marra et al. 1998; Webster et al. 2002; Sillett et al. 2000; Sillett and Holmes 2002; Newton 2004; Mazerolle et al. 2005). In the future, we must strive to gather the requisite information to accurately model effects of changes in availability or quality of breeding, migratory, and wintering habitats for populations of migratory species. Previously, the collection and analysis of such information has been hindered by difficulties associated with tracking movements of birds with vast and geographically disparate breeding and wintering ranges (Webster et al. 2002). However,

recent technological advances now make it possible to trace migratory linkages in birds and other wildlife (Hobson 1999; Rubenstein and Hobson 2004). In addition to helping us improve our understanding of the natural and anthropogenic factors affecting birds during the course of their annual cycle, these new tools will also assist in developing more effective conservation and management plans (Donovan et al. 2002; Webster et al. 2002; Hobson 2003a).

Avian migratory patterns and strategies are shaped by several factors including the spatial distribution and seasonality of resources, habitats, competitors, and pathogens (Webster et al. 2002; Alerstam et al. 2003). The extent of breeding populations intermixing on wintering areas (i.e., migratory connectivity) is a key piece of information needed to identify the requirements of birds over various temporal and spatial scales and for making accurate predictions about likely impacts of changes in environmental conditions on populations of migratory birds (Webster et al. 2002). Examples of well-known migratory patterns that typify migratory connectivity are leap-frog and chain migration (Fig.1.2), although migratory connectivity refers also to many forms of spatial linkages that do not necessarily correspond to latitudinal or longitudinal gradients in the segregation of populations on breeding and wintering areas (Webster et al. 2002). Recent research has demonstrated that events occurring during the wintering period of migratory birds can have important cross-seasonal, carry-over effects (i.e., seasonal interactions) to migratory and breeding events (Fig. 1.1; Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004). For instance, Marra et al. (1998) demonstrated that the quality of habitats used by birds on their wintering grounds affected spring body condition and timing of arrival on the breeding grounds, variables known to influence

reproductive success of individuals (e.g., Smith and Moore 2003, Wilson and Arcese 2003; Norris et al. 2004; Smith and Moore 2005a). Such studies demonstrate the importance of migratory connectivity for understanding the implications of cross-seasonal, carry-over effects (Hobson 1999; Webster et al. 2002).

Spatial linkages between breeding, migratory, and wintering areas have previously been investigated with extrinsic, biological, and biogeochemical markers (Webster et al. 2002; Rubenstein and Hobson 2004). Common extrinsic methods include tagging (i.e., banding) and remote-sensing methods, such as radio and satellite telemetry (reviewed by Webster et al. 2002). Attempts trace migratory movements with tagging approaches have been largely ineffective because the re-encounter rates of tagged individuals are extremely low (typically << 1%), particularly for non-game species (Hobson 2003a). Transmitter technology has proven useful for tracking migration, but currently this technique is only applicable to relatively large birds such as waterfowl and raptors (Hobson 1999). Further, because of the significant financial cost of transmitters, especially those with satellite capabilities, studies relying on this technology are often based on small sample sizes. This approach is also limited by potential negative effects of tagging on the behaviour of birds (e.g., Hamel et al. 2004). Intrinsic markers can be separated into two categories; those that are inherited and those that are acquired (e.g., biogeochemical markers). Inherited markers such as morphological, behavioural, and genetic traits have been applied with some success in previous studies (reviewed by Webster et al. 2002), although the resolution of these approaches is limited largely by levels of gene flow between populations (Kimura et al. 2002; Webster et al. 2002; Wennerberg et al. 2002; Clegg et al. 2003; Boulet 2004). Acquired markers such as

stable isotopes typically provide more population resolution than inherited markers. (Hobson 1999; Hobson 2003; Rubenstein and Hobson 2004) Well known isotopic patterns (i.e., spatial gradients in isotopic signatures) have been applied effectively to trace migratory linkages between isotopically-distinct areas used by birds (reviewed by Hobson 1999, and Rubenstein and Hobson 2004). In fact, since the late 1990s, the use of isotopic patterns for such purposes has grown exponentially (Fig. 1.3). Further, this research has improved our understanding of migratory connectivity and has provided novel perspectives on factors influencing the life history and population dynamics of migratory birds (e.g., Hobson et al. 1997a; Marra et al. 1998; Rubenstein et al. 2002; Mehl et al. 2004; Bearhop et al. 2004; Norris et al. 2004).

While isotopes of several elements have been used as tracers to study various aspects of avian ecology (Hobson 1999; Kelly 2000, Rubenstein and Hobson 2004), in North America, stable hydrogen isotopes are the most useful for making linkages between breeding, wintering, and migratory stopover periods of birds that perform latitudinal migration (Fig. 1.4; reviewed by Hobson 1999; Webster et al. 2002; Rubenstein and Hobson 2004). Natural concentrations of deuterium (depicted as $^{2}H/^{1}H$ or δD) in precipitation are incorporated through diet into the tissues of birds feeding within the local food web. Further, concentration of deuterium in precipitation varies roughly with latitude in North America and is transferred to metabolically inert structures such as feathers that permanently retain the isotopic signature of the food web where they were synthesized (Hobson 1999; Bowen et al. 2005). As a result, the origin of birds can often be inferred based on knowledge of the δD values of locally grown tissues and mean growing-season average precipitation.

1.2. STUDY SPECIES

My research focuses on white-throated sparrows (*Zonotrichia albicollis*), a short-distance migrant that breeds throughout most of Canada and winters primarily in southeastern United States (Fig. 1.4; Falls and Kopachena 1994). The white-throated sparrow is one of the most common songbird species breeding in the North America (Rich et al. 2004). Approximately 85% of the global population of this species breeds in the Canadian boreal forest (Rich et al. 2004). Breeding habitats used by white-throated sparrows consist primarily of low, dense cover next to open foraging areas (Falls and Kopachena 1994). During non-breeding seasons, these birds frequently forage along woodlot edges, hedgerows, and weedy fields (Falls and Kopachena 1994). They are also found commonly in urban areas during the non-breeding season. Its diet consists primarily of arthropods and seeds found on the ground during spring and summer, and fruits and seeds during fall and winter (Falls and Kopachena 1994).

The white-throated sparrow is among the most well studied songbird species in North America (Falls and Kopachena 1994). The great interest in this species stems in large part from its unique breeding system (Falls and Kopachena 1994; Lank 2002). White-throated sparrows exhibit plumage polymorphism with two distinct morphs – some individuals have white-striped- (WS) while others have tan-striped- (TS) eyebrows (Falls and Kopachena 1994). These morphs are maintained via negative assortative mating whereby each morph nearly always mates with the opposite morph (Falls and Kopachena 1994). In addition to identifying several differences in the breeding biology of WS and TS individuals, behavioural studies have also demonstrated that WS

individuals are socially dominant over TS individuals within each sex (Kopachena and Falls 1993, 1994).

White-throated sparrows undergo a complete moult at the end of the breeding season prior to fall migration (i.e., the preformative moult for young of the year and prebasic moult for adults) when they replace all feathers, and a partial moult prior to spring migration that involves only the replacement of body feathers primarily on the head and throat (i.e., the prealternate moult) (Falls and Kopachena 1994; Pyle et al. 1997). This makes it possible to estimate the wintering and previous breeding/natal locations of individuals by measuring the δD values of feathers grown during these stages of the annual cycle.

1.3. STUDY AREA

Fieldwork was conducted during spring and fall migration, 2002 and 2003, in the dune-ridge forest of Delta Marsh, MB (Fig. 1.5; 98°23'W, 50°11'N), although data collected from 1995 to 2003 by the Delta Marsh Bird Observatory were also used to evaluate patterns of differential migration in white-throated sparrows. Delta Marsh is one of the largest lacustrine marshes in North America, consisting of large basins and small sloughs connected to Lake Manitoba by several natural beaches (Mackenzie 1982). The study area represents a key staging ground for migratory songbirds *en route* to boreal forest located at least 65 km to the north (den Haan, unpublished data). Delta Marsh is located approximately 1,500 to 2,500 km from the wintering grounds of white-throated sparrows (Godfrey 1986; Falls and Kopachena 1994). Thus, all individuals sampled in this area are in transit to or from breeding areas. Capturing birds at major staging areas

provides a very efficient means of sampling individuals originating from geographically broad breeding and wintering areas.

1.4. THESIS OUTLINE

The general objectives of my thesis were as follows:

1) To evaluate levels of concordance between δD values of feathers, claws, and blood of migrating white-throated sparrows to determine which tissues provide useful information about origins of individuals. To date, studies that have investigated migratory connectivity with the stable hydrogen isotope approach have relied almost exclusively on feathers. However, for various reasons, it is not always possible to use feathers in such analyses.
2) To evaluate levels of variance in δD values of feathers of white-throated sparrows captured at a major staging ground in southern Manitoba. These estimates were used to evaluate the size of wintering and breeding ground catchment areas for the avian migration monitoring station where samples were collected. Based on these estimates, I was able to determine if a large enough segment of the species' range was sampled for evaluating migratory connectivity in white-throated sparrows.
3) To evaluate connectivity between breeding and wintering localities of populations using stable hydrogen isotope and band-encounter analyses. White-throated sparrows have been declining significantly during the past four decades in the eastern part of their range, while populations in the western part of their range have remained stable during this period (Fig. 1.6). Accurate information about migratory patterns and connectivity in this

species is a necessary prerequisite for evaluating factors responsible for geographic variation in population trends.

4) To evaluate differential migration of sex classes (with respect to distance travelled and arrival dates) using stable hydrogen isotope analyses of feathers grown on wintering areas. Delineating differential migration patterns in this species will lead to a better understanding of sex-specific ecological pressures and requirements on wintering areas. This information is also necessary for identifying potential cross-seasonal, carry-over effects resulting from the relationship between migration distance and timing of arrival of individuals at breeding areas, a parameter known to influence of reproductive success.

5) To investigate relationships between migration distance and body condition of individuals. Several hypotheses advanced to explain the occurrence of differential migration in birds assume that migration is costly and proportional to migration distance. However, few studies have validated this assumption. This study aimed at determining if body condition of birds captured *en route* to breeding areas was related to migration distances. Similar to the previous objective, this information is also necessary for identifying potential cross-seasonal, carry-over effects resulting from the relationship between migration distance and pre-breeding condition, a parameter known to influence reproductive success.

This research is the first to use isotope analyses of multiple feather types, representing different periods and geographic regions of the annual cycle, and to provide

new information on connectivity among breeding, wintering, and migratory stages of the annual cycle. I have organised the thesis into six chapters that are structured like journal articles, except for Chapter 1 and 6 that cover the general introduction and synthesis, respectively. Chapter 2, "*Estimating origins of short-distance migrant songbirds in North America: Contrasting inferences from hydrogen isotope measurements of feathers, claws, and blood"*, evaluates the first objective described above. Chapter 3, *"Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of white-throated sparrows at a migration monitoring station",* evaluates objectives two and three. Chapter 4, *"Patterns of differential migration in white-throated sparrows evaluated with isotopic measurements of feathers",* evaluates the fourth objective listed above, and finally, Chapter 5, "*Body condition of white-throated sparrows in relation to migration distance: Is there a cost to migrating longer distances?*", evaluates the fifth objective. Four appendices provide additional information about some of the methods and findings presented in these core chapters.

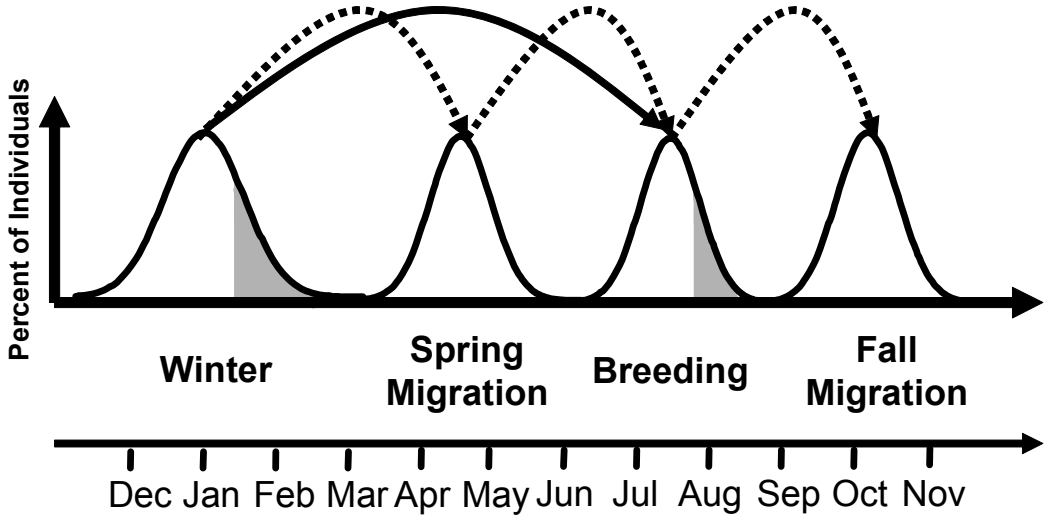

Fig. 1.1. Schematic diagram of the annual cycle of migratory birds and the *Seasonal-Interaction Hypothesis*. The solid arrow depicts interactions between events occurring on the wintering grounds with those occurring on the breeding grounds as explored by Marra et al. (1998). Dotted lines depict other potential carry-over effects between stages of the annual cycle of birds. The solid gray areas depict the timing of the prealternate and complete (i.e., the preformative moult for young of the year and prebasic moult for adults) moult of white-throated sparrows.

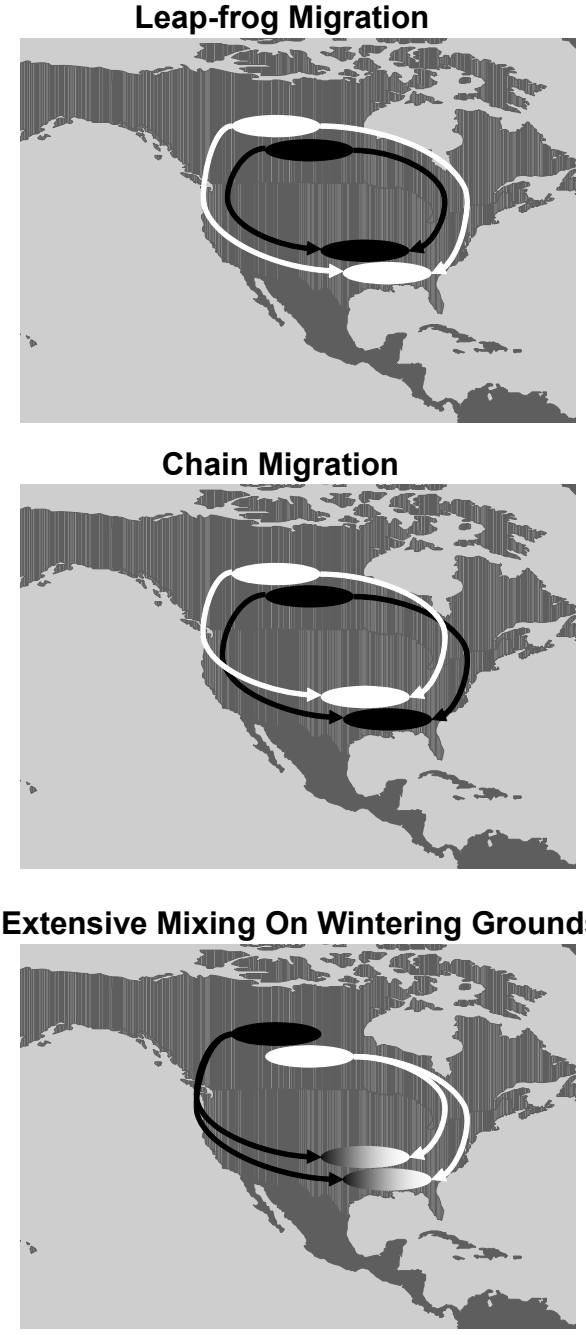

Fig. 1.2. Migratory patterns that can be studied well with stable hydrogen isotope tracers. Migratory connections are depicted with arrows, whereas breeding and wintering areas are depicted by ovals. The top two panels provide examples of breeding populations that exhibit strong migratory connectivity, whereas the bottom panel depicts populations with weak migratory connectivity (i.e., extensive intermixing of breeding populations on the wintering areas).

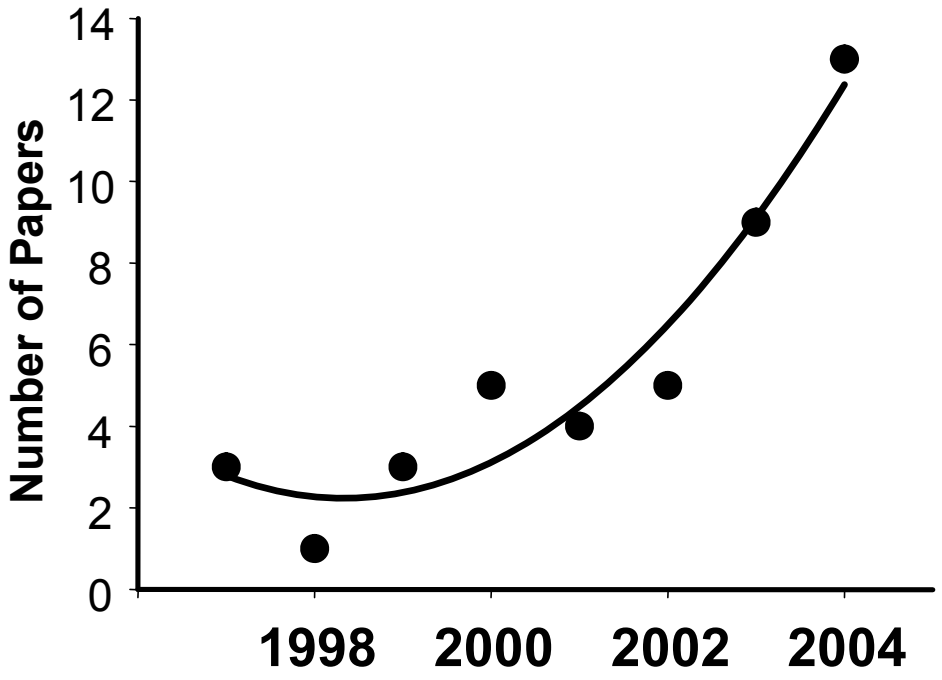

Fig. 1.3. Plot depicting the number of published studies focusing on the application of stable isotope analyses to track movements in birds in relation to year of publication. Estimates were based on an extensive review of the published literature including searches using the Web of Science database. Nearly all of these studies are based on δD, δC, or δN tracers used to track bird movements. Note that review papers are also included in the annual counts. See Martinez del Rio and Wolf (2004) for a related but broader analysis of the growth in the use of stable isotopes in animal and physiological ecology.

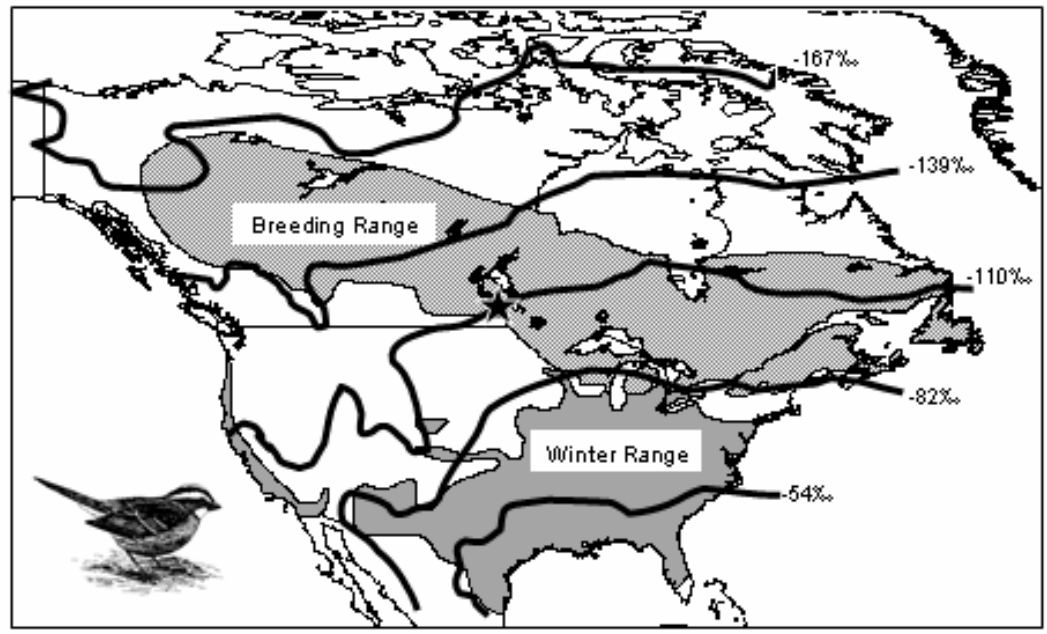

Fig.1.4. Map of the study area location (Delta Marsh, Manitoba, depicted by the black star), approximate limit of the breeding and wintering range of white-throated sparrows, and spatial variation in estimated δD values of feathers in North America based on a GIS-based model of mean growing-season δD of precipitation values corrected for altitude (Meehan et al. 2004) and an isotopic discrimination factor between mean growing-season precipitation δD and feather non-exchangeable δD of -25‰.

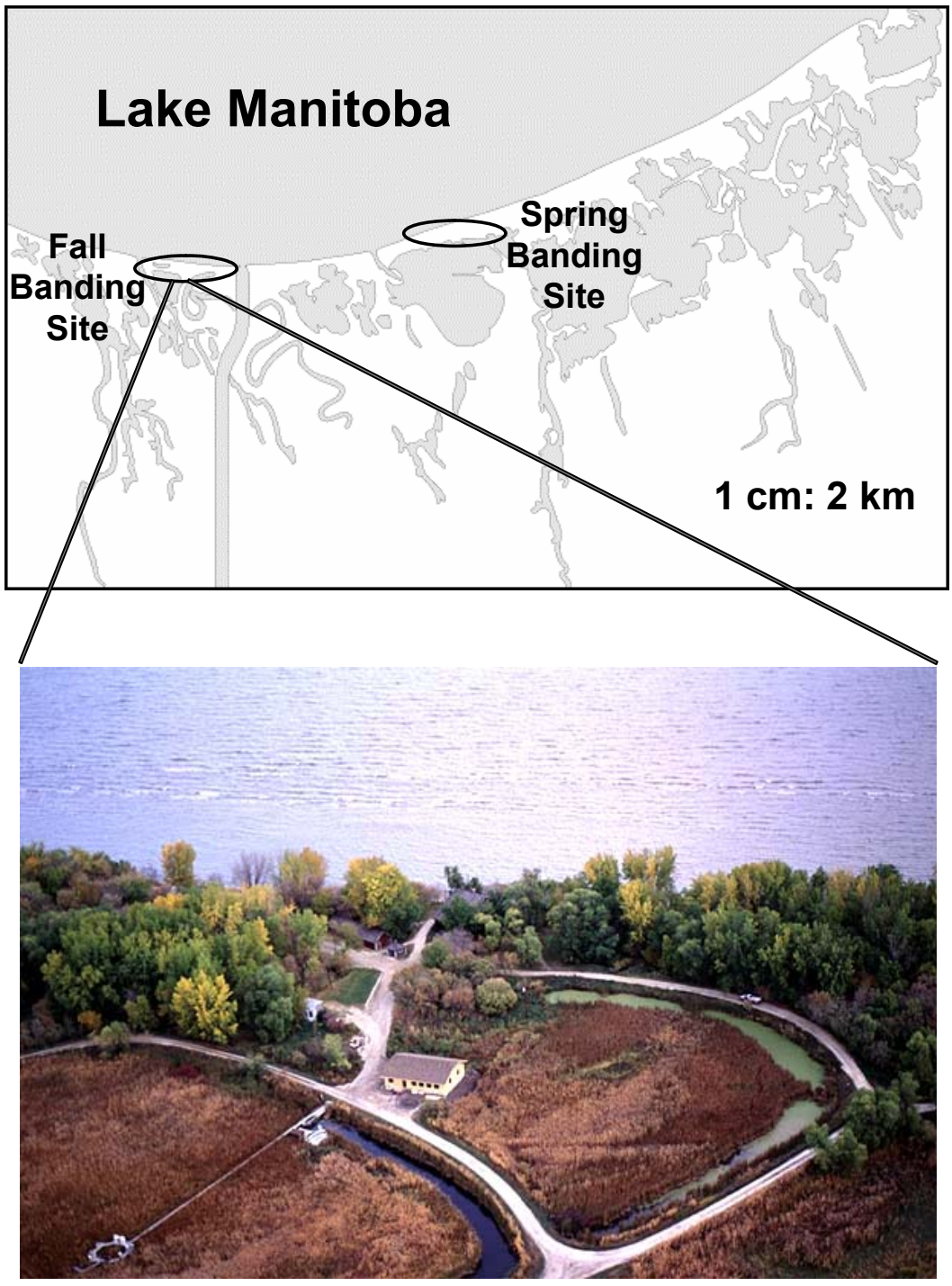

Fig. 1.5. Location of the spring and fall monitoring sites of the Delta Marsh Bird Observatory where samples of white-throated sparrows were collected (top panel) and an aerial view of the dune-ridge forest where the fall sampling took place (bottom panel).

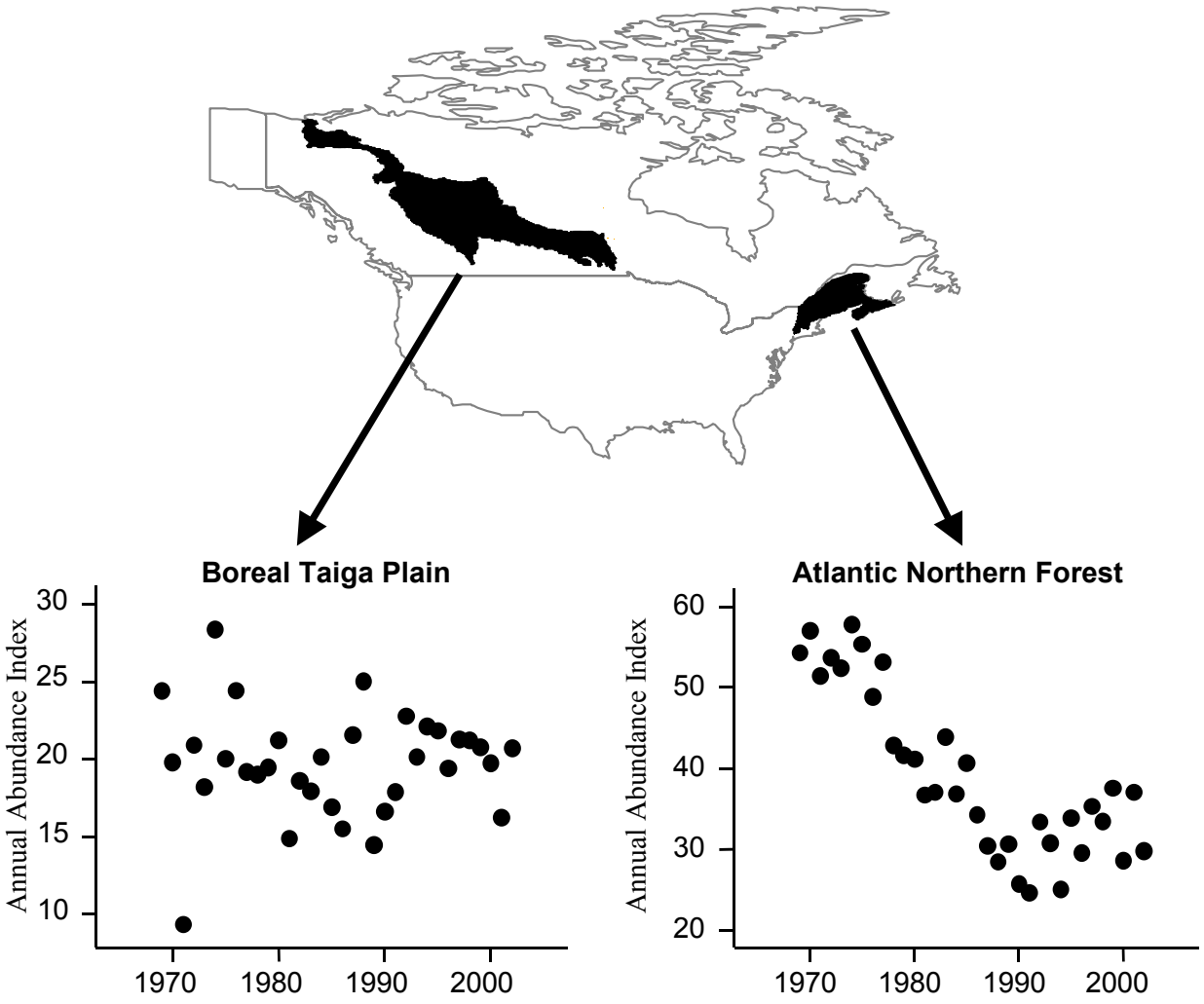

Fig.1.6. Geographic variation in population trends in white-throated sparrows. Indices of annual abundance of white-throated sparrows derived from the North American Breeding Bird Survey (BBS) are presented for the Boreal Taiga Plain (N = 98 routes) and Atlantic Northern Forest (N = 100 routes). BBS indices were taken from Downes et al. (2003). Note that the majority of surveys conducted in the boreal taiga plain region was biased towards southern locations.

CHAPTER 2: ESTIMATING ORIGINS OF SHORT-DISTANCE MIGRANT SONGBIRDS IN NORTH AMERICA: CONTRASTING INFERENCES FROM HYDROGEN ISOTOPE MEASUREMENTS OF FEATHERS, CLAWS, AND BLOOD

2.1. INTRODUCTION

Recent research based on stable-isotope tracers has demonstrated that events occurring during the wintering period can have carry-over effects on migratory birds to reproduction the following breeding season (reviewed by Webster et al. 2002, Rubenstein and Hobson 2004). While this concept is not new (Fretwell 1972), research investigating interactions among stages of the annual cycle of migratory birds using the isotope approach (Hobson et al. 1997a, Marra et al. 1998, Mehl et al. 2004, Bearhop et al. 2004, Norris et al. 2004) will almost certainly continue to provide novel and powerful analyses of factors influencing avian population dynamics. However, an incomplete understanding of which tissues most accurately reflect the isotopic signature of feeding locations used during specific periods of the annual cycle of birds currently limits the full potential of research elucidating seasonal interactions in migratory birds (Rubenstein and Hobson 2004).

Stable hydrogen isotope ratios (δD) in North American growing-season precipitation have been useful for tracing migratory connections in birds (Hobson and Wassenaar 1997, Chamberlain et al. 1997, Wassenaar and Hobson 2000, Rubenstein et

al. 2002). In North America, the pattern of δD values in precipitation follows a strong latitudinal gradient (Bowen and Revenaugh 2003, Meehan et al. 2004). The mean δD values of tissues and structures of living organisms feeding within local food webs generally reflect those of precipitation in a region (Yapp and Epstein 1982, Cormie et al. 1994, Hobson and Wassenaar 1997, Chamberlain et al. 1997). Feathers, which are metabolically inert, are permanently labelled with the isotopic composition of the food web at the location where they were synthesized, and as a result, the origin of birds can often be inferred from knowledge of the δD values of feathers compared to mean growing-season δD values from precipitation (Hobson 1999).

Researchers selecting tissues for isotope studies must take into consideration the elemental turnover rates of tissues since these rates determine how long tissues will retain information about previous feeding locations (Hobson and Clark 1992, Hobson and Clark 1993). Metabolically inert structures such as feathers and claws permanently retain the isotopic signature of the food web where they were synthesized (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Bearhop et al. 2003), whereas the temporal and spatial scales of feeding locations reflected by a metabolically active tissue is directly related to its elemental turnover rate. These tissue-specific elemental turnover rates range from a half-life of a couple of days for blood plasma to possibly years for bone collagen (Hobson and Clark 1992, Hobson and Clark 1993, Bearhop et al. 2002, Hobson and Bairlein 2003, Pearson et al. 2003, Evans-Ogden et al. 2004).

Currently, the only sample to have been used to estimate bird origins based on the stable hydrogen isotope techniques are feathers. However, while feathers have many characteristics that make them ideal for isotopic studies evaluating avian migratory

connectivity, it is not always possible to use feathers because some species moult only once a year, moult during migration, or have moult cycles that are poorly known (Pyle et al. 1997). Stable-carbon isotopes of blood have also been used in studies assessing migratory connections (Morrison and Hobson 2004, Norris et al. 2004). However, the metabolic turnover rates of blood remain poorly defined in wild birds (Evans-Ogden et al. 2004). Bearhop et al. (2003) demonstrated that claws of small passerines might provide a useful alternative. They found that the 1–2 mm tip of claws likely represents an integration of diet assimilated during a period of two to five months prior to the date of collection. This period corresponds to less than the duration of spring and fall migration for most North American migratory birds (Marra et al. 2005). Bearhop et al. (2003) suggested that claws could be useful for making estimates of the wintering and breeding latitudes of birds captured during spring and fall migration, respectively.

Here, I investigated δD values of feathers, claws, and cellular portions of blood from white-throated sparrows intercepted during migration, to determine if these measures provided concordant estimates of breeding and wintering latitudes. White-throated sparrows are short-distance migrants that breed primarily in the boreal forest of Canada and winter in the southeastern United States (Falls and Kopachena 1994). This species moults prior to fall migration (i.e., the preformative moult for young of the year and prebasic moult for adults) when they replace all of their feathers, and prior to spring migration (i.e., the prealternate moult) when they acquire their nuptial plumage (Howell et al. 2003). The latter moult involves only the replacement of body feathers, primarily in the head region (Pyle et al. 1997). Based on previous studies (described above) evaluating the integration of tissues grown at different periods of the annual cycle of

migratory birds, I constructed a diagram depicting hypothesized timescales reflected by the isotopic composition of various tissues sampled during spring and fall migration (Fig. 2.1). Further, for spring migrants, I compared the correspondence between δD values from three tissues that were expected to reflect the wintering grounds, specifically head feathers, claws (base and tip), and the cellular fraction of blood (Fig. 2.1). For fall migrants, I compared the correspondence between δD values from two tissues that were expected to reflect the breeding grounds of white-throated sparrows, specifically the tip of claws and tail feathers. Because migrating songbirds have high metabolic rates, I predicted that δD values of blood would provide estimates of origins that were poorly correlated with the δD values of tip of claws and head feathers, tissues grown on the wintering grounds and that have little to no metabolic activity. If considerable claw growth occurred during spring migration, I expected to find that claws would have more negative δD values than head feathers. Similarly, I expected that during fall migration claws would have more positive δD values than tail feathers. Further, if significant growth of claws occurred during migration, I also expected to find a difference between the δD values of the base (recent growth) and tip (older growth) of claws.

2.2 METHODS

2.2.1. Study Area

Fieldwork was conducted during spring and fall migration of 2002 and 2003 in the dune-ridge forest of Delta Marsh, Manitoba, Canada (98°23'W, 50°11'N). This area is a key staging ground for migratory songbirds *en route* to breeding grounds in boreal forest located 65 km to the north. Further, the study area is located approximately 1500-2500

m from the wintering grounds of white-throated sparrows (Godfrey 1986, Falls and Kopachena 1994).

2.2.2. Avian Samples

Ten mist nets were operated daily during spring (late April to early June) and fall (August to early October) in the dune-ridge forest abutting the southern shore of Lake Manitoba. Sampling protocols followed standard mist netting and banding procedures recommended by Hussell and Ralph (1995). To increase sample sizes, additional birds were captured in walk-in ground traps that were operated in the same area and during the same time period that mist nets were operated. Once a bird was captured, morphological measurements were taken, and a tail feather, approximately three head feathers, and a section of claw (2 - 4 mm) from the middle toe were collected from individuals. For some of the birds banded during 2002 spring migration, a small blood sample (25-100µl) was also collected from the brachial vein and using standard methods outlined in Campbell (1995). Microhematocrit tubes, used to collect blood, were centrifuged for 7 minutes at 12000 rpm using a clinical centrifuge (Thermo IEC IM-3411, Needham Heights, Massachusetts), and the plasma was removed and the cellular fraction of the blood was stored in 70% ethanol following Hobson et al.1997b. My field collections followed guidelines recommended by the Canadian Council on Animal Care.

2.2.3. Stable Isotope Analyses

Blood samples were freeze-dried, and feathers and claws were cleaned of surface oils using a 2:1 chloroform:methanol solution and allowed to air dry. Tip of tail feathers (0.31-0.37 mg), single head feathers (0.10-0.14 mg), base (proximal 2 mm) and tip

(distal 2 mm) of claws (0.31-0.37 mg), and blood samples (0.31-0.37 mg) were weighed out in silver capsules. Stable-isotope analysis of the nonexchangeable hydrogen was conducted using online continuous-flow isotope ratio mass spectrometry (CF-IRMS) performed on a Micromass Optima dual-inlet isotope ratio mass spectrometer (Micromass UK, Manchester, UK) as described Wassenaar and Hobson (2003). Estimates of deuterium concentration are expressed in the delta notation (δD), in units per mil (‰), and normalized on the VSMOW-SLAP standard scale. δD measurements of head feathers grown on the wintering grounds and tail feathers grown on the breeding grounds were highly repeatable (Chapter 3). Reproducibility of CF-IRMS and based on internal standards is ≤2.0 ‰ (Wassenaar and Hobson 2003).

2.2.4. Statistical Analyses

Certain head and tail feathers (<10% of samples) had δD values that corresponded to areas outside of the wintering and breeding range of white-throated sparrows, respectively. For tail feathers, this indicated that the preformative and prebasic moults were not completed prior to fall migration, or that certain tail feathers were replaced during fall migration or winter. For head feathers, these indicated that the prealternate moult was not complete (i.e., did not involve all head feathers) or was not completed prior to spring migration. Thus, I only used tail and head feathers that had δD values that fell within the possible range of values associated with the breeding ($\delta D_{feather} < -105‰$) and wintering ($\delta D_{feather} > -85‰$) range of white-throated sparrows, respectively, in my analyses. Concordance among δD values of claws, feathers, and cellular portions of blood was assessed with Pearson's correlations and paired-*t* tests. All analyses were two-tailed and performed with SPSS (version 9.0, Norušis 1998). Results are presented

as means and 95% confidence intervals and were considered significant at an alpha level of 0.05.

2.3. RESULTS

During spring migration, δD values of head feathers were positively correlated with those of tip of claws (Pearson's r = 0.43, N = 81, P < 0.001) but not with those of the base of claws (Pearson's r = -0.04, N = 27, P = 0.84). The tip of claws had more negative δD values than head feathers (Fig. 2.2; Paired *t*-test, t_{70} = 8.1, P < 0.001). Further, δD values of the base and tip of claws were positively correlated with each other (Pearson's r = 0.65, N = 36, P < 0.001) but tips had more positive δD values than bases (Mean, 95% C.I. of the difference between means = 8.8, 6.9 to 10.8 ‰; Paired *t*-test, t_{34} = 9.0, P < 0.001). During fall migration, δD values of tip of claws were positively correlated with those of tail feathers (Pearson's r = 0.73, N = 30, P < 0.001), although tail feathers had significantly more negative δD values than those of claws (Fig. 2.2; Paired *t*-test, t_{29} = -9.4, P < 0.001).

The δD values of the cellular portion of blood were not correlated with those of head feathers (Pearson's r = 0.43, N = 14, P = 0.13). One blood sample was an extreme outlier (δD value = -109 ‰; >3 SD from the mean) and had a very large influence on this correlation. Once this outlier was removed, the weak correlation between δD values of blood and head feathers was non-existent (Pearson's r = 0.06, N = 13, P = 0.84). In addition, the δD values of blood were not correlated with those of tip of claws (Pearson's r = 0.08, N = 25, P = 0.71) but were correlated with those of the base of claws (Pearson's r = 0.55, N = 18, P = 0.02).

2.4. DISCUSSION

I assessed the concordance between δD values of feathers with those of the cellular portion of blood and claws of birds intercepted during migration. I found that δD values of head feathers from spring migrants and tail feathers from fall migrants were correlated with those of the tip of claws, indicating that claw tips contained some information concerning wintering- and breeding-ground origins of spring and fall migrants, respectively. However, I uncovered compelling evidence that a significant amount of claw growth took place during both spring and fall migration. Thus, for migrating white-throated sparrows, I caution against claws as long-term position indicators. Further, because δD values of blood were correlated with those of base of claws, but were not correlated with those of the tip of claws or head feathers, δD values of blood cells contained little information on the wintering origin of white-throated sparrows captured during spring migration. Presumably, this would also be the case for the stable-isotope measurements of other elements (e.g., $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$).

Bearhop et al. (2003) found that claws of five European passerines grew at a rate of 0.04 mm per day. Thus, the distal portion of the claw would likely represent an integration of diet during the two to five months directly preceding the date of collection. My data suggest that claws of white-throated sparrows grow at a faster rate than those of the birds measured in Bearhop et al.'s (2003) study, since my results were consistent with a measurable amount of claw growth in white-throated sparrows most likely captured less than two months after leaving the wintering grounds. Specifically, δD values of white-throated sparrow claws were more negative than head feathers (representing wintering grounds) from birds captured during spring migration and more

positive than tail feathers (representing breeding grounds) from birds captured during fall migration. Further, the δD values of the base of claws were significantly different from the δD values of the tip of claws in spring migrants. These results are consistent with measurable effect of new growth on the δD values of claws, and can likely be explained in terms of the foraging tactics of this species. White-throated sparrows typically forage on the ground by clearing leaf litter with rapid kicking movements using both legs (Falls and Kopachena 1994). Such foraging tactics may cause considerable wear or stimulate increased rates of mitosis in claw tissues. Biases in estimates of origins of migrating birds provided by deuterium measurements might also be due to claw growth occurring not only from the base of the claw but also from the thin finger of pulp running down the center of the claw (Bearhop et al. 2003).

The δD values of the cellular portion of blood of migrating white-throated sparrows appeared to provide little to no information regarding wintering origins. One explanation for a lack of association between δD values of blood with those of head feathers and tip of claws is a rapid turnover rate of blood cells during migration. The high metabolic rates of migrating passerines (Blem 2000) could require high rates of erythropoiesis (production of new red blood cells), as found in other birds (Piersma et al. 1996). However, I am aware of three physiological processes that can result in a temporal mismatch between deuterium signatures of tissues and diet. First, it is possible that long-term energy stores are implicated in the synthesis of blood (Gannes et al. 1997). Second, protein catabolism occurring during migration releases water (Bauchinger and Biebach 1998, Jenni et al. 2000, Bauchinger and Biebach 2001), the hydrogen of which can be assimilated into the production of new tissues (Hobson et al.

1999). Lastly, evaporation of body water that occurs during migration (Landys et al. 2000) likely favors the lighter isotope of hydrogen (^{1}H) leading to an enrichment of deuterium in body water and, thus in newly synthesized blood cells (McKechnie et al. 2004). All three of these physiological mechanisms could have contributed to low correlations between deuterium measurements of cellular blood with those from feathers and claws.

Estimates of fractional turnover rates of blood have been shown to vary greatly among species and decrease interspecifically with body mass (Hobson 1999, Hobson 2003, Hobson and Bairlein 2003). However, no study has estimated the elemental turnover rates of deuterium in any bird tissue. Reported half-life estimates for carbon and nitrogen isotopes in blood of birds range from 3.9 days to 26.3 days (Hobson and Clark 1992, Haramis et al. 2001, Bearhop et al. 2002, Hobson and Bairlein 2003), although all tissue-specific half-life estimates of carbon and nitrogen isotopes in avian blood are based on birds in captivity (but see Morrison and Hobson 2004). Free ranging birds may have substantially higher metabolic rates, and consequently, faster turnover rates of isotopes in blood. Most estimates of isotope half-lives in avian blood are based on whole blood (cellular and plasma fraction). Hobson and Clark (1993) demonstrated that the half-life of carbon isotopes was approximately 30 days for the cellular portion of blood and 3 days for blood plasma of captive American crows (*Corvus brachyrhynchos*). Based on these captive studies and assuming that these estimates are representative of free-ranging birds, isotopic analyses of blood from species with relatively quick migrations (< 1 month) could provide some insights into bird origin during the premigratory period (Norris et al. 2004). However, my results suggest that

red blood cells of white-throated sparrows turn over too quickly to provide isotopic information associated with the wintering period.

In conclusion, I caution against the use of δD values of blood and claws as long-term position indicators for white-throated sparrows. I recommend that future studies use careful selection of tissues or evaluate multiple tissue types to assess the reliability of estimates of origins. Further, research is needed to determine the isotopic discrimination factors between deuterium concentrations of diet and blood and claws (Hobson et al. 1999) as these measurements will be needed to estimate signatures of food webs at avian breeding and wintering localities. This task will be complicated by the δD values of tissues being reflective of the deuterium signature of both diet and drinking water (Hobson et al. 1999; McKechnie et al. 2004). Additional growth rate estimates of avian claws would further enhance the usefulness of isotopic measurements of claws for tracking migration in birds. Furthermore, it is clear that more laboratory experiments are needed to evaluate the fractional turnover rates of tissues, and the extrinsic and intrinsic factors influencing these rates (Bearhop et al. 2002, Hobson, in press). As suggested by Hobson (in press), wind-tunnel studies evaluating the effects of flight on metabolic rates and turnover rates of stable isotopes in avian blood, would enhance our understanding of the utility of isotope analyses of blood cells to estimate pre-migratory conditions.

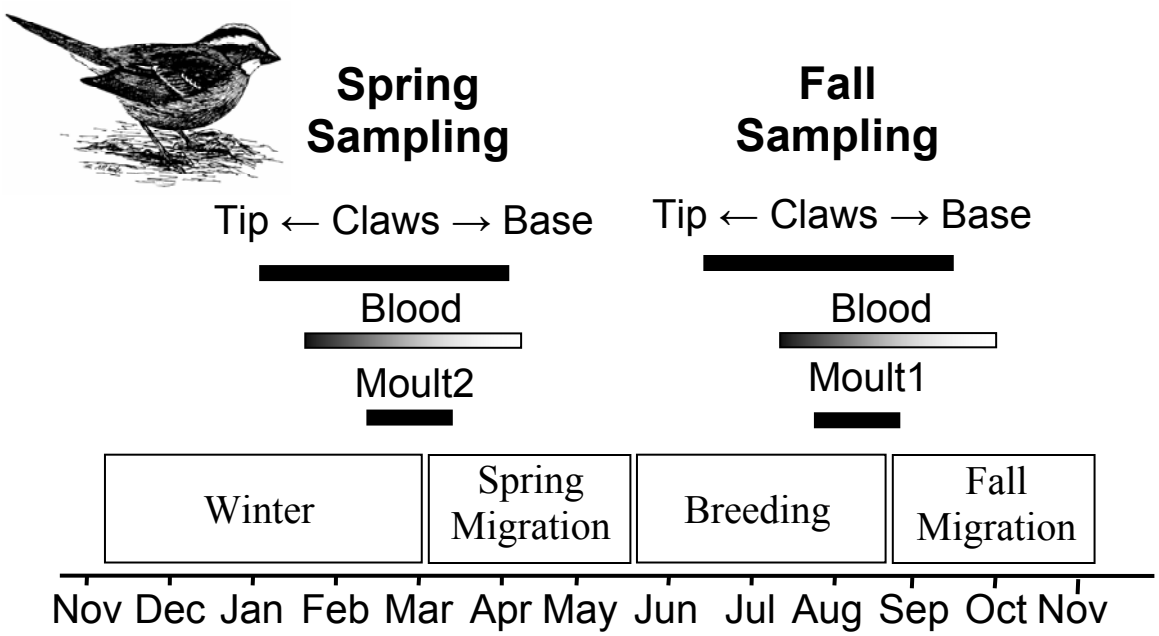

Fig. 2.1: Hypothesized timescales reflected by the isotopic composition of tissues of migratory passerines sampled during spring and fall. Blood, a metabolically active tissue, is represented as a gradient of timescales, and claws and feathers, metabolically inert structures, are represented as discrete time periods. The length of the bar also incorporates the variability in the timing of growth of tissues among individuals. Moult 1 denotes the preformative moult of young of the year and prebasic moult of adults. Moult 2 denotes the prealternate moult of after-hatch-year birds.

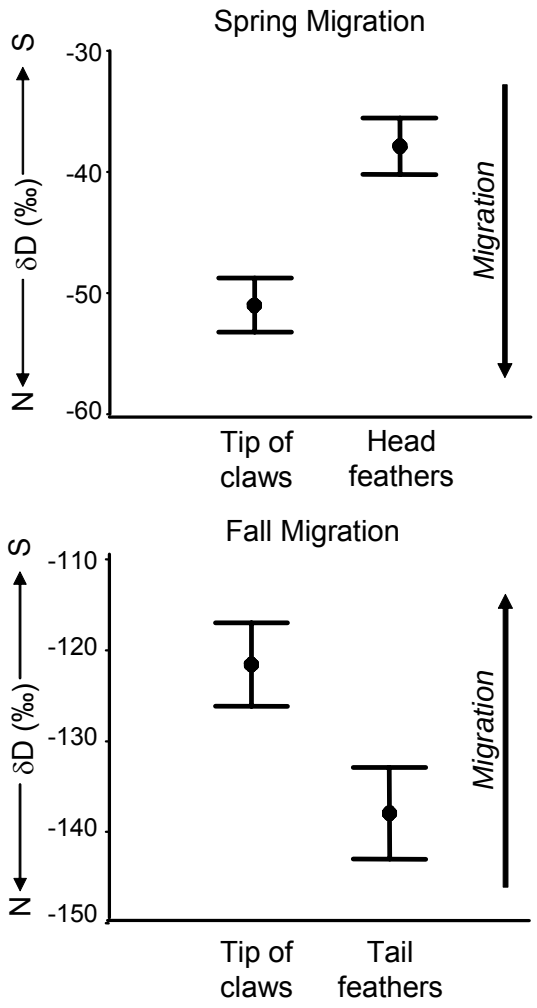

Fig. 2.2: δD values (mean, 95% C.I.) of paired claws and head feathers from white-throated Sparrows (N = 71) intercepted during spring migration, and of claws and tail feathers of individuals (N = 30) intercepted during fall migration at Delta Marsh, Manitoba, Canada. The concentration of deuterium in precipitation and avian tissues decreases with increasing latitude in North America. During spring migration, white-throated sparrows migrate from more northern latitudes with lower δD values to more southern latitudes with higher δD values, whereas during fall migration, the opposite occurs.

CHAPTER 3: STABLE ISOTOPE AND BAND-ENCOUNTER ANALYSES DELINEATE MIGRATORY PATTERNS AND CATCHMENT AREAS OF WHITE-THROATED SPARROWS AT A MIGRATION MONITORING STATION

3.1. INTRODUCTION

The conservation of North American migratory songbirds has been the focus of extensive recent research, motivated largely by evidence of long-term decline in populations of numerous species (reviewed by Rappole and Mcdonald 1994; Martin and Finch 1995). Population monitoring is essential for the conservation of North American migratory songbirds because it is crucial in estimating long-term trends in abundance and assessing the effectiveness of management actions (Dunn and Hussell 1995; Rich et al. 2004). The need for monitoring migratory passerines led to the establishment of the North American Breeding Bird Survey (BBS) (Sauer et al.1996; Sauer et al. 2003). The BBS, however, barely covers the mostly inaccessible Canadian boreal zone; a region hosting a major proportion of North America's breeding bird populations (Rich et al. 2004). Fixed migration monitoring stations (MMS), such as those operated by the Canadian Migration Monitoring Network (Fig. 3.1), apply constant-effort protocols to track changes in the abundance of migrating birds, and currently represent the only viable means of monitoring boreal songbird populations in North America; however, a major limitation in interpreting MMS data is that the geographical sampling (or

catchment) areas of each MMS are unknown (Dunn and Hussell 1995; Dunn et al. 1997; Wassenaar and Hobson 2001). Thus, observed population trends cannot be linked to causal events in specific geographical regions. Further, the traditional use of extrinsic markers (leg bands) and band-encounter analyses are inadequate for resolving catchment areas for nearly all bird species, because re-encounter rates of banded birds are extremely low and are biased to banding locations (Wassenaar and Hobson 2001). Thus, other approaches for quantifying origins of birds are needed to better delineate catchment areas of MMS and for tracing linkages between breeding, wintering, and stopover sites of migratory birds.

Linkages among events over the annual cycle of migratory birds and their ultimate effect on fitness (e.g., Marra et al. 1998; Norris et al. 2004) has stimulated considerable interest in the use of intrinsic tracers that provide information on areas used by birds at different times of the year (reviewed by Hobson 1999; Webster et al. 2002). Measurements of stable isotopes in animal tissues help in establishing migratory connections (Hobson and Wassenaar 1997; Chamberlain et al. 1997; Hobson et al. 2001; Meehan et al. 2001; Wassenaar and Hobson 2000, 2001; Kelly et al. 2002; Lott et al. 2003; Rubenstein et al. 2002; Pain et al. 2004). This approach is appropriate when birds move between areas having food webs with distinct isotopic patterns (Hobson 1999). One of the most important isotopic patterns used in making migratory connections is the continental pattern of hydrogen isotopes in precipitation, in North America (Bowen and Revenaugh 2003; Meehan et al. 2004; Hobson et al. 2004a). This isotopic pattern is useful because deuterium in rainfall is translated through diet into the tissues of living organisms feeding within local food webs (reviewed by Hobson 1999). Further,

metabolically inert tissues like feathers thereafter permanently record the hydrogen isotopic composition of the diet in the ecosystem where they were formed.

Patterns of migratory connectivity have important evolutionary, ecological, and conservation implications (Greenberg 1980; Berthold 1996, 2001; Webster et al. 2002). Increasingly sophisticated stable isotope approaches make it possible, in many cases, to critically assess the connectivity between breeding and wintering stages in songbirds (Hobson and Wassenaar 1997; Chamberlain et al. 1997; Kelly et al. 2002; Rubenstein et al. 2002; Webster et al. 2002). For example, δD values of feathers have been used to study latitudinal migration patterns in birds in North America (Kelly et al. 2002; Rubenstein et al. 2002; Smith et al. 2003). Two forms of latitudinal migratory patterns are chain migration and leapfrog migration (Berthold 2001). In chain migration, the latitudinal order of breeding populations remains the same on the wintering grounds. By contrast, in leapfrog migration the latitudinal order of breeding populations is the reverse of that on the wintering grounds. In chain migration, all breeding populations migrate approximately the same distance, whereas, in leapfrog migration, migration distances among breeding populations can differ tremendously. Identifying types of migratory patterns and determining whether connections between breeding and wintering localities are strong or weak will help predict the impact of changes in wintering ground conditions on breeding populations of birds and other animals (Rubenstein et al. 2002; Webster et al. 2002).

The objectives of this study were to use hydrogen isotope values of staging white-throated sparrows to: (1) determine wintering and breeding ground catchment areas of a MMS located in Manitoba, Canada; and to (2) evaluate the connectivity

between breeding/natal and wintering grounds of sparrows originating from these catchment areas. Unlike most North American migratory songbirds, reasonable numbers of banding encounters are available for white-throated sparrows banded in Canada and detected on the wintering grounds (Brewer et al. 2000). Thus, a secondary objective of this study was to evaluate the connectivity between breeding/natal and wintering localities using additional information provided by band-encounter analyses.

White-throated sparrows are short-distance migrants that breed primarily in the boreal forest (Godfrey 1986; Falls and Kopachena 1994), and winter primarily in the southeastern United States (Root 1988; Falls and Kopachena 1994). Kriged mean growing-season average δD of precipitation (δD_p) are available for the entire breeding and wintering range of this species (Meehan et al. 2004). White-throated sparrows undergo a complete moult (i.e., the preformative moult for the young of the year and the prebasic moult for adults) before fall migration, when they replace all of their feathers, and a partial moult (i.e., the prealternate moult) during late winter to early spring, which is completed before spring migration, with few exceptions (Falls and Kopachena 1994; Pyle et al. 1997; Howell et al. 2003). The latter moult involves only the replacement of body feathers primarily in the head region (Pyle et al. 1997). White-throated sparrows are largely site-faithful on the wintering (Piper and Wiley 1990) and breeding grounds (Falls and Kopachena 1994), and thus, δD values of tail and head feathers likely reflect the isotopic composition of food webs used in the area where the individual spent the majority of the breeding and wintering seasons, respectively. During spring, it may be possible to estimate wintering and previous breeding/natal locations of individuals by relating the δD values of feathers that were moulted during the winter (e.g., head

feathers) and previous summer (e.g., flight feathers) with modeled estimates of δD_p (Hobson and Wassenaar 1997, Meehan et al. 2004).

3.2. MATERIALS AND METHODS

3.2.1. Study Area

Fieldwork was conducted at the Delta Marsh Bird Observatory (DMBO) migration monitoring station during spring and fall migration, in the years 2002 and 2003, in the dune-ridge forest of Delta Marsh, MB, Canada (98°23′W, 50°11′N). This site is a key stopover location for migratory songbirds and is located 65 km from the southern edge of the boreal forest, the primary breeding grounds of white-throated sparrows. The wintering grounds of this species are approximately 1,500 to 2,500 km south of my study area (Falls and Kopachena 1994).

3.2.2. Avian Samples

Ten mistnets were operated daily during spring (late April–early June) and fall (August–early October). The large majority of the spring and fall passages of migrating sparrows fell within my sampling periods (DMBO, unpublished data). Sampling protocols followed the standard mistnetting and banding procedures recommended by Hussell and Ralph (1995). To increase sample sizes, additional birds were captured in ground traps that were operated in the same area and during the same time period as mistnets. Feathers were randomly selected from my total sample so that analyses would be representative of entire migratory passages and populations sampled by DMBO. Once a bird was captured, morphological measurements were taken and a tail feather (rectrix 4) and approximately three head feathers were collected from each individual. For some

individuals, I also collected a tertial feather and second tail feather to assess the repeatability of δD values.

3.2.3. Stable Isotope Analyses

Feathers were cleaned of surface oils using 2:1 chloroform:methanol solution and were air-dried. Single head feathers (0.1–0.14 mg), base and tip of tail feathers (0.31–0.37 mg), and tertial feathers (0.31–0.37 mg) were weighed out into silver capsules. Measurement of the non-exchangeable hydrogen δD of feathers was conducted using continuous-flow isotope ratio mass spectrometry, as described in detail by Wassenaar and Hobson (2003). Deuterium values are expressed in the delta notation, in units per mil (‰), and normalized on the VSMOW-SLAP standard scale. Like Wassenaar and Hobson (2001), I used an isotopic discrimination factor between δD_p and δD values of feathers of −25‰.

3.2.4. Band Encounter Analyses

Band encounters compiled from 1921 to 2002 by the US Geological Survey, Patuxent Wildlife Research Center, Bird Banding Laboratory were used to determine the connectivity between the breeding/natal and wintering locations of white-throated sparrows from Canada. Band returns from eastern (New Brunswick, Nova Scotia, Prince Edward Island, Newfoundland, and Labrador), central (Ontario and Québec), and western (Manitoba, Saskatchewan, Alberta, and British Columbia) Canada were analyzed separately to assess migratory connectivity of populations across the range of the species.

3.2.5. Statistical Analyses

I applied GLM to evaluate whether the δD values of head and tail feathers differed between spring and fall migration and between years (2002 vs. 2003). Competing models computed from GLM were ranked using Akaike's Information Criterion, corrected for small sample sizes (AIC_c) (Burnham and Anderson 1998). This method of model selection is based on the principle of parsimony (i.e., the best compromise of model fit and precision). Models with lower AIC values are more parsimonious, and it is generally accepted that models differing by <2, 2–4, 4–7, and >7 AIC_c units exhibit strong, some, little, and no support relative to other candidate models, respectively (Burnham and Anderson 1998). To facilitate model comparisons, I computed ΔAIC_c (the difference between a particular model and the model with the lowest AIC_c) and normalized Akaike weights (Burnham and Anderson 1998).

Pearson correlations were used to evaluate the repeatability of tail and head δD values for feathers grown on the breeding (δD values<−105‰) and wintering (δD values>-85‰) grounds, respectively. Significant within-site variability in δD values of feathers has been uncovered by previous studies (Hobson and Wassenaar 1997; Wassenaar and Hobson 2000; Meehan et al. 2001). I compared my estimates of variability in head and tail δD values with estimates of within-site variability of feather δD values from two previous studies (Clegg et al. 2003; Hobson et al. 2004b). Similar to this study, these studies focused on passerines and corrected for the exchangeable portion of hydrogen in feathers. I computed the mean within-site variance (weighted by sample size) for all sites used in both studies, except one site evaluated in Hobson et al. (2004b) that had an extremely large variance (s^2=52, 441) and influence on the mean

estimate of variance. I then used a variance ratio test to compare my estimates of variance in δD values of feathers to the mean within-site variance estimate to determine if it was probable that my birds originated from a localized area.

I computed 50% and 75% tolerance limits at 95% confidence levels (Walpole and Meyers 1993) for δD values of tail and head feathers to estimate the sparrow breeding and wintering ground catchment area, respectively, for DMBO. To delineate geographic catchment areas, I converted δD values of feathers to δD_p values (δD_p= δD of feathers − 25‰). Further, limits of the catchment areas were constrained by the boundaries of geographical range of the species and by the 50% and 75% tolerance limits of δD values. Consequently, the areas falling within the 50% and 75% tolerance intervals of δD values reflect areas from which 50% and 75%, respectively, of the individuals sampled at Delta Marsh originated. Catchment areas were generated using a geographic information system (GIS) based model of δD_p values (Meehan et al. 2004). While there is evidence suggesting that this feather discrimination value differs with age in raptors (Meehan et al. 2003), no such evidence has been found for songbirds (Hobson et al. 2004b).

I used a Pearson's correlation to evaluate the relationship between δD values of tail and head feathers grown on the breeding (δD values < −105‰) and wintering (δD values >85‰) grounds, respectively. I reasoned that a negative relationship between δD values of those feather types would be consistent with a leapfrog migratory pattern, whereas a positive correlation would be consistent with a chain migration pattern (Fig. 3.2, top panel). If there were no relationship between δD values of tail and head feathers,

it would indicate that there was no connectivity between breeding/natal and wintering latitudes of sampled populations.

To delineate approximate wintering origins of birds banded from 1921 to 2002 from eastern, central, and western Canada, I relied on Jenrich–Turner's range estimator (Jenrich and Turner 1969) computed using Arcview 3.2 and the extension, Animal Movement 2.0 (Hooge and Eichenlaub 1997). Only data that could be associated with one of the Canadian regions described above and contained information on the position of a bird during the wintering period (November–April) were used in these analyses. Jenrich–Turner's range estimator is robust to variations in sample sizes and assumes that locations are distributed normally along two axes. As such, it was suitable for the sample sizes and distributions of the banding data. I used a density distribution of 50% to identify the core wintering areas of individuals breeding or born in the three broad regions of Canada.

3.3. RESULTS

The δD values of 138 tail and 93 head feathers were measured for sparrows captured during spring migration in 2002, and 122 and 102 feathers, respectively, in 2003. During fall migration, 102 and 90 tail feathers were sampled in 2002 and 2003, respectively. The fall migration sample consisted of 136 hatch-year (HY) individuals and 56 after-hatch-year (AHY) individuals. As expected, mean δD values of tail and head feathers differed significantly (Figs. 3.3 and 3.4). Nearly all tail feathers reflected the expected δD_p for the breeding range of white-throated sparrows, whereas nearly all δD values of head feathers reflected those expected from the wintering range.

There was little to no evidence indicating that δD values of tail feathers differed between years (mean, 95% CI difference between means: −1.2, −4.6 to 2.2‰) but there was strong support for differences in these values between seasons (mean, 95% CI difference between means: 7.1, 3.7 to 10.5‰; Table 3.1). Differences between seasons, however, were due largely to feathers grown south of the breeding range (Fig. 3.3; areas with δD values > -105‰). Totals of 12 out of 138 (9%) and 13 out of 122 (11%) tail feathers had δD values associated with latitudes south of the breeding range. Among birds banded during fall migration, only 2 out of 192 (1%) tail feathers had values associated with latitudes south of the breeding range. δD values of tail feathers of HY and AHY individuals captured during fall migration did not differ significantly (mean, 95% CI difference between means: −2.9, −6.9 to 1.1‰). For head feathers, mean δD values did not differ between years (mean, 95% CI difference between means: 5.0, −1.8 to 11.8‰). Similar to tail feathers, there was clear evidence that some head feathers were moulted during a previous season (Fig. 3.4; migratory or breeding seasons). A total of 4 out of 93 (4%) and 11 out of 102 (11%) head feathers were apparently grown north of the wintering range (i.e., were from areas with feather δD values < −85‰) in 2002 and 2003, respectively (Fig. 3.4).

δD values of tail feathers grown on the breeding grounds (feather δD values < −105‰) were highly repeatable (Pearson's r, 95% C.I.=0.99, 0.96 to 1.0). Further, δD values of the base of tail feathers were highly correlated with (Pearson's r, 95% C.I. = 0.97, 0.93 to 0.98, N = 30) and did not differ from those of the tip of tail feathers (mean, 95% CI difference between means: −1.0, −2.2 to 1.8‰). Similarly, δD values of tertial feather (reflecting another feather type that is moulted during the complete moult prior

to fall migration) did not differ from (mean, 95% CI difference between means: 0.32, −2.21 to 2.86‰) and were highly correlated with those of the tip of tail feathers (Pearson's r, 95% C.I.= 0.93, 0.72 to 0.98, N = 10). δD values of head feathers reflecting the wintering grounds (>-85‰) were also highly repeatable (Pearson's r, 95% C.I.=0.91, 0.80 to 0.96, N = 22).

δD values of tail feathers corresponded to latitudes in the mid-boreal to high-boreal of western Canada (Fig. 3.5). Approximately one third of the birds that were banded during spring and fall migration at the monitoring station had tail δD values that corresponded to areas located north of the northern region covered by the current BBS (Fig. 3.3). δD values of head feathers corresponded to areas in the southeastern United States (Fig. 3.4). Variability among head δD values was more than three times the within-site levels of variability in δD values ($F_{195, 575} = 3.2$, $P < 0.001$), whereas variability in δD values of tail feathers was nearly two times more than the within-site levels of variability in δD values ($F_{452, 575} = 1.8$, $P < 0.001$). There was no relationship between δD values of head and tail feathers (Pearson's r, 95% C.I. = 0.07, −0.09 to 0.23, N = 195), indicating very weak connectivity between breeding/natal and wintering latitudes of populations originating from catchment areas.

Between 1921 and 2002, only 201 sparrows were banded in Canada and recaptured within their wintering range or were banded within their wintering range and recaptured in Canada. Of these, only 10, 57, and 40 encounters from western, central, and eastern regions, respectively, could be linked with the wintering period (November–April). Band recoveries were spread out over many years (>45 years) for all three zones (western, central, and eastern). Thus, there did not appear to be any substantial temporal

or spatial bias in the data. The 50% probability ellipses of birds from eastern and central Canada overlapped, although birds from western Canada were located primarily west of the wintering grounds of birds from eastern and central Canada (Fig. 3.6).

3.4. DISCUSSION

Stable hydrogen isotope analyses of feathers revealed that the migration monitoring stations sampled white-throated sparrow populations originating from a large catchment area including remote breeding areas that are currently not monitored by any other large-scale avian monitoring programs. Spring and fall δD values of tail feathers reflected δD_p (Meehan et al. 2004) expected at latitudes ranging from the very northern to the very southern extent of the western boreal forest. δD values of head feathers indicated that sparrows stopping at Delta Marsh during spring migration originated from a broad catchment region in the southeastern United States. Further, I found no evidence that breeding/natal and wintering locations of populations originating from the catchment areas were related, implying that there was extensive mixing of breeding populations from the catchment area on the wintering grounds; however, based on limited band returns, there appeared to be clear longitudinal segregation between the wintering grounds of breeding populations from western Canada from those from central and eastern Canada. The latter result suggests that white-throated sparrows have a parallel migration system. My study showed that white-throated sparrows, which moult different feather tracks on breeding and wintering grounds, can be sampled during spring migration to link both breeding/natal and wintering origins of individuals with a specific stopover site. As such, my findings corroborate the method of Wassenaar and Hobson (2001) who first suggested that δD values of feathers of staging migrants can be

used to delineate the breeding catchment areas of MMS (see also Meehan et al. 2001; Smith et al. 2003).

For many North American passerines, flight feathers are grown on or near the breeding grounds, and so these feathers form useful samples for conducting stable isotope analyses to estimate breeding/natal localities of birds (Hobson and Wassenaar 1997; Chamberlain et al. 1997; Wassenaar and Hobson 2000; Meehan et al. 2001, and Rubenstein et al. 2002). As shown, feathers moulted on the wintering grounds during the prealternate moult can be used to assess linkages between breeding/natal and wintering origins. For species that do not have a prealternate moult, stable isotope values of avian claws might provide a useful alternative wintering ground tracer for birds sampled during spring, although the usefulness of claw material for this purpose is dependent on wear and growth rates of claws and duration of migration (Bearhop et al. 2003; Chapter 2).

The assumption that flight feathers of migratory songbirds in North America are grown on or near the breeding/natal grounds (Rubenstein and Hobson 2004) is not valid for all migratory birds. Some species moult their flight feathers during fall migration (Winker et al. 1992; Wassenaar and Hobson 2001; Leu and Thompson 2002). Clearly, such moult-migration patterns would have significant impacts on isotope-based estimates of breeding/natal ground origins. I also evaluated whether moult-migration occurred in white-throated sparrows by comparing δD values of the tip (older material) and base (more recent material) of tail feathers and by comparing δD values of tail feathers with those of tertial feathers (a flight feather moulted during the prebasic moult but typically before the replacement of outer rectrices; Ginn and Melville 1983). I

reasoned that if flight feathers were grown south of the breeding grounds, the tip of tail feathers would have more negative δD values than the base, and that the tip of tail feathers would have more positive δD values than those of tertial feathers. My results showed that the δD values of these feather types were highly correlated and did not differ significantly from each other. Further, less than 4% of white-throated sparrows captured during fall migration were actively growing flight feathers (D.F. Mazerolle, unpublished data). Regarding head feathers, few individuals (<4%) that were captured at the monitoring stations had not fully completed their prealternate moult. Head feathers from individual sparrows also provided highly repeatable estimates of δD values. Together these findings suggest that moult during migration did not appear to have significant implications for my estimates of origins derived from δD measurements. I agree with the caution of Rubenstein and Hobson (2004) that future isotopic studies should assess the likelihood that feathers provide reliable and repeatable estimates of origins. Clearly, a greater understanding of moulting chronologies in migratory birds would greatly benefit future applications of stable isotope analyses for evaluating migratory connections. I suggest that the stable isotope technique is currently the best tool to evaluate delayed moult in birds that migrate latitudinally in North America.

Understanding migratory patterns and levels of connectivity is necessary to predict the effects of changes in wintering conditions on breeding populations (Rubenstein et al. 2002; Webster et al. 2002). I found that there was extensive mixing of breeding populations along a latitudinal axis within the wintering catchment area, indicating weak latitudinal connectivity between areas. Future studies will be necessary to determine if other factors, such as individual characteristics, have significant

influences on the distribution of birds on the wintering grounds (see Cristol et al. 1999). Based on band returns, there appeared to be clear segregation of breeding populations on the wintering grounds along a longitudinal axis at the scale of the entire geographical range of the species. This emphasizes that conventional techniques, such as banding, ought to be used to augment stable isotope approaches to making migratory connections by providing insights into the appropriate spatial scale of analysis (Smith et al. 2003).

White-throated sparrows have exhibited changes in population size during the past four decades; however, trends have been inconsistent across the breeding range, although I recognize that data from the BBS is only available for the southern portion of the range. Specifically, populations from eastern and central Canada experienced a marked decline starting in the mid-1970s that lasted for nearly 20 years, whereas populations from western Canada experienced only slight to no declines during this period (Downes and Collins 2003; Downes et al. 2003). Population declines that occurred in eastern and central populations have been associated with harsh weather conditions during the winters of the mid-1970s, which likely reduced survival of juveniles and adults (Sauer et al. 1996). My analyses reveal that there is little mixing between populations from western and eastern Canadian populations (see also Brewer et al. 2000) which leads me to suspect that geographical differences in trends of breeding populations were likely due to wintering-ground conditions.

In summary, the avian migration monitoring station provided new information on changes in populations of white-throated sparrows originating from very broad catchment areas, including birds from regions not monitored by any other large-scale monitoring programs. Such catchment delineations, which are otherwise extremely

difficult to estimate for nearly all migratory songbirds, enhance the value of population trend estimates derived from MMS. Similar to Wassenaar and Hobson (2001), my results also suggest that population trends detected by MMS are likely representative of large-scale, as opposed to local-scale, changes in demographic rates (see also Meehan et al. 2001; Smith et al. 2003).

Table 2.1: Summary output from competing general linear models approximating δD values of tail feathers of white-throated sparrows. Models are based on δD values of 138 and 102 birds captured during the spring and fall, respectively, of 2002 and 122 and 90 captured during the spring and fall, respectively, of 2003.

Model	*K*	Δ AIC_c	Akaike Weight
Season	3	0.00	0.74
Year + Season	4	2.51	0.21
Year + Season + Interaction	5	5.33	0.05
Intercept	2	13.82	0.00
Year	3	16.37	0.00

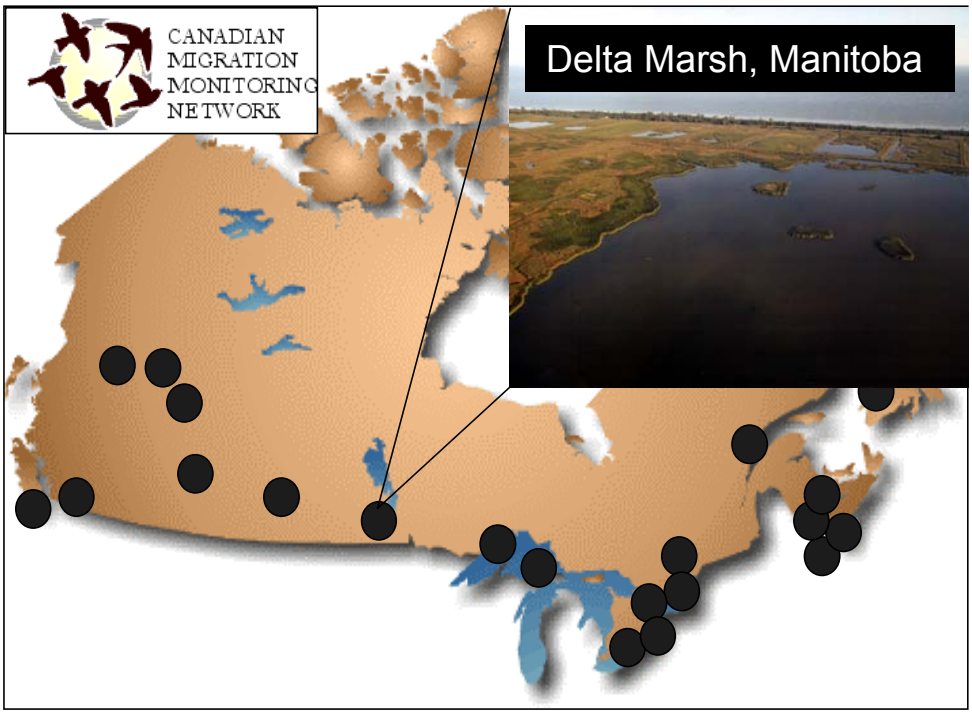

Fig. 3.1. Location of the monitoring sites forming the Canadian Migration Monitoring Network and aerial view of the monitoring site of the Delta Marsh Bird Observatory where samples of white-throated sparrows were collected for this study. Black circles represent avian migration monitoring stations forming the Canadian Migration Monitoring Network.

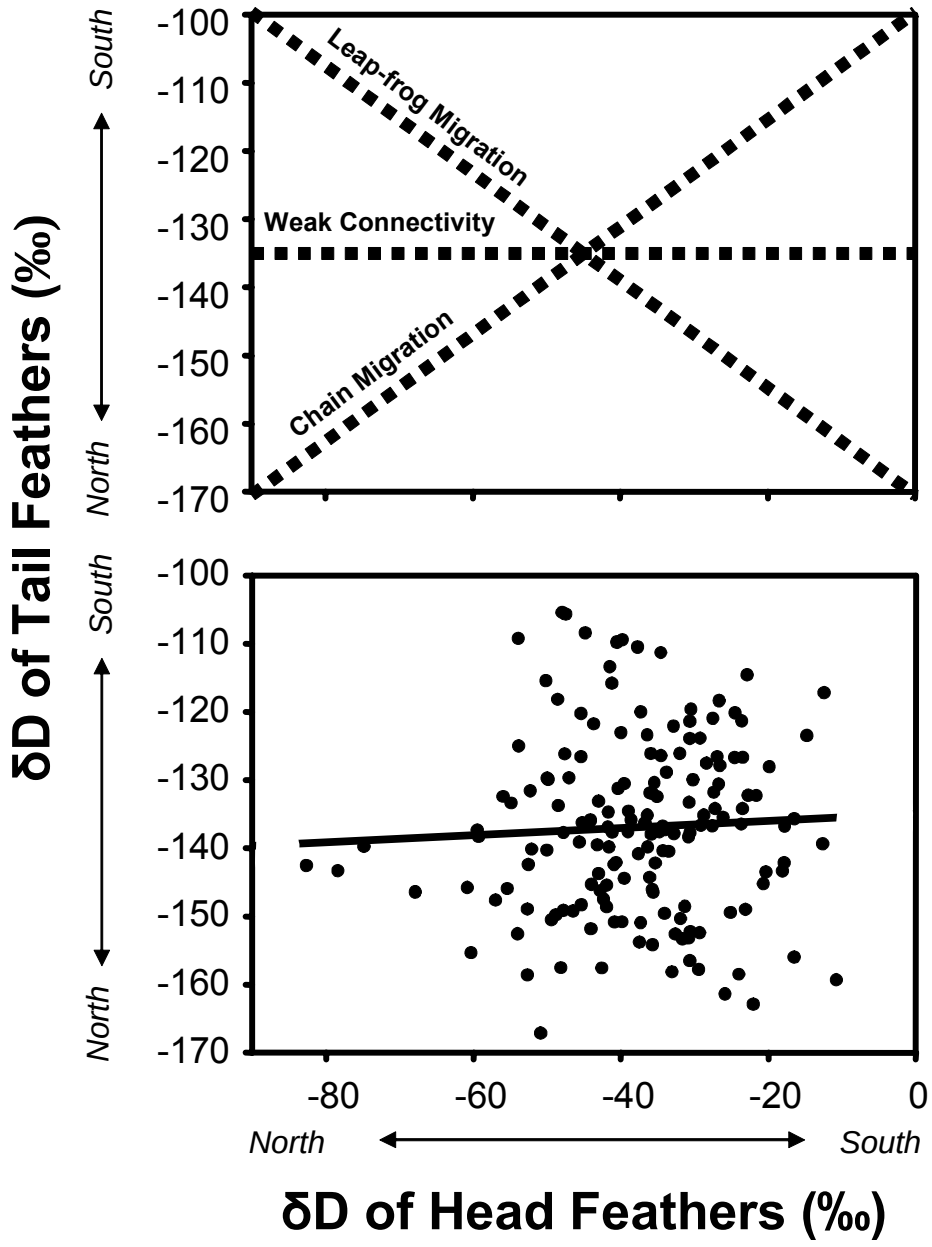

Fig. 3.2. Schematic diagram depicting the relationships between δD values of head and tail feathers expected with leap-fog migration, chain migration and with weak migratory connectivity (top panel). The bottom panel depicts the relationship between δD of head and tail feathers values measured for white-throated sparrows sampled during the spring of 2002 and 2003 at Delta Marsh, MB.

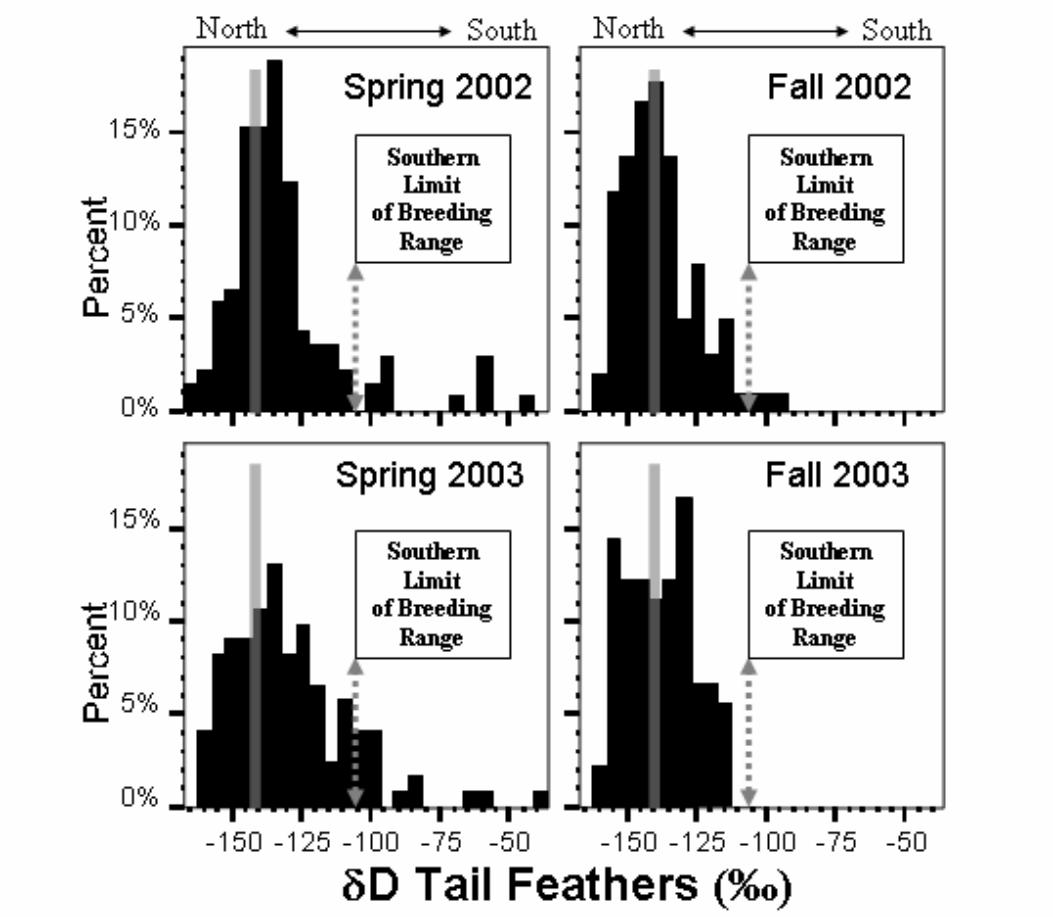

Fig. 3.3: Frequency distribution of the δD values of tail feathers (‰) of white-throated sparrows staging at Delta Marsh, Manitoba, during spring and fall migration 2002 and 2003. The solid grey bar indicates the approximate northern boundary of the coverage of the North American Breeding Bird Survey in western Canada.

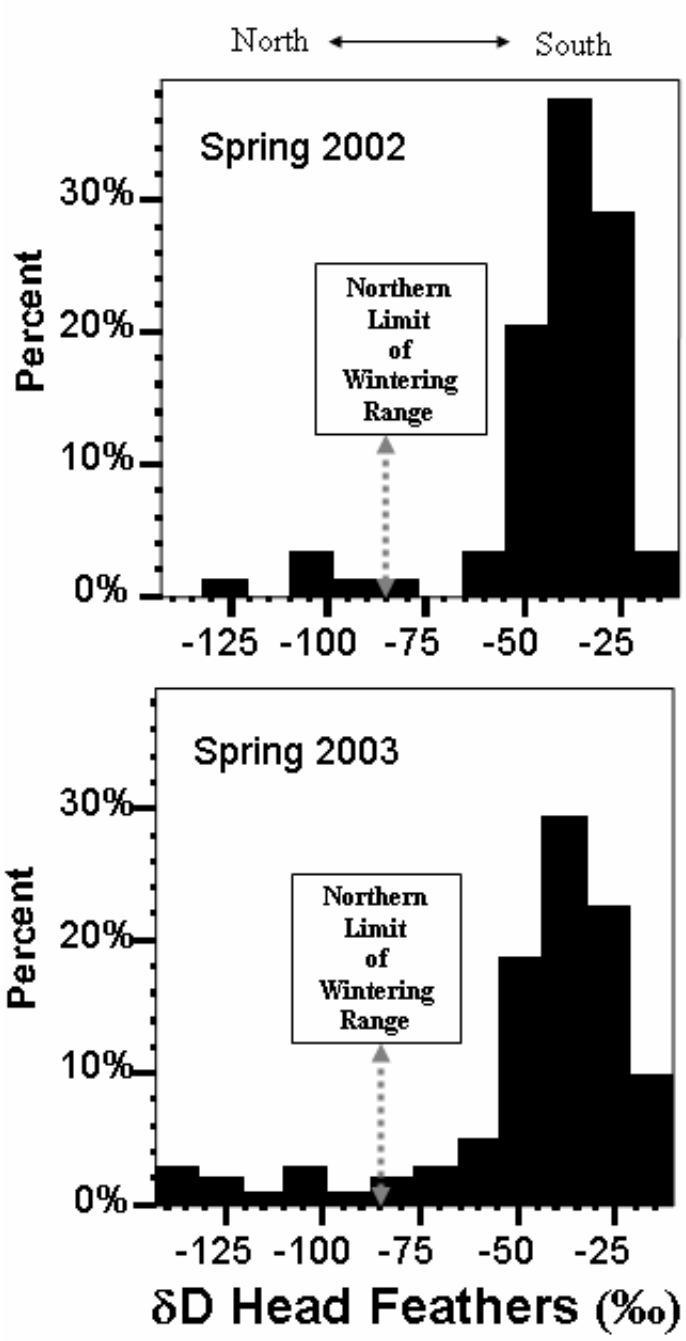

Fig. 3.4: Frequency distribution of the δD values of head feathers (‰) of white-throated sparrows staging at Delta Marsh, Manitoba, during spring migration 2002 and 2003.

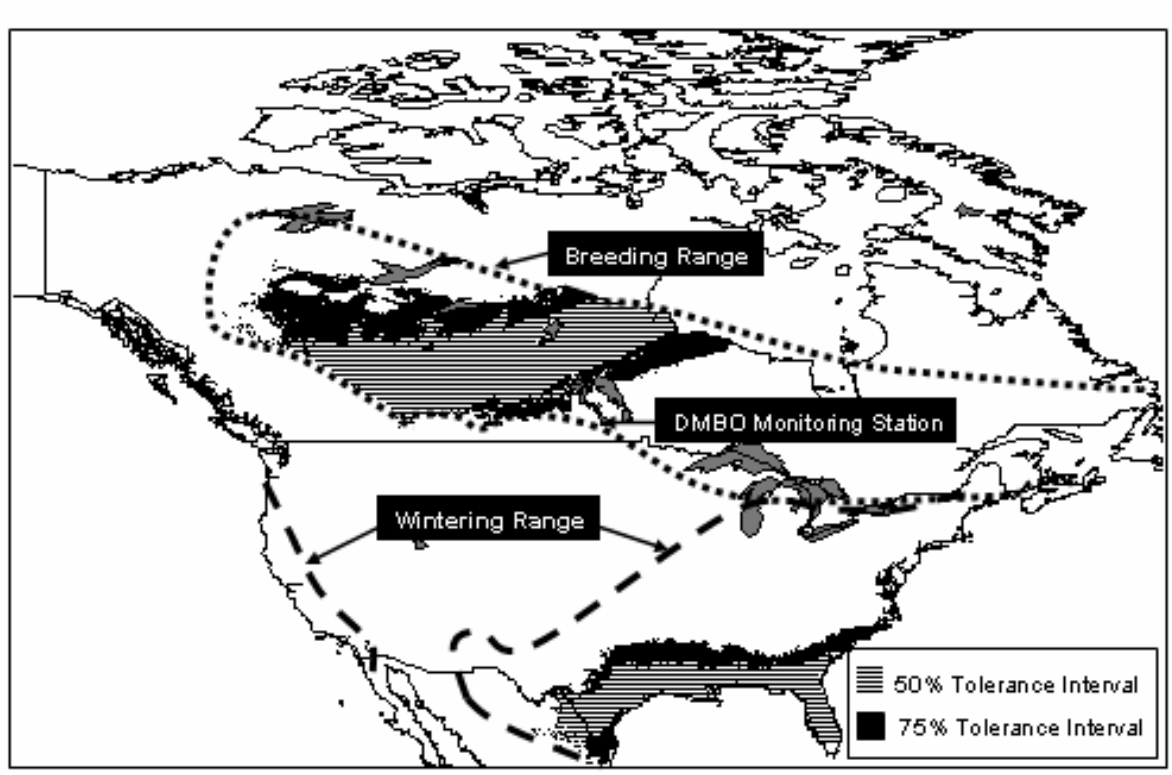

Fig 3.5. Probable breeding and wintering catchment areas of white-throated sparrows banded by the Delta Marsh Bird Observatory's (DMBO) migration monitoring station in Manitoba. Limits of the catchment areas were constrained by the boundaries of geographical range of the species and by the 50% and 75% tolerance limits of δD values of feathers (‰). These estimates were based on a level of confidence of 95%. The map was generated using a GIS based model of δD values of feathers.

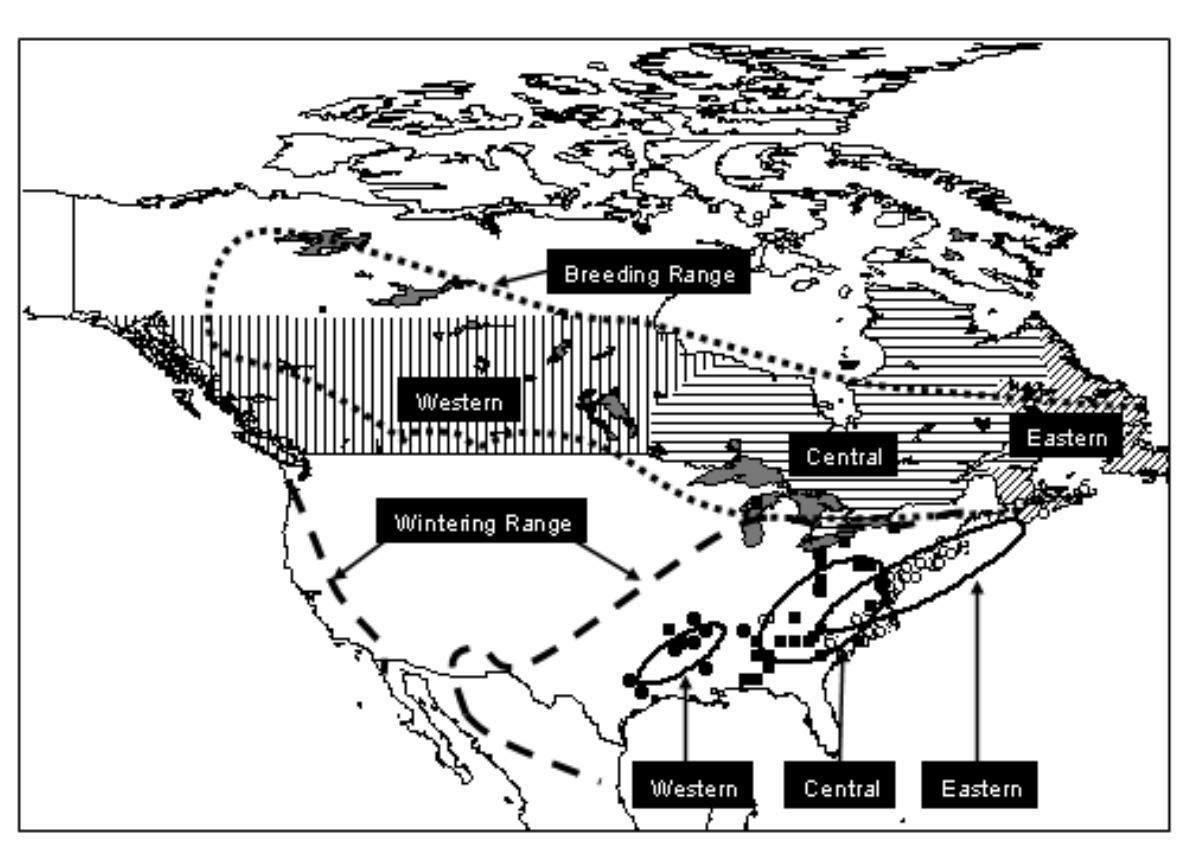

Fig. 3.6: Location of white-throated sparrows from western (●), central (■), and eastern (○) Canada encountered on the wintering grounds. Circles represent 50% Jenrich-Turner's range estimates for white-throated sparrows from eastern (N = 40), central (N = 57), and western (N = 10) Canada. No band returns of birds originating from areas north of the western Canadian provinces were available.

CHAPTER 4: PATTERNS OF DIFFERENTIAL MIGRATION IN WHITE-THROATED SPARROWS EVALUATED WITH ISOTOPIC MEASUREMENTS OF FEATHERS

4.1. INTRODUCTION

Knowledge of when and where birds migrate is basic to understanding their ecology and evolution (Berthold et al. 2003). Sexual segregation in space use during the non-breeding season is widespread in birds and has important implications for the evolutionary ecology and population dynamics of species (Cristol et al. 1999). Such segregation is thought to occur because of competitive exclusion between the sexes, mediated by differences in social dominance status or niche specialization in turn resulting from differences in morphology or reproductive roles between the sexes (Ketterson and Nolan 1976; Marra 2000; Phillips et al. 2004). Further, sexual segregation during the non-breeding season can take place at various spatial and temporal scales (Cristol et al. 1999) and can have important carry-over effects to the breeding season (Marra et al. 1998; Norris et al. 2004). One of the most common forms of sexual segregation in birds is differential migration, whereby females migrate farther from the breeding grounds than males (Ketterson and Nolan 1976; Cristol et al. 1999). A full evaluation of ecological factors responsible for the evolution of differential migration and potential carry-over effects to reproduction has been hampered by difficulties in tracking migratory individuals from winter to breeding localities (Marra et al. 1998; Cristol et al. 1999). Here, I evaluated factors responsible for differential

migration in a North American short-distance migrant, the white-throated sparrow. I examined linkages between the distributions of individuals during winter and timing of arrival at a stopover site near their boreal breeding grounds using stable hydrogen isotope (δD) measurements of feathers grown prior to fall migration from breeding grounds and those feathers grown on the wintering grounds.

Intrinsic tracers, such as stable isotope assays, provide powerful tools for analyzing ecological factors influencing the distribution of birds during the non-breeding season (Marra et al. 1998; Rubenstein and Hobson 2004). In particular, δD measurements provide one of the best available tracers for identifying latitudinal origins of North American migratory birds (Hobson and Wassenaar 1997; Rubenstein et al. 2002). Mean growing-season patterns of deuterium in precipitation (δD_p) are incorporated through diet into the tissues of birds feeding within local food webs (Hobson and Wassenaar 1997). δD_p varies approximately with latitude in North America and is transferred to metabolically inert structures such as feathers that permanently retain the non-exchangeable deuterium signature of the food web where they were synthesized. Consequently, it is possible to estimate moulting latitudes of birds by relating δD values of feathers with interpolated values of δD_p for the North American continent (Meehan et al. 2004).

In migratory passerines, differential timing of migration typically takes the form of protandry, whereby males arrive earlier than females on the breeding grounds (Morbey and Ydenberg 2001). This is thought to occur because costs, benefits, or constraints associated with early arrival differ between sexes and result in sex-specific optimal migration strategies (Francis and Cooke 1986; Morbey and Ydenberg 2001).

Competition among males for territories and mates results in intense selection for their early arrival on breeding grounds (Møller 1994; Kokko 1999). Females likely also benefit from arriving early on the breeding grounds; however, their arrival patterns are constrained by the energy requirements needed for egg production (Smith and Moore 2003). Due to their smaller size, the costs of early arrival may be greater for females than males because females are thought to be less able to survive harsh weather conditions associated with early spring (Francis and Cooke 1986; Weatherhead and Clark 1994; Kissner et al. 2003). Finally, protandry can also occur if selection acts indirectly via selection on a trait other than timing of arrival. In migratory birds, this may involve indirect selection on arrival dates via sex-biased differences in wintering distributions (Marra et al. 1998; Cristol et al. 1999). Such constraints can also occur within sexes and result in carry-over effects to reproduction by affecting the timing of arrival of individuals (Marra et al. 1998).

Three non-exclusive hypotheses have been suggested to explain the selective pressures responsible for latitudinal segregation of sexes on the wintering grounds (Cristol et al. 1999). The *arrival time hypothesis* predicts that the sex that experiences the most intense competition for breeding resources should winter farther north to facilitate early arrival to breeding areas in the spring (Myers 1981). This hypothesis is based on the empirical observation that the latitude at which a bird winters is closely related to its date of arrival on the breeding grounds, an assumption that has yet to be adequately evaluated (Cristol et al. 1999). The *body size hypothesis* suggests that larger individuals winter at more northern latitudes because they are better able to survive harsh weather conditions and prolonged periods with low food availability than smaller

individuals (Ketterson and Nolan 1976). This hypothesis is based on the assumption that differential migrant species exhibit sexual-size dimorphism (i.e., male body size > female body size). Further, the body size hypothesis assumes that larger birds are more likely to survive inclement weather conditions than smaller birds (Belthoff and Gauthreaux 1991; Cristol et al. 1999). Currently, there is little support for a relationship between intraspecific variation in body size and ability to survive inclement weather conditions (Ketterson and King 1977; Stuebe and Ketterson 1982; Weatherhead and Clark 1994). The *dominance hypothesis* is predicated on the notion that the more dominant sex migrates to the closest suitable wintering habitats, a strategy that is predicted to optimize survival, and forces the more subordinate sex to migrate farther south (Gauthreaux 1978). This hypothesis is based on the assumption that migration is costly and that the subordinate sex, typically females, is forced to migrate to more southern latitudes (Cristol et al. 1999). Evidence that females are subordinate to males during winter has been demonstrated in several species (Piper and Wiley 1989; Marra 2000). However, the role of dominance in the settlement of males and females latitudinally on wintering grounds remains unclear (Rogers et al. 1989; Cristol and Evers 1992), as do costs associated with migrating to more southern latitudes (Sandercock and Jaramillo 2002; Sillett and Holmes 2002).

Much of our understanding of factors influencing latitudinal segregation of sexes in birds stems from work conducted on only a few species (e.g., dark-eyed juncos *Junco hyamelis*; Ketterson and Nolan 1976). Further, differential migration could result from a combination of factors. Many studies have evaluated latitudinal segregation of sexes on wintering areas in birds, but none has been able to test hypotheses of differential

migration by linking simultaneously body sizes, arrival dates, and wintering latitudes of individual birds. Using δD measurements of feathers reflecting breeding and wintering latitudes to investigate differential migration in white-throated sparrows, I investigated if this species performed differential migration, both in terms of timing of spring arrival and wintering latitudes, and assessed the relative support for the timing of arrival and body size hypotheses, commonly used to explain latitudinal segregation of sexes on the wintering grounds. I also evaluated effects of spring weather conditions on arrival dates of males and females, degree of protandry, and relationship between wintering latitude and arrival dates of sparrows.

4.2. METHODS

4.2.1. Study Species

The white-throated sparrow is one of the most common, recognizable, and well-studied birds in North America (Falls and Kopachena 1994). Its breeding range encompasses Canada and the northeastern United States, whereas its wintering range is restricted primarily to the southeastern United States (Falls and Kopachena 1994). Previous studies have found patterns suggesting that male white-throated sparrows winter at more northern latitudes than females (Odum 1958; Jenkins and Cristol 2002).

White-throated sparrows undergo a complete moult (i.e., the preformative moult for young of the year and prebasic moult for adults) at the end of the breeding season prior to fall migration and a partial moult (i.e., prealternate moult) during late winter to early spring that is completed prior to spring migration with few exceptions (Falls and Kopachena 1994; Chapters 2 and 3). Therefore, during spring, it is possible to estimate the wintering and previous breeding or natal latitude of individuals by measuring δD of

feathers grown during these stages of the annual cycle. I have shown previously that δD values of head (wintering ground tracer) and tail (breeding ground tracer) feathers were highly repeatable for individuals but that a small percentage of head (7%) and tail (10%) feathers can be moulted away from the wintering and breeding grounds, respectively (Chapter 3; Wassenaar and Hobson 2001). Consequently, I opted to only use head and tail feathers that fell within the range of values reflecting the known wintering (> -85‰) and breeding range (< -105‰), respectively, to minimize the influence of these outliers on my analyses.

I used the criterion presented by Piper and Wiley (1991) (females = wing length ≤ 70 mm, and males = wing length >70 mm) to identify the sex of individual white-throated sparrows. More than 90% of individuals are sexed correctly using this criterion (Piper and Wiley 1991; Appendix 1). Although this measure provides an adequate sexing criterion, I also quantified latitudinal segregation of sexes on the wintering grounds based on an analysis weighted by the probability of correctly classifying sexes and based on individuals sexed with a more stringent criterion (females, wing length ≤ 69 mm; males, wing length ≥ 71 mm). Probabilities were computed based on a discriminant function analysis performed on the sample of 40 individuals for which the sex was known (Appendix 1). Analyses based on the more stringent sexing criterion and the weighted analysis produced similar results and conclusions as those presented below. Thus, I opted to present only the unweighted analyses based on the more inclusive sexing criterion.

4.2.2. Study Area

Fieldwork was conducted in the dune-ridge forest of Delta Marsh, Manitoba, Canada (98°23'W, 50°11'N). Sampling was conducted in a portion of forest (approx. 80m wide), abutted by Lake Manitoba on one side and an extensive cattail marsh on the other. During the spring of 2002, the first year for which isotopic data were available, ambient temperatures were among the top five coldest measured at Delta Marsh during the last 35 years (University Field Station, unpub. data). Atypically cold spring temperatures also occurred at southern stopover sites in the northern states of central U.S. The study area is a key stopover site for white-throated sparrows *en route* to boreal forest (located > 65 km to the north). Further, white-throated sparrows do not breed or winter at Delta Marsh and thus, all individuals sampled during spring originated from more southern latitudes and were destined for more northern latitudes (Falls and Kopachena 1994). Weather data were obtained from an Environment Canada Meteorological Station located on the study area. Spring temperatures varied greatly among years.

4.2.3. Avian Samples

Standardized constant-effort mist-netting was conducted every spring migration from 1995 to 2004 by the Delta Marsh Bird Observatory (DMBO). Intercepting birds during migration provides large numbers of individuals originating from or destined for broad geographical regions (Wassenaar and Hobson 2001; Chapter 3). One limitation of such an approach is that it is necessary to make the assumption that arrival dates of birds at this stopover site closely matche the arrival dates of the same individuals at breeding localities (Francis and Cooke 1986). As spring migrants typically stopover for no more than one to two days (den Haan, unpublished data) and the stopover site is located in

close proximity to their breeding range, I suspect that this assumption was valid (see also Francis and Cooke 1986).

Ten mistnets were operated daily during spring (late April to early June), weather permitting. To increase sample sizes, additional birds were also captured in walk-in ground traps that were operated in the same area and during the same time period. Sampling protocols followed standard mistnetting and banding procedures recommended by Hussell and Ralph (1995). When a bird was captured and banded, morphological measurements were taken, and in 2002 and 2003, a tail feather (rectrix 4) and approximately three head feathers were collected from each individual. Feather samples were randomly selected from the total sample so that analyses would be representative of entire migratory passages and populations sampled by DMBO. My field collections followed guidelines approved by the Canadian Council on Animal Care.

4.2.4. Stable Isotope Analyses

Feathers were cleaned of surface oils using 2:1 chloroform: methanol solution and allowed to air-dry. Single head feathers (0.1-0.14mg) and tip of tail feathers (0.31-0.37 mg) were weighed into silver capsules. Stable isotope analyses of the non-exchangeable hydrogen of feathers were conducted using continuous-flow isotope ratio mass spectrometry as described in detail by Wassenaar and Hobson (2003). Deuterium values are expressed in the delta notation, in parts per thousand (‰), and normalized on the VSMOW-SLAP standard scale. Similar to Wassenaar and Hobson (2001), I used an isotopic discrimination factor between mean growing-season precipitation δD_p and feather non-exchangeable δD values of feathers of -25‰.

4.2.5. Data Analyses

Principal component analysis (PCA) based on a correlation matrix using all morphological measurements was used to describe body size (Rising and Somers 1989). The first principal component (PC1) from this analysis was used as an index of structural size. PC1 accounted for 57% of the overall variance, and was characterized by the following morphological parameters and factor loadings: bill length, 0.36; tail length, 0.88; tarsus length, 0.72, and wing length, 0.88.

I used mean and 95% CI of differences between mean arrival dates to determine if white-throated sparrows exhibited protandry. Pearson's correlations were used to determine if timing of arrival of male and female white-throated sparrows and degree of protandry varied with mean minimum April temperatures at Delta Marsh. The degree of protandry was quantified as the $\log_{10}$-transformed mean arrival date of females minus $\log_{10}$-transformed mean arrival date of males. The transformation was applied to generate an estimate of protandry that was independent of scale (Møller 2004).

I used general linear models (GLM) to evaluate the importance of body size and timing of arrival as factors associated with wintering latitudes, as estimated with δD values of head feathers. In addition, since timing of arrival varies among years, I also evaluated models with combinations of time of arrival, year, and the interaction between time of arrival and year. As birds breeding at different latitudes could migrate according to different schedules, I also compared the model relating wintering latitude and time of arrival with a model based on date of arrival corrected for breeding latitudes, as estimated by δD values of tail feathers moulted during the previous summer. I reasoned that the breeding latitude of the previous year would be highly correlated with the

breeding latitude of the current year. However, I recognize that this correlation could be weaker for second-year (SY) birds than after-second year (ASY) birds because of lower natal vs. breeding philopatry (Weatherhead and Forbes 1994). I did not add a model approximating wintering latitude in relation to sex in my candidate set because the aim of these analyses was to evaluate mechanisms responsible for sex-specific wintering patterns, as oppose to describing distributions of males and females on wintering areas. Competing models computed from GLM were ranked using Akaike's Information Criterion, corrected for small sample sizes (AIC_c) (Burnham and Anderson 1998). This method of model selection is based on the principle of parsimony (i.e., best compromise of model fit and precision). Models with lower AIC_c values are more parsimonious, and it is generally accepted that models differing by < 2, 2 to 4, 4 to 7, and >7 AIC_c units exhibit strong, some, little, and no support relative to the other candidate models, respectively (Burnham and Anderson 1998). To facilitate model comparisons, I computed ΔAIC_c, as the difference between a particular model and the model with the lowest AIC_c, normalized Akaike weights, and 95% confidence intervals for parameter estimates (Burnham and Anderson 1998). Analyses were performed with SPSS version 12 for Windows (SPSS Inc. 2003).

4.3. RESULTS

A total of 1465 white-throated sparrows was captured at DMBO between 1995 and 2004. Males arrived earlier than females (difference between means = 5.5 days, 95% C.I. 5.0 to 6.0 days) every year (Fig. 4.1). Timing of arrival correlated strongly with mean minimum April temperatures (Fig. 4.2). However, annual variation in degree of protandry was not related to spring temperatures (slope ± SE = 0.001 ± 0.01 days).

Males wintered father north than females (Fig. 4.3). The best supported model approximating δD values of head feathers included date, year, and a date by year interaction (Table 4.1). This model received 87% of the support among the six candidate models. Wintering latitude of individuals had a significant effect on timing of arrival of white-throated sparrows in 2003 but not in 2002 (Fig. 4.4). The most parsimonious model was not improved significantly by using date of arrival corrected for δD values of tail feathers (i.e., the previous breeding or natal latitude tracer) moulted on breeding grounds (< 2 AIC_c units between the two models). In fact, δD values of tail feathers explained less than 5% of the variation in date of arrival. During 2003, there was also a clear relationship between wintering latitude on date of arrival within males (Pearson's r, N, 95% C.I. = 0.47, 43, 0.22 to 0.66). However, the relationship between wintering latitude and timing of arrival was non-existent within females (Pearson's r, N, 95% C.I. = 0.16, 37, -0.15 to 0.44). There was some support for a positive effect of body size on wintering latitude of individuals of both sexes combined (Table 4.1; β, N, 95% C.I. = -3.3, 195, -5.0 to -1.61; the beta term of this model is negative because δD values of head feathers is negatively correlated with latitude). This pattern also held in males (Pearson's r, N, 95% C.I. = -0.20, 98, -0.38 to -0.01) but not in females (Pearson's r, N, 95% C.I. = 0.01, 97, -0.19 to 0.20).

4.4. DISCUSSION

White-throated sparrows showed a clear pattern of differential migration both in terms of timing of arrival and wintering latitude. Males arrived earlier and wintered at more northern latitudes than females. Further, my analyses lend support to the timing of arrival hypothesis and, to a lesser extent, the body size hypothesis. Timing of arrival and

wintering latitude of individuals were correlated in one year but not in the other, a finding that can be attributed to pronounced differences in spring weather conditions between years. During 2003, the year when an effect was detected, the relationship between timing of arrival and wintering latitude was also present in males, suggesting that the distribution of males on the wintering grounds might have carry-over effects to reproduction.

From 1995 to 2004, male white-throated sparrows arrived approximately one week earlier than females during spring. This finding is consistent with those of others focusing on the spring arrival dates of white-throated sparrows at other locations (Knapton et al. 1984; Falls and Kopachena 1994). Male white-throated sparrows are the territorial sex, are larger than females, and winter at more northern latitudes (Odum 1958; Falls and Kopachena 1994; Jenkins and Cristol 2002; this chapter). Consequently, the sex-specific benefits, costs, and constraints of early arrival in this species all favor males arriving earlier than females. My results indicate that the timing of arrival of individuals is determined at least in part by the distribution of individuals on the wintering grounds as predicted by the seasonal-interaction hypothesis.

The timing of spring migration in sparrows at Delta Marsh was significantly correlated with mean minimum temperatures in April. The variable arrival dates and strong relationship between spring temperature and timing of arrival suggest that white-throated sparrows are "weather" migrants (Hagan et al. 1991), relying more on changes in weather and food supply as opposed to relying exclusively on endogenous rhythms and photoperiodic cues like "calendar" migrants (Berthold 1975). Given the strong negative relationship between spring temperatures and arrival dates, white-throated

sparrows should be less prone to "phenological miscuing" (when birds respond inappropriately to climate cues, including not responding at all) and "phenological disjunction"(when birds become asynchronous with their environment) than "calendar" migrants such as Neotropical migrant songbirds (Strode 2003). Phenological miscuing and disjunction in birds has recently been attributed to differential effects of spring conditions on males and females. Møller (2004) showed that the arrival dates of male barn swallows (*Hirundo rustica*) were affected by variation in spring weather conditions but female arrival dates were not. This reduced the ability of barn swallows to synchronize reproductive activities with optimal conditions for rearing offspring. My findings, based on a "weather" migrant, indicated that both male and females responded strongly to variation in spring weather conditions. These findings contrast with those of Møller (2004) on barn swallows and future studies are needed to evaluate whether the patterns observed by Møller (2004) occur in North American birds that migrate long distances. Data from avian migration monitoring stations would be well suited for this purpose.

My finding that male white-throated sparrows wintered farther north than females was consistent with those of Odum (1958), based on tower killed birds, and those of Jenkins and Cristol (2002), based on analyses of data from the North American Bird Banding Laboratory. Sexual segregation, including latitudinal segregation of sexes, in birds on wintering areas has been attributed to competitive exclusion of females at more northern latitudes by males or to differences in reproductive roles, metabolism, and morphology between males and females (Cristol et al. 1999).

I found moderate support for a positive relationship between body size and wintering latitude of white-throated sparrows. There was also evidence that males wintering at more northern latitudes were larger than males wintering at more southern latitudes. Since commonly used measures of size incorporate variation in feather measurements (e.g., wing lengths), some researchers have attributed such results to differences in the distribution of age groups in relation to wintering latitudes, since younger birds have shorter wings and arrive later than older birds (Francis and Cooke 1986). However, this likely does not explain my results since tarsus length, a measurement that does not vary with age in songbirds (Francis and Wood 1989), was also positively related to wintering latitude. Larger birds are expected to be better able to survive colder and snowier weather conditions that can result in extended periods during when food is unavailable (Ketterson and King 1977; Stuebe and Ketterson 1982).

I expected that breeding and wintering latitude of individuals would influence timing of arrival at the study area. However, I found that arrival dates at the stopover site were related to individual characteristics (i.e., sex) and wintering latitude but were not related to presumed breeding latitudes (Appendix 3). These findings are consistent with those of Hagan et al. (1991), based on an interspecific analysis of short- and long-distance migrant birds in North America, and those of Kelly et al. (2002), based on spring migration of Wilson' s warblers (*Wilsonia pusilla*), that showed breeding latitudes were not related to timing of spring migration. Nevertheless, I cannot dismiss the possibility that my findings could be influenced by changes in breeding latitude from one year to the next.

In birds, clear evidence for the role of dominance in mediating sexual-segregation among wintering habitats has been demonstrated previously (Marra et al. 1998; Marra 2000). However, evidence for the role of dominance in determining the latitudinal distribution of male and females is weak to non-existent (Cristol and Evers 1992; Rogers et al. 1989). I did not have any information on the dominance status of individuals and how that in turn related to their wintering latitudes. However, white-throated sparrows are polymorphic with morphs differing in levels of aggression (Falls and Kopachena 1994). White-striped birds are more aggressive than tan-striped birds of the same sex during spring migration and the breeding season (Kopachena and Falls 1993; Houtman and Falls 1994). However, the relationship between plumage morph and aggression during fall and winter is non-existent (Watt et al. 1984; Piper and Wiley 1989). I compared the wintering distribution of white-striped and tan-striped morphs and found no evidence that wintering latitudes differed between WS and TS birds of the same sex (Mazerolle and Hobson, unpubl. data). Further studies will be required to determine conclusively if sex-specific dominance status during winter influences wintering latitudes and how dominance status on the wintering grounds is acquired.

My use of stable isotope tracers and application of an information theoretic approach to model selection provides a novel and powerful analysis of hypotheses used to explain differential migration in migratory birds. Further, it demonstrated for the first time that wintering latitudes of individuals can affect the timing of arrival of birds on breeding areas. Isotopic approaches similar to the one applied in this study could prove very useful for further evaluating hypotheses that explain differential migration in other bird species. Such approaches would be especially useful if they were applied to

compare closely-related pairs of species that include differential and non-differential migrants (Cristol et al. 1999). As mortality rates of passerines are highest during migration, and males and females are exposed to different ecological conditions during winter (Sillett and Holmes 2002), latitudinal segregation of males and females on the wintering grounds could have important implications for sex-specific survival rates and population dynamics (Cristol et al. 1999). Further, sexual segregation on the wintering grounds could have important ramifications for the ability of migratory birds to respond to climate change because males and females will likely affected differently by shifts in climate (Newton 2004).

Table 4.1: Summary output from competing general linear models approximating δD values of head feathers (tracer of wintering latitude) of white-throated sparrows. Models are based on deuterium measurements on 115 and 80 individuals captured during spring, 2002 and 2003, respectively.

MODEL	*K*	Δ AIC_c	Akaike Weight
Arrival Date + Year + interaction	5	0.0	0.87
Body Size	3	4.0	0.12
Arrival Date	3	9.5	0.01
Arrival Date + Year	4	10.7	0.00
Intercept	2	11.3	0.00

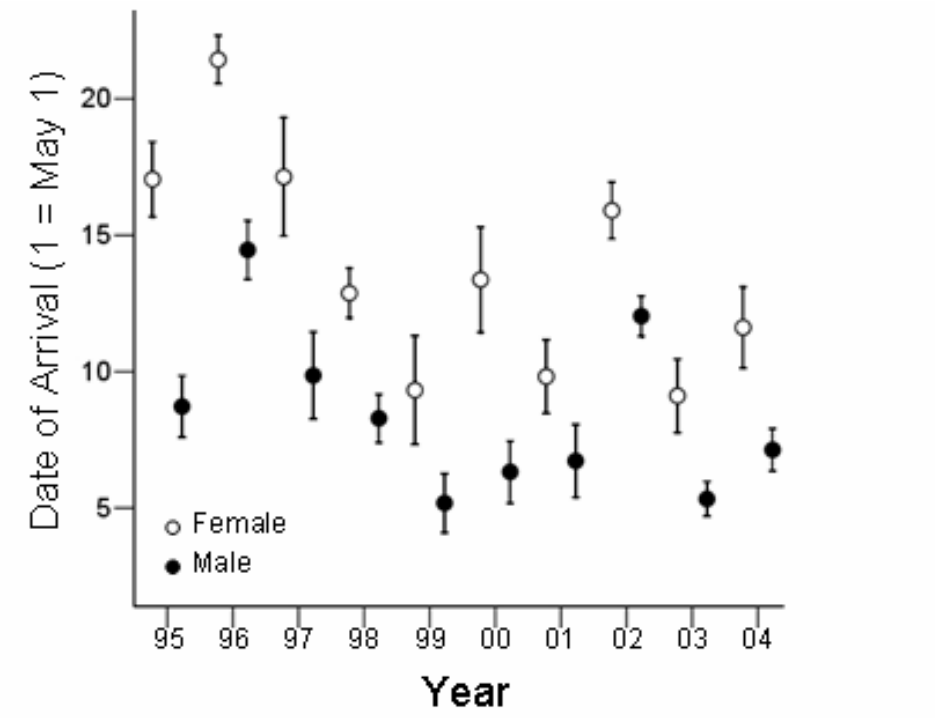

Fig. 4.1. Spring arrival dates (mean, 95% CI) of male (●) and female (○) white-throated sparrows at Delta Marsh, Manitoba, from 1995 to 2004.

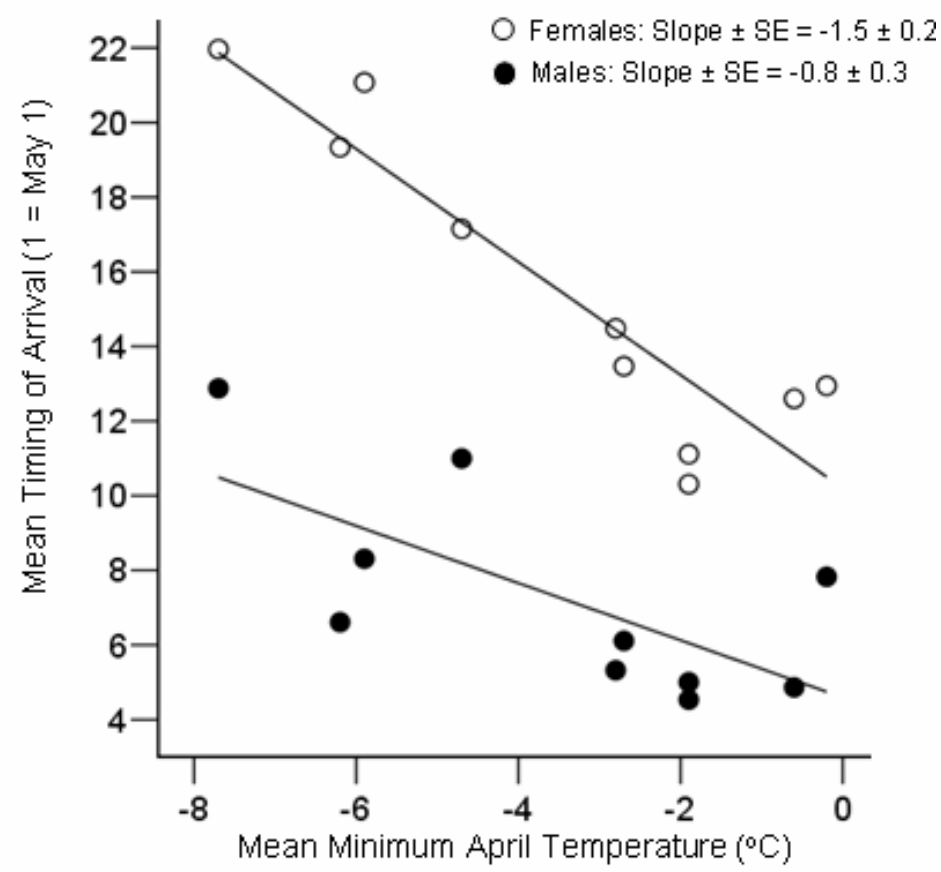

Fig. 4.2. Mean spring arrival dates of male (●) and female (○) white-throated sparrows at Delta Marsh, Manitoba, from1995 to 2004 in relation to mean minimum temperature in April (^{o}C) measured at Delta Marsh.

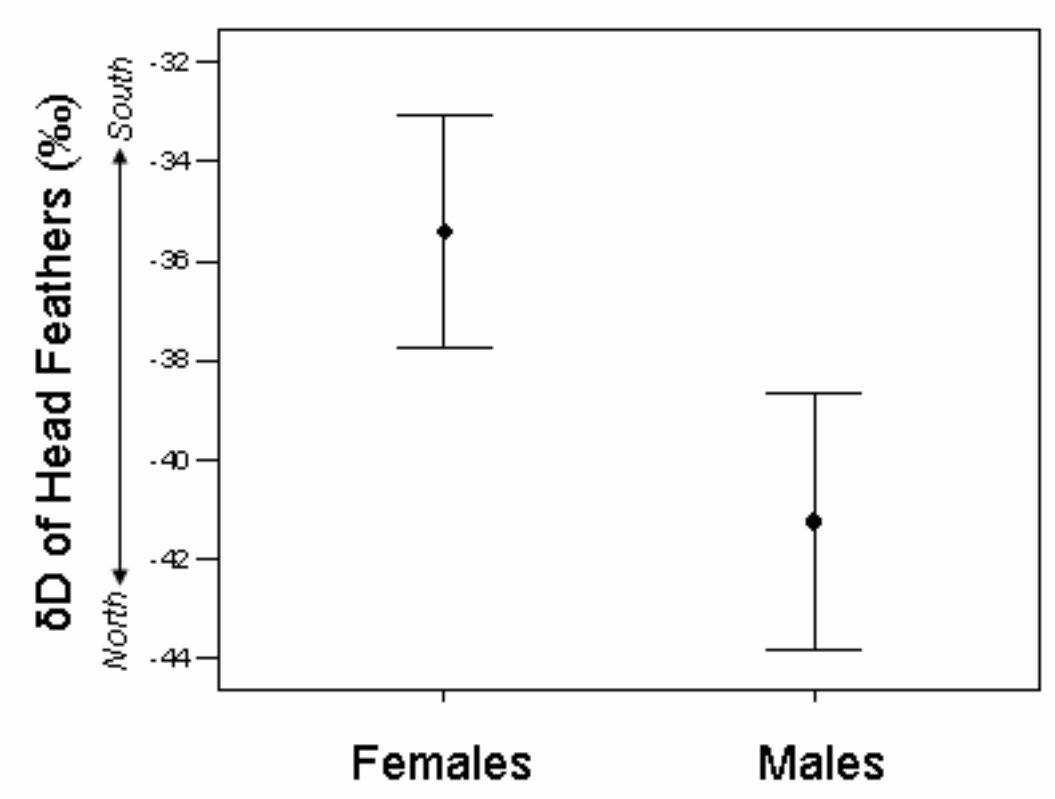

Fig. 4.3 δD values of head feathers (tracer of wintering latitude; mean, 95% CI) of male and female white-throated sparrows captured at Delta Marsh during spring, 2002 and 2003.

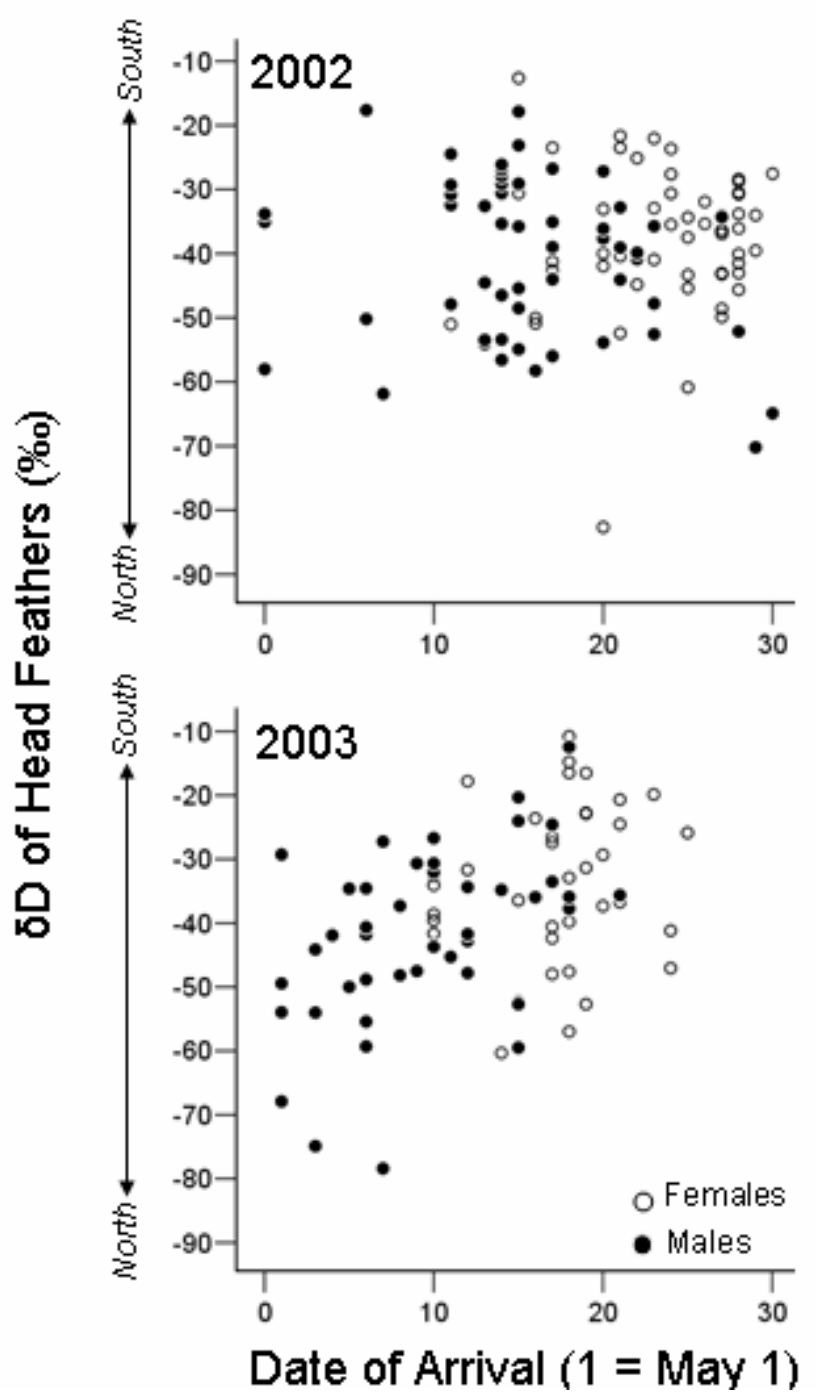

Fig. 4.4. δD values of head feathers (tracer of wintering latitude) in relation to arrival dates of male and female white-throated sparrows at Delta Marsh during spring, 2002 (top panel) and 2003 (bottom panel).

CHAPTER 5: BODY CONDITION OF WHITE-THROATED SPARROWS IN RELATION TO MIGRATION DISTANCE: IS THERE A COST TO MIGRATING LONGER DISTANCES?

5.1. INTRODUCTION

Migrating to temperate breeding areas to capitalize on superabundant food has clear benefits for avian reproduction (Fretwell 1972; Alerstam and Hedenstrom 1998). However, reaching these prime breeding areas is costly, for migration is the most energetically taxing and hazardous event in the annual cycle of migratory birds (Pienkowsky and Evans 1985; Owen and Black 1991; Blem 2000; Sillett and Holmes 2002). The cost of avian migration has been difficult to evaluate empirically because of difficulties associated with tracking migratory movements of birds (Webster et al. 2002; Smith et al. 2003; Rubenstein and Hobson 2004). Understanding these costs, both in terms of mortality and loss of reproduction output, has important implications for life-history theory and conservation (Sillett and Holmes 2002). Recently developed forensic tools, such as stable isotope tracers, provide a means of estimating origins of migratory birds and so facilitate research elucidating costs of migration (Chapter 1 and 2; Hobson 1999; Smith et al. 2003; Rubenstein and Hobson 2004; Smith et al. 2004).

Several hypotheses have been developed to explain migratory patterns observed in birds (e.g., differential migration, leap-frog migration, and chain migration), many of which are based on the assumption that the cost of migration is high and varies

proportionately with migration distance (Gauthreaux 1978; Belthoff and Gauthreaux 1991; Bell 1996; Cristol et al. 1999). Previous studies have attempted to quantify the cost of migration by correlating survival rates of species with the distance between breeding and wintering ranges (Greenberg 1980; O'Connor 1981; Morse 1989; Dobson 1990; Mönkkönen 1992; Sandercock and Jaramillo 2002). However, the findings of these interspecific analyses have yielded mixed results and may be suspect because of potential spurious correlations arising from covariation between migration distance and other life history traits such as habitat use (reviewed by Sandercock and Jaramillo 2002). Furthermore, nearly all inter- and intraspecific studies have related migration distance to annual survival rates, rather than to survival rates during the migratory period (Harrington et al. 1988; Hestbeck et al. 1992; Sandercock and Jaramillo 2002). Ketterson and Nolan (1982) found that annual survival rates (i.e., return rates) of dark-eyed juncos (*Junco hyemalis*) did not vary with wintering latitude (i.e., migration distance) but that wintering survival was lower at northern than at southern sites. Together, these results suggest that survival during migration maybe lower for individuals wintering farther from breeding areas. Consistent with Ketterson and Nolan's conclusion, Sillett and Holmes (2002) found that survival rates of black-throated blue warblers (*Dendroica caerulescens*) were approximately fifteen times lower during migration than during the breeding and wintering periods.

In addition to lowered survival rates, the cost of migration in animals is likely reflected in body condition of individuals (Sandberg and Moore 1996; Kinnison et al. 2001; Smith and Moore 2003). When different activities (e.g., migration versus reproduction) compete for limiting resources (e.g., nutrients and energy), physiological

trade-offs are expected to occur to divide these resources in a way that maximizes fitness (Stearns 1992). Since reproductive success in birds is influenced by pre-breeding body condition, the energetic costs of migration may have important carry-over effects to reproduction (Ankney and McInnes 1978; Sandberg and Moore 1996; Smith and Moore 2003). Further, if this cost is proportional to migration distance, individuals migrating longer distances could have less energy to invest in reproduction (Kinnison et al. 2001). This prediction has not been tested in birds, although results consistent with it have been found in migratory fish (Kinnison et al. 2001)

The objective of this study was to evaluate costs of spring migration of white-throated sparrows *en route* to boreal breeding grounds by relating migration distance to body condition indices reflecting immunological status (total white blood cell counts), parasitic infections (*Haemoproteus* and *Leucocytozoon* infections), oxygen-carrying capacity (hematocrit) and nutritional status (furcular fat scores and mass/size residuals). Stable hydrogen isotope analyses were used to estimate wintering latitude and previous breeding/natal latitude of individuals. With these tracers, I evaluated effects of wintering latitude (i.e., distance migrated) on body condition of individuals while controlling for potential effects of natal or previous breeding latitude (hereafter "breeding latitude") on body condition.

5.1.1. Background on Body Condition Indices

Blood parameters and measures of fuel stores are used frequently to estimate sub-lethal effects of stressors on birds (e.g. Maxwell et al. 1991; Hõrak et al. 1998, Ots et al. 1998; Norris and Evans 2000). Background information on body condition indices

used in this study, as well as the reasoning behind their predicted responses to migration distance, is provided below.

Maintaining immune function is energetically costly, and since resources are often limited, trade-offs are expected between immunological and other critical life-history functions (Lochmiller and Deerenberg 2000). Further, such trade-offs should be particularly pronounced during the most energetically taxing periods of the annual cycle (Owen 2004; Møller et al. 2004). This prediction is supported by recent research that has demonstrated that birds reduce investments in their immune system during migration (Deerenberg et al. 2002). For example, Owen (2004) found that total white blood cell count, a commonly used index of immunological status, of *Catharus* thrushes was significantly lower during migration than during the wintering and breeding seasons. Based on these studies, I predicted that birds that had migrated longer would have lower total white blood cell counts than birds with shorter migration distances.

Blood parasites can have significant negative impacts on the health and fitness of birds (Møller et al. 1990; Atkinson and van Riper 1991; Bennett et al. 1993; Ots and Horak 1998; Merino et al. 2000). Previous studies based on interspecific analyses have demonstrated that bird species migrating longer distances are more likely to be infected with blood parasites. This relationship is thought to occur because of the reduced immunocompetence of birds during migration and because species migrating greater distances are exposed to larger parasite fauna (Møller and Erritzoe 1998; Figuerola and Green 2000). Blood parasite infections are typically latent during the winter months and relapse during spring (Bennett and Fallis 1960; Deviche et al. 2001; Valkiunas et al. 2004) because of the energetic stress of spring migration and changes in the

concentration of sex hormones (Bennett and Fallis 1960; Deviche et al. 2001; Valkiunas et al. 2004). Since anti-parasite immune responses are costly (Lochmiller and Deerenberg 2000) and likely compete with other energetically demanding activities such as accumulating fuel stores for migration, I predicted that stress associated with migrating longer distances would trigger more prevalent and severe relapses in *Haemoproteus* and *Leucocytozoon* infections.

Hematocrit (Hct) consists of the proportional volume of red blood cells in the total blood volume (Campbell 1995). Increases in Hct are often associated with increases in oxygen-carrying capacity and nutritional condition (Campbell 1995; Ots et al. 1998). Alternatively, Hct levels can also increase through dehydration, as a result of a reduction in the volume of plasma, or decrease through anemias caused by starvation, dehydration, parasite infections, or hemolytic diseases (Campbell 1995). No bird sampled during this study was significantly dehydrated (Hct > 65%) or anemic (Hct < 35%). Since previous studies suggest that a significant breakdown of red-blood cells can occur during migratory flights (Piersma et al. 1996; Landys-Ciannelli et al. 2002), I predicted that birds with longer migration distances would have lower Hct levels than those with shorter distances.

Both furcular fat scores and mass/size residuals provide good indices of nutritional status in birds, including white-throated sparrows (Appendix 2; Blem and Shelor 1986). As migration is energetically costly in birds (Wikelski et al. 2003), I predicted that birds migrating longer distances would have less stored fat than birds migrating shorter distances (see also Smith et al. 2003). However, I also recognized that the size of fat stores in birds fluctuates greatly during migration (Dunn 2002).

Nevertheless, I reasoned that it was worth evaluating body fat indices in relation to wintering latitude, since Marra et al. (1998) found measurable long-term effects of wintering habitat use on estimates of pre-breeding body-fat levels of a migratory passerine (also see Norris et al. 2004).

5.2. METHODS

5.2.1. Study Area and Bird Sampling

Fieldwork was conducted at the Delta Marsh Bird Observatory (DMBO) migration monitoring station during spring and fall migration, 2002 and 2003, in the dune-ridge forest of Delta Marsh, MB, Canada (Fig. 5.1; 98°23′W, 50°11′N). This site is an important stopover location for migratory songbirds (Chapter 3; Wassenaar and Hobson 2001; den Haan, unpublished data) and is located ≈ 65 km from the southern edge of the boreal forest, the primary breeding grounds of white-throated sparrows. The wintering grounds of this species extend from approximately 1,500 to 2,500 km south of my study area (Falls and Kopachena 1994). White-throated sparrows do not breed or winter at Delta Marsh and thus, all individuals sampled during spring originated from more southern latitudes and were destined for more northern latitudes (Falls and Kopachena 1994).

Ten mistnets were operated daily during spring (late April–early June). The large majority of the spring passage of migrating sparrows fell within my sampling period (DMBO, unpublished data). Nets were opened one half hour before sunrise for a period of 6 hours, weather permitting, and were checked every 20 minutes. Sampling protocols followed the standard mistnetting and banding procedures recommended by Hussell and Ralph (1995). To increase sample sizes, additional birds were captured in ground traps

that were operated in the same area and during the same time period as mistnets. Estimates of fuel stores of individuals captured in ground traps were not used in the analysis described below because of the potential bias in estimates for individuals that foraged on seeds used to bait these traps. None of the other measured body condition indices were affected by the mode of capture. Further, there were no differences in the morphology, morph type, or sex of individuals captured with ground traps and mistnets. Feathers for stable isotope analyses were randomly selected from the total sample so that analyses would be representative (i.e., unbiased) of entire migratory passages and populations sampled by DMBO. Once a bird was captured, morphological measurements were taken and a tail feather (rectrix 4) and approximately three head feathers were collected from each individual.

5.2.2. Body Condition Indices

Within 30 minutes of capture, I collected a small blood sample (50 to 200 µl) using standard haematological methods outlined in Campbell (1995) and approved by the Animal Care Committee of the University of Saskatchewan. A sterilized needle (27-gauge) was used to make a small puncture in the brachial vein of captured white-throated sparrows. Hematocrits were quantified after centrifuging the remaining blood for 7 minutes at 12,000 rpm. For quantifying white blood cell composition, a thin coat of blood was smeared on a microscope slide, air-dried and stained with Giemsa-Wright solution with an Ames Hema-tek haematology slide stainer (Bayer, Ames Div., Elkhart, IN). Total white blood cell numbers (WBC) were estimated by counting the number of white blood cells per field at 400x and using the formula described in Lane (1996):

WBC = Mean Leukocytes per 400x field x 2000

Mean total white blood cell counts were computed based on examinations of ten fields of view that were focused on areas of the smear that formed a monolayer. Avian leukocytes can be classified as agranulocytes (lymphocytes and monocytes) or granulocytes (heterophils, eosinophils, and basophils). In response to stress and infections, counts of agranulocytes tend to decrease, whereas the number of granulocytes tends to increase (Campbell 1995). Leukocytes were identified based on descriptions in Luca and Jamroz (1961), Hawkey and Dennet (1989), and Campbell (1995). Based on a sample of white-throated sparrows (N = 82), I evaluated the proportion of different types of leucocytes in relation to WBC. As WBC increased, percentage of lymphocytes increased, while percentage of basophils and monocytes decreased (Appendix 4). The proportion of different types of white blood cells was determined by examining 100 white blood cells. The mean percentage of heterophils (8%), basophils (10%), eosinophils (4%), lymphocytes (73%), and monocytes (4%) did not differ significantly between sexes (Mazerolle, unpublished data). The proportions of these types of white blood cells in the blood of white-throated sparrows are very similar to those estimated for dark-eyed juncos (Leary et al. 1999)

Prevalence of parasites was quantified by scanning smears for five minutes under oil immersion (1000x) and for five minutes at 400x for the presence of *Haemoproteus* and *Leucocytozoon* species. Other species of parasites were detected (e.g., *Trypanosoma* sp. and microfilarial worms) but their prevalence was low and poorly quantified by scanning blood smears (Mazerolle, unpublished data; Fallon et al. 2003). Consequently, they were not considered further. Intensity of *Haemoproteus* infection was quantified by scanning 40 fields of view at 1000x, which represents the

approximate number of infected cells per 8000 red blood cells (Campbell and Dein 1984). The intensity of *Leucocytozoon* infections was not quantified because typically less than two to three cells infected with this parasite were found per 8000 red blood cells. Estimates of intensity of *Haemoproteus* infections were focused on parts of the smear that formed a monolayer.

Body lipids were estimated using furcular fat scores and mass/size residuals. The amount of visible fat in the furculum was measured using a five-point scale: 0 for none or trace; 1 for up to 1/3 full; 2 for 1/3 to 2/3 full; 3 for nearly filled; 4 for filled and 5 for overflowing. Mass and morphological measurements including bill length, flattened right wing length, tail length, and tarsus length were measured following the methods outlined in Pyle et al. (1997). These measures were used to estimate mass/size residuals (see Appendix 1). Furcular fat scores and mass/size residuals were combined in one linear axis using principal component analysis (PCA). Results from Appendix 1 indicated that fat scores and mass/size residuals in combination (the two measures were combined using PCA) explain approximately 70% of the variation in total body lipids of white-throated sparrows. The remaining variation in this measure can be attributed to variation in protein stores, water, and measurement error.

5.2.3. Stable Isotope Analyses

Stable isotope tracers have been shown to be effective for estimating wintering and breeding latitude of passerines (reviewed by Chapter 2 and 3; Hobson 1999; Rubenstein and Hobson 2004). For example, hydrogen occurs in two stable forms: a lighter more common form, ^{1}H, and the heavier deuterium, ^{2}H. The ratio of ^{2}H / ^{1}H (δD) in precipitation varies with latitude because of a southeast to northwestern gradient in

large-scale geological and climatic processes (Bowen et al. 2005). Feathers, which are metabolically inert, are permanently labeled with the isotopic composition of the food web at the location where they were synthesized (Hobson 1999). Many songbirds, including white-throated sparrows, undergo a complete molt at the end of the breeding season and a partial molt on wintering areas prior to the onset of spring migration (Pyle et al. 1997). Therefore, during spring, it is possible to determine wintering and previous breeding latitude of white-throated sparrows by analyzing feathers that were molted during the winter (e.g., head feathers) and previous summer (e.g., tail feathers).

Feathers were cleaned of surface oils using 2:1 chloroform:methanol solution and were air-dried. Single head feathers (0.1–0.14 mg) and tip of tail feathers (0.31–0.37 mg) were weighed out into silver capsules. Measurement of non-exchangeable hydrogen, δD, was conducted using continuous-flow isotope ratio mass spectrometry, as described in detail by Wassenaar and Hobson (2003). δD values of feathers are expressed in the delta notation, in units per mil (‰), and normalized on the VSMOW-SLAP standard scale.

5.2.4. Statistical Analyses

Values of all of the continuous body condition indices were normally distributed, except WBC and intensity of *Haemoproteus* infections. WBC values were normalized via $\log_e$-transformation. Intensity of *Haemoproteus* infections was so skewed by the large number of zero values that it was not possible to transform these data to meet the assumptions of parametric methods. However, $\log_e$-transformed intensity estimates were normally distributed among infected birds. Thus, I opted to analyze the influence of

migration distance on $\log_e$-transformed intensity of *Haemoproteus* infections using only infected birds. I also evaluated the repeatability of morphological measurements with intra-class correlations calculated from the variance components of one-way analyses of variance (Lessells and Boag 1987).

To reduce the number of parameters used in model selection, I corrected for the potential effects of year, date, and time of day on body condition indices prior to running the models. Effects of these temporal parameters were computed using general linear models (GLMs) with year, date, and time of day as explanatory variables and body fat, HCT, WBC, and intensity of *Haemoproteus* infection as response variables. These analyses indicated that body fat and WBC levels differed between years, that only intensity of *Hemoproteus* infections varied with date, and that none of the body condition indices varied with time of day. Further, based on logistic regressions, prevalence of *Haemoproteus* and *Leucocytozoon* did not vary with year, date, or time of day. Residuals, instead of raw values, from analyses correcting for nuisance variables that had a significant effect on body condition indices were used in analyses presented below. These corrections did not have an effect on any of the conclusions, except those pertaining to sex-specific differences in the intensity of *Haemoproteus* infections. Females had higher intensities of infections prior to but not after correcting for the effects of date. This finding can be attributed to spring relapses in infections and the fact that females were captured later than males during spring migration.

GLMs were used to evaluate effects of sex, breeding latitude, and wintering latitude on body fat, HCT, WBC, and intensity of *Haemoproteus* infection of sparrows. Logistic regressions were used to evaluate effects of these explanatory variables on the

prevalence of *Haemoproteus* and *Leucocytozoon* infections. I evaluated all possible models that allowed condition indices to vary in relation to estimated breeding latitude, estimated wintering latitude, and sex, including those that considered two-way interactions between explanatory variables. I inspected bivariate plots and LOESS trend lines for relationships between response variables and explanatory variables to determine whether a non-linear model would provide a better fit. However, there were no apparent non-linear relationships between response variables (raw or $\log_e$-transformed values) and any of the explanatory covariates. Competing models computed from GLMs were ranked using Akaike's Information Criterion, corrected for small sample sizes (AIC_c) (Burnham and Anderson 1998). This method of model selection is based on the principle of parsimony (i.e., best compromise of model fit and precision). Models with lower AIC values are more parsimonious, and it is generally accepted that models differing by < 2 AIC units are equally well supported (Burnham and Anderson 1998). To facilitate model comparisons, I computed ΔAIC_c, as the difference between a particular model and the model with the lowest AIC_c, and normalized Akaike weights (Burnham and Anderson 1998). All statistical tests were performed with SPSS version 12.0 (Norušis 1998).

5.3. RESULTS

Measures of WBC, HCT, body fat, and intensity of *Haemoproteus* infections were highly repeatable (Table 5.1). None of the body condition indices differed significantly between sexes (Table 5.2). Wintering latitude, as estimated by δD of head feathers, was not related to any of the body condition indices (Table 5.3 to 5.8). Prevalence of *Leucocytozoon* infections was the only parameter significantly related to breeding

latitude (Table 5.3 to 5.8). Specifically, prevalence in infections was negatively correlated with δD of tail feathers grown on the breeding grounds (Fig. 5.2; $\beta \pm SE = -0.03 \pm 0.01$). As δD of feathers are negatively correlated with latitude, prevalence of *Leucocytozoon* infections was greater for birds at northern than at southern latitudes.

5.4. DISCUSSION

Based on a suite of standard body condition indices, pre-breeding body condition of white-throated sparrows captured at a staging area near boreal breeding grounds did not appear to vary with migration distance. Moreover, none of the body condition indices measured in this study differed between males and females. Since females typically migrate longer distances than males (see Chapter 4), this finding further confirms the lack of a relationship between body condition and migration distance. Effects of previous natal/breeding latitude on body condition indices were also minimal. Only the prevalence of *Leucocytozoon* infections varied in relation to this measure, a finding that is consistent with suitable habitats for vectors of this parasite also varying with latitude. Overall, longer migrations in white-throated sparrows do not appear to have any detrimental effects on body condition.

White-throated sparrows make several stopovers during the course of their migration (Falls and Kopachena 1994). Since birds can replenish blood cells and fuel stores during migratory stopovers (Piersma et al. 1996; Dunn 2002; Landys-Ciannelli et al. 2002; Owen 2004), effects of migration distance on pre-breeding body condition might be less severe for this species than for others that stopover very infrequently or for very short periods. The isotope approach used in this study might yield interesting insights into sources of variation of pre-breeding body condition in bird species that do

not refuel frequently during migration. Moreover, the consequences of migration distance for reproduction could be especially significant for birds that rely heavily on endogenous reserves for producing eggs.

I found evidence of possible relapses of *Haemoproteus* infections. However, the severity of these suspected relapses was independent of migration distance. Significant effects of date on intensity of *Haemoproteus* infections were removed prior to running analyses on effects of migration distance. Previous research has evaluated condition-dependence in spring arrival patterns by relating the severity of *Haemoproteus* infections with arrival dates of individuals at breeding areas (e.g., Møller et al. 2004). However, I would caution against such an approach since the seasonal variation in blood parasite infections could generate spurious conclusions about links between timing of arrival and phenotypes of individuals. Future studies evaluating this condition-dependent hypothesis using parasite indices should attempt to capture individuals more than once to determine if they have parasite levels that are higher or lower than expected for a particular capture date.

Blood parasitism levels in birds are typically high in boreal ecosystems, as parasite vectors are abundant in this biome (Greiner et al. 1975). Further, in North America, birds breeding closer to the west coast tend to have a higher prevalence of blood parasites than do those breeding closer to the east coast (Greiner et al. 1975). Prevalence of *Leucocytoozoom* and *Haemoproteus* infections for white-throated sparrows sampled in this study and destined for western boreal forest (i.e., the area corresponding to the north-central Laurentian plateau) were significantly higher than those of white-throated sparrows from the eastern boreal forest (i.e., the area

corresponding to Great Lakes and northeastern Appalachian-Laurentian) (Greiner et al. 1975). I also found that prevalence of *Leucocytozoon* infections varied in relation to latitude within the western boreal forest. Specifically, individuals from more northern breeding latitudes were more likely to be infected with *Leucocytozoon* than birds from more southern breeding areas. Such an effect was not found in *Haemoproteus* infections. These findings are consistent with those of previous studies that found that the geographical distribution of *Leucocytozoon* is more restricted than that of *Haemoproteus* (Greiner et al. 1975; Smith et al. 2004). Differences in distribution between the two species are thought to occur because vectors of *Leucocytozoon* (i.e., black flies, *Simulium* spp.) are restricted to areas with fast-moving water (Bennett et al. 1995).

Overall, my study demonstrates the potential for using the stable-hydrogen isotope approach for evaluating trade-offs between migration and pre-breeding body condition and demonstrates that pre-breeding body condition was independent of migration distance for white-throated sparrows. The latter finding is inconsistent with the assumption that differential migration has evolved in response to the cost of migration. However, the cost of migration can also be reflected in survival rates. Approaches similar to the one applied by Sillett and Holmes (2002) and that compare populations that migrate different distances would provide more important insights into proximate mechanisms responsible for the evolution of migratory patterns.

Table 5.1. Repeatability estimates (intra-class correlations) of measurements of hematocrit (HCT), total white blood cell count (WBC), body fat, and intensity of *Haemoproteus* infections of white-throated sparrows sampled at Delta Marsh, MB, during spring migration of 2002 and 2003. * indicates no coefficient of variation could be computed for body fat because the mean of this parameter is zero (i.e., principal component of furcular fat score and mass/size residuals has a mean of 0 and a SD of 1). Note also that estimates of intensity of *Haemoproteus* infections were based only on infected individuals.

Parameters	CV	r	F ratio	DF
HCT (%)	6.4	0.96	50.61	267,268
WBC (cells / µl)	55.5	0.89	17.61	19,20
Body fat*	-	0.88	15.71	36,37
Haemoproteus (infected cells / 8000 erythrocytes)	189.4	0.99	145.31	65,66

Table 5.2. Estimates of body condition indices of male and female white-throated sparrows sampled during spring migration of 2002 and 2003 at Delta Marsh, MB. No parameter differed between sexes (see Table 5.3 to 5.8). Note also that estimates of intensity of *Haemoproteus* infections were based only on infected individuals.

Parameters	Females		Males	
	Mean ± SE	N	Mean ± SE	N
WBC (cells / µl)	9647 ± 519	110	9580 ± 461	129
HCT (%)	50.6 ± 0.3	168	50.7 ± 0.2	175
Body fat	-0.08 ± 0.07	212	0.08 ± 0.07	217
Haemoproteus (infected cells / 8000 erythrocytes)	65.1 ± 12.6	84	44.7 ± 8.7	107
Prevalence of *Haemoproteus* (%)	71	125	74.5	146
Prevalence of *Leucocytozoon* (%)	37.7	174	40.7	182

Table 5.3: Summary of competing general linear models approximating total white blood cell counts of white-throated sparrows with sex, breeding latitude (breeding) estimated with δD of tail feathers, and wintering latitude (wintering) estimated with δD of head feathers. Models are based on samples from 153 individuals captured during spring of 2002 and 2003. Interactions between explanatory factors were evaluated and are denoted as "*". Only the top ten most parsimonious models are shown.

MODEL	*K*	Δ AIC_c[a]	Akaike Weight[b]
Breeding	3	0.00	0.25
Null	2	0.37	0.21
Breeding + wintering	4	0.62	0.19
Wintering	3	1.96	0.10
Breeding + sex	4	3.09	0.05
Sex	3	3.42	0.05
Breeding + wintering + breeding*wintering	5	3.75	0.04
Breeding + wintering + sex	5	3.75	0.04
Wintering + sex	4	5.04	0.02
Breeding + sex + sex*breeding	5	5.23	0.02

[a] Difference between AIC_c of the current model and the minimum observed value.

[b] Normalized Akaike weight (Burnham and Anderson 1998).

Table 5.4: Summary of competing general linear models approximating hematocrit levels of white-throated sparrows with sex, breeding latitude (breeding) estimated with δD of tail feathers, and wintering latitude (wintering) estimated with δD of head feathers. Models are based on samples from 177 individuals captured during spring of 2002 and 2003. Interactions between explanatory factors were evaluated and are denoted as "*". Only the top ten most parsimonious models are shown.

MODEL	*K*	Δ AIC_c[a]	Akaike Weight[b]
Null	2	0.00	0.35
Wintering	3	1.81	0.14
Breeding + wintering +breeding*wintering	5	2.03	0.13
Breeding	3	2.23	0.11
Sex	3	2.74	0.09
Breeding + wintering	4	3.78	0.05
Wintering + sex	4	4.82	0.03
Breeding + sex	4	4.96	0.03
Breeding + wintering + breeding*wintering + sex	6	5.15	0.03
Breeding + wintering + sex	5	6.80	0.01

[a] Difference between AIC_c of the current model and the minimum observed value.

[b] Normalized Akaike weight (Burnham and Anderson 1998).

Table 5.5: Summary of competing general linear models approximating body fat of white-throated sparrows with sex, breeding latitude (breeding) estimated with δD of tail feathers, and wintering latitude (wintering) estimated with δD of head feathers. Models are based on samples from 155 individuals captured during spring of 2002 and 2003. Interactions between explanatory factors were evaluated and are denoted as "*". Only the top ten most parsimonious models are shown.

MODEL	*K*	Δ AIC_c[a]	Akaike Weight[b]
Null	2	0.00	0.25
Breeding	3	0.64	0.18
Wintering	3	1.18	0.14
Breeding + wintering	4	1.29	0.13
Breeding + sex+ sex*breeding	5	2.87	0.06
Breeding+ wintering + sex + sex*breeding	6	3.19	0.05
Sex	3	3.33	0.05
Breeding + sex	4	4.19	0.03
Breeding + wintering + sex	5	4.70	0.02
Wintering + sex	4	4.73	0.02

[a] Difference between AIC_c of the current model and the minimum observed value.

[b] Normalized Akaike weight (Burnham and Anderson 1998).

Table 5.6: Summary of competing general linear models approximating intensity of *Haemoproteus* infections among infected white-throated sparrows with sex, breeding latitude (breeding) estimated with δD of tail feathers, and wintering latitude (wintering) estimated with δD of head feathers. Models are based on samples from 108 individuals captured during spring 2002 and 2003. Interactions between explanatory factors were evaluated and are denoted as "*". Only the top ten most parsimonious models are shown.

MODEL	*K*	Δ AIC_c[a]	Akaike Weight[b]
Null	2	0.00	0.47
Breeding	3	2.56	0.13
Sex	3	2.86	0.11
Wintering	3	3.10	0.10
Breeding + Wintering + breeding*wintering	5	4.37	0.05
Breeding + sex	4	5.56	0.03
Breeding + wintering	4	5.75	0.03
Wintering + sex	4	6.00	0.02
Breeding + wintering + sex+ breeding*wintering	6	7.22	0.01
Breeding + sex + sex*breeding	5	8.44	0.01

[a] Difference between AIC_c of the current model and the minimum observed value.

[b] Normalized Akaike weight (Burnham and Anderson 1998).

Table 5.7: Summary of competing logistic regression models approximating prevalence of *Haemoproteus* infections in white-throated sparrows with sex, breeding latitude (breeding) estimated with δD of tail feathers, and wintering latitude (wintering) estimated with δD of head feathers. Models are based on samples from 177 individuals captured during spring of 2002 and 2003. Interactions between explanatory factors were evaluated and are denoted as "*". Only the top ten most parsimonious models are shown.

MODEL	*K*	Δ AIC_c[a]	Akaike Weight[b]
Null	2	0.00	0.27
Sex	3	1.12	0.15
Breeding	3	1.74	0.11
Wintering	3	1.86	0.11
Breeding + wintering + breeding*wintering	5	3.28	0.05
Breeding + wintering + sex	5	3.29	0.05
Breeding + sex	4	3.34	0.05
Breeding + sex + sex*breeding	5	3.38	0.05
Breeding + wintering	4	3.43	0.05
Wintering + sex	4	3.52	0.05

[a] Difference between AIC_c of the current model and the minimum observed value.

[b] Normalized Akaike weight (Burnham and Anderson 1998).

Table 5.8: Summary of competing logistic regression models approximating prevalence of *Leucocytozoon* infections in white-throated sparrows with sex, breeding latitude (breeding) estimated with δD of tail feathers, and wintering latitude (wintering) estimated with δD of head feathers. Models are based on samples from 177 individuals captured during spring of 2002 and 2003. Interactions between explanatory factors were evaluated and are denoted as "*". Only the top ten most parsimonious models are shown.

MODEL	*K*	Δ AIC_c[a]	Akaike Weight[b]
Breeding	3	0.00	0.25
Breeding + sex	4	0.96	0.15
Breeding + wintering	4	1.94	0.09
Breeding + wintering + breeding*wintering	5	2.07	0.09
Breeding + wintering + sex	5	2.73	0.06
Null	2	2.84	0.06
Breeding + wintering + sex+ breeding*wintering	6	2.87	0.06
Breeding + sex + sex*breeding	5	3.08	0.05
Sex	3	4.11	0.03
Wintering	3	4.44	0.03

[a] Difference between AIC_c of the current model and the minimum observed value.

[b] Normalized Akaike weight (Burnham and Anderson 1998).

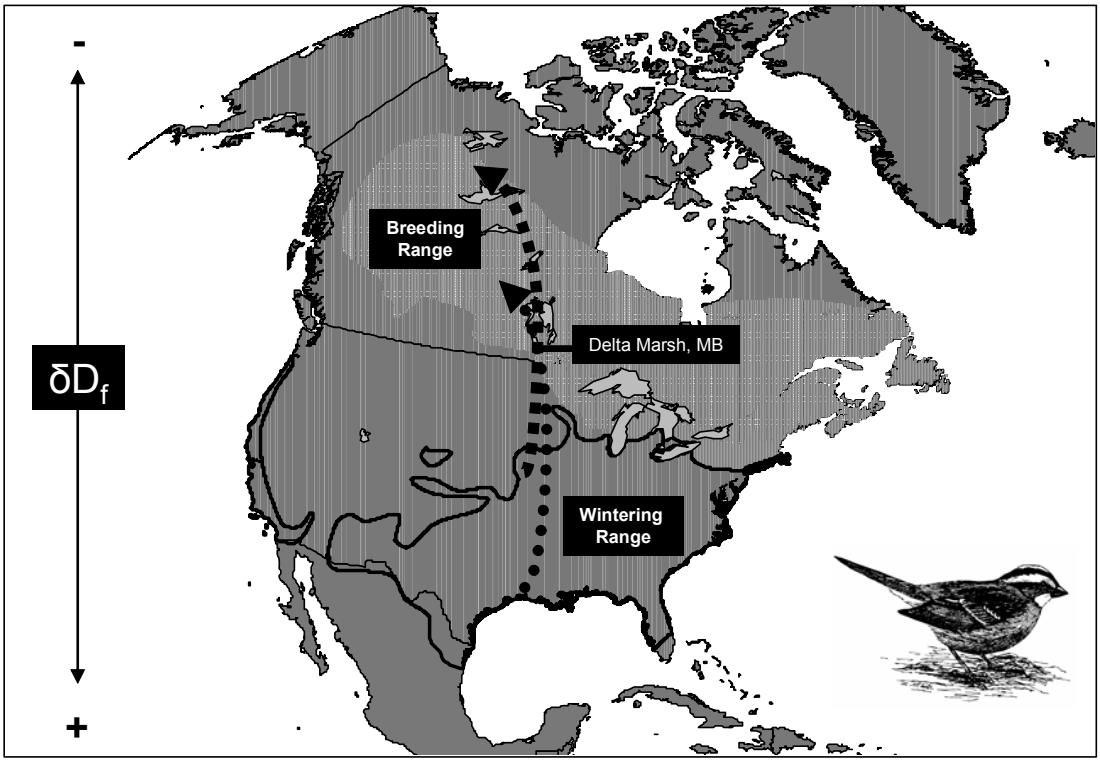

Fig. 5.1. Map depicting the wintering and breeding range of white-throated sparrows and two possible spring migration trajectories of individuals wintering within the catchment area of the monitoring station where birds were sampled. Note that the predicted mean growing-season δD values of precipitation (and feathers grown in these areas) decreases with increasing latitude in North America.

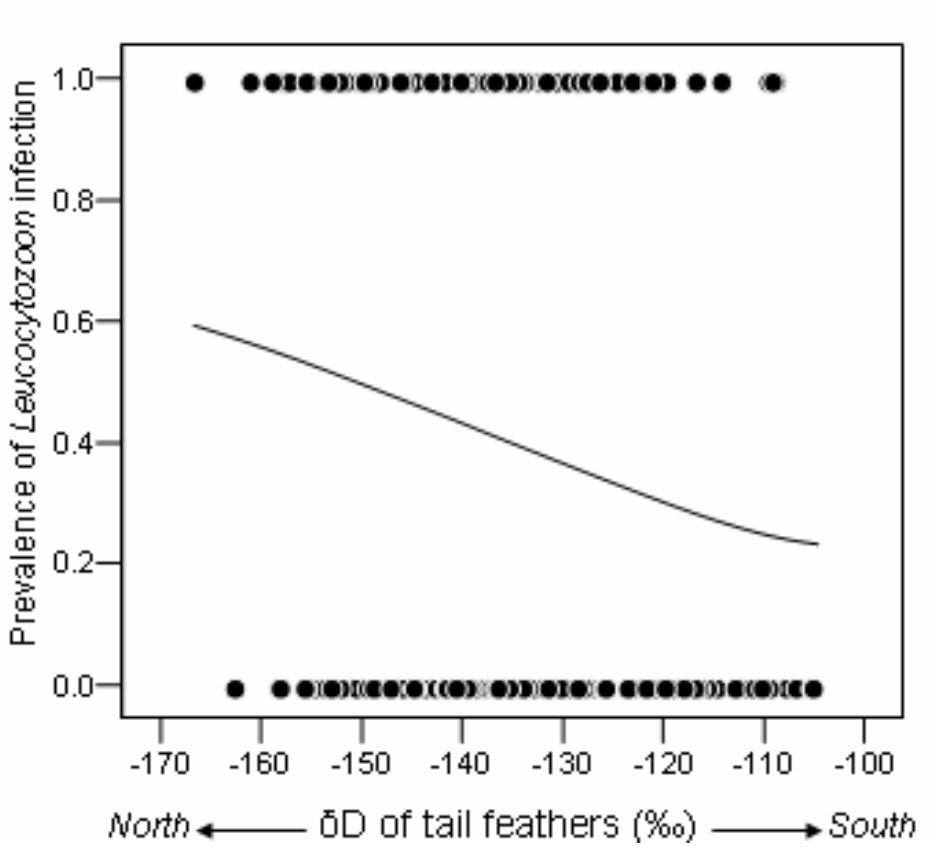

Figure 5.2. Predicted prevalence of *Leucocytozoon* infections in white-throated sparrows captured during spring migration of 2002 and 2003 in relation to previous breeding/natal latitude estimated by δD of tail feathers. The logistic regression analysis was based on a sample of 177 sparrows.

CHAPTER 6: SUMMARY AND SYNTHESIS

Intrinsic markers such as naturally occurring stable isotopes have received considerable attention because of their usefulness for evaluating migratory connections without the need to mark and recapture individuals (Hobson 2003; Rubenstein and Hobson 2004). For my thesis research, I relied on stable hydrogen isotope analyses of multiple feathers representing different periods and geographic regions of the annual cycle to: 1) provide key information about migratory patterns and population connectivity of white-throated sparrows, and 2) to investigate implications of migratory patterns for pre-breeding body condition and timing of spring of arrival. Below, I summarize the most significant findings of my research.

Establishing migratory linkages using stable-isotope markers hinges on knowing which tissues most accurately reflect the isotopic signature of previous feeding locations of interest. In Chapter 2, I assessed the correspondence among δD values of feathers, claws, and cellular portions of blood of white-throated sparrows intercepted during migration to determine if these measures provided concordant estimates of origins. δD values of claws from birds captured during spring and fall migration were positively correlated with δD values of head feathers grown on the wintering grounds and tail feathers grown on breeding grounds, respectively, indicating that claws contained information on origins of individuals. However, analyses contrasting δD measurements

of base and tip of claws, and of tip of claws versus head and tail feathers suggested a significant amount of claw growth occurred during migration resulting in biased estimates of breeding and wintering origins. Thus, for ground-foraging birds like white-throated sparrows, I caution against using isotope measurements of claws as long-term position indicators. δD values of blood were correlated with the δD values from the base of claws, which represented the most recent claw growth, but were not correlated with the δD values of claw tips or head feathers. Thus, it appears that the δD values of blood cells are not useful for approximating wintering latitudes of white-throated sparrows captured during spring migration at Delta Marsh, MB.

The stable-hydrogen isotope approach can provide information about origin and likely destination of birds at staging areas. This information can be important for determining the importance of specific staging areas for North American breeding bird populations, for delineating catchment areas of migration monitoring stations, and for assessing migratory connectivity at various spatial scales (Hobson 1999; Wassenaar and Hobson 2001; Hobson 2003; Rubenstein and Hobson 2004). In Chapter 3, I used δD values of feathers of white-throated sparrows moving through a migration monitoring station at Delta Marsh in Manitoba, Canada, to evaluate migratory connectivity in white-throated sparrows and to determine both wintering- and breeding-ground catchment areas monitored by this station. The δD values of tail feathers collected from spring and fall migrants delineated previous breeding or natal latitudes, ranging from the northern to the southern extremes of the western boreal forest. The δD values of head feathers grown on the wintering grounds and collected during spring migration revealed that individuals wintered in a broad region of the southeastern United States. This result

highlights the importance of Delta Marsh as a key staging ground for populations of white-throated sparrows. The isotope data showed no relationship between estimated breeding and wintering latitudes of white-throated sparrow populations. However, band encounter analyses indicated a clear east-west segregation of these sparrows across Canada, supporting connectivity among breeding and wintering longitudes at the scale of this species range. This finding suggests that white-throated sparrows have a parallel migration system.

Studies of avian population dynamics are relying increasingly on information about migratory connectivity to identify and evaluate potentially important environmental factors affecting population parameters of focal species and populations (Newton 2004). For example, recent studies have relied on information about migratory connectivity to predict impacts of El Niño / Southern Oscillation on the demography of specific breeding populations (see Sillett et al. 2000; Mazerolle et al. 2005). I would recommend that approaches similar to those applied by Sillett et al. (2001) and Mazerolle et al. (2005) be used to evaluate potential factors responsible for the remarkable spatial variation in long-term population trends of white-throated sparrows (Fig. 1.6). Presumably, the detailed account of migratory connectivity presented in this thesis would greatly facilitate such an endeavor.

Differential migration (i.e., latitudinal segregation of males and females on wintering areas) is one of the most common migratory patterns in birds. One of the key assumptions of differential migration hypotheses is that the timing of arrival of individuals is influenced by the distance between breeding and wintering areas. Males are thought to winter at more northern latitudes than females in part because wintering

in these areas allows them to reach breeding areas quicker during spring migration. In Chapter 4, I used the stable-hydrogen isotope approach to investigate differential migration in white-throated sparrows to clarify hypotheses about patterns and consequences of migration tactics. As expected, sparrows staging at Delta Marsh, Manitoba, exhibited sex-biased differential timing of spring arrival and latitude of wintering origin; specifically, females arrived later and originated from more southern latitudes. Further, there was a negative relationship between wintering latitude and arrival dates of individuals, although this relationship was only present during the second spring of the study, since atypical cold temperatures were associated with a pulse of late arriving sparrows during the first spring. The negative correlation between wintering latitude and arrival date was also present within males, suggesting that the distribution of males on wintering areas could have carry-over effects to reproduction.

Fretwell (1972) first theorized that events occurring during one stage of the annual cycle of birds could have residual effects on subsequent stages or seasons. In Chapter 5, I evaluated whether wintering latitude of white-throated sparrows *en route* to boreal breeding grounds had a measurable carry-over effect to pre-breeding body condition, an important determinant of reproductive success in birds (Ankney and McInnes 1978; Ots and Horak 1996; Hasselquist et al. 2001; Smith and Moore 2003; Møller et al. 2004; Moreno et al. 1999). I predicted that birds wintering at more southern latitudes would have lower body condition due to the stress associated with migrating longer distances. However, I found that none of the body condition indices measured in this study varied in relation to migration distance (i.e., distance between wintering areas and Delta Marsh).

To date, the use of stable isotopes for tracking cross-seasonal carry-over effects has been restricted to evaluations of residual effects of wintering habitat use (e.g., dry limestone forest versus mangrove forest) on reproduction (Marra et al. 1998; Bearhop et al. 2004; Norris et al. 2004). Wintering latitudes in differential migrants could also have important carry-over effects to reproduction by affecting pre-breeding body condition and timing of arrival at breeding areas, although I found support only for the latter. My findings set the stage for using the stable isotope approach to test the Seasonal Interaction Hypothesis in differential migrants such as white-throated sparrows.

For my analyses presented in Chapter 5, I controlled for potential effects of previous breeding or natal latitude on body condition indices. I reasoned that this was important particularly for blood parasites, since *Haematozoan* infections vary in relation to the spatial distribution of vectors (Greiner et al. 1975; Smith et al. 2004). I found that the prevalence of *Leucocytozoon* varied in relation to previous breeding or natal latitude. Specifically, individuals that had bred or were born at more northern latitudes were more likely to be infected by this protozoan. While this parasite did not negatively affect body condition of adult sparrows (Mazerolle, unpublished results), it could have important effects for the fitness of young birds that have not yet fully developed their immune system (Atkinson and van Riper 1991). Research is needed to evaluate latitudinal variation in parasitic infections and impacts of these parasites on body condition of hatch-year birds. If the impacts of these parasites are significant, they could have important carry-over effects to the wintering season.

Finally, the accuracy and precision of estimates of origins of birds based on the stable isotope technique, as applied in this study and several others, hinges on the

accuracy and precision of estimates of δD_p and the discrimination factor between δD_p and δD of feathers. The delineations of catchment areas in Chapter 3 were based on a GIS-based model of the mean growing-season δD_p (Meehan et al. 2004). This new model accounts for the effects of altitude on the δD of precipitation and the length of the growing season and provides more reliable estimates of δD_p than the earlier model produced by Hobson and Wassenaar (1997). Meehan et al. (2004) demonstrated that the elevation-corrected kriged estimates of δD_p accounted for large variations in δD values of feathers sampled across North America and that the slope between δD_p and δD values of feathers typically approached one, suggesting that the discrimination factor between these parameters is constant across regions. Similar to Wassenaar and Hobson (2001), I used a discrimination factor of 25‰ to relate my measured δD values of feathers with those of derived δD_p to determine origins. Similar offset values (± 5‰) have been found by other studies focusing on passerines and controlling for the portion of hydrogen in feathers that is exchangeable with ambient water vapor (Wassenaar and Hobson 2000; reviewed by Meehan et al. 2004). Nevertheless, the reliability of the stable isotope technique could be further enhanced with a greater understanding of 1) potential factors affecting the discrimination between δD_p and δD values of feathers, and 2) effects of inter-year and seasonal variation in δD of precipitation on precision errors of analyses estimating origins of individuals based on long-term mean growing-season δD of precipitation (Hobson 2003; Meehan et al. 2003; Rubenstein and Hobson 2004).

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APPENDIX 1: MORPHOMETRIC DISCRIMINATION OF THE SEXES IN WHITE-THROATED SPARROWS

A1.1 INTRODUCTION

Knowledge of the gender of birds is often essential for evaluating behavioral, ecological, and evolutionary questions. For some species, sex determination can be made easily based on visually discernable differences in plumage traits, morphology, or overall body size between males and females. However, for many songbird species, such differences do not exist, particularly when individuals are captured during the non-breeding season and males and females do not have fully developed cloacal protuberances or brood patches, respectively (Piper and Wiley 1991; Pyle et al. 1997; Wilson 1999). With such species, researchers often have to rely on precise estimates of morphological traits such as wing length or genetic approaches to identify the sex of individuals. Morphological measurements can provide useful measures for sex determination. For instance, Piper and Wiley (1991) demonstrated that more than 90% of white-throated sparrows, a species that is sexually monomorphic in color and for which males and females do not vary greatly in size, could be correctly sexed with measures of wing length. Similar approaches have been used successfully on several other species (reviewed by Pyle et al. 1997). However, as many species exhibit geographical variation in morphology (e.g., Rising 2001), the reliability of sexing criteria can be significantly reduced if individuals are sampled from across large areas (see also Van Franeker and ter Braak 1993).

Here, I assessed the reliability of wing length for discriminating between male and female white-throated sparrows originating from broad geographic areas. In addition, I assessed whether measurements of tarsus, tail, and bill lengths, in addition to

measures of wing lengths, would provide more accurate identifications of males and females.

A1.2. METHODS

A1.2.1. Study area and Sample Collection

Birds were captured in baited walk-in ground traps that were operated in the dune-ridge forest abutting the southern shore of Lake Manitoba, MB. Forty individuals (13 males and 27 females) were collected during spring of 2003 for another study. When a bird was captured, morphological measurements such as unflattened wing (measured to the nearest 0.5 mm), tail (measured to the nearest 0.5 mm), tarsus (measured to the nearest 0.1 mm), and bill length (measured to the nearest 0.1 mm) were taken using the methods described in Pyle et al. (1997). I measured all birds. For a subsample of the birds, I took repeat measurements of the same traits to quantify the repeatability of my measurements. Further, wing lengths of many of the sampled birds were also measured by other skilled banders, which enabled me to quantify among-observer error in wing-length measurements. The sex of individuals was determined by examination of reproductive organs following dissection. Bird collections were conducted under a C collection permit and using methods approved by the Committee for Animal Care at the University of Saskatchewan.

A1.2.2. Statistical Analyses

Repeatability of morphological measurements was quantified with intra-class correlations calculated from the variance components of one-way analyses of variance (Lessells and Boag 1987). Measurements used to compute repeatability estimates

included the dissected birds and other birds processed during the spring of 2002 and 2003. Body mass was not used to sex individuals because this measure varies considerably within and among individuals during the migratory period. Discriminant Function Analysis (DFA) was used to identify the morphological measurements that best discriminated between males and females. Since no differences in within-groups covariance matrices were detected (Box's M test, $P > 0.3$), within-groups covariance matrices were used. Percent correct classification of DFAs was computed using the jackknife procedure implemented in SPSS. Chance-corrected classification was also calculated to determine the effectiveness of the DFA while controlling for correct classification arising by chance alone (Titus et al. 1984). All analyses were performed with SPSS version 12 for Windows (SPSS Inc. 2003) and were considered significant at an alpha level of 0.05.

A1.3. RESULTS

Measurements of morphological traits were highly repeatable within (DFM) observers (Table A1.1), and unflattened wing length measurements were also highly repeatable between observers. All measured traits, except bill length, differed significantly between males and females (Table A1.2). However, as the repeatability estimates of bill length measurements were lower than those of all other morphological traits, I can not dismiss the possibility that the lack of a significant difference in this trait between sexes could have been caused by measurement errors. Using the sexing criterion described in Piper and Wiley (1991) (females = unflattened wing length ≤ 70 mm, and males = unflattened wing length >70 mm), 92% (12 /13) of males and 90% (27/30) of females were correctly identified. Unflattened wing length had the highest correct jackknifed

classification rates in 1-variable DFAs (Table A1.3). Including other traits did not substantially improve classification success. Probabilities of correctly classifying males and females in relation to unflattened wing length are presented in Fig A1.1.

A1.4. DISCUSSION

All morphological traits were larger in males, except bill length that was similar in size between males and females. Based on unflattened wing length measurements, I was able to correctly identify the sex approximately 90% of the sampled individuals. These findings are consistent with those of Piper and Wiley (1991), and suggest that unflattened wing length can be effective in predicting the sex of most white-throated sparrows even when individuals originate from wide ranging breeding and wintering latitudes. Measurements of additional morphological traits, including tail length, tarsus length, and bill length, did not increase the percentage of correct classification of males or females. Estimates of the probability of correct classification in relation to unflattened wing length presented in Fig. A1.1 can be used as a weighting variable in analyses comparing traits between sexes (as evaluated in Chapter 4).

Table A1.1: Repeatability estimates (intra-class correlations) of measurements of unflattened wing, tail, tarsus, and bill length of white-throated sparrows sampled at Delta Marsh, MB, during the spring migration of 2003. All measurements were highly repeatable ($P < 0.001$). Analyses used for computing estimates of between-observer repeatability for wing length measurements were based on comparisons of measurements taken by DFM and those taken by 5 other skilled banders.

Parameters	r	F ratio	DF
Unflattened Wing Length (mm) between observer	0.86	13.73	251, 252
Unflattened Wing Length (mm) within observer	0.97	63.82	21, 22
Tarsus Length (mm)	0.95	40.15	27, 28
Tail Length (mm)	0.95	37.58	19, 20
Bill Length (mm)	0.87	14.42	14, 15

Table A1.2: Descriptive statistics of morphological measurements of male and female white-throated sparrows collected at Delta Marsh, MB, during the spring of 2003.

Trait	Females				Males				P
	N	Mean	SD	SE	N	Mean	SD	SE	
Tarsus Length (mm)	27	23.0	0.5	0.1	13	23.7	0.6	0.2	***
Bill Length (mm)	27	11.8	0.4	0.1	13	12.0	0.4	0.1	
Tail Length (mm)	27	69.2	2.3	0.4	13	73.2	2.7	0.8	***
Unflattened Wing Length (mm)	27	68.4	1.7	0.3	13	72.9	1.9	0.5	***

*** $P < 0.001$

Table A1.3. Sex classification of white-throated sparrows sampled at Delta Marsh, MB during the spring migration of 2003. Separate analyses were computed for each morphological trait.

Parameter	Classified as female if	% Correct Classification	Cohen's Kappa[1]
Unflattened Wing Length (mm)	≤ 69.5	90	0.78***
Tail Length (mm)	≤ 70.5	82	0.62***
Tarsus Length (mm)	≤ 23.15	78	0.52***
Bill Length (mm)	≤ 11.8	57	0.12

*** $P < 0.001$

[1]Provides a measure of the chance corrected proportional agreement

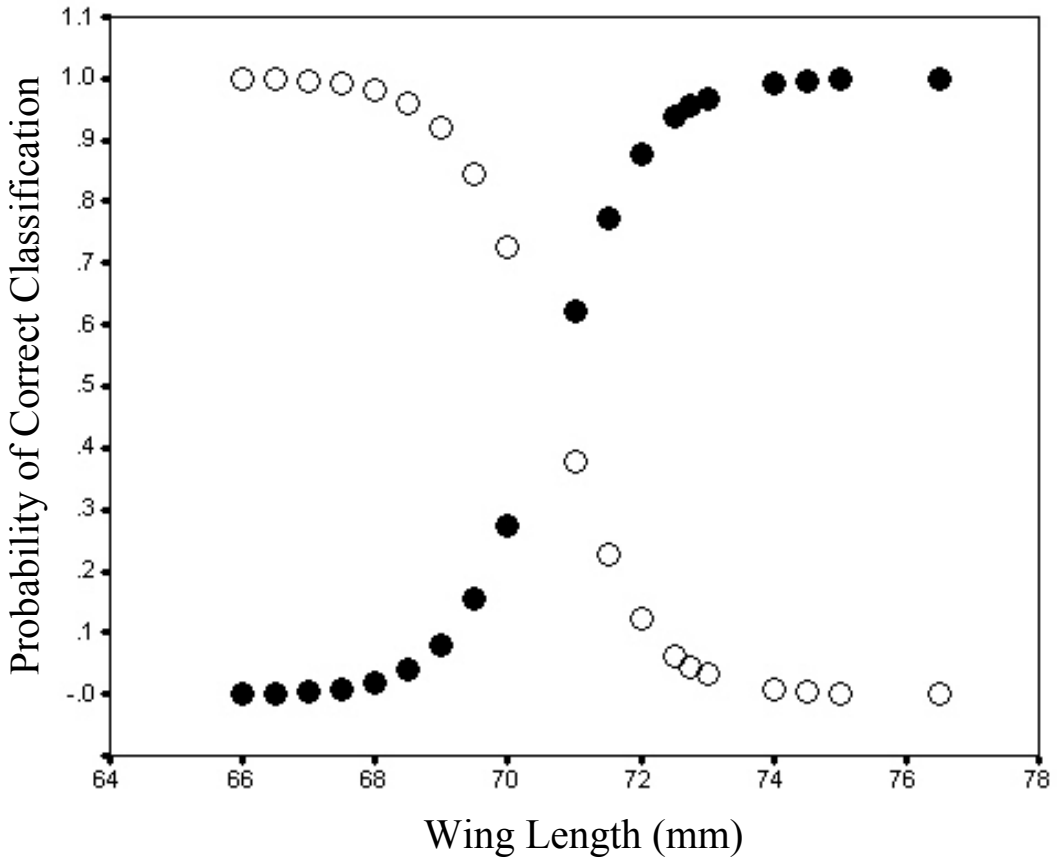


Fig. A1.1. Probability of correctly sexing white-throated sparrows with measures of unflattened wing length (●= males and ○ = females). Probabilities were computed with a discriminant function analysis based on a sample of 13 males and 27 females for which the sex was known.

APPENDIX 2: MORPHOMETRIC ESTIMATION OF FUEL STORES IN WHITE-THROATED SPARROWS: A VALIDATION OF THE USE OF MASS/SIZE RESIDUALS

A2.1. INTRODUCTION

Measures of animal body condition (i.e., size of fuel stores) are frequently used in behavioral, ecological, and evolutionary research (Blem 1990; Brown 1996; Speakman 2001). In birds, the most accurate indices of fuel reserves are those that involve direct measures of lipids and proteins derived using carcass analysis (Blem 2001; Speakman 2001). However, because of practical and ethical considerations, many studies require the use of non-destructive indices of fuel stores (Brown 1996). Several non-destructive methods have been evaluated (e.g., bioelectrical impedance analysis and total body electrical conductivity), although morphometric indices are the most frequently used (Green 2001). For instance, residuals from regressions of mass versus size (mass/size residuals) have been used extensively to estimate the relative size of energy stores, as the sign and magnitude of residuals are determined primarily by fat and protein mass (Blem 1990; Green 2001). Traditionally, mass/size residuals have been computed with ordinary least squares (OLS) regressions of mass against a measure of body size, although such methods have been recently criticized (e.g., van der Meer and Piersma 1994; Green 2001; Hayes and Shonkwiler 2001). Green (2001) described how regressions of mass versus size can violate certain assumptions of OLS regressions, producing biased estimates of fuel reserves. Both Hayes and Shonkwiler (2001) and Green (2001) stressed the importance of validating the accuracy of mass/size residuals for predicting the size of avian fuel stores and the need for critical evaluations of the statistical assumptions of regression models. Given the extensive use of mass/size

residuals and the debate over which regression models are most appropriate for calculating such residuals, additional studies evaluating the reliability of these measures as proxies of levels of fuel stores are warranted.

In addition to confirming that the index of the size of fuel stores is highly correlated with the true size of fuel stores, Green (2001) also suggested that researchers evaluate six assumptions inherent in the use of the mass/size residual method prior to using these indices as metrics of body condition. These assumptions are: 1) mass increases linearly with body size, 2) mass/size residuals and "true" condition are independent of body size, 3) the index of body size used in the regression is an accurate measure of body size, 4) the absence of a correlation between mass/size residuals with other structural attributes (i.e., shape) and the parameter against which the residuals are analyzed, 5) measures of body size are strictly independent of body mass, and 6) body size is measured without error. Green (2001) reasoned that most studies using mass-size residual method, especially those using OLS regressions, violated one or more of these assumptions. Consequently, he recommended that regression models such as reduced-major-axis regression (RMA) be used to compute mass/size residuals, instead of the OLS approach, since mass/size residuals derived with RMA regressions should be less biased and more highly correlated with the size of fuel stores. This recommendation, however, is inconsistent with the findings of Schulte-Hostedde et al. (2005) which demonstrated that mass-size residuals from OLS regression provided the best predictor of fuel stores for the three species of small mammals evaluated in their study. Similarly, Legendre and Legendre (1998) suggested that OLS regressions are more effective for making predictions (e.g., observed versus predicted mass) than RMA regressions.

Using an approach similar to that of Schulte-Hostedde et al. (2005), I sought to evaluate assumptions of the mass-size residual method and to determine which regression method (RMA versus OLS) provided residuals that best predicted fuel stores (total body lipids and proteins) in wintering white-throated sparrows.

A2.2. METHODS

A2.2.1. Study Area, Field Methods, and Laboratory Procedures

White-throated sparrows were captured by mist-netting throughout the winter (November 1979 to April 1980) in suburban west Richmond in western Henrico County (see Blem and Shelor 1986). Birds were captured at 3- to 4-day intervals over a wide variety of dates, time, and weather conditions. Upon capture, birds were euthanized via thoracic compression. Time of capture was recorded and birds were weighed in the field to the nearest 0.1g on a triple beam balance. Birds were temporarily stored on ice and transported to the laboratory where they were frozen and stored at -23^{o}C until further analyses could be conducted.

Wing chord was measured with calipers to the nearest millimeter. Tarsometatarsus (tarsus hereafter) was measured to the nearest 0.1mm. Length of the tarsus was defined as the distance between the notch formed by the joining of the tibiotarsus and tarsometatarsus distally to the last rigid undivided scale where the tarsometatarsus joins the phalanges. Bill length was measured from the external nares to the tip of the bill to the nearest 0.1mm. Furcular fat scores were determined using the classification scheme of Helms and Drury (1960), modified slightly in that each of their six classes was further subdivided so that intermediate conditions could be quantified.

Furcular fat scores can provide a usful index of total body lipids in many passerine species (Rogers 2003). For instance, fat scores in the white-throated sparrows sampled in this study explained 66% of the total body lipids (Blem and Shelor 1986).

Total body lipids were estimated via Soxhlet extraction. Lean dry weight was calculated as dry body weight minus total lipid, where total lipids correspond to the dry weight x lipid content (as a decimal fraction). All estimates of fuel stores and morphological measurements described above are described in detail in Blem and Shelor (1986).

A2.2.2. Statistical Analyses

Morphological measurements and body mass were log transformed. Principal component analysis (PCA) was computed from a correlation matrix using all morphological measurements (Rising and Somers 1989). The first principal component (PC1) from this analysis was used as an index of structural size. PC1 accounted for 41% of the overall variance, and was characterized by the following three morphological parameters and factor loadings: bill length, 0.13; tarsus length, 0.78; wing length, 0.79.

I determined whether the relationship between mass and size was linear by evaluating a bivariate plot of mass versus size and by contrasting the linear model with a quadratic polynomial regression model. I also used a covariance analysis that included sex and the interaction between sex and size to determine if the sexes should be evaluated separately.

Residuals (y-axis deviations) from both OLS and RMA regressions of mass vs. size were used as indices of the size of fuel stores. Unlike OLS regressions that minimizes the sum of squared y-axis deviations, RMA regressions minimizes the error

with respect to both x and y variables as a function of their joint product, which corresponds to a minimization of the sum of the areas of the triangle formed by the projection of the x and y value and the regression line (Legendre and Legendre 1998). Residuals were evaluated graphically and a 1-sample Kolmogorov-Smirnov test showed that they did not deviate from normality (Sokal and Rohlf 1995), but no violations were detected. I used Pearson's correlation to compare the strength of the relationship between mass/size residuals from OLS (OLSRESID) and RMA (RMARESID) and measures of total body lipids, lean dry weight, and water. Further, I combined mass/size residuals with furcular fat scores using PCA to generate a linear univariate measure of body condition. PC1 accounted for 80% and 78% of the overall variance for the analysis based on OLSRESID and RMARESID, respectively. The factor loadings for the mass/size residuals and furcular fat score were 0.90 and 0.89 for the PCA based on OLSRESID (OLSRESID + Fat Score = PCAOLSFAT) and RMARESID (RMARESID + Fat Score = PCRMAFAT), respectively. This index was then assessed against total body lipids, lean dry weight, and water to determine if it provided a better proxy of body condition than mass-size residuals alone. The slope and intercept of the RMA models were calculated using the program "Model II regression" (Legendre 2001). All other analyses were performed with SPSS version 9.0 (Norušis 1998). Results were considered significant at an alpha level of 0.05.

A2.3. RESULTS

Body composition estimates and morphological measurements were available for 52 females and 47 males. The index of size (PC1) was significantly correlated with mass (Fig. 1; Pearson's $r = 0.43$, $P < 0.001$). The addition of a quadratic term did not

significantly improve the regression model (P = 0.66). Further, adding sex (F = 0.38, P > 0.50) and the interaction between sex and size (F = 0.04, P > 0.80) did not significantly improve model fit. Body size was not significantly correlated with total body lipids (Pearson's r = 0.09, P > 0.53), but was significantly correlated with lean dry weight (Pearson's r = 0.45, P < 0.001). Both OLSRESID and RMARESID were positively correlated with each other (r = 0.85, P < 0.001) and with total body lipids, lean dry weight, and water (Table 1). However, OLSRESID were more highly correlated with the size of fuel stores than RMARESID (Table 1). Overall, PCOLSFAT was the best predictor of total body lipids, whereas OLSRESID was the best predictor of total body water and lean dry weight. (Table 1)

A2.4. DISCUSSION

Mass-size residuals were highly correlated with the size of fuel stores in white-throated sparrows. As expected, OLSRESID and RMARESID were highly correlated with each other (see also Omerod and Tyler 1990; Mazerolle and Hobson 2001). However, OLSRESID was better predictor of total body lipids, lean dry weight, and water than RMARESID. OLSRESID and fat score composite (PCOLSFAT) provided the best approximation of total body lipid. However, this measure predicted total body water and lean dry weight less well than OLS residuals. Thus, OLS residuals might be more appropriate than PCOLSFAT in studies where the consideration of protein stores is more important than fat stores. Overall, these findings validate the use of mass/size residuals for approximating body condition. Further, they indicate that mass/size residuals can predict more variation in total body lipids when they are combined with furcular fat scores using principal component analysis.

The assumptions inherent in the use of mass-size residuals as indices of body condition that I was able to assess were not violated or were violated only slightly. Specifically, body mass varied linearly with body size (assumption 1), and total body lipids was independent of body size, although body size was related significantly to lean dry mass (assumption 2). The latter could be due in small part to the influence of skeletal tissues and minerals on lean dry mass. While I was not able to directly test the assumption that PC1 of morphological measurements was an accurate measure of body size (assumption 3), previous studies have demonstrated that multivariate measures of size provide robust indices of structural size (Rising and Somers 1989; Gosler et al. 1998). Further, the use of multivariate measures of body size should also reduce the potential for correlations between body size indices and measures of other structural attributes (assumption 4). In addition, while body size was almost certainly measured with some degree of error (assumption 6), the use of principal components analysis minimizes violations in this assumption because measurement error tends to be relegated predominantly to the last principal components. (Gauch 1982)

My findings are consistent with those of Schulte-Hostedde et al. (2005) in that the mass/size residuals provide good proxies of fuel stores. This study is the first to directly evaluate the reliability of mass/size residuals generated from OLS and RMA regressions to predict fuel stores in birds. I found that the mass/size residuals generated using OLS regressions were better predictors than residuals generated using RMA regressions and that the best predictor of total body lipids was a measure that combined OLSRESID with furcular fat scores.

Table A2.1: Pearson correlation coefficients between y-axis residuals from mass/size regressions and total mass of body lipids (g), proteins (g), and water (g) of white-throated sparrows. See text for details on how residuals were computed.

	OLSRESID[1]	RMARESID[2]	PCRMAFAT[3]	PCOLSFAT[4]
Lipid (g)	0.77***	0.67***	0.81***	0.86***
Lean Dry Mass (g)	0.63***	0.30*	0.31***	0.49***
Water (g)	0.45***	0.07	-0.01	0.21*

* $P < 0.05$; *** $P < 0.001$

[1]Mass/size residuals from OLS regressions.

[2]Mass/size residuals from RMA regressions.

[3]PC1 from a PCA on RMARESID and furcular fat scores.

[4]PC1 from a PCA on OLSRESID and furcular fat scores.

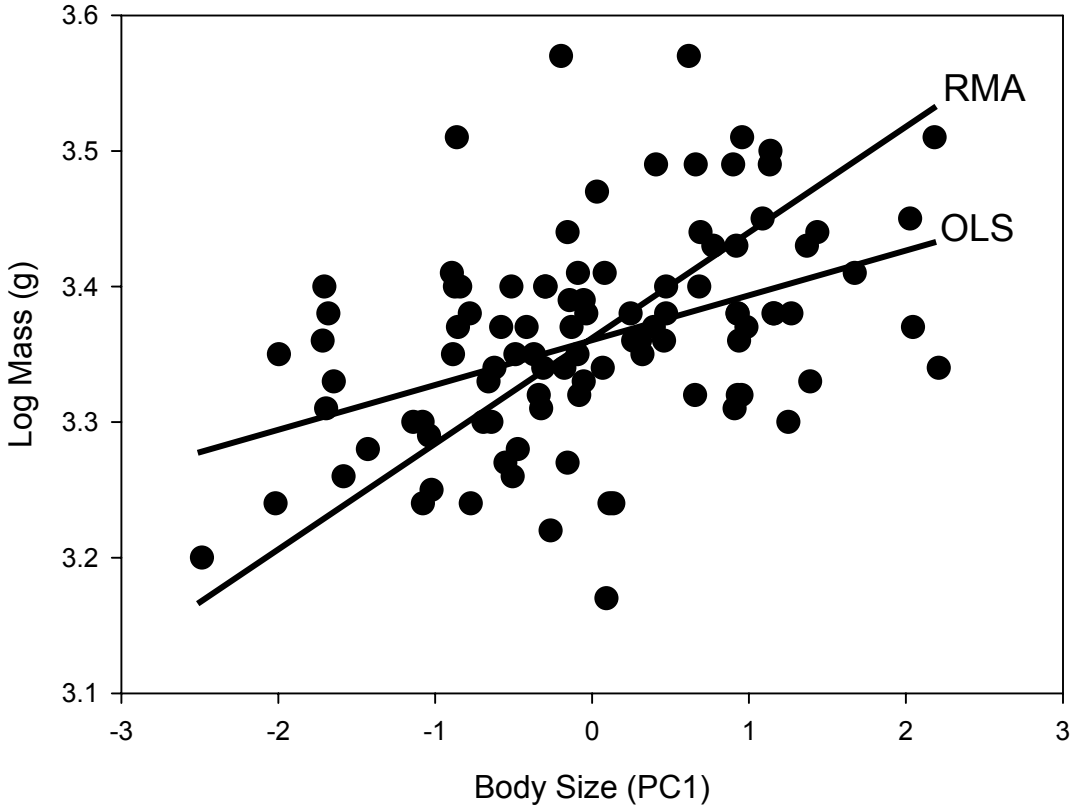
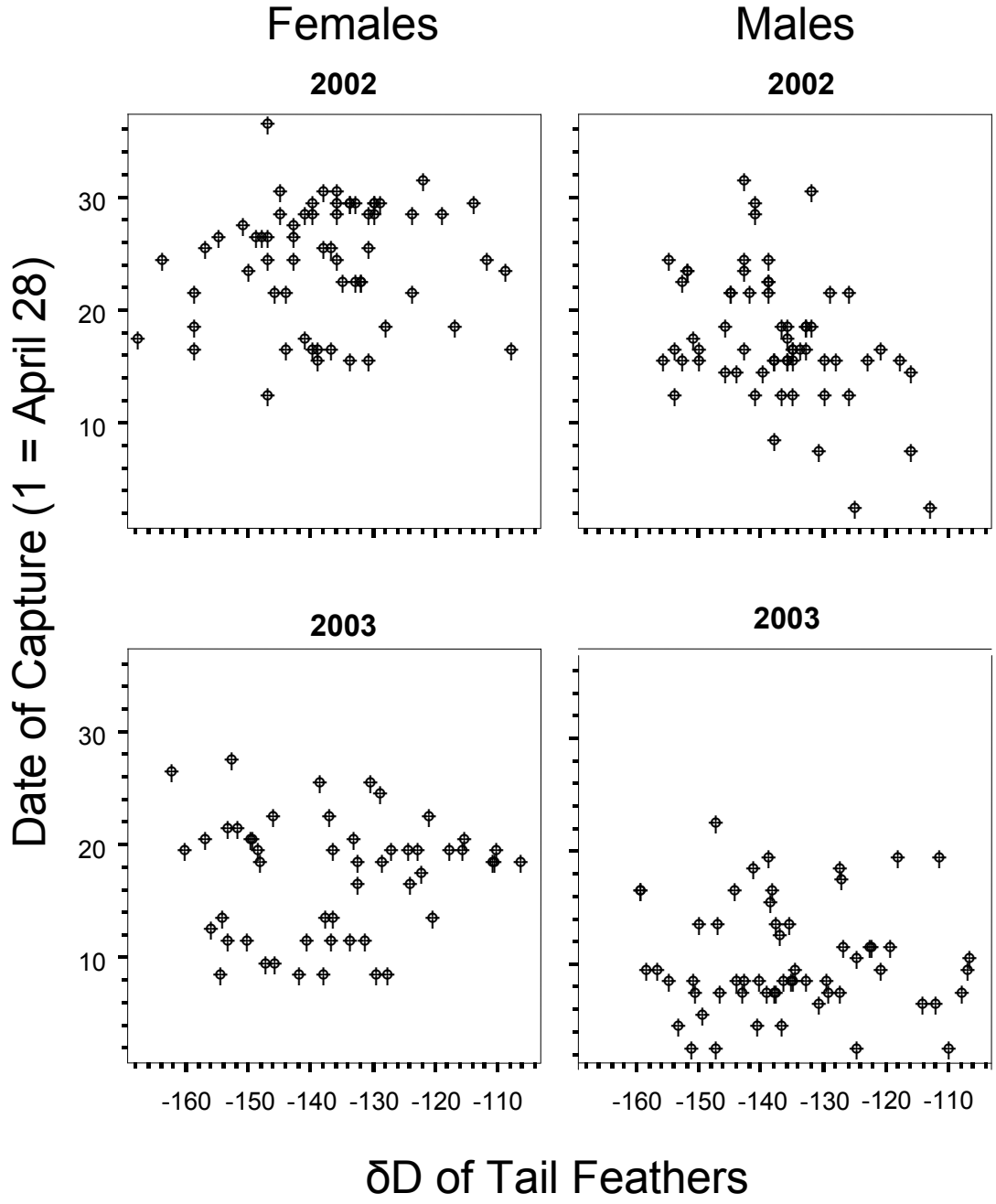


Fig. A2.1. RMA and OLS regression lines fitted to a plot of log body mass (g) against body size (PC1) in white-throated sparrows (N = 99). See text for details on the computation of body size and OLS and RMA regressions.

APPENDIX 3: RELATIONSHIP BETWEEN BREEDING LATITUDE, AS ESTIMATED WITH STABLE HYDROGEN ISOTOPE ANALYSES OF TAIL FEATHERS, AND CAPTURE DATES OF WHITE-THROATED SPARROWS SAMPLED DURING SPRING MIGRATION.



APPENDIX 4: RELATIONSHIP BETWEEN TOTAL WHITE BLOOD CELL COUNT AND COUNTS OF HETEROPHILS, EOSINOPHILS, BASOPHILS, MONOCYTES, AND LYMPHOCYTES. * P < 0.05.