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ABSTRACT

While wintering and breeding are geographically separated in migratory bird species, a growing body of evidence suggests that winter events and winter location may have effects that carry over and impact aspects of the breeding season. In this study, I investigated the effects of a winter event (prealternate moult) and winter location on breeding success in a short-distance migrant, the Ipswich Sparrow (*Passerculus sandwichensis princeps*). Ipswich Sparrows, a subspecies of Savannah Sparrow, breed almost exclusively on Sable Island, Nova Scotia; and winter along the Atlantic coast from Nova Scotia to Florida

My first goal was to describe the incidence, timing and extent of the partial winter (prealternate) moult of Ipswich Sparrows, and determine if relationships existed between prealternate moult and breeding performance or winter location. Prealternate moult only occurred in 25% of Ipswich Sparrows and was mainly restricted to tertials, rectrices and back feathers. Approximately half of the individuals that moulted were actively moulting during the breeding season; and stable isotope evidence suggests that some individuals moult during migration. There was no relationship between the incidence of prealternate moult and breeding performance, nor was prealternate moult related to winter location. My results suggest that prealternate moult is a relatively low-cost activity for Ipswich Sparrows, and that it may function to replace plumage degraded by sunlight.

My second goal was to determine if aspects of winter location impacted the breeding season in Ipswich Sparrows. I used hydrogen stable isotope analysis to determine wintering latitude and carbon and nitrogen stable isotope analysis to infer aspects of winter diet. My sample of sparrows wintered mainly in the northern and middle portions of the range. Males also wintered further north than females, and winter location impacted reproductive success in both sexes. Males that wintered in the northern part of the wintering range were in better condition, established territories earlier, and tended to produce heavier nestlings than those that wintered further south. Conversely, females that wintered towards the southern part of the wintering range had earlier first egg dates than those wintering further north. Individuals wintering further south relied mainly on a diet of C₄ plants, while those wintering further north incorporated C₃ plants in their diet. Nitrogen isotope ratios were not useful in determining trophic level, but were related to condition and therefore may provide information regarding quality of winter habitat.

LIST OF ABBREVIATIONS AND SYMBOLS USED

$\delta^{13}\text{C}$	The ratio of heavy carbon (^{13}C) to light carbon (^{12}C), expressed in parts per thousand (‰) relative to a standard
δD	The ratio of heavy hydrogen, or deuterium (^2H) to light hydrogen (^1H), expressed in parts per thousand (‰) relative to a standard
δD_p	The hydrogen isotope ratio (δD) of precipitation
δD_k	The hydrogen isotope ratio (δD) of claw keratin
δD_f	The hydrogen isotope ratios (δD) of feather keratin
$\delta^{15}\text{N}$	The ratio of heavy nitrogen (^{15}N) to light nitrogen (^{14}N), expressed in parts per thousand (‰) relative to a standard
$\delta^{34}\text{S}$	The ratio of heavy sulphur (^{34}S) to light sulphur (^{32}S), expressed in parts per thousand (‰) relative to a standard
AIR	Atmospheric nitrogen, the standard against which $\delta^{15}\text{N}$ is measured
BWB	Bowhead Whale Baleen
CAM	Crassulacean Acid Metabolism
CBC	Christmas Bird Count
CDT	Canyon Diablo Troilite, the standard against which $\delta^{34}\text{S}$ is measured
CFS	Chicken Feather Standard
CHS	Cow Hoof Standard
GNIP	Global Network for Isotopes in Precipitation
IAEA	International Atomic Energy Association
SARA	Species at Risk Act
TC/EA	High Temperature Conversion/Elemental Analyzer
VPDB	Vienna Pee Dee Belemnite, the standard against which $\delta^{13}\text{C}$ is measured
VSMOW	Vienna Standard Mean Ocean Water, the standard against which δD is measured.

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CHAPTER 1. INTRODUCTION

Migration, a seasonal movement between biomes, is common in the animal kingdom and particularly so in birds (Kelly and Finch 1998). However, studying the behaviour and ecology of migratory birds poses unique challenges, as their lives are divided into distinct periods (breeding and wintering) that occur in widely separated locations (Berthold 2001). To date, the majority of studies of migratory birds have taken place on their temperate breeding grounds; however, these animals may spend well over half the year migrating to and wintering in areas thousands of kilometers away from these breeding grounds (Marra et al. 1998, Norris et al. 2004a). Winter events (such as winter moult), winter ecology, and winter location remain unstudied for many species, and consequently there are large gaps in our understanding of the annual cycle of migratory birds. Furthermore, although wintering and breeding are distinct stages and may occur thousands of miles apart, they do not occur in isolation: each stage may impact or be impacted by the other. Therefore, in order to fully understand the factors shaping the population dynamics, behaviour and ecology of migratory birds, knowledge of the entire annual cycle is required.

Winter Events: Moulting

In birds, moulting is the process of replacing worn and abraded plumage (Humphrey and Parkes 1959). Most species undergo one complete moulting (the prebasic moulting) annually, during which all feathers are replaced. This moulting typically occurs on the breeding grounds following the breeding season (Humphrey and Parkes 1959), and has therefore been well studied. However, many species undergo additional complete or partial moultings (such as the prealternate moulting) during the year, which often occur on the

wintering grounds (Humphrey and Parkes 1959). Considerably less is known about the incidence, timing and extent of these moults.

Moult is an energetically costly process, as it involves growing new feathers and increased thermoregulatory costs due to feather loss (Payne 1972, Lindström et al. 1993). The temporary loss of flight feathers may also negatively impact flight ability and make individuals more vulnerable to predation (Hedenström and Sunada 1999, Lind 2001).

Because breeding is also a costly process, moult and breeding are frequently timed to minimize overlap (Ginn and Melville 1983). Therefore, the timing, duration and extent of moult may be impacted by breeding. Breeding individuals may moult at different times or for shorter periods (Meissner 2007, Allard et al. 2008), or moult fewer feathers (Brommer et al. 2003) than non-breeders. However, moult-breeding overlaps do sometimes occur. In these cases, individuals may produce smaller clutches (Lobato et al. 2006) or fledge fewer nestlings (Hemborg et al. 2001) than when the processes are temporally separated.

Moult may also impact or be impacted by winter location. Like moult and breeding, moult and migration are frequently temporally separated, presumably so individuals are not missing flight feathers during migration (Berthold 2001). Thus, moult strategies may be impacted by migration strategies. Migratory individuals or populations may moult at different times or more rapidly than sedentary individuals or populations (O'Hara et al. 2002, Munro et al. 2006, Serra et al. 2006). A relationship may also exist between moult and migratory distance, with individuals that do not moult migrating shorter distances (Nebel et al. 2002). When moult-migration overlap does occur, it often

results in fitness consequences such as decreased body condition (Pérez-Tris et al. 2001), or a reduction in feather quality (Norris et al. 2004b).

Winter Location

Many species of North American birds annually migrate thousands of miles between their temperate breeding grounds and southern wintering locations (Kelly and Finch 1998). There are many benefits associated with wintering in southern locations, such as increased winter food availability and more benign climatic conditions (Cox 1985, Greenberg et al. 2007). However, in many species, individuals migrate varying distances, and therefore the climatic and ecological conditions they experience during the winter differ radically (Nolan and Ketterson 1983, Castro et al. 1992). Consequently, migration does not entail the same costs and benefits for every individual.

There are several interrelated aspects of winter location that can affect breeding success. The length of an individual's migration, determined by the geographic distance between the wintering and breeding grounds, may play a role in determining individual arrival times on the breeding grounds. Birds that winter at distant southern locations may arrive on the breeding grounds later than those that winter at closer, northern locations (Bearhop et al. 2005). Earlier arrival times have been linked to increased reproductive success in a variety of species (e.g. American Redstarts (*Setophaga ruticilla*), Norris et al. 2004a, European blackcaps (*Sylvia atricapilla*), Bearhop et al. 2005); therefore, there may be substantial benefits gained by wintering closer to the breeding grounds. Additionally, the length of an individual's migration may influence their body condition when they arrive on the breeding grounds. Individuals that winter further away from the

breeding grounds and have a longer return flight may be in poorer condition upon arrival than those that winter closer to the breeding grounds, and thus have fewer resources to allocate to reproduction (Bearhop et al. 2005).

Winter location also determines the climate and habitat in which individuals winter (Nolan and Ketterson 1983, Castro et al. 1992), and these aspects of winter location may impact reproductive success in a number of ways. Variation in winter climate has been linked to variation in individual body condition and spring departure dates (Studds and Marra 2007), as well as measures of reproductive success such as clutch size and fledging success (Lehikoinen et al. 2006). Similarly, variation in winter habitat quality can impact winter body condition and hence timing of spring migration, with individuals on high quality territories departing before those on poor quality territories (Marra et al. 1998). The quality of winter territory can also impact body condition during migration (Bearhop et al. 2004), arrival times on the breeding grounds (Marra et al. 1998, Norris et al. 2004a), and measures of reproductive success such as clutch size (Saino et al. 2004).

The studies described above illustrate the connections between winter events, winter location and reproductive success and reinforce the importance of taking the nonbreeding season into account when attempting to understand factors affecting breeding success. This is especially important for species at risk, since the causes of population declines may be related to winter events and locations, and understanding the dynamics of links between wintering and breeding may improve the focus of conservation efforts (Wassenaar and Hobson 1998, Pain et al. 2004, Saino et al. 2004).

Historically, the complexities associated with following individuals throughout their annual cycle have made it very difficult to study the relationship between winter and breeding in migratory birds (Hobson 1999, Norris et al. 2004a). However, recent advances such as satellite telemetry and stable isotope analysis have allowed researchers to gain insight into the connections between the seasons (Hobson 1999, Webster et al. 2002, Hobson 2005).

To date, most studies using stable isotope analysis to look at links between wintering and breeding in migratory birds have focused on long-distance migrants and only considered variation in ecological conditions during the winter as a factor that might impact the breeding season. Many fewer studies have investigated the effects of migratory distance on reproductive success.

The purpose of my study was to determine how winter events (specifically, winter moult) and winter location affected breeding success in a short-distance migrant, the Ipswich Sparrow (*Passerculus sandwichensis princeps*), using stable isotope analysis. In the following sections of this introduction, I will describe how stable isotope analysis can be used to infer details about winter location and ecology, and I will discuss the annual cycle of my study species.

Stable Isotope Analysis

While recent studies underscore the importance of understanding the annual cycle of migratory birds in its entirety, this goal has historically been difficult to achieve, due to the vast distances involved in migration (Hobson 1999, Webster et al. 2002). The traditional method of marking and recapturing individuals often fails due to the sheer

improbability of seeing a few marked individuals among thousands (Kelly and Finch 1998, Webster et al. 2002). Recently, satellite tagging has been used to track individuals during migration (Liminana et al. 2007, Putz et al. 2007). However, this technique is limited to individuals large enough to carry heavy satellite tags, which excludes many migratory birds (Hobson 1999).

Over the past decade, stable isotope analysis has become an increasingly popular method of tracking individuals throughout their annual cycle (Hobson 2005). Isotopes are chemically different versions of the same element, which differ in the number of neutrons in the nucleus. For example, ^{12}C has six neutrons in the nucleus, while ^{13}C has seven. Often more than one isotope of an element is present in the natural world, and the ratio of one isotope to another may differ in a predictable way according to location (Webster et al. 2002, Hobson 2005). The ratio of isotopes at any given location is incorporated into the food web and therefore into animal tissues produced there (Hobson 1999, Webster et al. 2002, Hobson 2005). Consequently, the isotope ‘signature’ of animal tissue may provide information about the location where the tissue was grown (Hobson 1999, Hobson 2005). Isotope ratios are expressed in delta notation (δX , where X is the element in question) relative to a standard, and calculated according to the following equation:

$$\delta\text{X} = \left[\left(\frac{\text{R}_{\text{sample}}}{\text{R}_{\text{standard}}} \right) - 1 \right] \times 1000$$

where R_{sample} and $\text{R}_{\text{standard}}$ are the isotope ratios of the sample and a standard respectively.

Different elements provide information about different aspects of location. The elements used for isotope analyses in this study are discussed below:

Hydrogen Isotopes

The ratio of deuterium (^2H) to hydrogen (^1H) in precipitation, known as δD_p , varies along a latitudinal gradient in North America (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Bowen et al. 2005, Figure 1.1). Deuterium levels in precipitation are relatively high in the southeastern United States, and decrease progressively towards the north and west, producing corresponding patterns in δD_p (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Bowen et al. 2005). The hydrogen isotope ratio of precipitation is incorporated into the foodweb at a given location, and hence into animal tissue produced in that location (Estep and Dabrowski 1980, Chamberlain et al. 1997, Hobson and Wassenaar 1997). The strong gradient of δD_p in North America makes this continent particularly well-suited to animal movement studies using hydrogen isotope analyses, because δD signatures vary greatly between locations (Bowen et al. 2005).

Hydrogen isotope analyses have been used in a variety of ways in studies of migratory animals over the past decade. Most commonly, they have been used to determine the degree of migratory connectivity (the extent to which populations that breed together winter together, Webster et al. 2002) in various species of birds such as Bicknell's Thrushes (*Catharus bicknelli*, Hobson et al. 2001), Black-throated Blue Warblers (*Dendroica caerulescens*, Rubenstein et al. 2002), Aquatic Warblers (*Acrocephalus paludicola*, Pain et al. 2004), and European Blackcaps (Bearhop et al. 2005). Hydrogen isotope analyses have also been used to infer the location of origin of migrating or harvested individuals (Wassenaar and Hobson 2001, Meehan et al. 2001, Kelly et al. 2002, Hobson et al. 2006, Kelly 2006), to examine winter distribution of several species (e.g. Loggerhead Shrikes (*Lanius ludovicianus*), Hobson and Wassenaar 2001; White-throated Sparrows (*Zonotrichia albicollis*), Mazerolle and Hobson 2007),

and to locate previously unknown winter ranges (e.g. Coastal Plain Swamp Sparrows (*Melospiza georgiana nigrescens*), Greenberg et al. 2007).

While the hydrogen isotope signature of animal tissue is primarily determined by the latitude at which it is grown, a number of other factors may impact tissue δD and complicate this relationship. The δD signature of animal tissue differs from δD_p primarily because biochemical reactions tend to discriminate against one isotope (often the heavier), a process known as fractionation (DeNiro and Epstein 1981). However, as long as the degree of fractionation associated with the production of a given tissue is known, a correction factor can be applied. To date, two experimentally determined correction factors have been used in hydrogen isotope analyses of migratory bird feather and claw tissue: -19‰ (Bowen et al. 2005, Fraser et al. 2008) and -25‰ (Wassenaar and Hobson 2001). Tissue δD signatures may also differ from δD_p because they are subject to change after formation. Hydrogen bound to oxygen or nitrogen is only weakly bound, and may exchange freely with hydrogen in ambient water vapour (Hobson 2005).

Various laboratory methods have been developed to deal with this issue; most recently, a comparative equilibration technique (described in Chapter 2) has been used to account for the presence of exchangeable hydrogen in animal tissues (Wassenaar and Hobson 2003). Tissue hydrogen can also exchange freely with that found in drinking water (Hobson et al. 1999, Hobson 2005). While this is not necessarily a problem if there is little difference between the δD signatures of drinking water and diet, it can complicate interpretation of tissue δD values if the source of drinking water is isotopically distinct from the diet (Hobson 2005). Additionally, marine influence in mainly terrestrial foodwebs may obscure the relationship between latitude and tissue δD , as seawater

contains a high proportion of deuterium and hence has a high δD signature (Lott et al. 2003). Therefore, it is advisable to determine whether there is significant marine input in a system prior to conducting isotope analyses. Finally, there is evidence that δD signatures may vary within tissue samples. The δD_f of feather tissue may differ by as much as $\pm 3-5\%$ between different parts of a single feather (Wassenaar and Hobson 2006) and the δD_k of a given claw may vary if the central pulp of the claw is included with keratin in analysis (Fraser, pers. comm.).

Another source of uncertainty when relating tissue δD signatures to location lies in the determination of the δD_p signature of a given location. Currently available maps of global δD_p trends are based on interpolation of δD_p values taken from the Global Network for Isotopes in Precipitation (GNIP) database administered by the International Atomic Energy Association (IAEA) (Bowen et al. 2005, Hobson 2005). This database provides monthly averages of δD_p values based on up to forty years of data collection. Therefore, it is unlikely that tissue δD values (which represent one specific year) will exactly match those expected based on the average δD_p values in the database (Hobson 2005). There also may be some uncertainty (usually on the order of 2-6‰) associated with calculated δD_p values due to the interpolation process by which global grids are obtained (Bowen et al. 2005). Finally, there is substantial seasonal variation in δD_p , which may complicate interpretation of δD values for tissues produced over unknown timescales (Hobson 2005). However, this problem is largely avoided by using seasonal or annual average values of δD_p , since food webs reflect seasonal trends in hydrogen isotopes rather than short-term variation (Hobson 2005).

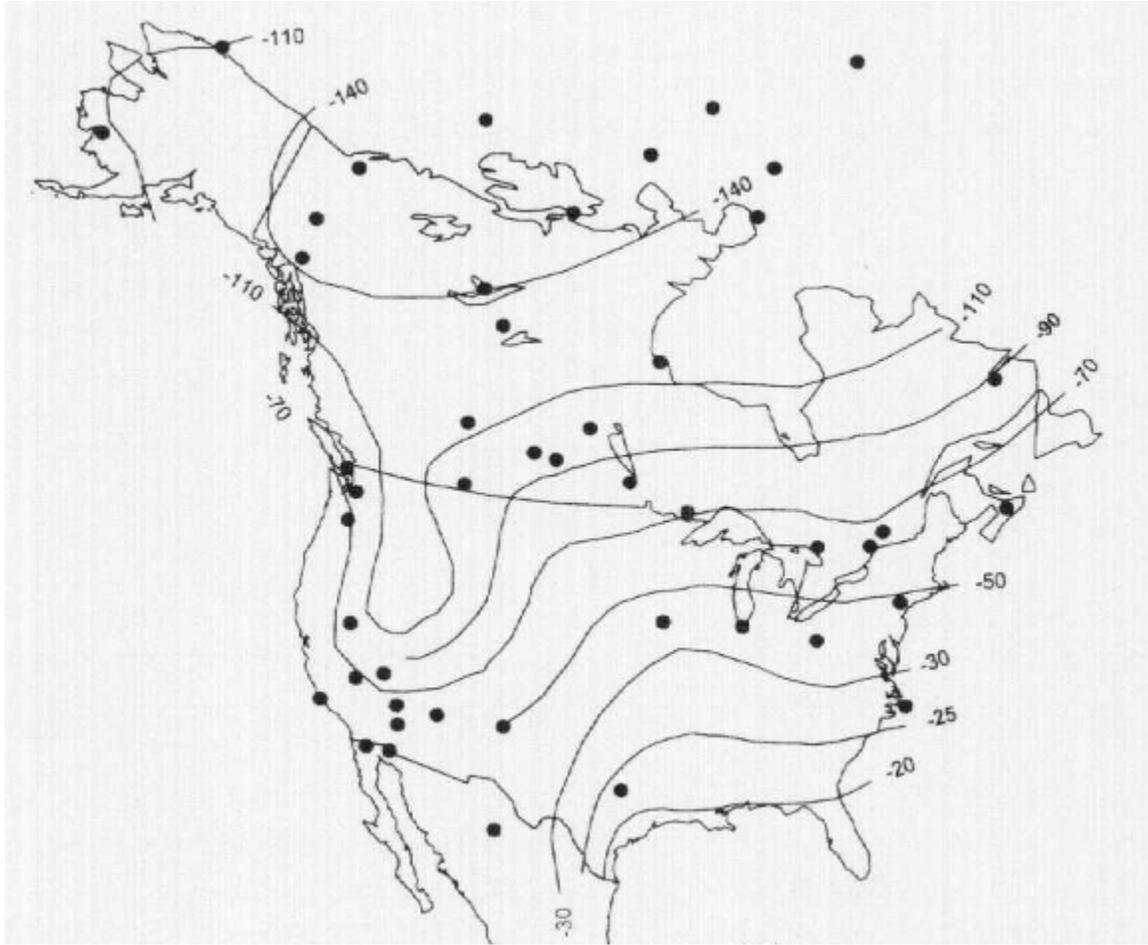


Figure 1.1. Patterns of precipitation hydrogen isotope (δD_p) signatures in North America. Contours are based on compilations of data by Hobson and Wassenaar (1997) and are constructed using averages of δD_p values throughout the growing season (months in which the mean temperature was above 0°C). Dots indicate precipitation sampling stations. Figure taken from Hobson et al. 2001.

Carbon Isotopes

Carbon stable isotope analyses primarily provide information about the photosynthetic pathway of the plants at the base of a food web, from which aspects of animal diet can be inferred (O'Leary 1981, Marra et al. 1998, Wassenaar and Hobson 2000, Norris et al. 2004a, Herrera et al. 2006). The ratio of heavy to light carbon ($^{13}\text{C}:^{12}\text{C}$; $\delta^{13}\text{C}$) varies between plants using a C_3 metabolic pathway and those using a C_4 or CAM metabolic pathway (O'Leary 1981). Rubisco, the enzyme that begins the photosynthetic process in C_3 plants, discriminates against the heavier form of carbon and hence C_3 plants have a lower $\delta^{13}\text{C}$ signature than C_4 or CAM plants (O'Leary 1981). Therefore, $\delta^{13}\text{C}$ can provide information about whether individual diets are based on C_3 or C_4/CAM food chains (Herrera et al. 2003, Herrera et al. 2006). Because the proportion of C_4 plants increases at lower latitudes, $\delta^{13}\text{C}$ signatures may also provide information about latitude, although on a much coarser scale than hydrogen stable isotopes (Kelly and Finch 1998).

Carbon stable isotope analyses have been used primarily in studies of the effects of winter habitat quality on migration and the breeding season. The relative proportions of C_3 and C_4 plants often differ between habitat types, and therefore $\delta^{13}\text{C}$ may also provide information about the type and quality of an individual's winter habitat (e.g. Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004a). For example, mesic habitats tend to have a higher proportion of C_3 plants than xeric habitats, and hence show lower overall $\delta^{13}\text{C}$ signatures. Mesic habitats are often also considered higher quality than xeric habitats, and are preferentially settled by dominant individuals, mainly older males (Marra et al. 1998, Marra 2000, Bearhop et al. 2004). Thus, the $\delta^{13}\text{C}$ signatures of tissue produced on the wintering grounds can provide information about aspects of winter

habitat, which can then be related to the reproductive success of breeding individuals (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004a).

Several factors other than photosynthetic pathway may play a role in determining the $\delta^{13}\text{C}$ signatures of tissues produced at a given location, and hence can complicate the interpretation of these signatures. Tissue $\delta^{13}\text{C}$ signatures increase slightly with marine input in a system, as C_3 plants in marine environments tend to be enriched in ^{13}C (Kelly 2000, Greenberg et al. 2007). Additionally, the degree of carbon isotope fractionation in plants changes with altitude (Körner et al. 1988) and also with latitude (Körner et al. 1991). At higher altitudes and latitudes, plants tend to discriminate less against the heavy form of carbon, and therefore plant $\delta^{13}\text{C}$ signatures increase with altitude and latitude. However, none of these effects are significant enough to obscure the differences in $\delta^{13}\text{C}$ signatures between C_3 and C_4 plants.

Nitrogen Isotopes

The ratio of heavy to light nitrogen ($^{15}\text{N}:^{14}\text{N}$, $\delta^{15}\text{N}$) in tissue is related to diet in a variety of taxa (Hobson 1990, Pearson et al. 2003, Herrera et al. 2006). The $\delta^{15}\text{N}$ signature of animal tissue is higher for animals at higher trophic levels, increasing by approximately 3.8‰ per trophic level (Hobson 1990). Thus nitrogen isotope analysis can provide information about an individual's position in the food web.

Nitrogen isotope analyses have been used to establish the proportion of various food sources in individual diets (Hobson 1990, Herrera et al. 2003, Herrera et al. 2005, Herrera et al. 2006), infer differences in foraging strategy between individuals and sexes (Bearhop et al. 2006), deduce diets of extinct birds such as the Great Auk (*Pinguinus impennis*; Hobson and Montevicchi 1991), and trace dietary shifts over time (Herrera et al. 2005, Emslie and Patterson 2007).

Several factors other than trophic level can impact tissue $\delta^{15}\text{N}$ values and complicate the determination of trophic level. $\delta^{15}\text{N}$ signatures are elevated by marine input, as well as a variety of anthropogenic inputs (e.g. fertilizer, effluent from urban areas) (Greenberg et al. 2007). Nutritional stress can also produce elevated $\delta^{15}\text{N}$ signatures (Hobson et al. 1993), and therefore make it appear that animals are feeding at higher trophic levels than they are in reality. Thus, these issues must be taken into consideration when interpreting $\delta^{15}\text{N}$ signatures.

Tissues Used in Stable Isotope Analysis

To date, a variety of tissues have been used in stable isotope analyses, including feathers (e.g. Hobson et al. 2001, Rubenstein et al. 2002, Bearhop et al. 2006), claws (e.g. Bearhop et al. 2004, Bearhop et al. 2005, Hobson et al. 2006, Fraser et al. 2008), blood (e.g. Norris et al. 2004a, Herrera et al. 2006), muscle tissue (e.g. Hobson et al. 1993, Marra et al. 1998) and bone collagen (e.g. Chamberlain et al. 1997). Stable isotope ratios of different tissues provide location information over different timescales, depending on the turnover time of the tissue (Hobson 1999, Bowen et al. 2005). Isotope ratios of bone collagen, which has a very slow turnover rate, may represent lifetime averages of dietary values (Hobson 1990), while the values of muscle tissue, which has a much faster turnover rate, may represent dietary intake over a period of a few weeks (Hobson 1990). Metabolically inert tissues, such as feathers and claws, are particularly useful in isotope analysis because they 'lock in' the isotopic signature of the location where they are produced (Hobson 2005). Thus, feathers only reflect the isotope signature of the location where they are grown and therefore are most useful in stable isotope analysis when the timing of moult is known (Hobson 2005). Claw keratin is also metabolically inert after growth and so similarly 'locks in' an isotope signature: however, claws are continuously

growing, and so only retain location information for a period of one to two months (Bearhop et al. 2003, Mazerolle and Hobson 2005, Fraser et al. 2008).

Study Species

Ipswich Sparrows are a subspecies of Savannah Sparrow (*Passerculus sandwichensis*, Zink et al. 2005) that nests almost exclusively on Sable Island, Nova Scotia (Stobo and McLaren 1975, Environment Canada 2006, Figure 1.2). Recent surveys indicate a population size of approximately 6000 individuals (Smith et al. 2003, Horn 2007). The breeding biology of Ipswich Sparrows was studied extensively in the early seventies (Stobo and McLaren 1975); unless otherwise stated, the following information is taken from that study.

Birds arrive on the island each year between the middle and end of April, and the breeding season extends into September. Males are territorial (Reid and Weatherhead 1988) and the majority of individuals are socially monogamous (pers. obs.), although a few males may be polygynous. Ipswich Sparrows are ground nesters, and most often build their nests in clumps of vegetation in the most densely vegetated areas of the island. Clutch sizes vary between 3 and 6, with a mean of 4.3, and eggs are incubated for approximately 12.5 days. Nestlings fledge after approximately 10 days, and are fed by both parents for up to two weeks after leaving the nest. Hatching and fledging success is high, likely due to the almost complete absence of predators on the island. Ipswich Sparrows are multi-brooded and may have as many as four broods over the course of a single breeding season. Individuals undergo a complete prebasic moult on Sable Island

in early fall, following the breeding season, and then depart for the wintering grounds in mid to late September each year.

Ipswich Sparrows appear to winter in the outer dunes along the Atlantic coast from Nova Scotia to Florida (44.5°N to 30°N), with a small proportion of the population remaining on Sable Island during the winter (Elliott 1968, Stobo and McLaren 1975, Figure 1.2). Overwinter mortality is approximately 75% (Stobo and McLaren 1975), and potentially higher for juveniles (Ross and McLaren 1981). A limited number of individuals may undergo a partial prealternate moult on the wintering grounds (Elliott 1968, Pyle 1997a). However, the incidence, timing and extent of this moult are currently unknown.

Only one other study has examined the winter distribution of Ipswich Sparrows. In February and March 1971, a survey of winter habitat was conducted at sites from South Carolina to Massachusetts, with a separate and later survey in Nova Scotia. Researchers surveyed 4-mile long sections of coast on foot, clapping to flush birds from cover. Based on these surveys, the highest abundance of Ipswich Sparrows apparently occurred between New Jersey and Virginia (39°N and 37°N, Stobo and McLaren 1971). Some attempt was also made to quantify microhabitat features believed to be of importance to Ipswich Sparrows: relief, vegetation cover and access to fresh water. However, only a relatively small proportion of the population (no more than 19 individuals at any one site) was actually seen on the wintering grounds, leaving open the question of where the majority of the population winters.

This 1971 study provided the first and only systematic survey of the wintering range of the Ipswich Sparrow to date. It did, however, have several limitations. The

entire wintering range was not covered, and the middle of the range was surveyed more extensively than other areas. Furthermore, evidence suggests that the winter ranges of many bird species have shifted northwards over the past few decades (La Sorte and Thompson 2007). It is possible that in the almost 40 years since the winter range of the subspecies was last examined, a similar shift has occurred. For these reasons, further investigation into the winter distribution of Ipswich Sparrows is warranted.

The Ipswich Sparrow was designated a Species of Special Concern under the Canadian Species at Risk Act (SARA) in June 2003, due mainly to its limited breeding range (Environment Canada 2006). Improving knowledge of its winter distribution is one of the goals set in the management plan for the subspecies (Environment Canada 2006), and is particularly important because the coastal wintering habitat of the Ipswich Sparrow is under heavy pressure from development (Crossett et al. 2004).

Purpose of the Study

The purpose of my study was to investigate whether winter events and winter location impact the breeding season in Ipswich Sparrows breeding on Sable Island, Nova Scotia, using stable isotope analysis of hydrogen, carbon and nitrogen. I examine the impact of a winter event (prealternate moult), and several aspects of winter location on breeding performance. Ipswich Sparrows are an excellent study organism with which to investigate the effects of winter on breeding success, as their winter distribution lends itself to stable isotope analysis. Their wide winter range means that winter experiences vary considerably among individuals, while their restricted breeding range theoretically allows individuals from across the winter range to be sampled in one location.

Furthermore, while they winter over a large range of latitudes, longitudinally their range is quite narrow. This is ideal for hydrogen isotope analysis because δD signatures provide a great deal of information about latitude, but very little about longitude (Hobson 2005).

In Chapter 2, I describe the incidence, timing and extent of prealternate moult in Ipswich Sparrows. To determine whether there is a relationship between moult and reproductive success, I investigate whether a selection of reproductive parameters vary with the incidence of prealternate moult. I also investigate whether a relationship exists between the incidence of prealternate moult and winter location, determined by hydrogen stable isotope analysis. In Chapter 3, I use hydrogen stable isotope analysis to determine the relative wintering location of Ipswich Sparrows and relate those locations to variation in reproductive success. To investigate whether the winter range of Ipswich Sparrows has shifted since the first winter census (Stobo and McLaren 1971), I also use survey data from the National Audubon Society's Christmas Bird Counts over the past 35 years to examine trends in the winter distribution of the subspecies. Finally, I investigate whether the impact of winter location on reproductive success could be due to variation in food availability by using carbon and nitrogen stable isotope analyses to infer aspects of Ipswich Sparrow winter diet. In Chapter 4, I conclude by summarizing my results and discussing the limitations of this study and possible avenues for future work.



Figure 1.2. Global breeding and wintering ranges of the Ipswich Sparrow. Figure taken from Environment Canada 2006.

CHAPTER 2. INCIDENCE, PATTERNS AND EFFECTS OF PREALTERNATE MOULT IN IPSWICH SPARROWS

Introduction

Moult is the process of plumage replacement in birds (Ginn and Melville 1983). Most bird species annually undergo at least one complete moult, in which all feathers are replaced (Humphrey and Parkes 1959). This moult, known as prebasic moult, is necessary because natural wear on feathers eventually impairs functions from thermoregulation to flight (Ginn and Melville 1983).

Prebasic moult varies in timing and duration between individuals, populations and species. Males often moult earlier than females (e.g. European Greenfinches (*Carduelis chloris*), Newton and Rothery 2005) and show a greater overlap between moult and breeding (e.g. Pied Flycatchers (*Ficedula hypoleuca*), Hemborg 1999). Individuals in better condition often moult earlier than those in poor condition (e.g. Barn Swallows (*Hirundo rustica*), Pérez-Tris et al. 2001), and breeding individuals frequently moult for shorter periods and at different times than non-breeders, minimizing moult-breeding overlap (e.g. Black-headed Gulls (*Larus ridibundus*), Meissner 2007; Northern Fulmars (*Fulmarus glacialis*), Allard et al. 2008). Similarly, migratory individuals often moult more rapidly and at different times than sedentary individuals, generally avoiding moulting while migrating (e.g. Western Sandpipers (*Calidris mauri*), O'Hara et al. 2002; Australian Silveryeyes (*Zosterops lateralis*), Munro et al. 2006; Grey Plovers (*Pluvialis squatarola*), Serra et al. 2006). Additionally, individuals that migrate greater distances may moult later and for shorter periods (e.g. Yellow Warblers (*Dendroica petechia*), Ryder and Rimmer 2003) than those that undertake shorter migrations.

The patterns described above are thought to be a consequence of the cost of moult (Salewski et al. 2004). Energy is required both to synthesize feathers (Lindström et al. 1993) and for increased thermoregulatory costs associated with feather loss (Payne 1972). Furthermore, wing gaps created by the loss of remiges may impair flight ability and increase vulnerability to predation (Hedenström and Sunada 1999, Lind 2001). These costs appear to be sufficient to cause decreases in condition and reproductive success when moult overlaps with other costly activities, such as breeding and migration. Moulting-breeding overlap has been associated with decreases in reproductive success (e.g. Pied Flycatchers, Hemborg et al. 2001, Lobato et al. 2006), while moult-migration overlap has been linked with decreases in individual body condition (e.g. Barn Swallows, Pérez-Tris et al. 2001).

To date, most moult studies have focused on patterns in the timing and duration of prebasic moult, as it is common to most bird species and often occurs on the breeding grounds, where the majority of studies are conducted. However, several other types of moult may occur during the annual cycle. Some species of birds undergo a second annual moult, known as prealternate moult, which often occurs on the wintering grounds (Humphrey and Parkes 1959), and therefore has not been well studied. Prealternate moult is often partial (not all feathers are replaced), and may also be limited (not all individuals moult) (Humphrey and Parkes 1959, Pyle 1997a). In some species, prealternate moult allows transformation into brightly coloured breeding plumage. In others, especially ground-foraging species, it may be necessary to replace severely abraded plumage (Humphrey and Parkes 1959).

Partial moults, such as the prealternate moult, may vary in timing, duration, extent and incidence between individuals, populations and species. Few studies have examined variation in prealternate moult, but studies on other partial moults (such as juvenile or supplemental moult) suggest the existence of patterns in partial moult strategies. Males frequently moult more feathers than females (e.g. Dark-eyed Juncos (*Junco hyemalis*), Mulvihill and Winstead 1997) or moult earlier and show a greater overlap with the breeding season (e.g. Savi's Warblers (*Locustella luscinioides*), Neto and Gosler 2006). Individuals in good condition may undergo a more extensive moult than those in poor condition (e.g. Great Tits (*Parus major*), Gosler 1991; Common Chiffchaff (*Phylloscopus collybita*), Catry et al. 2007), and breeding individuals may moult less extensively than non-breeders (e.g. Ural Owls (*Strix uralensis*), Brommer et al. 2003). Migratory species may show a higher incidence of partial moult than sedentary species (Terns (Sternæ), Bridge et al. 2007); however, migratory populations may also undergo less extensive moults than sedentary populations (e.g. Dark-eyed Juncos, Mulvihill and Winstead 1997). Individuals that migrate greater distances may moult later and more synchronously than those with shorter migrations (e.g. Red-eyed Vireos (*Vireo olivaceus*), Mulvihill and Rimmer 1997). Alternatively, moult may play a role in determining migration distance, with individuals that undergo partial moult migrating further than those that do not (e.g. Western Sandpipers, Nebel et al. 2002).

As is the case with prebasic moult, these patterns may be explained by the cost of partial moult. Although costs would be expected to be lower for moults in which only some feathers are replaced, partial moult may still entail some costs. For example, moulting feathers asymmetrically can impair flight ability and maneuverability (Thomas

1993), and this asymmetry persists after moult is complete, as new feathers are less worn than old feathers (Brommer et al. 2003).

Assuming there are indeed costs associated with partial moults, the variability of these moults may allow them to function as an honest signal of quality. For example, the extent of repeated moult (a partial moult in which a varying number of primaries and secondaries are replaced twice or even three times in a year) may be used as a means of evaluating mate quality in Common Terns (*Sterna hirundo*), and individuals may mate assortatively with respect to the extent of repeated moult (Bridge and Nisbet 2004).

The above studies are among relatively few that have investigated the patterns and impacts of partial moults like the prealternate. Very few studies exist on prealternate moult specifically; however, prealternate moult provides an excellent chance to investigate the forces that shape moult patterns. As only some individuals undergo prealternate moult, it offers an ideal opportunity to examine the relationship between moulting and breeding success, and moulting and migratory strategies within the same population.

The goal of my study was to describe the incidence, timing and patterns of prealternate moult in Ipswich Sparrows (*Passerculus sandwichensis princeps*), and to determine if relationships existed between this moult and breeding success. I was also interested in determining whether the incidence of prealternate moult was related to winter location. The existing literature suggests that Ipswich Sparrows undergo a complete prebasic moult on the breeding grounds in late summer and a partial and limited prealternate moult in February or March on the wintering grounds (Elliott 1968, Stobo and McLaren 1975, Pyle 1997a). However, current knowledge of Ipswich Sparrow

moult patterns, particularly the prealternate moult, is based largely on incidental observations by early natural historians (Elliott 1968) and patterns observed in Savannah Sparrows (Pyle 1997a). In this study, I describe the incidence, timing and nature of prealternate moult in Ipswich Sparrows and use hydrogen stable isotope signatures of claws and feathers to investigate whether this moult takes place exclusively on the wintering grounds. I also relate the incidence of prealternate moult to reproductive success on the breeding grounds and to winter location (and hence migration distance), determined using hydrogen stable isotope analysis of claw tissue.

Methods

Study Location

This study was conducted on Sable Island, Nova Scotia (44°N, 60°W) from 26 April to 2 July 2007. Sable Island is a crescent of sand approximately 45 km long (Smith et al. 2003) and 1.5 km wide (Stobo and McLaren 1975), located in the Northern Atlantic Ocean 150 km east of the Nova Scotia coast (Figure 2.1a). The north and south sides of the island are sand beaches, and the centre is composed of vegetated dunes, the highest of which rises approximately 25 m above sea level (Stobo and McLaren 1975).

The Ipswich Sparrow is endemic to Sable Island and approximately 3000 pairs breed there (Smith et al. 2003, Horn 2007). The only other birds breeding in significant numbers on the island are Herring and Great Black-backed Gulls (*Larus argentatus* and *L. marinus*) and Common and Arctic Terns (*Sterna hirundo* and *S. paradisaea*) (McLaren 1981). There are no mammalian predators, and relatively few avian predators, mainly crows (*Corvus brachyrhynchos*) and gulls (Stobo and McLaren 1975).

I monitored adult Ipswich Sparrows ($n = 124$) on two study sites (Figure 2.1b). The Main study site (11 ha) was located close to the west end of the island, and the Sparse study site (25 ha) was approximately 11 km east of the Main site, at the widest point of the island. These sites were first used to study Ipswich Sparrows by Stobo and McLaren (1975). At that time, the Main site was dominated by dense heath vegetation, while the Sparse site had much thinner vegetation cover, with large areas dominated by marram grass (*Ammophila breviligulata*). Birds on the Sparse site also began nesting almost two weeks later than those on the Main site, suggesting that the latter was a higher quality site (Stobo and McLaren 1975). However, during the course of my study, most birds nesting on the Sparse site were found within the areas covered with dense heath, similar to the Main site. Furthermore, mean hatch dates were similar for both sites in 2007 (Main: 20 June, $n = 32$; Sparse: 18 June, $n = 22$) suggesting that currently, these sites do not differ in quality. Therefore, for the purposes of this study, I pooled data from both study sites.

Capture, Banding and Tissue Sampling

Birds were captured in mist nets both before and during nest building and during incubation and nestling stages. Individuals were banded with a Canadian Wildlife Service (CWS) metal band and a unique combination of three colour bands. Birds were sexed using a combination of behavioural observations and morphological traits (brood patch/cloacal protuberance), and moult status was noted (see below). I measured wing chord, tail and tarsus lengths, and determined mass using a spring balance. I also clipped 1-2 mm of claw from the rear claw (C1) on each foot to be used in stable isotope analysis, and collected moulted feathers from those individuals that had undergone prealternate moult.

Reproductive Success

I monitored banded birds and their nests during the breeding season to determine reproductive success. I found nests by observing parents bringing food to nestlings or females returning to incubate eggs. If a nest was discovered before hatch, it was checked at least every other day to determine hatch date (the date the first egg hatched) and hatching success (number of eggs hatched per eggs laid). After nestlings hatched, the nest was usually checked only once until day 7 post-hatch. On day 7, I banded nestlings with a CWS metal band and weighed them using a spring balance. I also measured wing and tarsus length. From day 8 onwards, nests were again checked at least every other day to determine fledging date (the date all surviving nestlings left the nest) and fledging success (number of chicks fledged per chicks hatched). In cases where nests were located after hatch, I approximated hatch date by visually estimating the age of the nestlings and hatching success by relating the number of nestlings to the number of unhatched eggs.

Incidence, Timing and Patterns of Prealternate Moul

When birds were captured, I examined flight and body feathers for signs of moult. I considered birds to have undergone prealternate moult if moult limits were visible or if any of the feathers were still in sheaths. Moult limits are the line between new, recently moulted feathers and older feathers (Pyle 1997b). New feathers are darker and less worn than older feathers, and easily differentiated from worn plumage (Figure 2.2). Thus moult limits provide lasting evidence of incidence and extent of moult between seasons (Neto et al. 2006). They may last for as much as a year after moult is completed (Shizuka and Dickinson 2005), although in Ipswich Sparrows, moult limits are only expected to persist until the complete prebasic moult at the end of the breeding season. Feather

sheaths are present when feathers are still growing and hence provide evidence of continuing moult (Ginn and Melville 1983). I noted which feather tracts showed signs of moult, and placed birds into one of two categories based on moult observations: those that had undergone prealternate moult (Moult), and those that had not and were therefore still in full basic plumage (Basic).

To determine if Ipswich Sparrow prealternate moult took place exclusively on the wintering grounds, I used stable hydrogen isotope analysis of feather and claw keratin. The ratio of deuterium (^2H) to hydrogen (^1H) in precipitation, known as δD_p , varies along a latitudinal gradient in North America. δD_p values are highest in the southeast and decrease gradually to the north and west (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Bowen et al. 2005). The δD_p of precipitation at a given location is incorporated into the food chain, and hence into any tissues grown at that location (Estep and Dabrowski 1980, Chamberlain et al. 1997, Hobson and Wassenaar 1997). Thus the δD signatures of claw and feather keratin (δD_k and δD_f respectively) provide information about the latitude at which the tissue was grown. Higher δD_k and δD_f values correspond to southern latitudes.

Passerine claws grow relatively slowly, and therefore the signature of claw keratin reflects winter location for three to seven weeks after individuals arrive on the breeding grounds (Bearhop et al. 2003, Fraser et al. 2008 but see Mazerolle and Hobson 2005). Conversely, feathers grow quickly and incorporate the isotope signature of the location of moult (Hobson and Wassenaar 1997). To investigate the location of Ipswich Sparrow prealternate moult, I compared the δD_k signature of claw keratin and the δD_f signature of moulted feathers collected from nine Ipswich Sparrows. If prealternate moult took place

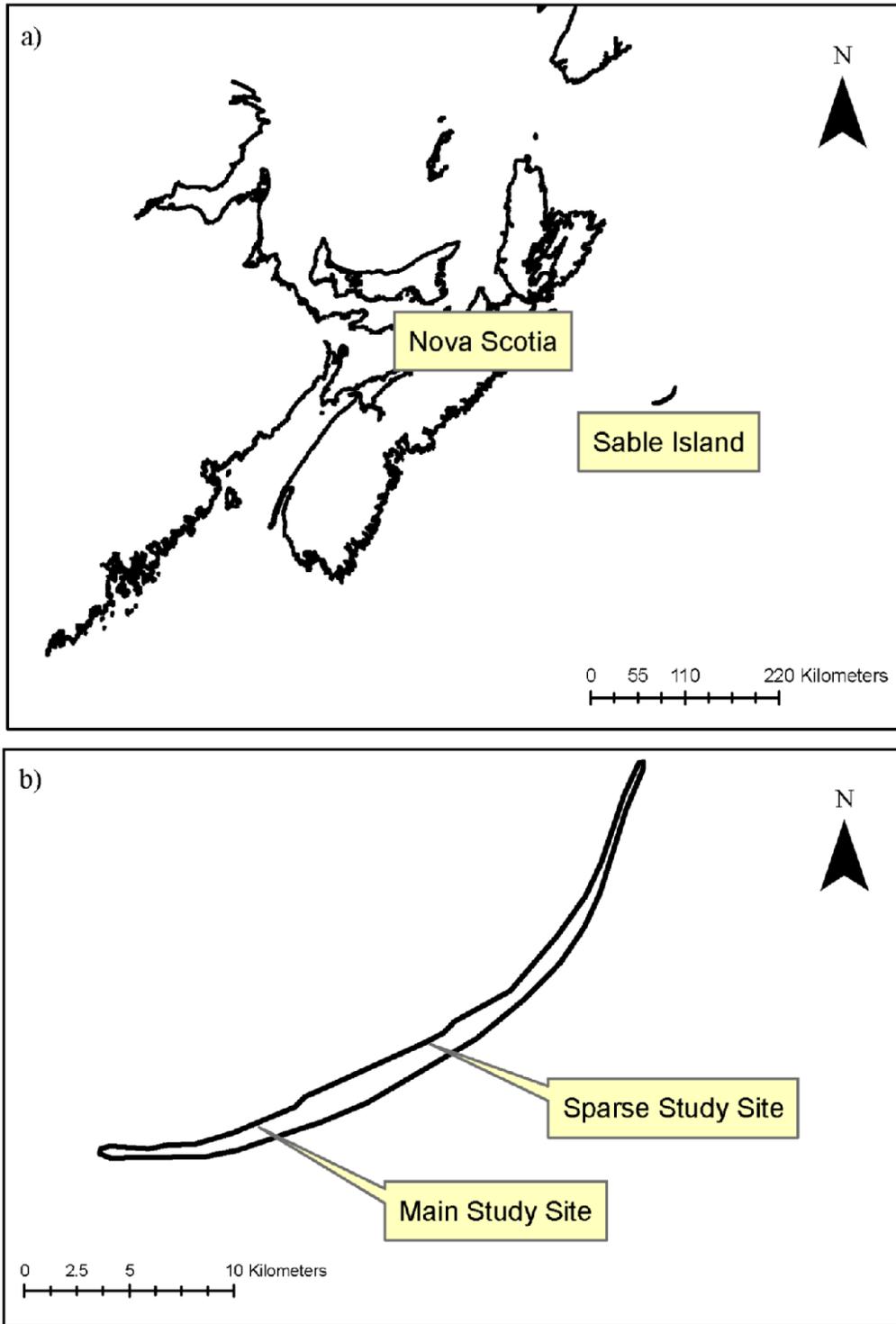


Figure 2.1. a) Location of Sable Island, Nova Scotia, Canada. b) Map of Sable Island showing the location of both study sites.



Figure 2.2. An adult Ipswich Sparrow with two moult limits. The innermost tertiary (S9) has been moulted on both wings, and the new, darker feathers stand out against the older, worn feathers.

entirely on the wintering grounds, I would expect the claw and feather keratin signatures to be similar. Signatures that differ by greater than 6‰ (approximately the level of variation in δD_k at any given location, Langin et al. 2007) suggest the tissues may have been grown in different locations.

Moult and Breeding Performance

To investigate whether moult strategies differ between the sexes, I examined whether the incidence of prealternate moult (proportion of individuals moulting) was similar for both sexes. I also looked at the relationship between moult strategies and performance on the breeding grounds by comparing body condition and timing of breeding initiation between Moulting and Basic birds; and comparing number and mean mass of nestlings between nests where one or both parents moulted and nests where neither parent moulted. Finally, I investigated whether Ipswich Sparrows moult assortatively with respect to moult strategy.

A measure of adult body condition, referred to as a condition index, was calculated for individuals by taking the residuals of a regression of mass on a measure of body size, in this case left wing (Robb et al. 1992, Jakob et al. 1996).

Timing of breeding initiation was defined differently for males and females. For males, I used the date birds were banded as a proxy for territory establishment date, which can be considered the beginning of the breeding season. Banding dates are likely to be a reasonable indicator of territory establishment dates because males were only responsive to the playbacks of male song used to lure them into nets when they were territorial (Temple 2000). I surveyed the study sites approximately every other day and attempted to capture singing males; thus, males were generally caught shortly after becoming territorial.

For females, banding date is less likely to reflect a biologically significant date, as territory settlement dates may not be related to breeding initiation in females (Stutchbury and Robertson 1987). Therefore, I used first egg date as a measure of timing of breeding initiation for females. Very few nests were found before clutch completion, so most females were already incubating at the time of nest discovery. In these cases, I approximated first egg date using hatch date. I assumed females had incubated for 12 days prior to hatch (Stobo and McLaren 1975, Ross 1980), and laid one egg per day (Stobo and McLaren 1975).

The number and average mass of nestlings produced at a nest was determined on day 7 post-hatch. Ipswich Sparrows leave the nest between 8 and 13 days after hatch (mean = 10.9, Stobo and McLaren 1975); therefore, by banding and measuring nestlings on day 7 post-hatch, I avoided force-fledging them.

Finally, if partial moults are costly, prealternate moult could function as an honest signal of quality and be used to evaluate potential mates. Therefore, I also looked for evidence of assortative mating with respect to the incidence of prealternate moult in Ipswich Sparrows.

Moult and Winter Location

I used stable hydrogen isotope analysis of claw keratin (δD_k) to infer winter location of individuals in the Moult and Basic groups. For these analyses, only claws collected prior to 20 May 2007 were used ($n = 59$ birds). Claws are expected to reflect winter location for approximately three to seven weeks after arriving on the breeding grounds (Bearhop et al. 2003, Fraser et al. 2008 but see Mazerolle and Hobson 2005). In 2007, spring sightings of Ipswich Sparrows on mainland Nova Scotia peaked between 7 and 14 April (range: 25 March – 19 May, McLaren 2007). Thus most birds likely arrived

on Sable Island in the third week of April, and 20 May represents a cutoff date of approximately five weeks after arrival, well within the time period during which claws should reflect winter values.

Stable Isotope Analysis

Stable isotope analyses were performed at the Stable Isotopes in Nature Laboratory at the University of New Brunswick in Fredericton, New Brunswick. Claw and feather samples were dried, powdered and weighed into silver capsules at approximately 0.2 mg. To account for exchangeable hydrogen (the proportion of hydrogen in keratin that exchanges with ambient water vapour), a comparative equilibration technique was used (Wassenaar and Hobson 2003). Standards with known hydrogen isotope ratios were weighed into silver capsules alongside sample material. These standards – Bowhead Whale (*Balaena mysticetus*) Baleen (BWB), Cow Hoof (CHS) and Chicken Feather (CFS) – and the samples were allowed to freely equilibrate with local water vapor for a minimum of 72 hours. Samples and standards underwent pyrolysis in a High Temperature Conversion/Elemental Analyzer (TC/EA) to produce hydrogen gas. This gas was delivered to a Thermo Finnigan Delta XP mass spectrometer via a ConFlo III interface. Resulting δD values were then adjusted to bring BWB, CHS and CFS standards to their known values (-108‰, -187‰, and -147‰ respectively). Comparative equilibrium makes all δD values relative to the VSMOW (Vienna Standard Mean Ocean Water) scale (Wassenaar and Hobson 2003). Based on repeated measurements of standard IAEA-85, the laboratory measurement error for δD_k and δD_f was estimated to be approximately $\pm 2.26\text{‰}$. Results of hydrogen stable isotope analysis are expressed in standard parts per thousand (‰) units.

Data Analysis

Statistical analyses were performed using Rcmdr (Version 1.3-8, Fox et al. 2007). Data were checked for normality using the Shapiro-Wilk test for normality, and non-normal data were analyzed using non-parametric statistics. Results were considered significant when p-values were 0.05 or lower.

T-tests were used to compare winter location, inferred from hydrogen isotope signatures (δD_k), between Moulting and Basic groups, and also to compare the condition of nestlings between nests where one or both parents moulted and nests where neither parent moulted. Kruskal-Wallis tests were used to compare condition indices between Moulting and Basic groups, as well as banding dates between males in each group and first egg dates between females in each group, and to compare number of nestlings between nests where one or both parents moulted and nests where neither parent moulted.

χ^2 tests were used to compare the proportion of males and females that underwent prealternate moult, and determine if evidence existed of assortative mating. For the latter analysis, only nests where the moult status of both parents was known were considered. I compared the number of nests where both, one or neither parents had moulted with the number of nests that would be expected in each category assuming 25% of individuals underwent prealternate moult.

Results

Incidence, Timing and Patterns of Prealternate Moult

Twenty-five percent of Ipswich Sparrows captured in 2007 (31/124) showed evidence of prealternate moult. Fifteen of the 31 (48%) birds showing evidence of moult were actively moulting at the time of capture on the breeding grounds.

Most birds were moulting more than one feather tract. Body feathers were the most commonly moulted, with body moult occurring in 25 of 31 moulting individuals (Figure 2.3). Back and crown feathers were the most frequently moulted body feathers. Remige moult was restricted to tertials, and was also fairly common, seen in 15 of the 31 birds that underwent prealternate moult (Figure 2.3). Both asymmetrical and symmetrical patterns of tertial moult were observed. Twelve of 31 birds had moulted rectrices. One individual appeared to have moulted several greater coverts, and three birds had moulted upper and under tail coverts (Figure 2.3).

Of the nine birds from which I collected both feather and claw material, three had feather stable hydrogen isotope (δD_f) signatures that were more than 6‰ more negative than their claw stable hydrogen isotope (δD_k) signatures. Four of nine individuals had δD_f and δD_k signatures within 6‰ of each other, and two individuals had δD_f signatures that were more than 6‰ more positive than their δD_k signatures (Figure 2.4).

Moult and Breeding Performance

The proportion of males moulting did not differ significantly from the proportion of females moulting (males: 0.23, $n = 60$; females: 0.35, $n = 50$; $X^2 = 0.10$, $df = 1$, $p = 0.75$), and the mean condition index was not significantly different for Moulting ($n = 31$) and Basic ($n = 93$) groups ($H = 0.0019$, $p = 0.97$).

The number of nests where both parents had moulted was not significantly different from the number expected in a population where 25% of individuals underwent prealternate moult ($X^2 = 3.81$, $df = 2$, $p = 0.15$).

For males, mean banding date did not differ significantly between the Moulting and Basic groups (Moulting: 137.71 ± 17.86 , $n = 14$; Basic: 138.17 ± 16.89 , $n = 46$; $H = 0.0093$, $p = 0.92$). Similarly, for females, first egg dates did not differ significantly between the

Moult and Basic groups (Moult: 157.56 ± 6.98 , $n = 10$; Basic: 153.56 ± 9.35 , $n = 35$; $H = 0.95$, $p = 0.33$).

Neither the number nor the mean mass of nestlings varied between nests where one or both parents moulted (One/Both) and those where neither parent moulted (None) (number: One/Both: 3.18 ± 1.67 , $n = 17$; None: 3.83 ± 0.86 , $n = 18$; $H = 0.99$, $p = 0.32$; mass: One/Both: $17.27 \pm 1.79\text{g}$, $n = 15$; None: $16.81 \pm 2.60\text{g}$, $n = 18$; $t = -0.60$, $df = 30.02$, $p = 0.55$).

Moult and Winter Location

δD_k values did not differ between Moult and Basic groups (Moult: $-71.08 \pm 8.63\text{‰}$, $n = 12$; Basic: $-68.43 \pm 9.31\text{‰}$, $n = 40$; $t = 0.88$, $df = 17.08$, $p = 0.39$, Figure 2.5).

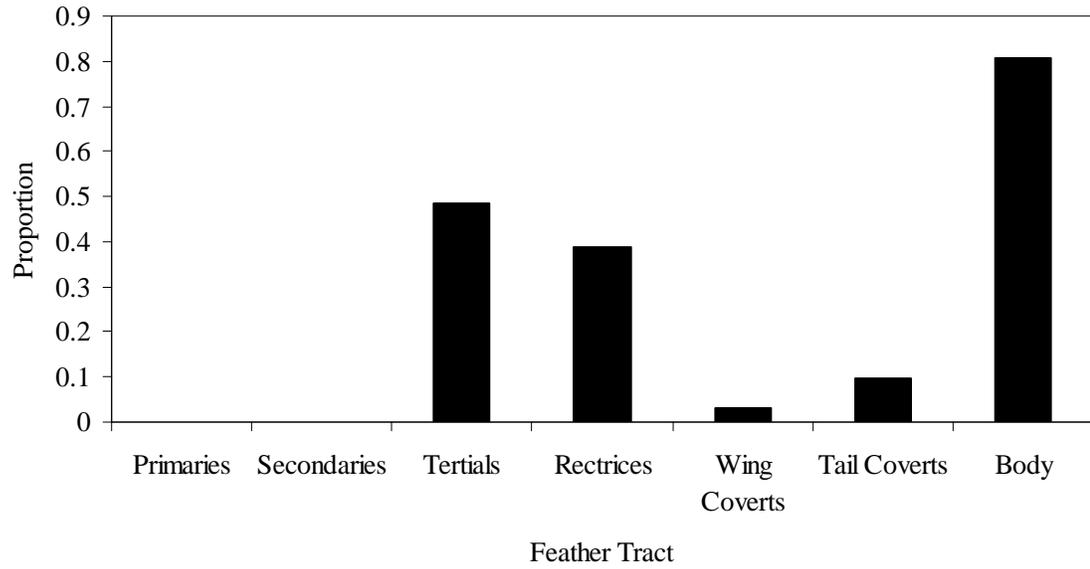


Figure 2.3. Proportion of Ipswich Sparrows captured in 2007 ($n = 31$) showing evidence of moult in indicated feather tracts.

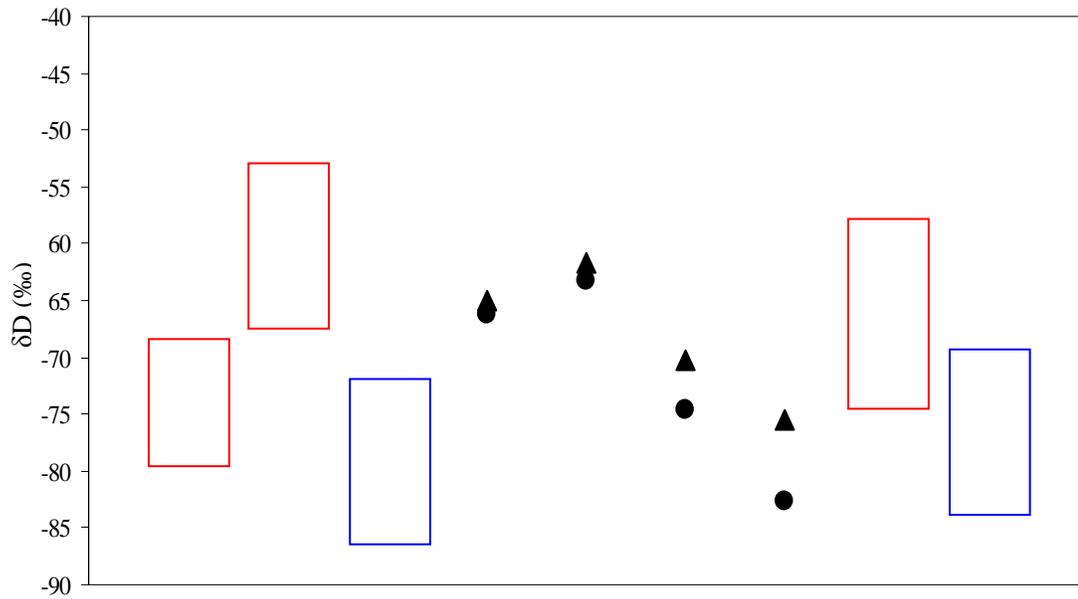


Figure 2.4. Claw (triangles, δD_k) and feather (circles, δD_f) stable hydrogen values for nine Ipswich Sparrows captured in 2007. Boxes indicate a difference greater than 6‰ between δD_k and δD_f . In three cases (red boxes), claw values are more positive than feather values. In two cases (blue boxes), claw values are more negative than feather values.

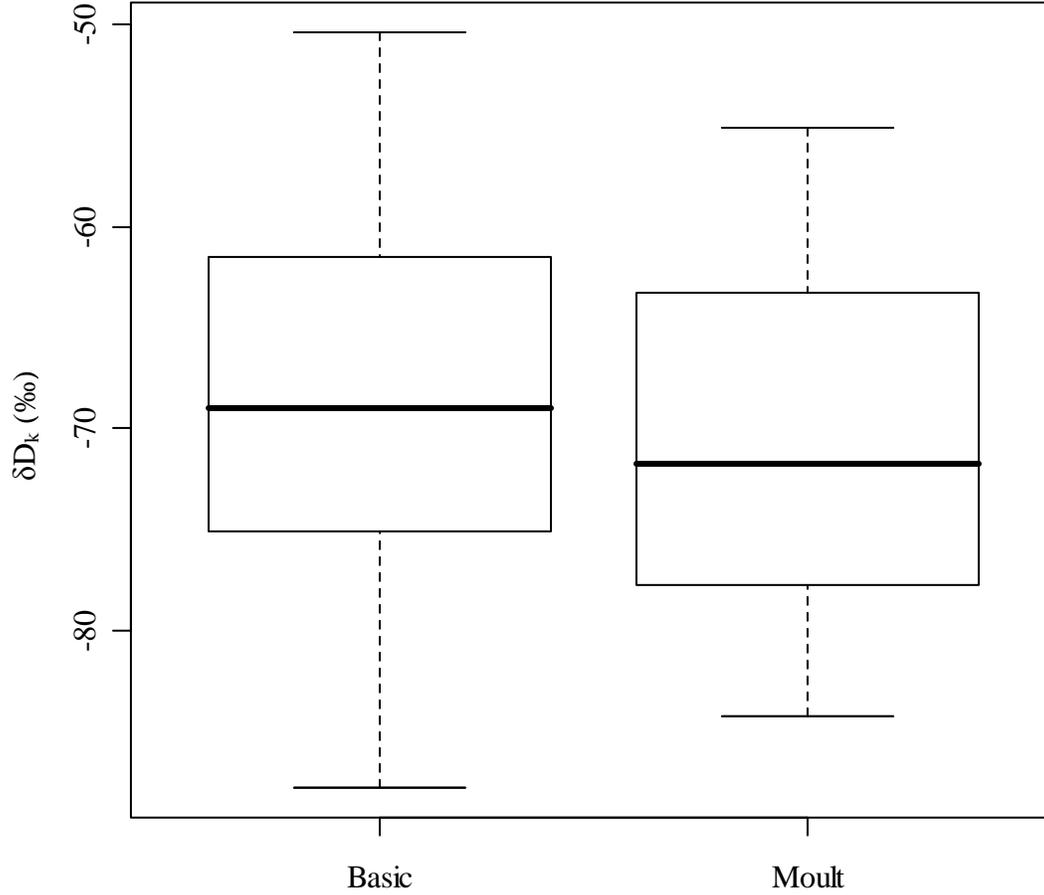


Figure 2.5. Boxplot illustrating claw hydrogen isotope signatures (δD_k , ‰) for Ipswich Sparrows that did not undergo prealternate moult (Basic, $n = 40$) and those that did (Moult, $n = 12$) in 2007. Lines within boxes indicate median δD_k values, while the top and bottom of boxes indicate upper and lower quartiles respectively.

Discussion

Only 25% of Ipswich Sparrows breeding on Sable Island showed evidence of prealternate moult. This was considerably lower than the 45% expected based on the literature available for Savannah Sparrows (Pyle 1997a, pers. comm.). One possible explanation for this difference is that Ipswich Sparrows winter farther north than many other subspecies of Savannah Sparrow. Northern wintering populations tend to moult less than populations that winter further south (Figuerola and Jovani 2001, Pyle, pers. comm.), likely because wintering further south entails longer migrations and increased exposure to ultraviolet radiation, resulting in a greater degree of feather wear (Ginn and Melville 1983, Nebel et al. 2002).

Roughly half of the Ipswich Sparrows showing evidence of prealternate moult were actively moulting at the time of capture on the breeding grounds, as late as the end of June. In fact, the proportion of birds that were actively moulting on the breeding grounds may be even higher than found in this study. Some individuals showing moult limits that were captured later in the breeding season may in fact have completed moult after arriving on Sable Island. The timing of prealternate moult in Ipswich Sparrows was unexpected, as the literature indicates that they undergo prealternate moult in February and March (Elliott 1968, Stobo and McLaren 1975). Furthermore, the timing of moult means that some individuals were actively moulting while breeding. While moult-breeding overlaps have been documented in several species (Pied Flycatchers, Hemborg et al. 2001, Lobato et al. 2006; Ural Owls, Brommer et al. 2003), such overlaps commonly occur at the end of the breeding season, when necessitated by the time constraints of impending winter.

Stable isotope analysis of claw and feather keratin also suggests that at least some individuals may be moulting during migration (Figure 2.4). For three of nine individuals from which both claw and feather material were collected, feather hydrogen isotope signatures (δD_f) were considerably more negative than claw hydrogen isotope signatures (δD_k). This pattern indicates that feathers were likely grown at more northerly locations than claws, possibly during northward migration. Moulting-migration overlaps have been documented for several other species (Barn Swallows, Pérez-Tris et al. 2001; American Redstarts (*Setophaga ruticilla*), Norris et al. 2004b), where they are usually associated with decreased feather quality, delayed arrival on the wintering grounds (Norris et al. 2004b) or a decrease in body condition (Pérez-Tris et al. 2001). Thus, like moulting-breeding overlaps, they usually occur at the end of the breeding season, when migratory birds face time constraints (Norris et al. 2004b), and are uncommon during spring migration. Conversely, two of nine individuals had δD_f signatures that were considerably more positive than δD_k signatures, suggesting feathers had been moulted south of the location where claws were grown. Stobo and McLaren (1975) suggested that Ipswich Sparrows may withdraw slightly from the northern parts of the range towards the end of the winter, and briefly move south. It is possible that these feathers were grown during this brief southern movement and thus reflect southern locations, while the claws reflect the location where the majority of the winter was spent.

The occurrence of spring moulting-breeding and possible moulting-migration overlaps in Ipswich Sparrows suggests that the cost of partial prealternate moult may be quite low. This interpretation is supported by the fact that I found no relationship between the incidence of prealternate moult and measures of reproductive success. It is likely that

prealternate moult was simply not energetically or aerodynamically expensive enough to impact other parts of the annual cycle. Because only some feathers are replaced during this moult, large amounts of energy may not be required to produce new tissue. Furthermore, as only one or two remiges are moulted per wing, feather gaps will be small and have little impact on flight ability (Lind 2001), particularly as tertials (the only remige moulted) are not among the most important feathers for flight (Neto and Gosler 2006, Pap et al. 2007).

It is also possible that I found no evidence that prealternate moult impacted reproductive success because only the highest quality birds moult. However, my results do not support this theory. If only the highest quality birds moult, I would expect birds that moulted to be in better condition than those that did not. This was not the case in my study: condition index did not differ significantly between birds that moulted and those that did not. Additionally, if only high quality birds moult, prealternate moult might act as an honest indicator of quality, similar to repeated moult in Common Terns (Bridge and Nisbett 2004). If this were the case, we might expect to see evidence of assortative mating with respect to prealternate moult in Ipswich Sparrows, which I did not find in this study.

Finally, it is possible that I did not measure those aspects of reproductive success that might have been impacted by moult. The majority of Ipswich Sparrow mortality occurs during the winter months (Stobo and McLaren 1975, Ross and McLaren 1981), and recruitment rates may be independent of many measures of reproductive success (Ross and McLaren 1981). Therefore, although not possible within the scope of this study, determining rates of return of nestling Ipswich Sparrows might have provided

additional insight into the relationship between prealternate moult and reproductive success.

While I detected no costs associated with prealternate moult, I also found no evidence of obvious benefits. Replacement of badly abraded plumage is necessary for birds in order to ensure efficient functioning of feathers (Ginn and Melville 1983). Thus, in a migratory species, we might expect those birds undertaking longer migrations to be more likely to undergo moult, as their feathers will be subject to increased wear (Nebel et al. 2002). However, my results show this is not the case for Ipswich Sparrows. Winter location did not differ between birds that had undergone prealternate moult and those that had not (Figure 2.5). The lack of a relationship between winter location and moult strategy suggests that prealternate moult does not function to ensure efficient migration in Ipswich Sparrows. The pattern of feather moult supports this hypothesis, as none of the most important flight feathers (primaries and secondaries) were moulted.

The function of prealternate moult in Ipswich Sparrows is unclear. Their alternate plumage is identical to their basic plumage, so the moult is not necessary for transformation to breeding plumage. Humphrey and Parkes (1959) proposed that the prealternate moult of Savannah Sparrows functioned to replace feathers that were badly abraded. Feather abrasion is thought to be particularly severe in ground-foraging species such as the Savannah Sparrow (Humphrey and Parkes 1959). However, the pattern of feather replacement seen in Ipswich Sparrows does not support this argument: back feathers and tertials were the most commonly moulted feathers, and these feathers are unlikely to come into contact with the ground. Back feathers and tertials are, however, the feathers most likely to be degraded by sunlight, which breaks down feather proteins

and causes wear and the loss of colour (Ginn and Melville 1983). Therefore, while prealternate moult in Ipswich Sparrows may function to replace severely abraded feathers, it is likely the abrasion is due to degradation by sunlight, rather than the result of foraging habits.

This study is the first to describe the incidence and timing of the prealternate moult in Ipswich Sparrows. The disparity between my findings and the information available in the literature suggests that moult strategies may differ widely among subspecies. The literature on moult patterns also suggests that in many species, moult is temporally separated from breeding and migration. However, Ipswich Sparrows were observed actively moulting during the early breeding season with no detectable consequences for reproductive success, and stable isotope evidence suggests that moult may also occur during migration. Therefore, the results of my study suggest that partial prealternate moult may not be a high cost activity for Ipswich Sparrows.

CHAPTER 3. WINTER LOCATION AND ITS EFFECTS ON THE BREEDING SEASON IN IPSWICH SPARROWS

Introduction

Approximately 350 North American bird species breed at temperate latitudes but spend well over half of each year migrating to and wintering in locations far south of their breeding grounds (Kelly and Finch 1998, Marra et al. 1998, Norris et al. 2004a). However, to date most studies of migratory birds have been conducted on the temperate breeding grounds, due mainly to difficulties associated with following individuals throughout the annual cycle (Marra et al. 1998, Hobson 1999, Norris et al. 2004a). Indeed, the winter range of some migratory bird species has only recently been discovered (Greenberg et al. 2007) or remains unknown (Pain et al. 2004).

Increasing knowledge of wintering ranges and winter ecology of migratory species is important for several reasons. In order to gain a complete picture of the annual cycle and habitat needs of these species, we must know where they winter. Additionally, there is a growing body of evidence suggesting that aspects of winter location can impact performance on the breeding grounds (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004a, Saino et al. 2004, Bearhop et al. 2005). Thus, in order to fully understand factors shaping reproductive success, we must have knowledge of individual and population wintering locations.

Several interrelated aspects of winter location may have effects that carry over and impact the breeding season. For example, the length of an individual's migration may affect breeding performance in a number of ways. Migration length may influence spring arrival times, with individuals that winter closer to the breeding grounds arriving earlier than those that winter further away (Bearhop et al. 2005, Mazerolle and Hobson

2007). Earlier spring arrival dates have been shown to increase reproductive success in a variety of species (e.g. American Redstarts (*Setophaga ruticilla*), Marra et al. 1998, Norris et al. 2004a; European Blackcaps (*Sylvia atricapilla*), Bearhop et al. 2005). Additionally, because migration can require up to 50% of an individual's annual energy budget (Drent and Piersma 1990), migration length may affect the amount of energy that can be devoted to reproduction (Berthold et al. 1992, Bearhop et al. 2005). Consequently, individuals that migrate shorter distances may have increased reproductive success (Bearhop et al. 2005).

Other aspects of winter location that may impact reproductive success are the climatic and habitat conditions experienced by individuals during the winter, which are partly determined by the distance individuals migrate (Nolan and Ketterson 1983, Castro et al. 1992), but may also vary independent of migratory distance (Studds and Marra 2007). Variation in winter climate has been shown to affect the timing of spring departure from the wintering grounds (Studds and Marra 2007), as well as body condition and measures of reproductive success such as clutch size and number of fledglings produced (Lehikoinen et al. 2006). Variation in quality of winter habitat can also impact reproductive success (Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004a, Saino et al. 2004). Individuals wintering in low quality locations may leave later for spring migration (Marra et al. 1998), be in poorer condition during migration (Bearhop et al. 2004), and arrive later on the breeding grounds (Norris et al. 2004a) than individuals wintering in high quality locations. Individuals wintering in poor quality habitat may also produce fewer fledglings than those wintering in high quality habitat (Marra et al. 1998, Norris et al. 2004a, Saino et al. 2004).

Several factors play a role in determining where individuals spend the winter. Both sex and age may influence an individual's winter location. Males and females of many species are separated latitudinally during the winter, with females wintering further south than males (e.g. Western Sandpipers (*Calidris mauri*), Nebel et al. 2002; European Robins (*Erithacus rubecula*), Catry et al. 2004; Common Chiffchaffs (*Phylloscopus collybita*), Catry et al. 2007; White-throated Sparrows (*Zonotrichia albicollis*), Mazerolle and Hobson 2007). Sex may also determine the quality of the habitat in which an individual winters, as females often obtain poorer quality winter territories than males (e.g. Black-throated Blue Warblers (*Dendroica caerulescens*), Wunderle 1995; American Redstarts, Marra 2000; European Robins, Catry et al. 2004). Similarly, age may influence the latitudinal distribution of individuals on the wintering grounds (e.g. Western Sandpipers, Nebel et al. 2002), and the quality of wintering habitat, as older birds often gain the highest quality winter territories (e.g. American Redstarts, Marra 2000; European Robins, Catry et al. 2004). Finally, populations that are separated during the breeding season often also winter separately. For example, populations that breed the furthest north may winter the furthest south (e.g. Wilson's warblers (*Wilsonia pusilla*), Kelly et al. 2002), or populations that breed at different latitudes may be segregated longitudinally on the wintering grounds (e.g. Black-throated Blue Warblers, Rubenstein et al. 2002).

The growing evidence that winter location often impacts reproductive success underscores the importance of understanding the connections between separate stages in the annual cycle of migratory birds. This is particularly important for species of conservation concern, as declines in productivity may be caused by factors outside the

breeding season, and thus causes may only be identified by increasing our knowledge of the species' winter ecology and the connections between the winter and breeding season (Wassenaar and Hobson 1998, Pain et al. 2004, Saino et al. 2004). However, it has historically been challenging to determine relationships between periods of the annual cycle due to the difficulties involved with following individuals once they have departed from the breeding grounds (Marra et al. 1998, Hobson 1999, Norris et al. 2004a).

Recently, techniques such as stable isotope analysis have provided a means of investigating the connections between the wintering and breeding grounds (Hobson 1999, Hobson 2005). Stable isotopes are intrinsic markers that vary systematically according to location, and thus provide a record of an organism's geographic history (Hobson 1999). Studies using stable isotope analysis to track migratory birds are largely responsible for our current knowledge of links between the winter and breeding seasons (e.g. Marra et al. 1998, Bearhop et al. 2004, Norris et al. 2004a, Bearhop et al. 2005). However, to date most of these studies have focused primarily on the effects of differences in winter habitat quality on reproductive success. To my knowledge, only two studies (Bearhop et al. 2005, Mazerolle and Hobson 2007) have considered migration distance as a factor that might significantly impact performance on the breeding grounds. Additionally, most stable isotope studies have considered the importance of winter location in long-distance migrants; short-distance migrants are considerably less studied.

The goal of my study was to determine if and how winter location impacts the breeding season in a short-distance migrant, the Ipswich Sparrow (*Passerculus sandwichensis princeps*). To address this question, I used stable isotope analysis of hydrogen (δD) to approximate the winter location of Ipswich Sparrows, a subspecies of

Savannah Sparrow (*Passerculus sandwichensis*) that breeds almost exclusively on Sable Island, Nova Scotia, Canada.

Sightings indicate the subspecies winters along the Atlantic coast from northern Florida to Nova Scotia (30-44.5°N), with a proportion of the population (~20%) remaining on Sable Island during the winter (Elliott 1968). A single study from 1971, based on surveys of a number of sites within the wintering range, found that the greatest proportion of the population wintered between New Jersey and Virginia (37-39°N, Stobo and McLaren 1971). The majority of the population, however, has never been seen on the wintering grounds and thus further investigation of the winter range of this subspecies is warranted. Additionally, it is possible that the winter distribution of Ipswich Sparrows has shifted in the almost 40 years since the first study was conducted. Several recent studies have shown that ranges and distributions of a variety of bird species have shifted northwards over the past few decades, possibly in response to climate change or regional habitat disturbance (Valiela and Bowen 2003, Brommer 2004, LaSorte and Thompson 2007). Thus, in addition to stable isotope analysis, I used survey data from the National Audubon Society's Christmas Bird Counts over the past 40 years to investigate possible changes in Ipswich Sparrow winter distribution.

Ipswich Sparrows are an ideal model species with which to investigate the effects of winter location on breeding success. Because of their wide winter range, winter experiences vary greatly among individuals, while their restricted breeding range allows individuals from across the wintering range to be sampled in one place. Furthermore, Ipswich Sparrow wintering grounds span a very narrow longitudinal range. This situation is ideal for hydrogen isotope analysis, as δD signatures provide a great deal of

information about the latitude at which tissues were grown, but very little regarding longitude (Hobson 2005).

Ipswich Sparrows winter exclusively in the outer dunes along the Atlantic coast; consequently, broad-scale winter habitat does not vary a great deal throughout the range. Microhabitat features (such as relief, vegetation cover, and access to fresh water) do vary throughout the winter range, but this variation is not related to latitude (Stobo and McLaren 1971). However, winter diet may vary with an individual's wintering latitude. During the winter, Ipswich Sparrows eat primarily beach grass seeds (marram grass, *Ammophila breviligulata*, and sea oats, *Uniola paniculata*), but may also eat insects when they are available (Elliott 1968). To date, no study has closely examined variation in Ipswich Sparrow diets across the wintering range. Therefore, I examined winter diet using carbon ($\delta^{13}\text{C}$) stable isotope analysis to determine whether Ipswich Sparrows were eating C_3 or C_4 plants during the winter, and nitrogen ($\delta^{15}\text{N}$) stable isotope analysis to determine whether individuals were eating insects in some locations.

Methods

Study Location

This study was conducted on Sable Island, Nova Scotia (44°N, 60°W) from 16 June to 18 August 2006 and from 26 April to 2 July 2007. For a full description of Sable Island and the two sites used in this study, see Chapter 2.

Capture, Banding and Tissue Sampling

Birds were captured in mist nets both before and during nest building (2007) and during incubation and nestling stages (2006 and 2007). For a full description of the banding process, see Chapter 2.

In 2006, I collected two feathers from each of 13 individuals displaying moult limits (indicating they had undergone prealternate moult, see Chapter 2). I took one moulted feather (back feather or flight feather) and one control feather (greater covert, moulted on Sable Island during the prebasic moult) from each individual. In 2007, I clipped 1-2 mm of claw from the back claw (C1) of both feet of birds captured before 20 May (n = 59, males = 38, females = 10, unknown sex = 11). I selected 20 May as a cutoff date for claw collection because previous studies suggest claw keratin reflects wintering ground isotope ratios for approximately three to seven weeks after birds arrive on the breeding grounds (Bearhop et al. 2003, Fraser et al. 2008, but see Mazerolle and Hobson 2005). In 2007, spring sightings of Ipswich Sparrows on mainland Nova Scotia peaked between 7 and 14 April (range: 25 March – 19 May, McLaren 2007). Thus most of the birds likely arrived on Sable Island in the third week of April, and 20 May represents a cutoff date of approximately five weeks after arrival, well within the time period during which claws should reflect winter values.

Reproductive Success

I monitored banded birds and their nests during the breeding season to determine nesting attempts, clutch sizes, and hatching and fledging dates. For a full description of methods, see Chapter 2.

Validating Hydrogen Isotope Analysis

I used stable hydrogen isotope analysis of claw and feather keratin to investigate the winter location of Ipswich Sparrows. The hydrogen stable isotope signature of precipitation (δD_p) varies along a latitudinal gradient in North America (Bowen et al. 2005). The δD_p at a given location is directly related to the hydrogen stable isotope signature of animal tissues produced at that location (Estep and Dabrowski 1980,

Chamberlain et al. 1997, Hobson and Wassenaar 1997). Therefore, the hydrogen stable isotope signatures of claw and feather keratin (δD_k and δD_f respectively) provide information about the latitude at which tissues were grown. δD signatures decrease as latitude increases; thus, higher δD values correspond to tissues produced at southern locations (Chamberlain et al. 1997, Hobson and Wassenaar 1997). For additional detail regarding hydrogen stable isotope analysis, see Chapter 1.

To verify that the δD signature of Ipswich Sparrow keratin reflects precipitation values (δD_p) and therefore provides information about location, I checked whether the δD_f signatures of greater covert feathers grown at a known location, Sable Island, matched the δD signature expected for keratin produced there. Greater coverts were chosen because they are almost exclusively grown during the prebasic moult (Pyle pers. comm.), which takes place on Sable Island in the fall (Stobo and McLaren 1975). I did not verify whether claw keratin also reflected δD_p , but the δD signatures of feathers and claws grown in the same locations are highly correlated (Hobson et al. 2006). Thus, I assumed that if feather keratin reflected δD_p , claw keratin would also.

The δD signature expected for keratin produced on Sable Island was calculated using values from an online database of isotopes in precipitation (see Acknowledgements). These values were obtained using methods described in Bowen and Revenaugh (2003) and Bowen et al. (2005). Because greater coverts are grown in the fall, they should reflect the average growing season δD_p of Sable Island. A correction factor of -19‰ was applied to the growing season δD_p to account for the fractionation associated with the production of keratin (Langin et al. 2007, Fraser et al. 2008).

The relationship between δD_p and δD_f or δD_k can be decoupled if there is marine input in the food web in which organisms are feeding. Seawater contains a higher proportion of deuterium than precipitation, and hence marine input in a system can lead to higher δD_f and δD_k values (Lott et al. 2003). However, seawater also has a high ^{34}S to ^{32}S ratio ($\delta^{34}\text{S}$) and this ratio can serve as an indicator of marine input in a system. A $\delta^{34}\text{S}$ signature of 10‰ or higher indicates likely marine input (Lott et al. 2003). To determine whether marine input was affecting hydrogen isotope signatures for Ipswich Sparrows, I used sulphur stable isotope analyses of 11 moulted flight and back feathers collected from individuals during the summer of 2006.

Winter Location of Ipswich Sparrows

Wintering latitude of individual Ipswich Sparrows was estimated using the hydrogen stable isotope values of claw keratin (δD_k) and the database of isotopes in precipitation (Bowen and Revenaugh 2003, Bowen et al. 2005). For each degree of latitude within the known wintering range of Ipswich Sparrows (30 to 44.5°N), average annual precipitation hydrogen isotope values (δD_p) and 95% confidence intervals were obtained from the database. Average annual values were used instead of average growing season values because there is a high degree of seasonal variation in δD_p (Hobson 2005), and it is currently unknown how long it takes foodwebs (and hence animal tissue) to mirror changes in δD_p . Furthermore, the exact time period represented by claw tips is unknown. Finally, for Ipswich Sparrows, their winter diet of seeds probably reflects growing season δD_p values, while the water they drink in the winter may be derived from winter precipitation or groundwater, and thus is likely isotopically distinct from their diet. Since tissue δD signatures are derived from both drinking water and diet (DeNiro and Epstein 1981, Hobson et al. 1999, Langin et al. 2007), it is unlikely

that claw keratin represents only growing season δD_p , and using average annual values allows for the incorporation of some winter precipitation values.

A correction factor of -19‰ was applied to average annual δD_p values and 95% confidence intervals to account for the fractionation of hydrogen isotopes associated with the production of keratin (Langin et al. 2007, Fraser et al. 2008), and a predicted hydrogen isotope range for keratin (δD_k) was estimated for each degree of latitude. The range of latitudes that could potentially produce the δD_k of claw keratin for each individual sparrow was determined to create a ‘latitude window’ of possible winter locations.

I divided the known winter range of Ipswich Sparrows into three approximately equal categories (North: 40-44.5°N; Mid: 35-40°N; South: 30-35°N), and assigned each sparrow to a category based on the latitude window associated with its claw δD_k value. Individuals with latitude ranges spanning more than one category were assigned to the category which included the greater part of the latitude window. In the three cases where the latitude window was divided equally between two categories, the individual was not assigned to a winter location category.

I compared the winter distribution of Ipswich Sparrows obtained using the above methods with the distribution estimated based on the only previous study of the Ipswich Sparrow winter range (Stobo and McLaren 1971). The distributions differed considerably, with a higher proportion of individuals in the northern part of the winter range in my study than was found by Stobo and McLaren (1971) (see Results). Therefore, I used survey data from the National Audubon Society’s Christmas Bird Counts (CBC) between 1971 and 2007 (National Audubon Society 2008) to investigate

the possibility of a shift in the winter range of Ipswich Sparrows. These surveys are conducted by volunteers annually in the period between 14 December and 5 January. Each survey takes place over one calendar day and encompasses a 12 km radius circle. All birds seen or heard are recorded, and final counts are corrected for survey effort by dividing the number of birds of each species seen by the number of hours of effort for each circle.

From these records, I calculated three measurements of the winter range: northern boundary, centre of occurrence and centre of abundance (La Sorte and Thompson 2007). These parameters were calculated for counts at intervals of three years (1971, 1974, 1977, ..., 2007).

Northern boundary was defined as the 95th quantile of the latitudes of circles in which Ipswich Sparrows were sighted, and centre of occurrence was defined as the median of the latitudes of circles in which Ipswich Sparrows were sighted. The centre of abundance was calculated according to the following equation:

$$y_{cm} = \sum m_i y_i / \sum m_i, i = 1 - n$$

where y_{cm} is the latitude of the center of mass for a collection of n CBC circles with masses m_1, m_2, \dots, m_n and latitudes y_1, y_2, \dots, y_n . Mass is defined as the total number of individuals observed during a CBC count divided by the total number of party hours (La Sorte and Thompson 2007).

I also investigated whether winter location varied with size or sex in Ipswich Sparrows. The differing reproductive strategies and energetic needs of males and females may lead to segregation on the wintering grounds by latitude or habitat (Catry et al. 2004, Catry et al. 2007, Mathot et al. 2007, Mazerolle and Hobson 2007). However,

another factor than can lead to the winter segregation of sexes is body size. Larger individuals may be able to withstand harsher winters and therefore may winter further north than smaller individuals (Ketterson and Nolan 1976). Male Ipswich Sparrows are, on average, larger than females (Stobo and McLaren 1975); thus, to determine if differential migration in Ipswich Sparrows was due to body size differences, I examined the relationship between winter location and a measure of size (left wing) within each sex.

Effects of Winter Location on Breeding Performance

I investigated whether δD_k and body condition were related in each sex, and examined the relationships between δD_k and territory establishment dates for males, and δD_k and first egg dates for females. I also looked at relationships between the δD_k signatures of parents and the number and average mass of nestlings on day 7. Analyses were conducted on first nests only and for males and females separately.

A condition index was calculated for each individual by taking the residuals of a regression of mass on left wing (Robb et al. 1992, Jakob et al. 1996).

I used the date that males were banded as a proxy for territory establishment date, which can be considered the beginning of breeding for males. Banding dates are likely to be a reasonable indicator of timing of territory establishment because males were only responsive to the playbacks of male song used to lure them into nets when they were territorial (Temple 2000). I surveyed the study sites approximately every other day and attempted to capture singing males; thus, males were generally caught shortly after becoming territorial.

For females, banding date is less likely to reflect a biologically significant date, as territory settlement may not be related to timing of breeding initiation in females

(Stutchbury and Roberston 1987). Therefore, I used first egg dates as a measure of breeding initiation for females. Very few nests were found prior to clutch completion, so most females were already incubating at the time of nest discovery. In these cases, I approximated first egg date using hatch date. I assumed females had incubated for 12 days (Stobo and McLaren 1975, Ross 1980), and laid one egg per day (Stobo and McLaren 1975).

The number and mean mass of nestlings was determined on day 7 post-hatch (Ross 1980). Ipswich Sparrows leave the nest between 8 and 13 days after hatch (mean = 10.9, Stobo and McLaren 1975); therefore by banding the nestlings on day 7 post-hatch, I avoided force-fledging nestlings.

Variation in Winter Diet

To assess trends in the winter diets of Ipswich Sparrows, I examined how carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures varied between sexes and with wintering latitude (approximated by δD_k). Carbon stable isotope values provide information regarding whether diet is derived mainly from plants using the C_3 metabolic path or those using the C_4 or CAM metabolic paths (Marra et al. 1998, Wassenaar and Hobson 2000, Norris et al. 2004a). C_3 plants discriminate against the heavier form of carbon (^{13}C) and hence have lower $\delta^{13}\text{C}$ values, as do the organisms feeding on them (O'Leary 1981). Marram grass, a C_3 plant, grows on the Atlantic coast from Nova Scotia to South Carolina (Watson and Dallwitz 2005, USDA 2008) and is the main component of Ipswich Sparrow diets in the northern part of their winter range (Stobo and McLaren 1975). Sea oats, a C_4 plant found along the Atlantic coast from Delaware to Florida (Watson and Dallwitz 2005, USDA 2008), is the staple food of Ipswich Sparrows wintering further south (Stobo and McLaren 1975). Thus we might expect to see variation

in claw $\delta^{13}\text{C}$ values across the Ipswich Sparrow winter range. Additionally, $\delta^{13}\text{C}$ signatures might provide insight into whether Ipswich Sparrows are eating primarily marram grass, primarily sea oats, or a combination of both in areas where both plants grow.

Nitrogen stable isotopes provide information regarding the trophic level at which individuals are feeding, as tissues become enriched with the heavy isotope (^{15}N) at higher trophic levels (Hobson 1990, Hobson and Montevecchi 1991, Herrera et al. 2006). $\delta^{15}\text{N}$ signatures increase by approximately 3.8‰ per trophic level (Hobson 1990). Thus, if Ipswich Sparrows eat insects in addition to seeds at locations throughout their winter range, I would expect to see elevated $\delta^{15}\text{N}$ values for birds wintering in these locations. However, because $\delta^{15}\text{N}$ values also increase when animals are under nutritional stress (Hobson et al. 1993), I also investigated the relationship between $\delta^{15}\text{N}$ and condition.

Stable Isotope Analysis

Hydrogen, carbon and nitrogen stable isotope analyses were conducted at the Stable Isotopes in Nature Laboratory at the University of New Brunswick in Fredericton, New Brunswick. For a full description of hydrogen isotope analysis methods for claw material, see Chapter 2. Claw δD_k values are expressed in parts per thousand (‰) deviation from Vienna Standard Mean Ocean Water (VSMOW). To determine precision of laboratory measurement of hydrogen isotopes, repeated measurements were made of hydrogen standard IAEA-85. Based on these measurements, the laboratory measurement error for δD_k was estimated at approximately $\pm 2.26\%$. Five claw samples were omitted from analyses because δD_k values were either missing or unreliable due to high or low H_2 amplifications (amount of H_2 gas produced by the sample).

The procedure followed for hydrogen stable isotope analysis of feathers was essentially identical to that of claw analyses; however, feathers were cleaned prior to analysis. They were first soaked in a 2:1 chloroform:methanol solution for 24 hours, then allowed to air dry for 48 hours. Based on repeated measurements of standard IAEA-85, the laboratory measurement error for the δD_f of the feathers was estimated at approximately $\pm 2.0\%$.

For carbon and nitrogen stable isotope analyses, claw samples were dried and powdered, and weighed into tin capsules at approximately 0.2 mg. Three standards (bovine liver, smallmouth bass (*Micropterus dolomieu*) muscle and nicotinamide) calibrated against IAEA standards (CH6, CH7, N1 and N2) were used to calibrate sample data. Samples were combusted in an NC2500 elemental analyzer to produce gas, which was analyzed in a Thermo Finnigan Delta XP mass spectrometer. $\delta^{13}C$ and $\delta^{15}N$ values are expressed in standard parts per thousand units (‰), relative to the Vienna Pee Dee Belemnite (VPDB) and atmospheric (AIR) scales respectively. To assess the precision of $\delta^{13}C$ and $\delta^{15}N$ measurements, isotope ratios of the standard acetanilide were measured multiple times. Based on this procedure, laboratory measurement error is estimated at approximately $\pm 0.14\%$ and $\pm 0.16\%$ for $\delta^{13}C$ and $\delta^{15}N$ respectively.

Sulphur stable isotope analyses were conducted in the Queen's University Facility for Isotope Research at Queen's University, Kingston, Ontario. Feathers were washed in a 2:1 chloroform:methanol solution for 24 hours, then allowed to dry for 48 hours. Samples were powdered and loaded into tin capsules at approximately 1 mg. The prepared samples were combusted in a Carlo Erba Elemental Analyser NCS 2500, and

analyzed in a Finnigan Mat 252 Mass Spectrometer. Sulphur isotope values are reported in standard parts per thousand units (‰) relative to Canyon Diablo Troilite (CDT).

Data Analysis

Statistical analyses were performed using Rcmdr (Version 1.3-8, Fox et al. 2007) and R (Version 2.6.0, R Development Core Team 2007). Data were checked for normality using the Shapiro-Wilk test for normality, and non-normal data were analyzed using non-parametric statistics. Results were considered significant when p-values were 0.05 or lower.

I used t-tests to compare the δD_f signatures of Ipswich Sparrow greater covert feathers to the expected δD signature for keratin produced on Sable Island, and to compare the claw δD_k , $\delta^{13}C$ and $\delta^{15}N$ signatures of male and female Ipswich Sparrows.

I used correlation tests (Pearson's Product-Moment and Spearman's Rank Correlations) to examine relationships between δD_k and size, as well as between δD_k and banding date (for males), first egg date (for females), body condition and number and mean mass of nestlings produced. Tests were conducted separately for males and females. I also used correlation tests to investigate relationships between δD_k and $\delta^{13}C$, and between δD_k and $\delta^{15}N$, and to examine the relationship between $\delta^{15}N$ and body condition.

The distribution of the latitudes of CBC circles in which Ipswich Sparrows were seen was left-skewed. Therefore, trends in the northern boundary and centre of occurrence of the Ipswich Sparrow winter range over time were analyzed using quantile regression. The trend in centre of abundance was analyzed using linear regression, where the latitude of the centre of abundance was the dependent variable and the year of the count was the independent variable.

Results

Validating Hydrogen Isotope Analysis

The greater covert feathers collected in 2006 had a mean δD_f value of $-64.06 \pm 7.40\text{‰}$ (Table 3.1), which was not significantly different from that expected based on the average growing season δD_p of Sable Island (expected $\delta D_k = -63.2\text{‰}$, $t = -0.42$, $df = 12$, $p = 0.69$). Eighty-five percent of greater covert δD_f values fell within $\pm 6.0\text{‰}$ of the mean value. Seven of the 11 back and flight feathers collected to check for marine input had $\delta^{34}\text{S}$ values greater than 10‰ (Table 3.2), the recommended cutoff point for detecting significant marine input (Lott et al. 2003).

Winter Location of Ipswich Sparrows

Latitude windows calculated for individual Ipswich Sparrows ($n = 54$) spanned the entire known wintering range but were concentrated in the northern and middle parts of the range (Figure 3.1). Approximately half (42%) of the birds sampled spent the winter in the northern part of the winter range, while the other half (46%) spent the winter in the middle part of the range. Only two individuals (4%) wintered in the southern part of the range (Figure 3.2a). My findings contrast with winter patterns extrapolated from surveys performed in 1971 (Stobo and McLaren 1971, Figure 3.2b), when relatively more sparrows were sighted per mile surveyed in the mid portion of the winter range than in the north or the south.

Neither the latitude of the northern boundary (95th quantile, slope = -0.007 , range: $-0.04 - 0.03$) nor the latitude of the centre of occurrence (50th quantile, slope = 0.005 , range: $-0.01 - 0.02$) showed any trend over time (Figure 3.3). However, the latitude of the centre of abundance decreased significantly over time ($R^2 = 0.35$, $df = 11$, $p = 0.03$, Figure 3.4).

Females had significantly higher δD_k signatures than males ($t = 3.55$, $df = 42$, $p < 0.01$, Figure 3.5), indicating that they wintered further south than males. However, there was no significant correlation between male or female body size (as measured by left wing) and δD_k (males: $r = -0.20$, $df = 33$, $p = 0.26$; females: $r = -0.52$, $df = 7$, $p = 0.15$).

Effects of Winter Location on Breeding Performance

Condition index was significantly and negatively correlated with δD_k values for males ($r = -0.43$, $df = 29$, $p = 0.02$, Figure 3.6) but not for females ($r = -0.52$, $df = 7$, $p = 0.15$).

For male Ipswich Sparrows, δD_k signatures were significantly and positively correlated with banding date, a proxy for territory establishment dates ($r = 0.37$, $df = 33$, $p = 0.03$, Figure 3.7), but there was no significant relationship between δD_k signatures and number of nestlings on day 7 ($r_s = 0.003$, $p = 0.99$). However, there was a trend for males with lower δD_k signatures to produce heavier nestlings ($r = -0.42$, $df = 18$, $p = 0.06$, Figure 3.8). In contrast, for females, δD_k signatures were significantly and negatively correlated with first egg dates ($r = -0.74$, $df = 6$, $p = 0.04$, Figure 3.9). No relationship existed between δD_k of females and number or mass of nestlings on day 7 (number: $r = -0.24$, $df = 5$, $p = 0.61$; mass: $r = 0.35$, $df = 5$, $p = 0.44$).

Variation in Winter Diet

$\delta^{13}C$ signatures of claw keratin ranged from -23.08 to -12.04% , with a mean value ($\pm SD$) of $-17.61 \pm 2.69\%$. Mean $\delta^{13}C$ values did not differ between sexes ($t = 1.27$, $df = 13.73$, $p = 0.11$), but were significantly and positively correlated with δD_k ($r = 0.41$, $df = 47$, $p < 0.01$, Figure 3.10). Individuals wintering at southern latitudes (higher δD_k values) had higher $\delta^{13}C$ signatures.

Claw keratin $\delta^{15}\text{N}$ signatures ranged from 4.02 to 14.5‰, with a mean value ($\pm\text{SD}$) of $8.53 \pm 2.45\text{‰}$. $\delta^{15}\text{N}$ values did not differ between sexes ($t = -0.50$, $df = 10.82$, $p = 0.63$), and were not correlated with δD_k ($r = 0.20$, $df = 50$, $p = 0.15$). However, $\delta^{15}\text{N}$ and condition index were significantly and negatively correlated ($r = -0.36$, $df = 46$, $p = 0.01$, Figure 3.11), with individuals in better condition showing lower $\delta^{15}\text{N}$ values.

Table 3.1. Mean and standard deviation of δD_f signatures (‰, relative to Vienna Standard Mean Ocean Water) for greater covert feathers collected from 13 Ipswich Sparrows during 2006.

Sample	δD_f (VSMOW, ‰)
1A	-66.1
2A	-66.3
3A	-66.5
4A	-74.1
5A	-62.7
6A	-58.7
7A	-68.2
8A	-59.9
9A	-70.1
10A	-62.9
11A	-63.5
12A	-69.9
13A	-43.9
Mean	-64.06
SD	7.40

Table 3.2. Mean and standard deviation of $\delta^{34}\text{S}$ values (‰, relative to Canyon Diablo Troilite) for back and flight feathers collected from 11 Ipswich Sparrows during 2006.

Sample	$\delta^{34}\text{S}$ (‰, CDT)
1B	14.7
2B	8.4
3B	6.7
4B	13.9
5B	4.7
6B	15.5
7B	16.0
8B	5.4
9B	15.4
10B	16.8
11B	14.5
Mean	12.0
SD	4.68

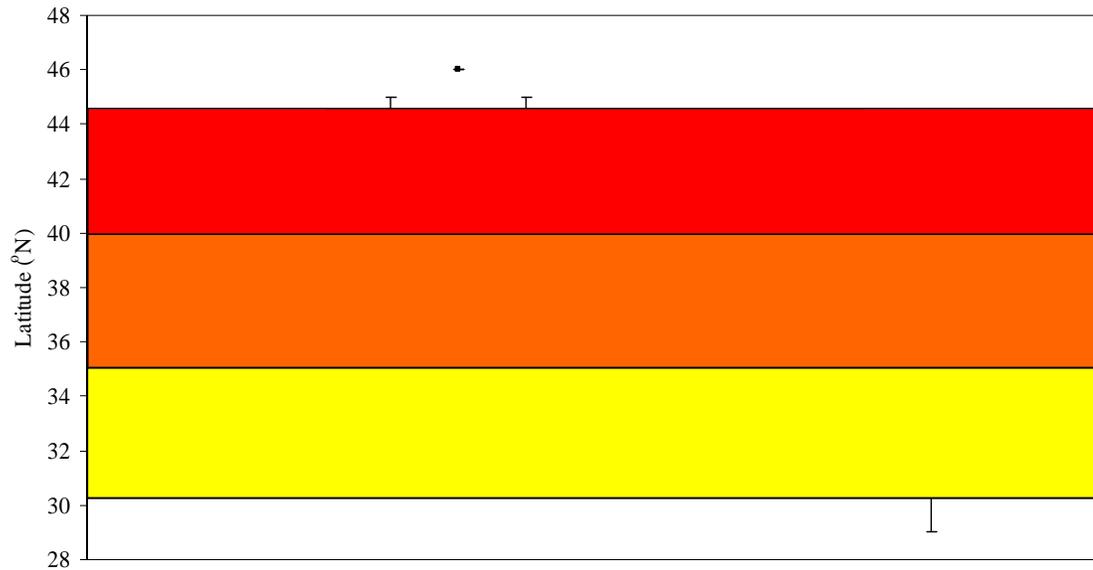
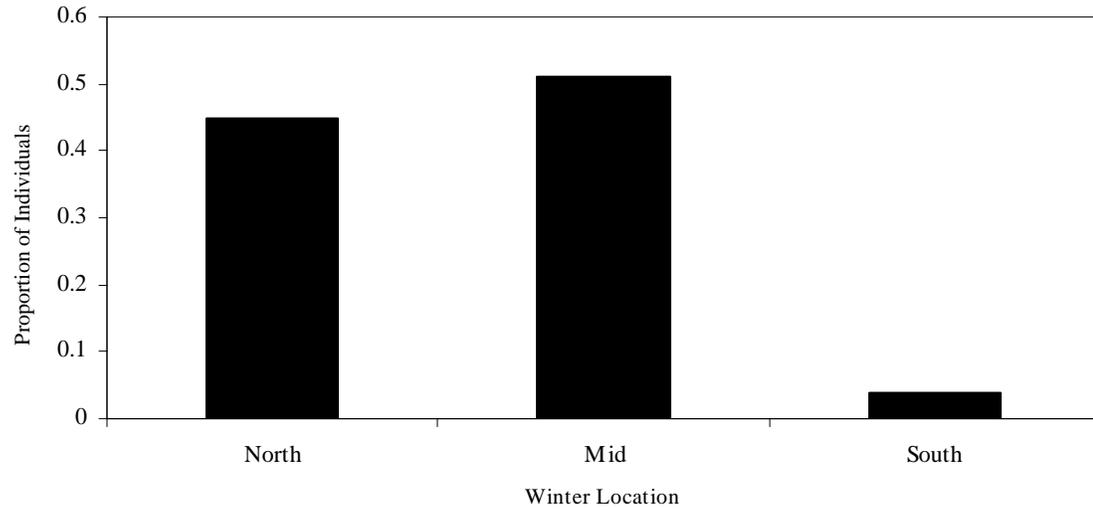


Figure 3.1. Latitude windows ($^{\circ}\text{N}$) based on claw δD_k signatures for 54 Ipswich Sparrows breeding on Sable Island in April and May 2007. Midpoints of latitude ranges are indicated. Colours indicate the division of the wintering range into three categories (North: red, 40-44.5 $^{\circ}\text{N}$; Mid: orange, 35-40 $^{\circ}\text{N}$; South: yellow, 30-35 $^{\circ}\text{N}$).

a)



b)

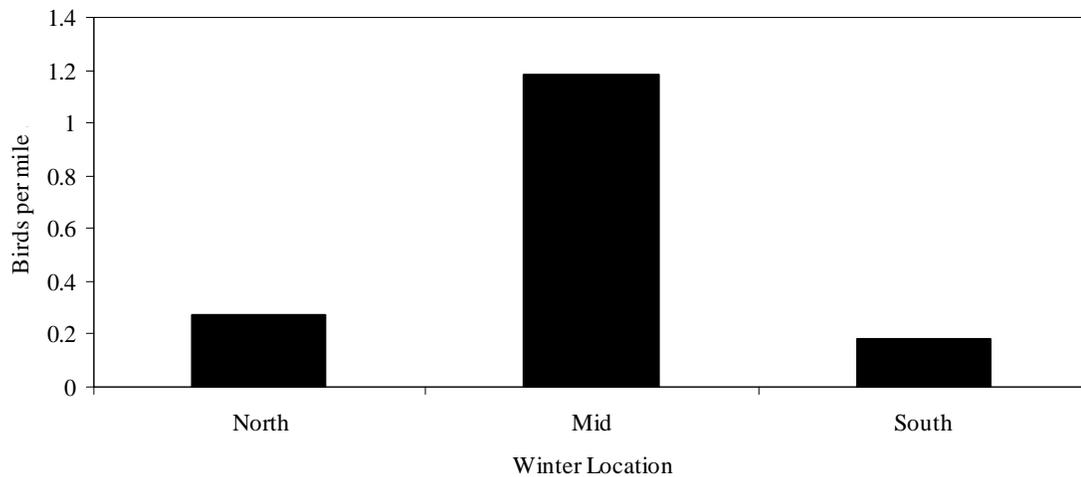


Figure 3.2. a) Proportion of Ipswich Sparrows ($n = 51$) wintering within each of three location categories, North ($40-44.5^{\circ}\text{N}$), Mid ($35-40^{\circ}\text{N}$) and South ($30-35^{\circ}\text{N}$), in 2007 based on latitude windows calculated from stable hydrogen isotope ratios (δD_k). **b)** Ipswich Sparrows sighted per mile surveyed in the same three location categories during March 1971. Data are taken from Stobo and McLaren 1971.

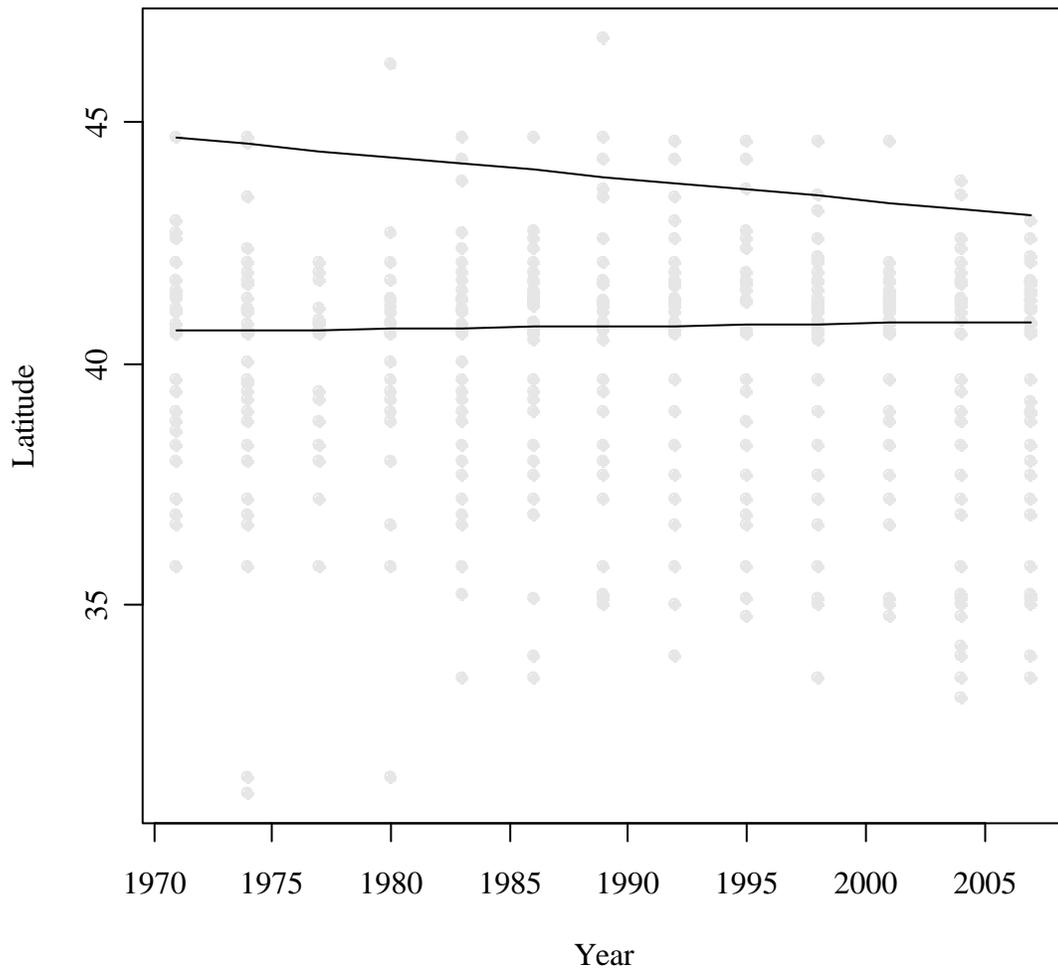


Figure 3.3. Trends in the latitude of the northern boundary (95th quantile, top line) and centre of occurrence (median, bottom line) of the Ipswich Sparrow winter range between 1971 and 2007. Grey points indicate the latitudes of all circles where Ipswich Sparrows were observed in a given year. Data are taken from the National Audubon Society's Christmas Bird Count.

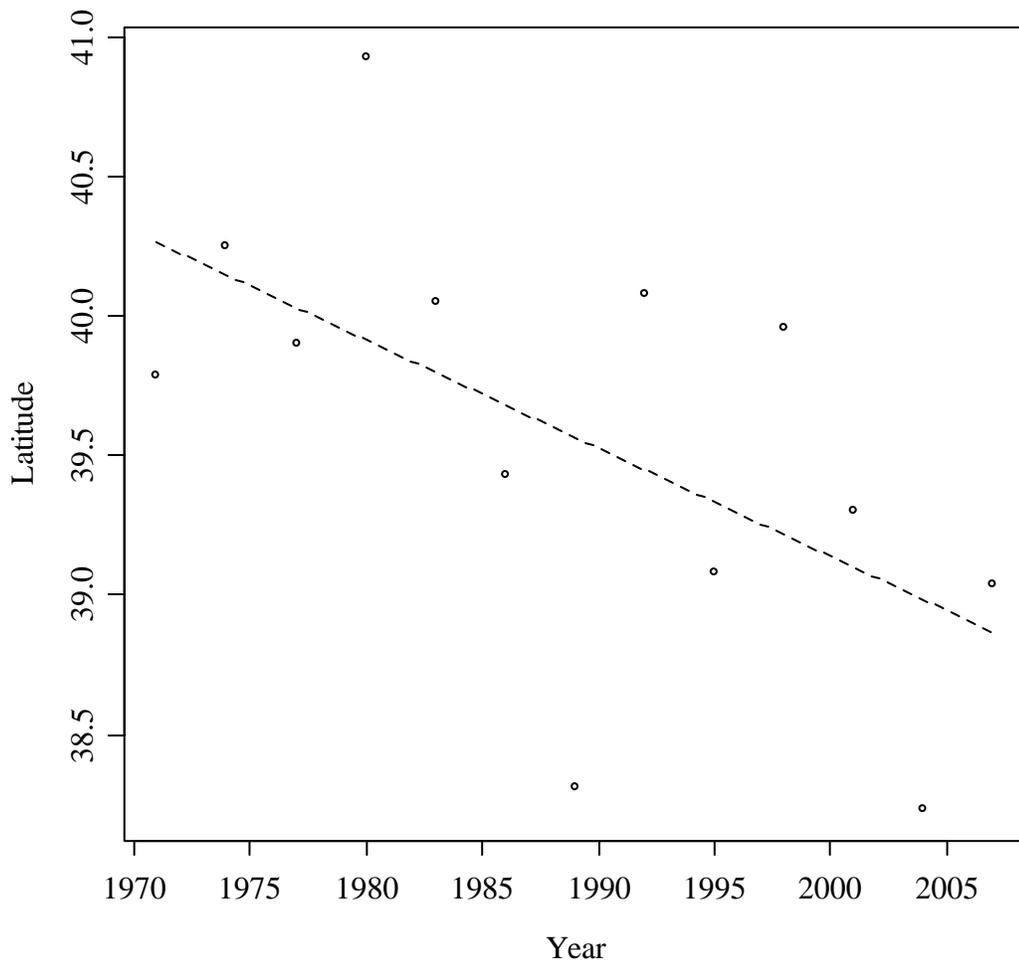


Figure 3.4. Trend in the latitude of the centre of abundance of the Ipswich Sparrow winter range between 1971 and 2007. Data are taken from the National Audubon Society's Christmas Bird Count.

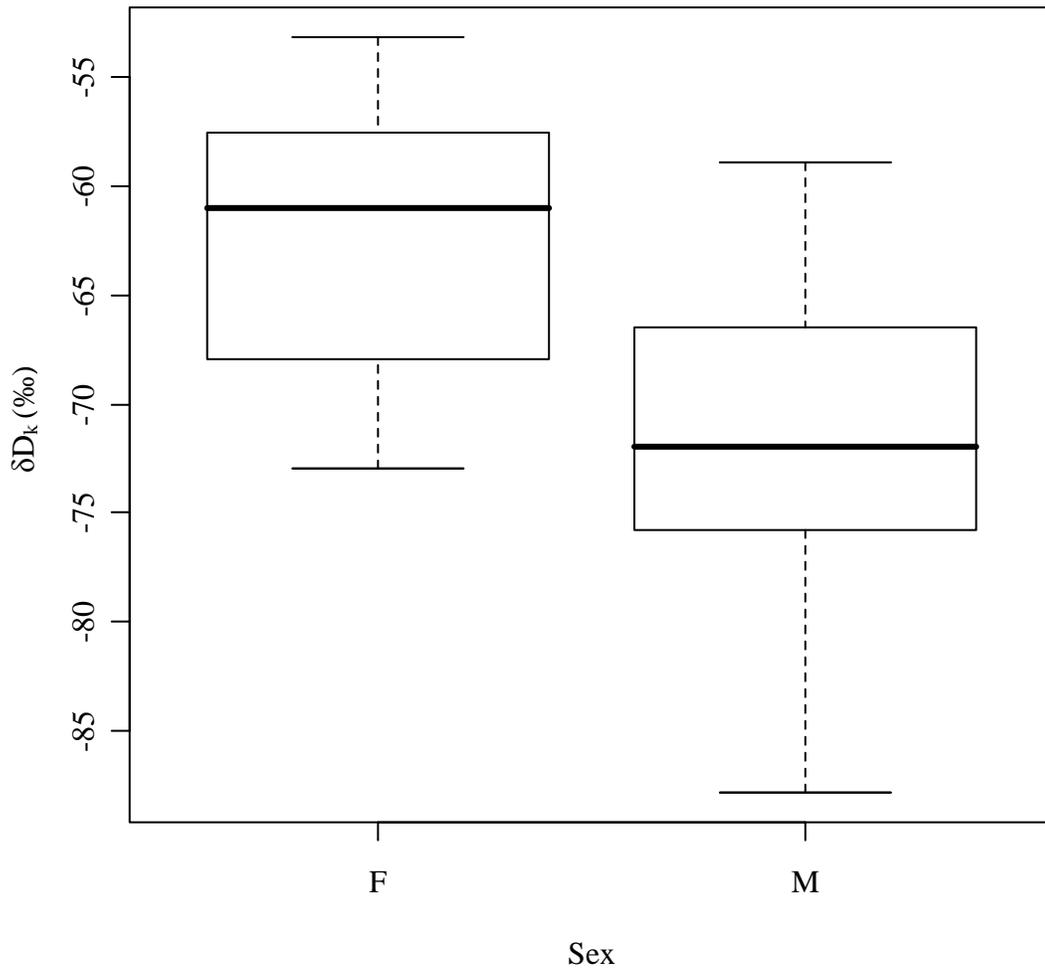


Figure 3.5. Boxplot illustrating claw hydrogen isotope signatures (δD_k , ‰) for female ($n = 9$) and male ($n = 35$) Ipswich Sparrows captured on Sable Island in 2007. Lines within boxes indicate median δD_k values, while the top and bottom of boxes indicate upper and lower quartiles respectively.

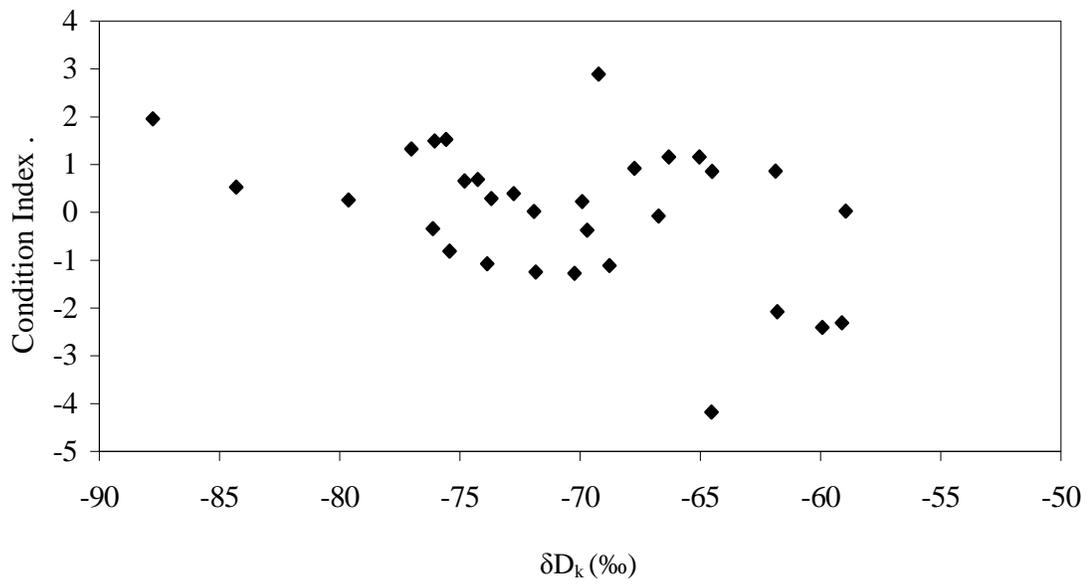


Figure 3.6. The relationship between condition index and δD_k for male Ipswich Sparrows captured in 2007 (n = 31).

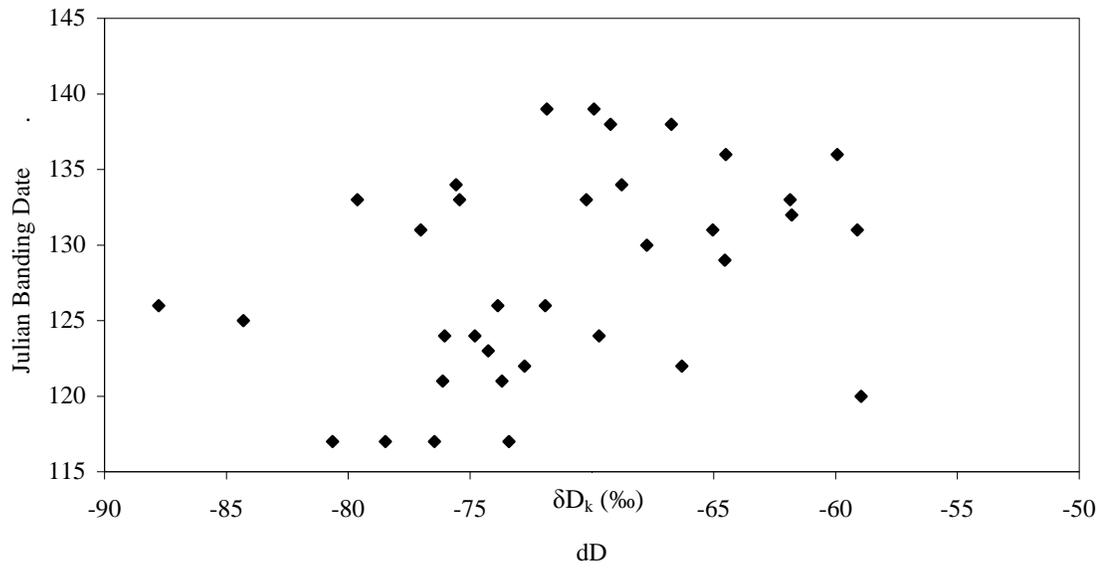


Figure 3.7. The relationship between banding date (a proxy for territory establishment date) and δD_k for male Ipswich Sparrows captured in 2007 ($n = 35$).

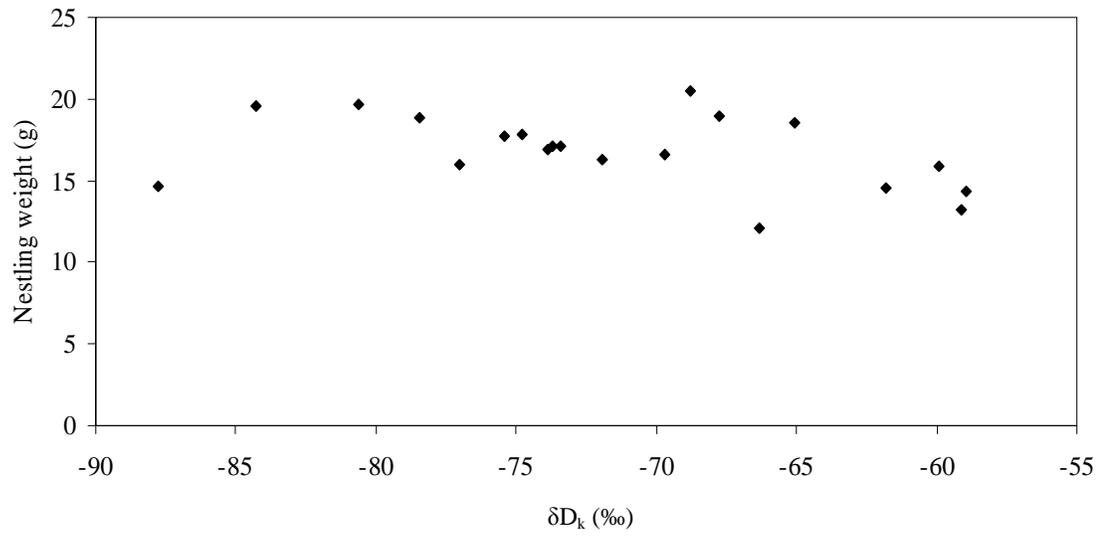


Figure 3.8. The relationship between mean nestling weight on day 7 (g) and δD_k for male Ipswich Sparrows captured in 2007 ($n = 20$).

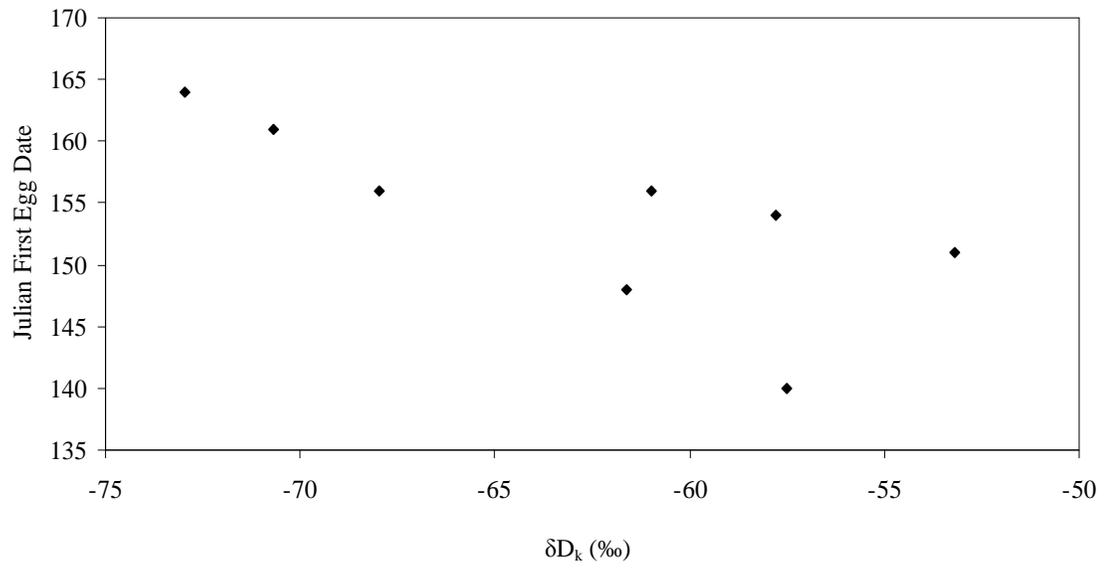


Figure 3.9. The relationship between first egg date and δD_k for female Ipswich Sparrows captured in 2007 ($n = 8$).

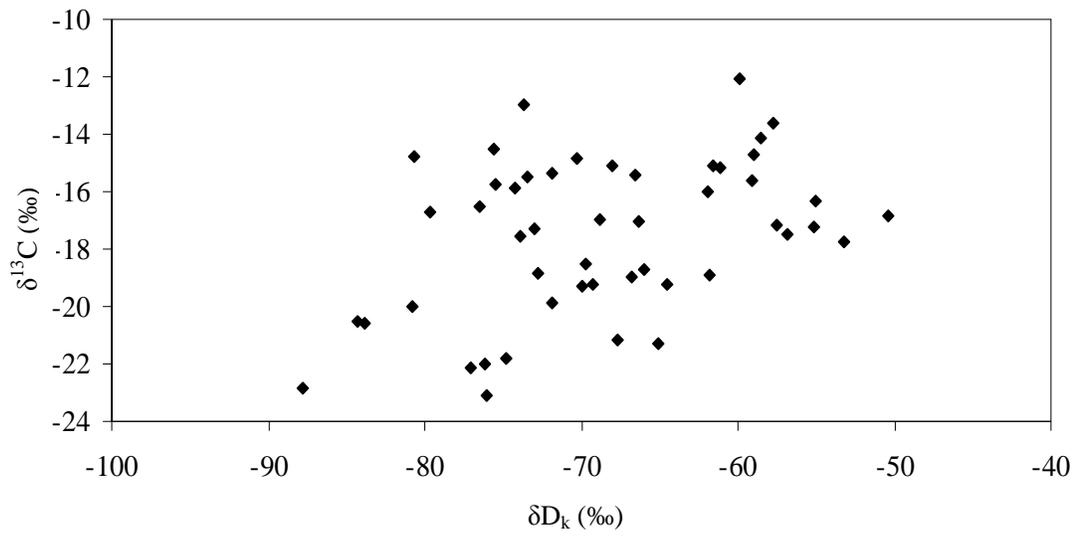


Figure 3.10. The relationship between claw carbon ($\delta^{13}C$, ‰) and hydrogen (δD_k , ‰) isotope signatures for Ipswich Sparrows captured in 2007 (n = 49).

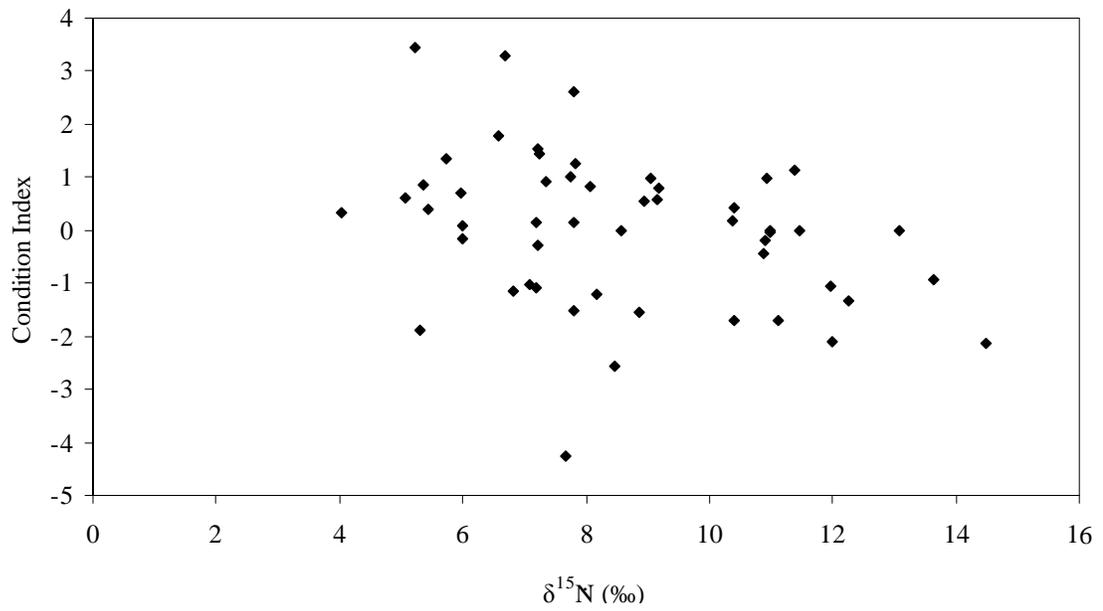


Figure 3.11. The relationship between claw nitrogen isotope signature ($\delta^{15}\text{N}$, ‰) and condition index for Ipswich Sparrows captured in 2007 ($n = 50$).

Discussion

Validating Hydrogen Isotope Analysis

Seven of the 11 Ipswich Sparrow feathers analyzed for sulphur stable isotopes had $\delta^{34}\text{S}$ signatures above the 10‰ threshold for detecting marine input (Lott et al. 2003). These values suggest marine input in the diet of at least some of the birds, which could distort the relationship between δD_k and δD_p . However, an alternative possibility is that the high $\delta^{34}\text{S}$ signatures observed may be the result of salt spray drying on the beach grass seeds ingested by the sparrows (Lott, pers. comm.), and thus δD_k values still reflect the δD_p signatures of winter locations.

There are several reasons to suspect that marine input is not a concern in this study, despite the results of the sulphur analyses. First, δD_f signatures of Ipswich Sparrow feathers grown on Sable Island were not significantly different from the expected value based on the growing season δD_p at this latitude, showing that feathers were still giving accurate information about location despite high $\delta^{34}\text{S}$ signatures. The variation seen in the δD_f values of these feathers (85% of observations within 6‰ of the mean) is similar to that predicted by Hobson (2005) and observed in a recent study by Langin et al. (2007). If marine input were distorting this relationship, I would expect feather δD_f signatures to be significantly higher than those expected for Sable Island and to show a greater degree of variation. Secondly, δD_f has been shown to accurately reflect wintering latitude in a recent study conducted in a similar system with possible marine input. Greenberg et al. (2007) conducted hydrogen stable isotope analysis on winter-grown feathers of Coastal Plain Swamp Sparrows (*Melospiza georgiana nigrescens*), which winter in coastal brackish habitats. Using the δD_f signatures of the feathers, they successfully located the previously unknown wintering grounds of the subspecies,

indicating that even a system with potential marine input, δD signatures may provide useful information about location.

Winter Location of Ipswich Sparrows

My results indicate that a high proportion of individuals sampled in 2007 (23 of 54) wintered in the northern part of the wintering range (40-44.5°N). This pattern differs from that found by the only other study conducted on the wintering range of this subspecies, in which the majority of individuals (94 of 107) were sighted in the middle portion of the range (35-40°N).

There are several possible explanations for the discrepancy between these results. First, because claws grow continually, the claws I collected might have incorporated isotope signatures from locations along the migration route, and hence reflected locations north of where the birds actually wintered. However, the winter distribution of Ipswich Sparrows found in my study is unlikely to be due to incorporation of δD signatures from outside the wintering grounds. If this were the case, I would expect birds caught later in the season to have more negative δD_k signatures. Instead, the opposite relationship was seen: birds caught later in the season tended to have more positive δD_k signatures (Figure 3.7).

Secondly, the sex ratio of the birds captured in my study might affect the observed winter distribution. My sample is heavily weighted towards males, with 35 of 44 known sex individuals captured being male; and analysis of δD_k values indicates that males winter further north than females (Figure 3.5). Therefore, due to the uneven sex ratio and the small proportion of the population sampled, it is unlikely that the winter distribution of my sample accurately reflects the winter distribution of the entire population. Similarly, the distribution observed by Stobo and McLaren (1971) may not

be an accurate representation of population winter distribution. In their study, the middle portion of the range was surveyed much more intensively than the northern or southern portions, and this difference in effort might have biased the results.

Another possibility is that the discrepancy between my study and that of Stobo and McLaren (1971) reflects real shifts in the winter distribution of Ipswich Sparrows. Northward range shifts have been observed for a variety of bird species, and have been linked to both climate change and local anthropogenic habitat disturbance (Valiela and Bowen 2003, Brommer 2004, LaSorte and Thompson 2007). The latter factor may be of particular importance to the winter distribution of Ipswich Sparrows, given that their coastal winter habitat is under high pressure from development (Crossett et al. 2004). However, my analysis of Christmas Bird Count data shows no trends in the latitude of the northern boundary or the centre of occurrence of Ipswich Sparrows over the past 36 years (Figure 3.3). These results suggest that there have been no systematic changes in the winter range of Ipswich Sparrows. Furthermore, while there was a significant trend over time in the centre of abundance of the Ipswich Sparrow winter range, it indicated a southward shift (Figure 3.4). The Christmas Bird Count data do not support the hypothesis that there has been a northward shift in the winter range of Ipswich Sparrows since 1971. It is more likely that the explanation for the discrepancy between my data and those of Stobo and McLaren (1971) lies in one or more of the methodological issues described above.

Stable isotope analysis also revealed that female Ipswich Sparrows wintered at more southerly locations than males (Figure 3.5). This result was unexpected, as a previous study of wintering Savannah Sparrows found no latitudinal pattern in sex ratio

(Rising 1988). However, differential migration according to sex, with females migrating further than males, has been observed in many migratory bird species (e.g. Dark-eyed Juncos (*Junco hyemalis hyemalis*), Ketterson and Nolan 1976; European Robin (*Erithacus rubecula*) Catry et al. 2004; White-throated Sparrows, Mazerolle and Hobson 2007), and several hypotheses have been advanced to explain this pattern. The ‘body-size hypothesis’ proposes that the largest individuals (normally the males) migrate the shortest distances, as larger individuals are more likely to be able to survive harsher winters (Ketterson and Nolan 1983). However, my results do not support this hypothesis as there was no relationship between winter location and size within sexes. The ‘arrival time hypothesis’ suggests that the sex responsible for establishing territories will migrate the shortest distance, in order to return earliest in the spring (Myers 1981). As male Ipswich Sparrows are responsible for territory establishment (Stobo and McLaren 1975), my data provide circumstantial support for this hypothesis. The ‘dominance hypothesis’ suggests that dominant males force subordinate females to migrate further (Gauthreaux 1978). However, while it is known that dominance interactions play a role in the settlement of winter territories (Marra 2000), there is little evidence so far suggesting that they cause the latitudinal segregation of sexes (Mazerolle and Hobson 2007). Finally, differential migration may be a consequence of differences in habitat preferences between the sexes (Catry et al. 2007); my results may provide some support for this hypothesis, as discussed below.

Effects of Winter Location on Breeding Performance

δD_k was significantly and negatively correlated with condition in males, suggesting that the distance males migrated affected the condition in which they arrived on the breeding grounds. Males with low δD_k signatures (those that wintered in the

northern portion of the wintering range) tended to be in better condition than those with higher δD_k signatures, possibly because their migration required less energy than that of birds wintering at southern locations (Berthold et al. 1992). In females, however, no relationship existed between δD_k and condition. This could be because at least some of the females we captured were likely gravid, which increased their mass and confounded my measurement of condition.

Males wintering in the northern part of the wintering range also established territories earlier than males wintering further south. Again, this is likely due to a shorter, faster migration resulting in earlier arrival (Bearhop et al. 2005, Mazerolle and Hobson 2005). Additionally, migratory cues such as longer photoperiods occur earlier at northern latitudes, possibly stimulating earlier migration (Berthold et al. 1992, Bearhop et al. 2005).

Early breeding has been associated with increased reproductive success in many species (e.g. American Redstarts, Marra et al. 1998, Norris et al. 2004a; European Blackcaps, Bearhop et al. 2005). Individuals that begin breeding earlier often produce larger clutches and fledge more offspring (Norris et al. 2004a, Bearhop et al. 2005), and breeding early is particularly important for Ipswich Sparrows, which are multibrooded and often raise as many as three or even four broods during the course of a breeding season (Stobo and McLaren 1975, Temple 2000). However, in this study δD_k was not correlated with the hatch date of the first clutch for males, suggesting that males that establish territories earlier do not necessarily produce nestlings earlier. Another advantage to breeding earlier, however, is that early breeders may obtain the best quality territories (Mitrus et al. 2006) which may then allow them to attract the best quality

females (Reid and Weatherhead 1990). The trend for northern wintering males to produce heavier nestlings (Figure 3.8) gives limited support to the hypothesis that Ipswich Sparrows that establish territories earlier get the best quality territories and mates, as it suggests males that winter further north produce higher quality offspring.

My data suggest that males wintering in the northern part of the winter range are in better condition and establish territories earlier than those wintering further south, and may also produce higher quality nestlings. However, the cause of this potential increase in reproductive success remains elusive: it is unknown whether males that winter at northern latitudes are in better condition and breed earlier due to a shorter migration and earlier arrival, or whether males that are inherently of high quality and in good condition are those that winter further north, as they can withstand harsher winter conditions.

Contrary to what I found for males, females wintering in the southern part of the wintering range may begin breeding earlier than those wintering further north (Figure 3.9). Females that wintered further south (those that had higher δD_k values) had significantly earlier first egg dates than those that wintered further north. As Ipswich Sparrows may produce as many as four broods in one season (Stobo and McLaren 1975), early first egg dates likely correspond to more time for additional broods and more nestlings produced over the course of the breeding season. Additionally, fledglings produced earlier in the season may be in better condition than those produced towards the end of the summer (Hochachka 1990, Norris 1993).

The pattern observed in females (southern wintering females breeding earlier) is somewhat counterintuitive, as the females that winter the furthest south also have the longest return flight and may arrive later than those wintering further north, with fewer

resources to devote to breeding (Bearhop et al. 2005). This pattern suggests that there are benefits associated with wintering at the southern end of the range that outweigh the costs of a longer migration. These results lend some support to the hypothesis that differential migration by sex is a result of differences in habitat or climate preference between the sexes (Catry et al. 2004, Catry et al. 2007, Mathot et al. 2007). In Ipswich Sparrows, males wintering in the northern part of the range may achieve higher reproductive success than those wintering further south; while females wintering in the southern part of the range may achieve higher reproductive success than those wintering further north. However, given the very small sample size of females in this study, results must be interpreted with caution.

Variation in Winter Diet

There were clear latitudinal trends in the type of plant material consumed by Ipswich Sparrows, as estimated by $\delta^{13}\text{C}$ values (Figure 3.10). Birds wintering further south (high δD_k values) tended to consume more C_4 plants, such as sea oats (high $\delta^{13}\text{C}$), than those further north. This pattern is likely due mainly to an increase in the proportion of C_4 plants available at southern latitudes (Kelly and Finch 1998), and supports previous reports of Ipswich Sparrow diets (Elliott 1968). The range of claw $\delta^{13}\text{C}$ values encompassed both values expected for birds feeding exclusively on C_3 plants (approximately -27 to -23‰, Hobson and Wassenaar 2000) and those expected for birds feeding solely on C_4 plants (approximately -16 to -12‰, Hobson and Wassenaar 2000). Birds that had δD_k signatures corresponding to the zone of overlap between marram grass and sea oats (Delaware to South Carolina, roughly -70 to -30‰) tended to have $\delta^{13}\text{C}$ signatures indicating they were consuming both C_3 and C_4 plants, suggesting that where both of these diet staples are available, the birds do not prefer one over the other.

The interpretation of Ipswich Sparrow claw $\delta^{15}\text{N}$ values is more problematic. The range of $\delta^{15}\text{N}$ values observed (4.02 to 14.5‰) spans three trophic levels, an unlikely result given what is known about Ipswich Sparrow diets. The lower portion of the range corresponds with what might be expected from birds dependent solely on plants, while the mid part of the range corresponds well with values found for Coastal Plain Swamp Sparrows ($10.8 \pm 0.4\text{‰}$), which consume arthropods (Greenberg et al. 2007). However, the higher $\delta^{15}\text{N}$ values (11.2 to 14.5‰) likely do not reflect actual trophic levels, as this would imply that Ipswich Sparrows are eating other secondary consumers. Several factors are known to cause ^{15}N enrichment, and hence high $\delta^{15}\text{N}$ values, among them anthropogenic nitrogen sources such as effluent from urban areas (Greenberg et al. 2007), and nutritional stress (Hobson et al. 1993). It is likely that both these factors are playing a role in shaping patterns of $\delta^{15}\text{N}$ in Ipswich Sparrows. The subspecies winters in some of the most developed areas of North America (Crossett et al. 2004), and thus exposure to anthropogenic nitrogen sources is likely. Additionally, data collected in this study suggests that $\delta^{15}\text{N}$ signatures are highest in individuals in poor condition (Figure 3.11), which may be an indication of nutritional stress. It is likely that these factors are confounding any relationships that might exist between δD_k and $\delta^{15}\text{N}$, and thus obscuring possible latitudinal patterns in diet. However, because $\delta^{15}\text{N}$ is correlated with condition, and condition is related to winter habitat quality in many species (Marra et al. 1998, Bearhop et al. 2004), nitrogen isotopes may still provide information about aspects of winter location.

Implications

Both male and female Ipswich Sparrows show evidence of carry-over effects of winter location: males that winter in the northern part of the range are in better condition and establish territories earlier than those wintering further south; while females that winter in the southern part of the range have earlier first egg dates than those wintering further north. This study adds to the growing body of evidence that winter location can impact reproductive success in migratory birds. This is one of the first studies, however, to show that carry-over effects exist in short-distance migrants, suggesting that even short migrations to relatively close wintering grounds can have significant implications for performance on the breeding grounds.

Ipswich Sparrows are a Species of Special Concern under the Species at Risk Act (SARA) (Environment Canada 2006). They are protected on the breeding grounds by the Sable Island Regulations of the Canada Shipping Act. However, the outer coastal dunes in which they winter are under development pressure throughout the winter range (Crosset et al. 2004). In order for conservation strategies for migratory birds to be effective, all important habitats used throughout the annual cycle must be protected (Norris et al. 2004a). One of the aims of this study was to provide information on Ipswich Sparrow winter distribution that might enable the informed prioritization of conservation efforts. Judging solely on distribution inferred from stable isotope analyses of hydrogen, efforts would be best concentrated in the northern parts of the range. However, isotope evidence also suggests that the females wintering in the southern parts of the range may have increased reproductive success; thus the conservation of this southern portion may also benefit the subspecies.

CHAPTER 4. CONCLUSION

Summary

The purpose of my study was to determine if and how a winter event (prealternate moult) and winter location impacted the breeding season in a short-distance North American migrant, the Ipswich Sparrow (*Passerculus sandwichensis princeps*).

Prealternate moult was considerably less common in Ipswich Sparrows than in other subspecies of Savannah Sparrow, and was seen in only 25% of individuals. There was evidence of a moult-breeding overlap, and stable isotope analysis suggested a possible moult-migration overlap (Chapter 2). However, prealternate moult did not affect reproductive success, and there was no relationship between the incidence of prealternate moult and winter location. These results suggest that partial prealternate moult may not be an energetically costly process. The pattern of feather replacement indicates that prealternate moult likely functions to replace feathers that have been degraded by exposure to sunlight.

My sample of Ipswich Sparrows wintered mainly in the northern and middle parts of the winter range, in contrast to the findings of the only study that has examined the actual distribution of Ipswich Sparrows on the wintering grounds (Chapter 3, Stobo and McLaren 1971). However, because males wintered further north than females, and my sample was male-biased, it is unlikely that my sample accurately represented the winter distribution of the entire population. I found evidence of carry-over effects of winter location on reproductive success for both male and female Ipswich Sparrows. Males that wintered further north were in better condition, established territories earlier, and tended to produce heavier nestlings than those that wintered further south. Conversely, females that wintered further south had earlier first egg dates than those that wintered in the

northern parts of the winter range. Only one aspect of diet was related to latitude: birds wintering further south had a diet based mainly on C₄ plants, while those to the north consumed more C₃ plants. Variation in nitrogen signature was not related to latitude and was more likely indicative of anthropogenic inputs and nutritional stress than trophic level. However, $\delta^{15}\text{N}$ signatures were negatively correlated with condition, and therefore have the potential to provide information about aspects of winter habitat quality.

Limitations of the Study

In this study, I inferred winter locations of Ipswich Sparrows based on known patterns of δD_p in North America, rather than ground-truthing tissue δD values throughout the wintering grounds. Consequently, there is some uncertainty associated with the assignment of individuals to winter locations. Several studies have shown that tissue hydrogen isotope signatures can vary by $\pm 6\%$ (Langin et al. 2007) or greater (Wunder et al. 2005) at a given location. There is also uncertainty associated with the calculation of δD_p values for specific locations based on large-scale patterns (Bowen et al. 2005, Hobson 2005). For these reasons, it has been suggested that determining location of origin for animals using stable isotope signatures should be done by assigning individuals to locations with known isotope values, rather than by predicting locations using known isotopic patterns (Wunder et al. 2005). My ability to determine winter location of Ipswich Sparrows would likely have been significantly improved had I been able to ground-truth hydrogen isotope values for tissue produced throughout the winter range of the subspecies.

In examining Ipswich Sparrow winter location, it would be particularly valuable to ground-truth tissues grown on Sable Island and on mainland Nova Scotia, in order to compare these signatures. Using only known patterns of variation in δD_p , I was not able to distinguish between birds that remained on Sable Island for the winter and those that migrated to the mainland. Climate can vary considerably between these two locations, and thus birds wintering on Sable Island experience very different winter conditions than those wintering on mainland Nova Scotia, with potential consequences for reproductive success. While it is unlikely that hydrogen isotope values would differ between these locations, as they are at similar latitudes, using multiple isotopes to develop an isotopic profile of locations may notably improve the ability to assign individuals to specific locations (Wunder et al. 2005). Sulphur isotope signatures in particular might be useful in differentiating between Sable Island and mainland Nova Scotia, as we would expect increased marine influence on Sable Island and thus higher $\delta^{34}S$ values (Kelly et al. 2005).

Finally, there was a significant sex bias in the sample of birds from which I collected claws. Males are easier to catch than females early in the season, and I caught many more males than females prior to the cutoff date for claw samples (20 May). As males appear to winter further north than females, my results do not provide a clear picture of the winter distribution of the subspecies. A larger, more balanced sample would prove invaluable in attempting to determine the winter distribution of Ipswich Sparrows using stable isotope analysis.

Future Work

A small proportion of the Ipswich Sparrow population does not migrate, instead remaining on Sable Island for the winter months. Historically, this proportion has been estimated at approximately 20% (Elliott 1968). However, there is some qualitative evidence that greater numbers of birds have been wintering on the island in recent years (G. Breed, Z. Lucas, pers. comm.). It remains unknown whether this is a reflection of the increase in population size over the past 40 years (Horn 2007), or whether a greater proportion of the population is becoming sedentary. This question is certainly worthy of further investigation, especially as a variety of anthropogenic influences are changing the migratory behaviour and winter ranges of a variety of migratory bird species (Berthold et al. 1992, La Sorte and Thompson 2007). Furthermore, because a proportion of the population winters on Sable Island, Ipswich Sparrows present an ideal system with which to compare the fitness benefits of migratory and sedentary lifestyles.

Finally, a longer term study of winter location in Ipswich Sparrows could provide insight into whether winter strategies remain the same from year to year, with individuals consistently wintering in the same locations, and whether juvenile birds tend to winter in similar locations as their parents.

Implications

This study reinforces the idea that in order to appreciate the forces shaping the ecology and behaviour of migratory bird species, we must understand the links between the various stages of the annual cycle. My results add to the growing body of evidence that winter location may impact reproductive success (Marra et al. 1998, Bearhop et al.

2004, Norris et al. 2004a, Saino et al. 2004, Bearhop et al. 2005), and is one of only a few studies showing that such effects may exist in short-distance migrants.

Ipswich Sparrows are a Species of Special Concern, and their winter range lies in an area that is under heavy pressure from development (Crossett et al. 2004). One goal of my study was to identify winter areas particularly important to the subspecies. The results of hydrogen stable isotope analysis suggest that the birds may be concentrated in the northern and middle portions of the winter range; however, further studies are necessary to determine whether this is representative of the winter range of the entire subspecies.

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