"There is nothing like looking, if you want to find something. You certainly usually find something, if you look, but it is not always quite the something you were after."

J.R.R. Tolkien

"Today's mighty oak is just yesterday's nut that held its ground"

-Anonymous

University of Alberta

Movements of the Northern Saw-whet Owl

by

Charles E. Priestley ©

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ABSTRACT

Movement patterns are fundamental traits of individuals and species. A tradeoff exists between potential benefits of movement such as decreased competition among relatives for resources, reduced probability of inbreeding and encountering new areas with more resources, and potential costs such as, increased predator encounters, being less efficient at resource acquisition while traveling through unfamiliar habitats and increased energetic requirements needed for movement. Dispersal movements of the Northern Saw-whet Owl (*Aegolius acadicus*) were studied using stable isotope analysis (SIA) of feather samples that were collected in central Alberta. In addition, DNA analyses were used to better understand morphological sex-specific differences of this bird. Based on SIA, I inferred that for this owl northward post-breeding dispersal preceded southern autumn migration, nomadism and year-round residency were exhibited, post-breeding dispersal exceeded post-fledging dispersal, female post-breeding dispersal exceeded that of males, and males were more likely to be year-round residents than were females.

Dedicated to my Mum, Gill Priestley, whose strength of character has always inspired me and to my wife, Lisa Priestley, whose nature has been built by her drive and dedication to do what is right - what is important.

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Finally, thank you to my family for all the encouragement and help along the way!

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Chapter 1: INTRODUCTION

Movements are an important aspect of an individual's life. Movement is associated with benefits such as decreased competition among relatives for resources, reduced probability of inbreeding and encountering new areas with more resources such as higher prey or nest densities. However, individuals also incur costs during movements such as increased chance of predator encounters, being less efficient at resource acquisition while traveling through unfamiliar habitats and increased energetic requirements needed for movement. The overall objective of the studies described herein is to better understand movement patterns as they relate to the Northern Saw-whet Owl (*Aegolius acadicus*).

The Northern Saw-whet Owl is one of the most abundant owls in North America (Cannings 1993). This nocturnal species is a secondary cavity nester that hunts from perches near forest openings. Its varied diet includes invertebrates and birds but its main prey is small mammals (Cannings 1993, Holt and Leroux 1996, Priestley et al. 2005). Like many raptors, it will feed opportunistically on prey that are temporarily abundant. For example, Northern Saw-whet Owls consume a higher proportion of songbird prey during songbird migration than at other times of the year (Cannings 1993). Therefore, these owls have the ability to move into new areas with different prey or to switch prey when the abundances of prey species change.

Northern Saw-whet Owls breed from southern Alaska, across Canada, and throughout much of the northern and western United States. During the non-breeding period of the year they can be found throughout their breeding range and across the entire continental United States except southern Texas and southern Florida.

Most studies of this species have been conducted during the autumn when large numbers of Northern Saw-whet Owls move. Most authors have called the autumn movement of this species migration. Taverner and Swales (1911) were first to suggest that the Northern Saw-whet Owl migrates. They reported four incidents to support their hypothesis. A large number of small owls landed on a fishing boat that was on Lake Huron during the autumn of 1903. During the autumn of 1906, 24 Northern Saw-whet Owls were among the 1845 dead migrants that washed up onto the shores of Lake Huron after a storm. The Northern Saw-whet Owl was not included in the list of 'Birds of Point Pelee' which was published in 1907 because its presence at Point Pelee, Ontario had not been confirmed. However, during the autumn of 1908, numerous Northern Saw-whet Owl carcasses were found at Point Pelee. During the autumn of 1910, autumn daytime searches at Point Pelee revealed the presence of 12 owls during a two-hour period. Taverner and Swales (1911) concluded that the Northern Saw-whet Owl, which had up to that point been considered a year-round resident, migrates in considerable numbers from the middle to the end of October.

Bent (1938), however, stated that the movements of the Northern Saw-whet Owl are too irregular to be considered true migration and that permanent year-round residency is more common for the species.

Further evidence for the migration of the Northern Saw-whet Owl was provided by Mueller and Berger (1967). They provided the first published attempt to capture and study the movements of these owls during the autumn. Owls were banded on the west shore of Lake Michigan in Wisconsin during the autumns of 1956 to 1964. During that period they trapped 213 owls, most of which (n = 168) were caught during the autumns of 1962 to 1964 when sampling effort was increased. They reported that their large sample of autumn-captured Northern Saw-whet Owls provided further evidence that the species migrated. However, they suggested that migration of Northern Saw-whet Owls could be locally irruptive in nature because their nightly capture index (number of owls per 1000m^2 of net per night) in 1962 was half what it was during 1963 and 1964.

Holroyd and Woods (1975) were first to present band recovery data to support the notion that Northern Saw-whet Owls migrated. They reported that the majority of owls that were banded in eastern North America and recovered within the same autumn moved southeast and that the majority of owls that were banded and recovered within the same spring moved north.

Initially autumn banding programs used passive mist netting to trap owls. During the autumn of 1986, an audiolure of the breeding call of the Northern Saw-whet Owl was placed adjacent to mist nets for the first time (Erdman and Brinker 1997). This new technique greatly increased capture rates. Erdman and Brinker (1997) reported that during the period 1971 to 1985, when passive netting was used, the average annual autumn capture rate was 57 at Little Suamico Ornithological Station near Green Bay, Wisconsin. In contrast, the average annual autumn capture rate at that site increased to 636 when audiolures and mist nets were used in combination between 1987 and 1995.

Banding programs for Northern Saw-whet Owls have become very popular because of (1) the owl's appealing nature, (2) large numbers involved in seasonal movement and (3) ease with which they can be caught. During the 10-year period 1997 to 2006, for example, 84 785 Northern Saw-whet Owls were banded in North America (Canadian Bird Banding Office unpubl. data). Most of these owls were banded during autumn at bird banding stations.

Despite the suggestive results from widespread autumn banding programs, the debate about whether the Northern Saw-whet Owl is a true migratory species has been recently renewed. Newton (1979 p. 180) defined migration as "a massive shift of birds twice each year between regular breeding and wintering ranges." In contrast, birds are nomadic when they "drift from one area to another, residing for a time wherever food is temporarily plentiful" (Newton 1979 p. 181). Marks and Doremus (2000) suggested that the Northern Saw-whet Owl could be nomadic based on low breeding-site fidelity in a 17-year nestbox study.

The different age and sex classes could have different movement strategies. Various authors have shown that more females than males are present in the autumn movements, and that after-hatch-year (AHY) owls are underrepresented compared to hatch-year (HY) owls. In order to determine any differences in the movements of these age-sex classes, an accurate method to determine the age and sex of owls is needed.

Measurement boundaries used to identify the sex of Northern Saw-whet Owls have been another topic of hot debate. Earhart and Johnson (1970), Sheppard and Klimkiewicz (1976), Weir et al. (1980) and Buckholtz et al. (1984) have all suggested different wing chord measurement boundaries to identify the sex of Northern Saw-whet Owls. More recently, Brinker et al., (1997) and Brinker (2000) suggested that wing chord and mass should be used in combination when assigning Northern Saw-whet Owls to gender.

In this thesis I present results from the application of (1) DNA analyses to understand Northern Saw-whet Owl morphological differences associated with gender and (2) stable-hydrogen isotope analyses of owl feathers to better understand seasonal movements of Northern Saw-whet Owls. The DNA samples were taken from owls trapped during autumn at three banding sites in central Alberta, Canada. In addition, a sub-set of DNA samples collected during the breeding season from AHY owls that could be clearly assigned to gender were used to test the accuracy of DNA analyses. Patterns of post-natal and post-breeding dispersal were inferred from isotopic analysis of feathers collected during autumn. Natal, breeding and winter dispersal patterns were inferred from feathers collected during the breeding season and winter.

The second chapter is an examination of the wing chord length and mass distributions of male and female, HY and AHY Northern Saw-whet Owls. External measurements can be used to sex birds and plumage can be used to determine the age of birds (Pyle 1997). These morphological data have been used to investigate temporal changes in age and sex-class ratios and whether different migration patterns exist between the sexes of various bird species (Murray 1966, Francis and Cooke 1986, Chandler and Mulvihill 1990, Woodrey and Chandler 1997).

Owls that were caught at Beaverhill Lake, Alberta during autumn were measured and weighed. DNA analyses were then employed to reveal the sex of these owls. The DNA samples were taken from owls trapped during the autumn at three banding sites in central Alberta. In addition, a sub-set of DNA samples were collected from known-sex AHY owls during the breeding season to test the accuracy of DNA analyses. These data were used to establish size variation between the sexes of Northern Saw-whet Owls, establish measurement boundaries for assigning Northern Saw-whet Owls to gender, and determine the accuracy of the sex identification techniques described by Weir et al. (1980), Buckholtz et al. (1984) and Brinker (2000).

In chapter three, I used stable-hydrogen isotope ratio analyses to investigate post-natal and post-breeding dispersal in the Northern Saw-whet Owl. Banding data have been used to investigate the movements of the Northern Saw-whet Owl. However, band recoveries may not have provided an accurate picture about the movements of this species. Stable isotope ratio analyses can reveal the general patterns of bird movements in a more unbiased way. This study (and the study reported in Chapter 4) is the first time that Northern Saw-whet Owl movements have been investigated using stable isotope ratio analyses.

In Chapter 4, I investigated natal, breeding and winter dispersals of the Northern Saw-whet Owl based on the results of stable-hydrogen isotope ratio analyses. Adult Northern Saw-whet Owls moult flight feathers on their breeding grounds and the moult of their remiges is usually incomplete (Evans and Rosenfield 1987, Cannings 1993). Therefore, stable isotope ratio analyses of feathers from the same bird that were grown in different years can reveal information about inter-year dispersal and reveal whether birds exhibit site fidelity.

At least two generations of feathers were collected from owls in the breeding season and winter in central Alberta. The stable isotope ratios of these feathers were used to (1) investigate the breeding origins of Northern Saw-whet Owls that were caught at various locations in central Alberta during the breeding and winter seasons, (2) determine whether breeding, natal and winter dispersal distances differed between sexes, (3) determine whether the owls travelled different distances during breeding, natal and winter seasons and (4) determine whether dispersal distances varied among years.

A summary of the main findings from chapters two, three and four are provided in the fifth chapter, along with suggestions for future research.

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Chapter 2: SEXING NORTHERN SAW-WHET OWLS

External measurements including wing chord and mass can be used to estimate age and sex of captured birds (Pyle 1997), and as a proxy for determining the physical condition of some bird species (Moore and Kerlinger 1987, Dunn 2000, Jones et al. 2002). In some species hatch-year (HY) and after-hatch-year (AHY) birds use different migration pathways or migrate at different times during the season (Ralph 1971, 1978, Hussell 1991). Migration stations have investigated how male:female ratios change between years and whether these ratios differ among species (Murray 1966, Francis and Cooke 1986, Chandler and Mulvihill 1990, Woodrey and Chandler 1997).

The Northern Saw-whet Owl (*Aegolius acadicus*) is commonly banded during autumn in North America. During the 10-year period 1997 to 2006, 84 785 individual Northern Saw-whet Owls were banded in North America (Canadian Bird Banding Office unpubl. data). This small raptor's autumn movements have been well documented, especially in eastern North America (Catling 1971, Holroyd and Woods 1975, Weir et al.

1980, Slack and Slack 1987, Cannings 1993, Brinker et al. 1997) and to a lesser extent in the west (Frye and Gerhardt 2003, Priestley and Priestley 2005). Weir et al. (1980) reported that females migrated earlier than males in two of the three years of their study in southern Ontario, Canada. Brinker et al. (1997) reported banding results from five migration stations located along the Atlantic coast and in the Northeastern USA. They reported that females were the most frequently netted sex-class and that the proportion of males netted increased with latitude. However, sexing Northern Saw-whet Owls in the field has been controversial because of doubt about the accuracy of sexing techniques (Mueller 1990).

In some species that are sexually dimorphic, sex of individuals can be inferred using morphological measurements. Raptors tend to exhibit reverse sexual dimorphism, with females being larger than males. Considerable overlap exists between the size of male and female Northern Saw-whet Owls (Earhart and Johnson 1970). This overlap is compounded by age-specific variation in size (Mueller and Berger 1967). Consequently, morphological differences between the sexes must be clearly determined before external measurements can be used reliably to draw conclusions about the sex-class structure of Northern Saw-whet Owl populations from owls that are caught at banding stations (Mueller 1990).

Earhart and Johnson (1970) determined that wing length and mass of museum specimens (*n* = 57) of Northern Saw-whet Owls differed significantly between the sexes. Owls with wing chords that were less than 134 mm were male and more than 141 were female.

Subsequently, Sheppard and Klimkiewicz (1976) concluded that Northern Saw-whet Owls with wing chords of less than 135 mm were male and wing chords greater than 139 mm were female. No reason was given for modifying the sexing criteria of Earhart and Johnson (1970).

Weir et al. (1980) modified these values for unflattened wing chord length to determine the sex of Northern Saw-whet Owls. Again, no explanation was offered for why the sexing criteria were changed. They called owls male when wing chords were ≤ 134 mm and female when wing chords were ≥ 141 mm.

Mueller (1982) criticized the accuracy of the Weir et al. (1980) sexing technique because (1) the authors did not take into account possible measurement differences between the age-classes even though Mueller and Berger (1967) had shown that wing length varies with age-class (HY versus AHY) and (2) the measurement boundaries were derived from museum specimens and therefore might have been shorter than what would have been found from living birds (Mueller and Berger 1968).

Buckholtz et al. (1984) modified the sexing criteria and recommended different wing chord size ranges for sex-classes of HY and AHY owls. Mueller (1990) criticized the Buckholtz et al. (1984) technique for (1) applying mathematical probability graphs to the distribution of wing chord lengths of owls with unknown sex and for (2) the presence of rounding errors in their measurement data.

Brinker et al. (1997) attempted to refine the sexing technique by suggesting that unflattened wing chord and mass should be used in combination when assigning sex-classes. However, they determined the sex of owls using DNA from a small sample of owls caught in the autumn (*n* = 10) and by the presence or absence of a brood patch from a small sample of owls caught during the breeding season (*n* = 7). Using breeding season mass to derive a sexing criterion for use throughout the year is problematic because differences between the mass of males and females are more pronounced during the breeding season than at any other time of the year (Cannings 1993). Overlap between the masses of owls during the breeding season is much less than during non-breeding periods of the year, therefore, breeding season mass should not be used to sex owls year-round. The sample size of owls of known sex increased since the initial 1997 publication and an updated version of the wing/mass sexing table is available on Project Owlnet's webpage (www.projectowlnet.org, Brinker 2000). This sexing technique has been widely accepted by bird banders and by the Bird Banding Office in Canada and the Bird Banding Laboratory in the United States. However, Brinker's (2000) version of the technique has not been published to clarify that using the revised table would allow banders to correctly identify the sex-class (male, female or unknown sex) of more than 95% of the Northern Saw-whet Owls that are trapped. The age-specific size variation that was reported by Mueller and Berger (1967) appeared to have been ignored by Brinker (2000). In addition, it is unclear how many known-sex owls were used to generate the latest version of Brinker's (2000) sexing table.

In order to establish the morphological boundaries for assigning owls to sex-classes, a large sample of owls with known-sex and known-ages is needed (Mueller 1982). The question is how to obtain information about gender. Fortunately, the sex of wild birds can now be determined reliably from tissue samples using molecular genetics. Recent innovations, in particular, multiple amplification via polymerase chain reaction (PCR), make it possible to extract DNA from small biological samples such as feather quills (Taberlet and Bouvet 1991). The use of feathers as a source of DNA is less invasive than collecting tissue samples such as muscle or blood (Bush et al. 2005) and has many advantages for work with field populations.

The objectives of this study were to: (1) use sex determination through DNA analyses to clearly establish size variation between the sexes of Northern Saw-whet Owls; (2) use data about size variation to establish measurement boundaries for assigning Northern Saw-whet Owls into sex-classes; and (3) use the known-sex and known-age data to determine the accuracy of the sexing techniques described by Weir et al. (1980), Buckholtz et al. (1984) and Brinker (2000). Here I report results from DNA analyses and measurements of Northern Saw-whet Owls caught during the autumns of 2004 and 2005 at three banding stations in central Alberta, Canada.

METHODS

Northern Saw-whet Owls were captured during the autumn 2004 and 2005 at Lesser Slave Lake Bird Observatory (LSLBO, 55°26.0′N,114°50.4′W), Beaverhill Bird Observatory (BBO, 53°22.9′N,112°31.5′W), and an acreage 8km south of Millet, 53°01.9′N,113°26.4′W). All sites are located in central Alberta and are separated by about 300km, north-south. Capture techniques at all three locations followed the protocol described in Priestley and Priestley (2005), using four mist nets and continuous broadcast play back of Northern Saw-whet Owl breeding calls at the centre of array of four mist nets.

All captured owls were fitted with numbered United States Geological Survey aluminum leg bands. Unflattened wing chord (mm) and body mass (g) were recorded for each owl and the bird's age was estimated using criteria outlined by Pyle (1997). In addition, five body feathers were plucked from along the flanks of each bird. Feathers were placed into #3 coin paper envelopes which were sealed with tape. All feather samples obtained from each owl were put into one envelope. Feather samples were stored dry and at room temperature for 10 - 16 months before processing.

Feather samples from 363 Northern Saw-whet Owls were analyzed for this study: 73 owls were caught at the LSLBO during the autumn of 2005; 50 and 185 were caught at the BBO during the autumns of 2005 and 2004 respectively; and 55 were caught near Millet during the autumn of 2004. Individual owls chosen for DNA analysis were a randomly selected subset of owls caught at each of the study sites.

Feather samples were removed from 69%, 39%, 54% and 68%, respectively, of owls caught at LSLBO during 2005, BBO during 2005 and 2004 and Millet during 2004.

DNA was extracted from feather quills using materials and protocols supplied in Qiagen DNeasy® Tissue Kits. Slight modifications used when following the Qiagen DNeasy® Tissue Kit extraction protocol are outlined in Bush et al. (2005, Table 1, sample type 5). Extracted DNA was stored at -20°C for a period of 1 - 18 months prior to amplification by PCR.

Feather samples were categorized for sex of the owl using 1273L/1272H primer sets. PCR cycling conditions followed the procedure of Kahn et al. (1998). Concentrations of the fifteen microlitre PCR solutions were made according to Bush et al. (2005). PCR products were visualized on an Applied Biosystems 3730 DNA analyzer with alleles scored using Genemapper (Applied Biosystems). Males were identified by presence of a single CHD-Z band and females were identified by the presence of both a CHD-Z band and a CHD-W band (Griffiths et al. 1998).

In addition, feather samples were analyzed from 18 AHY Northern Saw-whet Owls that were monitored during a nestbox study (Priestley et al. 2005) to verify the accuracy of the DNA sexing technique. Females (*n* = 8) were trapped at the nest while they were incubating eggs or brooding young and sexed in the field by the presence of a brood patch. AHY males were caught while they were delivering food to the nest using a modified version of the nest-mounted swing-door trap described by Saurola (1987) during May and June of 2004 and 2005. I did not use the second swing door between the back of the trap and the nest as suggested by Saurola (1987). Instead, hardware cloth was used to maintain separation between the male and the nest during trapping. When a male was caught the trap was removed from the front of the nest and the male was taken out of the trap on the ground. The prey item that the male was delivering was identified then put into the nest after the male was removed from the trap. Some males were reluctant to enter the trap while others did not appear to be suspicious of the trap but most entered without hesitation.

Leaving a trap up too long could have interfered with food delivery, especially for nests that were provisioned by a male that was trap-shy. Therefore, I did not attempt to trap a male for more than two hours per night and I maintained at least 5-day intervals between trapping attempts [the upper limit of the between-day interval suggested by Saurola (1987)]. Extra food was not added to nests during trapping attempts, as was suggested by Saurola (1987), to avoid affecting the stable isotope ratios of feathers from nestlings. Instead, the amount of time spent trapping males was limited (both within and between nights) so that prey delivery disturbance was minimized. Measurement data from AHY owls caught during the breeding season were not included in the data to develop sexing criteria because, as explained above, the differences between the mass of males and females is more pronounced during the breeding season than at any other time of the year (Cannings 1993).

One-tailed t-tests were used to test whether wing chord differed with age for each sex. The alternative hypotheses in these tests were: the mean wing chord of HY owls was smaller than the mean wing chord of AHY owls within each sex-class. One-tailed t-tests were also used for each sex to test whether body mass differed with age. The alternative hypotheses in these tests were: the mean body mass of HY owls was smaller than the mean mass of AHY owls. One-tailed tests were used because, as described above, Mueller and Berger (1967) reported that AHY Northern Saw-whet Owls had longer wing chords than HYs.

Sex criteria boundaries for each of both wing chord and body mass were independently established using the lower 95% confidence limit of the female owls (the larger sex) and the upper 95% confidence limit of the male owls (the smaller sex).

A discriminant function was established to differentiate between the sexes, using wing chord and mass measurements. Prior to calculating the discriminant function, I tested the data for homoscedasticity using Box's M test. Means and standard deviations of the male and female canonical discriminant function scores were calculated. Using these I then calculated the upper 95% confidence limit for males and the lower limit for females. The basis of my sexing technique is as follows: owls with canonical discriminant function scores that were less than the lower female 95% confidence limit were called male and those with canonical discriminant function scores that were larger than the upper male 95% confidence limit were called female. To help facilitate the use of this discriminant function I created a table that includes all Northern Saw-whet Owl measurements that are likely. All statistical tests were performed using SPSS 16.0.

RESULTS

Overall, 381 owls were sexed using the DNA sexing technique: 363 were migrants and 18 were breeding AHYs. All feather samples that were amplified through yielded results that could be interpreted using the DNA sexing technique.

In every instance, the DNA results from breeding AHY owls were consistent with the sex that was assigned to these owls in the field using breeding evidence criteria. Ten of the breeding owls were male and eight were female. DNA analyses indicated that 252 (69%) of the owls caught in the autumn were female and 111 (31%) were male.

I compared the body mass and wing chord of owls in my sample, in the proportion that they were encountered. The mean body mass of HY owls was smaller than the mean mass of AHY owls ($t_{361} = 2.31$, $P = 0.01$; Table 2-1). Similarly, the mean wing chord length of HY owls was shorter than the mean wing chord length of AHY owls ($t_{361} = 2.56$, $P = 0.005$; Table 2-2). However, when I made age-specific size difference comparisons for each sex separately, the size of owls did not differ by age. Body mass did not differ significantly between AHY and HY owls within the female sex-class ($t_{250} = -1.78$, $P = 0.076$) or the male sex-class ($t_{109} = 1.033$, $P = 0.15$) and wing chord length did not differ significantly between ages within the female sex-class ($t_{250} = -1.13$, $P = 0.13$) or the male sex-class ($t_{109} = -0.67$, $P = 0.25$). Therefore, I did not derive different sexing criteria for HY and AHY owls because I found no between-age-class differences for the wing chord and mass measurements within each sex-class.

Body mass varied between birds of the two sexes (Wilk's Lambda = 0.58, $F_{1,361} = 263.77$, $P < 0.001$). The lower 95% prediction limit for mass of the female sex-class was 83.69

g and the upper 95% prediction limit of the male sex-class was 96.83 g (Table 2-1). Therefore, masses $\leq$ 83.5 g could be called male and those that are $\geq$ 96.9 g could be designated as female if body mass is the only variable used to assign sex to owls.

Wing chord length was significantly longer in females than in males (Wilk's Lambda = 0.55, $F_{1,361} = 295.1$, $P < 0.001$). The lower 95% prediction limit for wing chord of the female sex-class was 135.01 mm and the upper 95% prediction limit of the male sex-class was 141.83 mm (Table 2-2). Therefore, Northern Saw-whet Owls with wing chords that $\leq$ 135 mm could be designated as male and those with wing chord lengths $\geq$ 142 mm could be designated as female if wing chord is the only variable used to assign sex to owls.

A discriminant function describing differences between known sexes on the function derived from wing chord length and body mass was significant (Wilk's Lambda = 0.45, $\chi^2_2 = 289.5$, $P < 0.001$). All data were homoscedastic (Box's M = 1.07, $P = 0.79$). The following unstandardized discriminant function was obtained using both wing chord length and body mass:

Discriminant score = (0.194 × wing chord (mm)) + (0.100 × mass (g)) − 36.324.

When all measurements were included in the discriminant analysis, 89.0% of the original grouped cases were correctly classified. The mean canonical discriminant function score for males (*n* = 111) was -1.67 and the standard deviation was 0.989. For females (*n* = 252), the mean was 0.74 and the standard deviation was 1.005. The upper 95% prediction limit of the canonical discriminant function score for males was 0.308 and the lower limit for females was -1.27. Therefore, discriminant scores < -1.27 can be reliably designated as male and those > 0.308 can be designated as female. Owls with discriminant scores that are ≥ -1.27 but ≤ 0.308 should be assigned to the unknown sex-class if this discriminant function is used to assign sex to Northern Saw-whet Owls. When the 'unknown-sex' category was used in the discriminant analysis, 98.1% of the original grouped cases were correctly classified as either male, female or unknown-sex. To facilitate use of this discriminant function, Table 2-3 provides the sex-class boundaries for all Northern Saw-whet Owl measurements that could reasonably be encountered.

Of the three sexing techniques derived with my known-sex data, the discriminant function that used wing chord length and body mass as independent variables performed best (Table 2-3). That technique had the lowest Wilk's Lambda (0.45) compared to the mass-only (0.58) and wing chord length-only (0.55) techniques. A higher proportion of owls could be sexed using the wing chord length and mass discriminant function compared to when only wing chord length or only mass was used alone. The wing chord and body mass discriminant function had the same error rate when body mass was used alone; however, use of wing chord length only assigned owls to the incorrect sex-class twice as often. The latter errors were biased towards incorrectly assigning females to the male sex-class. Ten of the 12 owls that were incorrectly assigned to a sex-class were females that were classed as males. Similarly, using body mass alone led to errors that were biased towards one sex. Five of the seven errors were males that were assigned to the female sex-class. Conversely, errors from the discriminant function based on both wing chord length and body mass were not biased according to sex. Four of the seven owls that were incorrectly assigned to a sex class were females that were classed as males and three were males that were classed as females.

DISCUSSION

Mueller (1982) stated that "We need data from a sufficient sample of known-sex, known-age Saw-whet Owls to establish reasonable estimates of the true means, standard deviations, and hence the 95% confidence intervals for determining sex." Using data from 363 Northern Saw-whet Owls with known-sex and known-age (HY versus AHY) I developed a discriminant function based on wing chord length and body mass that could be used for sexing Northern Saw-whet Owls.

This study is only the second to use a large sample of known-sex and known-age Northern Saw-whet Owls caught during the autumn to test existing sexing criteria for that species. Leppert et al. (2006) used DNA extracted from blood samples to sex 245 Northern Saw-whet Owls from Idaho and determine the effectiveness of the Brinker (2000) sexing technique. They found that the Brinker (2000) chart was accurate 96% of the time and concluded that the chart is reliable and could therefore be used to determine the sex of Northern Saw-whets caught throughout the United States (Leppert et al. 2006). My data, however, indicated that the Brinker (2000) technique was accurate only 93% of the time.

Differences between my findings and those of Leppert et al. (2006) could be explained by yearly variation, regional variation or both. The distance between Beaverhill Bird Observatory and Idaho Bird Observatory is 1125.7 km and 11° latitude. Owls that were caught in central Alberta may have been, on average, slightly larger than the owls caught in Idaho due to latitudinal variation (Bergmann's rule). The directionality of bias with the Brinker (2000) technique (i.e., males were erroneously called females and the majority of owls in the unknown-sex category were male) is consistent with the hypothesis that Northern Saw-whet Owls are larger in the north.

Leppert et al. (2006) did not report either the sex ratio of the unknown sex-class or the sex of misclassified owls. Therefore, it is not known whether the Brinker (2000) technique yielded a sex ratio both within the 'unknown' sex-class category and among owls sexed incorrectly that was female-skewed as it was with my data.

The new sexing technique reported here (Table 2-3) uses wing chord and body mass measurements to assign owls to sex-classes. Average wing chord measurements are not expected to vary between years. However, mass is a more plastic measure because physical condition and body mass can be correlated. This could cause the distribution of owl masses to vary between years (Brinker et al. 1997).

Whalen and Watts (2002) reported results from a Northern Saw-whet Owl autumn banding project that was conducted near Cape Charles, Virginia during a seven year period (1994 to 2000). They found that body condition scores and body masses of HY and AHY owls were significantly lower during years characterized by sudden involvement of an unusually large number of owls (i.e., 'irruptive events'). Unless this factor is taken into account, using mass to assign owls to sex-classes during these irruptive events could result in the erroneous assignment of more males. During nonirruptive years, more owls could be assigned to the female sex-class if body mass is used for identification.

Data that were used to generate the discriminant function table (Table 2-3) were collected during the autumns of 2004 and 2005. An irruptive movement of Northern Saw-whet Owls occurred at Beaverhill Lake in 2004 when the highest capture rate was recorded. During that year, fifty percent more owls were caught than the five-year average (32.3 vs. 22.9 owls caught per 100 net hours, SE of 2.9, 2002 to 2006; Priestley 2007). The capture rate during 2005 (21.4 owls per 100 net hours) was similar to the average capture rate and should therefore represent a nonirruptive year.

Whalen and Watts (2002) reported that during irruptive years HY Northern Saw-whet Owl mean body masses were 3.0 g lighter and AHY owl mean body masses were 2.3 g lighter. Owl mass at BBO were consistent because during 2004, the irruptive year, owls were 2.6 g lighter than 2005, the nonirruptive year. Since the discriminant function was generated during irruptive and nonirruptive years, the effect of between-year variation in mass should be incorporated.

Mueller and Berger (1967) stated that morphologically-based Northern Saw-whet Owl sexing techniques should vary by age because they found AHY owls were heavier and had longer wing chords than HYs. That conclusion was reached by comparing age-specific size differences for all owls rather than for male and female owls separately. My data showed a similar pattern when age-specific variation in size was compared irrespective of sex. However, when sex was taken into account I found that size did not vary by age. A higher proportion of the larger sex (females) were in the AHY sex-class (80% females : 20% males) than the HY sex-class (66% females : 34% males). Therefore, the difference detected when the sexes were grouped was not attributed to AHY owls being larger, rather, it was because more females (the larger sex) were in the AHY age class. Age-specific size differences reported by Mueller and Berger (1967) were also likely attributed to a larger proportion of females in the AHY age-class of their sample.

Of the three established field techniques used to identify the sex of Northern Saw-whet Owls (Weir et al. 1980, Buckholtz 1984 and Brinker 2000), the Weir et al. (1980) field sexing technique worked best. The Weir et al. (1980) technique correctly classified the highest portion of owls into one of the three sex classes (male, female or unknown sex); correctly assigned the lowest proportion of owls as either male or female; assigned the highest proportion of owls to the unknown-sex category; classified the lowest proportion of males, and highest proportion of females as unknown sex and; produced the lowest discrepancy between the number of males and females as sex unknown (Table 2-5, Table 2-6). In addition, the Weir et al. (1980) technique misclassified the smallest proportion of owls; misclassified the smallest proportion of males as female; misclassified the largest proportion of females as male and; produced the smallest discrepancy between the sex ratio of misclassified owls (Table 2-7).

In contrast, the Brinker (2000) sexing technique performed comparatively poorly because it correctly classified the lowest portion of owls into one of the three sex classes (male, female or unknown sex); correctly assigned the highest proportion of owls as either male or female; assigned the lowest proportion of owls to the unknown-sex category; classified the highest proportion of males, and lowest number of females as unknown sex and; produced the highest discrepancy between the number of males and females that were as sex unknown (Table 2-5, Table 2-6). In addition, the Brinker (2000) technique misclassified the largest proportion of owls; misclassified the largest proportion of males as female; misclassified the smallest proportion of females as male and; produced the largest discrepancy between the sex ratio of misclassified owls (Table 2-7).

The Buckholtz et al. (1984) technique was intermediate to Weir et al. (1980) and Brinker (2000) because of its performance with respect to the proportion of owls that were correctly assigned as either male or female; the proportion of owls that were assigned to the unknown-sex category; the portion of owls that were correctly classified into one of the three sex classes (male, female or unknown sex); the sex ratio of the unknown sex-class; the proportion of owls assigned to the wrong sex-class; had the smallest proportion of males that were misclassified as female and; the discrepancy between the sex ratio of misclassified owls (Table 2-5, Table 2-6, Table 2-7).

DNA sexing is the most reliable way to determine the sex of Northern Saw-whet Owls that are caught during migration (Leppert 2006). One of the main advantages of using this technique, in addition to its accuracy, is it does not have the unknown sex category that field sexing techniques have. However, the cost of doing DNA sexing will impede its widespread use. When DNA sexing is not possible, I recommend that criteria based on the chord and body mass discriminant function derived here be used. This function was derived from the largest known-sex and known-age sample of owls that has been published and none of the measurement data that went into the model were collected during the breeding season. This sexing technique should be tested using DNA sexing across the range of the Northern Saw-whet Owl to determine whether regional size differences exist. If they do, different field sexing criteria would have to be used across the Northern Saw-whet Owl's range.

TABLES

Table 2-1. Masses (g) of Northern Saw-whet Owls caught in the autumn at three banding stations in central Alberta[a]

	AHY-F	HY-F	AA-F	AHY-M	HY-M	AA-M
Mean	96.59	95.10	95.50	82.97	84.67	84.41
Standard deviation	5.99	5.84	5.91	5.55	6.36	6.25
Sample size	67	185	252	17	94	111
Upper 95% prediction limit	108.56	106.78	107.31	94.07	97.39	96.83
Lower 95% prediction limit	84.62	83.41	83.69	71.87	71.95	71.91

[a] AHY, HY, AA, F and M denote after-hatch-year, hatch-year, all ages, female and males respectively.

Table 2-2. Wing chords (mm) of Northern Saw-whet Owls caught in the autumn at three banding stations in central Alberta[b]

	AHY-F	HY-F	AA-F	AHY-M	HY-M	AA-M
Mean	142.36	141.80	141.95	135.76	135.18	135.27
Standard deviation	3.80	3.34	3.47	4.60	3.00	3.28
Sample size	67	185	252	17	94	111
Upper 95% prediction limit	149.96	148.48	148.89	144.97	141.18	141.83
Lower 95% prediction limit	134.76	135.12	135.01	126.56	129.18	128.72

[b] AHY, HY, AA, F and M denote after-hatch-year, hatch-year, all ages, female and males respectively.

Table 2-3. Wing chord length and mass discriminant function table for sexing Northern Saw-whet Owls

Wing Chord (mm)	**Mass (g)**			
	Male	**Unknown**		**Female**
125	≤108.0	>108.1	<123.8	≥123.9
126	≤106.0	>106.1	<121.8	≥121.9
127	≤104.1	>104.2	<119.9	≥120.0
128	≤102.2	>102.3	<118.0	≥118.1
129	≤100.2	>100.3	<116.0	≥116.1
130	≤98.3	>98.4	<114.1	≥114.2
131	≤96.3	>96.4	<112.1	≥112.2
132	≤94.4	>94.5	<110.2	≥110.3
133	≤92.5	>92.6	<108.3	≥108.4
134	≤90.5	>90.6	<106.3	≥106.4
135	≤88.6	>88.7	<104.4	≥104.5
136	≤86.6	>86.7	<102.4	≥102.5
137	≤84.7	>84.8	<100.5	≥100.6
138	≤82.8	>82.9	<98.6	≥98.7
139	≤80.8	>80.9	<96.6	≥96.7
140	≤78.9	>79.0	<94.7	≥94.8
141	≤76.9	>77.0	<92.7	≥92.8
142	≤75.0	>75.1	<90.8	≥90.9
143	≤73.1	>73.2	<88.9	≥89.0
144	≤71.1	>71.2	<86.9	≥87.0
145	≤69.2	>69.3	<85.0	≥85.1
146	≤67.2	>67.3	<83.0	≥83.1
147	≤65.3	>65.4	<81.1	≥81.2
148	≤63.4	>63.5	<79.2	≥79.3
149	≤61.4	>61.5	<77.2	≥77.3
150	≤59.5	>59.6	<75.3	≥75.4
151	≤57.5	>57.6	<73.3	≥73.4
152	≤55.6	>55.7	<71.4	≥71.5
153	≤53.7	>53.8	<69.5	≥69.6
154	≤51.7	>51.8	<67.5	≥67.6
155	≤49.8	>49.9	<65.6	≥65.7

Table 2-4. Proportion of Northern Saw-whet Owls in each sex-class using the wing chord-only, mass-only and wing chord/mass discriminant function techniques on owls that were caught in the autumn at three banding stations in central Alberta.

	M%	F%	U%	Error Rate%
Mass & Wing	23	49	28	1.9
Wing-only	20	39	41	3.9
Mass-only	17	29	54	1.9

Table 2-5. Summary of the comparison of sex determined by Weir et al. (1980), Buckholtz et al. (1984) and Brinker (2000) field techniques compared to sex of Northern Saw-whet Owls determined

by DNA (n=363)[c]

		Weir et al. 1980		Buckholtz et al. 1984		Brinker 2000	
	Case	n	%	n	%	n	%
Female cases	1	169	67.06	205	81.35	245	97.22
	2	4	1.59	2	0.79	0	0.00
	3	79	31.35	45	17.86	7	2.78
	Subtotal	252	100	252	100	252	100
Male cases	4	41	36.94	24	21.62	19	17.18
	5	3	2.70	13	11.71	27	24.32
	6	67	60.36	74	66.67	65	58.56
	Subtotal	111	100	111	100	111	100

[c] Case 1 is female by field technique and female by DNA sexing; case 2 is male by field technique and female by DNA technique; case 3 is unknown by field sexing technique and female by DNA sexing; case 4 is male by field technique and male by DNA sexing; case 5 is female by field technique and male by DNA sexing; and case 6 is unknown by field technique and male by DNA sexing.

Table 2-6. Characteristics of the Northern Saw-whet Owl sex-categories that were correctly classified as male, female or unknown using the Weir et al. (1980), Buckholtz et al. (1984) and the Brinker (2000) field sexing techniques. Percent of total number of owls (n=363) represented within categories are in brackets.

Description	Weir et al. 1980	Buckholtz et al. 1984	Brinker 2000
Correctly identified as male or female	210 (57.85%)	229 (63.09%)	264 (72.73%)
Unknown-sex category	146 (40.22%)	119 (32.78%)	72 (19.83%)
Correctly identified as male or female plus unknown	356 (98.07%)	348 (95.87%)	336 (92.56%)
Males in the unknown-sex category	67	74	65
Females in the unknown-sex category	79	45	7

Table 2-7. Characteristics of the Northern Saw-whet Owl sex-categories that were misclassified as male or female using the Weir et al. (1980), Buckholtz et al. (1984) and the Brinker (2000) field sexing techniques. Percent of total number of owls (n=363) represented within categories are in brackets.

Description	Weir et al. 1980	Buckholtz et al. 1984	Brinker 2000
Misclassified as male or female	7 (1.93%)	15 (4.13%)	27 (7.44%)
Males misclassified as females	3	13	27
Female misclassified as male	4	2	0

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Chapter 3: POST-NATAL AND POST-BREEDING DISPERSAL OF THE NORTHERN SAW-WHET OWL

Movement patterns are fundamental traits of individuals or biological populations (Hobson 1999). It is important to understand the movement patterns of birds when conservation strategies are being developed (Myers et al. 1987) because factors on the breeding grounds, on the wintering grounds and during movement between those areas can all influence conservation status (Sillett and Holmes 2002). Wildlife managers will know where conservation efforts should be directed when they understand (1) where and when species move, (2) the rigidity of movement patterns such as the degree of site fidelity and dispersal patterns and (3) the factors that influence survival and productivity in the areas that they occupy during all parts of their annual cycle.

Rappole and McDonald (1994) reviewed data for 109 Nearctic migrants to explore 14 predictions of the hypothesis that population declines are the result of breeding-ground events. Population changes were more strongly influenced by events that occurred on the wintering grounds than on the breeding grounds. Species, such as the Bicknell's Thrush (*Catharus bicknelli*), that are philopatric to breeding and wintering grounds are of particular interest because habitat changes in winter can be detrimental to specific breeding populations (Hobson et al. 2001).

Seasonal movements of the Northern Saw-whet Owl (*Aegolius acadicus*), that have generally been referred to as migration, have been well documented (Slack and Slack 1987, Cannings 1993, Brinker et al. 1997). During 1997 to 2006, 84 785 Northern Saw-whet Owls were banded in North America (Canadian Bird Banding Office unpubl. data). Studies migration in this species have explored the following topics: seasonal timing of migration (Catling 1971, Holroyd and Woods 1975, Duffy and Kerlinger 1992, Frye and Gerhardt 2003, Priestley and Priestley 2005), nightly timing of migration (Russell et al. 1991, Frye and Gerhardt 2003), age-class variation of migrants (Weir et al. 1980, Frye and Gerhardt 2003), sex-class variation of migrants (Weir et al. 1980), influence of weather patterns on migrant movements (Catling 1971, Weir et al. 1980, Russell et al. 1991), stopover patterns (Whalen and Watts 2002) and migration events characterized by sudden involvement of an unusually large number of owls (i.e., 'irruptive events')(Brinker et al. 1997, Whalen and Watts 2002).

Using data from band recoveries, Holroyd and Woods (1975) described two potential autumn migration routes in eastern North America. The first route had a southwest orientation that extended between central Ontario and Kentucky and the second had a southeast orientation that extended between Maine and North Carolina. Brinker et al. (1997) reported recovery of 39 banded owls moving among banding stations in the Eastern United States in Maine, Maryland, Minnesota, New Jersey, North Carolina, Virginia and Wisconsin and suggested that forests in the south-eastern United States might provide important wintering areas for Northern Saw-whet Owls. However, use of banding data to trace the movements of birds has been limited by low recovery rates (Meehan et al. 2001). In addition, band recovery data can introduce biases when they are used to understand movement patterns because locations of bird banding stations were not chosen randomly. In North America, most stations that band Northern Saw-whet Owls are located in the southeast (Priestley and Priestley 2005). Recovery of bird bands is also biased by patterns of human presence because the probability of recovering bird bands is greater in areas with high human density (Nichols and Kaiser 1999). Therefore, it may not be possible to correctly interpret movement patterns of bird populations from band recovery data.

Marks and Doremus (2000) suggested that Northern Saw-whet Owls could be nomadic in some parts of their range because they found low breeding-site fidelity at nest boxes in south-western Idaho. They reported that only one of the breeding after-hatch-year (AHY), and none of the 139 hatch-year (HY), Northern Saw-whet Owls that were banded at nests were recovered in their study area. In addition, one of the AHY males that was banded at one nest was found three years later more than 900km NNW from their study area.

Tracing movements of Northern Saw-whet Owls has been limited by the available techniques, including the weight of more advanced technology. The effectiveness of radio telemetry tracking migration movements is limited because the VHF transmitters that can be fitted to Northern Saw-whet Owls can only be detected within a limited range.

Satellite transmitters are too heavy to use on Northern Saw-whet Owls.

Recent innovations have enabled researchers to use chemical composition of body tissues to trace movements of animals (van der Merwe et al. 1990, Vogel et al. 1990). In the case of birds, the stable-hydrogen isotopic composition of feathers can be used to trace the breeding origins of individuals (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Feathers reflect the deuterium value of the precipitation in the area of feather growth. Deuterium values of precipitation gradually become more depleted along a southeast to northwest gradient across North America (Dansgaard 1964). Stable isotope ratio analysis is a major advancement in the ability of researchers to track movements because much more can be learned in a shorter amount of time with fewer financial resources (Kelly and Finch 1998, Hobson 1999). As a result, this gradient has been used as a tool to learn about animal movements in North America (for example see: Hobson 1999, Wassenaar and Hobson 2000, Hobson and Wassenaar 2001, Meehan et al. 2001, Hobson et al. 2001, Kelly et al. 2002, Rubenstein et al. 2002, Lott et al. 2003). Additionally, this new technique is not prone to the same problems that affect band recovery data because data about the origins of the migrants is not limited by the location of banding stations.

Lott and Smith (2006) created a base map of δD values for North American raptors using feathers from a sample of 264 raptors from 12 species (Fig. 3-1). Feathers were collected from 255 locations across North America. They used Sharp-shined Hawk (*Accipiter striatus*) feathers to demonstrate that this map can be an effective tool for exploring the origins of migrants.

Growth of juvenile Northern Saw-whet Owl remiges and rectrices is completed by the time they fledge (Cannings 1993). Despite undergoing a complete body plumage moult a few months after fledging, the first set of remiges and rectrices that are grown are retained for the first year (Cannings 1993). Therefore, stable isotope analyses of remex and rectrix feathers that are collected from HY owls during the autumn carry information about where they hatched.

AHY Northern Saw-whet Owls are believed to moult their flight feathers on their breeding grounds (Cannings 1993, Pyle 1997). Therefore, new flight feathers that are collected from AHYs during autumn were grown where the owl spent the most recent breeding season. The rectrices are usually completely renewed through moult every year (Cannings 1993) but the annual moult of the remiges is usually incomplete (Evans and Rosenfield 1987). A second-year owl typically carries juvenile inner primaries and secondaries, while some of the outer primaries and secondaries were grown during the most recent summer. Thus, feathers from these two years can be used to estimate natal dispersal and the breeding origin of migrant owls. After-second-year owls can carry feathers from three years reflecting the location of the owl over three breeding seasons (Pyle 1997). Consequently these feathers can be used to determine inter-year breeding dispersal. In this chapter I have used only the most recently grown feathers to determine origins of migrants.

Until this study, movement patterns of the Northern Saw-whet Owl have not been investigated using stable isotope ratio analyses. Therefore, I used stable isotope analyses to better understand the movements of the Northern Saw-whet Owl and to address the question posed by Marks and Doremus (2000): "Are Northern Saw-whet Owls Nomadic". My objectives were to (1) investigate the natal and breeding origins of Northern Saw-whet Owls that were caught in central Alberta, Canada during the autumn and (2) determine whether breeding origins vary between age-classes, and (3) between sex-classes.

METHODS

Samples from Migrants

Migration monitoring was conducted along the south-eastern shore of Beaverhill Lake at the Beaverhill Bird Observatory (BBO, 53°32.7′N, 113°29.4′W). Capture techniques followed the protocol described in Priestley and Priestley (2005), using four mist nets and continuous broadcasts of Northern Saw-whet Owl breeding calls.

All captured owls were fitted with numbered United States Geological Survey aluminum leg bands. Unflattened wing chord (mm) and body mass (g) measurements were taken. The sex of each owl was assigned based on the sexing technique developed in Chapter 2. The age of each owl was determined using criteria outlined by Pyle (1997). The remex and rectrix feather moult pattern of each bird was documented. Each remex and rectrix feather was classified as 'new', 'older' or 'oldest'. Generally, newer feathers are darker brown and less frayed; older feathers are lighter brown and more frayed (Fig. 3-2)(Pyle 1997). A new feather was clipped from the remex or rectrix feather tracts of each bird. Feathers were placed into #3 coin paper envelopes and these were sealed with tape. Feather samples were stored dry and at room temperature for a period of 12 - 38 months.

Feather samples from 181 Northern Saw-whet Owls were analyzed for this study. Thirty samples were randomly chosen from HY and AHY owls collected in the autumns of 2003, 2004 and 2005 except that 31 AHY owls were sampled in the autumn of 2005. Only one new feather (grown in the current year) from each bird was analyzed for this study because I was only investigating the travel between the location where the owl spent the most recent breeding season and the autumn monitoring station.

Nestling Samples

In addition, feather samples were collected from 11 Northern Saw-whet Owl nestlings from a nest box study (Priestley et al. 2005). The average distance between the nests where nestling feathers were collected from BBO was 30.1 km (range: 0.1 km to 45.0 km) to the west with an average true bearing of 268.5° (range: 245° to 316°). Feathers from nestlings were used to determine an expected stable isotope ratio value for Northern Saw-whet Owl feathers that were grown in the immediate area around Beaverhill Lake. These results provide a reference against which the migrant samples were compared.

Natal plumage of Northern Saw-whet Owl hatchlings is replaced by juvenile plumage, commencing at least seven days after hatching (Cannings 1993). Only juvenile plumage feathers were collected because the stable isotope analyses results from natal down can be more indicative of the diet of the female that produced the eggs than that of the young bird, itself, thus reflecting the prebreeding location of the food that was consumed by the AHY female while she was migrating (Duxbury et al. 2003).

The average distance between the nests where nestling feathers were collected from BBO was 30.1 km (range: 0.1 km to 45.0 km) to the west with an average true bearing of 268.5° (range: 245° to 316°).

Stable-hydrogen Isotope Ratio Analyses

Feathers were first soaked in a 2:1 solution of chloroform and methanol for at least 48 hrs. Samples were rinsed twice with clean 2:1 chloroform and methanol solution and then allowed to dry in a fume hood for at least 48 hrs.

Sub-samples were cut only from the tip of cleaned feathers to avoid possible variation of stable-hydrogen isotope ratios within feathers (Wassenaar and Hobson 2006). The mass of sub-samples, determined using a microbalance (Sartorius, Model CP2P), ranged between 0.237 mg and 0.675 mg. Weighed sub-samples were packed into small (3.5 × 5.0mm) silver capsules which were crushed into cubes and transferred into plastic 96-position sample trays. Packed samples were stored in the laboratory for at least 10 days prior to analyses.

Sub-samples were analyzed for stable-hydrogen isotope ratios at the Biogeochemical Analytical Laboratory at the University of Alberta. A EuroVector EuroEA3028-HT element analyzer was used to pyrolyse sub-samples. The resolved H_2 sample was analyzed with a GV Instruments IsoPrime mass spectrometer.

Lott and Smith (2006) reported systematic shifts in stable-hydrogen isotope ratios when feathers were reanalyzed several months to a year after feathers were first analyzed. This type of temporal effect could introduce unpredictable bias that might promote erroneous conclusions in comparing the results from different feather samples. To minimize this potential bias, all feathers for these comparisons were analyzed within 8 days (between 24 November and 1 December 2006). In addition, feathers were analyzed in collection-year batches to minimize potential biases in within-year comparisons (e.g., origins of age-classes and sex-classes). All feathers within each batch were analyzed on the same day. Results were reported in per-mil units (‰) and were normalized on the standard VSMOW-SLAP scale.

Data Analyses

To estimate the direction of dispersal in the autumn, I compared the distribution of δD values from local nestling owls and the values obtained from HY and AHY owls that were caught during the autumn. I used t-tests to determine whether (1) δD values obtained from HY owls differed between years, (2) δD values obtained from AHY owls differed between years, (3) δD values differed between sexes, and (4) δD values obtained from AHY owls differed from δD values obtained from HY owls for each year.

RESULTS

The average δD value of local nestling feathers was -127.8‰ (SD = 1.6, *n* = 11) and ranged between -125.2‰ to -129.6‰.

Post-fledging Dispersal

Of the δD values from HY migrants, 79% (*n* = 90) were above the range of samples for local nestlings and 9% and 12% were within, and below, the range respectively. A GLM (General Linear Model) ANOVA indicated that isotopic values differed significantly among years within the HY category among years ($F_{2,87} = 17.45$, $P < 0.01$)(Table 3-1, Fig. 3-3).

HY owls had: δD values that were increasingly depleted in 2003, 2004, and 2005 with significance of differences as follows: 2003 to 2004 $t_{58} = 3.18$, $P < 0.01$; 2003 to 2005 $t_{58} = 5.24$, $P < 0.01$ and 2004 to 2005 $t_{58} = 3.30$, $P < 0.01$. Within the HY age category, δD values of males ($n = 46$) and females ($n = 21$) did not differ ($t_{65} = -0.10$, $P = 0.46$).

Post-breeding Dispersal

In every case ($n = 91$), the δD values from the AHY migrants were higher than the range of δD values from the local nestling samples. A GLM ANOVA indicated that isotopic values differed significantly among years within the AHY age category ($F_{2,88} = 8.27$, $P < 0.01$)(Table 3-1, Fig. 3-4). AHY owls had δD values that were less depleted in 2003 than 2005 ($t_{59} = 4.02$, $P < 0.01$) and less depleted in 2004 than 2005 ($t_{59} = 2.27$, $P = 0.03$) suggesting that breeding origins were further north during 2005 than 2003 or 2004. For AHY owls, δD values did *not* differ significantly between 2003 and 2004 ($t_{58} = 1.78$, $P = 0.08$) suggesting that breeding origins were similar in these years. Within the AHY age group female ($n = 60$) δD values were less depleted than male ($n = 9$) δD values ($t_{67} = 1.62$, $P = 0.05$). Thus, I conclude that females travel further during post-breeding dispersal.

Post-fledging and Post-breeding Comparison

δD values differed significantly between HY and AHY owls in all years (2003: $t_{58} = -6.87$, $P < 0.01$; 2004: $t_{58} = -11.06$, $P < 0.01$; 2005: $t_{59} = -9.84$, $P < 0.01$). On average, δD values were more depleted for HY than for AHY owls, suggesting that owls traveled further post-breeding than post-fledging (Fig. 3-4). Variation in δD values of feathers tended to be less in HY than in AHY birds, except in 2003 when δD variation in HY birds was twice that measured in 2004 and 2005 (Table 3-1, Fig. 3-3). During 2003, the distribution of δD values for HY owls was skewed left, suggesting that a few HY owls traveled further during post-fledging dispersal that year, even though most HY owls originated in relative close proximity to Beaverhill Lake in all three years.

DISCUSSION

The isotope data indicate that the majority of Northern Saw-whet Owls caught at Beaverhill Lake in the autumn grew their most recent remix and rectrix feathers at latitudes south of the point of capture. Most of the owls caught in the autumn had δD values that were significantly less depleted than -127.8‰, the average δD value obtained from local nestling owls. HY owls grow remix and rectrix feathers before fledging and retain these feathers for their first year, moulting again as AHY owls after breeding but before autumnal movement (Cannings 1993). Therefore, I conclude that most Northern Saw-whet Owls caught during the autumn at Beaverhill Lake had spent the most recent summer at more southerly latitudes.

Lott and Smith (2006) produced a δD map for North American raptors but advised caution when comparing δD values from other studies to their map because they noted shifts in δD values between analyses. They suggested that new data should be calibrated (using a subset of the feathers that were used to create their original δD map) before the results from new analyses are plotted on their map. However, I did not calibrate my data using a subset of their feathers because δD data from nestling feathers that were collected locally were within the range reported for my area by the Lott and Smith (2006) map. Thus, I assumed that the data were comparable to that from the Lott and Smith (2006) map and used it to explore general patterns.

Seven percent (*n* = 6) of the HY owls had δD values that were larger than -90‰ (Fig. 3-4), showing that they traveled from a location that was south of the point of capture based on the maps of Lott and Smith (2006) and Cannings (1993). Eleven percent (n = 10) of HY owls had feathers with δD values that were greater than -99‰. These owls could not have originated in Alberta; however, 60% (n = 6) of these owls could have traveled east from southern British Columbia or west from southern Saskatchewan.

Sixty-four percent (*n* = 58) of the AHY owls had δD values that were more enriched than -90‰ (Fig. 3-4). These owls could only have traveled from a location that was south of the point of capture according to maps of Lott and Smith (2006) and Cannings (1993). Eighty-one percent (n = 74) of AHY owls had δD values that were insufficiently depleted to have originated in Alberta; however, 64% (n = 47) of these owls could have traveled east from southern British Columbia or west from southern Saskatchewan.

The magnitude of the distance between the inferred southern breeding origins of these owls and my field station is surprising in some cases. For example, 2% (*n* = 2) of the AHY owls had δD values that ranged between -40‰ to -50‰. Northern California is the closest location to the BBO from which these owls could have originated, according to Lott and Smith (2006). Ten percent (*n* = 9) of the AHY owls had δD values that ranged between -50‰ to -70‰. The simplest explanation is that these birds traveled from the state of Washington.

Autumnal movement of Northern Saw-whet Owls has been generally referred to as migration (Taverner and Swales 1911, Catling 1971, Holroyd and Woods 1975, Weir et al. 1980, Slack and Slack 1987, Russell et al. 1991, Duffy and Kerlinger 1992, Cannings 1993, Brinker et al. 1997, Whalen and Watts 2002, Frye and Gerhardt 2003, Priestley and Priestley 2005). Cannings (1993) stated that large numbers of Northern Saw-whet Owls 'migrate', even though some are year-round residents. Holroyd and Woods (1975) reported seasonal increases in the number of Northern Saw-whet owls that were banded during 1955-69 in eastern North America, and assumed that these birds were migratory. Further, they reported that the majority of the autumn banded owls recovered in the same season were found southeast of the original banding locations and spring banded owls recovered in the same season were found north of the banding locations, indicating that these populations exhibit a typical north-south migration pattern. Similarly, Brinker et al. (1997) reported autumnal movement between banding stations in the Eastern United States; all recovered owls were found south of the location where they were banded.

The idea that the Northern Saw-whet Owl is simply a migrant in Alberta is not corroborated by my isotope data. The following three hypotheses could explain this inconsistency: (1) post-breeding dispersal northwards precedes southern autumn migration, (2) Northern Saw-whet Owls are nomadic in Alberta, moving rather haphazardly, in response to prey availability and other factors and (3) different strategies are used to deal with seasonal change in prey across the owl's range.

Hypotheses to explain isotope-implied movements

(1) Post-breeding Dispersal then Southern Migration

Northern Saw-whet Owls could disperse generally northward after breeding and then migrate southward in the autumn. This would explain why δD values obtained from newly moulted feathers collected at Beaverhill Lake from migrants were more enriched than the δD values obtained from the nestlings near my study area.

Despite being rare, this pattern of northward post-breeding dispersal prior to autumn migration does occur in a few species. For example, Steenhof et al. (2005) reported on movement in female Prairie Falcons (*Falco mexicanus*) that were fitted with satellite telemetry transmitters in southern Idaho. Most female Prairie Falcons moved northeast onto the Great Plains, perhaps in response to prey abundance, after breeding to occupy summer grounds for a period of 1 - 4 months. The main prey of the falcons during the breeding season, the piute ground squirrel (*Spermophilus mollis*), move underground in the early summer to enter torpor and are no longer available to the falcons by early July (Steenhof and Kochert 1988, Van Horne et al.

1997). In late summer the falcons migrate south to reoccupy their wintering range.

Small mammals are the main prey of the Northern Saw-whet Owl but owls also opportunistically consume birds (especially during passerine migration) and invertebrates (Cannings 1993, Holt and Leroux 1996, Whalen et al. 2000, Priestley et al. 2005). These prey are available throughout the Northern Saw-whet Owl’s range during spring and summer periods. Unlike for the Prairie Falcon, the main prey of the Northern Saw-whet Owl does not become regularly unavailable post-breeding. Therefore, if Northern Saw-whet Owls undergo post-breeding dispersal they are likely motivated to do so for different reasons than Prairie Falcons are.

Southern (1974) analyzed band data from >18,000 Ring-billed Gulls and >6,500 reports of wing-marked Ring-billed Gulls (*Larus delawarensis*). After the breeding season a portion of the Ring-billed Gull population that bred in the Great Lakes Region dispersed northward prior to migrating south in the autumn. However, few gulls moved very far northward (e.g., Yukon, British Columbia, Saskatchewan, James Bay and

Quebec) and the region into which gulls moved was considered part of the secondary post-breeding range. Southern (1974) singled out 47 banded or wing-marked birds that showed unusual and large postbreeding dispersal distances. Of these, only 0.07% (*n* = 11 of the total banded or wing-marked birds) had moved north.

The isotope data indicate that a large portion of the Northern Saw-whet Owls that I caught in the autumn had southern breeding origins. Thus, it is unlikely that this population uses a strategy in common with gulls. In the case of Ring-billed Gulls, pre-migration northward dispersal appears to reflect only the wanderings of a few individuals, whereas a large portion of the Northern Saw-whet Owl population seems to move northward after breeding.

(2) Nomadism

Marks and Doremus (2000) suggested that Northern Saw-whet Owls are nomadic in some parts of their range because they found low breeding-site fidelity during a 14-year nestbox study in south-western Idaho. Cote et al. (2007), suggested based on trapping and banding results from the north-eastern edge of the owl's range in central Quebec, Canada that Northern Saw-whet owls were not migrating from more northerly latitudes. Instead, they suggested the owls could be simply dispersing northward after breeding or fledging. As an example, they reported that an AHY female banded during a nesting attempt was recovered 350 km north of its breeding site later the same year. Nonetheless, they pointed out, Northern Saw-whet Owls are regularly seen at their site in the autumn in large numbers and are therefore more likely migrating (Cote et al. 2007).

It is unlikely southern origin of all AHY and most HY owls is a function of nomadic movement. If the owls were moving nomadically my sample should have been represented by a larger proportion of owls that had moved from the north, east or west.

(3) More than one Strategy

Northern Saw-whet Owl movement patterns could vary across their range. For example, Northern Saw-whet Owls that occur in eastern North America could have a stronger propensity to migrate along north-south corridors, as described by Holroyd and Woods (1975). Nomadism might be more common in western North America, as suggested by Marks and Doremus (2000). In addition to exhibiting migratory and nomadic behaviour, some Northern Saw-whet Owls could be year-round residents. This 'mixed' strategy would not likely be detected by my study because data were only collected at one site and during the autumn season. Occurrence of year-round residency could be investigated using stable isotope ratio analyses of feathers collected from AHY owls at nests or by collecting feathers from owls that were caught at various sites during the winter period. It would be interesting to investigate what factors drive the switch in individual behaviour, or if this sort of variation has a genetic basis.

Other owl species exhibit more than one dispersal behaviour to deal with the winter period. Factors that influence which dispersal behaviour is employed can include breeding site latitude or longitude, prey abundance, and nest availability. The Short-eared Owl (Holt and Leasure 2006) and Long-eared Owl (Marks et al. 1994) both exhibit migratory movements, year-round residency and nomadism. The Elf Owl (*Micrathene whitneyi*)(Henry and Gehlbach 1999), Spotted Owl (*Strix occidentalis*)(Gutierrez et al. 1995), Burrowing Owl (*Athene cunicularia*)(Haug et al. 1993), Barn Owl (*Tyto alba*)(Marti 2005), Flammulated Owl (*Otus flammeolus*)(McCallum 1994) and Northern Pygmy Owl (*Glaucidium gnoma*)(Holt and Petersen 2000) all exhibit migratory movements and year-round residency. The Boreal Owl (Hayward and Hayward 1993) and Great Gray Owl (Bull and Duncan 1993) exhibit year-round residency and nomadism.

Other raptors also exhibit more than one strategy to help them get through times when prey availability is diminished. The Bald Eagle (*Haliaeetus leucocephalus*) exhibits migratory movements, year-round residency and nomadism (Buehler 2000). The Golden Eagle (*Aquila chrysaetos*)(Kochert et al. 2002), Northern Goshawk (*Accipiter gentilis*)(Squires and Reynolds 1997), Cooper's Hawk (*Accipiter cooperii*)(Curtis et al. 2006), Sharp-shined Hawk (*Accipiter striatus*)(Bildstein and Meyer 2000), Gray Hawk (*Asturna nitida*)(Bibles et al. 2002), Short-tailed Hawk (*Buteo brachyurus*)(Miller and Mayer 2002), Zone-tailed Hawk (*Buteo albonotatus*)(Johnson et al. 2000), Red-tailed Hawk (*Buteo jamaicensis*)(Preston and Beane 1993), Red-shouldered Hawk (*Buteo lineatus*)(Crocoll 1994), Common

Black-Hawk (*Buteogallus anthracinus*)(Schnell 1994), Peregrine Falcon (*Falco peregrines*)(White et al. 2002), Merlin (*Falco columbarius*)(Sodhi et al. 2005) and Osprey (*Pandion haliaetus*)(Poole et al. 2002) exhibit year-round residency and migratory movements.

Natal/Breeding Origins and Age-class

In all years, δD values of HY owl feathers were more depleted than δD values of AHY owls which implies that Northern Saw-whet Owls do not move as far during post-fledging dispersal as they do during post-breeding dispersal. Northern Saw-whet Owls are fed mainly by the male parent for at least one month after fledging (Cannings 1993). Therefore, HY owls are accustomed to waiting for food delivery. Once food is no longer provided, they must learn how to find and catch prey. Perhaps they are not inclined to travel great distances to search for food during this learning stage. Conversely, AHY owls have more hunting experience that would presumably include the ability to more effectively recognize good hunting habitat. Therefore, hunting experience could influence the distance that Northern Saw-whet Owls travel in search of prey.

HY owls could also be in better condition after fledging than the AHY owls that have just raised young and thus body condition might stimulate AHY birds to search for areas with higher prey abundance. During the breeding season, the adults expend a great deal of energy to produce the eggs (in the case of the female) and feed the young (in the case of the male). If the young were in better condition than the adults they could be less motivated than adult owls to leave the area near their nest to search out areas with higher prey densities.

Body mass is a common proxy for the condition of birds (Chastel et al. 1995). Heavier birds are assumed to be in better condition because they have been able to find enough resources to build fat reserves. Chapter 2 described the use of DNA to sex Northern Saw-whet Owls (n = 363) that were moving through the Beaverhill Lake area during the autumn. The average weight to wing mass index value for AHY females (mean = 0.68 g/mm, n = 67) did not differ from the value for HY females (mean = 0.67 g/mm, n = 185, t_{114} = 1.36, P = 0.18) in this sample of Northern Saw-whet Owls. Similarly, the average weight to wing mass index value for

AHY males (mean = 0.61 g/mm, n = 17) did not differ from the value for HY males (mean = 0.63 g/mm, n = 94, $t_{28} = -1.61$, P = 0.18). These results suggest that AHY age-class and HY age-class birds do not differ in condition for either sex. Therefore, it is unlikely that the difference observed between post-fledging and post-breeding dispersal distances is a function of differences in physical condition between age-classes.

The large difference in δD values between HY and AHY owls could, in-part, be explained by the reproductive output of the AHY owls in the most recent breeding season. Part and Gustafsson (1989) found that Black Kites (*Milvus migrans*) disperse further after a failed nesting attempt than after successful nesting. Perhaps AHY Northern Saw-whet Owls, whose feathers had the most enriched δD values, were dispersing following a nesting failure.

Breeding Origins and Sex-class

δD values from AHY females were less depleted than those from AHY males, suggesting that females move greater distances during post-breeding dispersal than males. In addition, the sample of Northern Saw-whet Owls caught during migration biased toward females (Chapter 2). Overall, 69.4% of the 363 birds that provided feather samples from BBO during the autumn were females. Thus, it seems likely that females are also more likely to disperse into the Beaverhill area after the breeding season than males.

Greenwood (1980) proposed that resource defense by males could explain female-biased dispersal. Reproductive fitness of male birds is generally determined by their ability to acquire and hold resources. Thus, females choose to mate with males that are able to supply the largest amount of resources. Males remaining on a territory would be more likely to hold and efficiently use territories than those that leave and have to re-establish themselves and re-learn the location of good hunting perches and nest structures (Greenwood 1980). As a consequence of that system, female dispersal facilitates gene flow and results in lower rates of inbreeding depression.

During the breeding season, male Northern Saw-whet Owls use breeding calls to attract mates (Cannings 1993). In addition, males will occasionally put prey into potential nests (C. Priestley pers. obs.) to further entice females to breed. The advertising call and tendency to cache prey in potential nests are behaviours that are consistent with Greenwood's (1980) hypothesis that males exhibit greater site fidelity where resources are available and that females tend to move around so that they will have the opportunity to choose males with the highest reproductive fitness.

Differences between male and female movement patterns have been reported for the Boreal Owl, the most closely related species to the Northern Saw-whet Owl (Lundberg 1979, Lofgren et al. 1986, Korpimaki 1988). Boreal Owl females change territories between breeding attempts but males generally remain on established territories after successful breeding. Korpimaki (1988) suggested that this discrepancy between the movement patterns of the sexes could be attributed to male defense of tree cavities for nesting. Similar to Boreal Owls, Northern Saw-whet Owls also nest in cavities. Thus, limited nesthole availability could contribute to the differences between the movement patterns of male and female Northern Saw-whet Owls.

TABLES

Table 3-1. Summary of hydrogen isotope analyses of feathers collected from Northern Saw-whet Owls at Beaverhill Lake, Alberta, Canada during the autumns of 2003, 2004 and 2005.

Sample	n	Mean +/- 1SD	95% CI	Range
HY				
2005	30	-124.2 +/- 8.2	+/-3.1	-137.9 to -108.3
2004	30	-117.0 +/- 8.6	+/-3.2	-130.7 to -90.8
2003	30	-105.6 +/- 17.5	+/-6.6	-129.2 to -60.6
AHY				
2005	31	-93.3 +/- 15.2	+/-5.6	-114.2 to -41.7
2004	30	-85.2 +/- 13.2	+/-4.9	-108.2 to -49.5
2003	30	-79.5 +/- 11.2	+/-4.2	-103.6 to -56.2

FIGURES

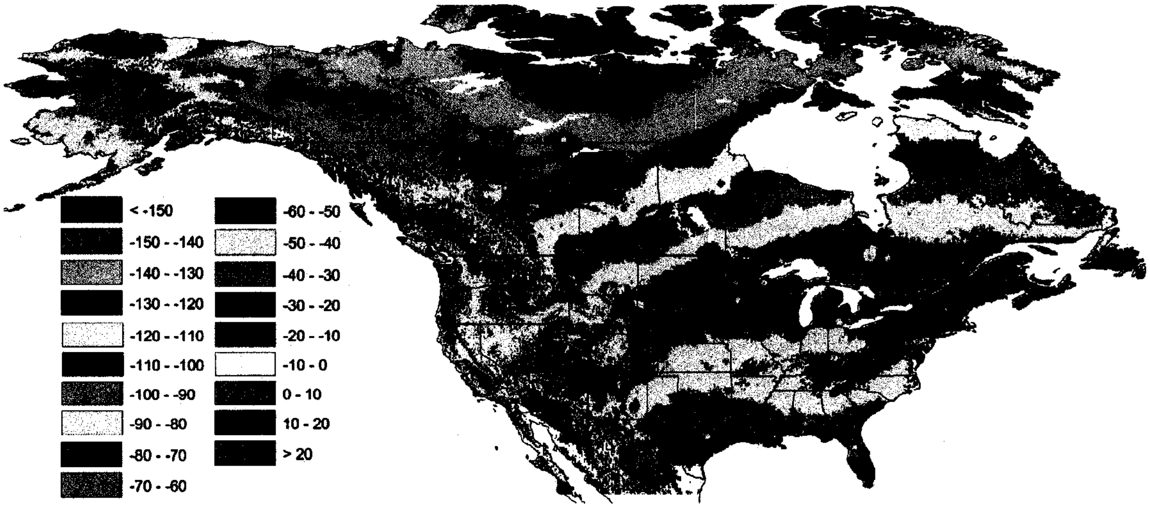

Figure 3-1. Map of δD_f for North American raptors reproduced from Lott and Smith (2006). Given standardized lab analysis, δD_f values from raptors of unknown origin captured during migration or at wintering sites can be matched to values on the map to suggest the area of owl origin. In general, δD_f values decrease with increasing latitude. However, regional complexity in spatial patterns of δD_f increases in areas of topographic relief and along the Pacific coast, making interpretation of results based solely on δDf problematic for some species, particularly in western North America. This map should be considered carefully in relation to the geographic range of a study species before sampling δD_f at migration or wintering sites to evaluate whether measurements of δD_f can clearly differentiate among potential source areas.

Figure 3-2. Second-year Northern Saw-whet Owl feather pattern. Bright pink outer primary feathers and inner secondary feathers are newly grown. Light pink inner primary feathers and outer secondary feathers are retained from the previous year.

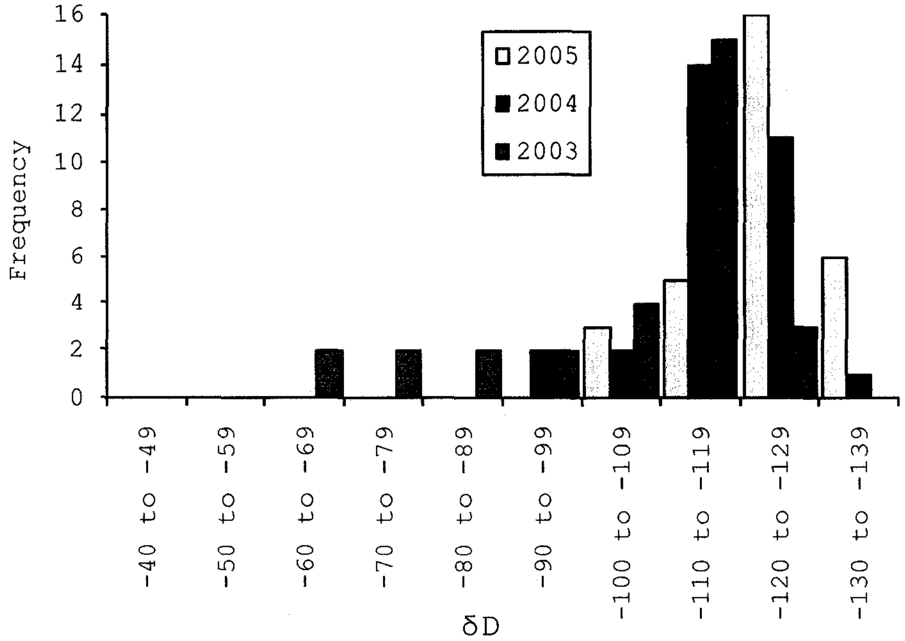

Figure 3-3. Frequency of stable hydrogen isotope values from HY Northern Saw-whet Owl feathers collected at Beaverhill Lake, Alberta, Canada during the autumns of 2003, 2004 and 2005.

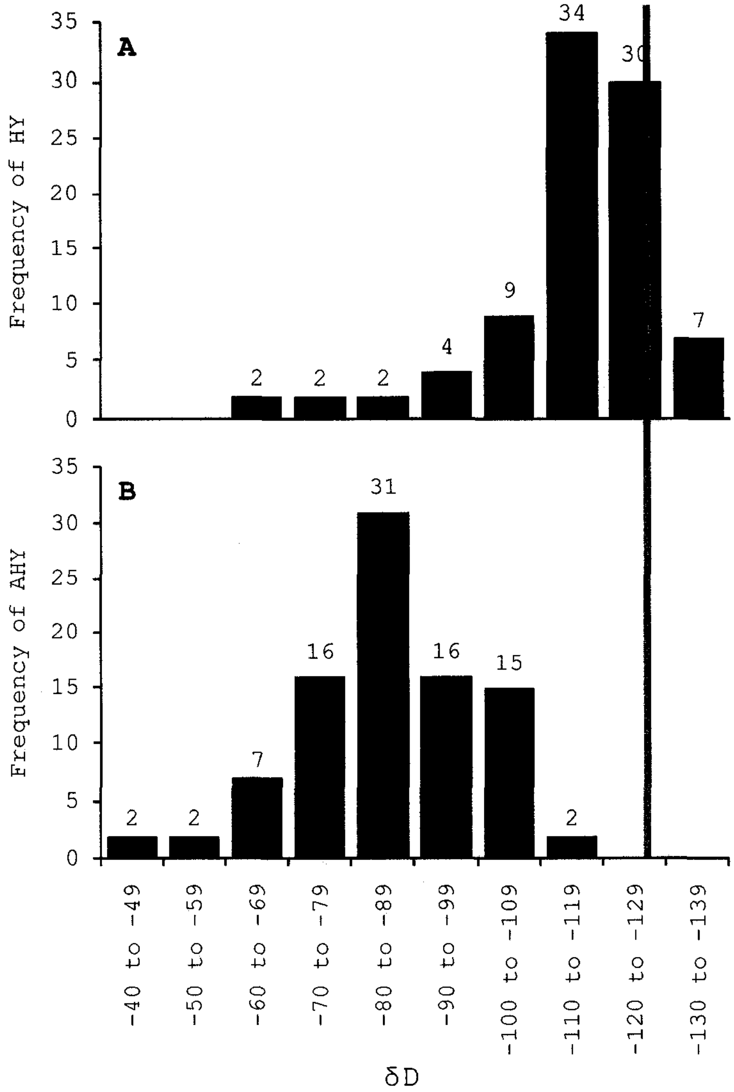

Figure 3-4. Frequency of stable hydrogen isotope values from (A) HY (*n* = 90) and (B) AHY (*n* = 91) Northern Saw-whet Owl feathers collected at Beaverhill Lake, Alberta, Canada. Data from 2003, 2004 and 2005 are pooled for each age-class. The grey line represents the average stable-hydrogen isotope value obtained from local nestlings (127.8‰).

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Chapter 4: NATAL, BREEDING AND WINTER DISPERSALS OF THE NORTHERN SAW-WHET OWL

The Northern Saw-whet Owl (*Aegolius acadicus*) is a strictly Nearctic species with breeding range extending from southern Alaska, across Canada to the east coast south of the treeline, south to the northeastern United States and throughout most of the western United States but excluding the Great Plains (Cannings 1993). During non-breeding periods it can be found throughout its breeding range and across the continental United States, except in southern Texas and southern Florida (Cannings 1993). The species can be found in various types of forest habitats but it tends to be more abundant in coniferous forests and forested riparian areas (Cannings 1993). It feeds on a variety of prey including birds and invertebrates but it mainly consumes small mammals (Cannings 1993, Holt and Leroux 1996, Whalen et al. 2000, Priestley et al. 2005).

Movement patterns of the Northern Saw-whet Owl have been a recent topic of debate, focused on whether or not these birds migrate. Newton (1979 p. 180) defined migration as "a massive shift of birds twice each year between regular breeding and wintering ranges." In contrast, nomadic birds "drift from one area to another, residing for a time wherever food is temporarily plentiful" (Newton 1979 p. 181). Many authors have called seasonal movements of the Northern Saw-whet Owl migration (Taverner and Swales 1911, Mueller and Berger 1967, Catling 1971, Holroyd and Woods 1975, Weir et al. 1980, Slack and Slack 1987, Russell et al. 1991, Duffy and Kerlinger 1992, Cannings 1993, Brinker et al. 1997, Whalen and Watts 2002, Frye and Gerhardt 2003, Priestley and Priestley 2005). Holroyd and Woods (1975) and Brinker et al. (1997) used banding data to support the idea that migration characterizes eastern populations of the Northern Saw-whet Owl migrates.

Bent (1938), however, stated that the movements of the Northern Saw-whet Owl are too irregular to be considered true migration and that permanent year-round residency is more common for the species.

More recently, Marks and Doremus (2000) suggested that the Northern Saw-whet Owl could be nomadic. They reported that only one of 52 adult Northern Saw-whet Owls that were banded during the breeding season at the Snake River Birds of Prey National Conservation Area in Idaho was recovered there in a future year as a breeding bird in their study area. One male that was breeding in their study area was found 900 km NNW of their study area in a subsequent year. They suggested that the high fecundity and low apparent survival rates of the Northern Saw-whet Owl were evidence that Idaho populations were, at least in-part, nomadic.

In Chapter 3 I reported results from stable hydrogen isotope analyses of Northern Saw-whet Owl feathers that were collected during the autumn in central Alberta, Canada. I showed that many owls moving through the Beaverhill Lake area in autumn had been to the south in the summer because the isotope values from the most recently moulted remiges and rectrices of after-hatch year (AHY) owls were indicative of a southern origin based on continental hydrogen isotope patterns (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Lott and Smith 2006). To explain the discrepancy between what the isotope data indicated about Northern Saw-whet Owl movement and what banding data have shown (Holroyd and Woods 1975), I hypothesized that owls in the west undergo a post-breeding dispersal which might be a nomadic movement.

In addition to exhibiting migratory movements and nomadism, some Northern Saw-whet Owls could be year-round residents. Other owl species employ multiple dispersal strategies, including year-round residency, to deal with seasonal changes in prey abundance. These species include Short-eared Owl (Holt and Leasure 2006), Long-eared Owl (Marks et al. 1994), Elf Owl (*Micrathene whitneyi*)(Henry and Gehlbach 1999), Spotted Owl (*Strix occidentalis*)(Gutierrez et al. 1995), Burrowing Owl (*Athene cunicularia*)(Haug et al. 1993), Barn Owl (*Tyto alba*)(Marti 2005), Boreal Owl (*Aegolius funereus*)(Hayward and Hayward 1993), Great Gray Owl (*Strix nebulosa*)(Bull and Duncan 1993), Flammulated Owl (*Otus flammeolus*)(McCallum 1994) and Northern Pygmy Owl (*Glaucidium gnoma*)(Holt and Petersen 2000). The analyses presented in Chapter 3 would not have detected individuals that stayed on site year-round because feathers were collected from owls during the autumn at one fixed point. In order to use stable isotope ratio analyses to identify residents, feathers would have to be collected from owls at various locations and during the seasons when owls were not dispersing such as the breeding season and possibly the winter.

The moulting pattern in Northern Saw-whet Owl is what Howell et al. (2003) called the Complex Basic Strategy (CBS; Fig. 4-1). This pattern is characterized by (1) annual moult cycles in which one basic plumage replaces a preceding basic plumage via prebasic moult and (2) a single (as in the case of the Northern Saw-whet Owl), or occasionally a second, additional moult (termed preformative moult) within the first moult cycle which yields a formative plumage. During the preformative moult Northern Saw-whet Owls replace all body plumage but do not replace either remiges or rectrices. These retained feathers are referred to as B1F(s) in this chapter. During the first moulting cycle, CBS birds develop the first basic plumage (subsequently referred to as B1, which is replaced by formative plumage (subsequently referred to as F1). In the second moult cycle the second basic plumage (subsequently referred to as B2) replaces F1, during the third moult cycle the third basic plumage (subsequently referred to as B3) replaces B2, and so on. Prebasic moults do not necessarily involve the replacement of all feathers.

For most species, prebasic moults occur during the late summer while birds are on their breeding grounds [as is the case with the Northern Saw-whet Owl (Pyle 1997)].

During each prebasic moult Northern Saw-whet Owls usually replace all rectrices (Cannings 1993) but only some remiges (Evans and Rosenfield 1987). When a Northern Saw-whet Owl is in its B2 plumage it usually possesses B1Fs and new feathers that were grown when the B2 commenced. These new feathers are referred to as B2F(s) here. The same rationale and terminology applies to subsequent moults. In addition to B3Fs and B2Fs, owls in B3 plumage also occasionally possess B1Fs. Unless B1Fs are present, it is not possible to determine whether a Northern Saw-whet Owl is in B3 or another subsequent basic plumage. I characterized the plumage of such owls as (B3 + x), where x refers to the unknown number of basic plumages that have occurred beyond B3. The range of x is 0 to ∞. Owls that are in their (B3 + x) usually possess (B3 + x - 1)Fs and new feathers that were developed when (B3 + x) commenced. These new feathers will be referred to as (B3 + x)Fs here. In addition to (B3 + x)Fs and (B3 + x - 1)Fs, owls that are in (B3 + x) may also occasionally possess (B3 + x - 2)Fs.

Northern Saw-whet Owls grow B1Fs [i.e., 'juvenile' feathers (Howell et al. 2003)] prior to fledging (Cannings 1993). B2Fs are grown at the end of an owl's first breeding season on the breeding grounds (Cannings 1993). Subsequent prebasic moults, that yield B3Fs and (B3 + x)Fs, occur at the end of subsequent breeding seasons.

Because Northern Saw-whet Owls moult their plumage on their breeding grounds, stable-hydrogen isotope ratio analysis of their feathers can be used to investigate natal, breeding and winter dispersal. Natal dispersal is the distance between an owl's fledging site and its first breeding territory. Breeding dispersal is the distance between successive breeding territories. Winter dispersal is the distance between fledging site or breeding site and where an owl was found during the winter.

In this chapter I used stable-hydrogen isotope ratios from feathers collected from Northern Saw-whet Owls during the breeding and winter seasons to better understand their movements. My objectives were to (1) determine natal dispersal distances of Northern Saw-whet Owls breeding in central Alberta, (2) determine breeding dispersal distance and direction of breeding Northern Saw-whet Owls, (3) determine winter dispersal distances and direction of breeding Northern Saw-whet Owls, (4) determine whether dispersal distances differ between sex classes, seasons or years. In this chapter I report results from stable hydrogen isotope ratio analyses of feathers collected from Northern Saw-whet Owls caught during the breeding seasons of 2004 and 2005 and the winters of 2003/04 and 2004/05.

METHODS

Breeding Season Samples

Feather samples were collected from nestling and breeding AHY owls during the breeding season at 18 nest boxes within 70km of Edmonton, Alberta, Canada.

Different methods were used to capture adult males and females. AHY female owls were caught at nests while they were incubating eggs or brooding young during May and June of 2004 and 2005. A small hand net was placed over the entrance hole of the nest and the female either jumped into the net or stayed in the nest and was taken out by hand. AHY males were caught while they were delivering food to the nest using a modified version of the nest-mounted swing-door trap described by Saurola (1987) during May and June of 2004 and 2005. I did not use the second swing door between the back of the trap and the nest that Saurola (1987) suggested. Instead, hardware cloth that was fixed to the back of the Saurola (1987) trap covered to entrance hole to maintain separation between the male and the nest during trapping. The trap was removed from the front of the nest to remove captured males from the trap on the ground. The prey item that the male was delivering was identified and then put into the nest after the male was removed from the trap.

Some males were reluctant to enter the trap while others did not appear to be suspicious of the trap. Leaving a trap up too long could have interfered with food delivery, especially for nests that were provisioned by a male that was trap-shy. Therefore, I did not attempt to trap a male for more than two hours per night and I maintained intervals between trapping attempts of at least five-days, the upper limit of the between-trap interval suggested by

Saurola (1987). Extra food was not added to nests during trapping attempts, as was suggested by Saurola (1987), to avoid affecting the stable isotope ratios of feathers developed by nestlings. Rather, the amount of time spent trapping males was limited (both within and between nights) so that prey delivery disturbance was minimized.

Breeding owls were aged using feather colour and wear, as described by (Pyle 1997). Owls that were breeding for the first time were called second year (SY); the following year they were classed as third year (TY); and for all subsequent years, classed as after-third-year (ATY). None of the feathers collected from SY owls were analyzed for this study because I wanted to focus on owls that had more than one generation of feathers present. The following feathers [terminology of Howell et al. (2003)] were collected from owls caught during the winter. A B2F and a B1F were analyzed from each of the third-year (TY) owls. A feather from each of the different basic plumages was analyzed from the after-third-year (ATY) owls.

Body feather samples were collected from single nestlings from 11 different nests encountered during a nest box study

(Priestley et al. 2005). These feathers were analyzed to determine the expected stable hydrogen isotope ratio value for Northern Saw-whet Owl feathers that were grown in the study area. The results provided a reference for interpreting isotope ratios of feather samples from breeding and winter adults.

Natal plumage of Northern Saw-whet Owls is replaced by B1 (juvenile plumage) commencing at least seven days after hatching (Cannings 1993). Only B1Fs were collected because the stable isotope analyses results of natal down can be more indicative of the diet of the female that produced the eggs than of the young itself, thus reflecting the prebreeding location of the food that was consumed by the adult female (Duxbury et al. 2003).

Winter Samples

Winter trapping was conducted at 10 locations within 60km of Edmonton, Alberta using a combination of mist nets and audiolure (Erdman and Brinker 1997). Two mist nets (12 m long, 2 m high and 60 mm mesh) and continuous broadcasts of Northern Saw-whet Owl breeding calls were used to capture the owls. Trapping started at least half an hour after sunset and occurred between two to four hours each night. For owls caught during the winter I analyzed A B2F and B1F feathers [terminology from Howell et al. (2003)] from owls in the SY/TY age category. Feathers from each of the different basic plumages were analyzed from owls in the ASY/ATY age category.

Field Techniques

All captured owls were fitted with numbered United States Geological Survey aluminum leg bands. Unflattened wing chord (mm) and body mass (g) were measured. During the breeding season, females were sexed by the presence of a brood patch and were trapped at the nest while they were incubating eggs or brooding young. Males were sexed by the absence of a brood patch and were caught while they were attempting to deliver food to the nest. Wire hardware cloth kept the female in the nest during male trapping attempts to be certain that it was the male that was delivering food to the nest. Sex of owls caught in the winter was assigned based on the sexing technique developed in chapter 2.

Age of each owl was estimated using criteria outlined by Pyle (1997). The remex and rectrix feather moult pattern of each bird was described as either: B1F, B2F, B3F or (B3 +x)F. These feathers can be differentiated because newer feathers are darker brown and less frayed than older feathers (Pyle 1997). The distal 4 cm of a flight feather representative of each age category was clipped from the remex or rectrix feather tracts of each bird for each feather generation that was present. Feathers were placed into #3 coin paper envelopes, subsequently sealed with tape and stored dry at room temperature for a period of 16 - 36 mo.

Stable-hydrogen Isotope Ratio Analyses

Feathers were first soaked in a 2:1 solution of chloroform and methanol for at least 48 hrs. Samples were then rinsed twice with clean 2:1 chloroform and methanol solution and allowed to dry in a fume hood for at least 48 hrs.

Sub-samples were cut only from the tip of cleaned feathers to minimize within-feather stable-hydrogen isotope ratio variation (Wassenaar and Hobson 2006). The weights of sub-samples, determined using a microbalance (Sartorius, Model CP2P), ranged between 0.237 mg and 0.675 mg. Weighed sub-samples were packed into 3.5mm × 5.0mm silver capsules; these were crushed into small cubes and transferred into plastic 96-position sample trays. Packed samples were stored in the laboratory for at least 10 days prior to analyses.

Sub-samples were analyzed for stable-hydrogen isotope ratios at the Biogeochemical Analytical Laboratory at the University of Alberta. A EuroVector EuroEA3028-HT element analyzer was used to pyrolyse sub-samples. The resolved H_2 sample was analyzed with a GV Instruments IsoPrime mass spectrometer.

Lott and Smith (2006) reported systematic shifts in stable-hydrogen isotope analyses results when feathers were reanalyzed several months to a year after a first analysis. If uncontrolled, this temporal effect could lead to erroneous conclusions when the results from the analyses of different feather samples are compared. Therefore I analyzed all feathers for this study on the same day (24

November 2006). Results are reported in per-mil units (‰) and are normalized on the standard VSMOW-SLAP scale.

Data Analyses

Through a series of calculations I converted stable-hydrogen isotope ratio values into natal dispersal isotope values, winter dispersal isotope values and breeding dispersal isotope values. Using the transformed data, I could compare breeding dispersal, natal dispersal or winter dispersal among sexes, dispersal types and years. The calculations are described below.

(1) Natal dispersal values

The stable-hydrogen isotope value of each individual owl's B1F was subtracted from the stable-hydrogen isotope value of its B2F. The products of these differences were called 'natal dispersal values'.

(2) Winter dispersal values

The average stable-hydrogen isotope value obtained from the local nestling feathers was subtracted from the stable-hydrogen isotope value obtained from the newest feather of each owl that was caught in the winter. The products of these differences were called 'winter dispersal values'.

(3) Breeding dispersal isotope values

The isotope value differences between feathers in consecutive moult series were calculated for owls caught in the breeding season and winter. For example, B3F was subtracted from B2F, (B3 + X) was subtracted from (B3 + x – 1), and (B3 + x – 1) was subtracted from (B3 + x – 2). These differences were called 'breeding dispersal values'.

I based this analysis of dispersal patterns in Northern Saw-whet Owls on the North American hydrogen-isotope gradient that has more negative δD values in the northwest and more positive δD values in the southeast (Hobson and Wassenaar 1997, Lott and Smith 2006). Therefore, dispersal values of 0‰ were assumed to indicate no dispersal. As dispersal values increased, the inferred dispersal distances increased. Positive dispersal values indicated northwestern dispersal and negative values indicated southeastern dispersal. In addition, dispersal values were converted to absolute values to investigate dispersal magnitude independently of dispersal direction.

Two-tailed t-tests were used to test whether breeding, natal and winter dispersal movements varied between males and females, seasons or years. In all cases, the null hypothesis in these tests was that owls in the two classes had equal mean dispersal isotope values. All statistical tests were performed using SPSS 16.0.

The proportion of individuals that had dispersal isotope values between 0 - 10‰ was determined for birds in each dispersal category. Owls with dispersal isotope values in this range either moulted feathers in the same area between seasons (because they remained in the same area year-round or because they returned to breeding in the same area) or moulted feathers along the same δD contour line between seasons. These low dispersal values could indicate site fidelity.

RESULTS

The average δD value of feathers from local nestlings was -127.8‰ (SD = 1.6; range -125.2‰ to -129.6‰). All nestling δD values were within the range reported by Lott and Smith (2006) for my study area.

A total of 37 feathers were collected from a group of 10 females and 8 male owls (11 ATY and 7 TY) captured during the summers of 2004 and 2005. A B2F and a B1F were analyzed from each of the TY owls. A feather from each of the two different basic plumages was analyzed from 10 of the after-third-year owls. Three feather generations were apparent in one of the after-third-year owls therefore it was possible to analyze feathers from three different basic plumages from that bird.

A total of 29 feathers were collected from 12 owls (6 females, 5 males and one of unidentifiable sex) during the winters of 2003-04 and 2004-05. Six were in the ASY/ATY age category and six were in the SY/TY age category according to criteria of Pyle (1997). A B2F and a B1F were analyzed from each of the SY/TY owls. Feathers from two different basic plumages were analyzed from one of the owls in the ASY/ATY age category. Three feather generations were apparent in five owls that were in the ASY/ATY age category therefore it was possible to analyze feathers from three different basic plumages from those birds.

Between-year comparisons

Isotope values indicative of natal dispersal did not differ between years (2003/04 compared to 2002/03: $t_{10} = -0.873$, $P = 0.40$). Winter dispersal isotope values did not differ between years (2004 to winter 2004/05 compared to 2003 to winter 2003/04: $t_9 = 1.022$, $P = 0.33$). Similarly, isotope values indicative of breeding dispersal did not differ between years (2004/05 compared to 2003/04: $t_{29} = 1.880$, $P = 0.07$; 2004/05 compared to 2002/03: $t_{18} = 1.84$, $P = 0.08$; 2004/05 compared to 2001/02: $t_{17} = 1.55$, $P = 0.14$; 2003/04 compared to 2002/03: $t_{11} = -0.682$, $P = 0.51$; 2002/03 compared to 2001/02: $t_{10} = 0.574$, $P = 0.58$; 2003/04 compared to 2001/02: $t_7 = -0.059$, $P = 0.96$). Therefore, I conclude that dispersal distances remained fairly similar between years. Thus subsequent comparisons were made with years lumped.

Natal dispersal

Isotope dispersal values indicated that natal dispersal movements could be substantial and were quite variable (Table 4-2A,B). Most (83.3%) values were negative, indicating that SY, TY, ASY or ATY owls caught in central Alberta tended to disperse southwest during natal dispersal.

Distribution of absolute natal dispersal isotope values was not skewed (γ_1 = 0.07;) and only 8% of them were between 0 - 10‰. This indicates that a relatively low proportion of first-time breeders nest in, or close to, the area where they hatched. Natal dispersal isotope values did not differ between males and females (t_{11} = -0.999, P = 0.34).

Winter dispersal

Winter dispersal movements also appeared to be quite large and variable (Table 4-2C,D). All winter dispersal isotope values were positive, indicating that Northern Saw-whet Owls caught in central Alberta during winter spent the most recent breeding season to the southeast.

The distribution of the absolute isotope dispersal values for winter dispersal was negatively skewed (γ_1 = -1.25) and 17% of them were between 0 - 10‰. Therefore, I conclude that most Northern Saw-whet Owls move a large distance to winter in Alberta, although a small proportion of owls over-winter close to where they spent the most recent breeding season. Winter dispersal isotope values did not differ between males and females (t_9 = 0.478, P = 0.64).

Breeding dispersal

Breeding dispersal movements also appeared to be quite large and variable (Table 4-2E,F). Most (65.9%) isotope values indicative of movements associated with breeding were positive. The δD values indicate that owls tended to disperse northwest between breeding seasons. Differences between δD values for feathers from local nestlings (the expected isotope value for my study area) and the newest feathers (grown during previous breeding season) were all positive. Thus, the breeding owls sampled at nests in central Alberta had been located to the southeast during the previous breeding season. In contrast, differences between isotope values of feathers grown during the two previous breeding seasons were negative for most (72.7%) owls, suggesting that these birds moved to the southeast between those seasons (Fig. 4-3).

Absolute δD values for breeding dispersal were positively skewed ($\gamma_1 = 1.01$), with 24% of breeding dispersal values 0 – 10‰ indicating that a proportion of adult owls nested in, or close to, the same area between years.

Although δD values indicative of breeding dispersal did not differ between the sexes ($t_{37} = -0.263$, $P = 0.79$), their distribution was positively skewed for males ($\gamma_1 = 1.68$); female values were not skewed ($\gamma_1 = -0.03$). For males 32% of breeding dispersal values were between 0 – 10‰ whereas, only 20% of values for females were in that range which suggests that more males than females breed in, or close to, previously occupied territories.

Comparisons of breeding, natal and winter dispersals

Dispersal values did not differ significantly between breeding and first year birds ($t_{49} = -1.572$, $P = 0.12$), nor did natal dispersal values differ from those for winter dispersal ($t_{23} = 0.955$, $P = 0.35$). However, isotope values for winter dispersal were larger than those for breeding dispersal ($t_{57} = -3.568$, $P = 0.001$), suggesting that distances between breeding and wintering sites are larger than inter-year distances between breeding sites.

DISCUSSION

Natal Dispersal

I found that 92% of the isotope values associated with natal dispersal were in the 11 - 50‰ range and that the distribution of these values was not skewed. This indicates that a large majority of Northern Saw-whet Owls move significant distances after fledging. In a meta-analysis of natal dispersal studies of terrestrial bird and mammal species Sutherland et al. (2000) showed that carnivores tended to travel greater distances during natal dispersal than non-carnivores. My findings are consistent with this pattern.

In chapter 3, I reported that Northern Saw-whet Owl movements leading to autumn distributions varied between HY and AHY owls. Stable isotope analysis showed in chapter 3 that AHY owls traveled further during post-breeding dispersal than did HY owls during post-natal dispersal. In contrast, there was no difference between the isotope values for breeding and natal dispersal. I suggest two possible explanations for those conflicting patterns. First, HY owls could continue to move throughout the winter and spring until the following breeding season. If this were the case, the continued dispersal of HY owls could account for the post-breeding to post-natal differences detected during the autumn. However, movement of Northern Saw-whet Owls in central Alberta starts in early September, gradually increases until it peaks in early October and then gradually decreases before ending in mid-November (Priestley and Priestley 2005). If owls continued to disperse throughout the winter it is unlikely that this pattern of movement would have been detected. A second more plausible explanation is that HY owls (which would become second-year owls after January 1st (Pyle 1997)) disperse further during spring movement than during autumn movement.

Winter Dispersal

I found that the majority (83%) of the isotope values indicative of winter dispersal fell in the 11 - 50‰ range. Thus, the majority of Northern Saw-whet Owls caught during winter in central Alberta had traveled a large distance. All the owls that were caught in the winter were south of the point of capture during the most recent breeding season based on what was inferred from the isotope values of their feathers.

Despite that the majority of owls appeared to disperse large distances between the breeding season and the winter, I found that 17% of the winter dispersal values were in the 0 - 10‰ range. A portion of the owls that I caught could have remained near their breeding territories during the winter and were detected in the winter sample but were missed during autumn sampling because they were resident.

Breeding Dispersal

Overall 76% of the isotope values indicating breeding dispersal of Northern Saw-whet Owls were in the 11 - 55‰ range. In addition, the direction of breeding dispersal varied among years. Comparison with the continent map showed that all owls that bred in central Alberta moved northwest following the previous summer and the direction of breeding dispersal between the two preceding summers tended to be southeast thus direction of movement varied among years. These data suggest that at least a portion of the Northern Saw-whet Owl population is nomadic, as suggested by Marks and Doremus (2000). In fact, my findings indicate that nomadism is the main strategy that Northern Saw-whet Owls employ to deal with presumed seasonal change in food supply in central Alberta.

Despite the strong evidence for nomadism in Northern Saw-whet Owls, the breeding dispersal values suggested that a smaller proportion (c. 24%, see Fig 4-4A) of owls remain on territory year-round. These owls could have been either (1) year-round residents, (2) owls that returned (after migrating) to nest on, or near, previously occupied territories or (3) owls that nested along the same δD contour line between seasons. It is reasonable to suggest that at least some of these owls stayed in or near their breeding territories because 17% (*n* = 2) of the owls caught in the winter registered dispersal values in the 0 - 10‰ range.

In contrast to the distribution of isotope values that I found associated with breeding dispersal, none of the values indicative of post-breeding dispersal of owls caught in autumn (Chapter 3) were in the 0 - 10‰ range (Fig. 4-4B). This was expected because the only year-round residents that would have been caught during the autumn would have resided near the trapping location, and the density of year-round residents was not likely to be high. Owls that were caught during the breeding season and winter, from which breeding dispersal isotope values were derived, could have been nomads, migrants or year-round residents. Year-round residents would be represented by owls that had dispersal values in the 0 - 10‰ range, as was the case with 24% of the breeding dispersal values. Therefore, inferences derived from autumn banding programs might not apply to the portion of the Northern Saw-whet Owl population that resides on territories year-round.

The Boreal Owl, the most closely related species to the Northern Saw-whet Owl, is considered a partial migrant.

AHY female and HY owls tend to move nomadically whereas AHY males tend to maintain year-round residency after their first breeding attempt (Lundberg 1979, Lofgren et al. 1986, Korpimaki 1988). Similar to the Boreal Owl, movement pattern of the Northern Saw-whet Owl seems to vary between the sexes. The female-biased sex ratios reported in Chapter 2 imply that either (1) females are more likely to disperse after the breeding season than males, or (2) females travel further than males during post-breeding dispersal. Although the isotope data contained here cannot effectively measure post-breeding dispersal, a higher proportion of male Northern Saw-whet Owls had breeding dispersal isotope values that were within the 0 - 10‰ range. This suggests that more males than females bred in, or near, previously occupied territories and that females were more likely than males to disperse after breeding.

Conclusions and Future Research Suggestions

Stable isotope ratio data can quickly provide insights about individual movement in various species (for example see: Hobson 1999, Wassenaar and Hobson 2000, Hobson and Wassenaar 2001, Meehan et al. 2001, Hobson et al. 2001, Kelly et al. 2002, Rubenstein et al. 2002, Lott et al.

2003); however, this technique has limitations. I used stable-hydrogen isotope ratios to infer the magnitude and direction of natal, breeding and winter dispersal for Northern Saw-whet Owls and to better understand movements typical of populations in central Alberta. Even though such studies shed light on movement patterns, one cannot track individuals continuously between seasons. Thus, it is difficult to interpret decisively the biological significance of the low isotope values. The data suggest that some Northern Saw-whet Owls are year-round residents, however, it is not possible to establish whether low δD vales for breeding dispersal resulted from (1) individuals that remained in the same area between seasons, (2) individuals that returned to the same breeding site between seasons, or (3) individuals that nested along the same δD contour line between seasons. Thus, I cannot reliably estimate the proportion of the population that remains in the area year-round. Other techniques, such as radio telemetry, could be used to track individual Northern Saw-whet Owls between seasons, and these might corroborate the hypothesis of year-round residency that I offer based on stable isotope ratio analyses.

The majority of feathers collected in autumn from AHY Northern Saw-whet Owls had less depleted δD values than the average value obtained from local nestling feathers. Thus, I concluded that the majority of AHY Northern Saw-whet Owls that were caught at Beaverhill Lake during autumn were located south of the capture site during the most recent breeding season. I offered three hypotheses to explain this south/north autumnal movement: (1) post-breeding dispersal northwards precedes southern autumn migration, (2) Northern Saw-whet Owls are nomadic in Alberta, moving rather haphazardly, in response to prey availability and other factors and (3) different strategies are used to deal with seasonal change in prey across the owl's range. Although the data presented here do not eliminate the first hypothesis, they do support the idea that more than one strategy, including nomadism and year-round residency, is used by the Northern Saw-whet Owl to deal with seasonal change.

Dispersal values described in this chapter clearly show that most Northern Saw-whet Owls travel large distances during natal, winter and breeding dispersal. Owls likely incurs costs during these movements such as (1) increased chance of predator encounters, (2) being less efficient at resource acquisition while traveling through unfamiliar habitats and (3) increased energetic requirements needed for movement. However, there are potential benefits of dispersing such as (1) decreased competition among relatives for resources, (2) reduced probability of inbreeding and (3) encountering new areas with more resources such as higher prey or nest densities. Because movement seems to be a regular feature in Northern Saw-whet Owl populations, we can assume that the advantages of dispersal outweigh the costs over much of the range of this species. A detailed analysis of populations with a mixed strategy, as characterizes the populations under study, could reveal how these factors interact to result in the observed distribution of tactics.

TABLES

Table 4-1. Variation in natal, winter and breeding dispersal isotope values of Northern Saw-whet Owls caught in central Alberta, Canada. All data are in absolute values.

Dispersal Type	n	Range (δD)	Mean (δD)	SE (δD)	Std. Dev. (δD)
Natal	12	9 - 46.2	27.0	3.4	12.3
Winter	12	1.1 - 50.6	32.0	4.1	14.2
Breeding	41	2.1 - 55.2	20.0	1.9	12.4

FIGURES

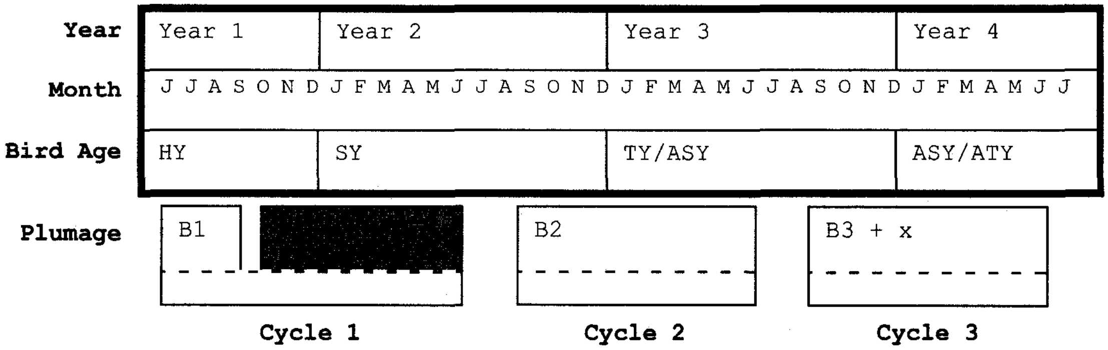

Figure 4-1. Moult pattern of the Northern Saw-whet Owl overlaid with relative dates and bird ages. Moult timing is from Cannings (1993). The plumage diagram follows Howell et al. (2003). Moults are represented by breaks between blocks. The area above the dashed line within each plumage cycle represents body feathers and the area below the dashed line represents flight feathers. HY = hatch-year; SY = second-year; TY = third-year; ASY = after-second-year; ATY = after-third-year; B1 = first basic plumage; F1 = formative plumage; B2 = second basic plumage; B3 + x = third basic plumage plus 'x' which is the unknown number of basic plumages beyond the B3 that have occurred. The range of x is 0 to ∞. All subsequent cycles have B3 + x plumages.

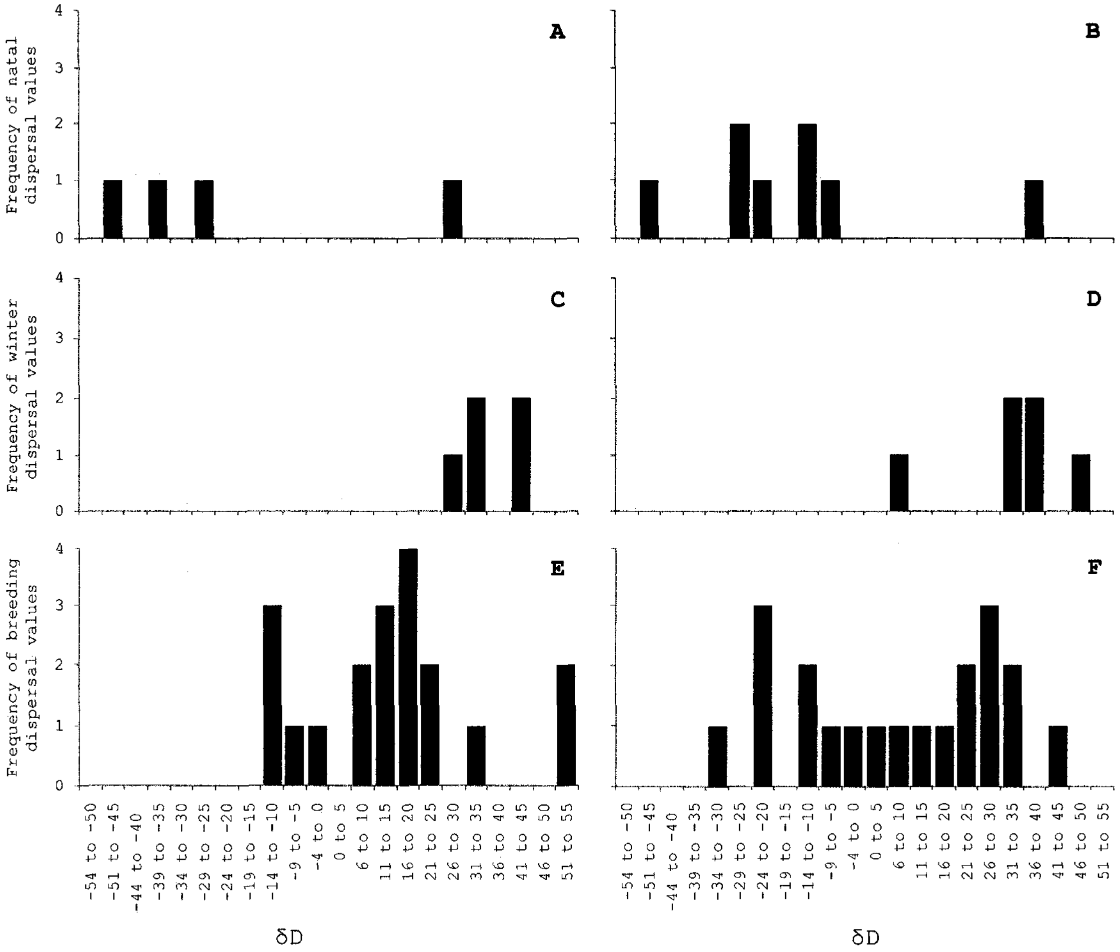

Figure 4-2. Frequency of (A) male (*n* = 4) and (B) female (*n* = 8) natal dispersal values, (C) male (*n* = 5) and (D) female (*n* = 6) winter dispersal values, and (E) male (*n* = 19) and (F) female (*n* = 20) breeding dispersal values of Northern Saw-whet Owl feathers collected in central Alberta, Canada.

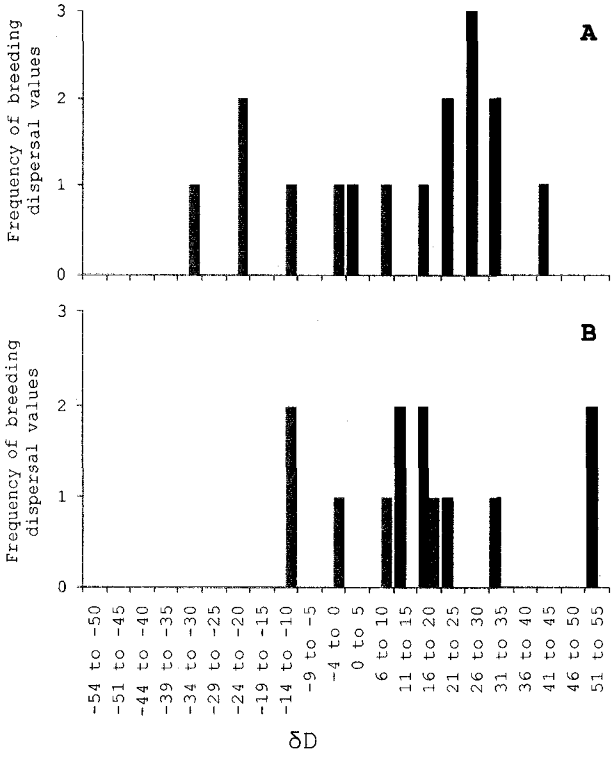

Figure 4-3. (A) Female (*n* = 16) and (B) male (*n* = 13) breeding dispersal values derived from Northern Saw-whet Owl feathers collected during the breeding season in central Alberta, Canada. Breeding dispersal between the nest in central Alberta where feathers were collected and the preceding summer are represented with black bars. Gray bars represent the breeding dispersal isotope values between the two summers prior to the summer when feathers were collected.

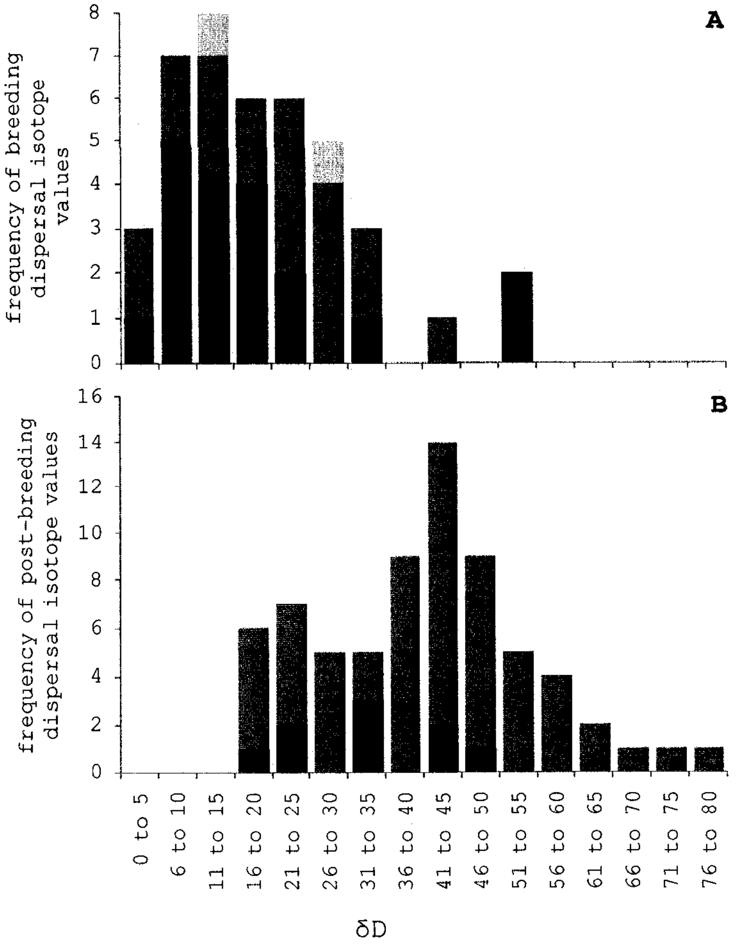

Figure 4-4. (A) Breeding dispersal isotope values (*n* = 41) of Northern Saw-whet Owl feathers collected during the breeding season and winter in central Alberta and (B) post-breeding dispersal isotope values (*n* = 69) of Northern Saw-whet Owl feathers collected during the autumn at Beaverhill Lake, Alberta (from chapter 3). Data from male, female and unknown-sex owls represented by black, dark grey and light grey bars respectively. All data are in absolute values.

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Chapter 5: CONCLUSION

Understanding the traits of species is a necessary prerequisite for effective conservation strategies. Movement patterns are a fundamental part of the traits of species and critically important to conservation management (Hobson 1999). It is important to understand timing of movement, dispersal strategies (i.e., year-round residency, migration or nomadic), degree of site fidelity to breeding sites, wintering sites and movement pathways including stopover points. With respect to the individuals dispersing, it is also important to know yearly composition of age and sex-classes, the timing of movement of individuals in different sex or age classes, and condition of birds that are moving.

SEXING CRITERIA

Sexing criteria for Northern Saw-whet Owls have been debated since the early 1970s. Earhart and Johnson (1970), Sheppard and Klimkiewicz (1976), Weir et al. (1980), Buckholtz et al. (1984), Brinker et al., (1997) and Brinker (2000) have all suggested different wing chord measurement boundaries for classifying the sex of Northern Saw-whet Owls.

In chapter 2, I presented a discriminant function based on wing chord length and body mass that provides a useful criterion for sexing Northern Saw-whet Owls in autumn. This was derived from the largest known-sex and known-age sample of Northern Saw-whet Owls that has been published to-date. None of the measurement data used to develop the model were collected during the breeding season because the difference between male and female body mass is more pronounced at that time of year (Cannings 1993). This sexing technique should be tested using DNA sexing across the range of the Northern Saw-whet Owl to determine its usefulness with respect to regional variation. In addition, this criterion should be tested throughout the year to determine whether it is effective during seasons other than autumn.

MOVEMENT PATTERNS

One of the main reasons given for operating migration banding stations is to obtain data about bird population trends (Vega and Rappole 1994). Dunn et al. (1997) showed trends of 13 obligate migrants that were caught in mist nets in southern Michigan during the autumns of 1979-91 were positively correlated with trends from the Breeding Bird Survey. They concluded that mist-netting operations can be an effective way to monitor bird populations, provided these efforts are intensive and follow standardized protocols.

Silkey et al. (1999), however, advised caution about determining population trends from mist netting, based on comparison of spot mapping and mist netting for four songbird species monitored at Point Reyes National Seashore, California during 1980-92. They found that capture rates of White-crowned Sparrow (*Zonotrichia leucophrys*), were not correlated with breeding density, although there were positive correlations for Spotted Towhee (*Pipilo maculates*), Song Sparrow (*Melospiza melodia*) and Wrentit (*Chamaea fasciata*). Therefore, data from mist netting during migration periods might not reflect actual population trends for all species.

Northern Saw-whet Owl banding is popular (Taverner and Swales 1911, Mueller and Berger 1967, Catling 1971, Holroyd and Woods 1975, Weir et al. 1980, Slack and Slack 1987, Duffy and Kerlinger 1992, Cannings 1993, Brinker et al. 1997, Whalen and Watts 2002, Frye and Gerhardt 2003, Priestley and Priestley 2005) and during 1997-06, 84 785 were banded in North America (Canadian Bird Banding Office unpubl. data). Most of these owls were trapped at banding stations during autumn.

Even though the Northern Saw-whet Owl moves seasonally, I found that populations in Alberta are partially nomadic and migratory and exhibit year-round residency. In chapter 3, I reported that all adult Northern Saw-whet Owls caught during the autumn spent the most recent breeding season at more southerly latitudes. The large breeding dispersal isotope values reported in chapter 4 indicated that Northern Saw-whet Owls did not return to the same breeding ground between years. These findings are indicative of a nomadic strategy, as suggested by Marks and Doremus (2000).

Korpimaki (1988) hypothesized that nomadism and polygyny are correlated in birds of prey. This notion was supported by comparing banding data from Ural Owls (*Strix uralensis*) and Tawny Owls (*Strix aluco*), which both have strong nest-site and mate fidelity, with data from Tengmalm's Owls (*Aegolius funereus*) and Common (or 'European') Kestrels (*Falco tinnunculus*), which tend to be nomadic and have low mate fidelity. Given that polygyny has been reported in the Northern Saw-whet Owl (Marks et al. 1989, Cannings 1993, C. Priestley pers. obs.), nomadism would be expected for this species according to the Korpimaki (1988) hypothesis.

Marks and Doremus (2000) noted that even though they seem to be nomadic, Northern Saw-whet Owls do not specialize on prey that undergo population abundance cycles. They referenced Marks and Doremus (1988), Swengel and Swengel (1992) and Cannings (1993) as evidence that voles with cyclical populations are not usually the main prey that Saw-whets use during the breeding season. However, the studies cited in evidence were conducted in the southern portion of the Northern Saw-whet Owl's range and may not necessarily reflect owl prey use further north. Priestley et al. (2005) reported that 15 of the 21 (71%) prey items found in, or being delivered to, nest boxes were voles. Of these, 8 (38% of total prey detected) were southern red-backed voles (*Clethrionomys gapperi*) and 7 (33% of total prey detected) were meadow voles (*Microtis pennsylvanicus*). Meadow vole densities cycle in 2 or 3 year intervals (Krebs et al. 1973), and though southern red-backed vole populations are not characterized by regular cycles, they do have high and low years at irregular intervals (Boonstra and Krebs 2006). Thus, voles with either cyclical populations or populations that vary at irregular intervals can comprise a large portion of this owl's breeding season diet at the north edge of its range. Nomadic behaviour of the Northern Saw-whet Owl could be related to this dietary feature.

Cote et al. (2007) also reported a positive relationship between number of 'migrating' Northern Saw-whet Owls that they caught in the autumn and rodent abundance. They made the following assumptions when interpreting their data: (1) the Northern Saw-whet Owls that they caught were migrating, (2) more Northern Saw-whet Owls were caught during years of high rodent abundance because the higher prey availability increased owl productivity. There is an alternate interpretation to explain why more owls were caught during years when rodent abundance was higher, as follows: (1) Northern Saw-whet Owls that they caught were not migrating, they were searching for food (moving nomadically) and (2) more owls were caught because more owls responded aggregative to increased rodent densities.

As Cote et al. (2007) stated, a stable isotope study of feathers collected at their site would clarify the origins of the owls encountered at their monitoring station. The site of my study (BBO) and the station used by Cote et al. (2007) are both at the northern edge of the Northern Saw-whet Owl's range. Comparison of results between the two stations would be interesting, especially with respect to the issue of longitudinal variation.

Given data about other owls, it would not be unexpected for the Northern Saw-whet Owl to behave nomadically. Of the nineteen North American owls, five are considered as nomadic in at least some populations. This includes Short-eared Owl (*Asio flammeus*) (Holt and Leasure 2006), Long-eared Owl (*Asio otus*)(Marks et al. 1994), Great Gray Owl (*Strix nebulosa*)(Bull and Duncan 1993), Northern Hawk Owl (*Surnia ulula*)(Duncan and Duncan 1998) and the most closely related owl to the Northern Saw-whet Owl, Boreal Owl (*Aegolius funereus*) (Hayward and Hayward 1993).

In addition to finding evidence that many Northern Saw-whet Owls disperse nomadically, I showed that a portion of the population could be resident year-round in central Alberta. The majority (69%) of owls caught during the autumn were female (Chapter 2). Males are more likely to remain on, or near, their territories year-round than females, and thus I'd expect to catch more dispersing females during autumn monitoring. The Boreal Owl, which is the most closely related species to the Northern Saw-whet Owl, exhibits this pattern (Lundberg 1979, Lofgren et al. 1986, Korpimaki 1988), with females shifting territories between breeding attempts while males generally remain on established territories after breeding. In chapter 3, I found that females traveled further during post-breeding dispersal than males. In a subset of owls (24% of those captured) with low breeding dispersal values most were male (chapter 4).

Northern Saw-whet Owl population trends derived from spring and autumn trapping at banding stations should be interpreted with caution, given the compelling evidence for nomadism and year-round residency presented here. It would simply not be possible to identify from such data whether trends result from population change, new areas being used by this species, or a change in the tendency for individuals to remain on, or near, their territories. Therefore, large-scale studies such as nocturnal calling surveys during the breeding season (Takats et al. 2001) should be used to evaluate population trends for the Northern Saw-whet Owl.

Despite the potential difficulty in interpreting trends obtained from spring and autumn banding stations and the potential negative costs to individual birds that are banded such as stress related to trapping and handling (which has not been well studied or quantified), banding stations provide a number of benefits including:

(1) Long term data from spring and autumn banding data can help interpret change, even if the connection to population trends is weak. For example, if breeding call surveys indicated that Northern Saw-whet Owl populations did not change but negative trends were found using spring and autumn banding data one might

hypothesize that more Northern Saw-whet Owls are remaining on, or near, their territories year-round.

(2) Data from banding stations can be used to determine how weather affects the movements of Northern Saw-whet Owls.

(3) Information about spring and autumn prey use can be gleaned from banding station operations.

(4) Seasonal changes in the age-class and sex-class ratios of dispersers can be illuminated and investigated at banding stations.

(5) Bird band recoveries provide insights about patterns of individual movement; however, band recoveries should not be generalized to depict movement patterns for a species.

(6) Feathers can be collected at banding stations for use in stable isotope ratio analyses. Such studies could provide insights about the movements typical in regional populations of any species.

(7) An easy and effective way to connect the general public to nature. A close encounter with a bird (such as an owl) facilitates conversation about environmental issues. Northern Saw-whet Owls are

appealing creatures and ideal ambassadors for conservation. This final benefit does not, on its own, justify the operation of a banding station. Rather, it should be considered a value-added benefit that complements a research or monitoring initiative.

RECOMMENDATIONS FOR FUTURE RESEARCH

Innovations in the fields of molecular genetics and stable isotope geochemistry have facilitated greater understanding about the movements of this owl. While the research described in this thesis sheds light on the movements of the Northern Saw-whet Owl, gaps in our knowledge of this owl's movements still exist. The following suggestions are provided to help direct future research efforts:

(1) The author recognizes the need for a more substantial analysis employing an ANOVA approach to adequately control for confounding and interaction dimensions of the analysis in Chapters 3 and 4. Such an analysis will be incorporated into a subsequent publishable manuscript.

(2) The wing chord/mass discriminant function table presented in chapter 2 should be tested across the range of the Northern Saw-whet Owl using the DNA sexing methodology illustrated in chapter 2.

(3) Summer trapping using protocols similar to spring and autumn monitoring (nets and audiolures) should be conducted in the summer to determine whether Northern Saw-whet Owls are moving at that time of year. Feathers should be collected from birds trapped in summer for stable isotope analyses to determine whether some owls move northward after breeding and then return southward during autumn.

(4) Stable isotope studies should be done using feathers collected during the autumn at 'migration monitoring' sites across the range of the Northern Saw-whet Owl to determine whether regional differences in movement patterns exist.

(5) Similar to recommendation (3), stable isotope studies should be done on feathers collected from owls at active nests and during the winter at sites across the owl's range to determine the various dispersal trends.

(6) A stable-hydrogen isotope map could be created for Northern Saw-whet Owls using juvenile plumage feathers collected at active nests. Such a map would be useful for interpreting stable isotope ratio data more accurately.

(7) Movement of Northern Saw-whet Owls is not monitored as commonly during the spring as in the autumn. Feathers should be collected from owls during spring so that possible differences between spring and autumn movements can be investigated using stable isotope ratio analyses.

(8) Data from spring and autumn Northern Saw-whet Owl banding operations should be compared to trend data obtained for this species using standardized nocturnal owl calling surveys (Takats et al. 2001).

Being a predator, the Northern Saw-whet Owl occurs at a high trophic level in the ecosystem it occupies. In addition, this owl requires mature trees for nesting. Because of these factors, learning the traits and habits of this bird (including its movements) will help us detect, and understand, possible changes in ecosystems.

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