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Dynamics of fat and lean mass in refuelling migrant passerines measured using quantitative magnetic resonance

Lisa V. Kennedy, *The University of Western Ontario*

Supervisor: Dr. Chris Guglielmo, *The University of Western Ontario*

A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology

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DYNAMICS OF FAT AND LEAN MASS IN REFUELLING MIGRANT
PASSERINES MEASURED USING QUANTITATIVE MAGNETIC RESONANCE

(Measuring Changing Fat And Lean Mass In Refuelling Migrant Passerines)

(thesis format: Integrated Article)

by

Lisa V. Kennedy

Graduate Program in Biology

A thesis submitted in partial fulfillment
of the requirements for the degree
of Master of Science

The School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

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THE UNIVERSITY OF WESTERN ONTARIO
School of Graduate and Postdoctoral Studies

CERTIFICATE OF EXAMINATION

Supervisor

Dr. Chris Guglielmo

Supervisory Committee

Dr. Graeme Taylor

Dr. Jack Millar

Examiners

Dr. Jack Millar

Dr. Zoe Lindo

Dr. Kathleen Hill

Dr.

The thesis by

Lisa Viola Kennedy

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ABSTRACT

Although fat deposition during stopover in migrating passerine birds has been extensively studied, changes in lean mass during refuelling are not well understood. I used quantitative magnetic resonance (QMR) analysis to measure the deposition of fat and lean mass for both recaptured and single capture migrant passerines in spring and fall at Long Point, Ontario. Both the recapture analysis and single capture regression analysis indicated a substantial contribution of lean mass to overall increases in total body mass. Some of the variation in the relative deposition of fat and lean mass was explained by sex, age and season. I then used radio-telemetry and mark-recapture analysis to investigate whether QMR affects a bird's magnetic compass or stopover duration. QMR had no effect on stopover duration and departure orientation of migrating Black-throated Blue Warblers. QMR slightly increased stopover duration in adult White-throated Sparrows in fall, but not in spring. My study demonstrates that lean mass deposition is substantial and dynamic, and that QMR is a safe and effective technology to study fuel deposition of migrant birds in the field.

Keywords: Quantitative magnetic resonance, migration, passerines, refuelling, body composition, orientation, telemetry

STATEMENT OF CO-AUTHORSHIP

All work within this thesis has been authored by Lisa V. Kennedy and will be published with Christopher G. Guglielmo and for Chapter two, specifically, will be published with Stuart A. Mackenzie.

Under the supervision of Dr. Guglielmo I was responsible for all intellectual and analytical aspects of the development and completion of this thesis. With the assistance of Bethany Thurber, Tara Crewe and Stuart A. Mackenzie I wrote the programs to create an assessment of migratory refuelling at a stopover site and generated encounter histories from bird banding data and telemetry and ran mark-recapture models. I performed the statistical analyses for all aspects of this thesis. Bethany Thurber, Tara Crewe and Stuart A. Mackenzie assisted in writing functions to assist in statistical modelling, as well as, offered other valuable analytical and technical support. All co-authors provided valuable editorial and intellectual guidance.

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I strive to never lose my child-like enthusiasm for the natural world and to remind myself that “a person who never made a mistake, never tried anything new”. ~ Albert Einstein

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LIST OF ABBREVIATIONS

LPBO – Long Point Bird Observatory

MA – Type II Major Axis Regression

QMR – Quantitative Magnetic Resonance

\hat{c} – overdispersion correction parameter

ϕ - daily survival probability or probability that an individual detected on day i will remain at the study site until day $i+1$

p – detection (recapture) probability for an individual in a given state within a multi-state recapture model and a recaptures-only model

τ – probability that an individual present on day i will not be present on day $i+1$

CMR – Capture-mark-recapture

NOSCAN – an individual bird or group of birds that has not been scanned using quantitative magnetic resonance

SCAN- an individual bird or group of birds that has been scanned using quantitative magnetic resonance

HY – Hatch Year Bird, hatched and fledged within one year

AHY – After Hatch Year Bird, is older than one year

SY – Second Year Bird, two years old

ASY – After Second Year, more than two years old

AIC – Akaike information criterion

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CHAPTER ONE: GENERAL INTRODUCTION

Animal migration is expressed across a wide variety of invertebrates and vertebrates (Dingle 1966). The largest migrant is the blue whale (*Balaenoptera musculus*) which makes large scale movements from tropical climates after giving birth, to Arctic waters for rich feeding areas (Burtenshaw *et al.* 2004). Yet long-distance migration is also observed in the very small animals, such as aphids (eg; Dingle 1972) which with wind assistance are capable of non-stop flights of over 1000 km (eg; Taylor 1974). In a broad sense, such efforts to migrate are driven by predictable changes in the environment that make it beneficial for animals to move to maximize growth, reproduction and survival. One cost of migration is the large investment of energy required to travel great distances. Fat loading to fuel migratory journeys is widespread across taxa including insects (eg; monarch butterfly (*Danaus plexippus*); Brower *et al.* 2006), fish (Mesa and Magie 2006), reptiles (eg; green turtle (*Chelonia mydas*); Kwan 1994), mammals (Boyd 2004) and birds.

Avian migration is one of the largest and most visible semi-annual movements globally and more than 50 billion birds are estimated to migrate every year (Berthold 1993). Long-distance migrants demonstrate impressive feats of energy expenditure. For example, bar-tailed godwits (*Limosa lapponica baueri*) fly for 6 - 9 days non-stop, directly from Alaska to Australia (~10,000 km) (Gill *et al.* 2009). Other species, such as the Garden Warbler (*Sylvia borin*), cross the Sahara Desert, an environment of extreme heat with limited access to water (Biebach 1998). Understanding fuel accumulation and changes in body composition is essential to deciphering how birds are able to fuel such

extreme migratory movements. Early work on fuel storage resulted in the “airplane refuelling paradigm” where all lean body components stayed constant, and only fat was used as fuel for flight (Odum *et al.* 1964). However, subsequent studies have shown that other body components such as muscles and organs also change in mass whereby lean mass is catabolized during flight (Klassen *et al.* 2000, Jenni-Eiermann *et al.* 2002, Schmidt-Wellenburg *et al.* 2008) and ‘rebuilt’ at stopover sites (Karasov and Pinshow 1998, Pierce and McWilliams 2004, Seewagen and Guglielmo 2010, Aamidor *et al.* 2011).

Although lean mass deposition seems to be widespread among birds, factors that determine variation in the relative deposition of fat and lean mass are poorly understood. Until recently it has been technologically challenging to measure fat and lean mass of animals non-invasively which is largely attributed to our lack of understanding of changes in body composition in migrating birds. The simplest method to assess body condition of migrating birds is to use body mass or a morphometric index such as size-corrected body mass (Peig and Green 2009). A scaled mass index generates size-corrected body mass for all individuals adjusted for the whole body composition to which it would have at average length (L_0) for the population, according to allometry (Peig and Green 2009). Other methods simply divide mass by a body length measurement to generate a rough ‘condition index’ (Merom *et al.* 2000). Additional information on the fat or lean mass composition of body stores can be derived from qualitative scoring of visible fat or muscle (Salewski *et al.* 2009, Bauchinger *et al.* 2011). Fat scores are used by researchers and bird banding stations all over the world to visually assess fat stores

(e.g. Kaiser 1993), but methods for scoring fat differ from place to place, and over time are subject to observer error. The primary method for measuring body composition is proximate analysis by chemical extraction because it directly measures tissues from a carcass. However, chemical extraction is destructive and prevents following body composition changes in the same individual. (Afton and Ankney 1991, Reynolds and Kunz 2001).

Sophisticated, non-invasive methods have been developed to allow for non-lethal measurement of body composition. The methods used on migrant birds include procedures such as heavy water dilution (Speakman 2001), total body electrical conductivity (TOBEC; Skagen 1991, Grant and Evans 1991, Karasov and Pinshow 1998), and dual x-ray absorptiometry (DEXA; Korine *et al.* 2004). The heavy water dilution technique is based on the fact that most of the total body water is distributed in lean tissues and fat is mostly anhydrous. A known quantity of deuterium or ^{18}O labelled water is injected into the animal and allowed to equilibrate with the body water pool. By measuring dilution of the label in a body water sample (from blood, tears or urine), one can calculate the mass of total body water, and thereby the wet lean mass of the animal. Fat is estimated by subtraction of lean mass from total body mass (Speakman *et al.* 2001). Heavy water dilution is reliable and accurate but can be cost-prohibitive and time consuming. TOBEC is based on the principle that fat and fat-free tissue differ in electrical properties. Conductivity readings can be used to estimate wet lean mass, which again can be used to estimate fat mass by subtraction (Scott *et al.* 2001). This method generally has greater error for measuring fat mass than other methods (eg; heavy water

dilution) and is not very useful for measuring body composition in small birds (Scott *et al.* 2001). DEXA uses x-rays to differentiate between bone, lean tissue and fat (Stevenson and Tets 2008), and is a very accurate and precise technique for measuring body composition in birds (Aamidor *et al.* 2011). This technique is difficult to use in field work since birds may require anaesthesia and post-treatment recovery time is required, the scanning area is small, and there are x-ray exposure issues for operators (Scott *et al.* 2001).

Quantitative magnetic resonance (QMR) is the newest non-invasive method for measuring body composition of live animals. This technology has been validated on a variety of taxa including small animals such as mice, rats, bats and birds (Taicher *et al.* 2003, Tinsley *et al.* 2004, McGuire and Guglielmo 2010, Guglielmo *et al.* 2011). QMR measures mass of fat, wet lean and total body water of small birds with precisions of $< \pm 3\%$, and accuracies of approximately $\pm 11\%$, $\pm 2\%$ and $\pm 2\%$, respectively (Guglielmo *et al.* 2011). When using QMR, no anesthesia is required, there are no operator risks, and many birds can be scanned each day because scanning takes < 2 minutes with zero recovery time (Guglielmo *et al.* 2011). As a result, QMR provides the opportunity to accurately and precisely measure small changes in fat and lean mass of migrant birds. With evidence of decreasing passerine populations globally (Wilcove and Wikelski 2008, Wilcove 2008), and continued need to conduct research on migrants, QMR uniquely provides opportunities to design body composition studies for migratory birds that have not previously been possible.

Orientation and Navigation

In addition to being physically capable of long-distance flight, birds require sophisticated orientation and navigation mechanisms. Migrating birds use several different compasses in combination with a map sense during migration (Able 2001, Åkesson 2003). All birds have a sun compass, which uses the position of the sun on its azimuth along with information on time of day to determine orientation (reviewed by Schmidt-Koenig 2001, Huttunen 2009). Generally, birds use the pattern of polarized light in the sky to determine sun position for their sun compass, and polarization is used in preference to the sun itself (Able 1982). This skylight polarization is particularly prominent at dawn and dusk, and is crucial for the calibration of the magnetic compass, and orientation before migratory flight is initiated (Åkesson and Backman 1999, Zapka *et al.* 2009). Birds are the only animals beside humans capable of using the stars to orient. The star pattern is used to determine the axis of rotation of the night sky, which indicates the position of the geographic pole (Emlen 1969).

One very prominent cue used in determining position and orientation during migration is the Earth's magnetic field. A geomagnetic compass has been detected not only in birds, but also in a great number of other animals including insects (Larue *et al.* 2006, Reppert *et al.* 2010), amphibians, sea turtles and bats (Wiltschko and Wiltschko 1995, Holland *et al.* 2006, Phillips *et al.* 2010). Geomagnetic sensing appears to be crucial to successful migration in birds (eg; Åkesson and Backman 1999, Åkesson *et al.* 2005, Holland 2010). Iron-mineral-based sensors appear to be present in the beaks of all birds (Cadiou and McNaughton 2010). They are thought to be involved in sensing

geomagnetic field strength, and play a role in navigation by providing information on current location (Zapka *et al.* 2009). A separate photopigment-based geomagnetic sensing system appears to be responsible for compass orientation in birds by detecting polarized light arranged in concentric circles around the sun (Zapka *et al.* 2009, Ritz *et al.* 2010) and when integrated with the solar azimuth can be used to determine position relative to the Earth's magnetic poles (Rossel *et al.* 1978). Current evidence indicates that the magnetic compass is calibrated each evening using twilight cues, especially skylight polarization, and then flight at night is primarily directed by the iron-mineral based magnetic compass (Åkesson and Backman 1998). Currently the exact mechanisms birds use and which are more important during migration is under debate, but magnetodetection is most likely used in conjunction with other compasses such as; polarized light patterns (Wehner 1998), star patterns at night (Weindler *et al.* 1996) and visual geographical landmarks (Mettke-Hofmann and Gwinner 2003, Mouritsen 2003).

There is concern that short-term exposure to a magnetic field during QMR analysis could affect a bird's magnetic senses. In general, the evidence suggests that birds should not be greatly affected by QMR. First, birds have been shown to recalibrate their magnetic compass each evening using celestial cues, particularly the skylight polarization pattern during sunset (Cochran *et al.* 2004). Second, the photopigment-based system that birds use to sense the Earth's magnetic inclination angle to orient should not be affected once the external magnetic field is removed (Zapka *et al.* 2009). On the other hand, QMR could potentially affect the iron-based sensors in the beak since little is known about how magnetite structurally responds to changes in the magnetic field.

Measuring Stopover Behaviours

Tracking migrating animals poses many challenges. For many years, specific movements and locations for breeding and winter grounds of many bird species remained a mystery (Bairlein 2008). Tracking becomes especially difficult when it requires monitoring movements of very small birds over large distances. Attempts to track and monitor migratory birds in North America began in 1920 with systematic banding efforts between US Fish and Wildlife Service and the Dominion Wildlife Service of Canada (Bairlein 2008). Consequently, general movements between breeding and wintering areas for birds in North America are fairly well known. Other recent techniques can now provide more refined spatial and temporal resolutions for migrating species. For example, satellite tracking (Gill *et al.* 2009), geolocation (Stutchbury *et al.* 2009), radio-telemetry (Taylor *et al.* 2011) and chemical and molecular markers (Norris *et al.* 2005) have solved many mysteries of bird migration and other movements birds make on daily and even hourly time scales. At stopover sites, radio-telemetry towers and hand-held tracking is extremely useful to measure and detect small scale movements birds make during refuelling periods. Recent studies have indicated that birds and bats may use stopover habitat on a broader spatial scale than originally thought, moving as much as 30 km between suitable habitats in the area to refuel (Taylor *et al.* 2011). Additionally, radio-telemetry has been used to track and capture individuals direct refuelling rates and true stopover duration (Goymann *et al.* 2010). Therefore, radio-telemetry is an effective method for measuring stopover behaviour of small birds and bats.

Other indirect methods for assessing stopover behaviour are mark-recapture models which can be used to generate estimates of certain stopover behaviours and statistically account for variation in aspects of population movement patterns (Pradel *et al.* 1997, Schaub *et al.* 2001, Schaub *et al.* 2004, Salewski *et al.* 2007). In the program MARK 5.2, simpler recapture-only models provide opportunities to include covariates while generating estimates of recapture (p) and survival (ϕ) probabilities, and provide evidence of differences in migratory stopover behaviour between selected groups. Further, extended models such as multi-state mark-recapture models generate estimates of changes between pre-determined states, specifically temporal displacements (Lebreton and Pradel 2002, Schaub *et al.* 2004). With regards to stopover behaviour, multi-state mark-recapture models allow for estimates for ‘transient’ behaviour (leaving a study site <24h after capture) and subsequent behavioural estimates from ‘non-transient’ individuals remaining beyond 24 hours while comparing selected groups. For example, Schaub *et al.* (2004) used both of these models to determine that wind and rain are factors that significantly impact decisions for daily emigration (transiency), departure probability, and stopover duration in migrating birds. They found that European Robins (*Erithacus rubecula*) were most likely to emigrate on nights where wind speed was low (<2.4 km/s) and there was no rain.

THESIS OBJECTIVES

QMR provides notable advantages for body composition analysis, allowing for quick, accurate and non-invasive repeated measures of individual birds. Thus, QMR gave me an unprecedented opportunity to study factors determining the dynamics of fat and

lean body mass of free-living birds in a magnitude that's never been done before. The primary objective of this thesis was to determine how factors like season, sex and age affect the deposition of fat and lean mass (migratory fuel) in passerines at a stopover site during migration. Developing an understanding of potential side effects of QMR is essential to ensure minimal adverse effects on migrating birds so my second objective was to assess the potential behavioural effects that QMR analysis may have on migrant songbirds in the field.

In Chapter two, I used individual and population level regression analyses to measure the relative contribution of fat and lean mass to change in body mass of passerines refuelling at a stopover site during migration. Songbirds depend on stopover sites during their annual migration to accumulate sufficient fat and lean mass to fuel long-distance flight and although it is now recognized that lean mass is an important component of fuel for birds, the factors that determine variation in the deposition of fat and lean mass during stopover periods are poorly understood. Therefore, to refine our knowledge of changes in body composition, I used QMR to measure fat and lean mass changes and investigated the influence of species, season, sex and age on fuel accumulation at a stopover site, in spring and fall, for 29 passerine species in Long Point, Ontario.

Field studies on refuelling in migrants are limited by sample size (number of birds captured) and time (migratory stopover duration at the study site). Though recaptured birds provide evidence to direct refuelling and body composition changes, most often recapture rate is low. Therefore, a major goal of chapter two was to compare an

individual level analysis of refuelling in recaptured birds to a population level analysis of single captured birds.

In Chapter three, I assessed the potential behavioural effects of QMR exposure on migrant passerines using two different approaches; radio-telemetry and mark-recapture modelling. Direct measurements of behaviour from radio-telemetry provided information on stopover duration and departure orientation for QMR treated and control birds. Indirect measurements of transiency (τ), recapture (p) and survival (ϕ) were determined from mark-recapture models to compare migratory decisions for both QMR treated and control birds. Both these approaches determine potential negative effects on orientation and stopover behaviour of QMR analysis.

In Chapter four, I conclude with a general discussion of results for studies in Chapters two and three. In Chapter two, I found that factors affecting the relative deposition of fat and lean mass were much more variable than I had predicted. Not only can fat and lean mass be affected by species, season, sex or age alone or in combination, but post hoc evaluation of the results also indicate a potential relationship between relative lean mass deposition and body size. In Chapter three, in general, results were as I predicted. By investigating transiency, departure orientation and stopover duration from radio-telemetry data and mark-recapture models, I determined that QMR had no effect on transiency or departure orientation on birds at stopover, however, it may affect stopover duration by delaying birds one to two extra days.

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CHAPTER 2: COMPOSITION AND RELATIVE DEPOSITION OF FAT AND LEAN MASS IN MIGRANT PASSERINES AT A STOPOVER SITE IN SPRING AND FALL

INTRODUCTION

Bird migration consists of intervals of endurance flight interrupted by refuelling at stopover sites. Stopovers are critical places where migrants replenish fuel stores for subsequent migratory flights (Mehlman *et al.* 2005). Because most passerine bird species do not feed during flight, they depend on fuel stored during periods at stopover sites to complete their journeys (Jenni and Jenni-Eiermann 1998). Birds spend the majority of the total time and energy of migration at stopover, and so the rate of fuel deposition significantly affects migration strategy (Hedenstrom and Alerstam 1997). Consequently, if rate of fuel deposition is a limiting factor, birds should optimize fuel storage behaviour. Optimal migration theory, initially described by Alerstam and Lindstrom (1990) suggests time-minimization may be the most prevalent migration strategy for birds (Hedenstrom 2008, Karlsson *et al.* 2012) and therefore migrant passerines obtain greater fitness through fast refuelling and departure from stopover sites.

Fat and lean mass are the two potential sources of energy for flight (Jenni and Jenni-Eiermann 1998, Gannes 2001, Jenni-Eiermann *et al.* 2002, Salewski *et al.* 2009). Fat yields 8 - 10 fold more chemical energy per gram of wet mass than carbohydrate or protein, and therefore fat is the preferred fuel source during flight (Jenni and Jenni-Eiermann 1998, Guglielmo 2010). Nevertheless, catabolism of lean mass (mostly protein) occurs to maintain stable blood glucose concentration, to provide key Krebs's cycle

intermediates, or to provide water (Jenni and Jenni-Eiermann 1998, Guglielmo and Williams 2003, Gerson and Guglielmo 2011).

Early work on fuel use suggested that only fat was used to fuel flight (eg. Odum *et al.* 1964), and it was not until the 1990's that the use of lean body components as an energy source was recognized as being substantial (Lindström and Piersma 1993, Karasov and Pinshow 1998, Jenni and Jenni-Eiermann 1998). For example, when Garden Warblers (*Sylvia borin*) migrate across the Sahara desert 70 % of mass lost is composed of fat (Biebach 1998). However, the remaining mass that is lost comes from lean tissue protein. The majority of protein is derived from the digestive tract, but breast and leg muscle mass was also reduced (Biebach 1998). After crossing the Sahara, the Garden Warbler requires 1-2 days before gut function and food intake returned to pre-flight levels (Biebach 1998). Additionally, wind tunnel flights have revealed that protein provides about 10 % of catabolised fuel for energy during flight (Klassen *et al.* 2000, Jenni-Eiermann *et al.* 2002, Schmidt-Wellenburg *et al.* 2008, Gerson and Guglielmo 2011) and this remains constant for varying levels of exercise up to a minimum 10 hours of flight time (Jenni-Eiermann *et al.* 2002). It is now widely accepted that many birds catabolise both fat and lean mass throughout migration (Biebach 1998, Karasov and Pinshow 1998, 2000, Bauchinger 2006) and subsequently rebuild both fat stores and depleted organ and muscle tissue.

It is important to know how much lean mass migrants are depositing during refuelling for a variety of reasons. First, predictive models of migration have generally assumed that all mass gained is fat and thus greatly overestimate potential flight distances

of individuals (Pennycuick 2008). Second, birds depositing lean mass may require high protein foods, such as insects, at stopover (Piersma and Jukema 2002, Aamidor *et al.* 2011, McCue *et al.* 2011). Quantifying food requirements and providing necessary resources in stopover habitats may aid in the conservation of migrant populations (Wikelski and Cooke 2006, Wikelski *et al.* 2007). It has recently been reported that lean mass may contribute up to 50 % of mass gained at stopover sites even when birds do not cross major barriers, like the Sahara Desert (Seewagen and Guglielmo 2010). Therefore, the general importance of lean mass deposition may be underappreciated.

Although lean mass deposition seems to be widespread among migratory birds, factors that determine variation in the relative deposition of fat and lean mass are very poorly understood. On one hand lean mass may make up a constant fraction of the fuel deposited, but it is possible that factors such as species, season, sex and age may affect ‘fuel mixture’. In this study I used both individual and population level analyses for a variety of species to understand the causes of variation in the deposition of fat and lean mass during stopover.

Seasonal differences in fuel accumulation may be attributed to different ultimate goals between spring (reproduction) and fall (overwintering), and in general food and weather conditions are more unpredictable in spring (Fransson 1995, Kokko 1999, Newton 2008, Yohannes *et al.* 2009). Greater fat mass accumulation may be expected in spring when northbound birds are in a hurry to reach their breeding grounds to ensure sufficient time to breed and fledge their young (Cherry 1982, Veiga 1986, Izhaki and Maitav 1998). In contrast, fall migration is generally thought to proceed at a slower pace

(Preston 1966). Previous studies indicate that body mass and fat scores are greater in the spring, but there is no information on seasonal variability in lean mass (Dunn 2000, Seewagen and Guglielmo 2011).

Fuel accumulation may differ between male and female birds and differences could change seasonally. Energetic requirements for migration do not differ between males and females, but in spring, males are under more pressure to arrive at the breeding site earlier since they are in competition for territories with other males (Otahal 1995, Yong *et al.* 1998, Morris *et al.* 2003, Seewagen and Slayton 2008,), while females are preparing for egg laying. Therefore, in spring males may carry less fat and lean mass than females, but males may accumulate a greater proportion of fat to lean mass. Conversely, sex-differences in fuel storage may be reduced or absent in fall.

Age could have a dramatic effect on fat and lean mass accumulation, particularly during fall. Passerine birds generally have low survival rates in their first year of life, and juvenile mortality may be especially great during migration (Menu *et al.* 2005). The energetic demands of migration may be greatest for juveniles since they have to spend more energy to maintain stored fuel relative to adults (Hedenstrom 1997, Swanson *et al.* 1999) since they are poorer foragers (Heise and Moore 2003, Vanderhoff and Eason 2007, 2008), choose poorer quality foods, and may be out-competed for food by adults (Marchetti and Price 1989, Sol *et al.* 1998). Differences in gut size and continued maturation in hatch year birds could also lead to differences in lean mass, particularly in the gut (Hume and Biebach 1996, Guglielmo and Williams 2003).

It is technically challenging to accurately measure fat and lean mass of animals non-invasively (Speakman 2001). Most migration studies use a morphometric approach, such as size-corrected body mass with or without additional qualitative scoring of visual fat or muscle to assess body composition (eg; Kaiser 1993, Pieg and Green 2009). More sophisticated procedures include heavy water dilution (Karasov and Pinshow 1998), total body electrical conductivity (TOBEC; Skagen 1991, Grant and Evans 1991, Karasov and Pinshow 1998) and dual x-ray absorptiometry (DEXA; Korine *et al.* 2004, Aamidor *et al.* 2011), but these techniques can be time consuming, may require anaesthesia (DEXA) or are no longer commercially available (TOBEC). Quantitative magnetic resonance (QMR) allows quick and accurate repeated measurement of fat and lean mass of individuals in the field. This technology has been validated on a variety of taxa including small animals like mice, rats, bats and birds (Taicher *et al.* 2003, Tinsley *et al.* 2004, McGuire and Guglielmo 2010, Guglielmo *et al.* 2011). QMR predicts fat, lean and total body water of small birds with precisions of $< \pm 3$ % error and accuracies of approximately ± 11 %, ± 2 % and ± 2 %, respectively (Guglielmo *et al.* 2011). As a result, QMR provides the opportunity to accurately measure small changes in fat and lean mass of migrants at stopover sites. Seewagen and Guglielmo (2010) used QMR to measure the relative deposition of fat and lean mass in migrant passerines at a stopover site. They found that on average 35 % of the total mass gained in recaptured birds was lean mass. These results were a novel finding and provided opportunity to investigate lean mass on a broader scale by including additional factors affecting fuel deposition.

There is limited understanding of the small scale changes in lean mass in individual birds during migration. The purpose of this study was to assess the composition of fuel accumulated at a stopover site at the individual and population level. If individual level assessment supported population level analysis, future studies on migrant refuelling would not rely on recapture, which usually results in very small and potentially biased samples. I hypothesized that both fat and lean mass are changing during refuelling at stopover in migrating passerines during spring and fall, and additional factors; species, season, sex and age, may affect the overall amount and relative deposition of both fat and lean mass. Further, I aspired to describe trends in deposition of fuel across a range of migrant passerines. I predicted that both fat and lean mass should contribute to increases in total body mass during refuelling. I examined whether variation in the relative deposition of fat to lean mass is explained by several factors. Specifically, I predicted that spring birds would accumulate a greater proportion of fat than lean mass and juvenile birds would accumulate less fat relative to adults. In spring, males would accumulate a greater relative proportion of fat to lean mass than females, and that sex differences would be reduced or absent in fall.

METHODS

Study Site and Data Collection

Passerine songbirds of 99 species were sampled during spring (35 sampling days, 1223 adults) and fall (50 sampling days, 183 adults, 1120 juveniles) of 2009 at Long Point, Ontario, Canada (42°34'57.71"N, 80°23'51.48"W) (Figure 2.1). At the Old Cut study site (located on Old Cut Blvd off Hwy 59) of the Long Point Bird Observatory

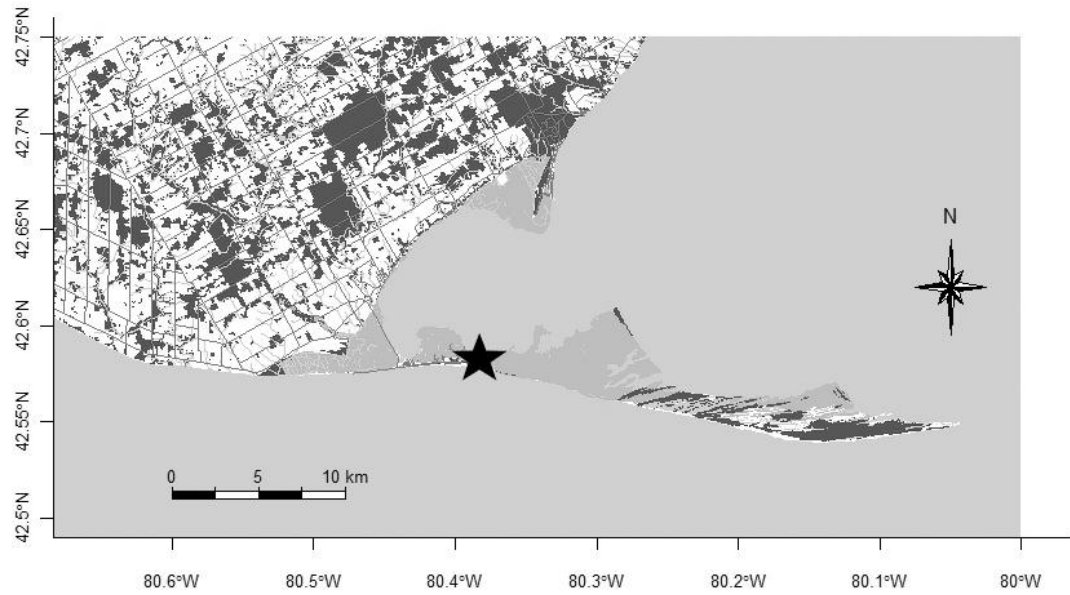


Figure 2.1 Long Point, Ontario, Canada ($42^{\circ}34'57.71''\text{N}$, $80^{\circ}23'51.48''\text{W}$). Solid black star indicates Old Cut study site.

(LPBO), 14 mist-nets (NABC 2001, Hussell and Ralph 2005) in a woodlot were opened 30 min before sunrise and remained open for 6 hours. Nets were not open during periods of heavy rain or wind. Birds were individually banded in the banding laboratory on site with a unique 9 digit number on a United States Fish and Wildlife Service/ Canadian Wildlife Service aluminum band. The following was recorded for each bird; age, sex, unflattened wing chord, mass (nearest 0.1 g), date, time and degree of skull ossification to determine age during fall (Jenni and Winkler 1994) by LPBO banding office staff. Individuals were identified and aged based mainly on species-specific plumage and moult criteria, eyes and/or tongue colouration described by Pyle (1997). Birds were classified as adult (AHY in fall or SY, ASY in spring) or juvenile (HY in fall) (Pyle 1997). Birds were then bagged again and brought to the mobile laboratory (~20 m from the banding laboratory) to be scanned in the Quantitative Magnetic Resonance (QMR) body composition analyzer (Echo-MRI-B, Echo Medical Systems, Houston, TX, USA). Birds were scanned once using the “small bird” (<50g) and “two-accumulation” settings as described in Guglielmo *et al.* (2011). Scanning once decreases precision compared to multiple scans, but allows one to scan many more birds. In my study the maximum number of birds scanned in a six hour period was 140. The QMR was calibrated daily by running a “system test” using a 94 g canola oil standard provided by the manufacturer. Scans of 5 g and 10 g oil standards were taken periodically throughout the day to ensure scanning accuracy (Seewagen and Guglielmo 2010, Seewagen and Guglielmo 2011).

Each bird was held for a 2 minute scan in a ventilated plexi-glass tube appropriate for the size of the bird; no anaesthesia was required. Birds were selected for scanning

after banding only if there was sufficient time for processing since no bird was held after capture for more than one hour. All birds were released immediately after scanning.

Thirty species of warblers, sparrows, wrens, and thrushes were selected for further study based on a minimum sample size criterion of ≥ 15 individuals. Birds recaptured on the same day were excluded. Fat mass and wet lean body mass values were adjusted to improve accuracy using two calibration equations (calibrated fat mass = raw QMR fat \times 0.94, and calibrated lean body mass = raw QMR wet lean body mass \times 1.021) (Guglielmo *et al.* 2011). Calibration equations were obtained from OLS regression for predicting body composition measured by chemical extraction from QMR body composition data from both house sparrows (*Passer domesticus*) and zebra finches (*Taeniopygia guttata*) (Guglielmo *et al.* 2011).

Measurement of Average Body Composition for Migrant Passerines Species Captured during Spring and Fall

Mean values of fat, lean mass and total body mass (g) (\pm SE) were measured to compare overall body composition for each species in various season, sex and age categories. Each species with ≥ 15 scans was selected. Means were compared using ANCOVA in SPSS 17.0 (SPSS Inc., Chicago, IL, USA) for all combinations of season/sex/age groups where applicable, with wing chord as a covariate to account for additional variation in structural body size. Only the first capture of recaptured individuals was used in the analysis. For many species, mean fat, lean and total body mass were not compared for all season, sex and age categories. Several species in spring and fall could not be sexed unless spring breeding physiology was observed so gender

comparisons were not made. For example, Hermit Thrush (*Catharus guttatus*) male and female birds have identical plumage and therefore sex could not be determined visually. In addition, all birds in spring are at least one year old and therefore were all identified as adult in this study.

In addition to season, sex and age, Mean body composition (fat and lean mass) were compared to estimates of migration distance. Each species was grouped into a bin (short- (~1600 – 2800 km), medium- (~3000 – 4000 km) and long-distance (~5000 – 8000 km) migrants) determined by estimating the mid latitude for breeding and wintering ranges and converting latitude degrees into distance (km) (1° latitude = 111.12 km). Migration distance for each bin was selected by comparing the shortest to longest distance migrant in the study. Classifying migration distances as short, medium and long are not standardized and therefore this method of classification is strictly for comparisons within this study. Body composition for each species and additional season, sex and age factors were compared to migration distance.

Individual-level Analysis of Fuel Deposition using Recaptured Birds

Birds recaptured were used to measure changes in fat and lean mass within individuals. Changes in body composition were calculated by determining the difference between final and initial capture for both fat and lean mass. Only species where there were ≥ 5 individuals recaptured were used. In order to determine how well QMR analysis measured total change in body mass during refuelling, I regressed total change in body mass (g) (Δ QBM) measured by QMR analysis (Δ QMR Fat mass (g) + Δ QMR Lean mass (g)) against total change in body mass measured in the banding lab on a balance. If

QMR accounted for 100 % of the changes in body mass, the slope of the relationship in a simple linear regression should be equal to 1 and intercept should equal zero. I then regressed Δ Fat and Δ Lean against Δ QBM to get a measurement of general change in fat and lean across species. There were four cases in the data set where direction of change in total mass measured by the balance was opposite to the Δ QBM. (ie; QMR indicated that birds gained mass while the balance indicated the bird lost mass). This error could be a result of a single QMR measurement not being accurate, or from rounding total body mass measurements on the scale in the banding lab. Since we could not explain the measurement discrepancy, 4 data points were removed out of 112 recaptured individuals. To calculate the relative deposition of fat and lean mass during refuelling, I used linear regression of change in fat or lean for each recaptured bird to Δ QBM. This method was chosen over calculation ratios because significant numbers of birds lost mass between captures and regression can accommodate positive and negative values to estimate slopes. These slopes, in turn, indicate the contribution of each body component to mass change.

Population Level Analysis of Fuel Deposition using Single Captures

For each species with ≥ 15 captures, the contributions of fat and lean mass to total change in body mass was determined by regressing fat or lean mass on size-corrected body mass (Piersma and Jukema 1990, Piersma and Van Brederode 1990, Wirestam *et al.* 2008, Seewagen and Guglielmo 2010). Within each species, a scaled mass index was used to adjust all body mass data to a common structural body size for each species using wing chord since it is a common and useful body size measurement (Schulte-Hostedde *et al.* 2005, Peig and Green 2009). Total body mass for each bird was adjusted (Eqn. 2, Peig

and Green 2009), but retained the original units of measure for the analysis. Adjustments were made only to species where fat, lean or total body mass was significantly correlated with wing chord. Type II major axis regression and line of best fit was used to examine the proportion of variation in total body mass explained by fat or lean mass indicated by the slope, since the dependent variables (fat or lean mass) and independent variable (size-corrected total body mass) both are likely to contain error (Sokal and Rohlf 1981, Warton *et al.* 2006).

In the past, similar studies using this regression approach with body composition data were criticized for over estimating the contribution of lean mass to total body mass variation since lean mass components are very likely to increase as structural body size increases (Lindstrom and Piersma 1993, van der Meer and Piersma 1994). However, most current work in avian migrants, in the field and in captivity, suggests that lean mass body components during migration are extremely variable and changes in lean mass occur independent of structural body size (Klassen and Biebach 1994, Klassen *et al.* 2000, Wirestam *et al.* 2008, Seewagen and Guglielmo 2010). Different migratory strategies across different landscapes shape the relation between flight muscle and body mass and therefore flight muscle is not always representative of body mass for both short- and long-distance migrants (Bauchinger and Biebach 2005). Additionally, phenotypic homeostasis in organ size is only restricted to the brain and lungs of migrating great knots (*Calidris tenuirostris*) (Battley *et al.* 2000). Therefore, original scaling predictions of lean mass (muscle + organ mass measured by QMR) and body mass parameters can no longer be expected.

For this analysis I focused only on the effects of sex and age within season. During spring migration, individuals that fledged during the previous summer cannot easily be identified from adult birds for all species. As a result, no age analyses were made during spring. During fall migration, there is a distinct group of adult and juvenile (recently fledged) migrants and more often these hatch year birds are reliably identified. Sex and age group comparisons were made where birds could be reliably classified in these groups.

Comparison of relative fuel deposition for fat and lean mass between season, sex and age groups were made using R (© R version 2.11.0 (2010-04-22)) ‘smatr’ package for R (© ‘smatr’ version 2.1 (2007-01-12), <http://bio.mq.edu.au/ecology/SMATR>). Major axis regressions were run for individual groups of sex and age within season using the “slope.test” function and compared using the “slope.com” function. Further comparisons of significantly different groups across seasons were made again using the “slope.com” function (see Appendix B).

RESULTS

Body Composition of Migrant Passerines in Spring and Fall

Fat, lean mass composition and total body mass varied widely among passerine species, and some season, sex and age effects were notable (Table 2.1). In general, fat mass was significantly greater in spring than fall for 11 of 25 species, although this trend was observed for 21 species (Table 2.1 and Figure 2.2). There were few cases where fat

mass differed between age or sex classes. Lean mass varied by season, sex or age in only 10 of 29 species (Table 2.1).

Migration distance appears to affect the relative difference between spring and fall fat loads. Species categorized as long distance migrants had the greatest difference spring to fall ratio of fat loads (Figure 2.3). In comparison, medium distance migrants and short distance migrants showed a trend towards decreasing spring:fall fat loads but these differences are not significant ($F_{2,22} = 1.13$, $p = 0.34$) (Figure 2.3).

Individual-level Analysis of Fuel Deposition using Recaptured Birds

My validation analysis indicated that changes in body components measured by QMR analysis are equal to changes in total body mass measured by a balance (Figure 2.4). Therefore, QMR measurements are detecting all changes in body mass of scanned birds. Further, after combining all species and regressing both fat and lean mass separately, recapture birds indicate that both fat and lean mass are deposited in equal amounts (Fat; $y = 0.50x + 0.006$, $R^2 = 0.65$, $F_{1,104} = 194.27$, $p < 0.001$, Lean; $y = 0.50x - 0.006$, $R^2 = 0.61$, $F_{1,104} = 160.97$, $p < 0.001$).

Fat and lean mass deposition varied across recaptured species (Table 2.2). Common Yellowthroats and Grey-cheeked Thrushes deposited equal amounts of fat and lean mass overall, however, in many cases, species deposited varying proportions of fat and lean mass (Table 2.2). Lean mass deposition varied from 27 – 74 % of total body mass gained. In White-throated Sparrows, where sample size was greatest, there was a significant difference in relative fuel deposition between fall and spring. Fall migrants

Table 2.1 Mean fat, lean and total body mass divided by sex, age and season for migrant passerine species. Group differentiation determined through comparison of means in © SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

Common name Species	Group	N	Fat (g)	Lean (g)	Total Body Mass (g)
American Redstart	SP ♂	14	1.27 ^a ± 0.12	6.02 ^a ± 0.10	8.61 ^b ± 0.16
<i>Setophaga ruticilla</i>	SP ♀	7	1.07 ^a ± 0.13	5.90 ^a ± 0.09	7.99 ^{ab} ± 0.15
(L)	F ♂	13	1.06 ^a ± 0.16	5.95 ^a ± 0.09	8.15 ^{ab} ± 0.19
	F ♀	11	0.89 ^a ± 0.06	5.85 ^a ± 0.08	7.94 ^a ± 0.10
Black & White Warbler	SP ♀	5	1.29 ^a ± 0.21	7.59 ^a ± 0.17	10.48 ^a ± 0.20
<i>Mniotilta varia</i>	SP ♂	6	1.14 ^a ± 0.29	7.76 ^a ± 0.21	10.22 ^a ± 0.40
(M)	F	4	1.09 ^a ± 0.44	7.67 ^a ± 0.14	10.25 ^a ± 0.33
Blackpoll Warbler	SP	7	2.27 ^b ± 0.43	9.52 ^a ± 0.16	13.59 ^a ± 0.63
<i>Dendroica striata</i>	FA	5	1.77 ^{ab} ± 0.59	9.00 ^a ± 0.48	12.44 ^a ± 1.03
(L)	FJ	12	1.13 ^a ± 0.13	9.20 ^a ± 0.10	12.03 ^a ± 0.20
Black-throated Blue Warbler	SP ♂	8	1.02 ^a ± 0.12	7.45 ^{ab} ± 0.09	9.95 ^a ± 0.14
	SP ♀	10	1.12 ^a ± 0.10	7.00 ^a ± 0.13	9.48 ^a ± 0.15
<i>Dendroica caerulescens</i>	F ♂	8	1.11 ^a ± 0.25	7.49 ^b ± 0.07	9.99 ^a ± 0.29
(S)	F ♀	15	0.96 ^a ± 0.06	7.27 ^{ab} ± 0.12	9.61 ^a ± 0.16
Canada Warbler	SP ♂	7	1.05 ^a ± 0.18	7.92 ^a ± 0.15	10.41 ^a ± 0.28
<i>Wilsonia canadensis</i>	SP ♀	16	1.01 ^a ± 0.14	7.70 ^a ± 0.05	10.26 ^a ± 0.16
(L)					
Cedar Waxwing	SP	7	3.68 ^a ± 0.59	25.11 ^a ± 0.36	32.30 ^a ± 0.93
<i>Bombycilla cedrorum</i>	F ♂	7	3.35 ^a ± 0.53	25.12 ^a ± 0.49	31.30 ^a ± 0.43
(M)	F ♀	7	3.06 ^a ± 0.55	25.56 ^a ± 0.54	31.56 ^a ± 0.96
Common Yellowthroat	SP ♂	15	1.29 ^a ± 0.15	8.17 ^c ± 0.12	10.95 ^c ± 0.15
<i>Geothlypis trichas</i>	SP ♀	15	1.24 ^a ± 0.15	7.41 ^a ± 0.09	10.09 ^a ± 0.24
(S)	F	22	0.97 ^a ± 0.14	7.81 ^b ± 0.10	10.23 ^{ab} ± 0.17
Chestnut-sided Warbler	SP ♂	7	0.95 ^a ± 0.08	7.41 ^a ± 0.12	9.71 ^a ± 0.17
<i>Dendroica pensylvanica</i>	SP ♀	8	1.34 ^a ± 0.18	7.39 ^a ± 0.14	10.05 ^a ± 0.15
(M)	FJ	5	0.92 ^a ± 0.16	7.17 ^a ± 0.06	9.40 ^a ± 0.25
Eastern White-crowned Sparrow	SP	14	5.53 ^a ± 0.53	22.80 ^a ± 0.37	33.16 ^b ± 0.74
<i>Zonotrichia leucophrys</i>	F	5	3.65 ^a ± 0.68	21.81 ^a ± 0.74	30.02 ^a ± 0.84
(S)					

Golden-crowned Kinglet <i>Regulus satrapa</i> (S)	F♂	23	0.85 ^a ± 0.07	4.34 ^a ± 0.06	6.28 ^a ± 0.11
	F♀	24	0.89 ^a ± 0.06	4.18 ^a ± 0.04	6.19 ^a ± 0.08
Gray-cheeked Thrush <i>Catharus minimus</i> (L)	SP	14	4.03 ^b ± 0.62	24.41 ^a ± 0.41	32.0 ^a ± 0.70
	F	28	2.51 ^a ± 0.19	25.83 ^a ± 0.41	32.31 ^a ± 0.61
Gray Catbird <i>Dumetella carolinensis</i> (S)	SP	50	3.26 ^a ± 0.31	27.37 ^a ± 0.28	35.43 ^a ± 0.52
	FA	13	4.62 ^a ± 0.86	30.11 ^b ± 0.40	39.96 ^b ± 0.71
	FJ	57	3.83 ^a ± 0.30	31.03 ^c ± 0.25	39.23 ^b ± 0.37
Hermit Thrush <i>Catharus guttatus</i> (S)	SP	25	2.65 ^b ± 0.23	21.08 ^a ± 0.21	28.24 ^a ± 0.36
	FA	8	2.65 ^b ± 0.58	23.84 ^b ± 0.31	30.92 ^a ± 0.73
	FJ	35	1.75 ^a ± 0.14	23.83 ^b ± 0.27	29.65 ^a ± 0.34
House Wren <i>Troglodytes aedon</i> (S)	SP	22	0.89 ^a ± 0.08	8.48 ^a ± 0.09	10.76 ^a ± 0.11
	FJ	16	1.14 ^b ± 0.10	8.32 ^a ± 0.10	10.90 ^a ± 0.13
Magnolia Warbler <i>Dendroica magnolia</i> (M)	SP	68	1.18 ^b ± 0.05	6.24 ^a ± 0.04	8.71 ^b ± 0.08
	F	84	0.87 ^a ± 0.04	6.17 ^a ± 0.04	8.36 ^a ± 0.06
Lincoln Sparrow <i>Melospiza lincolni</i> (S)	SP	16	2.96 ^a ± 0.33	13.00 ^a ± 0.15	18.36 ^a ± 0.39
	F	3	1.96 ^a ± 0.58	13.74 ^a ± 0.72	17.97 ^a ± 1.54
Yellow-rumped (Myrtle) Warbler <i>Dendroica coronata</i> (M)	SP♂	8	1.72 ^b ± 0.32	8.98 ^a ± 0.16	12.52 ^b ± 0.41
	SP♀	14	2.26 ^b ± 0.23	8.73 ^a ± 0.11	12.81 ^b ± 0.26
	F	77	1.30 ^a ± 0.05	1.30 ^a ± 0.05	11.80 ^a ± 0.07
Nashville Warbler <i>Vermivora ruficapilla</i> (M)	SP♂	7	1.80 ^b ± 0.34	6.79 ^b ± 0.43	9.56 ^b ± 0.49
	SP♀	12	1.38 ^{ab} ± 0.14	6.12 ^{ab} ± 0.10	8.62 ^{ab} ± 0.23
	FA	9	1.18 ^{ab} ± 0.16	6.30 ^{ab} ± 0.12	8.72 ^{ab} ± 0.19
	FJ	38	1.12 ^a ± 0.08	6.16 ^a ± 0.07	8.52 ^a ± 0.11
Ovenbird <i>Seiurus aurocapilla</i> (M)	SP	30	2.68 ^b ± 0.15	14.72 ^a ± 0.14	19.84 ^a ± 0.30
	F	7	1.32 ^a ± 0.16	15.67 ^b ± 0.45	20.27 ^a ± 0.63

Ruby-crowned Kinglet <i>Regulus calendula</i> (M)	SP	56	0.97 ^b ± 0.05	4.45 ^a ± 0.06	6.39 ^a ± 0.07
	FA♂	11	0.75 ^a ± 0.07	4.67 ^{ab} ± 0.06	6.52 ^a ± 0.01
	FA♀	5	0.98 ^{ab} ± 0.07	4.18 ^a ± 0.12	6.22 ^a ± 0.17
	FJ♂	46	0.74 ^a ± 0.03	4.73 ^b ± 0.04	6.60 ^a ± 0.06
	FJ♀	72	0.81 ^{ab} ± 0.03	4.41 ^a ± 0.04	6.27 ^a ± 0.05
Red-eyed Vireo <i>Vireo olivaceus</i> (M)	SP	10	2.63 ^b ± 0.53	13.74 ^a ± 0.34	18.77 ^b ± 0.64
	F	27	1.58 ^a ± 0.15	13.86 ^a ± 0.16	17.58 ^a ± 0.25
Song Sparrow <i>Melospiza melodia</i> (S)	SP	6	1.14 ^a ± 0.24	16.72 ^b ± 0.59	20.67 ^a ± 0.64
	F	14	1.89 ^a ± 0.26	15.24 ^a ± 0.27	20.06 ^a ± 0.44
Swamp Sparrow <i>Melospiza georgiana</i> (S)	SP	26	1.68 ^b ± 0.15	12.38 ^a ± 0.20	16.37 ^a ± 0.26
	F	9	0.92 ^a ± 0.12	12.59 ^a ± 0.35	15.72 ^a ± 0.31
Swainson's Thrush <i>Catharus ustulatus</i> (L)	FA	22	2.39 ^a ± 0.24	24.15 ^a ± 0.33	29.99 ^a ± 0.42
	FJ	97	2.41 ^a ± 0.11	23.99 ^a ± 0.16	29.87 ^a ± 0.22
Veery <i>Catharus fuscescens</i> (L)	SP	20	5.12 ^b ± 0.34	23.95 ^a ± 0.30	33.38 ^a ± 0.40
	FA	5	3.21 ^a ± 0.89	24.55 ^{ab} ± 0.51	31.46 ^a ± 1.33
	FJ	11	3.19 ^a ± 0.44	25.29 ^b ± 0.54	32.13 ^a ± 0.80
Wilson's Warbler <i>Wilsonia pusilla</i> (M)	SP	14	1.03 ^a ± 0.09	5.47 ^a ± 0.10	7.69 ^a ± 0.13
	F	4	0.84 ^a ± 0.28	5.55 ^a ± 0.24	7.57 ^a ± 0.52
Winter Wren <i>Troglodytes troglodytes</i> (S)	FA	5	1.13 ^a ± 0.11	6.38 ^a ± 0.36	8.80 ^a ± 0.42
	FJ	15	1.21 ^a ± 0.09	6.61 ^a ± 0.15	9.13 ^a ± 0.19
Western Palm Warbler <i>Dendroica palmarum</i> (M)	SP	13	1.26 ^a ± 0.07	7.39 ^a ± 0.11	10.01 ^a ± 0.24
	F	6	1.36 ^a ± 0.18	7.32 ^a ± 0.15	10.25 ^a ± 0.21
White-throated Sparrow <i>Zonotrichia albicollis</i> (S)	SP♂	22	3.97 ^b ± 0.36	20.29 ^c ± 0.29	28.14 ^b ± 0.56
	SP♀	35	3.46 ^b ± 0.22	17.75 ^a ± 0.15	24.62 ^a ± 0.34
	FA	23	1.98 ^a ± 0.16	19.83 ^{bc} ± 0.36	25.59 ^a ± 0.50
	FJ	117	2.29 ^a ± 0.08	19.46 ^b ± 0.12	25.11 ^a ± 0.16

SP-Spring, F-Fall, A-Adult, J-Juvenile, ♀-Female, ♂-Male

Fat = correctedfat from gravimetric equation (Guglielmo, 2011)

Total Body Mass = Raw Value

Lean = correctedlean from gravimetric equation (Guglielmo, 2011)

Fat/Lean/Total Body Mass = season* sex *age +wing (where applicable) (\pm SE)

(S)-Short – *Migration distance (~ 1600 - 2800 km)

(M)-Medium –* Migration distance (~ 3000 – 4000 km)

(L)-Long –* Migration distance (~ 5000 – 8000 km)

*Migration distance measured mid-latitude breeding range to mid-latitude wintering range: conversion 1° latitude = 111.12 km

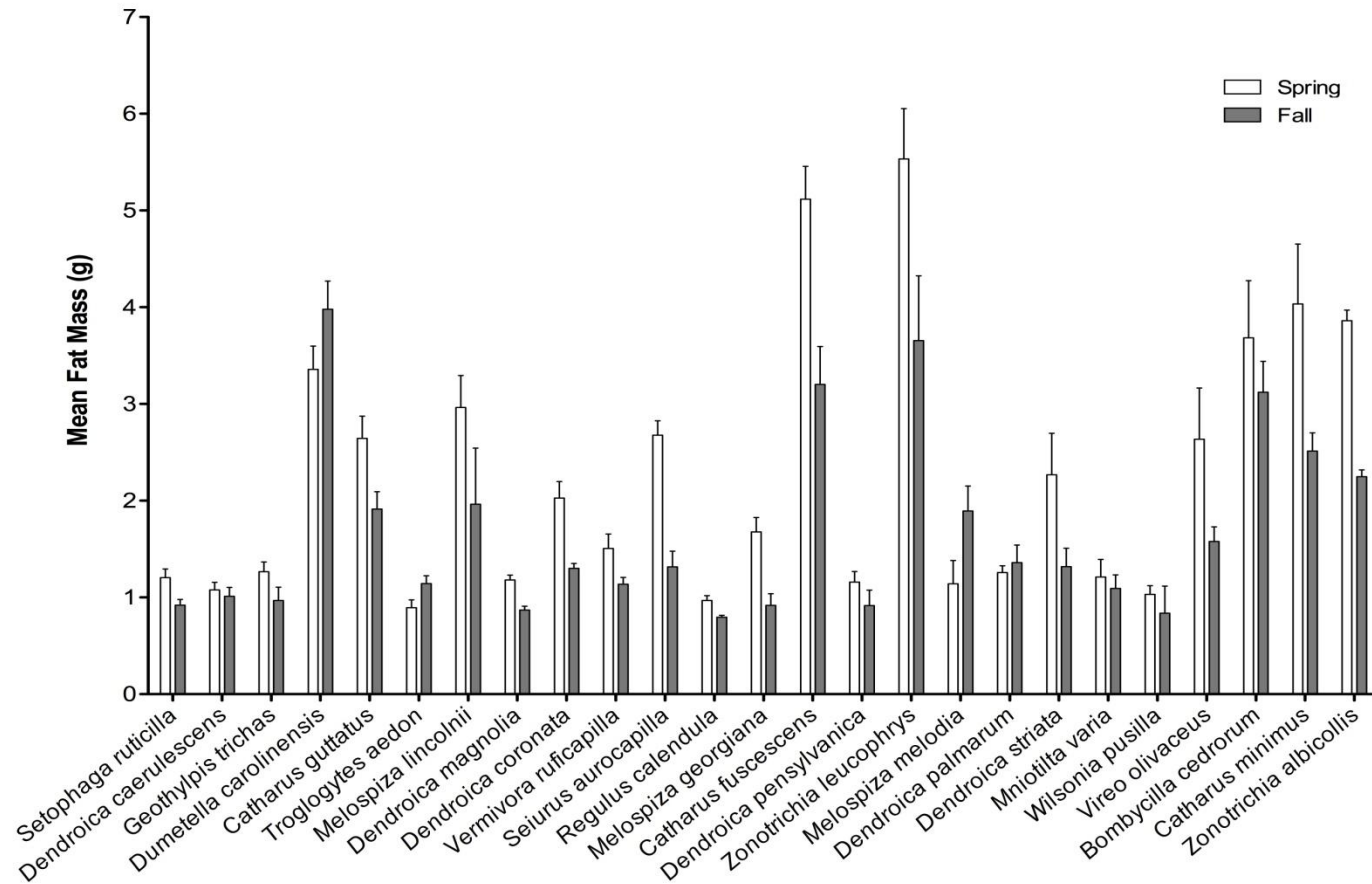


Figure 2.2 Fat mass (g) in spring and fall for 25 species of migrant passerines at a stopover site in Long Point, Ontario. Statistical comparison of seasons including sex and age are available in Table 2.1. Fat was measured using QMR and bars represent standard errors of the mean.

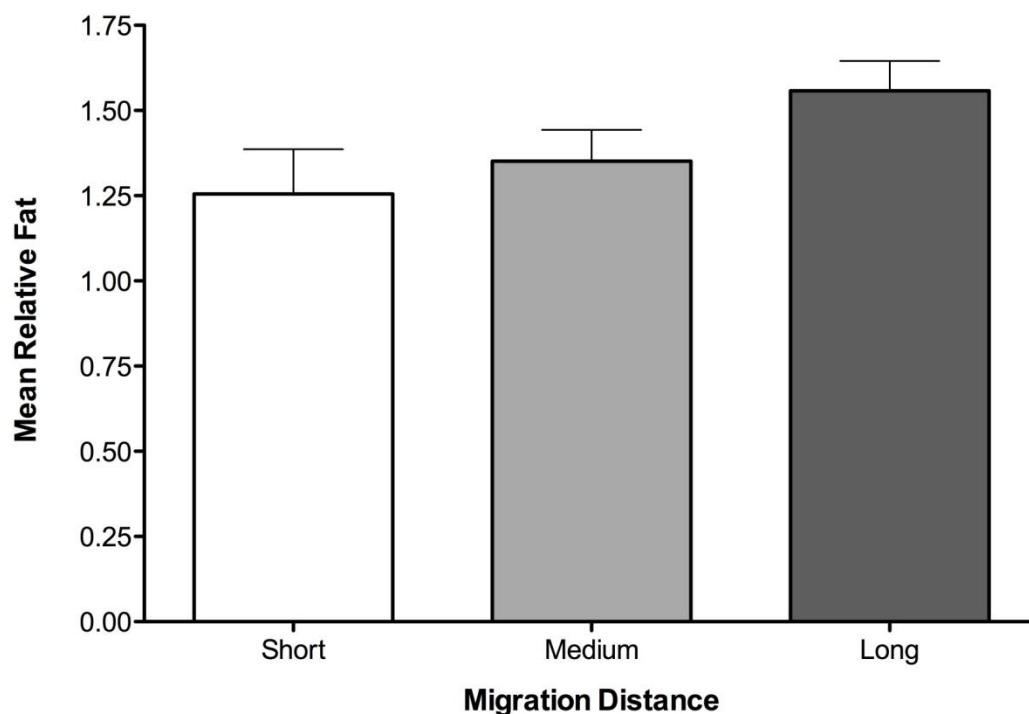


Figure 2.3 Mean (\pm SE) increases in relative fat in spring to fall from short distance migrants to long distance migrants. Differences among groups are not significant ($F_{2,22} = 1.13$, $p = 0.34$). The ratio of spring to fall fat load in passerines migrants in relation to migration distance. Migration distance bins are: 'Short' (~1600 – 2800 km), 'Medium' (~3000 – 4000 km) and 'Long' (~5000 – 8000 km) and corresponding number of bird species for each bin are ($n = 10, 11, 4$). Stored fat tends to be greater in spring than fall in birds flying longer migration distances.

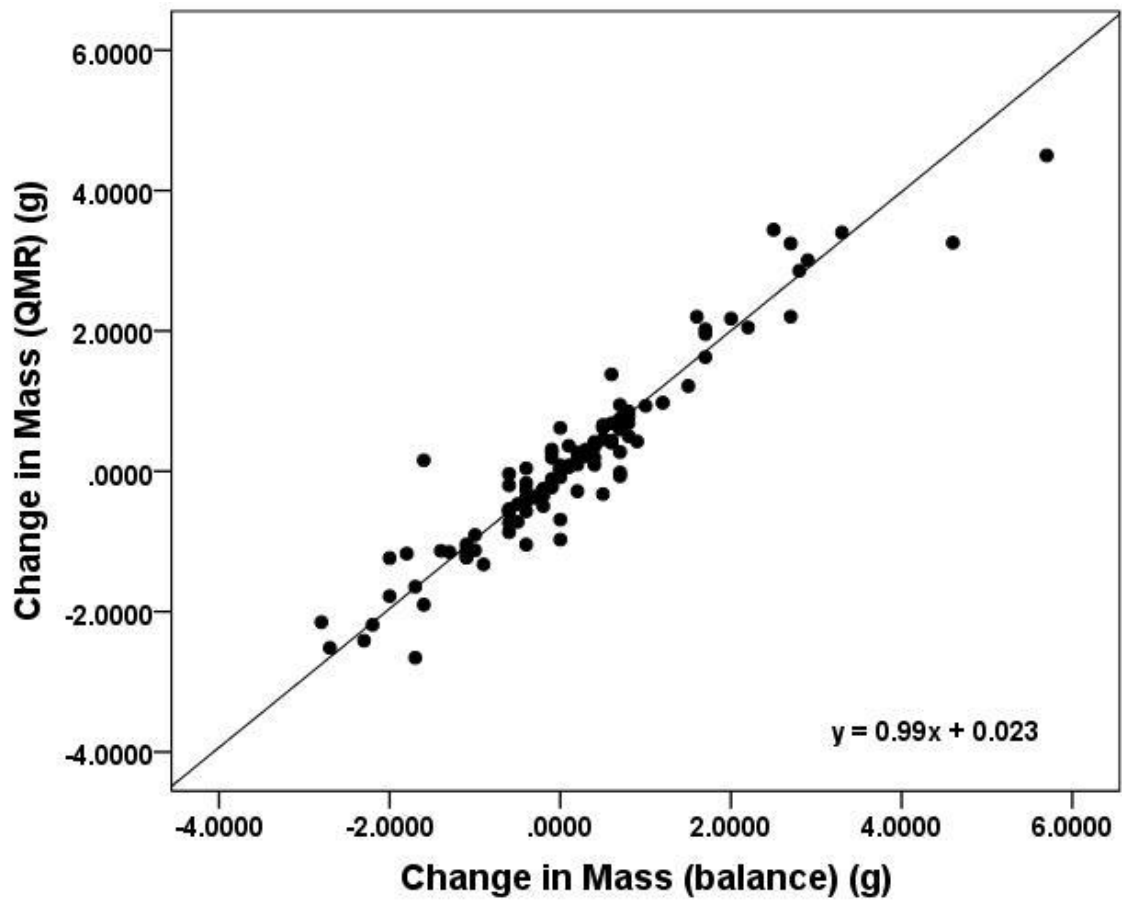


Figure 2.4 Change in fat plus lean mass measured by quantitative magnetic resonance (QMR) was positively related to change in total mass measured using a balance for individual recaptured birds ($R^2 = 0.91$, $F_{1, 104} = 1001.77$, $p < 0.001$).

Table 2.2 Recapture refuelling; % fuel change for lean and fat mass (g) relative to change in total mass (QMR).

Species	N	Initial Mass (g \pm SE)	Δ Mass (QMR) (g) (range)	Season	Fat Deposition (% change)	Significance	Lean Deposition (% change)	Significance
Common Yellowthroat	7	10.63 \pm 0.42	0.08 (-0.54 – 0.69)	SP	50.0	P = 0.04 R ² = 0.55	50.0	P = 0.04 R ² = 0.55
Hermit Thrush	8	27.93 \pm 0.35	0.00 (-1.13 – 2.05)	F/SP	37.4	P < 0.001 R ² = 0.90	62.6	P < 0.001 R ² = 0.96
Magnolia Warbler	5	8.48 \pm 0.37	-0.22 (-2.20 – 0.96)	F/SP	61.3	P = 0.001 R ² = 0.98	38.7	P < 0.01 R ² = 0.96
Ruby-crowned Kinglet	6	5.83 \pm 0.18	0.24 (-0.74 – 0.78)	F/SP	72.9	P < 0.001 R ² = 0.96	27.1	P = 0.02 R ² = 0.79
Grey-cheeked Thrush	7	31.68 \pm 0.97	0.65 (-1.78 – 3.01)	F/SP	51.4	P = 0.01 R ² = 0.74	48.6	P = 0.02 R ² = 0.72
Swainson's Thrush	8	29.76 \pm 0.59	-0.26 (-2.52 – 2.86)	F	26.0	P = 0.04 R ² = 0.52	74.0	P < 0.001 R ² = 0.90
White-throated Sparrow	8	24.4 \pm 0.56	-0.49 (-1.90 – 3.26)	F	43.8	P < 0.001 R ² = 0.79	56.2	P < 0.001 R ² = 0.86
White-throated Sparrow	25	25.96 \pm 0.44	0.08 (-2.45 – 4.50)	SP	71.7	P < 0.001 R ² = 0.84	28.3	P < 0.001 R ² = 0.44

SP-Spring, F-Fall

deposited relatively more lean mass and less fat than in spring. Low recapture rates restricted seasonal comparisons and only White-throated Sparrows were compared.

Changes in Fat and Lean Mass During Refuelling – Population Level Analysis

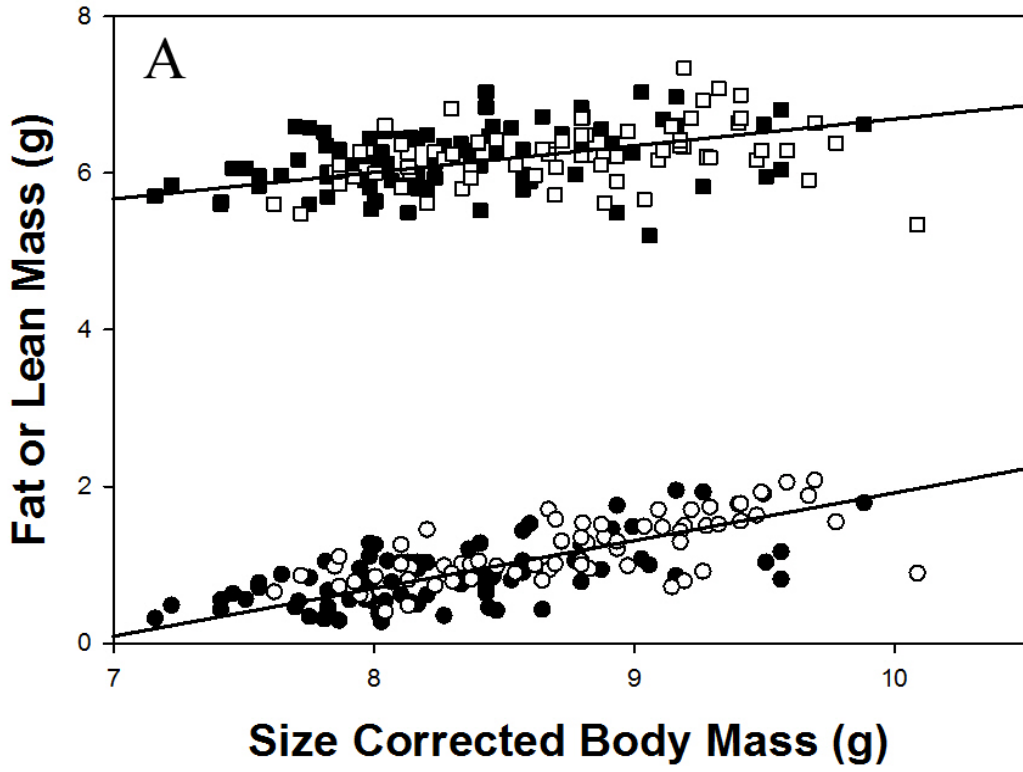
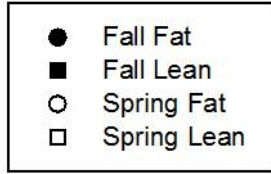
Major axis regression of fat and lean mass against size-corrected body mass showed that the relative contribution of fat and lean mass to mass change during refuelling differs among species. Similar to the pattern seen in recapture data, estimates from the population level single capture regression indicate that fat mass contribution varied from 22 - 77% and lean mass varied from -35 - 113% of total mass gained (Table 2.3). Season, sex and age also had effects depending on species and sample size and to demonstrate this, Figure 2.5A and 2.5B visually illustrate how including these factors may explain variation in relative deposition of fat and lean mass. White-throated Sparrows (Figure 2.5B) had a strong seasonal difference in relative deposition of fat and lean mass, whereas Magnolia Warblers (*Setophaga magnolia*) (Figure 2.5A) showed no seasonal difference in relative deposition of fat or lean mass as total body mass changed. Where there were seasonal effects, in all cases, there was greater relative deposition of fat in spring than fall and subsequently less relative deposition of lean mass in spring than fall. Sex and age differences in deposition of both fat and lean mass were not common. In conclusion, the majority of species did not have any sex or age differences in the relative deposition of fat and lean mass but in general migrants refuelling at stopover were depositing a greater proportion of fat mass in spring and lean mass in fall.

Additional Factors Explaining Differences in Relative Deposition of Fat and Lean Mass

After finalizing the individual and population level analyses of refuelling, it appeared that birds with larger body mass were selectively depositing a larger proportion of lean mass. It appeared that mean percent lean mass deposition was positively related to total body mass in recaptured and single scanned birds respectively but no significant trend was observed (recapture regression; $R^2 = 0.46$, $p = 0.09$, single scan regression; $R^2 = 0.16$, $p = 0.09$) (Figure 2.6).

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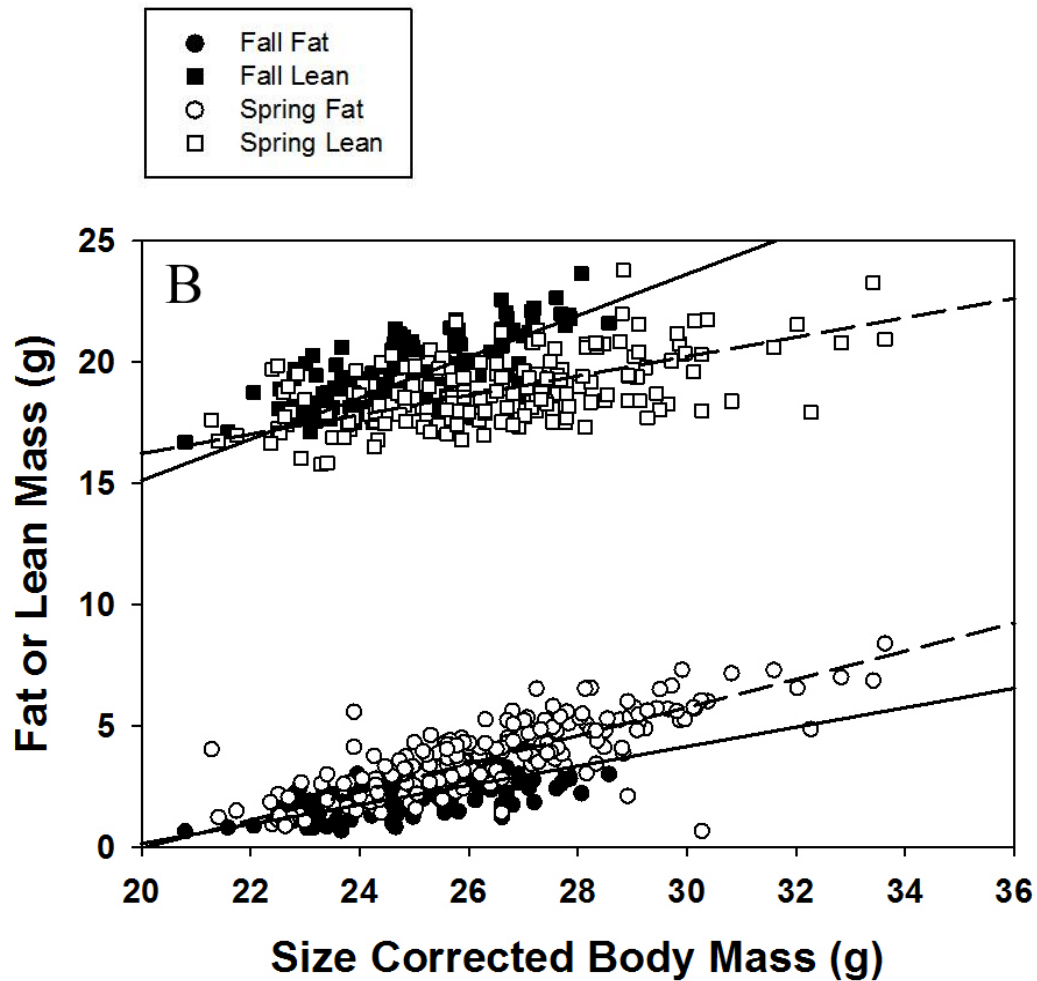


Figure 2.5 Example of seasonal comparison (spring- white, fall-black) for deposition of fat (circles) or lean (squares) mass for increase in 'size corrected body mass' for two species using major axis regression ($p < 0.05$), © R version 2.11.0 (2010-04-22); (A) Magnolia Warbler (*Setophaga magnolia*), no significant difference in relative deposition of fat or lean mass with increasing body mass by season, (B) Seasonal difference in White-throated Sparrows (*Zonotrichia albicollis*), deposition of both fat and lean mass is significantly different between spring and fall.

Table 2.3 Percent accumulation of fat and wet lean mass in migrant passerines in Long Point, Ontario, Canada, 2009. Group differentiation determined through comparison of slopes from major axis regression ($p < 0.05$), © R version 2.11.0 (2010-04-22).

Species	Group	N	% Fat	P	% Lean	P
Myrtle Warbler	SP	26	88(69-112)	0.29	19(0-41)	<0.01
	F	77	62(45-81)	<0.001		
	F♂	17			49(25-79)	0.01
	F♀	19			113(62-216)	0.65
Black-throated Blue Warbler ¹	SP	18	43(0-147)	0.12	82(47-137)	0.41
	F	23			50(29-74)	<0.01
	F♀	8	85(67-100)	0.18		
	F♂	15	17(0-46)	<0.01		
Nashville Warbler ¹	F & SP	67			47(28-70)	<0.01
	F♀	19	59(40-82)	<0.01		
	F♂	28	95(68-134)	0.78		
Blackpoll Warbler	SP	7	68(56-81)	<0.01	23(12-35)	<0.01
	F	17	59(44-76)	<0.01	41(26-59)	<0.001
Grey-cheeked Thrush ¹	SP	14	112(69-187)	0.60	16(Inf)	0.28
	F	28	25(13-38)	<0.001	75(58-95)	0.02
White-throated Sparrow ¹	SP	189	59(44-62)	<0.001	40(31-50)	<0.001
	F	140	40(32-49)	<0.001	85(70-100)	0.11
Ruby-crowned Kinglet ¹	SP & F	201			71(-74-64)	<0.001
	SP	56	62(53-72)	<0.001		
	F	145	43(34-54)	<0.001		
Gray Catbird	SP	50	60(47-75)	<0.001	46(28-66)	<0.001
	FA	13	122(95-160)	0.10	-35(-95-0.8)	0.04
	FJ	57	77(60-96)	0.02	33(3-69)	<0.01
Hermit Thrush ¹	SP & F	68	44(28-63)	<0.001	100(81-130)	0.77
Magnolia Warbler ¹	SP & F	152	61(52-71)	<0.001	34(21-49)	<0.001
American Redstart ¹	SP & F	64	74(64-87)	<0.01	36(20-53)	<0.001

Common Yellowthroat	SP & F	52	70(54-89)	<0.01	44(25-66)	<0.01
House Wren	SP & F	38	59(33-93)	0.03	69(37-113)	0.13
Golden-crowned Kinglet ¹	SP & F	47	39(24-55)	<0.001	5(0-23)	<0.001
Veery	SP & F	36	71(52-96)	0.03	46(19-81)	<0.01
Red-eyed Vireo	SP & F	37	70(56-87)	<0.01	38(19-60)	<0.001
Swainson's Thrush ¹	SP & F	122	22(15-29)	<0.001	42(35-50)	<0.001
Canada Warbler ¹	SP	26	75(60-94)	0.01	26(6-47)	<0.001

P-values indicated are for the individual slope from each regression whether it was significant or not.

Species were not included if sample size was insufficient for any sex, age or season comparison.

* SP-spring, F-fall, A-adult, J-juvenile, ♂-male, ♀-female

¹Total Body Mass corrected for size using wing chord (Peig and Green 2009)

Species names provided Appendix A.

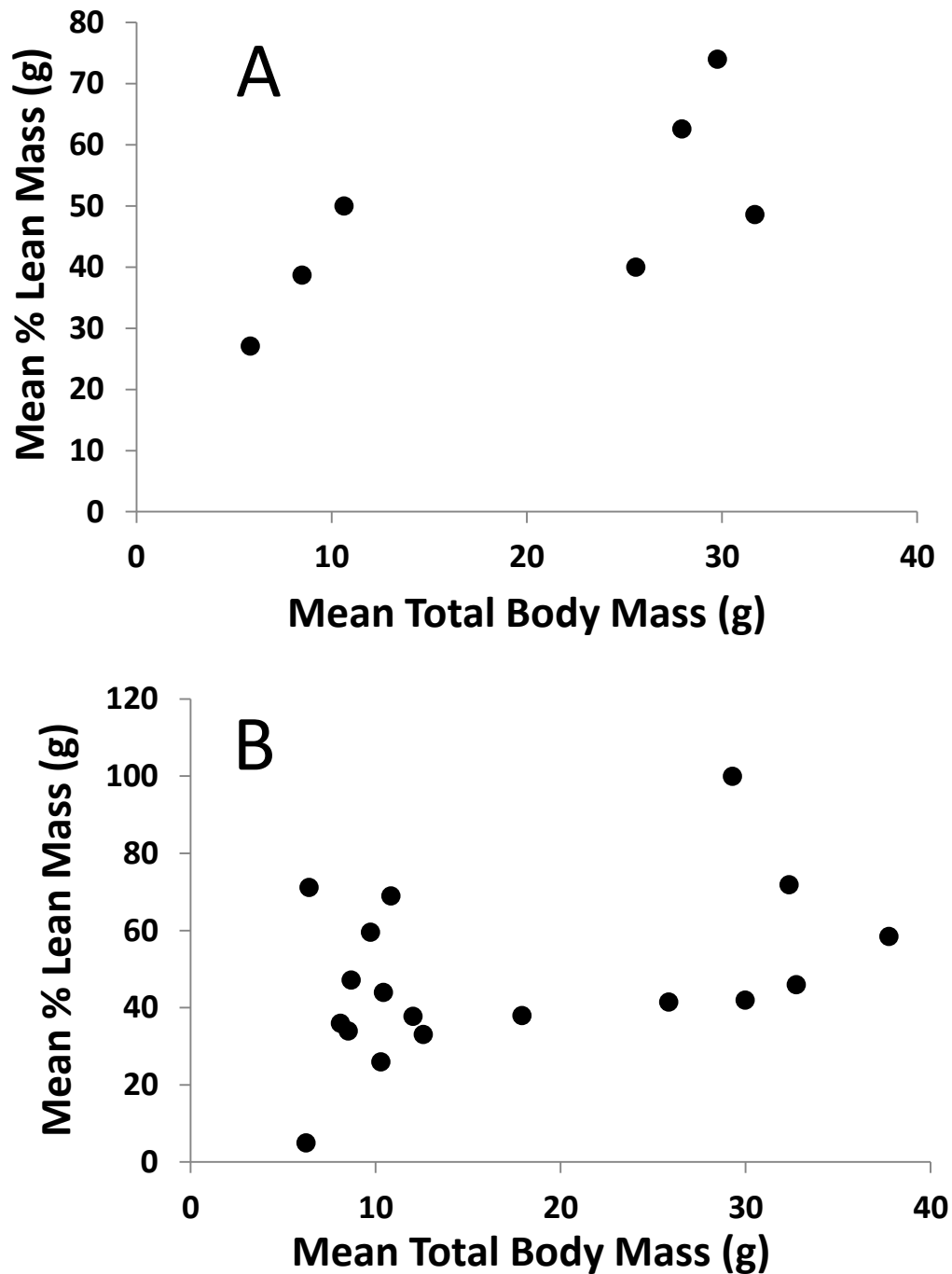


Figure 2.6 Mean relative percent lean mass deposited in refuelling passerines in relation to total body mass (g) at a stopover site in Long Point Ontario in spring and fall. Each black circle represents the mean % lean mass deposited during refuelling for a species. (A) Seven recaptured species (% estimates taken from Table 2.1) correlation analysis ($R^2 = 0.46$, $p = 0.09$). (B) Eighteen species from single scans (% estimates taken from Table 2.2) correlation analysis ($R^2 = 0.16$, $p = 0.09$).

DISCUSSION

Lean mass deposition is widespread among passerine species, and can be affected by season, sex, age, and potentially migration distance and body size. Seasonally, migrants generally deposited relatively more fat in spring than fall during refuelling, and sex and age effects were weak. Birds flying longer distances also carried more fat during the rushed spring migration than the more relaxed fall migratory journey. Though fat is the dominant fuel source (Jenni and Jenni-Eiermann 1998, Guglielmo 2010), interestingly, lean mass often contributed greatly to total change in body mass, and in some cases, contributed a greater proportion of mass increase than fat mass at stopover. Season, sex and age differences in lean mass stores and relative lean mass deposition in passerines were weak but there are potential effects of body size on relative deposition of lean mass, such that larger birds deposit more lean mass than smaller birds. My regression analyses to determine the relative deposition of both fat and lean mass in single scan birds using QMR data were highly variable, but still generally captured patterns in relative fuel deposition as found in recaptured birds. This was particularly true where sample sizes were large in both analyses, such as the White-throated sparrow, where recapture and single scan regression methods gave very close to the same deposition estimates for fat and lean mass. Overall, both fat and lean mass are dynamic body components in refuelling passerines during spring and fall migration and are important when considering energetic during migratory flights.

Average Body Composition for Migrant Passerines Species Captured during Spring and Fall

Most of the birds scanned for the first time were presumed to have arrived the previous night, and therefore their physiological condition is indicative of a nocturnal flight with little to no time dedicated to refuelling. However, within species, mean fat and lean mass stores between birds varied. Season, sex and age helped to explain some of the variation but it is possible that birds were not captured the first day they arrive and variation could be due to birds having been able to refuel for one or more days.

I predicted that migratory preparedness or overall fat and lean mass stores would differ by season, sex and age across species. Season explained the most variance in fat and lean mass stores. In 21 of 25 species, birds had larger fat stores in spring than fall. Other studies demonstrated the same trend using fat scoring techniques for visual fat stores like a standard scoring system (Kaiser 1993, Seewagen and Slayton 2008, Salewski *et al.* 2009). Mean lean mass stores were compared in 26 of the 29 species, and 10 species had differences by season but no universal trend towards greater proportion of lean mass in either fall or spring was observed. Therefore, even though lean mass stores may differ within species, the season, sex and age factors didn't entirely explained this variation. My results further indicate that body composition rarely differed by sex or age. Therefore, fat and lean mass stores did not consistently differ by season, sex or age but explained more variation in mean fat mass than mean lean mass.

Interestingly, long-distance migrants had the greatest difference between spring and fall in fat mass where long-distance migrants carried more fat in spring. Medium and

short distance migrants were less likely to have seasonal differences in fat loads. This may indicate that birds anticipating flying longer distances to reach breeding grounds, or facing more unpredictable weather conditions rely more on fat as fuel. Spring is considered the rushed migration (Cherry 1982, Veiga 1986, Izhaki and Maitav 1998) and perhaps the metabolic challenge of flying longer distances on a restricted time budget requires these species to store a greater amount of fat when compared to shorter distance migrants.

Relative Fat and Lean Mass Deposition in Refuelling Migrants at a Stopover Site

Previous studies indicate that in migrant passerines both fat and lean mass are catabolized during flight (ie; Bairlein 1985, Battley *et al.* 2000, Bauchinger and Biebach 2005) and both of these body components are recovered during stopover (Seewagen and Guglielmo 2011, Aamidor *et al.* 2011). I further investigated the relationship of fat and lean mass with total body mass of refuelling passerines at a stopover site across season, sex and age groups. This is a multi-factorial study to examine how these factors influence the relative deposition of both fat and lean mass in refuelling free-living birds during migration.

Validation for the use of QMR analysis using recaptured birds indicated that 100 % of change in total body mass measured on a balance was also measured by the QMR equipment. These results are similar to studies using the same QMR instrument (Seewagen and Guglielmo 2011). Interestingly, after combining all species, fat and lean mass contributions to mass gain were equal; for every unit of mass gained, on average 50 % was fat and 50 % was lean. During flight in a wind tunnel, Swainson's Thrushes derived

10 % of the energy for flight from lean mass, but this was x-y regression of the percent mass lost (Gerson and Guglielmo 2011). The conversion of energy supplied from lean mass tissues equates to ~50 % of the total mass lost in flight is derived from protein catabolized from muscles and organs (McGilvery 1983, Jenni and Jenni-Eiermann 1998). If 50 % of the mass a bird is burning comes from lean mass, relative lean mass deposition of ~50 % at a stopover site is plausible (Piersma and Jukema 1990, Lindstrom and Piersma 1993). QMR detected all changing body components and therefore provided a reliable method for generating estimates of relative fat to lean mass deposition.

Refuelling in recaptured birds, analyzed by species, indicated significant variation around the 50/50 average reported above. The relationship between change in fat and lean mass to overall change in total mass, measured using QMR, provided estimates of relative fuel deposition on a very fine scale at the individual level. At the population level, lean mass accounted for 22 – 105 % of the mass change across species. Gray Catbird, for example, lost fat mass upon arrival, substituted the loss of fat with gain in lean mass and still increased in total body mass overall, making the percent lean mass contribution greater than 100 %. Lean mass deposition during refuelling can in some cases be more dynamic than fat mass deposition and therefore it is important to understand and measure changes in lean mass when migrants are refuelling.

The greatest changes in lean mass during migration are in long-distance migrant shorebirds and Palearctic passerines crossing large ecological barriers, such as the Sahara Desert (Biebach 1998). Results in this thesis demonstrate that there are also changes in non-fat body components in many Nearctic-Neotropical passerine species that typically

demonstrate shorter flight bouts and use a greater number stopover sites during migration (Akesson *et al.* 1992, Bauchinger and Biebach 2005). Every bird examined in this study has its own migratory pathway originating from different breeding sites and ending at unique wintering grounds and notably, this variation in migratory body condition can be related to conditions from a previous night's flight (Bairlein 1985), an individual's sex or age (eg; Heise and Moore 2003, Vanderhoff and Eason 2007, 2008), the time of year (eg; Fransson 1995, Kokko 1999, Newton 2008) or the refuelling site relative to an individual's final destination (Cherry 1982). This would explain why grouping birds by season, sex and age only explained some differences among refuelling birds at stopover. However, my results from comparing mean deposition of lean mass for every gram gained compared to mean total body mass may be a reflection of Lindstrom's (1991) study which determined that rapid increases in body mass of migrating birds were proportional to body mass, such that, smaller birds deposited fat at a greater rate than larger birds. Perhaps smaller birds are sustaining energetic requirements for long distance flight by using fat and sparing lean mass, where larger birds rely more on subsidizing flight costs with protein catabolism. Therefore, in addition to aforementioned factors examined and additional environmental factors discussed affecting body condition and refuelling, body size may also attribute to refuelling efficiency and strategy during migration.

The ability to change lean body components, such as organs and muscles, must provide benefits aside from energy for flight. Current research provides evidence that lean mass catabolism during flight is directly related to relative humidity. Water balance

was maintained when flying during drier conditions as a result of depleted lean mass stores and subsequent release of metabolic and free water (Gerson and Guglielmo 2011). Depletion of lean body components during flight requires subsequent rebuilding of those components (eg; muscles and organs) during refuelling. Greater proportions of lean mass deposition in relation to fat upon arrival at a stopover site may be expected if birds are rebuilding organs. Fully functioning digestive organs are necessary for processing and building large fat stores needed for flight and therefore birds have an increasing reliance on high protein foods, such as insects (Aamidor *et al.* 2011).

It should be noted that many recaptured birds lost mass between captures. There are a number of reasons why some birds are recaptured and others are not. Typically, birds in poor body condition need to gain more mass at a stopover site than birds in good condition (Bairlein 1985). Refuelling takes time, and therefore, an increased stopover period is required, ultimately, providing more opportunity for recapture. Thus, recaptured birds may sometimes represent poorer migrants (less experienced, or less dominant individuals) and could help to explain why many birds I recaptured were not refuelling very well. However, whether a bird increases or decreases in mass, linear regression analysis used for both recapture and single scan relative deposition of both fat and lean mass estimates still represents overall positive or negative change in body components.

Overall, there is no general rule that songbirds follow when it comes to refuelling at a stopover site during migration but this does not suggest that season, sex or age do not affect relative deposition of both fat and lean mass. For example, White-throated Sparrows deposit more fat in spring than they do in fall. Other species, such as Magnolia

Warbler, did not demonstrate any differences in seasonal deposition of fat or lean mass. Evidence of variation within species highlights the importance of refining samples into informative groups such as sex, season and age when doing refuelling assessments of migrant passerines and demonstrates how even at the individual level, birds are responding to stopover differently.

Comparing Analysis of Recapture Regression Deposition Estimates to Analysis of Single Scanned Regression Deposition Estimates of Refuelling Passerines

Recapture rates of migrant passerines at a stopover site within the same season are often low. They are also biased towards individuals that stopover longer which may not represent an average migrant. Low recapture rates and small sample size make it difficult to study refuelling in free-living birds. Studies using single captures have greater sample sizes and represent a more accurate sample of the population. A comparison of regression analyses of recaptured individuals and a different regression analysis using single scanned individuals was done to determine the reliability of predicting relative deposition of fat and lean mass in passerines while refuelling during migration. Only 7 of the species out of the 18 used in the single scan regression analysis had sufficient sample size for recapture regression. However, in a number of cases, slope estimates from the two methods were the same or within 10% of each other. In other cases where single scan regression under or over estimated fat or lean mass deposition, the relative ranking of fat/lean values was always the same. For example, Hermit Thrush single scan analysis over estimated both fat and lean mass deposition in comparison to recapture regression, but estimates for both regressions predicted a greater proportion of mass gain to be lean

mass. Using both recapture and single capture analysis supports a potential positive relationship between average percent lean mass deposited at stopover and body size.

Conclusion

Although the species used in this study were not preparing for, or recovering from, crossing a large ecological barrier, they were refuelling at an inland stopover site, and were mostly temperate, short-distance migrants, each of my analyses suggests that non-fat body components change significantly during refuelling. In comparison to extreme long-distance migrants, such as shorebirds, and birds crossing ecological barriers, where energy from fat mass may be limiting, temperate migrants do not face the same energetic demands. North American temperate migrants have more opportunity to stop and refuel, yet they still change non-fat body components dramatically. Refuelling variation may differ between stopover sites (Cherry 1982) due to different environmental conditions. Also, deposition of fat and lean mass may vary with the relative location of the staging site to expected migration distance (Bairlein 1985) and the previous flights energy use (Gerson and Guglielmo 2011). As a result, relative deposition of fat to lean mass is a reflection of migratory strategy in relation to an individual's final destination and recovery from previous migratory flights. Regardless, lean mass contribution to changes in total body mass in short-and long-distance migrants with or without frequent stopover site use, is substantial, ranging anywhere between -35 – 113 % of mass increase.

My thesis presents strong empirical evidence of changing lean mass in refuelling free-living migrants. For decades, researchers have developed complicated models for interpreting fat scores taken from banding stations all over the world in an attempt to

decipher physiological changes in migrating birds (eg; Biebach 1986, Dunn 2000). Until the early 1990's it was generally thought that lean mass was an unchanging body component. There is now empirical evidence that lean mass significantly contributes to changes in total body mass in refuelling free-living birds during stopover.

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CHAPTER 3 : A FIELD TEST OF THE EFFECTS OF BODY COMPOSITION ANALYSIS BY QUANTITATIVE MAGNETIC RESONANCE ON SONGBIRD STOPOVER BEHAVIOUR

INTRODUCTION

Migratory birds have remarkable abilities to orient in unfamiliar locations and navigate over thousands of kilometres to travel between breeding, wintering and moulting areas (Newton 2007, Holland *et al.* 2009). It is widely accepted that one source of information birds use to orient and navigate is the Earth's geomagnetic field (eg: Wiltchko and Wiltchko 1995, Akesson 1999, Muheim 2007), and recent studies have begun to reveal the mechanisms underlying the geomagnetic senses of birds. Quantitative Magnetic Resonance (QMR) is a newly-available technology used to measure body composition of small birds in the field (Seewagen and Guglielmo 2010, Seewagen and Guglielmo 2011, Guglielmo *et al.* 2011). Birds undergo a one to three minute scanning procedure that exposes them to a horizontal magnetic field approximately 1,000 times stronger than the natural geomagnetic field. It is unknown if QMR analysis will affect their geomagnetic senses and therefore, orientation and navigation ability.

Current evidence suggests that birds should not be affected by QMR. First, although manipulation of the magnetic field can cause migratory birds to alter their orientation (Muheim *et al.* 2006, Henshaw *et al.* 2010, Wiltchko *et al.* 2007), when the artificial magnetic field is removed, birds can recalibrate their magnetic compass using celestial cues, particularly the skylight polarization pattern during sunset (Cochran *et al.* 2004, Muheim *et al.* 2007). Second, the photopigment-based system that birds use to

sense the Earth's magnetic inclination angle to orient, should not be affected once the external magnetic field is removed (Zapka *et al.* 2009). On the other hand, QMR could potentially affect the iron-mineral-based sensors in the beak which may be involved in sensing geomagnetic field strength and play a role in navigation by providing information on their current location (Zapka *et al.* 2009). A growing body of evidence suggests that birds use both the iron-mineral-based and the photopigment-based mechanism to orient during migration (Wiltschko and Wiltschko 2002, Muheim *et al.* 2002, Fleissner *et al.* 2003, Beason 2005, Davila *et al.* 2005, Mouritsen and Ritz 2005). Therefore, birds may have more than one mechanism for detecting, orientating to and navigating with the Earth's geomagnetic field.

I hypothesized that migrating birds would not be affected by QMR analysis. I used direct and indirect measurements of migratory behaviour of songbirds to determine if QMR analysis affects a birds' ability to refuel and orient at a stopover site. Radio-telemetry allowed us to make direct measurements of stopover duration and departure direction of individual birds, but had the disadvantage of relatively small sample size. Capture-mark-recapture analysis of banding data was used to make indirect measurements of stopover behaviour. I tested for differences in transience (τ) (departure from a stopover site <24 hours after arrival) and stopover duration (converted from estimates of daily survival (ϕ)) between QMR scanned and control birds to determine behavioural effects of QMR analysis during stopover. I predicted there would be no difference in stopover duration or departure direction between birds exposed to the magnetic field from QMR scanning and the control in the radio-telemetry study and no

difference in transience or stopover duration estimates between QMR scanned birds and control birds from Capture-mark-recapture analysis.

METHODS

Study site and bird handling

Long Point Bird Observatory (LPBO), is located on Long Point, Ontario, Canada; (42°34'57.71"N, 80°23'51.48"W) a 35-km sand spit extending east into Lake Erie. This study site is a World Biosphere Reserve and a globally Important Bird Area and, as a result, is an important area for numerous species of migrant passerines. At the Old Cut banding lab, 14 mist-nets and 4 ground traps (NABC 2001, Hussell and Ralph 2005) were opened 30 min before sunrise and remained open for 6 hours. Nets were not open during periods of heavy rain or wind. Birds were individually banded with a unique 9 digit number on a United States Fish and Wildlife Service/ Canadian Wildlife Service aluminum band. Birds were classified as adult (AHY in fall or ASY in spring) or juvenile (HY in fall, SY in spring) (Pyle 1997). Birds were then released or bagged and brought to a climate-controlled mobile laboratory to be scanned in a QMR body composition analyzer (model Echo-MRI-B, Echo Medical Systems, Houston, TX, USA; QMR and lab described in Guglielmo *et al.* 2011). Birds were scanned using the "small bird" (<50g) and "two-accumulation" settings of the Echo-MRI software producing fat mass and wet lean body mass measurements to 0.001g. Each morning we calibrated the QMR using a 94g canola oil standard provided by the manufacturer. Scans of 5g and 10g oil standards were taken periodically throughout the day to ensure scanning accuracy (Seewagen and Guglielmo 2010, Seewagen and Guglielmo 2011). Fat mass and wet lean body mass

values were adjusted to improve accuracy using two calibration equations (calibrated fat mass = raw QMR fat X 0.94, and calibrated lean body mass = raw QMR wet lean body mass X 1.021) derived from a laboratory validation developed from house sparrows (*Passer domesticus*) and zebra finches (*Taeniopygia guttata*) (Guglielmo *et al.* 2011). Birds were selected for scanning only if there was sufficient time after banding for QMR scanning. We did not include a control group for the extra handling associated with the QMR scan because we wanted to maximize the amount of data collected on body composition for use in other studies. Therefore, our conclusions apply to the entire process of being handled and QMR scanned, rather than the effects of magnetic field exposure alone.

Radio-Telemetry Study

Black-throated Blue Warblers (*Dendroica caerulescens*) were captured between September 9 and October 12, 2009. Nine HY fall birds were scanned by QMR (SCAN), and 11 HY fall birds were used as an unscanned control group (NOSCAN). Each bird was outfitted with an ANTC-M1-1 or ANTC-M2-1 digital transmitters (Lotek Wireless, Newmarket, Ontario, Canada). The transmitters were attached to the bird by elasticized loops around the hips and over the back (Rappole and Tipton 1991). Masses of the transmitters average 0.3g, (Thurber 2010) which is below the 5 % recommended upper limit for passerine sized birds (Caccamise and Hedin 1985). Tagged individuals were released within one hour of capture.

The movements of individuals were monitored continuously by means of an array of radio-telemetry receivers and antennas, situated at five locations both near and on

Long Point (see Taylor *et al.* 2011). Local movements were more precisely monitored at least twice daily throughout range of the peninsula by means of manual tracking, using a handheld SRX600 receiver and 5-element Yagi antenna from Lotek Wireless (Newmarket, Ontario, Canada) as described by Taylor *et al.* (2011) . Minimum stopover duration was estimated from the day the bird was captured to the day the bird's tag was no longer detected by automated or manual tracking. Minimum stopover duration is a conservative estimate of total stopover duration assuming the day of capture is the day of arrival to the stopover site. Departure orientation was defined as the direction travelled during a nocturnal movement or a daily movement from within to beyond the area covered by radio-telemetry array. Flight movement was determined from sharp increases in radio-telemetry signal strength from the initial detection pattern from one or more towers and subsequent detection over several minutes which provided the direction of movement (Taylor *et al.* 2011). Daily movements are considered emigration to other surrounding areas but were included in our analysis due to limited sample size (refer to Table 3.1). Departure direction from the stopover area has been demonstrated to reflect migratory direction (Goymann *et al.* 2009, Thurber 2010) and therefore appropriate departures were expected to be in a southerly direction.

Capture-mark-recapture Study

White-throated Sparrows were captured in spring (April 26 – May 19) and fall (September 25 – October 15) 2009. Migratory behaviour at the stopover site was quantified from constant-effort banding and recapture data using both a multi-state mark-recapture model (no.1 below) and a recaptures-only model (no.2 below). These models

allow estimation of parameters specific to migrant behaviour such as daily transiency probability (τ) (leaving a monitored site within 24 h of first capture) (Lebreton and Pradel 2002, Schaub *et al.* 2004) and daily survival (ϕ). Survival estimates can be used to create stopover duration following Schaub *et al.* 2001 (eqn 3). All estimates were generated for both groups; SCAN and NOSCAN within each model for spring and fall. All CMR models were written and run in MARK 5.2. Due to a limited sample size, all models built for this study were time invariant. Encounter histories were generated for White-throated Sparrows (*Zonotrichia albicollis*) across dates where captures and recaptures were greatest for each season (spring, fall).

Model No.1

A multi-state mark-recapture model was used to assess movements made within 24 hours of first capture by taking all birds from an ‘initial’ state upon first capture and moving them to either a ‘transient’ or ‘non-transient’ state using a logit-link function (Schaub *et al.* 2004, Mackenzie 2010). Estimates of transiency (τ) were derived from this model for both groups and compared using the calculated 95 % confidence intervals for all individuals in SCAN and NOSCAN groups for spring and SCAN and NOSCAN groups for fall. Three encounter histories were generated in fall; 1) “all birds” (SCAN/NOSCAN), 2) “HY birds only” (SCAN/NOSCAN) and 3) “age groups” (adultSCAN, adultNOSCAN, juvenileSCAN and juvenileNOSCAN) to determine potential contribution of age effects. In general, sample size for fall adult birds was limited (SCAN AHY = 23, HY = 112; NOSCAN AHY = 24, HY = 75). Sample size is essential when considering model selection in multi-state models (like model no. 1) when

survival and encounter probabilities are state-specific (Lindberg and Rexstad 2002, Lindberg 2010). Distinguishing between states in model no. 1 may be challenging when sample size is small and in order to take this into consideration with software MARK (White and Burnham 1999, Lindberg 2010) multiple encounter histories were generated to determine if sample size affected model deviance and outcome. A goodness-of-fit test was performed on the model using the bootstrap method in MARK (Mackenzie 2010) and a commonly used overdispersion correction factor (\hat{c}) was derived to determine variance inflation of the model (Anderson and Burnham 2002, Cooch and White 2008) and applied to the AIC and parameter estimates.

Model No.2

A recaptures-only model was used to assess daily survival probability between SCAN and NOSCAN groups for spring and SCAN and NOSCAN groups for fall. Three encounter histories again were generated in fall; 1) “all birds” (SCAN/NOSCAN), 2) “HY birds only” (SCAN/NOSCAN) and 3) “age groups” (adultSCAN, adultNOSCAN, juvenileSCAN and juvenileNOSCAN) to determine potential contribution of age effects. Again, the number of adult birds captured in fall was relatively small. However, single-state recapture-only models can accommodate smaller sample sizes. This model included additional covariates; handling time and bird abundance to account for additional variation in daily survival and recapture probability estimates. Handling time was averaged for each group from the time of capture to the time of release over the days included in the encounter histories. Bird abundance was calculated from the total number of birds banded of all species on the days included in the encounter histories. Handling

time was included to determine if model estimates were influenced by additional stress from treatment duration as opposed to QMR analysis. Bird abundance was included to prevent bias in sampling; greater proportions of birds were scanned on days with few birds captured than days with many birds captured. Estimates of daily survival (ϕ) probability and daily recapture (p) probability for each group were determined for each handling time/bird abundance model combination. A goodness-of-fit test was performed on the most general model ($p_{\text{handtime*birdabundance}}$, $\phi_{\text{handtime*birdabundance}}$) again to determine an overdispersion correction factor (\hat{c}) and applied to the AIC and parameter estimates. Survival estimates were used to calculate stopover duration (days) for each group using $\{-1/\ln(\phi)\}$ (Schaub *et al.* 2001).

Potential Violations of Model Assumptions

Both mark-recapture models (no.1 & no.2) have the same two general assumptions that may not be upheld in our analyses (Bachler and Schaub 2007). All data used in these models were derived from banding data collected at a stopover site during migration. Both models assume that the encounter probability at time i is the same for all individuals present at time i ; to account for this assumption model no. 2 included other sources of variation such as handling time and bird density (methodological influences). However, there are other sources of variation that could influence recapture probability such as environmental or behavioural variation (Simons *et al.* 2004, Bachler and Schaub 2007, Bonter *et al.* 2008). Results of recapture probability generated from model no. 1 were not included in this study as these results did not best represent potential variation from additional influences. Secondly, both models assume that every individual captured

at the study site at time i has the same probability of survival (or probability of remaining at the site) until time $(i + 1)$. However, this is often violated as the probability of remaining at the study site during migration should decrease with time after arrival (Bachler and Schaub 2007). As a result, survival estimates were not used in their raw form but converted to stopover duration in days using Schaub *et al.* (2004).

RESULTS

Radio-Telemetry

Telemetry data provided both minimum stopover duration and departure direction from the Long Point area for each Black-throated Blue Warbler. Mean minimum stopover duration in fall did not differ between HY SCAN (5.36 d, SD = 1.804, n = 11) and HY NOSCAN (7.33 d, SD = 3.77, n = 6) birds (unequal variances $t(6.273df) = 1.205$, $p = 0.272$). Due to the limited sample size of our departure orientation data (Table 3.1), statistical analysis would be inappropriate (Fisher 1993), but a visual comparison of departure direction from Long Point between SCAN (treated QMR) and NOSCAN (control) birds indicates that no bird, regardless of group, departed Long Point in an inappropriate direction for fall migration (Figure 3.1). Some birds departed along the shoreline of Lake Erie and others travelled south across the lake. Sample sizes and tag fates are provided in Table 3.1.

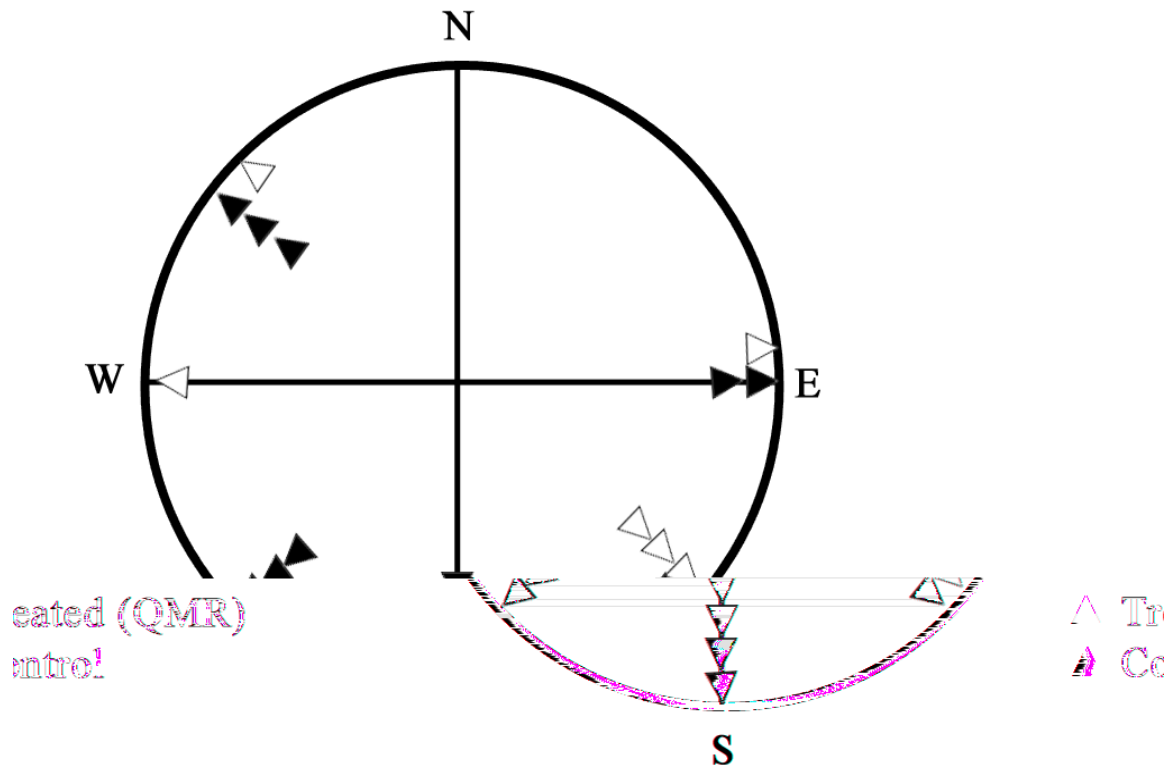


Figure 3.1. Departure orientation for Black-throated Blue Warblers (*Dendroica caerulescens*) from Long Point, Ontario, Canada using radio-telemetry between birds treated by Quantitative Magnetic Resonance (QMR) analysis (open triangles) and control birds (solid triangles).

Table 3.1 Sample size and tag fate for each group of Black-throated Blue Warblers captured in Long Point in fall 2009.

Group	n	Age	Sex	Fate
NOSCAN	11	15 HY	7 ♀, 4 ♂	3 lost tags 1 deceased 3 emigration movements, 8 definite departures
SCAN	6	9 HY	5 ♀, 4 ♂	2 lost tags 1 deceased 3 emigration movements, 3 definite departures

*HY: Hatch year bird (juvenile)

*lost tags: tag was recovered but no bird

Capture-Mark-Recapture Models

Overdispersion values (\hat{c}) that were <3.0 for each model suggested appropriate goodness-of-fit for the data (Burnham and Anderson 2002). All model results for each encounter history (1, 2 and 3) were compared for best goodness-of-fit.

Model no. 1 deviance for models with encounter histories “all birds”, “HY birds only” and “age groups” respectively ($D = 252.9, 42659.1, 53694.5$) demonstrates that “all birds” best supports the data. Extreme difference in model deviance in “HY birds only” and especially “age groups” is mostly likely attributed to sample size restrictions in this multi-state model. Transience probability estimates for White-throated Sparrows, generated in model no. 1 (encounter history “all birds”), were generally high for both SCAN and NOSCAN groups (Figure 3.2). Similar means and substantial overlap in confidence intervals indicates these groups were not different. Encounter histories “HY birds only” and “age groups” transiency estimates for SCAN and NOSCAN groups were generally lower, but 95 % confidence intervals extended beyond 0-1 (range for daily transiency estimate) therefore suggesting sample size restricted proper assessment from the model.

Model no. 2 deviance for encounter histories “all birds”, “HY only” and “age groups” respectively ($D = 275.1, 344.9, 436.0$) suggested that sample size was not a factor in the simpler single-state model. To address potential age effects since deviance output no longer indicated inadequate sample size, encounter history no. 3 “age groups” was selected for fall.

Model AIC results for spring and fall models, indicate daily survival estimates for White-throated Sparrows were influenced more by bird abundance ($p_{\text{bird abundance}}$, $\phi_{\text{bird abundance}}$) than handling time, even though handling time was significantly longer in both spring and fall respectively for SCAN birds (spring 67.9 minutes, SD = 24.0, n = 222; fall 58.1 minutes, SD = 28.1, n = 162) than NOSCAN birds (spring 43.9 minutes, SD = 34.8, n = 913; fall 36.2 minutes, SD = 23.4, n = 247) ($t(474) = 12.09$, $p < 0.001$; $t(407) = 8.574$). AIC weight indicated that handling time had little to no effect, and therefore was it not included in the final model. Multi-model inferences for model no. 2 are indicated in Table 2.2.

In spring, White-throated Sparrow stopover duration, corrected for bird abundance, was not significantly different between SCAN (2.41 d, LCI= 2.09, UCI = 2.82) and NOSCAN birds (1.96 d, LCI=1.53, UCI = 2.56). In fall, White-throated Sparrow stopover duration, corrected for bird abundance, was estimated for the following; adultSCAN (6.75 d, LCI = 2.56, UCI = 19.19), adultNOSCAN (0.39 d, LCI = 0.27, UCI = 0.66), juvenileSCAN (2.11 d, LCI = 1.62, UCI = 2.81), juvenileNOSCAN (1.00 d, LCI = 0.78, UCI = 1.32). AdultSCAN and juvenileSCAN birds had a significantly longer stopover duration than both adult- and juvenileNOSCAN groups.

Daily recapture probability was significantly greater in SCAN ($p = 0.50$, LCI = 0.43, UCI = 0.58) than NOSCAN ($p = 0.08$, LCI = 0.05, UCI = 0.12) White-throated Sparrows in spring. Fall daily recapture probability for White-throated Sparrows was significantly greater for adultNOSCAN ($p = 0.99$, LCI = 0.02, UCI = 0.99) and

juvenileNOSCAN ($p = 0.45$, LCI = 0.42, UCI = 0.49) than adultSCAN ($p = 0.12$, LCI = 0.06, UCI = 0.23) and juvenileSCAN birds ($p = 0.22$, LCI = 0.15, UCI = 0.32).

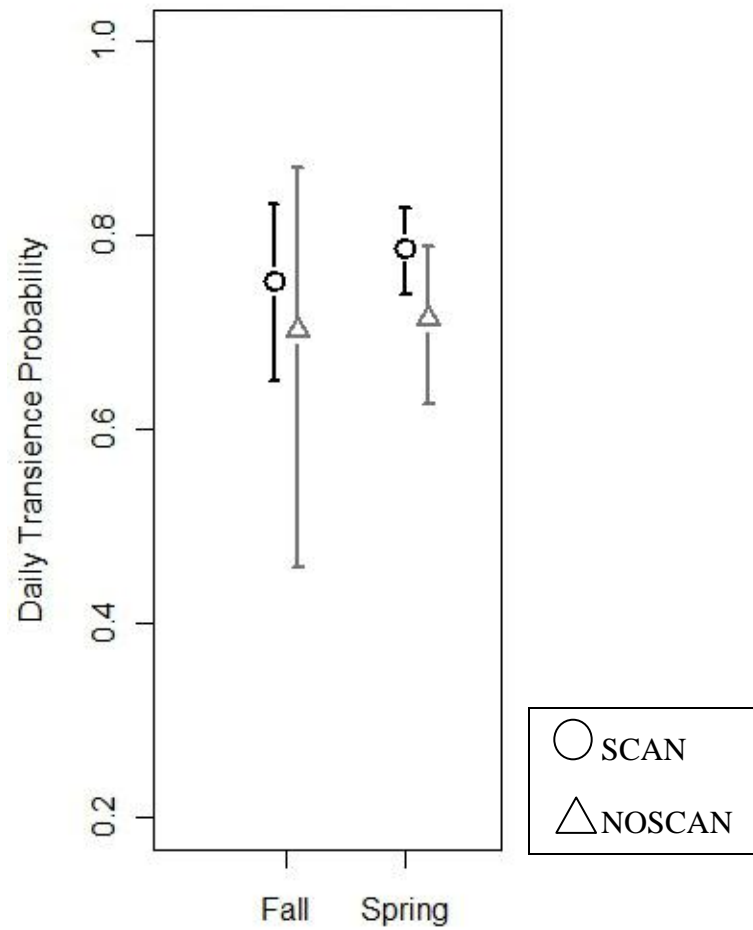


Figure 3.2 Daily transience (τ) probability estimates for White-throated Sparrows in Fall and Spring of 2009. QMR SCAN birds (circles) and control NOSCAN birds (triangles) with 95% confidence intervals.

Table 3.2 Multi-model inferences for spring and fall model no. 2 multivariable analysis of survival in White-throated Sparrows encounter history 3; “age groups”.

Rank	Covariates	(<i>Q</i>)Dev	<i>K</i>	(<i>Q</i>)AIC _c	(<i>Q</i>)ΔAIC _c	(<i>Q</i>) <i>w</i>
1	<i>Model (S) + b.abund</i>	1134.2	5	1984.4	0.0	0.7
2	<i>Model (S) + b.abund+ h.time</i>	1134.2	6	1986.4	2.0	0.3
3	<i>Model (S) + h.time</i>	1144.1	5	1994.2	9.8	0.0
1	<i>Model (F) + b.abund</i>	436.0	6	721.8	0.0	-
2	<i>Model (F) + h.time</i>	437.7	6	723.5	1.7	-
3	<i>Model (F) + b.abund + h.time</i>	436.0	7	723.9	2.1	-

*Headers for columns:., Dev = Deviance, *K* = number of parameters, AIC_c = corrected AIC, ΔAIC_c = change in AIC relative to the optimal model, *w* = AIC weight, (*Q*) = corrected using \hat{c} -hat value.

*Model and covariates: (*S*)-Spring, (*F*)-Fall, *b.abund* = bird abundance, *h.time* = handling time

DISCUSSION

Radio-telemetry

The telemetry array provides reliable, direct measurement of departure time and direction (Taylor *et al.* 2011), and my analysis indicated that QMR analysis had no effect on minimum stopover duration or departure direction of Black-throated Blue Warblers. Though the effect was not statistically significant, the average stopover for QMR scanned birds tended to be ~2 days longer, but this was influenced by 2 birds out of 6 in the SCAN group that stayed longer than all others (caught in the afternoon of September 30, 2009 and October 1, 2009 staying 12 and 11 days respectively). A larger sample size may have revealed such idiosyncratic stopovers in the NOSCAN group as well, and these occasional long stopovers have been observed with other species in other studies (Schaub and Jenni 2001, Schaub *et al.* 2001, Salewski *et al.* 2007). All QMR scanned Black-throated Blue Warblers were able to depart in about the same amount of time as any other radio-tagged bird in this study.

All fall migratory departures from Long Point for both SCAN and NOSCAN Black-throated Blue Warblers were in an appropriate southerly direction or appropriate direction for the surrounding landscape (following the shoreline). Previous work at Long Point has indicated that in the fall Black-throated Blue Warblers, Swainson's Thrushes (*Catharus ustulatus*) and Hermit Thrushes (*Catharus guttatus*) depart: 1) directly east off the tip of the peninsula of Long Point, 2) directly south, or in some cases 3) west to follow the shoreline on the north side of Lake Erie (Mackenzie unpublished data, Mills *et al.* 2011). Most importantly, if QMR altered orientation, each bird was able to recalibrate their geomagnetic compasses prior to departure. All SCAN birds departed Long Point

more than 24 hours after capture, providing a minimum of one sunset/sunrise to recalibrate using celestial information (Cochran *et al.* 2004, Muheim *et al.* 2007). Holland (2010) demonstrated that birds altered their departure direction after undergoing a magnetic pulse designed to shift their orientation from the magnetic poles. However, the magnetic pulse (0.1 T) applied was designed to alter the magnetic field orientation, not cause disorientation. In our study, magnetic forces experienced in QMR analysis were neither directional (zero inclination angle) nor comparable in intensity to the Earth's geomagnetic field (0.05T for QMR versus 30-60 μ T), and therefore my treatment cannot be compared to the Holland (2010) study.

How iron-mineral sensors in birds respond to directional changes in the magnetic field is unknown. Magnetotactic bacteria reverse their swimming direction after an applied antiparallel magnetic pulse, and therefore, similar effects can be anticipated in magnetite (Blakemore 1975, Blakemore *et al.* 1980). Pulse treatments in birds are a 'black box' since there have been no direct measurements of the effects of a pulse on iron-minerals in the bird magnetic sensory system, either *in vivo* or *in vitro* (Holland 2010). Therefore, it is currently unknown what aspects exactly are affected in avian iron-mineral-based systems from a magnetic pulse treatment (Fleissner *et al.* 2003). Regardless of the effects QMR may have had on iron minerals in the treated birds, there is no evidence that birds were unable to 'recalibrate' their magnetic compass after treatment. Overall, after exposure to QMR at a stopover site in fall, Black-throated Blue Warblers showed no evidence that their navigation or orientation sensory mechanisms were impaired by exposure to QMR.

Capture-Mark-Recapture Models

Capture-mark-recapture modeling indicated that White-throated Sparrows demonstrated some differences in migratory behaviour after QMR analysis. In model no. 1., transiency estimates were the same for both SCAN and NOSCAN groups when comparing “all birds”, and these estimates greatly overlap transiency estimates generated in a comparable model by Mackenzie (2010) for passerines in Long Point, Ontario. Model no. 2 indicated that stopover duration in White-throated Sparrows was not affected by QMR in spring, but in fall, QMR adult scanned birds stayed four to five days longer than unscanned adults and scanned juveniles stayed about one day longer than unscanned juveniles (scanned adults = 6.75 d, control adults = 0.39 d, scanned juveniles = 2.11 d, control juveniles = 1.00 d). Such a substantial difference in stopover duration of scanned adult birds is most likely attributed to the fact that only five of the twenty-three adult scanned birds included in the model were recaptured and only two of the birds were recaptured three to four times over six to twelve days. In a relative sense scanned juvenile birds stopping for two days compared to 1 day in unscanned juveniles represents a doubling of stopover duration for scanned birds. However for juveniles the one day stopover in the control group is very short and atypical for passerines in light of other studies at Long Point and elsewhere (Schaub and Jenni 2001, Mackenzie 2010, Seewagen *et al.* 2010). If QMR affects geomagnetic orientation or navigation systems, one day may be insufficient for recalibration with celestial cues. During a more typical multi-day stopover, recalibration may be completed and thus not constrain departure. Black-

throated Blue Warblers refuelled for five to seven days and showed no effects of QMR on stopover duration.

Typical for fall migration in Long Point Ontario, the vast majority of individuals captured and included in this study were juvenile birds. The energetic demand of migration poses stress on passerines, and juvenile birds tend to have to work harder to maintain stored fuel relative to adults (Hedenstrom 1997). Hatch year birds in fall may be poorer foragers (Heise and Moore 2003, Vanderhoff and Eason 2007, 2008), choose poorer quality foods, and may be out-competed for food by adults (Marchetti and Price 1989, Sol *et al.* 1998). Ultimately, HY birds often have a longer stopover duration in comparison to their experienced AHY competitors (Mackenzie 2010). However, my stopover duration estimates for juveniles were very short. Migratory stopover duration estimates for ovenbirds in North America have estimated these refuelling periods can last 3 days on average and range from 1-10 days (Seewagen *et al.* 2010). Most studies are estimates of migrants in Continental Europe, these estimates range from 4-12 days (Schaub and Jenni 2001, Schaub *et al.* 2001, Salewski *et al.* 2007). If birds require 1-2 sunsets to completely recalibrate their magnetic compass after exposure to QMR, this effect is minimal over the course of a complete migration since migrants often can be delayed at stopover by other environmental factors like rain or wind (Schaub *et al.* 2004). Finally, daily recapture probability was greater in treated birds during spring. However, control adults and juveniles were more likely to be recaptured than scanned birds in fall. Overall, recapture probability differences were not a reflection of length of stay but more of a reflection of an affinity for the study site.

Conclusion

Birds are extremely resilient travellers, avoiding starvation, predators, variable weather conditions and other challenges to navigate hundreds or thousands of kilometres during migration. Quantitative magnetic resonance analysis offers a powerful, non-invasive method to study energetics and fuel metabolism during migration. My study indicates that QMR did not affect orientation or a bird's ability to refuel while at a stopover site. Birds departed from Long Point in an appropriate migratory direction regardless of treatment group, and small differences in stopover duration, with the exception of the longer stopover duration estimated for scanned adult sparrows in fall, indicate that after QMR analysis birds were not confused and disoriented in a manner that affected their ability to refuel. Many techniques, including banding, blood sampling, or radio tagging likely have small and transient effects on bird behaviour and physiology. However, birds in the field are able to cope with these perturbations and quickly return to normal activity. Thus, QMR is a useful technique to acquire accurate measurements of body condition (Guglielmo *et al.* 2011), which will increase opportunities for novel research of free-living birds.

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CHAPTER 4: GENERAL DISCUSSION

To understand passerine migration as a whole, one must assess the broad and fine scale challenges migrants face en route between breeding and wintering grounds. During migration, birds spend 90 % of their entire journey at stopover sites refuelling for subsequent flights (Hedenstrom and Alerstam 1997). Through experimental studies and theoretical models, a great deal of work has been dedicated to stopover site refuelling since it is commonly defined as the limiting factor by optimal migration theory (Alerstam and Lindstrom 1990). Prior understanding of refuelling physiology has relied on a variety of techniques, such as carcass analysis, heavy water dilution (Karasov and Pinshow 1998), total body electrical conductivity (TOBEC; Skagen 1991, Grant and Evans 1991, Karasov and Pinshow 1998), and dual x-ray absorptiometry (DEXA; Korine *et al.* 2004). In this thesis, I used data collected using quantitative magnetic resonance (QMR) to refine our understanding of the relative changes in body composition of a large number and variety of birds refuelling at a stopover site in Long Point, Ontario. Further, I assessed the potential side effects of QMR in the field to determine if magnetic resonance technology affects a bird's ability to orient and migrate normally.

Thesis Summary

In Chapter two, I showed that a major axis regression analysis for single-scanned individuals represents relative deposition of fat and lean mass reasonably well when compared to a regression analysis of refuelling measured directly in recaptured birds. Use of single-scan regression is advantageous because a larger sample size provides a better representation of the population and may be less biased than recapture. Relying on

recaptured birds means a much smaller sample size, and those individuals recaptured may exhibit unusual behaviour or may not be the best quality birds (Bairlein 1985). This can skew the results and deviate from the general population trend.

Baseline amounts of fat and lean mass provide evidence that migrant condition cannot be based solely on quantity of stored fat. Individuals of a species with the same mass do not necessarily have the same condition, since some were 'meatier' or 'fatter'. Therefore, large fat stores may not exclusively dictate migratory 'preparedness'. Interestingly, fat stores did differ seasonally depending on migration distance. The difference in fat stores between spring and fall was greater in species with longer migration distance.

Relative deposition of fat and lean mass was more variable than I predicted in both recapture and single-scan regressions. Even using sex, age, and season comparisons, there was no universal rule to help explain how fat and lean mass was changing between and within species. However, my results support recent studies suggesting that lean mass is a dynamic body component during migration in all short-, medium- and long-distance migrant passerines. An interesting generality to derive from Chapter two is that there is evidence to support that smaller birds deposit relatively less lean mass per gram gained than larger birds from estimates of lean mass deposition taken from recapture and population level regression analyses. Even though both analyses were close but not significant, results were consistent for both recaptured birds and single-scanned birds.

In Chapter three, I showed that exposure to QMR scanning did not affect transiency or departure direction, and slightly affected stopover duration. Although

previous studies using magnetic pulse treatments show that a bird's orientation and navigation can be manipulated by externally applied magnetic fields, magnetic forces experienced during QMR were neither directional nor comparable to the Earth's geomagnetic field. There is considerable evidence in my study, corroborating other work (ie; Able 1982, Cochran 2004, Muheim *et al.* 2007), that if a bird's magnetic compass was altered after scanning, an individual can re-calibrate their compass within one to two sunsets. Previous work suggests that juvenile birds are most likely to be affected by magnetic treatment (Åkesson *et al.* 2005). However, my analysis of radio-telemetry data did not indicate any significant differences between QMR treated and control juvenile birds. In addition, mark-recapture model no. 2 suggested minimal differences between QMR treated and control juveniles. The longer stopover duration of adult QMR treated birds in fall may be attributed to a small sample size and the extensive recapture of only 2 individuals. Though at these stages of analysis for QMR in the field it is important to acknowledge this difference in stopover duration however, these results do not suggest a universal negative effect of QMR exposure on a bird's ability to successfully rest, refuel and depart normally. Although there are still unanswered questions regarding the exact mechanisms birds use to detect and interpret the Earth's geomagnetic field, evidence from radio-telemetry tracking and generated mark-recapture model results do not indicate any permanent negative effects of QMR.

Future Directions

Although QMR is relatively new, its accuracy, precision, and quick, non-invasive procedure will only increase its future use in the field. The methods and analyses

presented in this thesis provide a framework for determining refuelling physiology and ecology of migrant birds at stopovers, and collectively the data support current evidence that lean mass is an important body component to measure when considering the physiology of migration. Since the original objective of this thesis was a broad investigation of relative fuel deposition in passerines during migration, its recommended for future studies to focus on specific species at other stopover site locations. For example, a study with similar methodology could be conducted but at multiple stopover sites during the same season. Thereby moving with the birds and comparing relative deposition of fat and lean mass between sites the study would give an overall impression of potentially changing fuel mixtures. More specifically, I think it would be very interesting to scan birds upon arrival after crossing the Gulf of Mexico and compare the fuel deposition of the same species to a stopover site further inland. Do the same migrant species in North America selectively deposit more lean mass after crossing an ecological barrier than they do inland?

QMR has many applications in addition to studying refuelling in migrant birds. Body composition is also important during the pre-breeding and nesting stages of adult birds, as well as body composition in growing nestlings. Both of these have been studied in Tree Swallows (*Tachycineta bicolor*) using QMR (Boyle, Winkler, and Guglielmo, unpublished data). QMR can also be used to measure body composition of salvaged carcasses, responses of birds to changes in diet (Guglielmo and Gerson unpublished data), and energetics and fuel selection during flight (Gerson and Guglielmo 2011). Recently QMR was used in wind tunnel experiments where fuel use and water balance were

measured by scanning birds before and after flights (Gerson and Guglielmo 2011). It is anticipated that the convenience of QMR will make this technology a highly sought-after tool for many ecological and physiological studies.

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Appendix A- Bird species used in the analysis of this thesis.

Species	
American Redstart <i>Setophaga ruticilla</i>	Chestnut-sided Warbler <i>Dendroica pensylvanica</i>
Black-throated Blue Warbler <i>Dendroica caerulescens</i>	Eastern White-crowned Sparrow <i>Zonotrichia leucophrys</i>
Canada Warbler <i>Wilsonia canadensis</i>	Song Sparrow <i>Melospiza melodia</i>
Common Yellowthroat <i>Geothlypis trichas</i>	Western Palm Warbler <i>Dendroica palmarum</i>
Gray Catbird <i>Dumetella carolinensis</i>	Winter Wren <i>Troglodytes troglodytes</i>
Hermit Thrush <i>Catharus guttatus</i>	Brown Creeper <i>Certhia americana</i>
House Wren <i>Troglodytes aedon</i>	Blackpoll Warbler <i>Dendroica striata</i>
Lincoln Sparrow <i>Melospiza lincolni</i>	Black and White Warbler <i>Mniotilta varia</i>
Magnolia Warbler <i>Dendroica magnolia</i>	Wilson's Warbler <i>Wilsonia pusilla</i>
Yellow-rumped Warbler <i>Dendroica coronata</i>	Red-eyed Vireo <i>Vireo olivaceus</i>
Nashville Warbler <i>Vermivora ruficapilla</i>	Cedar Waxwing <i>Bombycilla cedrorum</i>
Ovenbird <i>Seiurus aurocapilla</i>	Swainson's Thrush <i>Catharus ustulatus</i>
Ruby-crowned Kinglet <i>Regulus calendula</i>	Grey-cheeked Thrush <i>Catharus minimus</i>
Swamp Sparrow <i>Melospiza georgiana</i>	White-throated Sparrow <i>Zonotrichia albicollis</i>
Veery <i>Catharus fuscescens</i>	Golden-crowned Kinglet <i>Regulus satrapa</i>

Appendix B – Functions and R code used for QMR data processing, written by LV. Kennedy, B. Thurber and T. Crewe (2010-2012). Functions and R code written for recapture data written by P. Taylor and LV Kennedy to convert into encounter history matrices; written in the R language for statistical computing in MARK software (copyright to be added here).

i) Function name: total2009

Function purpose: To extract all files containing QMR data from the Echo-MRI program and LPBO banding data, merge into one working file by date and band number, convert time date into one column for day-month-year and eliminate missing data and outliers.

```
##To open all fall data (mr/band)
fallmr <-read.csv("J:/MR Data/Fall/Fall 2009 MR Data.csv",header=TRUE)
attach(fallmr)
names(fallmr)
fallmr$date.fix <- with(fallmr, as.POSIXct(strptime(paste(date), "%b-
%d-%Y", tz = "GMT")))
fallband<-read.csv("J:/MRData/Fall/LPBOFallBanding
2009.csv",header=TRUE)
attach(fallband)
names(fallband)
fallband$date.fix<-with(fallband,as.POSIXct(strptime(paste(date),
"%d-%b-%y", tz = "GMT")))
totalfall <- merge(fallmr, fallband, by = c("date.fix", "band.no"))
totalfall <- subset(totalfall, weight != 0)

##To open and merge all the spring data (mr/band)
springmr<-read.csv("J:/MRData/Spring/Spring2009MRData.csv",header=TRUE)
attach(springmr)
names(springmr)
springmr$date.fix<-with(springmr,as.POSIXct(strptime(paste(date),
"%b-%d-%Y", tz = "GMT")))
springband<read.csv("J:/MRData/Spring/LPBOSpringBanding2009.csv",
header=TRUE)
attach(springband)
names(springband)
springband$date.fix<- with(springband,as.POSIXct(strptime(paste(date),
"%d-%b-%y", tz = "GMT")))
totalspring <-merge(springmr,springband, by = c("date.fix", "band.no"))
totalspring <- subset(totalspring, weight != 0 & weight != "NO WEIGHT")
totalspring <- subset(totalspring, wingcrd != 0)
##this is to double check that all the weight = 0 has been removed
length(totalspring$weight[totalspring$weight == 0])
##this is to double check there are no wing.chords == 0
length(totalspring$wingcrd[totalspring$wingcrd == 0])
##this is to remove the outlier (wing.chord) band.nos I don't want in
the data
totalspring <- subset(totalspring, band.no != "2580-34894")
```

```
total2009 <- rbind(totalspring, totalfall)
#End of function
```

ii) Function name: test.1

Function purpose: to statistically compare slopes for corrected fat QMR data regressed with size-corrected total body mass between groups; sex, age and season, using a Type II Major Axis Regression for each species.

```
##each species is analyzed separately for season, sex and age
require(smatr)
## SPECIES ##
species <- read.csv("J:/Analysis/Species Excel files/species all
individuals.csv",header=TRUE)
test.1 <- slope.com(correctedfat, correctedmass, group, method = 'MA',
  alpha = 0.05,
  data = species, intercept = TRUE,
  V = array(0, c(2, 2, length(season))), ci = TRUE, bs = TRUE)
#End of function
```

iii) Function name: test.2

Function purpose: to statistically compare slopes for corrected lean QMR data regressed with size-corrected total body mass between groups; sex, age and season, using a Type II Major Axis Regression for each species.

```
##each species is analyzed separately for season, sex and age
require(smatr)
## SPECIES ##
species <- read.csv("J:/Analysis/Species Excel files/species all
individuals.csv",header=TRUE)
test.2 <- slope.com(correctedlean, correctedmass, group, method = 'MA',
  alpha = 0.05,
  data = species, intercept = TRUE,
  V = array(0, c(2, 2, length(season))), ci = TRUE, bs = TRUE)
#End of function
```

iv) Function name: test.A, test.3

Function purpose: to analyze and output slope, intercept, p-value, r^2 and 95% confidence intervals for Type II Major Axis regressions of corrected fat by size-corrected total body mass for all significantly different sex, age and season groups of each species.

```
require(smatr)
```

```
## SPECIES ##
species<-read.csv("J:/Analysis/SpeciesExcelfiles/ species
allindividuals.csv",
header=TRUE)
test.A <- slope.test(correctedfat, correctedmass, test.value = 1,
  data=species, method = 2,
  alpha = 0.05, V = matrix(0,2,2), intercept = TRUE)
test.3 <- line.cis(correctedfat, correctedmass, alpha = 0.05,
  data=species, method = "MA", intercept = TRUE,
  V = matrix(0,2,2), f.crit = 0)
#End of function
```

v) Function name: test.B, test.4

Function purpose: to analyze and output slope, intercept, p-value, r^2 and 95% confidence intervals for Type II Major Axis regressions of corrected lean mass by size-corrected total body mass for all significantly different sex, age and season groups of each species.

```
require(smatr)
## SPECIES ##
species<-read.csv("J:/Analysis/SpeciesExcelfiles/species
allindividuals.csv",
header=TRUE)
test.B <- slope.test(correctedlean, correctedmass, test.value = 1,
  data=species, method = 2,
  alpha = 0.05, V = matrix(0,2,2), intercept = TRUE)
test.4 <- line.cis(correctedlean, correctedmass, alpha = 0.05,
  data=species, method = "MA", intercept = TRUE,
  V = matrix(0,2,2), f.crit = 0)
#End of function
```

i) Function name: banded

Function purpose: to generate encounter histories for MARK programming data analysis.

```
require(lattice)
#####PREPARING THE MATRIX FOR SEASON AND SPECIES OF INTEREST#####
#create banding data file
work.datrunc <- read.csv("J:/Analysis/Chapter 2, stopover duration
estimate files/lpbo_alldata_2009.csv", header = TRUE)
work.dat <- work.datrunc
## Script to convert banding data to encounter history format for MARK .
##### SPECIFY THE YEAR ##
y <- 2009
```

```

#####
# make a POSIX date for the banding file
work.dat$date <-
with(work.dat,as.POSIXct(strptime(paste(Day,Month,Year),"%d%m%Y")))
work.dat$doy <- as.numeric(format(work.dat$date,"%j"))
qmrbirds <- read.csv("J:/Analysis/Chapter 2, stopover duration estimate
files/WTSP, QMR, spring.csv",header=TRUE)
attach(qmrbirds)
names(qmrbirds)
work.dat <- merge(work.dat, qmrbirds, by = "Bandnum", all= TRUE)
work.dat$scan[is.na(work.dat$scan)]<-0
work.dat$noscan[is.na(work.dat$noscan)]<-1
##### SPECIFY THE SPECIES, LOCATION, YEAR, OTHER SPECIFICS (E.G.
MIST NETS ONLY, NO NON-STANDARD BANDING...) #####
# first subset data to include only HETH and the variables actually
used later
work.dat <- subset(work.dat, Spcd == "WTSP", select =
c(Bandnum,Bandstat,Spdc,Year,Month,Day,date,doy,Sex,Age,Location,Wingcr
d,Weight,Timecap,Fat,Trap,NSB,scan,noscan))
# subset to include e.g. only location 13[OldCut], years "y" , Trap=MN,
and GT (for HETH it happens), User9!=X
work.dat <- subset(work.dat, Location==13)
work.dat <- subset(work.dat, Year==y)
work.dat <- subset(work.dat, NSB!="X" & NSB!="x")
work.dat <- subset(work.dat, Trap !="MX")
#work.dat <- subset(work.dat, User10 !="X")
work.dat$Age<-as.factor(work.dat$Age)
##### SPECIFY THE RANGE OF DATES TO INCLUDE
## WTSP Fall date range = c(268,288)
## RCKI Fall date range = c(267,290)
## WTSP Spring date range = c(116, 139)
## RCKI Spring date range = c(117, 139)
date.range <- c(116,139)
#make a dataset with just the first encounters
#add the time, so that multiple encounters on the first day are dealt
with properly
work.dat$doytime <- work.dat$doy + work.dat$Timecap/2400
work.dat.first <-
aggregate(work.dat$doytime,list(Bandnum=work.dat$Bandnum),min)
names(work.dat.first)[2] <- "doytime" # for first day/time observed
work.dat.first$fdoy <- trunc(work.dat.first$doytime) #so we have a doym
too

#and merge in the rest of the data for the individual on its first
encounter
work.dat.first <-
merge(work.dat.first,work.dat,all.x=T,by.x=c("Bandnum","doytime","fdoy"
),by.y=c("Bandnum","doytime","doy"))
#create a vector of the full range of dates
all.doy <- seq(date.range[1],date.range[2]) # a vector of all possible
doy, since some might be missing
#head(all.doy)
#remove all bandnumbs where the first encounter is before or after the
date range
work.dat.first <- subset(work.dat.first,fdoy %in% all.doy)

```

```

#remove all birds from work.dat that were NOT first banded within the
period
work.dat <- subset(work.dat,Bandnum %in% work.dat.first$Bandnum)
#create recaps and banded vectors for summary script at end (calc of #
recaps)
recaps<- subset(work.dat, Bandstat == "R")
summary(recaps)
banded<- subset(work.dat, Bandstat == "1")
#make doy and BandNum factors, which lets the table function create
zero entries for dates with no effort
work.dat$doy <- factor(work.dat$doy,levels=all.doy)
work.dat$Bandnum <- factor(as.character(work.dat$Bandnum))
#make a table of the encounters, using the day of year and BandNum
work.dat.tab <- with(work.dat,table(Bandnum,doy))
work.dat.tab[work.dat.tab>1] <- 1 # replace any same day recaps (2 or
more) with 1
work.dat.tab[work.dat.tab==1] <-2 # and replace all 1s with 2s for the
MARK input
head(work.dat.tab)
#now convert the table to a data frame
work.dat.tab.df <- as.data.frame(array(work.dat.tab, dim(work.dat.tab),
dimnames(work.dat.tab)))
work.dat.tab.df$Bandnum <- row.names(work.dat.tab.df)
#head(work.dat.tab.df)
#merge the individual bird data with the encounter dataset
work.dat.all <-
merge(work.dat.tab.df,work.dat.first,by=c("Bandnum"),all.x=T)
#cycle through each individual and change the first encounters back to
1 (i.e. intial state=1, all other N-encounters =2)
for (i in 1:length(work.dat.all$Bandnum))
{work.dat.all[i,as.character(work.dat.all$fdoy[i])]<-1}
# head(subset(work.dat.all, Bandstat == "1"))
# at this point all first encounters are 1's - no recaps
#calculate total number of birds N and total number of time periods T
N <- length(work.dat.all$Bandnum)
T <- diff(date.range)+1
# write out the encounter histories in array format
x.dat <-
t(array(t(work.dat.all[,as.character(date.range[1]:date.range[2])]),dim
=c(T,N))) #the encounters; need t to transpose the array that results
# to format for easy reading
out.hist <- matrix(x.dat, nrow = N, ncol = T, byrow=FALSE)
# MARK needs blank columns separating the groups, and a column of ; at
the end of the histories...
blank.col <- rep(" ", length(out.hist[,1]))
end.col <- rep(";", length(out.hist[,1]))
MARK.data <- cbind(out.hist, blank.col, work.dat.all$scan, blank.col,
work.dat.all$noscan, end.col)
# calculate the total number of records including recaps
tmp.ls <- list()
tmp.ls[1] <- sum(recaps$scan)
#tmp.ls
# calculate the number of individuals without recaps
tmp.ls <- list()
tmp.ls[1] <- sum(banded$scan)

```

```
#tmp.ls <- as.data.frame(tmp.ls)temp
#tmp.ls
recap.table<- c(y,sum(recaps$scan))
recap.table
banded.table<- c(y,sum(banded$scan))
banded.table
summary(banded)
write.table(MARK.data, quote=FALSE,
file=paste(y,"_Seasonspeciesmatrix.inp", sep=""), row.names=FALSE,
col.names=FALSE, sep="")
} # End of function
Write.csv(banded,"Season.year.species.BANDED.csv
```

Appendix C – Animal Use Protocol Renewal form.



03.01.09
 *This is the 3rd Renewal of this protocol
 *A Full Protocol submission will be required in 2010

Dear Dr. **Guglielmo**

Your Animal Use Protocol form entitled:

Physiological ecology of migratory birds during stopover

has had its yearly renewal approved by the Animal Use Subcommittee.

This approval is valid from **03.01.09** to **02.28.10**

The protocol number for this project remains as **2006-014**

1. This number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this number.
3. If no number appears please contact this office when grant approval is received.
 If the application for funding is not successful and you wish to proceed with the project, request that an internal scientific peer review be performed by the Animal Use Subcommittee office.
4. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

REQUIREMENTS/COMMENTS

Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

c.c. J Wasylenko, D Cheshuk

The University of Western Ontario
 Animal Use Subcommittee / University Council on Animal Care
 Health Sciences Centre, • London, Ontario • CANADA – N6A 5C1
 PH: 519-661-2111 ext. 86770 • FL 519-661-2028 • www.uwo.ca/animal

CURRIULUM VITAE

April 2012

NAME: Lisa Viola Kennedy

PLACE of BIRTH: Brampton, Ontario, Canada

UNDERGRADUATE WORK:

2004-2008 University of Western Ontario, London, Ontario

B. Sc. H Biology

Research supervisor: Dr. Scott Petrie

Title of Thesis: Season, sex and age related differences in migrating tundra swans in Long Point, Lake Erie.

GRADUATE WORK:

2010-2012 University of Western Ontario, London Ontario

M. Sc. Biology, stream: Ecology and Evolution

Research supervisor: Dr. Chris Guglielmo

Title of Thesis: Dynamics of fat and lean mass in refuelling migrant passerines measured using quantitative magnetic resonance

ACADEMIC AWARDS AND GRANTS:

Western Graduate Research Scholarship (University of Western Ontario)

annually (Institutional, 2010-2012)

Canadian Society of Ornithologists Conference, honourable mention for top 4 presentations (Moncton, August 2011)

RESEARCH INTERESTS

My research focuses on migratory refuelling physiology and stopover site behaviour in migrant passerines. In particular, I am interested in the relative deposition of both fat and lean mass upon arrival at a stopover site and potential impacts of stopover site behaviour from quantitative magnetic resonance analysis.

EMPLOYMENT

September 2010 - April 2012. University of Western Ontario, Biology Department. London, Ontario.

Teaching Assistance; Assigned to using quantitative magnetic resonance equipment in the Field Laboratory for Integrative and Ecological Research on migrant passerines.

April - May, September – October 2009. University of Western Ontario, Biology Department. Long Point, Ontario.

Research Assistant/ Field Biologist; Prepared and presented lab material for First Year University biology laboratory and Third Year University wildlife management. Evaluated students on scientific writing skills in Second Year University Scientific Writing module in scientific methods in biology course.

July 2006 - October 2009. Taxidermy, Tillsonburg, Ontario.

Avian Taxidermist; customer mounts including ducks, swans, geese, raptors.

PUBLICATIONS

Kennedy, LV. Mounting a perfect raptor: Richard Davis method. Breakthrough Magazine, Issue 92 Fall 2008.

Badzinski SS, Kennedy L, Petrie SA and Schummer ML (2011). Variation in body composition and digestive organs of Tundra Swans during migration at Long Point, Lake Erie. Waterbirds (-in press)

PRESENTATIONS:

Kennedy, LV and Petrie, S. Season-, sex-, and age-related comparisons of body condition and digestive organ size in migrant Tundra Swans at Long Point, Lake Erie. Honours Departmental Seminar Series, date. (Seminar talk).

Kennedy, LV. Factors affecting fat and lean mass deposition in migrant passerines during stopover . Friday Philosophical Graduate Student Seminar Series, October, 2011. (Departmental Seminar talk)

Kennedy, LV. Lean mass: a dynamic body component in migrant passerines & Does quantitative magnetic resonance have an effect on orientation?. Friday Philosophical Graduate Student Seminar Series, November 4, 2011. (Departmental Seminar talk)

Kennedy, LV. Factors affecting fat and lean mass deposition during stopover in White-throated Sparrows measured by quantitative magnetic resonance. Canadian Society of Ornithologists, August 2011. (Seminar talk)

CURRENT SOCIETY MEMBERSHIP:

Society of Canadian Ornithologists