

**Northern Saw-whet Owls:
Migration and Population
Trends in Manitoba**

By

Christopher C. De Ruyck

A Thesis
Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements
For the Degree of

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Of

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Abstract

Little is known about the Northern Saw-whet Owl's distribution, or migratory behaviour within the prairie provinces. I examined saw-whet migration and population trends using the migration monitoring data collected by the Delta Marsh Bird Observatory (DMBO), Manitoba (2000-2007). Multiple regression suggested that populations were stable, however, the analysis had low power to detect trends. Correlation between saw-whet data from DMBO and the Manitoba Nocturnal Owl Survey suggested that population fluctuations were synchronized over large regions. Correlations between saw-whet owl and small mammal abundance from southeastern Manitoba suggested that saw-whet density and reproductive success were influenced by cycles of mammal abundance, which also synchronized over large regions. Finally, I used hydrogen isotope analysis on owl feathers to identify the latitudinal origins of saw-whet owls migrating through Delta Marsh. However, adult feathers showed large deuterium enrichment patterns, indicating that this technique cannot be used to track adult owl movements without further refinement.

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NORTHERN SAW-WHET OWL MIGRATION AND POPULATION TRENDS IN MANITOBA

CHAPTER 1 – INTRODUCTION

1.1 Background and Rationale

The northern saw-whet owl (*Aegolius acadicus*) is one of North America's most abundant forest owls (Rasmussen *et al.* 2008). It breeds throughout Canada's boreal forests, as well as farther south in mixed forest types and at moderate elevations from 1,000 to 10,000 feet. Despite their abundance, data on saw-whet owls are limited and population trends and migratory behaviour are poorly known throughout much of their range. This is especially true in the prairie provinces of Canada, which contain almost half of Canada's boreal forest habitat, but where monitoring efforts are sparse and there is little literature regarding saw-whet owl behaviour, population trends or distribution from within this vast area (Kirk and Hyslop 1998, Rasmussen *et al.* 2008).

Habitat alterations such as loss of mature forest (and suitable nesting cavities) through timber harvest, human encroachment, and climate-change induced outbreaks of insect pests and wildfire are increasingly affecting Manitoba's boreal forests (Manitoba Conservation 2005). These alterations can directly affect saw-whet owl populations (Johnson and Anderson 2003, Hinam and St. Clair 2008, Rasmussen *et al.* 2008).

Therefore, it is important to accurately monitor their distribution and population trends in Manitoba so that possible declines can be detected. This will encourage the timely development of conservation measures and research to mitigate threats to saw-whet owl populations.

To effectively conserve a migratory species, it is necessary to understand its migratory behaviour and the habitats used throughout its life cycle. Autumn saw-whet owl migration monitoring programs alone cannot link detected population trends with their underlying causes. This is because it is unknown from where the owls originate, and it is unknown whether yearly changes in the number of individuals migrating and the distance of migration are of significant magnitude to obscure actual population trends. This is a shortcoming of the few long-term migration monitoring programs in the prairie provinces, such as Delta Marsh in Manitoba, Last Mountain Lake in Saskatchewan, and Beaverhill, Inglewood Bird Sanctuary and Lesser Slave Lake in Alberta (www.bsc-eoc.org/national/cmmn.html). My research addresses this shortcoming by using stable-isotope analysis to identify the latitudinal origins (within $\approx 2^\circ$ latitude) of saw-whet owls that pass through Delta Marsh, Manitoba, in fall. This information links the population data collected from current migration monitoring to the geographical area from which migratory owls originate, and allows future research and conservation efforts to be focused towards areas experiencing declines.

Currently, two monitoring programs in Manitoba may be used to detect changes in saw-whet owl population numbers. The Spring Nocturnal Owl Survey (NOS) coordinated by Manitoba Conservation censuses territorial owls, including saw-whets, throughout southern and central Manitoba (Duncan and Duncan 1997). The Northern Saw-whet Owl Fall Migration-Monitoring program conducted by the Delta Marsh Bird Observatory (DMBO) monitors migrating saw-whet owls in the fall during the only constant effort trapping and banding program in Manitoba (den Haan and Grief 1999,

De Ruyck unpublished data). Band returns reported through the U.S. Fish and Wildlife office have provided evidence that owls breeding at least as far away as northern Alberta, and wintering as far south as southern Wisconsin, pass through Delta Marsh during migration (Bird Banding Laboratory 2008).

I assessed the population trends and migration patterns of saw-whet owls migrating through Manitoba by analyzing the 8 year DMBO data set. This analysis was complemented by a comparison with results produced by the Spring Nocturnal Owl Survey. Stable-isotope analysis was used to determine the geographic origins and breeding areas of saw-whet owls migrating through Delta Marsh. Combined, this research redresses our lack of understanding about saw-whet owl populations and migratory behaviour in Manitoba, and provides a basis for the development of future conservation programs and research.

CHAPTER 2 – LITERATURE REVIEW

2.1 Conserving Migratory Species

Knowledge of the movement patterns of migratory birds is vital to understanding their ecology and life-history traits, and is required for their effective conservation (Ralph *et al.* 1993, Bock and Jones 2004, Dunn 2005, Dunn *et al.* 2006). This is especially true of many boreal forest species, whose breeding ranges lie primarily north of the Breeding Bird Survey (BBS) coverage and other monitoring programs (Bart *et al.* 2004, Rich *et al.* 2004, Bart and Ralph 2005). For example, in Saskatchewan and Manitoba the northernmost BBS routes are located at 55-56° latitude, but occur at a lower density than farther south and provide sparse coverage of large areas of boreal forest habitat (www.pwrc.usgs.gov/BBS/routemaps).

Migration monitoring programs such as those working through project owlnet (<http://www.owlnet.org>) and the Canadian Migration Monitoring Network (CMMN, <http://www.bsc-eoc.org/cmmn.html>) are used for detecting trends in northern breeding saw-whet owl populations by counting individuals as they migrate south each fall. However, there is a general lack of knowledge about the geographic origins of birds captured during migration (Bart *et al.* 2004, Rich *et al.* 2004, Dunn 2005). Therefore, these programs alone cannot effectively direct conservation efforts, as it is difficult to link detectable population trends to specific geographic areas/habitats and possible underlying causes.

Linking migratory populations to their breeding grounds is further complicated because saw-whet owl populations in different regions vary in their breeding and

migratory behaviour. For example, saw-whet owls near the southerly limits of their breeding range in Idaho are nomadic, which is characterized by an absence of breeding in years with low prey abundance, and an abundance of owls and young produced in years of high prey abundance (Marks and Doremus 2000). Annual fluctuations are also observed as “irruptive” years, which primarily consist of large numbers of migrating juveniles and are occasionally recorded in the eastern United States and Canada (Weir *et al.* 1980, Duffy and Kerlinger 1992, Brinker *et al.* 1997, Whalen and Watts 2002). As well, saw-whets may exhibit a migratory strategy similar to boreal owls (*Aegolius funereus*), in which males winter on or near breeding territories and familiar nesting cavities, whereas females migrate in much larger numbers and winter farther south to be closer to stable food supplies (Korpimäki 1986, Korpimäki 1988, Duffy and Kerlinger 1992, Brinker *et al.* 1997, Erdman *et al.* 1997).

Differences in migratory behaviour can also result in differences in migratory timing among age and sex classes, for example, in eastern Canada female saw-whet owls were observed to migrate earlier than males in some years (Weir *et al.* 1980), perhaps due to the longer distances travelled. Young birds were also observed to migrate before adults in irruption years (Weir *et al.* 1980, Stock *et al.* 2006), which could be caused by increased competition for food (Newton 2006). In contrast, other researchers have observed little to no differences in migration timing among different age and sex classes (Mueller and Berger 1967, Duffy and Kerlinger 1992, Brinker *et al.* 1997). Effective saw-whet owl migration monitoring programs therefore require a clear understanding of saw-whet migratory behaviour and patterns to define where owls originate from, which

habitats are used when and by which demographic groups, and whether annual variability is of significant magnitude to obscure actual population trends.

Despite the saw-whet owl's abundance, "... much remains to be learned about its populations, distribution, and behaviour and breeding biology" (Rasmussen *et al.* 2008, p.1). This is especially true of western Canada, which contains approximately half of the continent's boreal forest breeding habitat. However, nocturnal owl populations are poorly monitored by existing multi-species surveys, such as the Breeding Bird Survey (Kirk and Hyslop 1998). As well, my literature search indicated that there is only one peer-reviewed publication in the literature regarding saw-whet owl migratory behaviour or migration monitoring data from within the prairie provinces. Therefore, it is important to learn more about saw-whet owl ecology, migration and population trends to enable their effective monitoring and conservation.

2.2 Sustainable Development Implications

There is a pressing need for this research because little is known about saw-whet owl population trends or distribution in the prairie provinces. Habitat alterations such as loss of mature forest (and suitable nesting cavities) through timber harvest, fire and insect pest outbreaks and climate change are becoming more widespread in Manitoba's boreal forests (Manitoba Conservation 2005). These changes may have direct effects (e.g., habitat loss) and indirect effects (e.g., altered prey abundance cycles) on saw-whet owl populations.

The research will also contribute towards several sustainable development issues present within Manitoba.

“Preventing species from becoming rare or at risk can be more cost-effective than recovery programs for species at risk” and “[w]e have little to no data on the population status or trends for the vast majority of species native to Manitoba.” (Manitoba Conservation 2005, p. 12).

It is important to accurately monitor the population trends of this owl so that declines are detected early. This will allow conservation efforts to be focused towards areas demonstrating declines and address potential threats to saw-whet populations, thus allowing greater flexibility in conservation measures.

“Conserving biodiversity is essential for maintaining the health of ecosystems and essential services they provide to human society.”(Manitoba Conservation 2005, p. 13).

This project will enable us to gauge the accuracy of saw-whet owl monitoring in Manitoba and assess their conservation status based on migration monitoring data. The study will indirectly contribute to broader biodiversity conservation efforts by expanding the available baseline information from which to derive measures of forest ecosystem health.

This research contributes to our knowledge of saw-whet migration in Manitoba and their distribution in the prairies, and provides baseline data to encourage future research. Dissemination of the project results to governments, conservationists and the public will generate environmental awareness, and better inform environmental and natural resource use decision-making processes.

2.3 Goals and Objectives

Goals

1. To quantify and understand the migratory behaviour and population trends of saw-whet owls breeding in and migrating through Manitoba.
2. To improve current monitoring programs to assess and track saw-whet owl population trends, distribution and conservation status within the prairie provinces.
3. To contribute towards sound natural resources management by broadening the available ecological data on which to base forest and resource use management decisions.

Objectives

1. Determine the population trends and migration patterns of saw-whet owls migrating through Delta Marsh, Manitoba, by analyzing the long-term migration monitoring data obtained from the Delta Marsh Bird Observatory (DMBO).
2. Determine the amount of agreement between annual changes in abundance estimates observed in the DMBO and Manitoba Nocturnal Owl Survey (NOS) data, and explore the extent and possible causes of regional variation in saw-whet owl abundance by comparing the DMBO and NOS data to small mammal population indices obtained from eastern Manitoba.

3. Determine the geographic origins of saw-whet owls that migrate through Delta Marsh and assess the degree of site fidelity and sex-biased migratory behaviour by analyzing feather samples using stable-isotope analysis.

The remainder of this thesis is divided into three chapters. Chapter 3 addresses objectives 1-2, and chapter 4 address objective 3, including background information, methods, results, and a discussion. Chapter 5 summarizes the research and explores saw-whet owl conservation strategies and future research based on the results.

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CHAPTER 3 - SAW-WHET OWL MIGRATORY BEHAVIOUR AND POPULATION DEMOGRAPHICS AND TRENDS IN MANITOBA

3.1 Abstract

The Northern Saw-whet Owl (*Aegolius acadicus*) is widespread throughout wooded areas of Canada and the northern U.S., however, very little is known about their population numbers, trends, or migratory behaviour within the prairie provinces. The Delta Marsh Bird Observatory (DMBO) has collected fall migration monitoring data on saw-whet owls since 2000. I examined saw-whet demographics and migratory timing using the DMBO data. I also examined trends in owl abundance over time using multiple regression and generalized linear models. The trend results suggest a stable saw-whet population migrating through Manitoba, however, large annual fluctuations in owl abundance resulted in a low power to detect relatively large trends. Comparison of the DMBO data to spring saw-whet abundance data available from the Manitoba Nocturnal Owl Survey correlated strongly, providing confidence that the annual owl abundance estimates are representative of actual changes in owl abundance, and suggests that population trends are synchronized over large geographic regions. I also observed a significant positive correlation between saw-whet owl and small mammal abundance from widely separated regions of Manitoba, suggesting that the breeding density and reproductive success of saw-whet owls is affected by annual cycles of small mammal abundance, which may synchronize over similar sized regions.

3.2 Introduction

The Northern Saw-whet Owl is endemic to North America, and breeds throughout Canada's boreal forests, as well as farther south in other forest types at moderate elevation from 300 to 3,000 meters (Rasmussen *et al.* 2008). Although saw-whet owls are considered numerous, with estimates of 50,000 to 150,000 pairs within Canada (Kirk and Hyslop, 1998), saw-whet owl demographic data are limited and population trends are largely unknown. Some data suggest that they are slowly declining due to increasing habitat loss (Kirk and Hyslop 1998, Rasmussen *et al.* 2008).

Habitat alterations such as loss of mature forest (and suitable nesting cavities) through timber harvest, human encroachment, and climate-change induced outbreaks of insect pests and wildfire are increasingly affecting Manitoba's boreal forests (Manitoba Conservation 2005). This can have direct and indirect effects on saw-whet owl populations (Johnson and Anderson 2003, Rasmussen *et al.* 2008, Hinam and St. Clair 2008). Therefore, it is important to accurately monitor their distribution and trends in Manitoba so that changes in population size can be detected. This will allow for the timely development of conservation measures and research to mitigate threats to saw-whet populations.

3.2.1 Saw-whet Owl Migration.- Each fall, many saw-whet owls breeding in northern latitudes migrate to wintering grounds in the eastern and southern U.S. (Holroyd and Woods 1975, Grigg 1992, Brinker *et al.* 1997, Rasmussen *et al.* 2008). Some populations of saw-whet owls are nomadic (Brinker *et al.* 1997, Marks and Doremus 2000), of a form that is characterized by low breeding and winter site fidelity, and large

annual variation in the extent, timing and number of migrating individuals, principally in response to fluctuating food supplies (Anderson 1980, Korpimäki 1987, Newton 2006). For example, Whalen and Watts (2002) found captured hatch-year saw-whet owls to have lower average mass during peak/irruptive years, which suggests a relationship between predator-prey density, its effect on owl body condition, and the number of owls migrating. Poor condition can also increase the length and frequency of stopovers during migration, while food abundance affects the time taken to replenish energy reserves (Cherry 1982, Whalen and Watts 2002).

Saw-whet owls may also exhibit a sex-biased migratory strategy similar to boreal owls (*Aegolius funereus*) where males winter on or near breeding territories (and nest cavities), and females and young migrate in much larger numbers and winter farther south to be closer to stable food supplies (Löfgren *et al.* 1986, Korpimäki 1987, Duffy and Kerlinger 1992, Brinker *et al.* 1997, Erdman *et al.* 1997).

Differences in migratory behaviour can also result in differences in migratory timing among age and sex classes, for example, in eastern Canada female saw-whet owls were observed to migrate earlier than males in some years (Weir *et al.* 1980), perhaps due to the longer distances travelled. Young birds were also observed to migrate before adults in irruption years (Weir *et al.* 1980, Stock *et al.* 2006), which could be caused by increased competition for food (Newton 2006). In contrast, other researchers have observed little to no differences in migration timing among different age and sex classes (Mueller and Berger 1967, Duffy and Kerlinger 1992, Brinker *et al.* 1997). Effective saw-whet owl migration monitoring programs therefore require a clear understanding of

saw-whet migratory behaviour and patterns to define where owls originate from, which habitats are used when and by which demographic groups, and whether annual variability is of significant magnitude to obscure actual population trends.

The annual fall saw-whet migration south provides an excellent opportunity to study these otherwise elusive owls, because many yearling and adult owls can be efficiently sampled over a short period. Mist-netting and audiolure techniques have been developed that allow large numbers of owls to be netted, banded, measured and released while en route to their wintering grounds (Duffy and Matheny 1997, Erdman *et al.* 1997).

Most information available on saw-whet owl migratory behaviour is generated through migration monitoring stations using standardized constant effort mist-netting protocols. Constant effort mist-netting is widely used to effectively monitor and detect population trends in many species of boreal forest breeding birds (Ralph *et al.* 1993, Dunn and Hussell 1995, Silkey *et al.* 1999, Ballard *et al.* 2003, Bart *et al.* 2004). There are approximately 97 stations collecting data on saw-whets throughout North America (<http://www.sawwhetnet.org>). They are distributed primarily along the great lakes and eastern seaboard, with fewer stations scattered throughout the prairies, the mid-western United States and the west coast. For example, there is one station in Manitoba, four in Saskatchewan, four in Alberta, one in British Columbia, one in Washington, four in Minnesota, one in Montana, and none in the Dakotas (total = 16; Figure 1).



Figure 1. Northern Saw-whet Owl Migration Monitoring Stations in Project Owlnet. (Location data from D. Brinker, www.projectowl.net)

The Delta Marsh Bird Observatory (DMBO) has the only saw-whet owl migration-monitoring program in Manitoba and is uniquely situated for studying large numbers of migrating saw-whets as they pass between Lake Manitoba and the large Delta Marsh. The DMBO is a member of the Canadian Migration Monitoring Network administered by Bird Studies Canada, has had a saw-whet owl migration monitoring program operating since 2000, and follows a standardized protocol used by banding stations across Canada and the U.S. (www.bsc-eoc.org/national/cmmn.html).

Data collected by DMBO permits a description of saw-whet owl demographics, population trends and migratory timing through Manitoba. Data from band returns reported through the U.S. Fish and Wildlife office have provided evidence that owls breeding at least as far away as northern Alberta, and wintering as far south as southern Wisconsin, pass through Delta Marsh during migration (Bird Banding Laboratory, 2008).

3.2.2 *Trend Estimates from Multiple Sources.*- The reliability of population trends estimated through migration monitoring programs can be assessed by comparison with data from other sources (Dunn and Hussell 1995, Bart *et al.* 2004, Bart 2005). For example, Dunn *et al.* (1997) found strong correlations between species trends estimated by constant-effort mist netting and trends estimated by the Breeding Bird Survey. I compared annual saw-whet owl abundance estimates from the DMBO analysis to estimates generated by the springtime Manitoba Nocturnal Owl Survey (Duncan and Duncan 1997).

The Manitoba Nocturnal Owl Survey (NOS) has collected data on several owl species (including saw-whets) since 1991 and provides a unique opportunity to compare eight consecutive years from an independent data set that is also tracking saw-whet owl population trends. However, the regions sampled by the two programs only partially overlap. Saw-whets sampled at DMBO originate from south and central Manitoba and eastern Saskatchewan (see Chapter 4), whereas the spring NOS mainly samples owls in southern Manitoba (Figure 2). It is also unknown whether saw-whets are on territory or still migrating when the NOS survey takes place. Therefore, some of the saw-whets counted in the spring may still be moving north to settle within breeding areas sampled by the DMBO monitoring.

To further examine the geographic scale of patterns observed in saw-whet owl abundance, I also compared DMBO and Manitoba NOS data to Saskatchewan NOS data (Alan Smith, pers. comm.). The regions sampled by the Saskatchewan NOS and DMBO data also partially overlap (Chapter 4); however, it is unlikely that the Manitoba and

Saskatchewan Nocturnal Owl Surveys are monitoring owls within overlapping regions, because the owl censuses are from widely separated areas at the same time in the spring.

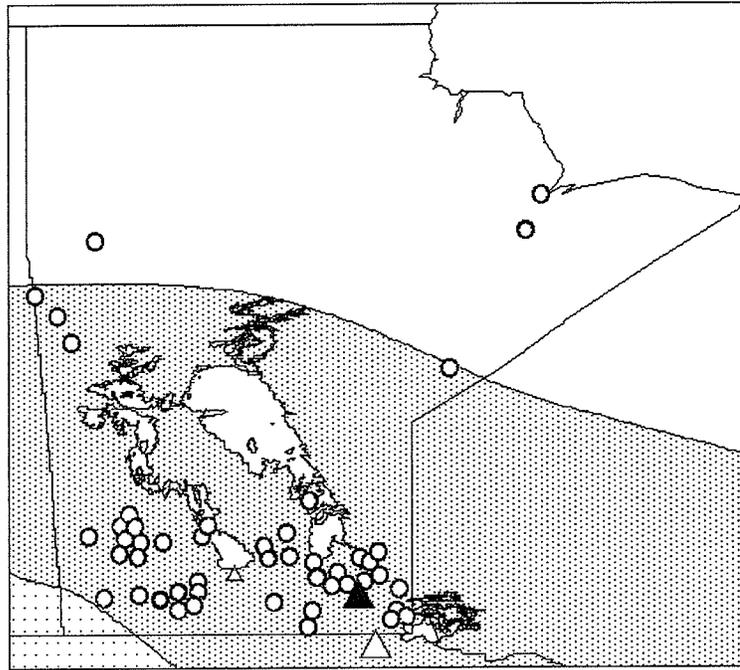


Figure 2. Manitoba Nocturnal Owl Survey transects and small mammal sites.
○ = Transect locations 2006 (Duncan *et al.* unpublished data).
▲ = Spruce Siding, small mammal trap site. △ = Roseau Bog, small mammal trap site.
Δ = DMBO. Dark stippling = Saw-whet owl year-round range. Light stippling = Saw-whet owl winter range. (Rasmussen and Sealy 2007).

A high correlation between the DMBO and NOS data sets would suggest that either both programs sample the same migratory populations, or that the populations sampled exhibited fluctuations that are synchronized over a relatively broad region. For example, population sizes of other holarctic owl species vary synchronously over large regions due to their relationship to cyclical prey (Korpimäki 1986, Sundel *et al.* 2004, Newton 2002, 2006). Alternatively, a weak correlation between the data sets would

indicate that the populations differ and the fluctuations observed are due to local prey abundance and habitat change, or that the fluctuations recorded by one or both programs do not indicate actual changes in owl abundance.

3.2.3 Relationship between Owl and Small Mammal Abundance.- Northern ecosystems such as the boreal forest exhibit 3 to 7 year productivity cycles, and rodent populations also are known to cycle synchronously in northern regions (Ranta *et al.* 1997, Cheveau *et al.* 2004, Sundell *et al.* 2004, Lima *et al.* 2006, Falls *et al.* 2007, Côte *et al.* 2007, Bowman *et al.* 2008). For example, the fruiting patterns of boreal conifer species can synchronize over regions 500-1000 km apart (Koenig and Knops 2000), which leads to a similar pattern in seed-eating mammals (Ranta *et al.* 1997, Lima *et al.* 2006, Falls *et al.* 2007). Mammal cycles synchronized over large regions may also influence the density of predators over similar geographic scales (Korpimäki 1986, Newton 2006).

Red-back voles (*Clethrionomys gapperi*), meadow voles (*Microtus pennsylvanicus*), and deer mice (*Peromyscus* sp.) are common breeding season diet items for saw-whet owls in the prairie provinces (Underwood and Sealy 2002, Priestly *et al.* 2005), as well as small birds, shrews (*Sorex* sp.), and jumping mice (*Zapus* sp; Rasmussen *et al.* 2008). However, reports of many varied prey items also suggest that saw-whet owls hunt opportunistically (Rasmussen *et al.* 2008).

Significant positive correlations have been observed among Manitoba and Wisconsin NOS indices and vole population indices pooled from southeastern Manitoba and Northern Minnesota, suggesting a close relationship between saw-whet owl abundance and prey density (Swengel *et al.* 2008). Comparing spring owl abundance to

fall mammal abundance is a valid approach as mammal abundance in the fall tends to covary with spring abundance, especially in high and low abundance years (Mihok *et al.* 1985, Falls *et al.* 2007). Similar relationships between prey and owl abundance have been described for other holarctic owl species (reviewed by Newton 2002, 2006) including saw-whet owls in northern Quebec (Cheveau *et al.* 2004, Côté *et al.* 2007). I compared DMBO fall migration saw-whet numbers to fall small mammal abundance data available from southeastern Manitoba to evaluate whether annual fluctuations in saw-whet numbers might be caused by population cycles in their prey abundance, and to evaluate whether these cycles are synchronous over large geographic areas.

3.3 Objectives

My objectives were to determine the population trends and migration patterns of saw-whet owls migrating through Delta Marsh, Manitoba, by analyzing the long-term migration monitoring data obtained from the Delta Marsh Bird Observatory (DMBO). I complimented this analysis by comparing the DMBO annual abundance estimates to those produced by the Spring Nocturnal Owl Survey. I also determined whether fluctuations in saw-whet owl numbers are related to fluctuations in their prey abundance by comparing DMBO fall indices to fall small mammal population indices from southeastern Manitoba.

Combined, this research redresses our lack of understanding about saw-whet owl populations and migratory behaviour in Manitoba, and provides a basis for the development of future conservation programs and research.

3.4 Methods

3.4.1 *Study site.*- The DMBO owl banding site lies on the south shore of Lake Manitoba (50°13'N, 98°21'W), on a treed ridge running east to west between the lake and the expansive Delta Marsh. From 2000 to 2004 the site was located where there were two 40-m wide ridges separated by an approximately 200-m wide back marsh. The nets were positioned on the southern ridge farther from the lakeshore. The vegetation mainly consisted of relatively short (<10 m) Manitoba maple (*Acer negundo*), bur oak (*Quercus macrocarpa*), peach-leaved willow (*Salix amygdaloides*), and choke cherry (*Prunus virginiana*). In 2005, the netting site was moved approximately 8 km west along the ridge to a permanent location near the University of Manitoba, Delta Marsh Field Station. The site is positioned on the 80-m wide single ridge between lake and marsh, approximately 50 m from the lake shore amid relatively taller stands (<25 m) of Manitoba maple, cottonwood (*Populus deltoides*), green ash (*Fraxinus pennsylvanica*), and peach-leaved willow.

3.4.2 *Migration Monitoring Protocol.*- Northern saw-whet owls were captured in mist nets using methods similar to those described by Project Owl-Net (www.projectowl.net.org/dunnowl.html). Each net site consisted of four 12-m long, 1.8-m tall, 60-mm gauge mist-nets, placed in a closed square around an audiolure. Four additional 12-m long, 36-mm gauge nets were placed on either side of the audio lure, two at 50-m distances east and west of the lure and two more at 100-m distances east and west.

The audio lure was an mp3 player connected to two speakers, which were placed 1 m off the ground, directed east and west, respectively, and approximately 30° upwards. The playback consisted of the monotonous male saw-whet territorial call interspersed regularly with short bouts of silence. The playback was played continuously throughout the netting period, at a volume that carried at least 200 to 300 m in moderate winds, and up to 2 km in calm conditions (De Ruyck, unpublished data). As the treed ridge in which the owls move is less than 200 m wide at both net sites, we expected that all owls on the ridge could hear the audiolure. Therefore, variation in hearing distance due to wind is unlikely to significantly bias our results, however, a small increase in catch-rate was expected at the latter site because the narrower ridge causes owls to pass closer to the nets.

We banded owls from 15 September to 31 October. These dates were calculated to encompass approximately 98% of the migratory passage based on data from 1999, 2000 and 2001 (P. Viola, unpublished data). Banding was conducted nightly, unless gusts of wind or precipitation would have affected the owls' safety. Nets were opened one-half to one hour after sunset and remained active for at least four hours. This period was the "standard" period and is consistent with owl banding protocols commonly used at other stations. Nets remained open beyond the standard period on nights of high, or expected high owl activity. The non-standard period aided in increasing the total number of owls banded and helped better estimate the number of owls migrating during large passage nights. Owls trapped during the standard period are referred to as "standard" owls, likewise owls caught during non-standard hours are "non-standard"

owls. Statistical analyses were restricted to standard owls to provide meaningful comparisons among years.

Nets were checked for owls every half hour 2000 to 2004. In 2005, the duration was increased to 40 minutes to accommodate the increased travel time between the banding lab and nets at the new site. The 40-minute period between net checks was well within standard owl netting protocols (<http://www.sawwhetnet.org>). During net checks, strict effort was made to keep the level of disturbance and time spent at the nets to a minimum. Owls were extracted from nets by trained personnel (University of Manitoba Animal Protocol # F06-034). Captured owls were conveyed in individual cloth bags to a nearby banding lab where the time of capture was noted. The owls were then banded with a size 4 "short-butt" U.S. Fish and Wildlife Service aluminium band, and sexed by a discriminant function using a combination of wing chord and weight (Brinker 2000). Wing chord was measured to the nearest 1.0 mm using a specialized wing chord ruler. Birds were weighed to the nearest 0.1 g using a digital scale and a customized "top-loading" container to constrain the bird briefly on the scale. The sexing criteria are at least 95% accurate (Leppert *et al.* 2006). Owls were then aged based on remex moult patterns described by Pyle (1997). Complete primary and secondary moult patterns were recorded for every bird. It was possible to accurately age most owls as either hatch-year (HY = hatched this year), second-year (SY = hatched last year), or after-second-year (ASY = hatched at least the year before last). After processing, owls were released out of doors onto the palm of the bander's hand, where they were allowed to adjust to the darkness and fly away at their leisure.

We recorded weather observations every half hour, which consisted of a temperature reading, estimates of wind speed and direction (Beaufort wind scale), cloud cover (clear, broken, obscured, heavy overcast,) and light/moon conditions (very dark, dark, average, bright and ultra bright).

Banding operations were developed and conducted by P.Viola (1999-2002) and C. De Ruyck (2003-2008) with the assistance of H. den Haan and volunteers throughout.

3.5 - Statistical Analysis

3.5.1 Migratory Behaviour.- I analysed differences in the timing and number of individuals migrating among different sex and age classes to assess whether males, females and young exhibit similar migratory timing or whether a difference exists that could indicate different migratory cues, speeds or travel distances. I calculated migration windows consisting of the 5th percentile, median, 95th percentile and peak migration dates (maximum nightly count) for each age/sex class using passage dates from all years to examine whether there are any observable differences in migratory timing. I also calculated annual migration windows for each age class for each year and used ANOVA to test whether a statistical difference existed in the 5th, 95th, and median migration dates among age classes.

I also examined the relationship between average owl body condition and observed stopover lengths (measured by recaptures), and between body condition and the number of young and adult birds captured each year. I used annual averages of individual mass/wing-chord indices (mass/wing-chord^{1.6929}) as a measure of average owl

body condition (Norberg 1981, Whalen and Watts 2002). I raised the wing chord to a scaling exponent equal to the slope of the relationship between $\log(\text{mass})$ and $\log(\text{wing-chord})$, which I calculated from the DMBO data (slope = 1.6929, $F_{1,1686} = 1034.94$, $p < 0.0001$). This method eliminates the residual correlation between body condition and wing chord and is robust to structural size differences among owls (Whalen and Watts 2002). I used Pearson correlation to examine the relationship between the average annual $\text{mass/wingchord}^{1.6929}$ index to the annual number of owls migrating per net-hour and to the number of hatch-year owls migrating per net-hour.

Finally, I tested for a bias in captures between males and females due to the audiolure by comparing proportions of owls of each sex captured in the “square” of nets around the audiolure, versus the proportion of owls of each sex captured in the 4 “passive” nets set at a distance from the audiolure. This test was also performed separately for each age class to determine whether the bias due to the audiolure differed between the age classes. For example, adult females (of reproductive age) may respond more to the audiolure than immature HY-females. The difference in captures between the square and passive nets may indicate a bias due to the audiolure, however, it is not a control that can be used to quantify this bias because the audiolure is easily heard at all nets and may have affected the catch-rate at the passive nets as well.

3.5.2 Foreign Recaptures.- I submitted band recovery information to the Bird Banding Laboratory, which provided us with details of the original capture of 10 owls recaptured at Delta Marsh but originally banded elsewhere (Bird Banding Laboratory, 2008, Appendix 1). I also occasionally obtained further information by sharing data with

other saw-whet monitoring stations on the project owl net list server

(www.projectowl.net.org/dunnowl). I examined the age and sex of foreign recaptures to assess migratory behaviour, distances, speed, and migratory routes/direction.

3.5.3 Comparison of Saw-whet Owl and Small Mammal Population Abundance Indices.-

I also analysed correlations between standardized DMBO saw-whet owl population indices and small mammal population indices to assess the degree of synchrony between saw-whet numbers and prey abundance. I obtained small mammal population indices from J. Duncan (pers. comm.), who calculated the indices from fall trapping efforts in southeastern Manitoba (Spruce Siding) and northeastern Minnesota (Roseau Bog) during the falls of 1986-2007 (Duncan 1987, Swengel *et al.* 2008). Trapping occurred in late September to mid-October and consisted of 300 stations, spaced 10 m apart at each site. Each station had one museum special snap trap, baited with peanut butter and monitored over 3 nights. Traps were checked each morning, trapped mammals were removed, and traps were reset/re-baited as required. The average trap nights/year was 1774.8 nights/year (range 1582-1814). Mammal indices were calculated as number mammals trapped per number of trap nights per year (Duncan 1987).

DMBO indices were calculated as number of standard owls per number of standard net-hours per year. I standardized small mammal and DMBO indices from each data set by converting them to z-scores, which have a normal distribution with a mean of zero and a standard deviation of one (Quinn and Keough 2002). Pearson correlations of standardized z-scores were used to measure their relationship to DMBO indices. A strong correlation would suggest that at a broad scale, small mammal

population cycles and saw-whet owl abundance is synchronous, and that small mammal population sizes may drive saw-whet owl populations.

3.5.4 Comparison of Fall Migration and Spring Calling Abundance Indices.- I

compared annual capture rates at DMBO to saw-whet owl call detection rates from the springtime Manitoba Nocturnal Owl Survey (NOS, Duncan *et al.* unpublished data).

Volunteers conduct the NOS survey annually in late March to early April, which consists of fixed listening stations spaced 1.6 km apart along a series of road transects. (Duncan and Duncan 1997). Volunteers started 30 minutes after sunset and finished at least 30 minutes before sunrise. The listening period was 2 minutes per stop and all owls detected were recorded. Volunteers surveyed on average 1378.7 km/year (range 946-2403 km; J. Duncan unpublished data).

I used Pearson correlation to quantify the correlation between annual fall-capture rates from DMBO and spring-density indices from the Nocturnal Owl Survey for the years 2000-2007. The DMBO abundance indices were the number of owls captured each year corrected for trap effort (# owl captures/net-hour). The NOS indices were the number of owls detected each year corrected for survey effort (# owls/km). Saw-whet indices available from the Saskatchewan Nocturnal Owl Survey from 2002-2007 were also included in this analysis. I standardized indices from the three data sets by converting them to z-scores, which are normally distributed with a mean of zero and a standard deviation of one (Quinn and Keough 2002). I then examined same year and lag-year correlations between the three sets of indices. I performed a *post hoc* power

analysis using G*POWER 3 (Erdfelder *et al.* 2007) to examine the power and sensitivity of the correlations to detect relationships between the datasets.

3.5.5 Population Trend Analysis.- I used multiple regression to examine annual changes in population numbers and age/sex class proportions over time using data collected at DMBO since 2000 following procedures described by Dunn and Hussell (1995, 2003) and Francis and Hussell (1998). I also did the same analysis using a generalized linear model (GLM), to compare the fit and results of the two modelling methods.

Both the regression and GLM methods involved modelling the relationship between nightly owl counts and the effects of day, year, and variables of wind speed and direction, temperature, and number of days to/from the new moon. Second-order and third-order effects of these variables were also explored (e.g., date^2 , date^3). The nightly count data are skewed due to the presence of many small count nights and a few large count nights. The large counts arise from combinations of weather and seasonal factors such as windspeed, cloud cover and lunar phase (Clark and Anderson 1997, Jobs 2002), and are more variable with less precise estimates than small counts. Therefore, the purpose of Dunn and Hussell's method is to reduce the effects of variability and error in large count nights and model an overall annual trend on all count nights. This model equation was then used to calculate annual population indices, which were analyzed with regression to measure the linear trend over time. These methods are consistent with other standard constant effort mist-netting analyses

(Dunn and Hussell 1995, Francis and Hussell 1998, Badzinski 2003) and generate trends in units comparable to the Breeding Bird Survey (Dunn and Hussell 2003, Dunn 2005).

3.5.6 Multiple Regression. - I used multiple regression to model nightly count data relative to effects of date, "date²", dummy variables for every year against a reference year and weather variables of wind speed, wind direction, date from new moon, "date from new moon²", and temperature using methods described by Dunn and Hussell (2003) and Farmer *et al.* (2007). I obtained weather data produced by the Environment Canada weather station located at Delta Marsh (<http://climate.weatheroffice.ec.gc.ca>). I supplemented missing data from this database with weather recordings taken during DMBO owl banding activities. Date and date² were centered on the median migration date to minimize the effects of collinearity (Quinn and Keough 2002). Date from new moon and (date from new moon)² were also centered. I calculated accumulated wind speed and direction by vector addition of 4 hourly wind measurements taken over the standard period for each count night. The accumulated wind speed variable was centered. I categorized wind direction into 4 variables of east, southeast, south, and southwest. Negative values of east, southeast, south and southwest correspond to westerly, northwesterly, northerly and northeasterly winds respectively. I calculated an index of temperature by averaging 4 hourly measurements taken during the standard period and subtracting it from the long term daily average calculated by Environment Canada (<http://climate.weatheroffice.ec.gc.ca>).

3.5.7 Model Selection and Fitting. - I fit the multiple regression model to count nights occurring within the 5th and 95th percentile migration window dates to avoid

possible negative values of expected nightly counts (Dunn and Hussell 2003). I calculated the dependent variable “nightly count” by dividing the number of birds captured for each night by the number of net-hours for each night to correct for effort. I multiplied the corrected count per unit effort by 1000 to obtain numbers greater than one. Migration count data generally exhibit a Poisson distribution (Dunn and Hussell 2003). Therefore, I transformed the effort-adjusted count variable by adding one and taking the natural log to approximate a normal distribution (Quinn and Keough 2002). I weighted the multiple regression model with each count night weighted by its net-hours relative to the total number of net-hours across all years. Weighting the regression model accounted for variability due to uneven trap effort (Dunn and Hussell 2003).

I did not want to include unnecessary parameters in the Dunn and Hussell model (2003) that did not contribute significantly to the models fit. Therefore, I compared Akaike’s information criterion (AIC) values of variables within the model to choose the model with the lowest AIC (Burnham and Anderson 2002). The variables “date³”, “temperature”, “date from new moon”, and “date from new moon²” were not included in the multiple regression. The variable (date)³ increased AIC by 1.924, temperature increased AIC by 1.877, date from new moon increased AIC by 1.150, and (date from new moon)² by 1.386. The wind speed and wind direction variables were included in the model as their inclusion decreased AIC by 10.579.

I calculated average annual owl abundance indices (relative to a reference year) from the model by entering mean values for each variable into the model equation +/- the slope estimate for each year’s dummy variable. I added half the variance to each

year's index calculation so that the index value represents the mean number of birds and not the median (Dunn and Hussell 2003). I back-transformed annual indices from the log scale and subtracted one to put the indices in the form of real bird numbers. Indices were then log-transformed again (without adding one) to put the indices back into the log-linear scale of proportionate rate of change per year (Dunn and Hussell 2003).

Finally, I fit a linear regression model to the log-transformed indices with year as the independent variable to obtain the annual proportion of linear change in population over the eight years of monitoring. The distribution of residuals for all analyses were examined using diagnostic plots.

I performed this analysis individually on counts of HY, SY, and ASY birds to calculate trends of the different age classes separately and to explore demographic variability in trends. However, it is difficult to define what a biologically significant population trend is. For example, a small annual decline will become ecologically significant given enough time; conversely large trends over the short term likely have ecological significance, but may be stable over the long term (Reed and Blaustein 1996). Therefore, as recommended by Thomas (1997), I calculated confidence intervals to demonstrate the amount of certainty for each trend estimate, and I used TRENDS (Gerrodette 1993) statistical software to perform a *post hoc* power analysis. I used variance terms estimated from the regression of abundance indices on year and calculated the model's statistical power ($1-\beta$) of detecting annual population changes of 10% and 5% per year at a significance of $\alpha = 0.1$. I also calculated the number of years required for the model to achieve a power = 0.8 at $\alpha = 0.1$. I selected an *a priori*

significance of $\alpha = 0.1$ in the trend analysis to lower the probability of Type II error.

From a species conservation standpoint I considered there to be a less serious biological consequence for making Type II errors (falsely concluding there is no significant trend; Quinn and Keough 2002). Also note that the power analysis was based on the t -distribution and only applies to the power of detecting a linear trend over time in the annual indices with linear regression. The power analysis did not incorporate error associated with the calculation of saw-whet owl abundance indices from the multiple regression model.

3.5.8 Generalized Linear Model.- I also performed the above analyses using a generalized linear model (GLM) instead of multiple regression to explore the usefulness/appropriateness of GLMs for analysing this type of data and to compare the model fit and results of the two modelling methods. A GLM may provide a better fit to the data because it does not require the dependant variable to have a normal distribution and can model other distributions such as Poisson (Quinn and Keough 2002). Therefore, the GLM does not require log transformation of the nightly-count variable to approach normality prior to analysis. The scale units of the annual indices produced by the GLM are not equivalent to those produced by the multiple regression. However, the slope of the regression line through the annual indices will be directly comparable as they both represent proportionate change on a log-linear scale.

3.6 Results

3.6.1 *Population Demographics of Migratory Saw-whet Owls.*- A total of 1,691 saw-whet owls was banded at DMBO between 2000 and 2007. Of these, 1,324 (78.3%) were captured during the nightly standard period. There were also 76 same-year recaptures, and 10 owls recovered at DMBO but previously banded elsewhere (Table 1).

Table 1. Annual counts of saw-whet owl age and sex, banded at Delta Marsh, Manitoba, 2000-2007.

Year	HY	SY	ASY	AHY	Female	Male	Unknown	Total
2000	145	24	16	2	123	23	41	187
2001	56	38	16	4	84	10	20	114
2002	44	25	10	1	59	5	16	80
2003	63	31	7	5	70	14	22	109
2004	68	35	20	2	89	9	27	125
2005	134	57	23	13	165	26	36	227
2006	194	64	27	3	200	25	68	288
2007	103	59	28	4	133	20	41	194
Total	807	336	147	34	922	132	270	1324

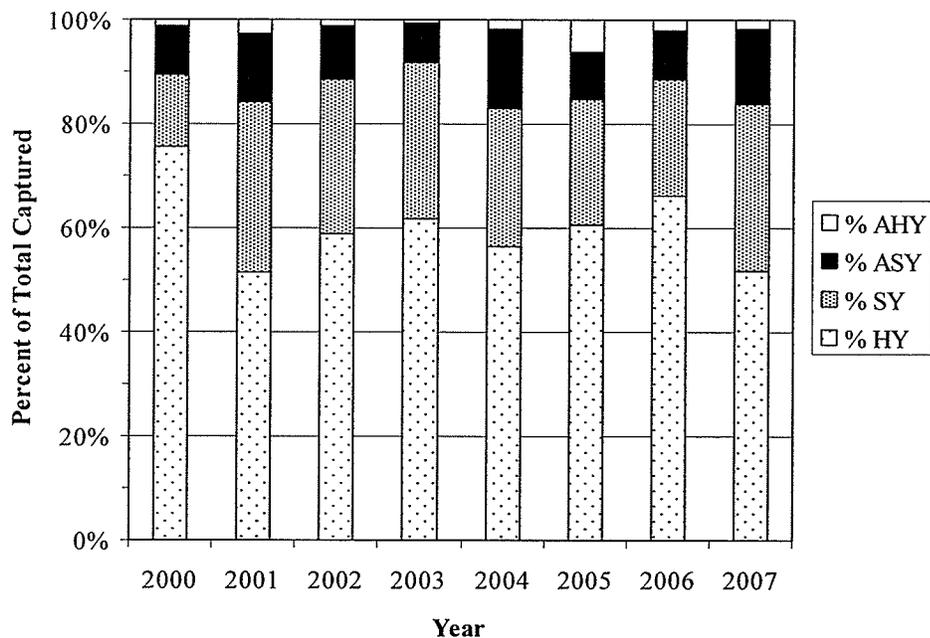


Figure 3. Age distribution of saw-whet owls, Delta Marsh, Manitoba, 2000-2007. HY = hatch year, SY = second year, ASY = after second year, AHY = after hatch year.

In total, 61% of owls captured were HY, 25.4% were SY, 11.1% were ASY, and 2.6% were AHY (unknown age adult owls that may be SY or ASY). Though the total number of owls within each age class varied considerably among years (Table 1), age-class proportions were more consistent, with annual averages: HY = 59.3 %, SD = 7.9, SY = 26.46 % SD = 6.2, and ASY = 11.4 %, SD = 2.8, $n = 8$ years (Figure 3).

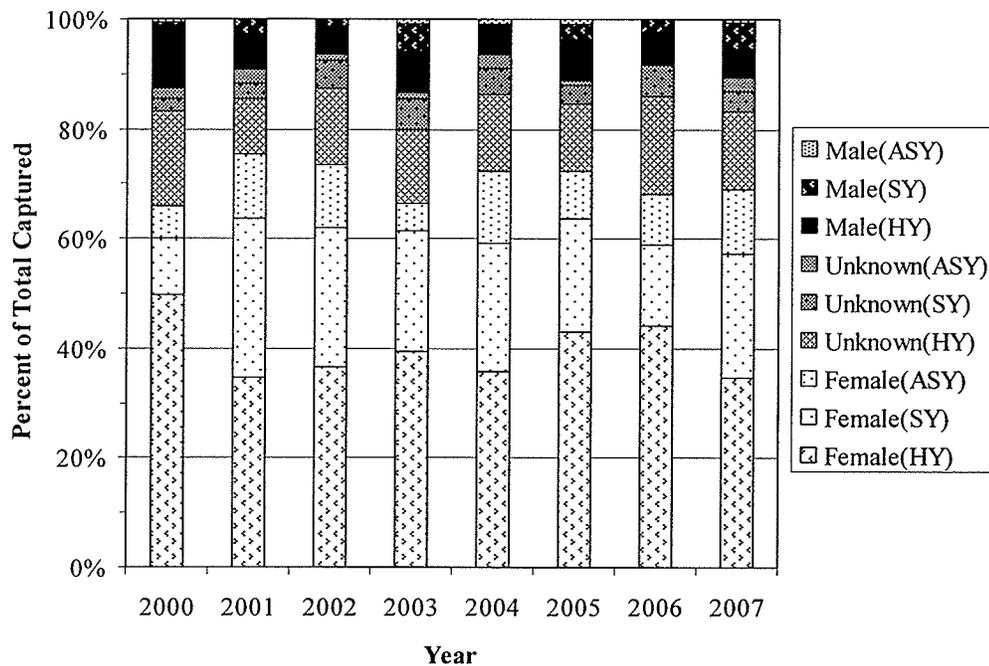


Figure 4. Proportions of sex accorded to age class of saw-whet owls, Delta Marsh, Manitoba, 2000-2007. HY = hatch year, SY = second year, ASY = after second year.

I identified 69.8% of captured owls as female, 9.8% as male, and 20.1% as indeterminate. This pattern was consistent among years, mean = 69.8% female, SD = 2.3, $n = 8$ years (Figure 4). These proportions varied between owls captured in nets surrounding the audiolure (relatively more females) and those captured some distance from the audiolure (relatively fewer females and more of unknown sex), which indicates

that passive and audiolure nets captured a different sub-sample or proportion of the migrating population (Table 2). However, the proportions are skewed towards females in both cases. Females are also more common in the adult age classes than in HY birds and there are fewer adults of unknown sex (Table 3).

Table 2. Proportions of male and female saw-whet owls captured in Passive vs. Audiolure nets, Delta Marsh Bird Observatory, Manitoba, 2000-2007. Passive nets not adjacent to audiolure; Audiolure nets adjacent to audiolure.

Sex	Passive Nets (<i>n</i> = 396)		Audiolure Nets (<i>n</i> = 928)	
	<i>n</i>	%	<i>n</i>	%
Male	53	13.35	80	8.61
Unknown	97	24.43	172	18.51
Female	246	61.96	676	72.77

Table 3. Sex proportions (%) of saw-whet owls by age class, Delta Marsh, Manitoba, 2000-2007

Sex	HY		SY		ASY	
	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>
Male	11.59	94	8.98	30	3.85	6
Unknown	23.19	187	14.66	49	13.19	19
Female	65.22	526	76.36	257	82.97	122

3.6.2 Migratory Timing.- The median migration date among all years was 8 October, and the dates corresponding to the 5th and 95th percentiles of owl passage were 23 September and 25 October, respectively (Figure 5, Table 4). The earliest median migration date was 5 October, which occurred in both 2002 and 2004, and the latest median migration date was 10 October, in 2005. Annual differences in the 5th and 95th percentile migration periods were of similar magnitude. The overall median migration dates for all age and sex classes fell between 7 October and 9 October (Table 4). There

were no significant differences in annual median migration date among HY, SY and ASY-owls ($F_{2,22} = 0.6497, p = 0.5324$).

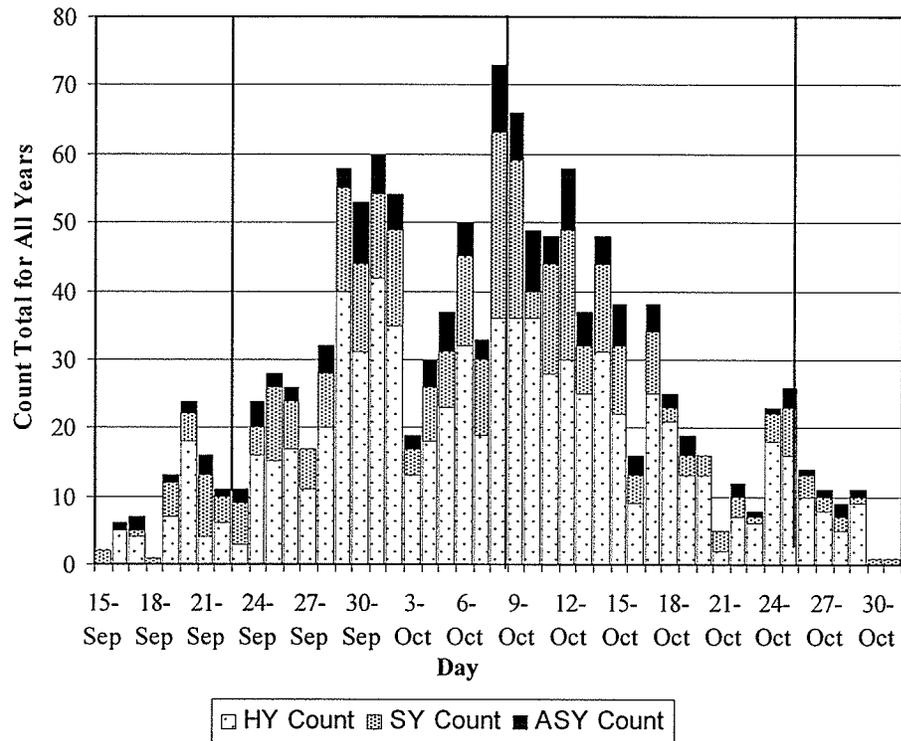


Figure 5. Nightly saw-whet owl captures by age class (hatch year, second year, after second year), Delta Marsh, Manitoba, 2000-2007. Lines = 5th, median, 95th quartiles.

Table 4. The 5th, Median, 95th and Peak Migration nights of saw-whet owls, Delta Marsh, Manitoba, 2000-2007.

Age-Sex	5th	Median	95th	Peak
Female	21-Sep	8-Oct	26-Oct	8-Oct
Male	24-Sep	9-Oct	26-Oct	9-Oct
HY	21-Sep	8-Oct	25-Oct	1-Oct
SY	21-Sep	7-Oct	25-Oct	8-Oct
ASY*	21-Sep	8-Oct	25-Oct	8-Oct
Female SY	21-Sep	8-Oct	24-Oct	8-Oct
Male SY	25-Sep	8-Oct	25-Oct	9-Oct

*ASY is not divided by sex because only 6 ASY males were captured.
 HY=hatch year, SY=second year, ASY=after second year.

3.6.3 *Saw-whet Owl Recaptures and Stopover Time.*- We recaptured relatively few owls on subsequent nights of the same year. In total, 76 owls were recaptured, which was 5.7% of all owls captured from all years (Table 5); 68.4% of the recaptures were HY, 22.4% were SY and 9.2% were ASY. In addition, 71.1% of the recaptures were female, 7.9% were male and 21.1% sex was not determined. These values are similar to the proportion of original captures.

Table 5. Saw-whet owls retrapped at Delta Marsh, Manitoba, 2000-2007.

Year	Retraps	Female	Male	Unknown	HY	SY	ASY	Foreign Recoveries
2000	14	7	1	6	13	0	1	1
2001	8	8	0	0	2	6	0	0
2002	13	11	1	1	11	2	0	2
2003	7	2	2	3	6	1	0	1
2004	9	4	1	4	6	3	0	1
2005	0	0	0	0	0	0	0	3
2006	11	9	1	1	6	1	4	0
2007	14	13	0	1	8	4	2	2
Total	76	54	6	16	52	17	7	10

Of the retrapped owls, 51% were caught the following night, and 73% were caught within 3 nights, which suggests that owls stopping over at Delta Marsh typically stay for a minimum of 1-3 days.

A change in mass was frequently observed between subsequent captures. The average weight change between recaptures was +0.29g SD = 9.99 as many birds lost weight between captures as well as gained weight. The average magnitude of weight change between captures was 3.67g SD = 3.94. The number of re-traps each year was too small and variable to allow meaningful comparisons of annual weight change and stopover duration with the number of owls caught/net-hour.

Only 2 owls were recaptured in a subsequent year at DMBO. An SY-female was recaptured 4 October 2004 and originally banded as an HY on 5 October 2003, and another SY-female was recaptured 13 October 2008 and originally banded a HY on 10 October 2007. In addition, 10 owls that had been banded previously at other locations were recaptured at DMBO (Figure 6; Appendix 1). All but one of the foreign recaptures at DMBO were female.

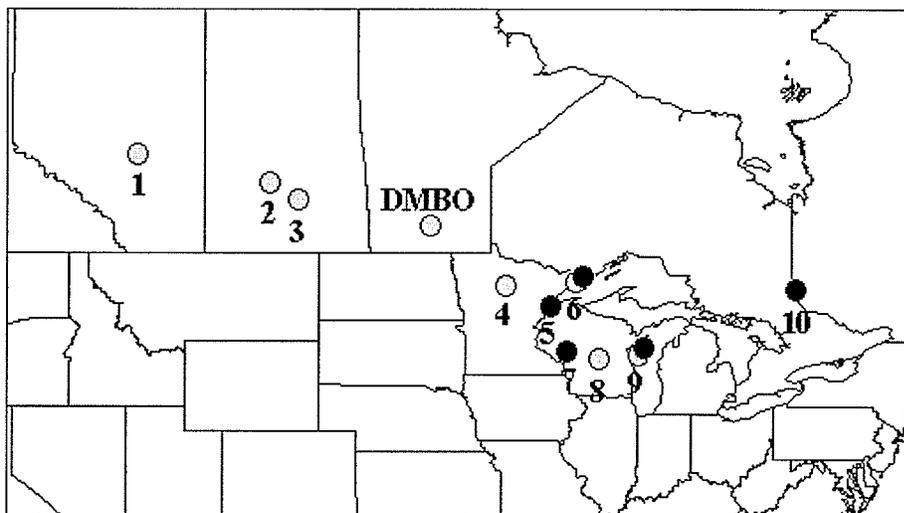


Figure 6. Foreign recaptures of saw-whet owls, Delta Marsh, Manitoba, 2000-2007. 1 – Opal, Alberta. 2 – Dalmeny, Saskatchewan. 3 – Last Mountain Lake, Saskatchewan. 4 – Dora Lake, Wisconsin. 5 – Linwood Springs, Wisconsin. 6 – TOFTE, Minnesota. 7 – Beaver Creek, Wisconsin. 8 – New Rome, Wisconsin. 9 – Little Suamico, Wisconsin. 10 – Ville-Marie, Quebec. ○ = Owls banded elsewhere and recaptured at Delta Marsh. ● = Owls banded at Delta Marsh and recaptured elsewhere.

A female owl recaptured in 2004 is noteworthy as it was first captured 20 days earlier near Dalmeny, Saskatchewan, approximately 630 km away (Figure 6). This equates to an average movement of 31.5 km per night assuming a straight East-South-East course. Another DMBO banded female was recovered 19 September 2006 near

Duluth, MN and then re-trapped 24 October 2006, near Beaver Creek, Wisconsin. This translates into an average movement of 14.4 km per night assuming a straight South course. Finally, a female banded 20 September 2006 at DMBO was re-trapped 21 October 2006 near Duluth, Minnesota, translating into an average of 18.6 km per night assuming an East-South-East course. Similar movement rates have been observed around the Great Lakes and along the east coast (Brinker *et al.* 1997).

3.6.4 Annual Fluctuations in Saw-whet Owl Abundance.- The total standard owls captured per year ranged from 80 - 293. This variation in owl numbers is largely attributable to the number of HY birds captured (Table 1). Overall, I observed a high-low-high cycle in the number of captured owls with six years between the high of 2000 and the peak in 2006. The two high points in the cycle corresponded to the greatest number of HY-birds caught (Table 1) and greatest proportion of HYs: 2000 = 77.5% and 2006 = 67.4% (Figure 3). The year following each high (2001 and 2007) showed moderate number of HYs caught and the lowest proportion of HYs (49.1% and 53.1%, respectively) due to the larger proportion of adult owls caught (Figure 3), which are presumably surviving SY-birds from the high productivity of the year before. The ASY category does not display a similar 2-year lag because the age class is made up of variously aged adult birds.

The average owl mass/wing-chord^{1.696} index was similar among years: min = 0.0212, max = 0.0217, SD = 0.00026, and did not correlate significantly with the annual number of owls caught/net hour (Pearson $r = 0.0659$, $p = 0.8767$, $n = 8$).

3.6.5 Relationship between Saw-whet Owl Migration Numbers and Small Mammal

Population Indices. - Small mammal population indices derived from southeastern Manitoba (Spruce Siding) were significantly correlated with the DMBO data. Total small mammal indices from Spruce Siding showed similar peaks in 2003 and 2006, as well as a peak in 1999, the year previous to the start of DMBO monitoring (Table 6; Figure 7). Individual species of small mammals showed slightly weaker correlations with DMBO saw-whet owl indices. Indices of mammal species from the Roseau Bog site were not significantly correlated with DMBO saw-whet owl indices, however meadow voles were near significant (Table 6). The power of the DMBO and Small Mammal indices to detect a correlation of 0.7295 is $1-\beta = 0.69$, $\alpha = 0.05$. Power analysis also indicated that a sample size of 11 years is required to achieve a power of $\beta = 0.80$ for this analysis. Finally, this analysis had a power of $1-\beta = 0.972$, to detect a perfect correlation.

Table 6. Pearson correlation of Delta Marsh saw-whet owl indices and small mammal indices (Duncan, unpublished data), Manitoba and Minnesota, 2000-2007.

Species	Spruce Siding, MB		Roseau Bog, MN	
	<i>r</i>	<i>p</i> -value	<i>r</i>	<i>p</i> -value
Total Small Mammals	0.7295	0.0404	0.2452	0.5583
Red-backed Vole	0.6959	0.0553	-0.0337	0.9369
Meadow Vole	0.6399	0.0875	0.5556	0.1528
Shrews	0.6945	0.0559	0.3219	0.4368

Correlations with mammal indices were also analysed with owl indices separated by age class into HY, SY and ASY. HY indices showed slightly stronger correlation with Spruce Siding data ($r = 0.7352$, $p > 0.0377$; appendix 2). SY owls showed weaker non-significant correlation ($r < 0.61$, $p > 0.10$; appendix 3), except with shrews ($r =$

0.6515, $p = 0.0801$). ASY indices showed very little correlation to Spruce Siding data ($r < 0.21$, $p > 0.61$).

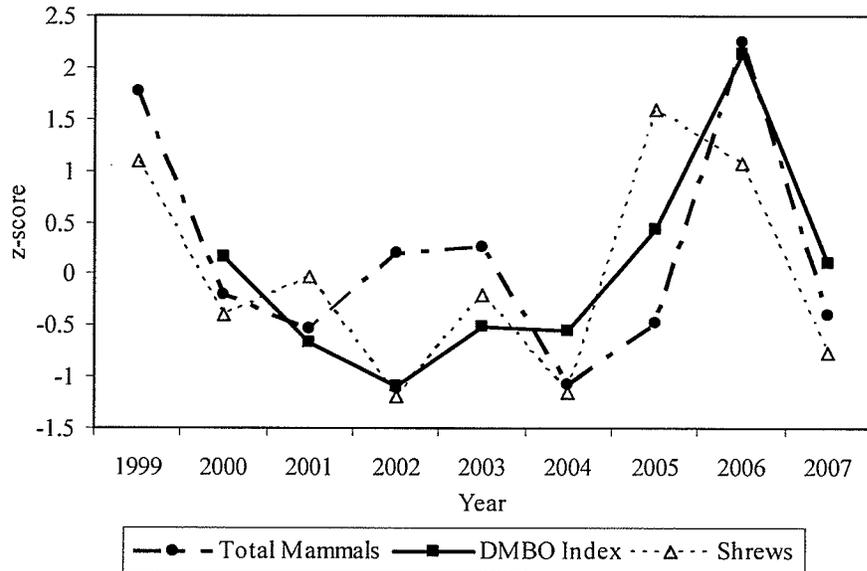


Figure 7. Standardized abundance indices of saw-whet owls at Delta Marsh, total small mammals (including shrews), and shrews at Spruce Siding, Manitoba, 1999-2007.

Lag year indices (this year's mammal index with the following year's owl index) showed little to no correlation for all sites, owl age classes and mammal species ($r < 0.29$, $p > 0.51$), except with shrews. Shrew indices showed a weak correlation (nonsignificant) with next year's saw-whet owl indices ($r = 0.5995$, $p = 0.1547$, $n = 6$ years).

3.6.6 Relationship between Saw-whet Owl Fall Migration Numbers and Spring

Abundance.- Annual abundance indices of the Manitoba Nocturnal Owl Survey (NOS) and the DMBO Migration Monitoring program were correlated. Both indices showed similar amounts of annual variation, and both showed the same 6-year high-low-high cycle (Figure 8).

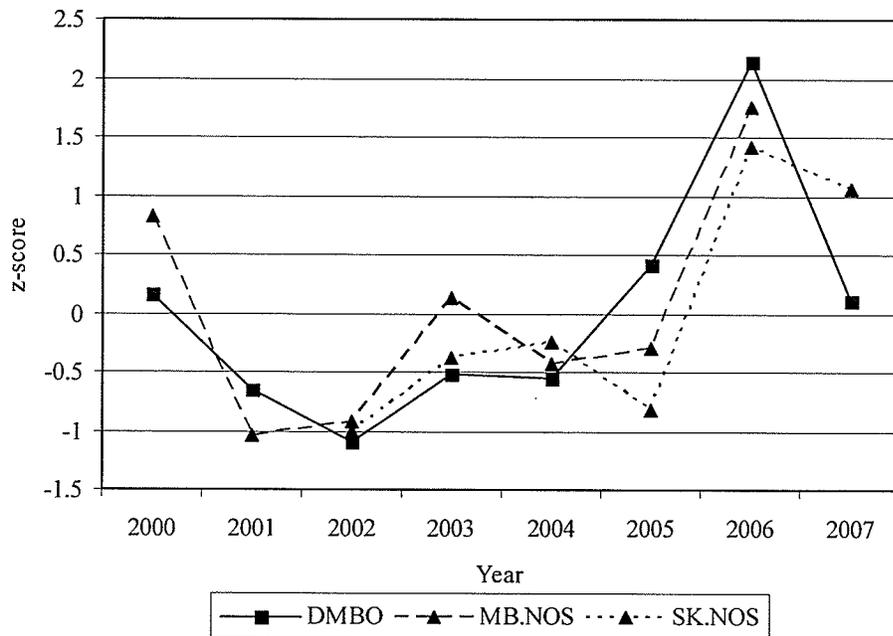


Figure 8. Standardized indices of saw-whet owl abundance from Delta Marsh Bird Observatory, and Manitoba and Saskatchewan Nocturnal Owl Surveys, 2000-2007.

The same-year DMBO and Manitoba NOS standardized abundance index values (z-scores) were significantly correlated ($r = 0.8693$, $p = 0.0110$, $n = 7$ years). DMBO indices also showed a nonsignificant correlation with Saskatchewan NOS values ($r = 0.7383$, $p = 0.0938$, $n = 5$ years). There was a high correlation between the Manitoba and Saskatchewan NOS values ($r = 0.9543$, $p = 0.0117$, $n = 5$ years). There was little to no correlation between DMBO fall values and the following year's spring Manitoba NOS or Saskatchewan NOS values ($r < 0.39$, $p > 0.83$; Appendix 4). The power of the DMBO and MB NOS analysis to detect a correlation of 0.8693 is $1 - \beta = 0.8302$, $\alpha = 0.05$. This analysis had a power of $1 - \beta = 0.9950$, $\alpha = 0.05$, to detect a perfect correlation (effect size of 1). Overall, I had high power to detect the observed correlations among these indices. More years of data will help better establish the relationship between DMBO and NOS indices,

however, the results of this 7-year analysis provides evidence that a strong positive relationship exists.

3.6.7 *Population Trend Estimates using Multiple Regression.*- The independent variables of day, day², dummy variables for each year, and the selected weather variables regressed significantly with the dependant count variable (log-transformed nightly count adjusted for effort): $r^2 = 0.4429$, $F_{15, 174} = 9.2230$, $p < 0.0001$. This equation was then used to calculate annual population indices, which allow for an estimate of the average annual change in nightly counts for each year relative to a reference year (2000).

Performing the multiple regression with each count night weighted by its net-hours relative to the total number of net-hours across all years produced a slightly poorer fit than the unweighted model: $r^2 = 0.4212$, $F_{15, 174} = 8.44$, $p < 0.0001$. However, the weighted regression equation produced annual indices with less variability. Therefore, the resultant linear regression of indices on year produced a better fit and greater power to detect linear change over time (Dunn and Hussell 2003).

I fitted weighted models independently for HY, SY and ASY birds to calculate separate annual indices for each age class (Table 7).

Table 7. Multiple Regression model fit of nightly saw-whet owl counts, Delta Marsh Bird Observatory, Manitoba, 2000-2007

Dependant Variable	r^2	F -value (df = 15,174)	p -value
All Owls	0.4429	9.223	1.22E-15
All Owls (weighted)	0.4212	8.441	2.51E-14
HY Owl	0.3911	7.452	1.28E-12
HY Owl (weighted)	0.3837	7.221	3.29E-12
SY Owl	0.2524	3.916	4.79E-06
SY Owl (weighted)	0.2364	3.591	2.01E-05
ASY Owl	0.1590	2.192	0.0082
ASY Owl (weighted)	0.1598	2.206	0.0078

I calculated annual indices from the weighted model and used linear regression to model the linear change among years (Table 8). The slope of this regression equation (β_1) is interpreted as the proportionate linear change in population indices over time. Multiplying the slope by 100 represents percent change per year. The slope (β_1) did not differ significantly from 0 ($\beta_1 = 0.0777$, 90% confidence interval (-0.1302, 0.3640), indicating a non-significant annual increase averaging 7.8% in owl numbers each year over the time period 2000-2007.

Table 8. Weighted linear trend analysis of Delta Marsh Bird Observatory, Manitoba saw-whet owl migration monitoring, 2000-2007

Age class	β_1 (slope)	S.E.	r^2	F-value (df = 1,6)	p-value
All Owls	0.0777	0.0936	0.1031	0.6894	0.4382
HY	0.1169	0.1272	0.1235	0.8452	0.3934
SY	0.1512	0.0643	0.4795	5.526	0.0590
ASY	0.1815	0.1050	0.3326	2.99	0.1345

HY and ASY birds showed statistically non-significant changes in population numbers over time (β_1), whereas SY birds showed a significant increase (Table 8). Overall, all β_1 estimates were positive (between 7.8 % and 18.2 %). Therefore, the migration monitoring analysis suggests that saw-whet populations are stable or slightly increasing over the monitoring period. However, *post hoc* power analysis indicated that the statistical power of detecting a large linear change of 10% per year with 8 years of data was low ($1-\beta = 0.26$, $\alpha = 0.1$). The power to detect a moderate change of 5% per year was ($1-\beta = 0.15$). Power analysis also indicated that 15 years of migration monitoring data would be required to detect a 10% per year linear change with a power of 0.8 ($\alpha =$

0.1), and 22 years to detect a 5% linear change. Finally, our analysis ($n = 8$ years) had a power of 0.8 to detect a 28% per year change ($\alpha = 0.1$).

3.6.8 Population Trend Estimates using a Generalized Linear Model.- I used a weighted GLM using the same variables as the multiple regression, and using the same relative effort weights as the multiple regression (using SPLUS default settings). The model fit parameters were: Null deviance = 32,549.83, $df = 186$. Residual deviance = 16794.49, $df = 172$. The ratio of residual deviance to degrees of freedom is ≈ 100 , indicating a poor fit to the data. I also fit the GLM separately for each age class (Table 9).

Table 9. Generalized Linear Model fit of nightly Saw-whet owl counts, Delta Marsh Bird Observatory, 2000-2007

Dependant Variable	Null Deviance (df=189)	Residual Deviance (df=173)
All Counts	34460.8	19118.2
Allcounts (weighted)	32715.1	18053.3
HY Count	24030.7	13251.4
HY Count (weighted)	23280.2	12573.2
SY Count	14088.2	10214.6
SY Count (weighted)	13664.1	10240.0
ASY Count	9657.3	7251.7
ASY Count (weighted)	9549.9	7241.8

I calculated annual indices from the model using the same method as the multiple regression (without back-transformation). I regressed the GLM indices on year, which produced non-significant population trend estimates (β_1) ranging from 9.9% to 12.3% (Table 10). These estimates are similar to those produced by the multiple regression (Figure 9), but the range of β_1 values among age classes is smaller (Table 10). Again, the trend for SY birds is the only statistically significant result, $\beta_1 = 0.1228$, 90% confidence interval (-0.0389, 0.2381), $r^2 = .6448$, $F_{1,6} = 10.89$, $p = 0.0164$.

Table 10. Weighted GLM trend analysis of Delta Marsh Bird Observatory, Manitoba saw-whet owl migration monitoring, 2000-2007

Age class	β_1 (slope)	S.E.	r^2	F-value (df = 1,6)	p-value
All owls	0.0996	0.0708	0.2481	1.978	0.2091
HY	0.0989	0.0932	0.1581	1.127	0.3292
SY	0.1228	0.0372	0.6448	10.89	0.0164
ASY	0.1125	0.0798	0.2487	1.987	0.2084

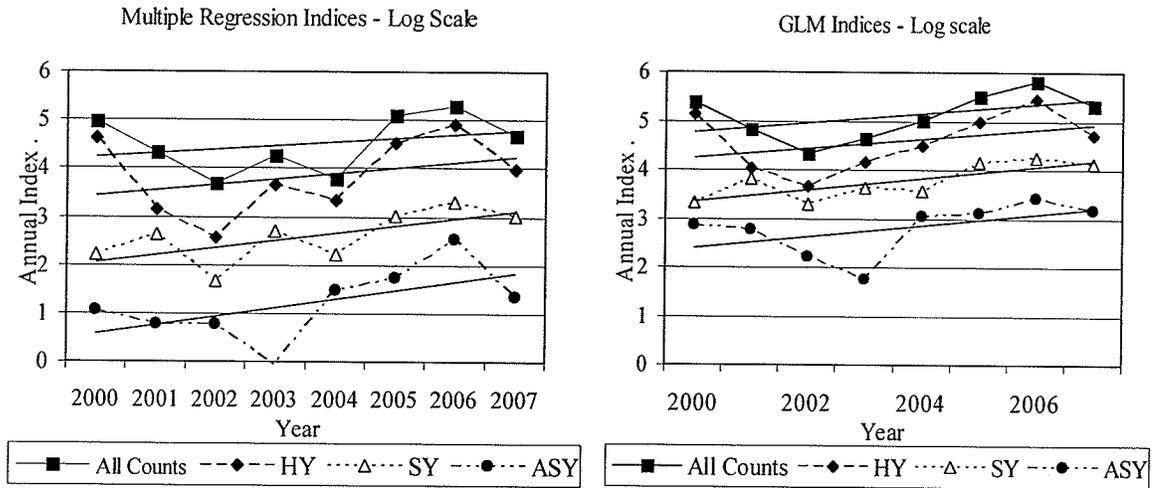


Figure 9. Linear regression of annual indices on year of each age class (Hatch Year, Second Year, and After Second Year), Delta Marsh, 2000-2007. Straight line fitted by least squares.

QQ-normal plots indicated that the residuals produced by the GLM are less skewed and better approach a normal distribution than those produced by the multiple regression (Figures 10 and 11). However, the large ratio of residual deviance to degrees of freedom indicated that a significant amount of variability is unaccounted for by the model. Therefore, the annual indices calculated from the GLM are correspondingly imprecise (e.g., wide confidence interval for each year's index value).

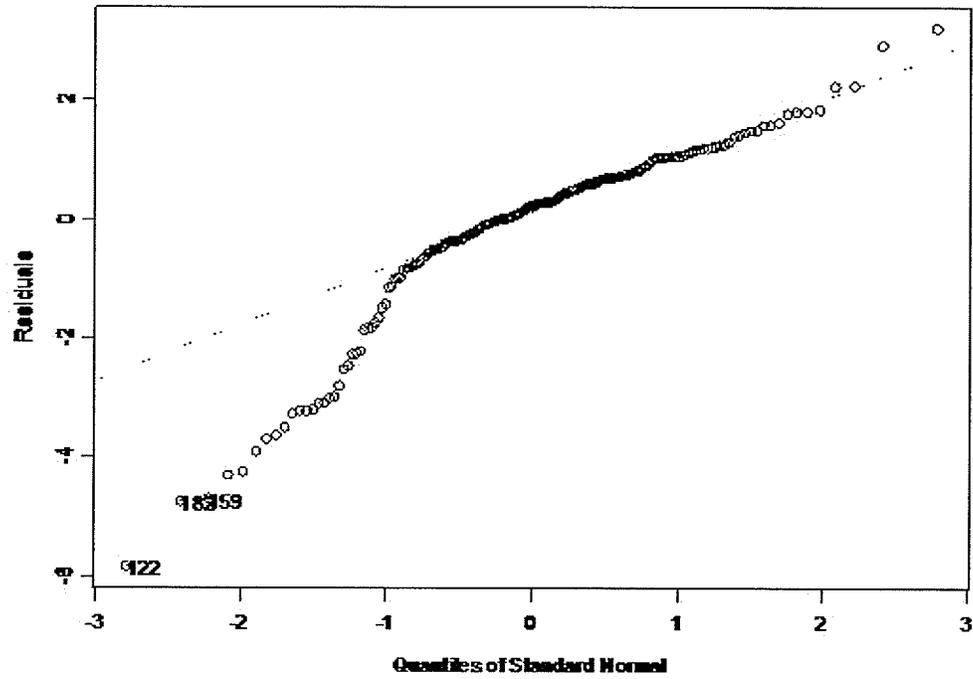


Figure 10. Q-Q-Normal plot of residuals for multiple regression fit to migration monitoring data. Dotted line represents a normal distribution of residuals.

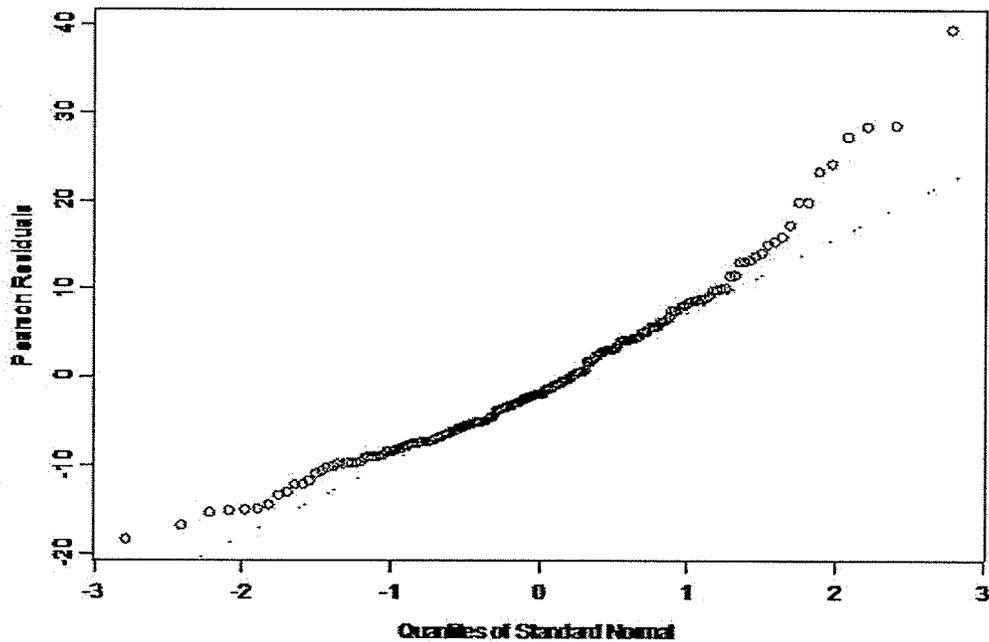


Figure 11. QQ-Normal plot of residuals for generalized linear model fit to migration monitoring data. Dotted line represents a normal distribution of Residuals.

Post hoc power analysis of the regression of GLM indices on year showed a slightly higher power to detect population trends over time than the multiple regression. The GLM analysis had a power of 0.35 ($\alpha = 0.1$) to detect a 10% linear change in owl numbers with 8 years of data, and a power of 0.17 to detect a 5% linear change. Power analysis also indicated that 13 years of migration monitoring would be required to detect a 10% change with a power of 0.8 ($\alpha = 0.1$) and 19 years to detect a 5% change. Finally, the GLM analysis has a power of 0.8 to detect a population change of 21% ($\alpha = 0.1$).

3.7 Discussion

3.7.1 *Saw-whet owl Demographics and Migratory Behaviour.*- The number of saw-whet owls in each age and sex class observed in the DMBO data is similar to proportions at a number of saw-whet monitoring stations around the Great Lakes (Brinker *et al.* 1997). My observation regarding skewed sex ratios towards females also suggests that more females migrate in fall than males, especially among the adult age classes, which are more strongly skewed towards females than young.

Brinker *et al.* (1997) suggested that differential migration in saw-whet owls may follow a similar pattern to that of boreal owls (*Aegolius funereus*) in Fennoscandia (Korpimäki 1986, 1988, Löfgren *et al.* 1986). Korpimäki (1988) showed that female Boreal Owls migrate farther and in greater numbers to winter where there is more access to food (resulting in better condition for breeding), whereas experienced males stay on or near the breeding grounds to increase their probability of securing or retaining nesting

holes and territories in the spring. In North America, females may overwinter farther south than males to avoid the extremes of cold and snow cover experienced in the northern interior in winter. As well, male saw-whets provide almost all of the food to their females and young during incubation and brooding (Rasmussen *et al.* 2008, Hinam and St. Clair 2008). Therefore, there is a large reproductive advantage afforded to males that hold territories in high-quality habitat (Hinam and St. Clair 2008), as well as an advantage to retaining familiarity and experience with a territory to facilitate hunting (Korpimäki 1986, 1988). This finding also supports the mating system hypothesis argued by Greenwood (1980) stating that philopatry is more likely to be exhibited by the sex that defends resources, in this case, males.

My results and similar observations from other saw-whet owl monitoring stations suggest that saw-whet owls commonly exhibit sex-biased migratory behaviour. However, there is a bias observed between the proportion of owls of each sex captured in passive nets versus those caught using an audiolure. For example, Duffy and Matheney (1997) and Erdman *et al.* (1997) found evidence that more females are captured when using an audiolure versus passive netting. The DMBO data also showed this difference in proportions of males and females between owls captured in nets around the audiolure versus owls caught 100-200 m away from the audiolure. This could result from a greater proportion of the total population being captured when using the audiolure, or from a difference in catch rate of males and females between passive netting versus audiolure netting. For example, Erdman *et al.* (1997) suggested

that passive netting mainly captures actively hunting owls, while the audiolure attracts both hunting and migrating owls.

Owls stopping migration to hunt are more likely to hit passive nets than actively migrating owls because they are lower to the ground and spend more time in a given area. Hunting owls requiring food will also be lighter than migrating owls on average, which might result in fewer female hunting owls correctly identified as female and more falling into the unknown sex category (based on wing-chord and weight). The DMBO data support this conclusion by showing an increase in the proportion of unknown owls and decrease in female owls in passive versus audiolure nets. It is also reasonable to assume that migrating males may have to stop to hunt more frequently than females because they are smaller, which results in a greater proportion of males stopping over and being captured in passive nets relative to audiolure nets. In contrast, nets near the audiolure catch owls passing within earshot of the lure and are actively attracted to it. The hundred-fold increase in catch rate between active and passive nets may be attributable to a greater number of actively migrating owls being captured. Erdman *et al.* (1997) also showed that the average owl mass was greater in audio-lure nets vs. passive nets further supporting the conclusion that passive nets catch a greater proportion of hungry, hunting owls.

The DMBO data showed sex proportions skewed strongly towards females in audiolure nets and moderately skewed towards females in passive nets. Therefore, it is reasonable to conclude that owls captured at DMBO exhibited a differential migration

pattern wherein females appeared to migrate in greater numbers than males, but perhaps not to the degree indicated by the total proportion of females captured.

3.7.2 Migratory Timing.- The migration windows calculated from the DMBO data indicate that the timing of saw-whet migration is very consistent among years in southern Manitoba. This is a characteristic of a regular migration based largely on a seasonal stimulus (Newton 2006), as opposed to a nomadic or irruptive migration, which is typically triggered by changes in food abundance (Korpimäki 1988, Cheveau *et al.* 2004, Newton 2006). The similarity of median migration dates among age and sex classes also seem to indicate regular migration stimuli such as seasonal factors, which likely affect different age and sex classes similarly (Bauchinger and Klaassen 2005, Newton 2006). This finding agrees with saw-whet owl patterns observed by others such as Whalen *et al.* (1997) in Virginia.

The presence of an earlier “peak” migration date in HY owls may be due to the consistent early arrival of owls successfully breeding relatively near to DMBO. Populations originating near DMBO would presumably arrive in more concentrated numbers than those coming from farther away and “diffusing” through different migratory routes, thereby increasing the variability of their arrival time at DMBO.

3.7.3 Foreign Recaptures.- The same-year recaptures associated with DMBO suggest a southeast movement of owls from Saskatchewan and Manitoba towards Minnesota and Wisconsin near the Great Lakes where many saw-whets winter (Rasmussen *et al.* 2008, Erdman *et al.* 1997, Brinker *et al.* 1997, Swengel *et al.* 2008). This pattern may result from saw-whets concentrating along the southern boundary of boreal

forest/aspen parkland during migration rather than travelling south across open grassland and agricultural lands. However, saw-whets are also captured within forested areas in the middle of prairie Saskatchewan indicating more southward movements. Also, there are no banding stations north of DMBO or Prince Albert, and very few in the central U.S., to allow detection of more southward or westward movements.

DMBO recoveries occurring after one or more seasons are widespread. The original banding locations range from as far northwest as northern Alberta and as far south as Wisconsin. Owls banded at DMBO and recovered elsewhere show similar distances of dispersal, including one owl that was recovered northeast of the Great Lakes on the Ontario-Quebec border. Although few in number, these recoveries suggest that movements of female and young during spring and fall migration are widespread, of variable distances and directions, and that adult females may travel 500-1400+ km between successive breeding seasons. Therefore, breeding populations in the prairie provinces are likely well mixed by females originating from regions that vary year to year. This mixing of individuals on the wintering and breeding grounds suggests that saw-whets exhibit a degree of panmixia, wherein separate subpopulations or regions share a common gene pool and exhibit population dynamics/trends interdependently due to individual movements among regions (Esler 2000). The frequent movements of females and young between different breeding and wintering grounds (perhaps in response to cyclical prey abundance) also suggests that the trends observed in saw-whet numbers in one region may be linked to increases or decreases in another, perhaps up to

distances over 1000+ km away. Future comparison of DMBO data to saw-whet owl monitoring from other regions will be useful to assess the degree of relatedness in population trends.

3.7.4 Annual Fluctuations in Saw-whet owl Abundance.- The observed 3 to 6 year cycle in the DMBO data are similar to other stations in the east that have observed 3 to 5 year cycles in saw-whet numbers (Grigg 1992, Brinker *et al.* 1997, Rasmussen *et al.* 2008). The large annual variation in the number of owls captured is mainly attributable to changes in the number of HY birds captured. This degree of variability in reproductive success may result from annual cycles in food abundance during the breeding season. For example, Marks and Doremus (2000) found a significant positive correlation between nest-box occupancy by saw-whets and small mammal population indices in southwestern Idaho. A strong relationship was also observed between the abundance of *Aegolius* owls and small mammals in Canada's eastern boreal forest (Cheaveau *et al.* 2004, Côte *et al.* 2007). Similarly, the annual breeding success of specialist predators of small mammals such as the boreal owl was correlated with small mammal abundance in Fennoscandia (Sundell *et al.* 2004).

3.7.5 Implications of Correlation with Small Mammal Indices.- The significant positive correlation among saw-whet owl abundance indices observed by DMBO and the Manitoba NOS to small mammal abundance in southern Manitoba suggests that the breeding density and reproductive success of saw-whet owls is affected by annual cycles of small mammal abundance, which may be synchronized over large regions (Swengel *et al.* 2008). Northern ecosystems such as the boreal forest can exhibit 3- to 7-year

productivity cycles and rodent populations also cycle synchronously in northern regions (Ranta *et al.* 1997, Sundell *et al.* 2004, Lima *et al.* 2006, Falls *et al.* 2007, Côte *et al.* 2007, Bowman *et al.* 2008), though the mechanisms producing synchrony are complex and may vary spatially and temporally (Krebs *et al.* 2002, Korpimäki *et al.* 2004, Sundell *et al.* 2004, Bowman *et al.* 2008). The correlation of DMBO and NOS indices with small mammal indices from southeastern Manitoba suggests that broad-scale regional synchronization occurs in saw-whet owl populations, and this may be mediated through the owls' relationship with small mammal population cycles that synchronize over similar scales.

Saw-whet owls could influence the synchronization of small mammal cycles through a top-down effect of predation and long-range dispersal and migration. Avian species of specialist small mammal predators can reduce the densities of alternative prey species, thereby inducing a synchronous low phase in small mammal population cycles (Korpimäki *et al.* 2004, Korpimäki 2005) over hundreds of square kilometres (Norrdahl and Korpimäki 1996). Therefore, small mammal populations in Manitoba may synchronize over large areas as a result of the regular long-range movements of saw-whets and other avian predators that settle in areas of high prey abundance in the spring and fall. Alternatively, annual saw-whet abundance may also be determined by bottom-up factors influencing small mammal populations. For example, small mammal abundance may synchronize over large distances due to extrinsic environmental factors such as climate or seed production (Ranta *et al.* 1997, Bowman *et al.* 2008). The fruiting patterns of boreal conifer species can synchronize over regions 500-1000+ km apart

(Koenig and Knops 2000) and could lead to a similar pattern in seed-eating mammals (Ranta *et al.* 1997, Lima *et al.* 2006, Falls *et al.* 2007). Environmental or climatic factors influencing small mammal populations are also evidenced by changes in the amplitude and magnitude of population cycles with increasing latitude or elevation (Sundell *et al.* 2004). Finally, the effects of other nomadic/dispersing avian or mammalian predators may also play an important role in small-mammal predator-prey dynamics and it would be difficult to tease out their effects separate from that of saw-whet owls alone.

The analysis presented here is limited by the small sample size ($n = 8$ years), the large distance separating the small mammal study site from the region sampled by DMBO, and the lack of information on small mammal cycles from other parts of Manitoba during the monitoring period (e.g., within the catchment area of DMBO). The geographic scale of synchrony in small mammal populations in Manitoba is also generally unknown. For example, Mihok *et al.* (1985) found little evidence of synchrony among annual abundance indices of various small mammal species near Pinawa, Manitoba (1968-1978). This is in contrast with small mammal observations from Spruce Siding, Manitoba and Roseau Bog, Minnesota from 1986-2007 (~100 km apart), which show varying degrees of synchronization over time (Duncan pers. comm.). As a consequence, my results cannot conclusively demonstrate a causal relationship between saw-whet owls and small mammal populations. However, the research suggests a potential mechanism that might explain regional synchrony in small mammal and owl populations. More time-series information on small mammal populations is required from different parts of Manitoba and different seasons to determine whether inter- and

intra-specific population synchrony exists, and what the spatial and temporal dimensions of synchrony are.

3.7.6 Implications of Correlation with NOS Abundance Indices.- The DMBO and NOS monitoring programs detected similar trends in saw-whet owl abundance, and suggested the same cyclical pattern and amount of annual variation in owl numbers. The strong agreement between the two monitoring methods provides greater confidence that the observed trends are representative of changes in saw-whet owl abundance, rather than due to systematic biases inherent in either monitoring program.

The correlation between the DMBO and NOS indices is striking because each monitoring program samples owls from widespread regions. Isotope analysis indicates that saw-whets captured at DMBO originate from southern and central Manitoba/Saskatchewan (see Chapter 4), whereas Manitoba NOS saw-whet data are mainly obtained from southern Manitoba. However, there may be some additional overlap in the populations monitored because males may still be migrating north during the springtime NOS (Duncan and Duncan 1997). Also striking is the seasonal difference in the timing of data collection between the two monitoring programs, which results in a different demographic sample of the monitored populations; the NOS records data on calling males in the spring, whereas the DMBO monitoring counts migrating juveniles and adult females after breeding has taken place. Thus, the observed correlation implies that the trends observed occurred over a large area and that different demographic groups of the population exhibited similar trends.

The combined area encompassed by the monitoring programs is on the scale of province-wide or larger, for example, the Manitoba NOS incorporates an area of over 210,000 km² among its route locations (my estimate based on area calculated in ARCVIEW). Therefore, the correlations observed suggest a degree of synchrony in saw-whet owl populations across a large region, consistent with Swengel *et al.* (2008). The correlations observed among the Saskatchewan NOS and Manitoba NOS and DMBO abundance indices further support this conclusion.

Large synchronous irruptions of saw-whets and other northern forest owls have been recorded elsewhere in North America. For example, Cheveau *et al.* (2004) found Boreal Owl irruptions to be synchronized over an area encompassing the western Great Lakes, southern Ontario and Quebec. Similarly, a large saw-whet irruption was observed in the autumn of 1995 throughout the western and eastern Great Lakes, New Jersey, Maryland and Virginia (Brinker *et al.* 1997). These movements of northern owls are generally thought to be related to the abundance of their prey and the associated predator-prey density affects on reproduction and competition (Löfgren *et al.* 1986, Korpimäki 1988, Newton 2002, 2006, Cheveau *et al.* 2004, Sundell *et al.* 2004, Côté *et al.* 2007). For example, interspecific competition causes more owls to disperse farther in high abundance years (Löfgren *et al.* 1986, Korpimäki 1988). This is particularly likely to occur during the crash phase following a mammal population peak, in which prey shortages cause large irruptions of dispersing owls that are in relatively poor body condition (Newton 2002).

The strong correlation between these two data sets also indicates that the number of calling males in the spring is a reliable indicator of the number of adults present, and the number of young produced, both of which then migrate through Delta Marsh in the fall. One explanation is that saw-whet male calling rates are related to individual body condition, which is correlated with habitat quality (Holschuh 2004), and abundant resources may also attract higher densities of males to an area (Marks and Doremus 2000, Hinam and St. Clair 2008). Therefore, high calling rates observed during the spring NOS probably coincides with good habitat quality factors such as high prey abundance (Marks and Doremus 2000). Assuming sex-biased migratory behaviour (Brinker *et al.* 1997), the increased calling rates and density of males may then attract a greater number of females to an area as they arrive from the south in spring. Polygyny has also been observed in saw-whets, and may increase in high habitat quality years (Marks *et al.* 1989). Additionally, the good habitat quality may also favour greater production and survival of young (Newton 2002, Hinam and St. Clair 2008). This would explain why the migration monitoring at DMBO detects a corresponding higher abundance of adults and young during the fall migration.

Overall, the correlation between the DMBO and NOS abundance indices suggests synchronization in saw-whet owl numbers can occur over province-wide regions or larger, similar to patterns observed in eastern North America (Brinker *et al.* 1997, Cheveau *et al.* 2004). The correlation also indicates that the springtime density of saw-whet males has a strong relationship to the abundance of migrating adults and young observed by DMBO in the fall. This relationship may be due to annual cycles of

prey abundance, which affects the density of breeding owls (Korpimäki 1988, Marks and Doremus 2000, Sundell *et al.* 2004), and their reproductive success (Cheveau *et al.* 2004, Côté *et al.* 2007, Hinam and St. Clair 2008).

3.7.7 Comparison of Trend Analyses Methods.- Annual abundance indices produced using the GLM show very similar trends to the multiple regression. The GLM also showed an increasingly better fit with more normally distributed residuals through the HY-ASY age classes relative to the multiple regression. However, the ratio of residual deviance to the degrees of freedom indicated an overall poor fit of the GLM and suggests that a large amount of model error is incorporated into the calculation of the annual abundance indices. Therefore, the indices produced by the GLM can not be considered as accurate estimates of saw-whet owl annual abundance. For this reason, I only considered the results of the multiple regression in interpreting saw-whet owl abundance trends

3.7.8 Trend Analysis Results.- Second year owls were the only age class to show a statistically significant increase. It is unlikely that this is due to an actual increase in SY owls relative to other age classes because the trend for SY owls falls within the range of trends estimated for the other age classes. Rather the estimated trend for SY owls is significant mainly because of the lower amount of variation present in the SY annual indices. Less variation in SY owl indices may have resulted from their numbers responding less than HYs to underlying factors such as food abundance. For example, the density of SYs present in an area of high prey abundance will be restricted by territory size, and can only change through dispersal of individuals to/from other areas,

whereas the number of HY owls is determined both by territory size and by the number of young produced per territory/breeding pair (ranging from 0 – 7 per clutch, Rasmussen *et al.* 2008). Therefore, there is more inherent variability in the numbers of HY birds than in SY numbers. Additionally, SY birds are caught in greater numbers than ASY birds and show less skew (from a normal distribution) in the form of “0” counts in the nightly data. Therefore, the multiple regression may provide a better fit to the SY counts compared to ASY counts resulting in annual estimates with less variability due to model error caused by skew.

Alternatively, the number of SY owls migrating may have increased relative to HY and ASY numbers. This could potentially occur if HY recruitment increased over the monitoring period due to more favourable wintering conditions, or if more SY birds moved into the monitored area from outside the catchment area. Another explanation is that the increase in SY abundance leading up to and following the peak in 2006 is due to a lag effect between small mammal abundance and SY abundance. Generally, the number of SY owls should decline one year behind the number of HYs and the magnitude of SY decline may be partially offset by a greater number of SYs breeding the year following a peak year. As well, the monitoring period included in the analysis may not have extended long enough past the peak year to record a further drop in SY abundance, thereby giving the appearance of an increasing linear trend relative to that of hatch year birds.

3.7.9 Interpretation of Trend Analysis Results.- The linear trends produced by the multiple regression suggest a stable or slightly increasing saw-whet population

migrating through Delta Marsh. However, these results must be considered cautiously. The statistical power of the analysis to detect a relatively large 10% linear rate of population change is low. Therefore, the eight years included in this analysis are insufficient for detecting small rates of long-term change and the trends observed are not certain. Power analysis also indicated that 22 years of data collection are required to detect a 5% per year trend with a power of 0.8, which demonstrates that it is generally beyond our ability to detect smaller rates of saw-whet population change within a time period relevant to the development and evaluation of potential management strategies. For example, the "Partners in Flight" initiative defined an effective monitoring scheme as having a 90% power of detecting a 50% decline over 25 years (Finch and Stangel 1992), which is equivalent to detecting a 2% decline per year with 25 years of data. The multiple regression does not achieve this level of power and sensitivity.

The large annual fluctuations in owl abundance did not exhibit a linear relationship over time, which contributed to the low power of the linear regression to detect trends. For example, a polynomial model fit using a smoothing spline (Fewster *et al.* 2000) describes the cyclical relationship between population indices and year much better than the linear model (Figure 12). As more years of data accumulate (e.g., 5-10 more years encompassing more periods of the cycle), analysis using a generalized additive model and a smoothing spline fit to the abundance indices may be suitable for detecting changes in the frequency and magnitude of the population cycle (Fewster *et al.* 2000). For example, detection of a lessening of owl abundance during peak years, or an increase in period length between peak years could indicate a decline in owl numbers

not detectable by the linear regression. Therefore, analyzing changes in the frequency or magnitude of saw-whet owl cycles could be more appropriate for providing forewarning of potential changes to saw-whet owl populations, thus allowing research and development of conservation measures should the need arise.

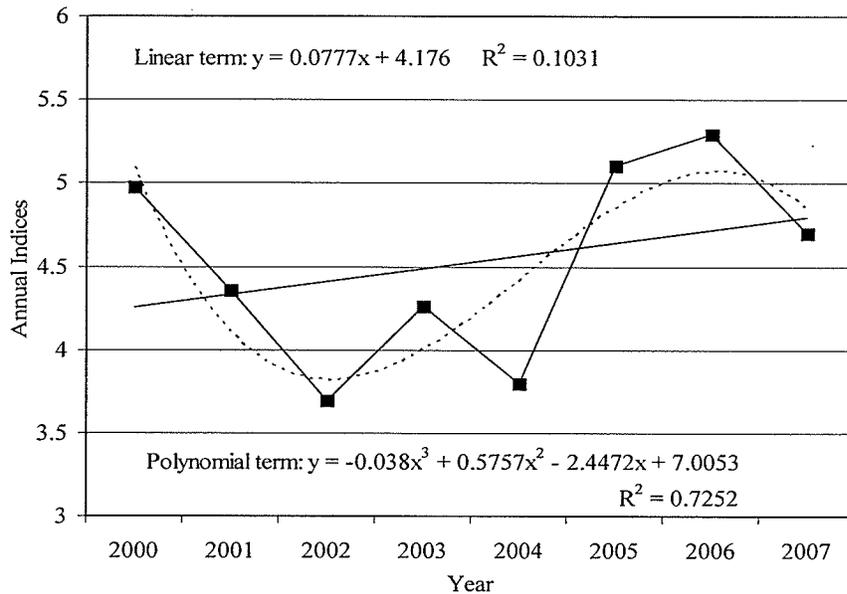


Figure 12. Linear versus curvilinear fit of Saw-whet owl annual indices, Delta Marsh, Manitoba, 2000-2007. Solid line = least squares fit. Dashed line = smoothing spline fit.

Another consideration for interpreting the trend results is that the changes observed in migrating owl numbers do not necessarily represent true population change. For example, moving net sites in 2005 may have increased the proportion of total owls captured because migrating owls had to pass through a narrower ridge and at a closer distance to the nets than at the first site. Lake noise may also have interfered with the owl's response to the audiolure more at the first site than the second.

Potential differences in catch rates between the two banding sites at Delta Marsh are difficult to separate from variation in the number of owls migrating. However, the effects of a change in catch rate would be small compared to the magnitude of variation observed in annual owl numbers, which has varied by as much as 107 owls/year and 96 owls/year from the two netting sites, respectively. For example, a measure of influence in regression (Cook's D; Quinn and Keough 2002) show that the years 2005-2007 only have a moderate amount of influence on the slope of the trend line (Cook's D = 0.24, 0.08, 0.3 respectively), compared to the influence of the high-catch year in 2000 (Cook's D = 0.8). Also, the effect of lake noise varies with the amount of wind so that the initial regression, which models the effect of wind will also somewhat account for the effects of lake noise between the two sites. In addition, the strong correlation between the annual abundance indices produced from the DMBO and NOS data provide more confidence that the trends observed are due to actual changes in saw-whet owl numbers rather than a bias resulting from switching net sites.

A final consideration for interpreting the DMBO trend results is that female dispersal between different breeding areas each year could obscure the population trends observed at a single site such as DMBO, whose catchment area encompasses a small portion of the total breeding range. Female dispersal may obscure trends in adult numbers by changing from year to year independently of population size. However, the annual variation observed at DMBO is mainly the result of variation in HY numbers, presumably due to changes in breeding effort and success. Therefore, the results of the DMBO analysis can be considered a good measure of the annual reproductive output

from within DMBO's catchment area, which can be considered a proxy for estimating population change (Rich *et al.* 2004). As well, the panmictic character of saw-whet migration suggests that the trends observed in adult and HY numbers are average values representing the cumulative change of numerous semi-independent breeding populations both within and outside the DMBO catchment area. Consequently, future comparison of the DMBO trends with other monitoring stations from the western provinces and Ontario will be very useful to assess population trends over broader scales and examine how trends among regions may relate to one another.

The potential effect of switching net sites on estimation of long-term trends will lessen as more years of data accumulate. The continuation of saw-whet migration monitoring at Delta Marsh is also important to increase the statistical power of detecting trends for future assessments of population change. In addition, I wish to encourage other monitoring stations to compare their long term data sets with the DMBO data to allow an assessment of saw-whet populations on broader scales and enable an examination of the relationship in trends observed among other regions. This comparison would especially be useful to see to what degree different regions coincide in their high-low-cycle so that a clearer picture of saw-whet population trends can be obtained.

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CHAPTER 4

DEFINING ORIGINS OF MIGRATORY SAW-WHET OWLS USING STABLE ISOTOPE ANALYSIS OF FEATHERS OBTAINED FROM DELTA MARSH, MANITOBA, 2006-2007

4.1 Abstract

The Northern Saw-whet Owl is widespread throughout northern wooded areas of Canada, the U.S. and into Mexico. However, little is known about its population trends or distribution within the prairie provinces. I used hydrogen isotope analysis on saw-whet owl feathers to identify the latitudinal origins of saw-whet owls captured during fall migration at the Delta Marsh Bird Observatory (DMBO), Manitoba (2006-2007). This allows the DMBO saw-whet monitoring data to be linked to specific regions and possible underlying mechanisms of population change. However, saw-whet feathers showed deuterium enrichment well beyond predicted values based on inferred patterns of saw-whet owl movements and the Lott and Smith (2006) isotope surface. This effect was primarily observed in adult feathers, whereas deuterium values of young owl feathers mainly fell within expected ranges. These results indicate that hydrogen isotope analysis techniques cannot be used to track adult owl movements without further research into the mechanisms of deuterium enrichment in feather tissues. Additionally Carbon and Nitrogen isotope analysis were used to compare the diets of young and adult owls. This analysis indicated that adults may feed on higher trophic level prey during moult than what young are fed in the nest.

4.2 Stable Isotope Analysis

To effectively conserve a migratory species, it is necessary to understand its migratory behaviour and the habitats used throughout its life cycle. This is especially true of migratory birds, which can live in distantly separated areas between their breeding and wintering grounds. The Northern Saw-whet Owl (*Aegolius acadicus*) is one of North America's most abundant forest owls (Rasmussen *et al.* 2008). It breeds throughout Canada's boreal forests as well as farther south in other forest types at moderate elevation of 300 to 3,000 meters (Rasmussen *et al.* 2008). Each fall, many saw-whets breeding in northern latitudes migrate to wintering grounds in the eastern and southern U.S. (Holroyd and Woods 1975, Grigg 1992, Brinker *et al.* 1997, Rasmussen *et al.* 2008).

Migration monitoring programs such as that run by the Delta Marsh Bird Observatory (DMBO) collect population information on saw-whet owls during migration. However, migration monitoring programs alone cannot link population trends to local areas and causes of population change. This is because it is unknown from where in western Canada the "counted" owls originate, and whether annual changes in the proportion of individuals migrating and the distance migrated are of significant magnitude to obscure actual population trends.

4.2.1 Deuterium isotope analysis.- Stable-hydrogen analysis allows the derivation of approximate geographic areas of origin in North America through measurement of deuterium isotope ratios ($^2\text{H}/^1\text{H}$) in feathers (Rubenstein and Hobson 2004, Hobson 2005,

Mazerolle and Hobson 2005). The technique is based on the isotopic ratio of deuterium to hydrogen in rainfall (δD_p), which varies predictably in a broad-scale latitudinal pattern across North America (Chamberlain *et al.* 1996, Hobson and Wassenaar 1996, Meehan *et al.* 2004). The precipitation weighted mean annual hydrogen isotope ratio in rainfall is reflected in the local food web (Cormie *et al.* 1994), and is transmitted to avian tissues through their prey and drinking water (Hobson and Wassenaar 1996, Chamberlain *et al.* 1997, Rubenstein *et al.* 2002). Geo-referenced hydrogen-isotope landscapes (“isoscapes”) are then modeled based on measurements of deuterium in the hydrosphere, and the quantified relationship between this abundance and that in avian tissues (δD_t ; Hobson and Wassenaar 1996, Meehan *et al.* 2004, Lott and Smith 2006). Therefore, measurements of δD in metabolically inert tissues such as feathers can be used to infer the geographic location of where the feathers were grown. In the case of saw-whets, feather samples from hatch-year birds can be used to determine natal origins, and samples from multiple feather generations on adult owls can be used to determine their moult locations over several years. Moult in saw-whet owls is believed to occur on/near the breeding grounds prior to migration (Rasmussen *et al.* 2008), and therefore new adult feather samples should represent breeding areas. Information on adult owl’s breeding locations over successive years indicates the degree of site fidelity/nomadism exhibited by saw-whets and also permits assessment of differences in male and female migratory distances and behaviour.

Measurements of δD_t have been used successfully to determine breeding and natal origins of several passerines and non-passerine species (Wassenaar and Hobson

2000, 2001, Meehan *et al.* 2001, Rubenstein *et al.* 2002, Smith *et al.* 2003, Dunn *et al.* 2006, Lott and Smith 2006). The accuracy of estimating origins depends on various factors including laboratory techniques (Wassenaar and Hobson 2006, Smith *et al.* 2009), the relationship between mean annual growing season δD_p values and δD_f values (Hobson 2005, Lott and Smith 2006), and variation in year and regional effects on δD_p and its relationship to δD_f (Chamberlain *et al.* 1997, Bowen *et al.* 2005, Lott and Smith 2006, Smith *et al.* 2008). Variation in δD_f also occurs between individuals in a population due to behavioural and physiological factors such as differences in individual diet, micro-habitat preferences, and behaviours adapted to regulate body temperature (Hobson and Wassenaar 2001, Meehan *et al.* 2003, McKechnie *et al.* 2004). Taking these factors into account, Meehan *et al.* (2001) estimated their accuracy to be approximately +/- 1.5 degrees latitude in their determination of moult origins of Cooper's Hawks (*Accipiter cooperii*). Hobson (2005) considers this estimate to be a best-case scenario. Given the relatively predictable deuterium-isotope pattern in precipitation weighted mean (δD_p) rainfall through the northern prairie provinces (Meehan *et al.* 2004, Lott and Smith 2006) and improving laboratory techniques (Hobson 2005, Wassenaar and Hobson 2006), I predicted similar latitudinal accuracy in our results with saw-whet owls. However, the relationship between δD_p and δD_f has not been specifically examined for saw-whets.

4.2.2 *Carbon and Nitrogen Isotope Analysis.*- Carbon-isotope ratios ($^{13}C/^{12}C$, measured as $\delta^{13}C$) differ between C_3 , C_4 and CAM plants due to a differential fractionation of carbon-isotopes through their respective photosynthetic pathways and mechanisms of C_3 water-use efficiency (Marshall *et al.* 2007). Carbon isotope ratios are

transferred with fractionation into the tissues of plant consumers (reviewed by Kelly 2000) and can be analyzed to determine whether an organism feeds in a C₃ (e.g., forest plants), C₄ (e.g., agricultural/corn) or CAM (e.g., desert plants/cactus) dominated ecosystem (reviewed by Kelly 2000, Hobson 2007).

Nitrogen isotope ratios (¹⁵N/¹⁴N, measured as δ¹⁵N) vary considerably throughout different ecosystems and landscapes (reviewed by Kelly 2000, Marhsall 2007). However, ¹⁵N is preferentially incorporated into consumer's tissues, resulting in a stepwise pattern of enrichment with each trophic level within an ecosystem (reviewed by Kelly 2000, Hobson 2007). Stable nitrogen isotope analysis of a consumer's tissues allows inferences about the trophic level at which an organism feeds and is also used to make comparisons in diet between individuals, species, or groups (Kelly 2000, Hobson 2007). This approach can be used on saw-whet owls based on the assumption that the foodwebs in which saw-whet owls feed do not significantly vary isotopically throughout the range of owls captured at Delta Marsh.

4.3 Objectives

My objectives were to use δD_r to estimate the geographic origins of owls migrating through Delta Marsh. This will describe the probable regions monitored by DMBO, and provides a spatial focus for future research linking ecological variables on the breeding grounds to population changes observed at DMBO. The stable-isotope analysis also provided information on the migratory routes and behaviour of saw-whets migrating through Manitoba, and provided a geographical framework on which to base

the interpretation of long-term saw-whet owl data collected from the monitoring programs.

I also analyzed $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers of a subset of saw-whet owls to examine the amount of variability in trophic feeding level, and to make comparisons in diet between adult and hatch-year owls (Duxbury and Holroyd 1997, Hobson 2005).

4.4 Methods

4.4.1 Feather collection.- I conducted δD_f analysis on feather samples obtained during DMBO migration monitoring operations during 2006 and 2007. The analyses were conducted by snipping a 0.5 cm tip off the first primary feather from individual hatch-year owls to determine the natal grounds of migrating yearlings. We also snipped a 0.5 cm tip from each mature feather generation present on the wings of adult owls (determined by feather wear) of secondaries or primaries. Samples were taken alternately from each wing to minimize asymmetry in the flight feathers (maximum 3 samples taken per individual). This was to track adult movements over two to three consecutive years and allowed assessment of the amount of annual movement between consecutive breeding grounds.

The collecting procedure took approximately 10 – 30 seconds per individual. There was negligible risk to the animal and no measurable impacts to the birds' health following the procedure have been documented (den Haan, pers.comm.). I stored feather samples at room temperature in brown paper envelopes prior to laboratory preparation.

4.4.2 Feather Sample Preparation.- In January 2008, I cleaned feathers in a 2:1 chloroform-methanol solution to remove surface oils and contaminants. I encased feather sample into silver capsules using methods described by Wassenaar and Hobson (2006). Only feather-vein material was used in each sample. Stable-hydrogen isotope analysis was completed at the Environment Canada stable-isotope laboratory in Saskatoon, using the comparative equilibration method described by Wassenaar and Hobson (2003), which produced standardized estimates of non-exchangeable hydrogen by using calibrated keratin isotope reference material (Hobson *et al.* 2006). Isotope measurements were performed on hydrogen derived from high-temperature flash pyrolysis of feathers using continuous-flow isotope-ratio mass spectrometry (Wassenaar and Hobson 2006).

4.4.3 Statistical Analysis.- I conducted δD_f analysis on 200 feather samples, 100 samples each from 2006 and 2007 (all age and sex classes combined). I presented results from the stable-isotope analysis in delta (δ) notation, in per-mil units (‰), which are normalized on the Vienna Standard Mean Ocean Water scale (Michener and Lajtha 2007). I used SPLUS 8.0 to conduct all statistical analyses and ARCVIEW 3.2 to depict geospatial information.

I used Welch modified *t*-tests and ANOVA to examine whether deuterium values (i.e. origins) differed among age/sex classes, feather generations, and years. Feather generations (FG) were designated relative to the year sampled. Therefore, FG1 = feather grown in current year, FG2 = feather grown in year previous to sample year, and FG3 = feather grown two years previous to sample year. I used Welch modified *t*-tests

to compare the δD_f of FG1 feathers between each age class. I combined the sexes in each age class in 2006 as there were no significant differences in δD_f values between males and females that year. I performed *t*-tests separately for each sex in 2007 due to the high degree of enrichment shown in SY-Males that year.

Geographic origins were plotted using a georeferenced altitude-corrected deuterium isotope in feather (δD_f) isoscape created by Lott and Smith (2006), which models the spatial relationship between δD in precipitation (δD_p) and δD in raptor feathers (δD_f). I assumed that saw-whet owls exhibit a similar relationship between δD_p and δD_f as diurnal raptors; however, there is no similar dataset based on nocturnal raptors.

I calculated tolerance limits at 95% confidence to depict latitudinal origins of 50% (TL₅₀), 75% (TL₇₅) and 90% (TL₉₀) of the population sampled at Delta Marsh. Tolerance limits represent the limits at which a specific proportion of the sampled population will fall at a given confidence level and are appropriate when all samples derive from a single population (i.e., single capture site). They also produce conservative estimates of origin that are robust to variability in the relationship between δD_p and δD_f (Hobson *et al.* 2007). For example, they are robust to modelling errors associated with the Lott and Smith (2006) δD_f isoscape.

I considered longitudinal origins of saw-whet owls by examining saw-whet owl band recovery data from the bird banding laboratory from Alberta, Saskatchewan, Manitoba, Ontario, Montana, North Dakota, Minnesota, and Wisconsin, between 1995

and 2007, to assess migratory distances and direction (number of recaptures = 1500+; Birds Banding Laboratory 2008). I calculated travel distances between consecutive trap locations for individual owls by subtracting lat./long. coordinates of the original and retrap locations to obtain lat./long distances and then calculating the hypotenuse. I also specifically looked for evidence of northward fall movements in saw-whets to see if geographic origins of owls south of Delta Marsh could be reasonably ruled out.

Lastly, I obtained ecoregion/habitat information from the Manitoba Land Initiative (<http://mli2.gov.mb.ca/environmental/index.html>) to differentiate between boreal forest habitat and prairie/prairie parkland habitats. This allowed me to further delimit the probable catchment area by excluding non-forested biomes.

4.4.4 Stable Carbon and Nitrogen Isotope Analysis.- I analysed a subset of adult and hatch-year feather samples for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (25 samples each for adult and hatch-year owls). The $\delta^{13}\text{C}$ values of terrestrial C_3 plant tissues (e.g., forest plants) range from -21‰ to -35‰, and C_4 plant tissues (e.g. corn) range from -10‰ to -14‰, with avian tissues showing slight amounts of enrichment (1-2‰) for each trophic step (Kelly 2000). However, some variation in $\delta^{13}\text{C}$ may also be caused by differences in water use efficiency of plants from more xeric habitats (Rubenstein and Hobson 2004). Taking these considerations into account, I defined two categories: $\delta^{13}\text{C}$ values less than ~ -18 ‰ indicated owls that mainly fed in agricultural areas, and values greater than ~ -21 ‰ indicated owls feeding in forested areas. Additionally, $\delta^{15}\text{N}$ commonly varies by approximately 3‰ (range 1-5‰) in animal tissues for each trophic step (reviewed by Kelly 2000). Therefore, assuming that foodwebs within the DMBO catchment did not

vary isotopically, $\delta^{15}\text{N}$ values were used to compare the trophic levels at which adults and hatch-years feed and compare males to females (Duxbury and Holroyd 1997, Hobson 2005). I used ANOVA to test whether significant differences in δC and δN existed between age and sex classes.

4.5 Isotope Analysis Results, 2006-2007.

4.5.1 Deuterium Analysis Summary.- A large proportion of feather samples showed abnormally high δD_f enrichment over expected values based on the Lott and Smith (2006) isoscape and an inferred southward migration patterns. The abnormal δD_f values occurred in adult feathers, while the δD_f values of HY-owls mainly fell within expected ranges (Table 11).

Table 11. Summary of current year δD_f values by age and sex, Delta Marsh, 2006-2007.

2006	Min.	Mean	Max.	Std. Dev.	<i>n</i>
HY-male	-107.35	-82.96	-47.14	20.67	10
HY-female	-110.75	-83.25	-52.55	17.88	15
SY-male	-77.42	-44.57	-1.43	25.65	6
SY-female	-98.64	-48.42	-13.98	22.00	14
ASY-female	-58.62	-28.72	-2.72	19.80	16
2007					
HY-male	-91.08	-68.68	-29.06	25.35	6
HY-female	-98.31	-67.00	-40.70	21.90	14
SY-male	-85.64	-75.52	-56.33	11.13	6
SY-female	-83.59	-45.90	-24.80	18.57	13
ASY-female	-69.44	-19.43	55.60	34.95	14

I assumed δD_f enrichment values of -70‰ or greater to be abnormal and due to an unknown eco-physiological mechanism. I chose a maximum acceptable value of -70‰ by taking the average expected δD_f of birds originating at Delta Marsh (-75‰ , Lott

and Smith 2006, assuming no northward migratory movements) and calculating an interval of +/-15% around this value (upper bound = -70‰). δD_f values from a single population have been observed to vary by up to 15% (Rubenstein and Hobson 2004). 37 individuals (61.7%) from the 2006 data and 46 individuals (76.7%) from the 2007 data showed this degree of abnormal enrichment (Table 12).

Table 12. Counts of current year saw-whet owl feather samples with δD values $> -70\text{‰}$, Delta Marsh, Manitoba, 2006 - 2007.

2006	<i>n</i> > -70	<i>n</i> -total	Percent	2007	<i>n</i> > -70	<i>n</i> -total	Percent
HY	5	25	20%	HY	12	24	50%
SY	16	19	84%	SY	18	20	90%
ASY	16	16	100%	ASY	16	16	100%

4.5.2 Relationships among Age, Sex, and δD_f Enrichment.- Fewer HY-owls showed abnormal enrichment values, and SY δD_f values were enriched in the recent feather generation, whereas their natal feathers from the previous year were not. This pattern is apparent when comparing multiple feather generations of adult birds (Figure 13). Feather generations (FG) are designated relative to the year sampled. Therefore, FG1 = feather grown in current year, FG2 = feather grown in year previous to sample year, and FG3 = feather grown two years previous to sample year.

Welch modified *t*-tests and paired *t*-tests ($\alpha = 0.05$) indicated that in SY-birds, FG1 was significantly more enriched than FG2 for both sexes in both years except SY-males in 2006 (Table 13). There were no significant differences between feathers in ASY birds except between FG2 and FG3 in samples taken in 2006 (Table 14). This is also apparent when comparing the FG3 values of ASY owls to HY owls in 2006 (Figure 13).

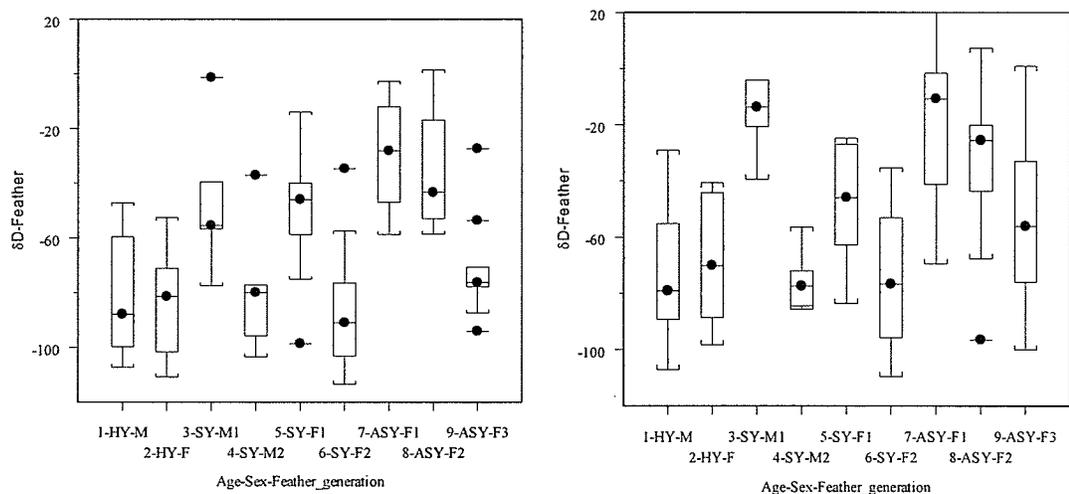


Figure 13. Box-plot of δD_f by age, sex, and feather generation of feather samples collected at Delta Marsh, Manitoba. Left plot = 2006, Right plot = 2007.

1 = Hatch Year male, 2 = Hatch Year female, 3 = Second Year male, new feather, 4 = Second Year male, year old feather, 5 = Second Year female, new feather, 6 = Second Year female, year old feather, 7 = After Second Year female, new feather, 8 = After Second Year female, year old feather, 9 = After Second Year female, 2 year old feather.

Table 13. *t*-tests comparing δD_f values between second year (SY) feather generations, 2006-2007.

Age-Sex-Year	FG1 Mean	FG2 Mean	<i>t</i> -value	df	<i>p</i>
SY-Male-2006	-46.08	-78.626	-1.9006	7.92	0.0942
SY-Female-2006	-48.42	-85.92	-4.5329	26	0.0001
SY-Male-2007	-10.49	-75.52	-6.3099	7.27	0.0003
SY-Female-2007	-47.78	-73.69	-3.0909	24.46	0.0049

Table 14. *t*-tests comparing δD_f values between after second year (ASY) feather generations, Delta Marsh, Manitoba, 2006-2007.

Age-Year-FG	Mean 1	Mean 2	<i>t</i> -value	df	<i>p</i>
ASY-06, FG1 v. FG2	-29.40	-35.17	-0.7638	27.27	0.4516
ASY-06, FG2 v. FG3	-35.17	-71.0	-4.2974	17.15	0.0005
ASY-07, FG1 v. FG2	-17.92	-33.02	-1.5550	30.24	0.1303
ASY-07, FG2 v. FG3	-33.02	-51.09	-1.6023	15.74	0.1290

To further explore the δD_f enrichment observed in FG1 samples, I examined whether δD_f values varied by age and sex. In HY owls, there was no significant

difference in δD_f between the sexes in either year. Neither was there a significant difference in SY owls in 2006; however, males had significantly enriched δD_f compared to females in 2007 (Table 15). The magnitude of δD_f enrichment found in males in 2007 adds certainty that the difference between male and female samples in 2007 is due to varying effects of the enrichment factor and not due to differences in origins, which would have shown a much smaller difference in δD_f values.

Table 15. *t*-tests comparing current year δD_f values between sexes, Delta Marsh, Manitoba, 2006-2007.

Age-Year	Mean-Male	Mean-Female	<i>t</i> -value	df	<i>p</i>
HY-2006	-82.96	-83.25	0.0362	17.4314	0.9716
HY-2007	-68.68	-67.00	-0.1407	8.3803	0.8915
SY-2006	-46.08	-48.42	0.1674	5.8193	0.8728
SY-2007	-10.49	-45.90	3.3394	8.2388	0.0098

New feather (FG1) δD_f values were significantly enriched between each age class in each year (sexes combined), 2006 ($f_{2,45} = 26.587$, $p < 0.0005$), 2007 ($f_{2,45} = 14.85$, $p < 0.0005$). HY birds showed the least enrichment (mean = -76‰), SY birds showed intermediate enrichment (mean = -42‰), while ASY feathers were the most enriched (mean = -24‰).

4.5.3 Predicted Origins of Saw-whet Owls.- The eco-physiological mechanism of δD_f enrichment primarily affected the δD_f values of adult feathers, therefore, I only used HY owl feathers to plot origins. These included both HY feathers from 2006 and 2007, as well as older feathers (FG2) on SY-owls from 2006 and 2007. This resulted in four separate samples representing the origins of owl captured at DMBO over three years (2005-2007). I calculated tolerance limits at 95% confidence ($\alpha = 0.05$) to estimate origins

of 50% (TL50) and 75% (TL75) of the saw-whet population sampled each year and plotted the results on the Lott and Smith (2006) isoscape (Figure 14; Table 16).

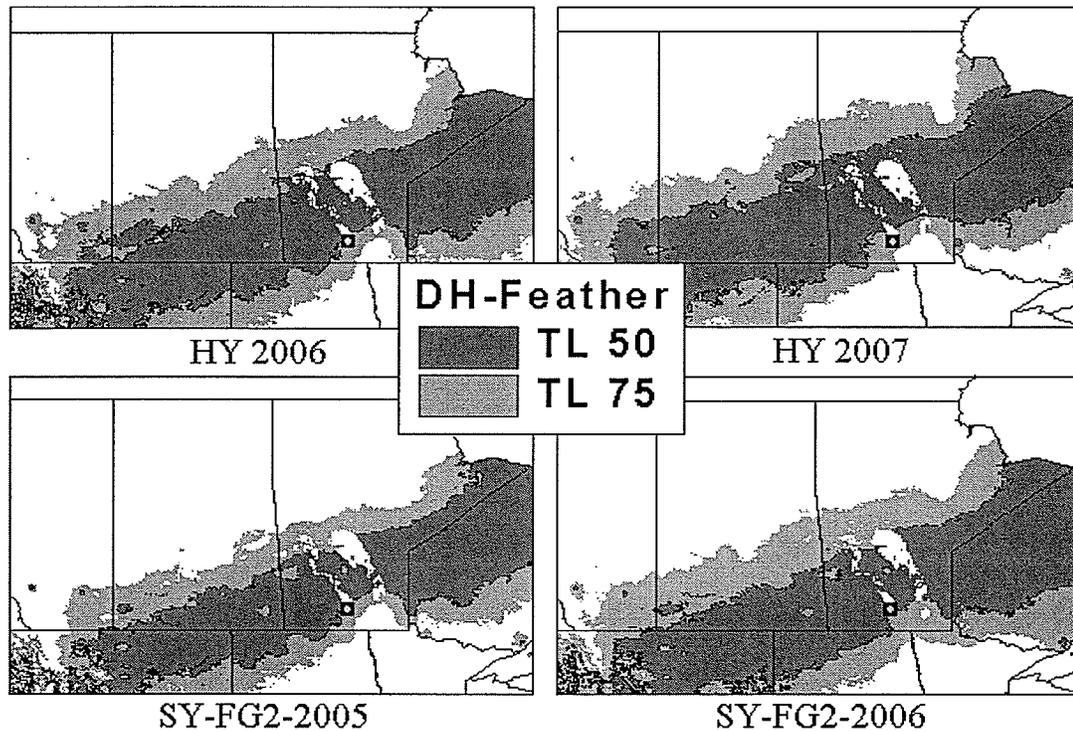


Figure 14. Tolerance limits defining natal origins of 50% and 75% of Saw-whet owl population migrating through Delta Marsh, 2006-2007.

HY 2006 = Origins of Hatch Year owls captured in 2006.

HY 2007 = Origins of Hatch Year owls captured in 2007.

SY-FG2-2005 = Natal origins of Second Year owls captured in 2006.

SY-FG2-2006 = Natal origins of Second Year owls captured in 2007.

Table 16. Tolerance Limits calculated from δD_r of Hatch Year saw-whet owl feather samples and Second Year feather samples of previous year feathers (FG2) collected at Delta Marsh, Manitoba, 2006 and 2007, values > -70 omitted.

TL50	lower	upper	TL75	lower	upper	<i>n</i>
HY-06	-102.48	-77.98	HY-06	-111.12	-69.34	20
SY-FG2-05	-98.66	-77.68	SY-FG2-05	-106.06	-70.28	15
HY-07	-105.84	-80.56	HY-07	-114.75	-71.65	16
SY-FG2-06	-100.39	-73.89	SY-FG2-06	-109.73	-64.55	13

In addition, I combined the δD_f values of the four separate samples and calculated TL50 and TL90 limits for all the samples combined. I plotted the regions defined and overlaid this information with land cover information differentiating regions of boreal forest from regions of prairie and prairie parkland habitat.

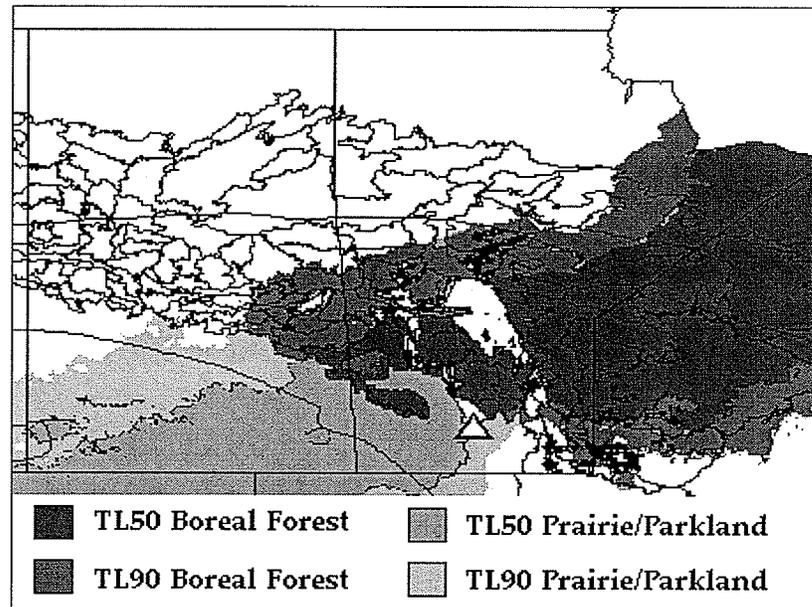


Figure 15. Manitoba Ecoregion data depicting Boreal Forest and Prairie Habitat combined with Tolerance Limits depicting the origins of 50% and 90% of the saw-whet owl population captured at DeltaMarsh, Manitoba (2005, 2006, and 2007 feather samples combined). Δ = Delta Marsh

4.5.4 Stable Carbon and Nitrogen Isotope Analysis.- I obtained $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope analysis data on 24 HY and 25 AHY feather samples. $\delta^{13}\text{C}$ was consistent among years and age classes (Figure 15). However, there were three outlying values: -17.0‰ and -17.4‰ in 2006, and -18.5‰ in 2007, indicating that these individuals were foraging within a C_4 plant dominated habitat (agricultural), rather than C_3 dominated forest (Hobson, pers. comm., reviewed by Kelly 2000).

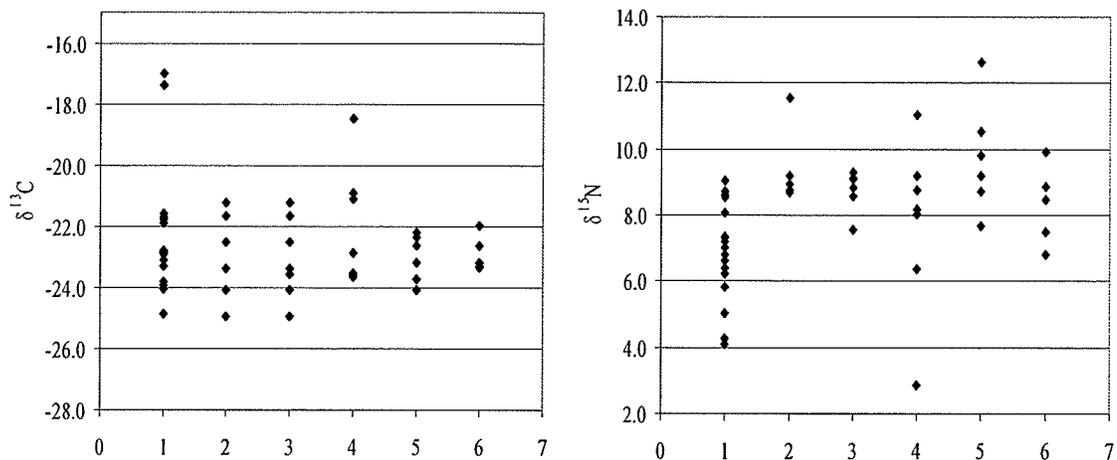


Figure 16. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by age and year, Delta Marsh, Manitoba, 2006-2007. 1 – HY'06, 2 – SY'06, 3 – ASY'06, 4 – HY'07, 5 – SY'07, 6 – ASY'07.

$\delta^{15}\text{N}$ values were less consistent among years and age class. $\delta^{15}\text{N}$ was depleted in HY feathers compared to adult age classes (SY and ASY), especially in 2006 (Figure 15). A Welch modified *t*-test on $\delta^{15}\text{N}$ values (2006 and 2007 combined) indicated a significant difference in $\delta^{15}\text{N}$ between HY and AHY age classes: HY (mean = 7.18, SD = 1.83), AHY (mean = 9.07, SD = 1.24), $t = -4.24$, $df = 42.39$, $p = 0.0001$.

4.6 Discussion

4.6.1. Deuterium Enrichment. - The δD_f values of saw-whets captured at Delta Marsh indicated that an unknown mechanism enriches saw-whet owl δD_f above δD_p well beyond the rate of 20 - 25‰ observed in passerines and other raptors (Meehan *et al.* 2001, 2004, Lott and Smith 2006, Hobson 2007). The southern origins indicated by the δD_f values can be reasonably ruled out as a possibility, because of the lack of evidence for long-range northward fall movements of saw-whet owls in the band recovery data

(1500+ recaptures in Alberta, Saskatchewan, Manitoba, Ontario, Montana, North Dakota, Minnesota, and Wisconsin 1995-2008; Bird Banding Laboratory 2008), as well as the magnitude of deuterium enrichment over expected values. The δD_f results also indicate that the enrichment mechanism is mainly observed in adult owls, and may also cause differences in δD_f between adult males and females.

The observed δD_f enrichment in saw-whet owls may be due to aspects of their physiology related to thermoregulation. Saw-whet owls are nocturnal, live in a relatively cold climate and are small bodied (females about 100g, males about 75 g, Rasumussen and Sealy 2007). Therefore, they show physiological cold temperature adaptations such as low rates of metabolism that decrease energy requirements, and also have effective systems of evaporative cooling to withstand higher ambient temperatures (Ligon 1969). For example, gular fluttering and panting are utilized by saw-whets in temperatures above 32° to increase evaporative heat loss and maintain their body temperature (Ligon 1969). However, body water loss through evaporation enriches the δD of the remaining body water pool due to fractionation of protium water (water molecule with ^1H) preferentially over deuterium-water (water molecule with ^2H , Sulzman 2007). For example, Wolf and Martinez del Rio (2000) found that the body water pool of white-winged doves could be enriched 20-40‰ above water source values. As well, the enrichment of body water δD over inputs varies with temperature, relative humidity, and the ratio of evaporative water loss to total water flux (McKechnie *et al.* 2004).

The amount of hydrogen contributed to feather tissues from the body water pool is unknown for most species. However, Hobson *et al.* (1999) demonstrated that 26-32% of hydrogen in feathers is derived from drinking water, and McKechnie *et al.* (2004) concluded that the δD of body water can significantly affect δD_f values. Therefore, enrichment of the body water pool during moult will likely result in a corresponding enrichment in the δD values of feathers.

The evaporative water loss mechanism of δD enrichment may also lead to the differences observed between young and adult owl δD_f , and between adult male and female δD_f . Fully feathered, active adults may rely more on evaporative heat losses to maintain body temperature than young, which initially are unable to thermoregulate and only develop endothermy over time (reviewed by Dunn 1975). Therefore, remiges may start growing in young before the mechanism of evaporative heat loss begins to function or work efficiently; however, this is speculative as this is unstudied in saw-whet owls.

Behavioural differences may also contribute towards the difference observed in δD_f between second year males and females, as suggested by Meehan *et al.* (2003). For example, males provide nearly all the food during incubation and brooding (Hinam and St. Clair 2008); therefore, they may have higher energetic demands and potentially elevated rates of evaporative heat loss than less active females when molt begins after or near the end of breeding.

Similarly, fasting has been observed to reduce evaporative water loss by 50% in boreal owls (Hohtola *et al.* 1994). Therefore, differences in food intake could significantly affect the amount of δD enrichment due to evaporative water loss between individuals and potentially between sexes. For example, females rely on male provisioning while incubating and brooding young (Hinam and St. Clair 2008). Therefore, they may be subject to different levels of nutritional stress/fasting than males prior to moult, which results in different amounts of evaporative water loss and deuterium enrichment.

The presence of the enrichment mechanism invalidated our approach of using deuterium isotope analysis to determine origins of adult owls, make comparisons between origins of breeding males and females, and to track individual adult origins over multiple years. Therefore, further research into the behavioural and physiological characteristics of saw-whets and their effect on deuterium enrichment in body tissues is required before the large advantages of deuterium isotope analysis techniques can be realized for this species. This research can likely only be accomplished with captive saw-whets, fed isotopically known diets, and subject to controlled conditions (Hobson pers. comm.).

The difference observed in δD between young and adult owls is similar to that found in Cooper's Hawks (Meehan *et al.* 2003), and suggests that the enrichment mechanism may be a feature of other raptor species as well. For example, Meehan *et al.* (2003) suggest that the δD_t enrichment in Cooper's Hawks could be caused by the

presence of neo-tropical passerines in the hawks' diet during moult. Neo-tropical passerines will have body tissues with enriched δD values reflecting their tropical origins (Hobson 2005) and may be incorporated into the keratinous structure of cooper's hawk feathers during moult (Meehan *et al.* 2003). Similarly, saw-whet owls are known to prey on passerines during the breeding season (Underwood and Sealy 2002), and therefore may share this enrichment mechanism with Cooper's Hawks. Finally, variance in δD_f within feathers and between feathers on the same individual could be caused by differential feather growth rates during the moulting period in raptors (Smith *et al.* 2008). For example, faster growing feathers should incorporate less deuterium into their structure during growth than slower growing feathers (Smith *et al.* 2008). This mechanism also suggests that young owls (showing relatively depleted δD_f values) grow their flight feathers faster than adults (showing enriched δD_f values), however, feather growth rates are also unstudied in saw-whet owls.

4.6.2 *Geographic Origins of Hatch Year Owls.*- The δD_f values of hatch year owls fell mainly within expected values. Also, the δD_f of old feathers from second year owls were also "normal" and closely matched those of HY owls. Therefore, the consistency of results suggests that the δD enrichment mechanism has much less effect or is not present in HY owls, and that the regions from where HY-owl originated was consistent from 2005 to 2007. Consequently, confidence is warranted in the determination of latitudinal origins derived from these samples. As well, tolerance limits are fairly robust to differences in the assumed relationship between δD_p and δD_f , and provide a conservative estimate of population origins (Hobson *et al.* 2007).

The δD_f values of hatch-year owls indicated that males and females originated from similar latitudes during fall migration. This suggests that the differential migration pattern observed between adult females and males is not exhibited as strongly in young saw-whets, which seem to be dispersing similar distances during their first fall migration.

The δD_f results identified the latitudinal origins of owls, but the longitudinal origins of saw-whet owls captured at Delta Marsh is essentially unknown. Band recaptures provide evidence of an East-Southeast movement of owls from Saskatchewan, through Manitoba down to Minnesota and Wisconsin (Bird Banding laboratory 2008). The two same-year recaptures of owls banded north of Saskatoon and then arriving at Delta in mid-October (during peak migration) also suggest that a significant proportion of owls captured at DMBO are originating in central Saskatchewan. However, the lack of stations north and south of Delta Marsh prevents more southward movement of owls from being observed. Therefore, it is unknown what proportions of owls caught at Delta Marsh originate North or Northeast of Delta Marsh relative to Northwest.

The depiction of boreal forest habitat helps further identify the likely origins of saw-whet owls. However, some owls likely breed in forested stands within prairie parkland and prairie ecoregions as well. The three outliers in the carbon isotope data also suggest that a small proportion of saw-whet owls captured at DMBO forage in agricultural areas (see below).

Future work with saw-whet isotope data may help refine the precision of defining latitudinal origins. An examination of the relationship between isotope ratios of hydrogen and oxygen may enable us to determine the extent of deuterium enrichment due to the unknown enrichment factor, and isotope research of captive and known origin saw-whet owls will help determine what the enrichment mechanisms are and perhaps how to account for it when interpreting δD_t results.

4.6.3 Diets of Young and Adult Saw-whet Owls.- $\delta^{13}C$ values fell within the range expected of birds feeding in C_3 plant dominated forest ecosystems (reviewed by Kelly 2000). The enriched outlying $\delta^{13}C$ values found in three HY owls suggest that a small portion of owls captured at DMBO originate near and feed within C_4 plant dominated agricultural habitat or more xeric dryland habitat (Kelly 2000, Rubenstein and Hobson 2004, Hobson pers. comm.). This is not unexpected, as saw-whet owls are often detected in aspen parkland within forested stands surrounded by agricultural fields.

The difference in $\delta^{15}N$ values between HY and AHY owls indicates that adult saw-whets may feed on higher trophic level prey during molt, compared with what young are fed in the nest during feather development (DeNiro and Epstein 1981, Hobson 1999, Kelly 2000). Underwood and Sealy (2002) found small birds made up approximately 25.2 % of the biomass found within the pellets of a saw-whet breeding at Delta Marsh (pellets obtained 29 May). Insectivorous birds represent a longer trophic chain than granivorous small mammals, and therefore likely have more $\delta^{15}N$ enriched body tissues in a given isocape (De Niro and Epstein 1981, reviewed by Kelly 2000,

Hobson 2007). Accordingly, the difference in $\delta^{15}\text{N}$ between adults and young may be due to adult owls feeding on a higher proportion of insectivorous birds than nestlings, which are primarily fed mice and voles (Rasmussen and Sealy 2008). However, the relationship between $\delta^{15}\text{N}$ and trophic level can be complex in terrestrial systems (reviewed by Kelly 2000). For example, the possibility of insectivory by adult saw-whet owls, or the incorporation of another trophic level through feeding on insectivorous shrews, makes conclusions about specific dietary items speculative. Indeed, trophic levels are more appropriately represented along a continuous gradient, rather than an ordinal one (e.g., Pauly et al. 1998).

The seasonal timing of feather growth may also influence the difference observed in the diet of young and adult owls. For example, small birds may be less abundant in the early spring when saw-whet nestlings are growing feathers (March-April, Rasmussen *et al.* 2008), whereas greater numbers of migratory passerines have arrived and produced young when adult saw-whets moult at the end of breeding. Therefore, seasonal passerine abundance relative to alternative prey may influence the proportion of passerines in the diets of young and adult owls. In conclusion, the δN analysis suggests a difference in diet between young and adult saw-whets, but a number of differing alternatives could lead to this result.

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CHAPTER 5

SAW-WHET OWL CONSERVATION: POPULATION TRENDS AND MIGRATORY BEHAVIOUR IN MANITOBA

5.1 Overview of Research Results

This research has brought together eight years of migration monitoring data from the Delta Marsh Bird Observatory (DMBO), the Manitoba Nocturnal Owl Survey, small mammal population indices from southeastern Manitoba, and a large literature source on northern owl and boreal ecology. I also utilized recent developments in stable isotope techniques to learn where saw-whet owls migrating through Delta Marsh originate. Taken together, the research results provide detailed information on saw-whet owl ecology, migratory behaviour, distribution and population fluctuations in Manitoba, and provides a framework with which to interpret the monitoring data generated each fall by the DMBO.

5.2 Saw-whet Owl Conservation and Management Strategies

5.2.1 Climate Change and the Boreal Forest.- Perhaps the largest threat to saw-whet owl populations and other boreal species is due to the uncertain effects of climate change on the boreal forest. The uncertainty arises because of the unknown extent of climate change itself, as well as the complex biological response of boreal ecosystems to climate change. For example, many global climate models predict that climate warming will be experienced first and to a greater degree in high latitude regions (Slaughter *et al.* 1995). Rising temperatures have the potential to greatly change the distribution of

permafrost (Slaughter *et al.* 1995), the water balance of precipitation, drought, and fire regimes (Larson 1980, Bergeron and Flannigan 1995, Hogg and Hurdle 1995, Henry 2002), and insect and disease outbreaks (Fleming and Volney 1995). In turn, these physical and biological processes could greatly change the distribution, composition and ecology of the boreal forest on which saw-whet owls and many other species depend (Slaughter *et al.* 1995, Sykes and Prentice 1995, Bergeron and Flannigan 1995, Henry 2002).

Monitoring saw-whet owl populations so that possible declines can be detected is important for encouraging research and the timely development of conservation measures. Broadly, changes in saw-whet owl populations may also provide another indication of changes occurring in the ecosystem dynamics of the boreal forest. For example, changes in the frequency or magnitude of northern small mammal cycles may be reflected in saw-whet owl population fluctuations (Cheveau *et al.* 2004, Côté *et al.* 2007).

5.2.2 Continuation of Saw-whet Owl Migration Monitoring.- The population trend analysis results indicated that saw-whet owl numbers were stable and potentially increasing over the monitoring period. The analysis also identified the limits of detecting small-to-moderate rates of change in saw-whet populations using migration monitoring data and current linear regression methods. These results illustrate the importance of continuing migration monitoring at DMBO to improve our ability to detect and assess potential changes in saw-whet owl population numbers in the future.

They also suggest that there is a need to develop conservation strategies for saw-whet owls before a need for them becomes readily apparent.

Accumulating more years of migration monitoring data will also allow more accurate modelling of annual fluctuations in owl numbers with curvilinear models so that changes in the magnitude and frequency of saw-whet abundance can be analyzed using methods such as Generalized Additive Models (Fewster *et al.* 2000). This will provide more information about changes in saw-whet owl populations than that which can be obtained by analyzing linear trends over time. For example, a proportional decrease in magnitude of both the low and high phases of owl abundance could indicate a significant change in saw-whet owl population dynamics, but it would not affect the slope of linear population change through time.

The strong correlation between the DMBO migration monitoring and Manitoba NOS indicates a degree of redundancy in saw-whet owl monitoring effort in Manitoba. However, the additional data generated by the two programs is sufficiently diverse to preclude the discontinuation of either program. For example, The NOS gathers data on a variety of owl species and the inclusion of saw-whet owls in the survey protocol has a very small marginal cost. Additionally, the band returns and demographic data generated by DMBO provides much more comprehensive information on annual changes in saw-whet owl populations, as well as generating precise data on migration routes and longevity. Therefore, the redundancy between the two programs is beneficial as it provides a measure of validation for the trends observed in either program.

Finally, I would like to encourage future comparisons of owl abundance data across regions as more overlapping years of coverage accumulate among different migration monitoring stations in Ontario, Saskatchewan, Alberta, Minnesota and Wisconsin. This will provide more information on the scale of regional synchronization in population trends, and the degree to which local populations vary interdependently.

5.2.3 Understanding Saw-whet Owls and Small Mammal Abundance.- There is a nomadic component to saw-whet owl breeding ecology evidenced by the large annual fluctuations in owls that are observed to be related to prey abundance here and elsewhere (Cheveau *et al.* 2004, Côté *et al.* 2007). This suggests that saw-whet owl annual recruitment is mainly restricted by prey availability rather than habitat loss or competition for scarce nesting cavities. Therefore, better knowledge about small mammal populations and cycles in Manitoba would be beneficial to understanding the mechanisms of saw-whet owl population fluctuations, as well as providing a basis for future conservation and management strategies. For example, forestry practices that retain snags and encourage cavity builders (e.g., woodpeckers to create suitable nesting cavities) could be combined with management options such as burning or harvesting variable patch sizes that also maintain or bolster natural cycles in small mammal abundance.

The observed relationship between saw-whet owl and small mammal abundance also points towards the possible mechanisms of regional synchrony in small mammal and owl populations. For example, large regional synchronization in saw-whet owl abundance might be due to a bottom-up effect of the synchronized cycles of their prey,

and/or saw-whet owls could influence the synchronization of small mammal cycles through a top-down effect of predation and long-range dispersal and migration. Therefore, an opportunity exists to combine further research into predator-prey dynamics in the boreal forest with research that also contributes to understanding saw-whet owl population trends.

5.2.4 Refining Deuterium Isotope Analysis Techniques to Better Estimate Saw-whet owl Origins.- The deuterium isotope analysis of saw-whet owl feathers provided an estimate of the geographic origins from where owls captured at Delta Marsh originate. This information provides a spatial focus for the population trend information collected by DMBO. Therefore, if saw-whet population declines are detected in the future, there is a pre-defined region in which research into possible causes related to saw-whet breeding ecology can be focused. The origins depicted also give some idea of the amount of potential overlap between DMBO, the Saskatchewan Nocturnal Owl Survey and migration monitoring stations in Saskatchewan. This information will be useful for future comparisons of saw-whet owl data among stations, especially if combined with stable isotope analysis data from owls captured in Saskatchewan.

The isotope analysis results also highlighted the shortcomings of using deuterium isotope ratios to define origins of adult saw-whet owls. The large amount of deuterium enrichment found in adult saw-whet feathers invalidated the use of this approach to estimate adult origins and track adult breeding areas over consecutive years. Therefore, research into the mechanisms of deuterium enrichment is required before the full advantages of isotope analysis can be realized for this species. The three

focuses of this research should be to examine potential δD_f enrichment mechanisms related to evaporative water loss in saw-whet owls, to examine the effects of δD enriched dietary tissue on δD_f , and to examine the effects of differential feather growth rates on δD_f enrichment. Understanding the mechanisms of δD_f enrichment in adults may allow δD_f values to be corrected for when interpreting origins.

As well, research into the relationship between δD and δO within feather tissues may provide a method of determining the degree of δD enrichment that took place during the feathers development K. Hobson (pers. comm.). In future studies, δD and δO information could then be used to determine which of the observed δD_f sample values were abnormally enriched and which were not. This would be a good improvement on the method used for this research, in which an upper limit to "normal" δD_f values was assigned based on expected values.

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Appendix 1. Delta Marsh, Manitoba foreign recaptures of saw-whet owls banded elsewhere, 2000-2007.

Recovery Date	Originally banded	Age	Original Location	Distance (km)
15 Oct '00	13 Oct '98	ASY-f	Little Syamico, WI	1,040
17 Oct '02	29 May '01	SY-f	Opal, Alberta	1,090
08 Oct '03	16 Oct '02	ASY-f	New Rome, WI	940
11 Oct '04	21 Sep '04	ASY-f	Dalmeny, SK	620
01 Oct '05	02 Oct '04	ASY-f	Duluth, MN	630
11 Oct '05	02 Oct '04	ASY-f	Duluth, MN	630
11 Oct '05	29 Mar '05	ASY-f	Dora Lake, MN	416
22 Sep '07	20 Oct '06	SY-f	Last Mnt. Lake, SK	500
03 Oct '07	14 Oct '06	SY-m	Dora Lake. MN	416

Saw-whet owls banded at Delta Marsh and recovered elsewhere, 2000-2007.

Recovery Date	Originally banded	Age	Recovery Location	Distance (km)
07 Oct '01	30 Sep '00	AHY-f	Little Suamico, WI	1,040
19 Sep '06	06 Oct '05	ASY-F*	Duluth, MN	630
08 Oct '06	18 Oct '05	ASY-F	Ville-Marie, QB	1,440
21 Oct '06	20 Sep '06	HY-f	Duluth, MN	630
24 Oct '06	06 Oct '05	ASY-f*	Beaver Creek, WI	830
18 Oct '07	09 Oct '06	SY-f	Matador, SK	665
20 Oct '08	25 Sep '06	HY-f	Beaver Creek, WI	830

* This is the same individual caught at two different stations south of DMBO in the same fall. It travelled 347 km southeast. HY = hatch year, SY = second year, ASY = after second year, f = female, m = male.

Appendix 2. Pearson Correlation between fall abundance indices of small mammals from Spruce Siding, Manitoba, and Roseau Bog, Minnesota (Duncan unpublished data), and Hatch year owls (Delta Marsh), 2000-2007.

Species	Spruce Siding, MB		Roseau Bog, MN	
	<i>r</i>	<i>p</i> -value	<i>r</i>	<i>p</i> -value
Total Small Mammals	0.7352	0.0377	0.2269	0.5889
Red-backed Vole	0.7138	.0467	-0.0052	0.9904
Meadow Vole	0.6471	0.0829	0.6648	0.0721
Shrews	0.6442	0.0847	0.1929	0.6471

Appendix 3. Pearson Correlation between fall abundance indices of small mammals from Spruce Siding, Manitoba and Roseau Bog, Minnesota (Duncan unpublished data) and Second Year owls (Delta Marsh), 2000-2007.

Species	Spruce Siding, MB		Roseau Bog, MN	
	r	p-value	r	p-value
Total Mammals	0.6123	0.1066	0.2260	0.5904
Red-backed Vole	0.5559	0.1525	-0.0849	0.8417
Meadow Vole	0.5485	0.1592	0.0511	0.9044
Shrews	0.6515	0.0801	0.5308	0.1759

Appendix 4. Pearson Correlation of Manitoba and Saskatchewan Nocturnal Owl Survey indices (Spring) and saw-whet owl abundance indices from Delta Marsh Bird Observatory (fall), 2000-2007. Lag year = Spring NOS following DMBO fall.

Correlation	r	p-value	Period	n (# years)
MB NOS v. DMBO	0.8693	0.011	2000-2006	7
MB NOS v. DMBO (lag year)	0.389	0.8998	2001-2007	7
SK NOS v. DMBO	0.7383	0.0938	2002-2007	6
SK NOS v. DMBO (lag year)	-0.1548	0.8307	2002-2006	5
MB NOS v. SK NOS	0.9543	0.0117	2002-2006	6