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Senior Thesis

An Examination of the Fueling Strategies and Energy Sources Utilized by Neartic-Neotropic Migrants

Jacqueline M. Fiala*
Department of Biology
Lake Forest College
Lake Forest, Illinois 60045

Preface

This thesis presents a detailed examination of the fueling strategies and sources of energy used by Neartic-Neotropic migrants to complete their journey. In chapter one, I provide a literature review on the fueling strategies and sources of energy used by migrants to fulfill the tremendous demands of migration. I focused on migrant songbirds of the New World, but I also drew on literature from Old World migrants, as well as shorebirds. I explored the use of fuel storage compounds by examining the advantages and deficits of each and I reviewed the usage of each compound during flight, in relation to the needs of the migrant and the availability of stopover sites.

Furthermore, I reviewed the energetics of migration using field and lab based studies, and I discussed the importance of refueling at stopover habitats, which led to a discussion on the costs associated with visiting stopover sites. I examined the use of an energy conservation strategy, in which digestive organs are shut down and reduced in size, by reviewing the correlation among migrants using this strategy and the distance they must travel, as well as the availability of stopover sites *en route*. I then compared birds using this strategy to short distance migrants that forage frequently *en route* to demonstrate the existence of a tradeoff birds must make due to the physiological condition of their digestive organs, which I used to explain why short-distance migrants must refrain from utilizing this strategy. In addition, I examined the use of protein stores *en route* by evaluating the relation among birds that must resort to "burning" their digestive organs, and the type of terrain they must cross. I also looked at the influence of migrants' diet composition before and during migration, and its relation to the amount of protein migrants use during flight, as well as the dietary influence on the building of depleted protein and fat stores during periods of refueling.

In chapter two, I present original research from Dr. Caleb Gordon's lab obtained from six years of mist netting at a stopover site in Illinois. I build on research presented in Benjamin Larsen's thesis (2007). Ben provided two predictions for classifying the fueling strategies of eastern migratory songbirds, he proposed the existence of an associated taxonomic classification among these strategies, and demonstrated that two methods used commonly in research for measuring mass change are useful for indicating two types of tissue assimilation because they rely on different time scales. I added more years of mist net data, as well as more songbird species to the data set. I also examined evidence for mass-gain thresholds among within season recaptured birds, and looked for evidence of divergent fueling strategies among sexes within the same species. In addition, I refined the two divergent fueling predictions previously set forth, as well as the tests and analyses Ben previously used to examine the data.

In this chapter, I examined two possible approaches used by eastern songbirds to fueling migration in an effort to determine the proportional reliance on nutrient stores acquired prior to beginning flight versus nutrients obtained *en route* at stopover habitats because migrants that fuel frequently during flight are important for conservation reasons. I also looked for evidence of mass-gain thresholds among recaptured birds, which would provide support for the proposed tradeoff migrants must make when "choosing" to utilize one fueling strategy over the other. I examined fueling differences among sexes within the same species in an effort to determine, if sexes fuel differently, which would aid in understanding, and explaining complex fueling behaviors that prohibit the classification of species into one of the two categories. I presented this chapter in the form of a manuscript intended for publication in the ornithological journal, *The Auk*.

Chapter One: The Importance of Protein Reserves as Emergency Migratory Energy and the Associated Physiological Consequences

Overview

This chapter provides a review on the sources of fuel and migratory strategies used by New and Old World migrants in order to fulfill the energy demands to complete their journey. Although fat is the densest energy source, migrants crossing harsh geographic barriers encounter difficultly refueling at stopover sites *en route* due to their unavailability or poor quality. If glycogen and fat stores become depleted and cannot be readily replenished, a bird must then use protein mobilized from functional tissues such as muscle or digestive organs as an emergency source of energy. Currently, there is still much to learn about migrants' proportional reliance on protein and when during the course of migration, functional tissue is utilized as an energy source. Thus, the use of protein as a source of fuel for migration, as well as the mechanism behind its utilization, and the associated consequences, are an active research frontier in migratory bird biology.

Fueling Migration

Sources of Energy Storage

Prior to beginning migration, many birds undergo a period of active hyperphagia during which they eat more than normal and store large amounts of energy as fat (McWilliams and Karasov 2001). This phase is characterized by elevated mass, length, and volume of digestive organs (McWilliams and Karasov 2005), positive mass gains, and elevated triglyceride levels (Cerasale and Guglielmo 2006). Glycogen stores increase as well and provide an additional source of energy, which is useful for prolonging the depletion of subcutaneous fat, as well as delaying the breakdown of protein reserves (Gannes 2001; Hill et al. 2004). Glycogen also provides glucose for the brain, and contributes to the production of ATP, which is used by the bird's skeletal

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muscles to continue flight until the bird can refuel at the next stopover (Hill et al. 2004).

In the past, fat and glycogen were regarded as the only sources of fuel used by migrants to power their journey (Klaassen et al. 2000), yet now it appears as though protein may also serve as a source of much needed energy and water during migration (Klaassen 1996). Previous theories once described migrants as "airplanes" that maintained a constant structural mass throughout flight, filling and emptying only, their fuel tanks (Battley et al. 2000). However, migrants have been observed altering the size and activity of their assimilation organs and the mass of their flight muscle, using a destructive metabolic process known as catabolism (Battley et al. 2000).

Protein vs. Fat: Which is the Preferred Energy Source?

Although fat, glycogen, and protein provide energy, fat is the preferred choice of fuel when comparing the energy density and hydration ratios of these fuel sources (Table 1). The oxidation of one gram of fat provides 9.0 - 9.5 kcal of energy, whereas, one gram of protein or glycogen yields only four kcal (Blem 1990). One reason why fat provides more energy per gram than protein is that it is stored in an anhydrous state of less than 5% water (McWilliams et al. 2004). In contrast, carbohydrates and proteins exist in a very high aqueous environment consisting of 70-80% water (McWilliams et al. 2004), resulting in a 2.5 water content ratio for glycogen and 2.2 for protein (Pennycuick 1998). Therefore, it would be advantageous for a bird attempting to carry the most energy possible and the least amount of mass, to store a larger amount of fat as opposed to protein or glycogen (Pennycuick 1998).

Despite the energetic shortcomings of protein and glycogen, there are advantages to using these sources of energy. The high water content in glycogen and protein provides a large amount of water for the bird once it is catabolized, which can delay the onset of dehydration during flight (Klaassen 1996). Protein stores are also valuable intermediates in the citric acid cycle and can be used for gluconeogenesis to generate glucose and fuel for the brain during periods of starvation onset (Battley et al. 2000). In addition, protein can still serve as a source of "emergency" energy for the migrant, even though it only provides four kcal/g (Blem 1990). In fact, 5-15% of long distance migrants' energy source originates from protein stores (McWilliams et al. 2004).

Although not common among all migrants, some species have been observed storing protein in conjunction with fat, as "fuel tissues" (Lindstrom and Piersma 1993). Bar-tailed Godwits (*Limosa lapponica*) have been found to contain fat stores consisting of 35% nonfat components, specifically protein and water (Lindstrom and Piersma 1993). The advantage to storing both protein and fat is that the migrant can rely on assimilated tissue stores for energy before resorting to the burning of functional tissues, such as digestive organs. However, the downside to this storage mechanism is that for every gram of fat tissue composed of 75% fat and 25% hydrated protein, 22% less energy is available compared to the amount contained in one gram of pure fat (Klaassen 1996). As a result, the distance a migrant can travel using these "mixed" energy stores is shortened (Klaassen 1996).

Where do protein stores originate?

Energy originating from protein is not stored in the form of subcutaneous deposits like fat; instead, it exists in the form of functional tissues such as skeletal muscle and digestive organs, which must be catabolized to release needed energy. These tissues can be degraded because their size and activity does not remain constant, with the exception of the brains and lungs, but instead they undergo periodic fluctuations over the course of several hours or days, referred to as phenotypic flexibility (McWilliams and Karasov 2005). This physiological adjustment enables migrants to adapt to changes in their environment by providing emergency sources of energy when food resources are unavailable (McWilliams and Karasov 2005). Phenotypic flexibility of digestive organs can be monitored by following fluctuations in a bird's basal metabolic rate (BMR) under thermo-neutral conditions because several studies have shown that a large portion of the BMR is generated by organs in the abdominal cavity (Lindstrom et al. 1999). Therefore, fluctuating basal metabolic rates can be used to measure the activity of metabolically active digestive organs, specifically, when the mass of these organs decreases because this would result in a reduction in the BMR as well (Lindstrom et al. 1999; Weber and Piersma 1996).

Calculated Total Migratory Energy Expenditure

Although studies have suggested that migration takes a lot of energy, the ability to quantify the amount of energy a migrant must expend is useful for understanding the ecology of migratory birds (Wikelski et al. 2003). Such data could aid in determining the proportional amount of energy acquired by migrants prior to beginning their flight in comparison to how much must be obtained *en route*. In addition, if the amount of energy required per kilometer can be found, this can be correlated with the amount of fat carried at the start of a flight in order to determine when a migrant must use protein from muscles and organs. Although flight energy requirements have been measured for several species, few studies have been able to measure this for long-distance migrants, making it difficult to produce theories and conclusions (Klaassen et al. 2000).

To gain better insight on the amount of energy required to fly a distance of several thousand kilometers, an energetic budget was created for Swainson's Thrushes (*Catharus ustulatus*) using an aerodynamic model (Pennycuick 1989a) and morphological measurements for this species (Yong and Moore 1994) (Table 2). The underlying basis of this aerodynamic model originates from observations of birds in flight, which were used to create of an equation for wing beat frequency, useful for estimating the mechanical power supplied by a bird's wings to complete migration (Pennycuick 1989b). Furthermore, this model relies on mechanical power measurements obtained from wind tunnel experiments as a basis for comparison and modifications of the equation if needed (Pennycuick 2000). This aerodynamic model is useful because it provides the distance a migrant can travel on pre-acquired fat stores until depletion, in addition to the amount of fat and protein used to reach this point (McWilliams et al. 2004). It also accounts for variations in flight altitude, body mass, morphometry, air density and other factors that affect flight costs, but most importantly it accounts for the progressive changes in performance that occur as the mass of the bird declines during the course of the flight (McWilliams et al. 2004; Pennycuick 1998).

Based on the energetic budget created for Swainson's Thrushes, it is evident that migration requires a substantial amount of energy that cannot all be stored as fat, but instead requires several stopovers *en route* to replenish (Pennycuick 1989a). In order to fly a total distance of 6752 km from South America to Canada, a Swainson's thrush would require 5140.93 kJ supplied from both fat and protein stores (Pennycuick 1989a; Sibley 2000). Over the course of their flight, these birds would need to replenish their fat and protein stores approximately 7 times because their initial fat stores only provide 539 kJ, which can be used to travel 746 km (Table 3) (Pennycuick 1989a). Swainson's Thrushes may require more energy than estimated using this model because there are still several variables such as wind, temperature, and adverse weather conditions that would cause the bird to expend additional energy. In addition, many migrants will be unable to obtain a consistent amount of energy from each stopover site they visit because of the variance in resource abundance among habitats. For example, if a Swainson's Thrush were to acquire 5140.93 kJ from its diet alone, it would need to consume 3698.5 large (22-25 mm) *Tenebrio molitor* larvae since each larva provides 1.39 kJ of energy (Moore and Simm 1985). This is a large number of larvae that Swainson's Thrushes must obtain during their stopover visits and these birds will most likely encounter several sites with limited food, causing the bird to make additional stops to acquire the energy they needs, which will result in more energy expended than predicted with the budget.

Although fat is a good source of energy, a bird cannot possibly carry enough fat to fuel their entire migration because the size of fat deposits are physiologically limited and also energetically expensive due to the extra weight the bird must carry. If a Swainson's Thrush were to carry 5140.93 kJ as fat, it would have to pack on an additional 131.82 g of fat, since 1 g of fat contains 39 kJ of energy, which is not realistic because, on average, Swainson's Thrushes weigh 31 g (Sibley 2000). A 35% increase in a bird's fat mass requires two times the normal amount of flight power, whereas a 50% fat mass increase requires three times the flight power (Alerstam and Hedenstrom 1998). In fact, a bird that carries fat stores that are 50% of its mass and flies until they are depleted actually expends 40% more energy than a bird that carries only 10% of its body mass in fat and travels the same overall distance (Alerstam and Hedenstrom 1998). To cope with this, many migrants strengthen their flight muscles before beginning flight (Alerstam and Hedenstrom 1998); however, the increased flight power requirement still leads to an increased consumption of energy, which requires the bird to make frequent stops to replenish their fat stores. On the other hand, when *Catharus* Thrushes stopped 10 times during the course of their flight and increased their fat stores by 5% of their body mass, they were able to achieve a 20% longer flight distance than if they deposited all their fat stores (50% their body mass) at one site (Yong and Moore 1997). Although carrying smaller fat deposits saves energy, it provides a low safety margin in the event that several consecutive stopover habitats are of poor quality (Yong and Moore 1997).

The energetic budget presented here for Swainson's Thrushes varied slightly from a budget created using field-based data for these birds (Wikelski et al. 2003), but this was expected based because energetic budgets created using aerodynamic models have been found to vary by 13% in comparison to field-based budgets (McWilliams et al. 2004). Wikelski et al. (2003) calculated energy expenditure for Swainson's Thrushes using labeled water experiments in which the birds were injected with ^{2}H and ^{18}O isotopes and their energetic expenditure was tracked based on the amount of water they produced from fat and protein catabolism. Based on these experiments, in order to fly a total distance of 4800 km from Panama to Canada, Swainson's (*Catharus ustulatus*) and Hermit Thrushes (*Catharus guttatus*) would need to expend 4450 kJ. A further breakdown of this energy expense shows that these birds would expend 0.93 kJ/km (Wikelski et al. 2003) whereas; based on the results in Table 3, Swainson's Thrushes would use 0.76 kJ/km (Pennycuick 1989a). This provides evidence that the aerodynamic model is useful for providing estimates of flight costs, but they may not accurately represent the amount of energy expended by birds in the field due to several environmental factors previously discussed.

Stopover Sites Provide Needed Energy

Energetic Cost of Foraging at Stopover Sites

Spending time at stopover sites to forage is energetically costly in itself, because of the large number of unpredictable variables migrants face, such as varying resource availability, and severe competition among additional migrants and resident species. These environmental factors can delay a migrant's obtainment of sufficient energy resources and increase the amount of energy they expend (Graber and Graber 1983). In addition, migrants must regulate their body temperatures, which is not costly during the day, but can be at night (Bowlin et al. 2005). Although most migrants attempt to leave stopover sites before nightfall, some migrants will not resume their flight until temperatures and wind speeds are ideal even though their fat stores are sufficient (Bowlin et al. 2005). Bowlin et al. (2005) found that thrushes initiated their flight only when the daily temperature was above 21 ºC and when surface winds during departure were below 10km/hr. The disadvantage of waiting for ideal conditions is that the bird consumes stored energy intended to power its flight, to maintain its body temperature (Bowlin et al. 2005). In fact, migrants that flew for 2-3 hours expended the same amount of energy used by migrants that chose not to fly due to low temperatures (Bowlin et al. 2005). Therefore, in order to prevent unnecessary energy loss, a migrant should power a short migratory flight on a cold night instead of staying at the site for an additional night (Bowlin et al. 2005; Wikelski et al. 2003). However, it is difficult to ascertain which birds remaining at a stopover site are awaiting ideal weather conditions as opposed to foraging to increase their mass.

Resource Availability Affects Stopover Fueling Rates

Resource availability at the habitat is important because if a bird is unable to find sufficient nutrients, or it expends more energy foraging than it is able to acquire, stopover periods become a hindrance by delaying the bird's arrival at its breeding grounds (Long and Stouffer 2003). Some birds, such as Northern Waterthrushes (*Seiurus noveboracensis*), are unable to avoid extended stopover visits because they are unable to gain mass until they have established territories, which can take 2-3 days (Alerstam and Hedenstrom 1998; Rappole and Warner 1976). However, for most birds, stopover sites set the pace of their migration especially since they spend a large amount of their flight time at them (McWilliams et al. 2004).

Temperature variance at a habitat can have a significant affect on resource availability because of its adverse affect on plant and insect activity (Dunn 2002). For example, there were low mass changes observed during spring migration compared to fall at a site in Southern Canada, which may have been due to the fluctuating spring temperatures ranging from near freezing to greater than 20°C (Dunn 2002). Migrants carrying large fat stores may not be as affected by low food availability at stopover sites because they can afford to wait to refuel at the next stopover site. However, birds with very little fat deposits are vulnerable to limited resources and may remain at the site foraging until they can find adequate energy to continue their flight. Studies have shown that among lean birds with depleted fuel sources, the probability of remaining at a stopover site depended largely on the quality of the habitat (Yong and Moore 1997). For example, White-crowned Sparrows (*Zonotrichia leucophrys*) arriving at a site with depleted fuel sources needed to remain at the site for longer than fat birds because of their poor body condition (Yong and Moore 1997). In addition, if the site White-crowned Sparrows arrive at provides minimal food resources, then their stay could be further lengthened due to habitat quality, resulting in increased energy expenditure due to longer foraging periods (Cherry 1982).

Stopover Habitats Vary in Quality

One indication of habitat quality is whether migrants foraging experience mass gains or mass losses, which can be qualitatively assessed by examining plasma metabolite levels. Beta-hydroxyl butyrate (B-OH) and uric acid are two metabolites used for identifying periods of starvation and intensive exercise because B-OH is prevalent when lipid oxidation is high and elevated uric acid levels are present during protein catabolism (Acevedo Seaman et al. 2006; Cerasale and Guglielmo 2006). In contrast, elevated triglyceride levels indicate periods of feeding and the active uptake of lipids and their storage, which can be used to identify good quality sites (Acevedo Seaman et al. 2006; Cerasale and Guglielmo 2006).

Stopover sites vary in food availability, which is indicated by the number of birds at the site experiencing mass gains and elevated triglyceride levels, as well as birds losing weight and burning fat (Dunn 2001, 2002). Acevedo Seaman et al. (2006) found that among the majority of the sites visited by Western Sandpipers (*Calidris* mauri), the migrants' triglyceride and B-OH levels varied little among all sites within the same year and also during following years, indicating that all these sites were of similar quality. Although most Western Sandpipers were observed gaining mass at these sites, there was one site deemed poor because birds at that site exhibited much lower triglyceride levels in comparison to the levels observed at other sites (Acevedo Seaman et al. 2006). Guglielmo et al. (2005) compared the metabolite levels of birds at two stopover sites in Long Point, Ontario and determined that one site was of better quality than the other was because migrants foraging at that site had much higher triglyceride levels and lower B-OH levels compared to birds foraging at the site deemed poor.

Although the rate of mass gain among foraging migrants is a good indicator of stopover habitat quality, variations among diet preferences across species can make this classification difficult. One site can be bountiful for some species, while others may find the same habitat useless. For instance, small insectivores, such as warblers and flycatchers, did well at several sites in Canada, in addition to several sparrows, which consume seeds as well as small insects, yet Swainson's Thrushes (*Catharus* ustulatus) that visited the same sites, actually lost mass. Dunn (2001, 2002) concluded that this was due to the type of soil, and lack of ground cover at the site, which may have affected insect availability. However, an alternative explanation may be that the Swainson's Thrushes did not need to refuel because they were already carrying adequate fat deposits, which may explain why these birds did not gain mass despite foraging at an excellent stopover site in Long Point, Ontario (Guglielmo et al. 2005). These unexpected results demonstrate that complex fueling patterns and diet preferences across species can often impede the classification of stopover habitat quality.

Pre-migratory Digestive Organ Shrinkage Minimizes Energy Expenditure

If migrants completing a long-distance flight are unable to feed frequently *en route*, shrinking their digestive organs is a good way to decrease the mass they must carry, but it also reduces unnecessary energy expenditure by lowering the metabolic rate of these organs (McWilliams and Karasov 2005). Some migrants, such as Eared Grebes (*Podiceps nigricollis*) (Jehl 1997) and three different wader species (Piersma 1998) have been observed catabolizing their intestines, liver, and stomach, prior to their migratory flight. Concurrently, these species increased the size of their heart to accommodate impending increases in flight muscle activity (Lindstrom et al. 1999).

There appears to be a correlation among the distance traveled by migrants who atrophy their organs prior to migration, and the extent at which their organs were atrophied. An Alaskan subspecies of Bar-tailed Godwits (*Limosa lapponica baueri)* completes a trans-oceanic flight in which stopover sites are extremely limited during the first 5000 km of their 11000 km route and most encountered thereafter are of poor quality (Piersma 1998). In contrast, the Wadden Sea-Siberia subspecies (*Limosa lapponica lapponica)* encounters at least one suitable stopover habitat at least half way through their 4500 km route (Piersma and Gill 1997; Piersma 1998). Interestingly, Wadden Godwits maintain a considerable amount of their digestive tissues, whereas Alaskan Godwits eradicate much of their organ tissue before beginning their strenuous flight (Piersma 1998). The migratory flight undertaken by these two subspecies of Bar-tailed Godwits (*Limosa lapponica)*, varies significantly, which may explain the variation among the mass of their digestive organs, when comparing the two subspecies (Piersma and Gill 1997; Piersma 1998). Similar to the Alaskan Godwits, the Bristle-thighed Curlews (*Numerius* tanitiensis) also reduce their digestive organ mass before beginning their 4000 km journey from Alaska to Hawaii because of the lack of stopover sites (Piersma 1998).

Imposed Tradeoff due to the Reduction of Digestive Organs

Migrants that conserve energy by shrinking their digestive organs prior to migration must sacrifice rapid refueling rates upon landfall until these organs can be "rebuilt," which may explain why only birds crossing terrains with limited stopover sites utilize this strategy (Jehl 1997; Piersma 1998). These mass-gain thresholds occur due to the loss of tissues from digestive organs, which consequently reduces their capacity and function (Karasov and Pinshow 1998, 2000). It is not until digestive organs return to pre-migratory conditions that high feeding rates and digestion can occur (Lee et al. 2002). Garden Warblers (*Sylvia borin*), for example, exhibited a 1-2 day lapse period before gut passage time and metabolic intake significantly increased (Hume and Biebach 1996).

Mass-gain thresholds can last for several days, dependent on how atrophied the assimilation organs are, which results in delayed rates of mass gains among migrants new to the habitat (Gannes 2002). Field evidence involving Blackcaps (*Slyvia atricapilla*) has shown that birds who have just completed a flight across the Negev desert, exhibit no mass gain for 3-4 days following their landfall (Gannes 2002). However, once the bird overcomes this threshold, it can experience high mass gains of up to 7% of its body mass on a daily basis (Alerstam and Lindstrom 1990). Blackcaps fasted in lab experiments ate less during their first 2 days of recovery, but did not gain mass at a slower rate than food-restricted Blackcaps suggesting that the imposed fueling limitation fasted Blackcaps experienced was due to emaciated organs that were unable to hold a large amount of food once feeding resumed (Gannes 2002; Karasov and Pinshow 2000).

To counter the effects of atrophied digestive organs, Bar-tailed Godwits (*Limosa lapponica*) utilize a strategy of organ hypertrophy during periods of refueling, and atrophy in preparation for resuming their flight (Engelmoer and Roselaar 1998). During the initial four weeks of fueling, lean mass components such as the stomach, liver and intestines increase in order to accommodate increases in food intake, however, when the migrants began to prepare for takeoff after refueling, their organs decrease in size (Landys-Ciannelli et al. 2003; Piersma et al. 1999b). At this same time, they increase their flight muscles and heart, which suggests that organs necessary for flight are hypertrophied and unessential organs are atrophied (Piersma et al. 1999b). In addition, Bar-tailed Godwits *(Limosa lapponica*) and Red Knots (*Calidris canutus islandica*), with "lighter" assimilation organs, showed a preference for softer prey due to its digestive ease (Piersma et al. 1993; Piersma et al. 1999a). This diet switch may have aided in the absorption of nutrients since their organs were still handicapped during their initial arrival at the stopover site and soft prey was easier to digest.

For other species, the risks associated with atrophying digestive organs may be so great that they abstain from this strategy entirely. Based on the small number of stopover sites Icelandic Red Knots (*Calidris canutus islandica*) encounter *en route,* they would be expected to shrink their digestive organs to save energy (Piersma 1998). Contrary to this prediction, Red Knots sustain a high ratio of digestive organ size (Piersma 1998). One reason may be related to the extremely cold temperatures they endure, which necessitates the ability to obtain nutrients rapidly when available to ensure survival (Piersma 1998). In this case, expenses due to thermoregulation in Arctic conditions are very demanding, thus energy is sacrificed to maintain metabolically active organs to ensure rapid fueling rates upon stopover arrival.

Maintenance of Digestive Organs en route Allows for Rapid Refueling

While some migrants can sacrifice their fueling capacity to save energy, birds that cross-terrains with at least one stopover site, maintain active organs to allow for rapid digestive rates since they eat frequently *en route*. A study by McWilliams and Karasov (1998) found that after restricting the diet of Yellow-rumped Warblers, they were still able to feed and digest at high rates, immediately following ad libitum (free-feeding) because they maintained a 37-48% spare digestive capacity (Lee et al. 2002). This occurred despite the 18-22% decrease of their liver, pancreas, and small intestine in comparison to controls (Lee et al. 2002). Another study involving Blackcaps (*Sylvia atricapilla*) found that food restricted birds were able to restore high feeding rates immediately following ad libitum because they maintained active organs despite the limited food that they were receiving (Karasov and Pinshow 2000).

Maintaining active digestive organs during flight is also beneficial for the resumption of hyperphagia, which allows migrants to replenish their energy stores in a shorter period (King 1963). For example, during a stay at a stopover site, White-crowned Sparrows (*Zonotrichia leucophrys*) were able to gain mass immediately following their arrival, permitting them to leave the site during impending evening hours (Cherry 1982). In contrast, Blackcaps (*Sylvia atricapilla*) arriving at stopover sites with reduced digestive organs exhibited a low state of hyperphagia, resulting in slow initial feeding rates (Gannes 2002; Langslow 1976).

Protein Used *en route* as an Emergency Energy Source

In the event that a migrant catabolizes all of their glycogen and fat stores, and stopover sites are unavailable or poor quality, protein reserves must be burned. A bird's flight muscles are a potential source of protein and provide a large "backup" energy supply since these tissues comprise 40-45% of a migrant's skeletal muscle (Swain 1992). Flight muscle can be consumed during flight because the power required from them decreases by a factor between two or three as fuel is used during flight (Pennycuick 1975) and it also may help birds fly faster because degrading flight muscles decreases their body mass (McWilliams and Karasov 2005). Swain (1992) found that during a fasting period designed to simulate flight, the proteolytic enzyme doubled activity in the flight muscle of Horned Larks (*Eremophila* alpestris) and the observed protein reduction was disproportionate to that of the liver (Swain 1992). However, the major downside to reduced flight muscle is that it may decrease the bird's flight capacity and performance, putting it at a greater risk for predation (Pennycuick 1975).

Although protein catabolism can occur among flight muscle, it appears to involve primarily digestive organs, with very little of it, if any at all, originating from flight muscles (Gannes 2001). After crossing the Sahara Desert and Mediterranean Sea, Garden Warblers (*Sylvia borin*) showed a 40% smaller digestive tract, but only a 20% reduction of their breast and lower leg muscles (Battley et al. 2000). Another study also observed a 50% decrease of the digestive tract and a 63% decrease of the small intestine among Garden Warblers, but no mass loss in their flight muscles (Hume and Biebach 1996). After limiting the food intake of White-throated Sparrows (*Zonotrichia albicollis*), 20% of the mass loss experienced by the birds was due to a reduction of lean mass from their stomach, small intestine, and liver (Pierce and McWilliams 2004).

Long distance migrants, especially those crossing oceans and deserts, exhibit a greater reliance on protein from their digestive organs than do short distance migrants because long distance migrants fly for extended periods without fueling. For example, Great Knots (*Calidris tenuirostris*), showed a decrease in lean tissue mass primarily among their digestive organs after completing a transoceanic flight from Australia to China (Battley et al. 2000). When the BMR of Great Knots was evaluated before and after their 5500 km flight, there was a 42% decrease in the BMR, of which 33% of this decrease was due to the reduction of digestive organs (Battley et al. 2001). Akesson et al. (1992) found that European Robins (*Erithacus rubecula*) had leaner body masses, flight muscles, and liver masses after completing a long distance route compared to shorter distance flights. Another study involving Pied Flycatchers (*Ficedula hypoleuca*), Garden Warblers (*Sylvia borin*), Barn Swallows (*Hirundo rustica*), and Willow Warblers (*Phylloscopus trochilus*) found that during their flight across the Sahara and Mediterranean Sea, there was a marked decrease in their protein stores once fat stores were near depletion (Schwilch et al. 2002).

Similar to the tradeoff experienced by transoceanic migrants that shrunk their digestive organs prior to beginning flight, migrants that must resort to functional tissues for emergency energy also experience slow mass-gain rates upon stopover arrival until their digestive organs return to pre-migratory conditions (Gannes 2002; Karasov and Pinshow 1998). However, the alternative is that the bird exhausts their energy stores and cannot continue their flight. Therefore, rapid refueling rates are sacrificed in order to provide a constant source of energy to meet the demands of migration.

Importance of Diet for Rates of Protein Catabolism and Anabolism

A migrant's diet prior to beginning migration may heavily influence the amount of protein it oxidizes during its flight because a bird's diet composition determines what form of energy it stores and it also instills specific nutrient demands from the bird's body based on the types of food it has become accustomed to receiving, particularly protein. Omnivores are able to store a larger amount of glycogen because their diets are rich in carbohydrates, whereas carnivores are unable to store large glycogen deposits because they consume a large amount of protein during hyperphagia (Gannes 2001). Gannes (2001) found that omnivores such as Blackcaps (*Sylvia atricapilla*) and Garden Warblers (*Sylvia borin*) catabolized less protein than carnivores such as Redstarts (Phoenicurus phoenicurus) and Orphean Warblers (*Sylvia hortensis*). A comparison of birds' metabolites showed that omnivores contained a much lower amount of uric acid and instead showed a higher rate of lipid catabolism (Gannes 2001). Birds with a diet consisting of primarily fruits may catabolize less protein than birds with a diet consisting of a large amount of insects because they do not rely heavily on proteins in their typical diet (Gannes 2001). Species with a high oxidation rate are at a disadvantage because they must restore a much larger amount of lost protein before significant nutrient stores can be rebuilt (Gannes 2001). Ultimately, the rate of protein oxidation varies from species to species, thus the time it takes for a migrant to begin showing significant mass changes varies greatly as well.

Importance of Fruit vs. Protein for Rebuilding Tissues during Migration

During tissue assimilation, protein is anabolized, during which energy must be used to build these tissues from smaller molecules (Hill et al. 2004). This process alone can take a considerable amount of time regardless of the available resources. For example, Hummingbirds (*Selasphorus rufus*) weighing less than 3.5 g, on average, took several days to three weeks to increase their mass up to 4.6 g (Carpenter et al. 1992). Among birds with a starting mass of less than 3.5 g, the initial mass gains were slow and appeared to consist of non-lipid deposits; however, additional mass changes that occurred once the bird reached a mass of 3.5 g appeared to be due to fat stores (Carpenter et al. 1992).

For some birds, protein and fat are anabolized simultaneously, which aids in reducing the migrants' time spent at the stopover site. Karasov and Pinshow (1998) found that Blackcaps (*Sylvia atricapilla*) showed a positive correlation between protein and fat gain, in which every gram of mass gain consisted of 37-42% lean mass. Blackcaps arriving in southern Israel after their flight across the Negev desert deposited substantial amounts of lean mass, implying that fat and protein were both catabolized during flight (Karasov and Pinshow 1998). Rufous Hummingbirds (*Selasphorus rufus*) also replenished lost protein stores during stopover visits in which they gained 3.5 g of non-lipid mass (Carpenter et al. 1992).

According to the nutrient limitation hypothesis, migrants must replenish depleted protein stores originating from functional tissues, especially their digestive organs, before they can deposit fat (Levey and Grajal 1991). Among these recovering birds, diets rich in protein such as grains and insects provide higher amounts of energy and are much more nutrient dense, therefore they enable the bird to replace lost body reserves much faster than if fed only a fruit diet (Levey and Grajal 1991). Pierce and McWilliams (2004) found that food-limited White-throated Sparrows (*Zonotrichia albicollis*) fed a diet consisting of grain during recovery were able to increase both their food intake and digestive organ mass, and regain mass during their 3 day recovery period. Long and Stouffer (2003) found that Hermit Thrushes (*Catharus guttatus*) fed only arthropods were able to gain a greater amount of mass and subcutaneous fat deposits compared to birds fed a mixed fruit and arthropod diet; in which fruit was fed ad libitum and insects were given in a reduced amount.

Minimal fruit should be consumed during this recovery period because of the indigestible fiber and plant secondary components it contains, but the major problem with fruit is its high water content (Levey and Grajal 1991). Although some birds, such as hummingbirds are able to process excessive amounts of water because they feed on nectar, most terrestrial vertebrates cannot (Pierce and McWilliams 2004; Sabat et al. 1998). The low mass gain seen among fruit fed birds may be due to the low energy and protein fruit contains, as well as its quick digestive passage, which delays the complete absorption of essential carbohydrates, proteins and lipids (Long and Stouffer 2003). Not only can a fruit diet impede mass gain, but it can also be toxic for birds consuming large amounts of it. The processing of copious amounts of water by the kidneys leads to the dilution of blood plasma and a subsequent decrease in several important solutes, such as sodium, which are needed to carry out important physiological processes (Faenestil 1977; Hill et al. 2004). Paleartic songbirds fed only a fruit diet were unable to rebuild shrunken digestive organs and depleted muscles rapidly; and were unable to maintain their body mass (Bairlein and Gwinner 1994; Berthold 1976). Similar results were seen among food-limited White-throated Sparrows (*Zonotrichia* albicollis), which were unable to increase their food intake or regain lost body reserves when fed a "recovery" diet of fruit for 3 days (Pierce and McWilliams 2004). Despite consuming 2.5 times the normal amount of wet food on a daily basis, these White-throated Sparrows were still obtaining 35% less energy compared to birds fed all grain (Pierce and McWilliams 2004).

Energy Source	**Energy Density (kcal/g)**	**Hydration Ratio**
Fat	9-9.5	0
Protein	4	2.2
Glycogen	4	2.5

Table 1. Energy densities for various sources of migratory energy(Blem 1990; Pennycuick 1998)

Morphological Variables	**Measurement Recorded for Swainson's Thrushes**
Mass of whole body (kg)	0.02765
Wing span (mm)	0.09863
Wing area (m2)	0.014177
Fat fraction	0.50*

* Long distance migrants have been shown to carry 50% or more of their mass as fat and Swainson's Thrushes are long distance migrants (Sibley 2000)

Table 2. Morphological measurements for Swainson's Thrushes (Yong and Moore 1994)

Variable	**Measurement Obtained When Level of Depleted Fuel Stores Reached**
Flight time (hr)	12.7
Distance (km)	746
Fat Burned (kJ)	539
Protein Burned (kJ)	28.3
Total Fuel Burned (kJ)	568

Table 3. Energetic budget for migrating Swainson's Thrushes (Pennycuick 1989a)

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Chapter 2: Divergent Spring Migration Fueling Strategies in North American Songbirds

Abstract

Recent growth in stopover biology research has yielded a wealth of information on mass changes and food acquisition by migrating birds both prior to migration and *en route*, however, it is still unknown how much of the energy required for migration is acquired prior to, versus during migration. We analyzed stopover mass change trends and subcutaneous fat deposits using 6 years of mist netting data from a spring migrant stopover site in Illinois, to describe differences in fueling strategies across taxa and sexes in 27 species of songbirds. We developed a set of predictions based on a hypothesized trade-off between pre-bulking and *en route* fuel accumulation as follows: "capital-based" migrants should show mass change over days spent at a stopover site indicative of replenishing tissue stores of energy, but should not show mass change on an hourly basis, as many individuals with full reserves may be unlikely, or even unable to fill their guts, merely resting until the next opportunity to resume their migration. Furthermore, such birds should frequently carry heavy stores of visible subcutaneous fat. In contrast, income-based migrants should exhibit mass change on an hourly time scale indicative of stomach filling, but should lack daily changes in mass and should possess minimal fat stores as they rely to a lesser degree on carrying large stores of energy in their tissues. Of the 27 species analyzed, Swainson's and Gray-cheeked Thrushes fulfilled all of the predictions of a capital-based migration strategy, Canada Warblers fulfilled the predictions of the income-based model, and Northern Waterthrushes and White-throated sparrows appear to employ mixed fueling strategies. Among the 27 species analyzed, eight species were capable of being sexed based on plumage traits. Of these eight species analyzed, Canada Warblers and Golden-winged Warblers showed significant stomach filling among males only, whereas, Black-and-white Warblers, American Redstarts, Common Yellowthroats, and Mourning Warblers showed significant stomach filling among females only. We conclude that species and sexes of North American migrant songbirds exhibit significant variation in their proportional reliance on stored energy reserves to fuel migration. This finding carries significant conservation implications, as income-based migrants may rely on finding resource-rich stopover habitats along their route.

Introduction

Every spring, many Neartic-Neotropic migrants undertake energetically demanding flights from their wintering grounds to their breeding grounds located thousands of kilometers away. Recent growth in stopover biology research has yielded a wealth of information on mass changes and food acquisition by migrating birds both prior to migration and *en route*, yet this information has not been integrated into a comprehensive understanding of fueling strategies in migrant birds. In particular, it is unknown how much of the energy required for migration is acquired prior to migration versus *en route*.

The energetic costs associated with fueling migration are similarly demanding to those associated with breeding, therefore, the proposed fueling strategies used by breeding Kestrels (*Falco tinnunculus*) (Drent and Dann 1980) may apply well to those utilized by migrants to fuel their flight. Drent and Dann (1980) proposed that two fueling methods underlie the decision made by Kestrels to lay a second clutch of eggs. The capital-based method relies solely on pre-acquired fat stores and therefore, the conditions of the environment have minimal impact on Kestrels' decision to lay another clutch (Drent and Dann 1980). The income-based method relies on frequent feeding to obtain needed energy because fat deposits are not mobilized, thus, if the bird's body condition is poor and there are limited food resources, she will not lay additional eggs due to an insufficient energy supply (Drent and Dann 1980). Similar to the breeding condition of these Kestrels, North American migrants may "decide" which strategy they will use to obtain their energy resources for flight, either by pre-bulking prior to beginning their flight, as in the capital-based strategy, or by acquiring their energy *en route* at stopover sites, as in the income-based strategy.

Migrants may experience a tradeoff between energy storage in tissues, and *en route* refueling capacity, which may force birds to evolutionarily "choose" to rely on one or the other strategy to fuel their migration. Alaskan Godwits (*Limosa lapponica baueri*) and Bristle-thighed Curlews (*Numerius* tanitiensis) both have been observed shrinking their digestive organs prior to beginning their trans-oceanic flights to save energy, since they encounter limited stopover sites *en route* (Piersma 1998). In addition, Blackcaps (*Sylvia atricapilla*) sacrifice their ability to feed *en route* by temporarily shutting down their digestive apparatus in order to reduce energy expenditure during their migration across the Negev desert (Gannes 2002). As a result, they cannot put on weight upon land arrival for 3-4 days, due to the shrunken condition of their assimilation organs (Gannes 2002; Karasov and Pinshow 2000). Mass gains cannot occur until these organs have returned to their pre-migratory size and activity (Gannes 2002; Karasov and Pinshow 2000; McWilliams and Karasov 2005). In contrast, some birds do not shrink their digestive organs, "deciding" instead to carry the extra weight in order to maintain their capacity to feed and refuel quickly at stopover sites (Lee et al. 2002). Migrants that do not decrease the size of their digestive organs, such as Yellow-rumped Warblers (*Dendroica coronata*), are able to feed and digest at high rates immediately following resumption of ad libitum feeding because they retain spare digestive capacity (Lee et al. 2002).

In this study, we set out to test whether or not differences in fueling strategies exist across taxa and sexes in eastern songbirds. Two methods for measuring mass change during migratory stopover visits allowed us to predict the mass change patterns that should be observed among capital-based and income-based migrants. The first method, often referred to as the "direct" method, involves measuring mass changes on a multi-day time scale in individual birds recaptured on multiple days at the same stopover site. It indicates tissue assimilation because this is a progressive process that requires the bird to acquire large amounts of food over multiple days.

The second method, which we term the "indirect" method, measures the trend of mass through time in all captured birds at the scale of hours within a day. At this scale, observed mass changes are indicative of stomach filling, and a large portion of the added mass may be comprised of water and/or indigestible materials, such as the keratinous exoskeleton of insects, which do not add to the birds' energy stores.

We developed two testable fueling strategy predictions based on our hypothesis that migrants exhibit a tradeoff between the acquirement of energy prior to beginning migration and obtaining energy *en route*. We predicted that capital-based migrants would show mass changes with the direct method, indicative of tissue assimilation, but should not show mass increases with the indirect method, as many individuals arrive with large tissue stores of energy, rendering feeding at the stopover site unnecessary. In addition, these birds should regularly carry large stores of subcutaneous fat. In contrast, we predicted that income-based migrants would gain mass with the indirect method, indicative of stomach filling because these birds carry minimal fat deposits and must acquire their energy frequently *en route*. However, these birds would not exhibit mass change with the direct method because they do not rely on large tissue stores of energy, therefore they do not need to rebuild these tissues over multiple days. These birds should be carrying minimal fat stores as well.

Methods

Mist Netting Procedure: This study was conducted at the Shaw Woods portion of the Skokie River Nature Preserve in Lake Forest, IL (N42º 15' 37.2" W87º 51' 34.0"). This location has been described in detail by Gordon et al. (2002) and Bueter et al. (2006). Six years of mist-netting data were collected (2002-2007) using 12-15 12 m, 30 mm mesh nylon mist nets opened May 1 thru May 31. The total net hours for each year were as follows: 744 in 2002, 1151 in 2003, 1221 in 2004, 1380 in 2005, 1614 in 2006 and 2250 in 2007. Mist nets were opened for 5 hours beginning at dawn and checked at the beginning of every hour. Upon removal from the nets, birds were placed in breathable bags and labeled with the time and net number.

At the central banding station located on site, the time and net number were recorded, and individually numbered aluminum bands issued by the U.S. Federal Bird Banding Lab were placed on a leg of each captured bird. We then weighed each bird to the nearest 1.0 g using a 25 g or 100 g spring scale during the 2002-2005 seasons. During the 2006-2007 seasons, we used a digital scale to measure mass to the nearest 0.1 g. Wing chord was measured to the nearest mm, and we examined subcutaneous fat deposits on the lower abdomen, furcular hollow, and wing pits, scoring them on a three-level fat scale to reduce observer error. Scores were assigned as follows: 0 = no visible fat, 2 = fat deposits full and bulging, 1 = intermediate. Birds were aged and sexed to the extent possible based on plumage and wing chord criteria described in Pyle (1997) and Sibley (2000).

Mass Change Calculations: We used two methods, both commonly employed in published literature, to measure changes in birds' mass at our stopover site (Bonter et al. 2007; Dunn 2001, 2002). To obtain mass change information for these birds via the direct method, the mass of the bird at its initial capture was subtracted from the mass of the same bird at its subsequent capture. This method can only be applied to individual birds that were captured on multiple days during the same season at our site, indicating stopovers of at least 1 day in duration. The indirect method does not rely on recaptures of individual birds. Instead, the condition index (CI) (mass x 100/wing chord) was plotted against the hour of capture for all captured birds. We used condition index in these calculations in order to correct for variation in body size among birds and obtain a more accurate representation of the variation in body conditions, or soft tissue mass, of birds over time (Winker 1995). The minimum sample requirement for our mass-change analysis with the direct method was 10 within-season recaptures, and for the indirect method, it was 24 single captured birds. Locally breeding species were excluded.

We performed multiple linear regressions of mass or CI over time for both these methods and the statistical significance of these relationships were tested with ANOVA, using JMP, version 7.0.1 (SAS Institute, 2007).

Mass-gain Threshold Analysis− Standardized cumulative mass change was calculated by subtracting the initial-capture mass from the final-capture mass divided by the initial-capture mass (Gannes 2002). These values were then plotted against the length of stay at the stopover site. The absence of overlapping SE bars was used as an indicator of significant mass changes that occurred between individual stopover durations. The minimum sample size was 48 within-season recaptured birds.

Subcutaneous Fat Analysis: The percentages of individuals with each fat score were determined for each species. We used the ratio of 2:0 scores to reflect the general frequency of birds with large, visible subcutaneous fat deposits. Species with a ratio of 0.1 or less were classified as "flying lean," and birds with a ratio of 1.0 or greater were classified as "flying fat". The minimum sample size was 25 birds.

Results

Stopover Mass Change Analyses: The direct method analysis was restricted to species that do not breed at the site, and for which we obtained a minimum sample size of 10 within-season recaptures. Of the nine species tested, four showed significant mass change on a daily scale (Table 1). Among these were two thrushes, the Gray-cheeked and Swainson's, and two warblers, Magnolia and Northern Waterthrush (Table 1).

The indirect method analysis was restricted to species with at least 24 single captured birds. Among the 27 species analyzed, six species exhibited a significant increase in condition index over time on an hourly time scale, including five species of warbler and one sparrow (Table 1).

Sexual Fueling Differences: Of the eight species analyzed, six showed divergent hourly mass change patterns among sexes (Table 2). Two species of warblers showed significant hourly condition index increases among males only and four species of warblers showed significant hourly condition index increases among females only (Table 2).

Mass-gain Threshold Analysis: The minimum sample size for this analysis was 48 within-season recaptured birds. Of the three species analyzed, Swainson's Thrushes were the only species that showed an indication of a mass-gain threshold. Individual Swainson's Thrushes did not appear to increase in mass until they had been at the site for more than 7 days (Fig. 1A). The remaining two species analyzed, Ovenbird and Northern Waterthrush, did not show mass-gain thresholds (Figs. 1B and 1C).

Subcutaneous Fat Analysis: The minimum sample size requirement for this analysis was 25 birds. Most individuals of all species were scored as "1" on our subcutaneous fat scale. Of the 27 species analyzed, four species were classified as "flying fat," including Swainson's and Gray-cheeked Thrushes, White-throated Sparrow and Tennessee Warbler (Table 1). Of the 27 species examined, 13 were classified as "flying lean," including eight species of warblers, two species of sparrows, and three species of flycatchers (Table 1).

Discussion

Despite frequent treatments of the indirect and direct method as interchangeable indicators of mass change at stopover sites (Bonter et al. 2007; Dunn 2001, 2002), these two methods reflect different mass gain processes because of the different time scales over which they are measured. Birds relying to different degrees on stored energy reserves should exhibit different mass change trends at these different time scales because of the different fuel acquisition and storage strategies they employ. The direct method measures mass change on a multi-day time scale and therefore reflects tissue assimilation or loss, whereas the indirect method measures mass change on an hourly basis and therefore reflects shorter-term processes such as stomach filling.

Swainson's and Gray-cheeked Thrushes fit our predictions of a capital-based migration fueling strategy. Birds from these two species carried large subcutaneous fat reserves, indicating that they rely heavily on pre-acquired fat deposits to supply the energy they need for migration. These species did not gain weight on an hourly time scale, indicating that most individuals did not fill their stomachs over the course of a morning at our site. Among recaptured individuals on multiple days at our site, mass gain occurred on a multi-day time scale indicating that these individual birds were increasing their tissue and fat stores presumably because they arrived at our site with tissue energy reserves depleted. These results are consistent with the results of Bonter et al. (2007) and Dunn (2001, 2002) who found no stopover mass change using the indirect method, and Othal (1995) and Yong and Moore (1997) who found stopover mass change using the direct method.

Canada Warblers fit our predictions for an income-based migration fueling strategy. Birds from this species were not carrying large fat loads and were observed gaining mass on an hourly time scale, indicative of stomach filling. In addition, among recaptured birds, there was no mass change observed on a multi-day time scale, indicating that these birds were not rebuilding fat and tissue stores.

Our finding of a divergence between capital and income-based migrants provides an explanation for enigmatic patterns from previous studies of plasma metabolites and stopover mass gain patterns in Swainson's Thrushes. Since capital-based migrants carry large fat stores, they may not need to fuel at each stopover site they encounter because they have sufficient energy stores to allow for the continuation of their flight. Instead of foraging, which is energetically costly in itself and increases the bird's risk for predation, capital-based migrants such as Swainson's Thrushes, may use stopover habitats as a resting place until they are ready to resume their flight (Wikelski et al. 2003). This may explain why Guglielmo et al. (2005) Swainson's Thrushes visiting an excellent stopover habitat did not exhibit mass changes on an hourly basis or show indications of fueling based on their plasma metabolites levels.

The divergence between capital and income-based migration strategies may be driven by a tradeoff that results from the physiological "decision" to shrink down and shut off the digestive system for efficient long-distance flight. Doing so may reduce flight mass and provide an additional source of fuel, but may require the bird to sacrifice its refueling capacity, resulting in slow rates of mass gain upon arrival at a stopover site (McWilliams and Karasov 2005). Despite the inherent limitations associated with this strategy, capital-based migrants using it can reduce the costs incurred by maintaining metabolically active organs, and offset the energetic costs associated with carrying added mass, which can constitute up to a 40% increase in energy expended (Alerstam and Hedenstrom 1998). Capital-based migrants can employ this strategy because they rely heavily on fat stores accumulated prior to the start of migration and can afford to shut down their digestive system since they do not feed frequently *en route*, whereas income-based migrants must maintain active digestive organs to allow for quick refueling at stopover sites.

Delays or thresholds in migrants' stopover mass gain patterns provide further evidence of a tradeoff between fuel storage and refueling capacity. Although our results are not as clearly defined as the thresholds found by Gannes (2002) among migrating Blackcaps (*Sylvia atricapilla*), they still suggest that shrinking the size and activity of digestive organs limits refueling capacity (Gannes 2002; Karasov and Pinshow 2000). Our results indicate that Swainson's Thrushes were unable to add significant weight until they had been at our site for at least eight days (Fig. 1A). The mass-gain threshold observed for Swainson's Thrushes is similar to the 3-4 day threshold experienced by Blackcaps following landfall (Gannes 2002; Karasov and Pinshow 2000). Ovenbird and Northern Waterthrush did not exhibit such thresholds (Figs. 1B and 1C), consistent with the significant hourly mass gains observed in both of these species, indicative of stomach filling with digestive organs maintained in an active state during migration (Table 1).

The existence of income-based migration fueling strategies in some birds carries an important conservation implication: providing resource-rich stopover habitats along their migration route may be essential for them to complete their migration successfully. Among Blue-winged Warblers, Yellow-rumped Warblers, Wilson's Warblers, Swamp Sparrows and three species of flycatchers there was no indication of stomach filling, despite the fact that these birds were flying lean. Canada Warblers, in contrast, were also flying lean but were able to stomach fill during their stay at the stopover site (Table 1). This may indicate that the former species are income-based migrants who are unable to find food during a morning spent at our site. Not only does stopover habitat quality vary from site to site (Dunn 2001, 2002), but our results demonstrate that habitat resources may not always meet the demands of all species due to diet differences. Dunn (2001) found at a Canadian site that small insectivores, such as warblers and flycatchers did very well, whereas Swainson's Thrushes actually lost mass. This variation among species demonstrates the importance of providing several excellent fueling sites for income-based migrants since the diet requirements of migrants varies from species to species.

Combined long-term fuel/storage and short-term stomach filling in Northern Waterthrushes and White-throated Sparrows suggests that this site is preferentially selected by these species for refueling, even though they rely, in general, on a capital-based strategy. This possibly provides a small bit of insight into the poorly understood processes of *en route* habitat selection. Two years of data collected using migratory window kills, nocturnal flight calls and mist netting at SWAMP showed that SWAMP had a much larger representation of Northern Waterthrushes compared to the other two methods (Schramm et al.in press). Northern Waterthrushes may exhibit both stomach filling and tissue assimilation at this stopover site because it is a "magnet" for these birds since it provides abundant resources that meet their needs. This demonstrates that migrants may adjust their fueling strategies *en route* based on the quality of the habitat they are foraging at, in order to acquire more energy at a lesser cost, or to conserve energy if food is not available.

Our analysis revealed divergence across sexes in migration fueling strategies in several species, though there was no consistency in which sex employed which strategy.

Golden-winged Warblers showed indirect fueling among males only, however when both sexes were sampled together, the species as a whole showed no mass change due to the 3:1 sex ratio (Table 1 and 2). Although both males and females exhibited divergent fueling patterns, we did observe more females stomach filling than males, which may be related to the energetic costs of breeding (Table 2). Laying eggs requires female birds to be in good condition; as a result, most migrating female birds, such as Pectoral Sandpipers (*Calidris melanotos),* increase their nutrient consumption prior to arriving at their breeding grounds and put on larger fat loads than males to improve their fitness (Fairner and Wiens 1999; Skagen 2006).

At the current time, it is difficult to classify all species or sexes into income versus capital-based migration strategies. Future studies should be conducted in order to further illuminate the fueling strategies employed by migrating birds, and to evaluate the role of unknown variables on the fueling rates of migrants, including the diet preferences of species in correlation with the composition of resources available at fueling sites, and intra-feeding differences among sexes and ages involving a larger span of species.

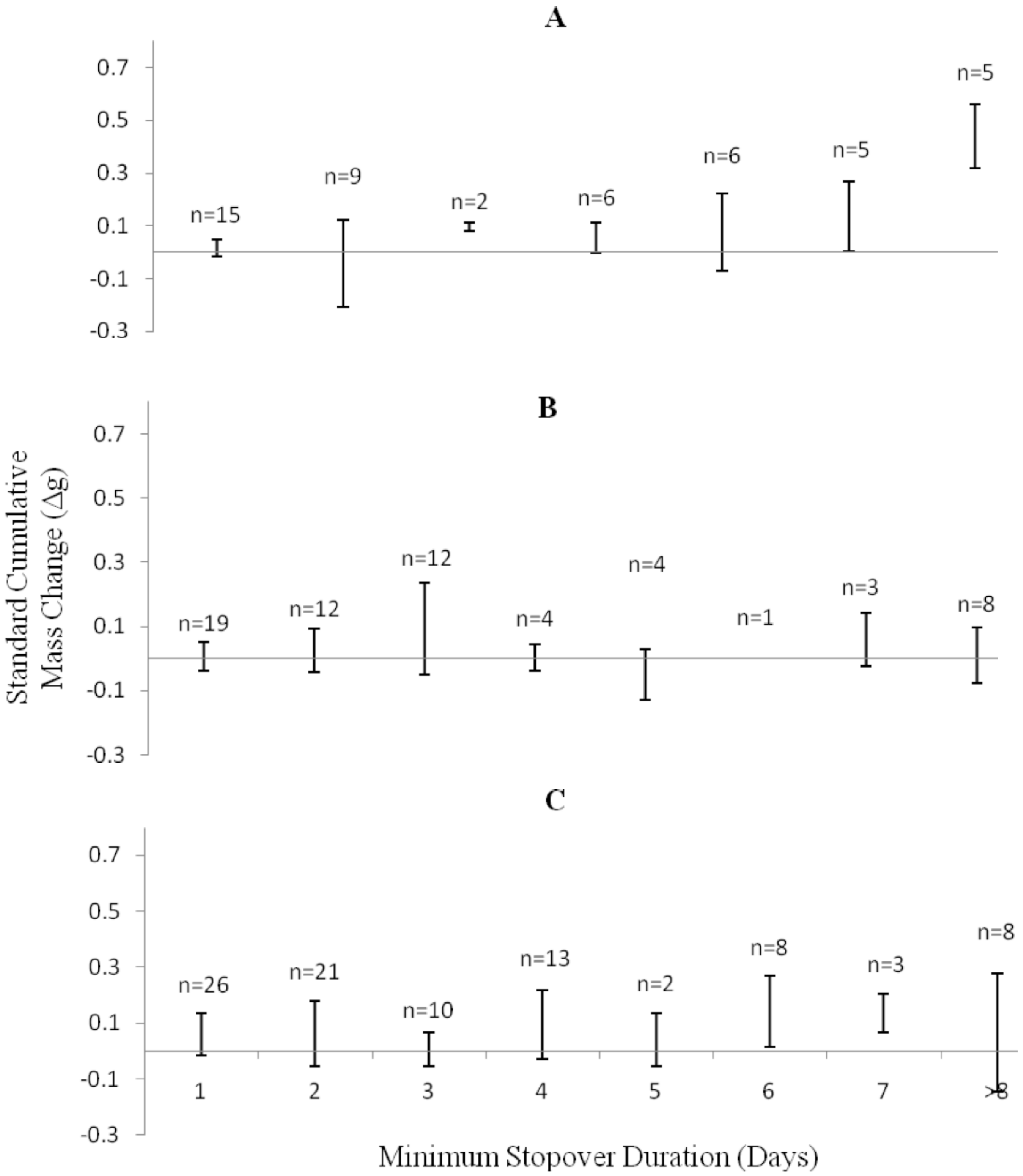

Figure 1. Direct method mass gains as a function of minimum stopover duration (±SE) for recaptured individuals caught at the SWAMP Illinois stopover site (2002-2007). Only species with at least 48 within-season recaptures were included. The absence of overlapping SE bars indicates the existence of a mass-gain threshold, before which individual birds are unable to gain mass rapidly. One out of three species analyzed showed a mass-gain threshold. Swainson's Thrushes (A) showed a fueling threshold between day 7 and 8. The remaining two species, Ovenbird (B) and Northern Waterthrush (C) did not show evidence of a mass-gain threshold.

Common Species Name	Stopover Mass Change Analyses				Subcutaneous Fat Analysis		
	Indirect		Direct		n	Fat Score Ratio	Fueling Strategy
	n	p value	n	p value			
Yellow-bellied Flycatcher	98	0.1162			98	0^	
Alder Flycatcher	74	0.3910			74	0^	
“Traill's” Flycatcher	91	0.6743			90	0^	
Ruby-crowned Kinglet	348	0.4697	32	0.9106	317	0.422	
Gray-cheeked Thrush	134	0.9389	20	**<0.0001**	116	5.1*	C
Swainson's Thrush	704	0.1221	48	**<0.0001**	656	2.97*	C
Hermit Thrush	30	0.9106			27	0.250	
Blue-winged Warbler	28	0.6678			27	0^	
Golden-winged Warbler	41	0.8207			38	0.154	
Tennessee Warbler	37	0.5050			36	1.875*	
Orange-crowned Warbler	34	0.3612			33	0.100^	
Nashville Warbler	98	**0.0282**			98	0.958	
Chestnut-sided Warbler	72	0.8412			70	0.130	
Magnolia Warbler	732	0.3636	40	**0.0015**	690	0.129	
Yellow-rumped Warbler	58	0.7301			57	0.077^	
Black-and-white Warbler	135	**0.0396**	10	0.4820	125	0.172	
American Redstart	375	0.0860			368	0.150	
Ovenbird	475	**0.0197**	63	0.7167	411	0.153	
Northern Waterthrush	609	**0.0417**	91	**0.0113**	508	0.061^	M
Common Yellowthroat	273	0.0558			269	0.019^	
Wilson's Warbler	249	0.8924	25	0.4871	224	0.080^	
Canada Warbler	300	**0.0386**	11	0.8620	288	0.006^	I
Mourning Warbler	184	0.0670			178	0.051^	
Lincoln’s Sparrow	51	0.6431			50	0.100^	
Swamp Sparrow	65	0.3995			63	0.051^	
White-throated Sparrow	245	**0.0005**			232	1.05*	M
White-crowned Sparrow	24	0.5809			24	0.111	

^Denotes “Flying Lean” (0.1 and less)
*Denotes “Flying Fat” (1.0 and greater)
C = Capital
I = Income
M = Mixed

Table 1. Results for stopover mass change and subcutaneous fat analyses. Subcutaneous fat analysis and two mass change analyses (see text) in spring migrant songbirds captured at an Illinois stopover site (2002-2007). Multiple linear regressions of condition index (indirect method) or mass (direct method) change over time were all positive, and p values denoting statistical significance of these trends were obtained using ANOVA. Six species showed significant mass change increase over hourly time with the indirect method, while four showed significant mass change across days with the direct method (see text). Our analysis of subcutaneous fat deposits resulted in 12 species, plus “Traill’s” Flycatcher, as “flying lean”, and 4 species as “flying fat”. The fueling strategy column presents the classifications made based on our predictions for income and capital-based strategies (see text). Swainson’s Thrushes and Gray-cheeked Thrushes fit the predictions of capital-based migrants, Canada Warblers of an income-based migrant, and Northern Waterthrushes and White-throated Sparrows demonstrated mixed strategies.

Species	**n**	**Male p Values**	**n**	**Female p Values**
Females Show More Stomach Filling than Males				
Black-and-white Warbler	53	0.5076	82	**0.0540**
American Redstart	199	0.6167	169	**0.0720**
Common Yellowthroat	161	0.4823	109	**0.0185**
Mourning Warbler	121	0.4170	61	**0.0793**
Males Show More Stomach Filling than Females				
Canada Warbler	204	**0.0747**	89	0.3413
Golden-winged Warbler	10	**0.0659**	30	0.5543
No Obvious Sexual Differences				
Ruby-crowned Kinglet	55	0.4829	288	0.3617
Tennessee Warbler	15	0.5915	17	0.4549

Table 2. Results for sexual fueling differences among sexes using indirect method analysis. Sexual differences in hourly mass gain trends in eight species of plumage-sexable songbirds, caught at an Illinois spring stopover site (2002-2007). P values are from ANOVA showing the significance of condition index change over time (hours). All trends were positive.

Conclusion

The basis for my research presented in Chapter two originated from a significant amount of published findings in this field and it goes one step further by expanding on these topics of migratory fueling strategies by providing new findings that encourage the growth of these theories and concepts. In an effort to provide a better understanding of how my work contributes to this field of research I have provided a comparison of previous knowledge and how my original research expands upon these findings.

Currently, capital and income-based fueling strategies have only been applied to breeding Kestrels (*Falco tinnunculus*) (Drent and Dann 1980). My research presented in this thesis contributes to this concept of divergent fueling strategies among birds through my examination of capital and income-based migratory fueling strategies among North American songbirds. In addition, I devised predictions related to the stopover mass change patterns and subcutaneous fat deposits that birds utilizing these two strategies should exhibit, which can be used to classify the fueling behaviors of migrating birds.

Previous studies have shown that female breeding Pectoral Sandpipers (*Calidris melanotos)* consume a larger amount of food and put on larger fat deposits than males, prior to arriving at their breeding grounds (Fairner and Wiens 1999; Skagen 2006). My finding of divergent fueling strategies among sexes within several species of warblers contributes to these previous findings by demonstrating the existence of this pattern among eastern migrating songbirds.

Dunn (2001, 2002) has shown through stopover mass change analyses that stopover sites vary greatly in quality and may provide adequate resources for some species, while providing minimal for other species. My finding that migrating songbirds utilize an income-based strategy, and that several species predicted to utilize this method are not stomach filling, necessitates the need to examine the quality of stopover sites across North America, both for their quality and the diversity of the resources they provide. In addition, previous enigmatic findings that Swainson's Thrushes were not observed gaining mass at an excellent stopover site (Guglielmo et al. 2005) might be explained by the fueling strategy utilized by these migrants. My finding that Swainson's and Gray-cheeked Thrushes employ a capital-based strategy suggests that these birds may not need to refuel at every stopover site and instead use them as a place to rest before resuming their flight.

Much of the current research involving migratory fueling behaviors at stopover sites have relied on only one of the two mass change analyses for measuring stopover mass change. For example, Yong and Moore (1997) and Othal (1995) measured stopover mass change for Swainson's Thrushes using only the direct method, whereas, Dunn (2001, 2002) used only the indirect method for measuring mass change for birds from this species. My research involving stopover mass change patterns among North American migrants has shown that mass changes found using either one of these methods indicate two different types of mass change patterns because of the different time scales they rely on, therefore, both methods should be used in conjunction with one another.

Gannes (2002) and Karasov and Pinshow (2000) demonstrated that Old World migrating Blackcaps experience a mass-gain threshold due to the "burning" of their digestive organs. In my research, I applied this concept to North American migrating songbirds and found an indication of a mass-gain threshold among capital-based migrants, but not income-based migrants, which can be explained by the divergent fueling strategies they utilize and the tradeoff they must make as a result.

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