

SEASONAL INTERACTIONS BETWEEN MIGRATION AND WINTER IN A
MIGRATORY SONGBIRD, THE MAGNOLIA WARBLER (*DENDROICA*
MAGNOLIA)

A Thesis

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ABSTRACT

Populations of many species of Nearctic-Neotropical migratory songbirds have been declining over the past several decades. Investigations of these declines have historically been focused on events occurring in temperate breeding grounds and tropical wintering grounds. Recent research on Nearctic-Neotropical migratory songbirds has emphasized the importance of events occurring during migration and interactions among breeding, wintering, and migratory phases of the annual life cycle. Stable isotope analysis has been instrumental in revealing seasonal interactions and migratory connectivity in migratory songbirds, but little research has addressed interactions between events occurring in tropical wintering and migratory stopover areas.

From May to early June in 2004 and 2005, I investigated seasonal interactions within the annual cycle of Magnolia Warblers (*Dendroica magnolia*) captured during migratory stopover in northwestern Ohio (Ottawa and Lucas counties). Birds were captured using mist nets placed in dogwood shrubland, mature deciduous forest, and beach-ridge forest habitat. A total of 615 Magnolia Warblers were captured, banded, measured, weighed, aged and sexed. In 2005, approximately 200 individuals were sexed using molecular techniques, and the extent of pre-alternate molt (plumage-status) was assessed by counting the number of freshly replaced wing coverts and quantifying the amount of dark breast streaking with digital photo analysis. Feathers grown in pre-

alternate molt in wintering areas were collected from 555 individuals and used for stable-carbon isotope analysis.

Stable-carbon isotope ratios ($\delta^{13}\text{C}$) of feathers ranged between -25.4‰ and -19.9‰ for both years, and this range corresponds to $\delta^{13}\text{C}$ values reported other species of wood-warblers that wintered in mesic tropical forest (generally considered high quality) and more xeric scrub. I tested for relationships between winter-specific habitat use (i.e., $\delta^{13}\text{C}$ values) and capture date, energetic condition (size-adjusted body mass), and plumage-status of transient Magnolia Warblers. I predicted that warblers that had wintered in more xeric habitats (enriched $\delta^{13}\text{C}$ values) would migrate later, be in lower energetic condition, and have lower plumage status (i.e., completed less molt in tropical wintering areas). Overall, results suggested that migration timing, energetic condition, and extent of pre-alternate molt completed by Magnolia Warblers were not influenced by wintering in either mesic or more xeric tropical habitats. I believe that Magnolia Warblers that wintered in more xeric locations may not have been negatively impacted or were able to regain mass during migration. Little published information exists on the wintering ecology of Magnolia Warblers. Additional information is needed to understand how winter habitat associations impact survival, energetic condition, migratory timing, and feather molt. Establishing the quality of various tropical habitats used by Nearctic-Neotropical migrants is important for the effective conservation of these species. A better understanding of the interactions among phases in the annual cycle of Nearctic-Neotropical migratory songbirds will be useful for developing comprehensive conservation planning that spans geographic and political boundaries.

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CHAPTER 1

INTRODUCTION

Nearctic-Neotropical migratory landbirds winter primarily in tropical regions of Mexico, the Caribbean, Central America, and northern South America, and migrate to temperate areas of North America to reproduce (Faaborg 2002). Populations of many species of Nearctic-Neotropical migrant landbirds have been declining in recent decades (Sauer et al. 2000). Hypotheses proposed to explain these population declines have historically focused on events occurring in either temperate breeding areas or tropical wintering areas. Habitat loss and fragmentation on the breeding grounds are likely important factors limiting populations of migratory landbirds (Robinson et al. 1995), however, Neotropical migrants spend the majority of their lives on the wintering grounds where extensive tropical deforestation may also negatively impact their populations (Terborgh 1980).

The highest population concentrations of wintering Neotropical migratory songbirds occur in Mexico and the Greater Antilles, with numbers decreasing southward through the Caribbean islands and into Central America and northern South America. Up to 50% of all Neotropical migrant landbirds spend the winter months in Mexico, the Bahamas, Cuba, and Hispaniola (Terborgh 1980). This tropical wintering region is only

one-seventh the size of the temperate breeding areas occupied by forest-breeding Neotropical migrants. As a result, Neotropical migrants typically occur in denser concentrations than they do breeding habitats. This has important conservation implications because the destruction of a relatively small amount of Neotropical forest may disproportionately impact migrants that breed in a much larger area of temperate habitat (Terborgh 1980).

The relatively small area of tropical forest suggests that habitat availability may limit Neotropical migrants. If wintering habitats are limiting, birds should compete for high quality habitats (Sherry and Holmes 1996). Differing densities of migrants in various habitats is a potential indirect indicator of intraspecific competition because optimal habitats can support a greater number of birds than corresponding suboptimal habitats (Faaborg 2002). The American Redstart (*Setophaga ruticilla*) winters primarily in the Caribbean and Central America and has been a focal species in studies of winter habitat quality and intraspecific competition in wet lowland and mangrove forest ecosystems and scrub ecosystems of Jamaica (Sherry and Holmes 1997). Densities of redstarts differ significantly among habitats in Jamaica (Sherry and Holmes 1996). However, because population densities are not always accurate indicators of habitat quality, other factors should be taken into consideration (Sherry and Holmes 1996).

LITERATURE REVIEW

Winter Habitat Quality

The availability of food resources likely influences the distribution of Neotropical migrants (Johnson and Sherry 2001) and may represent a reliable indicator of habitat quality for wintering migrants (Sherry and Holmes 1997). Tropical forests characteristically exhibit high floristic complexity, which may typically be associated with higher food availability (Sherry and Holmes 1996) than structurally simple shrub habitats, such as shrubland. Arthropods may also vary temporally in their availability among habitats. Parrish and Sherry (1994) found that mangrove forests supported temporally more persistent canopy structure and greater insect biomass than adjacent xeric scrub. Annual climatic fluctuation influences microhabitat characteristics (e.g., soil moisture content and standing water), and this, in turn, impacts arthropod prey abundance. Mesic riparian ecosystems, for example, are more resistant to climatic fluctuation and may provide higher quality habitats for wintering migrants because of greater consistency in food availability on an annual basis (Sherry and Holmes 1996).

Another indicator used to assess winter habitat quality is the change in energetic condition of individual birds. American Redstarts occupying suboptimal coastal scrub forest experienced a decrease in body condition (i.e., size-adjusted body mass) as the season progressed, whereas birds occupying higher quality mangrove and mature tropical forest habitats showed no significant decline in body condition (Sherry and Holmes 1996). Other research with American Redstarts revealed poorer body condition and

lower annual survival and longevity of individuals occupying sub-optimal shrub habitats (Marra and Holmes 2001). Redstarts in these shrub habitats also revealed higher levels of plasma corticosterone (Marra and Holberton 1998), a stress hormone that promotes the catabolism of muscle proteins and can contribute to poor physical condition (Marra and Holmes 2001).

In contrast to redstarts, ground-foraging Ovenbirds (*Seiurus aurocapillus*) occupying shade coffee forest and dry limestone forest in Jamaica showed a decrease in body condition through the winter, whereas Ovenbirds occupying second growth scrub did not decrease in body condition during one winter season (Strong and Sherry 2000). Change in body condition and feather growth rates of Ovenbirds were significantly related to ant biomass, which is their preferred prey during winter in Jamaica. Interestingly, ant biomass was associated to amount of rainfall, and during one relatively dry winter low ant biomass resulted in a decreased with a corresponding decrease in Ovenbird body condition from early to late-winter (Strong and Sherry 2000).

Winter Territoriality

Higher quality habitats, by definition, should contain resources that are vital to the survival of animals, particularly Nearctic-Neotropical migrant songbirds (Rappole 1995). These important resources may induce territorial behavior among wintering Neotropical migrants (Gauthreaux 1978). Territoriality is well documented among Neotropical migrants on the wintering grounds (Rappole 1995) and it influences the distribution of birds among habitats throughout the tropics (Terborgh 1989, Marra et al. 1993).

Territoriality and densities of wintering migrants may cause misleading interpretations of habitat quality (Fretwell 1972). In effect, higher quality habitats may have lower densities of migrants than expected because aggressive behaviors of dominant individuals limit the number of individuals that occur there (Marra and Holmes 2001).

Adult male redstarts primarily occupy high quality habitats, such as mangrove forests, whereas the majority of females and young males occur in low quality scrub habitats (Marra 2000). Some research suggests that habitat segregation among redstarts is a result of dominant, aggressive behavior by males (Marra et al. 1993). Typically, redstarts arriving in Jamaica after fall migration randomly distribute themselves in both mangrove forest and scrub habitat. This initial pattern of settlement does not suggest that redstarts segregate according to innate propensities for specific habitat types. As time progresses, the number of individuals occupying a particular habitat become increasingly skewed with regard to sex, and this is likely a result of territorial exclusion by more dominant individuals (Marra et al. 1993, Johnson and Sherry 2001). Removal experiments further support the dominance-mediation hypothesis because redstarts preferentially reoccupy empty mangrove territories over empty scrub territories, and more females reoccupy empty male territories than do males. It also seems likely that younger individuals are excluded from certain winter habitats (Marra et al. 1993).

In the Yucatan Peninsula of Mexico, sexual habitat segregation also occurs in American Redstarts and other sexually dimorphic warblers [Northern Parula (*Parula americana*), Magnolia Warbler (*Dendroica magnolia*), and Hooded Warbler (*Wilsonia citrina*)]. The typical pattern for all of these species is that males occupy more mature

forest habitats, whereas females inhabit the younger second-growth habitats, such as dune scrub, mangrove scrub, and seasonally flooded scrub. Hooded Warblers show clearly defined habitat segregation with regard to sex, whereas species such as the Magnolia Warbler show smaller, yet significant levels of habitat segregation (Ornat and Greenberg 1990). Magnolia Warblers occupy a variety of winter habitats, and show a distribution bias with females in scrub (64% of observations) and males in more forested habitats (60% of observations) (Ornat and Greenberg 1990).

As previously indicated, American Redstarts exhibit remarkable habitat segregation in wintering habitats, and, as a result, individuals in female-biased habitats (lower quality shrubland) tend to lose mass during winter while those individuals in male-biased habitats (higher quality mangrove forest) either gain mass or maintain constant mass (Marra et al. 1998). Poor physical condition resulting from use of lower quality (more xeric) winter habitat affects the date of departure of both males and females on spring migration. Furthermore, through the utilization of stable isotope analysis, birds arriving in poorer condition in temperate breeding areas were determined to have wintered in lower quality habitats (Marra et al. 1998). In another study involving stable isotope analysis, Norris et al. (2004a) demonstrated that redstarts of both sexes that wintered in low quality habitats experienced reduced reproductive success.

Migration

Many authors have suggested that events occurring in tropical wintering areas (e.g., tropical deforestation) have the potential to impact migratory songbird populations

(Terborgh 1989). More recent research suggests that migration events may significantly limit migrant populations. For example, using long-term demographic information from breeding areas in New Hampshire and tropical wintering areas in Jamaica, Sillett and Holmes (2002) estimated that approximately 85% of annual mortality in adult Black-throated Blue Warblers (*Dendroica caerulescens*) occurs during migration. Such studies highlight the need for continued research on the ecology of migratory landbirds during migratory periods.

Most species of Neotropical migrants are unable to reach their breeding destinations in one migratory leap. These migrants use a series of habitats (stopover habitats) in between their breeding and wintering grounds. Neotropical migrants spend approximately 2-3 months of the year at migratory stopover areas (Moore et al. 1995), but until recently, ornithologists have devoted little attention to the importance of events that occur during migration.

Migration presents an entirely different set of challenges for Neotropical migrants (Moore et al. 1995); migration is energetically demanding, and migrants require quality stopover habitats to replenish their energetic stores and to take shelter from predators that may take advantage of fatigued individuals. In addition, migrants must cope with limited availability of stopover habitats in some areas (Barrow et al. 2000). As a result, stopover habitats represent a critical link that spring migrants require to reach the breeding grounds, defend a territory, and successfully reproduce (Moore et al. 1995).

Much evidence suggests that migrant songbirds actively select stopover habitats during migration (Petit 2000). Given the food resource requirements of Neotropical migrants, active selection of habitats is expected, especially where habitat availability is

not limiting. The primary factors driving habitat selection during migration certainly include vegetation structure and food availability (Moore et al. 1995), but may also involve heterospecific attraction (Rodewald and Brittingham 2002), intraspecific and interspecific competition, and presence of predators (Petit 2000). However, the relative importance of these factors and the process by which selection occurs is not well understood (Moore and Aborn 2000).

The energetic condition of a migrant landbird is vital to the successful completion of migration (Woodrey 2000). Migrants use stores of body fat to fuel migratory flight (Blem 1980). Migrants can rapidly add mass in bouts of hyperphagia, and some species, such as shorebirds, nearly double their body mass before migrating. During migratory periods, migrants have high rates of lipogenesis and synthesize fat reserves from ingested lipids (e.g., essential fatty acids) and pre-existing carbohydrate reserves (e.g., glycogen reserves in the liver), and adjust their metabolic activities to use only fat stores (Berthold 1993). Fat is deposited in several subcutaneous reserves where it is readily available as an energy source to power sustained periods of flight (Blem 1980).

Energetic condition during spring migration may have significant consequences during the breeding phase of the life cycle. The first waves of migrants to arrive on breeding grounds may experience low food availability due to the delayed phenology of northern regions. Birds with excess fat stores accumulated during stopover periods can cope more effectively with periods of low resource availability. For example, American Redstarts with excess fat stores might be able to focus on breeding activities (e.g., territory and mate assessment, acquisition of specific nutrients needed for breeding, singing and territory maintenance) instead of concentrating on self-maintenance activities

needed for survival (Smith and Moore 2003). Although excess arrival fat may not be directly used for egg development, it may indirectly enhance reproductive success. Female redstarts with endogenous fat stores tend to produce larger egg clutches, larger eggs, and nestlings with higher mass (Smith and Moore 2003). There is also a positive correlation between endogenous fat stores of male redstarts and egg mass which suggests that fatter females paired with fatter males (Smith and Moore 2003).

Seasonal Interactions and Stable Isotope Analysis

Since populations of Neotropical migrants are likely limited by events occurring throughout their annual cycle (Latta and Baltz 1997), successful conservation planning for migratory birds requires a better understanding of interactions between the various events of a migrant's annual cycle (Rubenstein et al. 2002, Chamberlain et al. 2000). Understanding seasonal interactions is important because each event in a migrant's annual cycle has potential to influence a subsequent event (Webster et al. 2002).

It has been extremely difficult to study seasonal interactions and to link geographically separate breeding and wintering ranges because traditional marking methods (e.g., leg bands/rings, neck collars, patagial markers) provide inadequate data on seasonal movements because of low mark recovery frequencies (Hobson 1999). Radio telemetry has become a valuable tool for tracking individual birds at local spatial scales (Diehl and Larkin 1998), but is generally not useful on broader geographic scales for small-bodied species. Technological advances in satellite telemetry promise remarkable potential for tracking individual migratory birds over broad spatial scales. Unfortunately,

satellite telemetry is often not economically feasible, and currently, is only available for groups of larger birds such as certain raptors and seabirds (Steenhof et al. 2005, Ristow et al. 2000). Furthermore, these tracking technologies may prove inadequate for examining movements and habitat use at local spatial scales.

During the past several years, stable isotope analysis has become an increasingly popular tool for examining the feeding origins and movements of organisms, including connections between life cycle events of migratory birds (Webster et al. 2002). Stable isotope analysis is an efficient and relatively inexpensive way to track Neotropical migrants over continental spatial scales (Rubenstein et al. 2002) and to link physical conditions and reproductive consequences of migrants in one geographic location with previous events that occurred in geographically distant locations (Marra et al. 1998, Norris et al. 2004a, Norris et al. 2004b Bearhop et al. 2005). Organisms reflect isotope ratios of their environment by incorporating isotopic information into their tissues and feathers through their food webs (Marra et al. 1998). Migratory birds then carry this information through various phases of their annual life cycles. The duration to which a particular individual carries isotopic information depends on the elemental turnover rate of the tissue in question. Therefore, careful consideration of which tissue to analyze should be exercised in light of the questions being asked (Hobson 1999, 2005).

Isotopes are atoms of a particular element that have the same atomic number but have a different atomic mass. Stable isotopes are non-radioactive forms of elements, and they naturally occur throughout the earth. For example, carbon and nitrogen both have “heavy” and “light” isotopes (e.g., $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$). Light isotopes are much more common than heavy isotopes. Stable isotope analysis is a highly developed field in

analytical chemistry (Hobson 2005). Mass spectrometers can measure the ratios of light to heavy isotopes in samples (e.g., animal and plant tissues, soils, and water). Sample isotope ratios are compared to ratios found in standard materials (e.g., Pee Dee Belemnite for carbon and atmospheric air for nitrogen) because deviations in the machine readings or the isotopic composition of the samples may occur from day to day (Lajtha and Michener 1994). Stable isotope values are reported in 'delta' (δ) notation [i.e., δ (‰) = $(R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000$].

Stable carbon isotope ratios are of particular importance in ecological research on animals because they can be used to examine ecosystem associations through their feeding origins (Marra et al. 1998). The photosynthetic pathways of plants (i.e., C₃, C₄, Crassulacean acid metabolism) incorporate "heavy" ¹³C at varying degrees. This fractionation of ¹³C is mainly a result of physical and enzymatic differences between the three photosynthetic pathways (Lajtha and Michener 1994). C₄ plants have more enriched ¹³C isotope ratios measuring from -7 to -15‰, and C₃ plants have more depleted ¹³C isotope ratios measuring from -20 to -35‰. Plants using CAM photosynthetic pathways cannot be reliably separated from C₄ plants by using stable-carbon isotope analysis because of significant overlap in ¹³C isotope ratio values (-10 to -22‰) (Ehleringer 1989).

These isotopic distinctions become important when trying to determine relationships between plants and plant-dependent organisms. C₃ plants generally dominate cool mesic habitats, whereas warmer, more xeric habitats contain proportionally more C₄ and CAM plants (Marra et al. 1998). Stable-carbon isotope ratios also differ among C₃ plants because of differences in water use efficiency. C₃ plants

living under relatively xeric conditions experience higher degrees of water use efficiency than C₃ plants living under more mesic conditions (Hobson 2005). As a result, less atmospheric CO₂ is exchanged through leaf surfaces (i.e., epidermal stomata), and most intercellular CO₂ (both heavy and light) is involved in the initial enzymatic reactions of C₃ photosynthesis (Farquhar et al. 1989). This decrease in ¹³C fractionation results in C₃ plant tissues with more enriched (i.e., less negative) δ¹³C values (Lajtha and Michener 1994).

Stable carbon isotopes have been used to determine avian habitat associations (e.g., Marra et al. 1998, Bearhop et al. 2004). Birds incorporate the isotope ratios of plant tissues (e.g., leaves, seeds, fruit) or organisms that consume plant tissues (e.g., phytophagous insects.) For example, tissues of American Redstarts show an isotope signature that reflects the proportion of C₃ and C₄/CAM plants and possibly the degree of water-use efficiency of C₃ plants associated with mesic and more xeric tropical habitats used during winter (Marra et al. 1998). Isotopic information incorporated into feather keratin becomes metabolically inert once tissue growth ceases (Bearhop et al. 2003). These isotopic markers are then carried with the individual until the next feather molt and provide an opportunity to examine geographic migratory connectivity (Chamberlain et al. 2000, Rubenstein et al. 2002) and interactions between life cycle events (Marra et al. 1998, Bearhop et al. 2004).

A few studies utilizing stable-carbon isotopes to investigate seasonal interactions in songbirds have focused on linking habitat use during winter with arrival timing and condition, and reproduction in breeding areas (Marra et al. 1998, Norris et al. 2004a). However, very little research has examined interactions between migration and winter

events in migratory birds. Certainly, seasonal interactions observed in American Redstarts arriving on temperate breeding grounds suggest that outcome of winter events (e.g., late departure, lower energetic condition) should be apparent during migratory stopover. Bearhop et al. (2004) used stable-carbon isotope analysis to assess winter habitat use of transient Black-throated Blue Warblers captured in the Bahamas during northbound migration. They found that warblers with more mesic isotope signatures had higher body condition than those with more xeric isotope signatures. It should be noted that these migrating warblers were captured just north of their Caribbean wintering range and were relatively close to their points of wintering origin. It is not known whether impacts of using low quality winter habitat could be ameliorated through use of stopover habitats *en route*. In addition, essentially all research on seasonal interactions in the new world has been focused on two species (e.g., American Redstart and Black-throated Blue Warbler). Interactions between life cycle events need to be investigated for other species since the importance of such interactions may vary among species. A more thorough understanding of the annual cycles of Neotropical migratory birds and the interactions among life cycle periods is important to conservation efforts for these migrants (Webster et al. 2002).

STUDY SYSTEM

My research took place in a highly fragmented landscape of northwestern Ohio (Lucas and Ottawa counties) along the shore of Lake Erie. This glaciated region is dominated by agricultural, urban, and lakeshore housing developments with scattered

patches of woodland, shrubland, and wetlands. Historically, northwestern Ohio consisted of extensive bottomland swamp forest known as the Great Black Swamp (Cooperrider et al. 2001). Beginning in the early 19th century, European settlers took great strides to drain, clear, and control this landscape in order to make it suitable for farming (Peacefull 1996). Lakefront property is in high demand, and development is extensive and ongoing in the western basin of Lake Erie. Within 2 kilometers of the lakeshore are scattered wetlands, beach-ridge forests, and woodlots that largely occur within a series of state wildlife areas and national wildlife refuges. More inland areas (2-5 km from lakeshore) are characterized by scattered woodlots, shrublands, and wetlands. Conservation areas used in my study, included both Ottawa and Cedar Point National Wildlife Refuges, Maumee Bay State Park, Crane Creek State Park, and various state wildlife areas (Turtle Creek, Magee Marsh, and Little Portage).

My study sites included three different terrestrial habitat types and were part of a larger project investigating landbird stopover ecology. Sites were located in shrubland, beach-ridge forest, and mature deciduous forest. Shrubland habitats were characterized by dense dogwood (*Cornus* spp.) shrub thickets with few shrubs or trees over 5 meters in height. Beach-ridge forests were located on the lakefront and were heterogeneous in structure with a relatively open canopy and moderate amounts of understory vegetation. Common canopy trees in beach-ridge forests included eastern cottonwood (*Populus deltoides*) and ash (*Fraxinus* spp.), and common understory plants included tartarian honeysuckle (*Lonicera tatarica*), dogwood shrubs, European buckthorn (*Rhamnus cathartica*), and saplings of native tree species. Mature deciduous forests had a tall, more closed canopy with generally sparse amounts of understory vegetation. Common canopy

trees in mature deciduous forests included ash spp., oaks (*Quercus* spp.), and hickories (*Carya* spp.). Shrubland and mature deciduous forest sites were located 2-5 km from the Lake Erie shoreline.

Habitats along the southern shore of Lake Erie are ideal for sampling Neotropical migratory songbirds because large numbers and high species diversity occur during spring passage (Shieldcastle et al. 2004). Migrant songbirds are often reluctant to cross large bodies of water (Diehl et al. 2003), and this reluctance coupled with specific weather conditions often results in large concentrations of transient songbirds in the region. Certain locations along the southwestern shore of Lake Erie (e.g., Magee Marsh boardwalk at Crane Creek State Park) are known as some of the best locations for watching birds in North America (Pollick 2002). Over three spring migration periods, we captured and banded approximately 11,000 songbirds with the use of mist nets. The species constituting the bulk of transient songbird captures were Yellow-rumped “Myrtle” Warbler (*Dendroica coronata coronata*), Yellow Warbler (*Dendroica petechia*), White-thoated Sparrow (*Zonotrichia albicollis*), Gray Catbird (*Dumetella carolinensis*), “Western” Palm Warbler (*Dendroica palmarum*), Magnolia Warbler, Common Yellowthroat (*Geothlypis trichas*), and Swainson’s Thrush (*Catharus ustulatus*).

The Magnolia Warblers is a numerous Neotropical migrant songbird during spring passage in northwestern Ohio and was selected as the focal species of my research. On many days following large movements of Neotropical migrant passerines during mid-to late-May, Magnolia Warblers is among the most frequently encountered songbirds in this region of Ohio. This species is appropriate for examining seasonal interactions

between winter and spring migration events because in addition to being numerous during spring it possesses easily identifiable molt patterns (Pyle et al. 1997) that permits accurate collection of feathers containing winter-specific isotopic information. In addition, Magnolia Warblers are territorial in tropical wintering grounds (Hall 1994), and, therefore, stable-carbon isotope signatures should reflect tropical habitat use.

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CHAPTER 2

LINKING MIGRATION AND WINTER EVENTS IN A LONG-DISTANCE MIGRATORY SONGBIRD USING STABLE-CARBON ISOTOPE ANALYSIS

ABSTRACT.—Recent research on Nearctic-Neotropical migratory songbirds has emphasized the importance of events occurring during migration and interactions among breeding, wintering, and migratory phases of the annual life cycle. Stable-isotope analysis has been instrumental in revealing seasonal interactions and migratory connectivity in migratory songbirds, but little research has addressed interactions between events occurring in wintering and migratory stopover areas. From May to early June of 2004 and 2005, I investigated seasonal interactions within the annual cycle of Magnolia Warblers (*Dendroica magnolia*) captured during migratory stopover in northwestern Ohio. A total of 615 Magnolia Warblers were captured in mist nets, banded, measured, weighed, aged and sexed. Feathers grown in pre-alternate molt in wintering areas were collected from 555 individuals and used for stable-carbon isotope analysis. Stable-carbon isotope ratios ($\delta^{13}\text{C}$) of feathers ranged between -25.4‰ and -19.9‰ for both years, and this range corresponds to $\delta^{13}\text{C}$ values reported for other species of wood-warblers that winter in mesic tropical forest (generally considered higher

quality) and more xeric scrub. I tested for relationships between winter-specific habitat use (i.e., $\delta^{13}\text{C}$ values) and capture date, energetic condition, and plumage-status of transient Magnolia Warblers. I predicted that warblers that had wintered in more xeric habitats (enriched $\delta^{13}\text{C}$ values) would migrate later, be in lower energetic condition, and have lower plumage status (i.e., completed less molt in tropical wintering areas). Overall, results suggested that migration timing, energetic condition, and extent of pre-alternate molt completed by Magnolia Warblers were not influenced by wintering in either mesic or more xeric tropical habitats. I believe that Magnolia Warblers that wintered in more xeric locations may not have been negatively impacted or were able to regain mass during migration. There is a need to better understand interactions among phases in the annual cycle of Nearctic-Neotropical migratory songbirds, which will ultimately be useful for developing conservation plans for migratory birds.

INTRODUCTION

Events occurring in temperate breeding areas, tropical wintering areas, and migration may interact to impact populations of migratory songbirds, underscoring the need for research that addresses connections between life cycle events (Webster et al. 2002). Until recently, examining interactions between geographically separate phases in a migrant's annual cycle was extremely difficult, if not impossible. Technological advances in analytical chemistry have improved the ability to examine these interactions.

Stable-isotope analysis, in particular, has become an increasingly popular method for addressing a variety of ecological questions (Hobson 2005). It is a relatively inexpensive tool that can be used to understand seasonal interactions and migratory connectivity within the annual life cycles of migratory songbirds (Hobson 1999).

Isotopes are atoms of a particular element that have the same atomic number but different atomic mass; e.g., carbon has one heavy isotope (^{13}C) and one light isotope (^{12}C). Environmental ratios of these heavy and light stable-carbon isotopes vary among plant communities across spatial scales. C_3 plants in more xeric environments may have more enriched $\delta^{13}\text{C}$ than C_3 plants in more mesic habitats because of differences in water-use efficiency associated with different environments (Hobson 2005). In addition, C_3 plants incorporate these two isotopes into their tissues differently than C_4 and CAM plants (Lajtha and Michener 1994). As a result, mesic forests, which are dominated by C_3 plants, have more depleted $^{13}\text{C}:^{12}\text{C}$ ratios (expressed as $\delta^{13}\text{C}$) than more xeric habitats, which have proportionally more C_4 and CAM plants (Marra et al. 1998).

Organisms reflect environmental isotope ratios acquired from the particular food webs that they occupy (Hobson 1999). In molting birds, stable isotope ratios in the environment are fixed in feather keratin (a metabolically inactive tissue) during feather growth. Birds carry these habitat-signatures in their feathers until their next molt (Bearhop et al. 2003). Thus, sampling appropriate feather groups (or other appropriate tissues) of migratory birds can allow researchers to determine habitat use during a previous season and examine how this may impact ecology and behavior in other seasons.

Stable isotope analysis has recently been used to elucidate previously unknown seasonal interactions in a few species of long-distance migratory songbirds. For example, in Jamaica wintering male American Redstarts (*Setophaga ruticilla*) occupy high quality mangrove forest, and females and young males occupy lower quality scrub habitat (Marra et al. 1993). Throughout the winter, individuals in higher quality habitats maintain body condition whereas the body condition of individuals in lower quality scrub decreases as winter progresses (Marra et al. 1998). In addition, upon arrival in breeding areas in New Hampshire redstarts that possessed stable-carbon isotope signatures corresponding to lower quality xeric habitats arrived later and had lowered energetic condition (Marra et al. 1998). Subsequent research in southern Ontario, Canada that used stable-carbon isotope analysis revealed that individuals that wintered in poor quality habitats also experienced reduced reproductive success (Norris et al. 2004a).

Very little research has examined interactions between winter and migration events in migratory birds. Bearhop et al. (2004) used stable-carbon isotope analysis to assess winter habitat use of transient Black-throated Blue Warblers (*Dendroica caerulescens*) captured in the Bahamas during northbound migration. They found that warblers with more mesic isotope signatures had higher body condition than those with more xeric isotope signatures.

I used stable-carbon isotope analysis to assess winter habitat use of transient Magnolia Warblers (*Dendroica magnolia*) that were present in northwestern Ohio during spring migratory stopover in 2004 and 2005. I examined the relationship between winter habitat use (i.e., isotope value) and energetic condition, migratory timing, and plumage-

status of Magnolia Warblers. I predicted that warblers that had wintered in more xeric habitats (enriched $\delta^{13}\text{C}$ ratios) would migrate later, be in lower energetic condition, and have lower plumage status (i.e., completed less molt in wintering areas). Plumage-status was assessed because growth of plumage is affected by environmental factors such as food availability (Veiga and Puerta 1996) and habitat quality (Stratford and Stouffer 2001, Yosef and Grubb 1992), and therefore, may provide additional information on events occurring during winter. The appearance of the plumage is potentially important for migrants during breeding activities, such as mate selection (e.g., Norris et al. 2004b). Such information should be valuable for assessing the relative importance of winter and migratory events within the annual cycles of migrants. A better understanding of migratory connectivity in populations of Neotropical migratory songbirds will be useful for developing comprehensive conservation planning for migratory species.

METHODS

The Magnolia Warbler was selected as a focal species to investigate relationships between events occurring in tropical wintering areas and migration in northwestern Ohio. The species is an abundant spring transient in northwestern Ohio that breeds in second-growth and mature stands of spruce, hemlock, and other coniferous trees from the Yukon, east through boreal Canada into northeastern portions of the U. S. and south through the northern Appalachians (Dunn and Garrett 1997). Magnolia Warblers primarily winter in a relatively narrow latitudinal range from southeastern Mexico south through Central America to central Panama and east into the West Indies (Hall 1994). Magnolia

Warblers are territorial on the wintering grounds where they use a range of habitats from mesic forests (e.g., gallery woodland, agricultural woodland, evergreen tropical forest, and medium height subdeciduous and subperennial forest; Hall 1994, Rappole and Warner 1980, Ornat and Greenberg 1990) to more xeric habitats such as coastal dune scrub and second growth scrub (Ornat and Greenberg 1990). In the Yucatan Peninsula, Magnolia Warblers exhibit sexual habitat segregation that may be dominance-mediated, with males occupying mesic subperennial forest (60% of sightings) and females occupying more xeric early successional scrub (64% of sightings) (Ornat and Greenberg 1990). In Mexico, the species forages predominately by gleaning slow moving insects from vegetation surfaces (Rappole and Warner 1980). Importantly, Magnolia Warblers also undergo a partial pre-alternate molt in wintering areas from February to early March (Hall 1994) which includes most, if not all, body feathers and some greater secondary coverts (Pyle et al. 1997). As a result, sampling freshly molted feathers will reveal $\delta^{13}\text{C}$ signatures that reflect the tropical habitat used by an individual during its molt.

From May to early June of 2004 and 2005, research on transient Magnolia Warblers was conducted along the southwestern shore of Lake Erie in northwestern Ohio where large numbers of migrating songbirds concentrate annually (Diehl et al. 2003). Study sites were located in Lucas and Ottawa counties and within Ottawa National Wildlife Refuge, Cedar Point National Wildlife Refuge, Maumee Bay State Park, Turtle Creek Wildlife Area, and Little Portage Wildlife Area. Study sites were grouped into three focal habitat types including dogwood (*Cornus* spp.) shrubland, mature deciduous forest, and mature beach ridge forest. Dogwood shrublands were dense, 3-5 m tall, and had a few scattered taller trees. Mature deciduous forests had a tall, mostly closed

canopy with generally sparse amounts of understory vegetation. Beach-ridge forests were heterogeneous in structure with a relatively open canopy and moderate amounts of understory vegetation.

Approximately half of all Magnolia Warblers were captured at 12 sites (4 sites for each of 3 habitats). Most sites were visited 4 times per year with each visit consisting of a two-day sampling period. Additional Magnolia Warblers were captured at a mist netting operation run by Black Swamp Bird Observatory within the Navarre Unit of Ottawa National Wildlife Refuge. The Navarre site was sampled regularly during the study and consisted of beach ridge forest.

Magnolia Warblers and other landbirds were passively captured with the use of 2.6 m x 12 m mist nets (30 mm mesh). Between 7 and 12 mist nets were randomly located within a one-hectare area at each of the 12 sites and 21 nets were located at Navarre. Nets were opened one half hour before sunrise and operated for 7 hours each day. Birds were removed from nets every 20-30 minutes and held briefly in cloth bags before processing. I recorded time of capture and each warbler received a U.S.G.S. aluminum leg band. Age and sex of individuals were determined and classified as either second-year female (SY female), after second-year female (ASY female), second-year male (SY male), or after second-year male (ASY male). Age was determined by examining wear and molt limits within wing coverts (Mulvihill 1993, Pyle et al. 1997) and rectrix shape (Morris and Bradley 2000). Individuals were sexed by examining specific plumage characteristics, such as crown color, thickness of flank streaking, amount of white in the second pair of rectrices, and amount of black in lores, auricular, and back (Pyle et al. 1997). Extent of wing molt was recorded by counting the number of

median coverts, greater coverts, and tertials replaced in the pre-alternate molt. I measured unflattened wing chord using a wing ruler and tarsus length was measured with calipers. Body mass was measured to the nearest 0.1 g with an electronic balance. Subcutaneous body fat was visually estimated using the 6-point ordinal scale of Helms and Drury (1960).

Digital Photography and Photo Analysis

To provide a permanent visual record of captured Magnolia Warblers, at least four digital photographs were taken of each individual using a Canon Powershot A95 camera. Macro photographs of the opened right wing and spread tail were taken to aid in age assessment. Additional photographs of the side and dorsal view of each bird were taken to depict overall plumage characteristics, such as coloration of the mantle, crown, auriculars, and lores, and the amount of flank streaking. A standardized macro photograph of the center of each warbler's breast was also taken using an apparatus consisting of two pieces of 2.5 cm x 10 cm pine board joined together in an "L"-shape. A metric ruler was vertically mounted to the upright board of the photo apparatus. Each photograph was taken with the camera attached to a table-top tripod placed at a set distance along the base board.

Warblers were held in a standardized upright position with the wing tips and upper tail held between the index and middle finger, while the tibiotarsi were held between the thumb and index finger. Birds held in this manner were not able to contort their bodies, which could distort the total area of breast streaking. The bird was

positioned with the side of its body held flush against the edge of the photo board and the underparts facing the camera. Photos were taken at a focal length of 16 mm. To minimize shadow on the breast, the camera's flash was fired in each photograph, regardless of lighting conditions. Each digital photo file was labeled with the band number of the individual bird.

Digital photos were used to quantify the total area of dark streaking on the breast and were analyzed using *Image J* software (developed by the National Institute of Health, <http://rbs.info.hih.gov/ij/>). Photographs were rotated so that the edge of the ruler in each photograph was oriented at 90° to facilitate consistent cropping and rescaling. One photograph was randomly chosen to act as a standard. Each subsequent photograph was then cropped and rescaled so that an 8 cm ruler segment (the length that included all streaking) matched an 8 cm ruler segment in the standard photograph. Each photograph was converted to an 8-bit gray scale to quantify the number of dark pixels corresponding to dark streaking. The threshold function in *ImageJ* was used to convert each pixel to either black or white using a threshold value of 55. This value eliminated minor shading on the breast that was not eliminated by the camera flash. A freehand cutting tool was used to isolate the streaked area. The area of streaking was calculated using the particle analysis function, which calculated area as the total number of black pixels in each photograph.

Feather Collection and Stable Isotope Analysis

Three freshly molted greater secondary-coverts were collected from each wing of an individual bird ($n=6$ feathers) and placed in a labeled envelope. Pre-alternate molt of

greater secondary-coverts is incomplete and begins with the innermost feather and progresses outward (Pyle et al. 1997). Molt limits define the boundary between coverts of alternate and basic plumages (Pyle et al. 1997), and I consistently collected the freshly replaced greater secondary coverts that lied next to the molt limit (Figure 2.1). Isotope signatures from these late developing alternate coverts should best represent habitat occupied immediately prior to migratory departure from individual winter territories. In the rare event that there were no freshly molted greater coverts, several freshly molted flank or breast feathers with dark centers were collected.

Stable-carbon isotope analysis was conducted on feather samples at the Stable Isotope Facility at the University of California-Davis. We prepared feather samples for stable-carbon isotope analysis according to the protocol of Hobson et al. (2003). To clean surface oils and contaminants, feathers were soaked in a solution of 1 part chloroform and 1 part methanol for approximately 5 hrs. After soaking, feathers were rinsed with methanol using a disposable pipette and placed in labeled glass containers to dry overnight under a fume hood. Using a microbalance, dried feathers (1.2 ± 0.1 mg) were weighed and sealed in a tared tin capsule. Samples were combusted in an elemental analyzer that was coupled to a Europa Hydra 20/20 continuous flow isotope ratio mass spectrometer. Stable-carbon isotope values of samples were compared to a PeeDee Belemnite standard and were reported in a relative δ notation ($\delta^{13}\text{C}_{\text{standard}} = [\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1] \cdot 1000$).

Blood Sampling and DNA Sex-determination

In 2005, blood samples were collected for molecular sex determination. Blood was obtained from each warbler through brachial vein puncture with a 27-gauge needle. Blood was drawn into non-heparinized capillary tubes, and one drop (approximately 20 μ L) was placed into Queen's lysis buffer solution. Styptic powder was applied to the brachial puncture to promote clotting. Samples were stored in 1.5 mL cryoviles and placed in a freezer for storage.

Molecular sex determination was performed in a laboratory at Ohio State University. DNA was extracted from blood samples by using *Qiagen* animal tissue extraction kits. Polymerase chain reaction (PCR) for each sample followed the protocol of Griffiths et al. (1998). The primers P2 (5'-TCTGCATCGCTAAAT-CCTTT-3') and P8 (5'-CTCCCAAGGATGAGRAAYTG-3') were included in 10 μ L PCR amplification volumes for each sample. Electrophoresis was used to run PCR products for approximately one hour on a 2.5% agarose gel in order to facilitate separation of the two product bands. Gels were stained with ethidium bromide and photographed under UV light to visualize product bands. Samples were assigned to sex class based on the presence of either one band (male) or two bands (female).

Data Analysis

An index of plumage-status was created using the calculated number of black pixels corresponding to the area of breast streaking and the count of freshly molted greater secondary coverts, median coverts, and tertials on the right wing (i.e., wing count). Feather counts for the right wing were used because not all individuals had

counts for both wings. The values for wing count and black pixels of each individual were ranked from lowest to highest. The sum of the two rank-scores was divided by the product of the term (total number of individuals multiplied by 2). The resulting value was considered an index of plumage status for each individual.

Data were analyzed separately by year because in 2005 birds were assigned to age and sex class using molecular sex-determination and digital photo records, which likely resulted in more accurate age class assignments. Two-sample *T*-tests were used to test for differences between capture dates of males and females and to test for differences between age classes within each sex class. One-way analysis-of-variance (ANOVA) was used to test for a difference in $\delta^{13}\text{C}$ ratios among age and sex classes. To account for individual differences in structural size, a principle component analysis (PCA) of variables describing skeletal structure (i.e., tarsus length and wing chord) was used to calculate structural size. The first principle component scores (PC1) of the PCA were regressed with body mass (Marra and Holmes 2001), and the residuals from this regression were used as an index of size-adjusted body mass. General linear models were created using Proc GLM in SAS (SAS Institute 2003) to examine the relationship between $\delta^{13}\text{C}$ ratios (independent variable) and size-adjusted body mass, capture date, and the index of plumage-status (dependent variables). Age (second-year and after second-year) and sex (male and female) were included as factors in each analysis.

RESULTS

During spring 2004 and 2005, I captured and processed 615 Magnolia Warblers (362 in 2004 and 253 in 2005; Table 2.1). The large majority of sampled individuals were captured in beach ridge forest sites (89.9%), with much smaller samples from dogwood shrubland (7.8%) and mature deciduous forest (2.3%). Magnolia Warblers were captured between 3 May and 4 June, with 98.5% of individuals captured during May and few individuals captured in early June. In both years, males preceded females in capture date (2004: $T_{242} = 4.78$, $P < 0.001$; 2005: $T_{249} = 8.64$, $P < 0.001$; Figure 2.2a & b, Figure 2.3a & b). Similarly, in both years older (ASY) males preceded young (SY) males (2004: $T_{80} = -4.61$, $P < 0.001$; 2005: $T_{114} = -3.46$, $P = 0.001$) and ASY females preceded SY females (2004: $T_{61} = -2.17$, $P = 0.034$; 2005: $T_{121} = -2.63$, $P = 0.01$). In 2004 and 2005, median capture date for males were 17 and 19 May (respectively), and 20 and 26 May (respectively) for females. Median capture date for ASY males was 13 May (2004 and 2005) and for SY males was 18 and 17 May (2004 and 2005, respectively). ASY females had median capture dates of 18 May (2004) and 21 May (2005), whereas median capture dates for SY females were 21 May (2004) and 23 May (2005).

In 2004, male Magnolia Warblers accounted for 72% of individuals that were aged and sexed (Table 2.1). Young (SY) birds accounted for 64.9% of captured birds with 57.6% of all captures being SY males. In 2005, molecular sex-determination was successful for 91.5% of birds with blood samples ($n = 200$), and these individuals were 50.8% female and 49.2% male. Second-year birds of both sexes were more abundant in our 2005 sample than older (ASY) birds (Table 2.1)

Stable-carbon isotope analysis was performed on feathers obtained from 555 individual birds (309 in 2004 and 246 in 2005; Table 2.1). When a small number of outliers ($n = 7$) was ignored, stable-carbon isotope ratios of feathers ranged between -25.4‰ and -20.5‰ in 2004 (Figure 2.4) and between -25.0‰ and -19.9‰ in 2005 (Figure 2.5). ANOVA indicated a difference in stable-carbon isotope ratios among age and sex classes in 2004 ($F_{3,305} = 2.94$, $P = 0.033$; Table 2.2). Further inspection of $\delta^{13}\text{C}$ revealed that older males had the most enriched ratios while young females had the most depleted ratios. In 2005, there was no difference ($F_{3,242} = 0.59$, $P = 0.622$; Table 2.2) among age and sex classes for stable-carbon isotope ratios.

I found no significant relationships ($\alpha = 0.05$) between $\delta^{13}\text{C}$ ratios and body condition (i.e., size-adjusted body mass) of transient Magnolia in either 2004 ($F_{1,304} = 0.49$, $P = 0.483$; Table 2.3, Figure 2.6) or 2005 ($F_{1,231} = 0.56$; $P = 0.453$; Table 2.3, Figure 2.7). In 2004, sex was significantly associated with body condition ($F_{1,304} = 17.06$, $P < 0.001$), with males having higher condition scores than females (Figure 2.6). In 2005, there was a trend towards older birds showing higher condition scores than young birds, but results were not significant ($F_{1,231} = 3.12$, $P = 0.079$; Figure 2.7).

I found no significant relationship between $\delta^{13}\text{C}$ and capture date of Magnolia Warblers in either 2004 ($F_{1,305} = 1.06$, $P = 0.304$; Table 2.3) or 2005 ($F_{1,242} = 0.68$, $P = 0.409$; Table 2.3). Age class (2004: $F_{1,305} = 18.56$, $P < 0.001$; 2005: $F_{1,242} = 15.30$, $P = 0.001$) and sex class (2004: $F_{1,305} = 22.83$, $P < 0.001$; 2005: $F_{1,242} = 81.33$, $P < 0.001$) were each associated with capture date with males and ASY birds being captured at earlier dates than ASY females or SY birds (Figures 2.2a & b; 2.3a & b).

The amount of black ventral streaking and number of replaced wing coverts showed substantial variation within an age and sex class. I found no significant relationship between $\delta^{13}\text{C}$ and plumage status ($F_{1,220} = 0.20$, $P = 0.656$; Table 2.3) in 2005, although sex ($F_{1,220} = 239.80$, $P < 0.001$) and age ($F_{1,220} = 7.03$, $P = 0.009$) were strongly associated with plumage status. Males showed higher plumage-status than females, and older birds showed higher plumage-status than young birds (Figure 2.8).

DISCUSSION

This study found no significant relationships between the winter-specific isotope signature of feathers grown during the winter pre-alternate molt and either size-adjusted body mass, capture date, or plumage status. These findings suggest that Magnolia Warblers that wintered in habitats that varied in moisture content (which has been linked to habitat quality for wintering migrants; Marra et al. 1998, Bearhop et al. 2004) did not differ in energetic condition or migration timing in a stopover area that is relatively close to northern breeding areas. Similarly, winter habitat use did not seem to influence the extent of pre-alternate wing and body molt completed in wintering areas, and therefore the physical appearance of individuals upon arrival in breeding areas.

The range of stable-carbon isotope ratios (-25.4‰ to -19.9‰) represented in feathers of transient Magnolia Warblers in northwestern Ohio suggested that individuals wintered in both mesic and more xeric habitats. This range of $\delta^{13}\text{C}$ values encompassed ranges reported for transient Black-throated Blue Warblers in the Bahamas (-25.5‰ to -22.2‰; Bearhop et al. 2004), and American Redstarts arriving in temperate breeding

areas (-24.7‰ to -22.6‰; Marra et al. 1998). These ranges of stable isotope values correspond to values measured from songbirds sampled directly from mesic forests and more xeric scrub. Marra et al. (1998) reported ranges of $\delta^{13}\text{C}$ ratios in American Redstarts wintering in mesic lowland (approximately -24.6‰ to -23.9‰) and mangrove forests (approximately -22.9‰ to -22.6‰) and more xeric scrub (approximately -22.6‰ to -21.2‰).

In contrast to these results, Marra et al. (1998) found that American Redstarts wintering in xeric Jamaican scrub had lower energetic condition and departed at later dates in spring than birds that wintered in nearby mesic lowland and mangrove forests. In addition, relationships between habitat and body condition were (on average) maintained through the migratory period because redstarts arriving at later dates on breeding territories in New Hampshire had low body condition and significantly enriched tissue values for $\delta^{13}\text{C}$ (Marra et al. 1998). Similarly, transient Black-throated Blue Warblers captured in the Bahamas during northbound migration with more depleted $\delta^{13}\text{C}$ (i.e., more mesic) signatures had higher body condition than individuals showing more enriched $\delta^{13}\text{C}$ (i.e., more xeric) signatures (Bearhop et al. 2004)

There are a few possible explanations for these results including, 1) Magnolia Warblers that wintered in more xeric locations may not have been negatively impacted, 2) Magnolia Warblers experiencing reduced physical condition from wintering in more xeric habitat were able to regain mass during the migratory period, and 3) Magnolia Warblers wintering in more xeric habitat are more likely to die during northbound migration.

The best evidence to support the notion that Magnolia Warblers may be less negatively affected by their winter habitat association was that plumage-status was not significantly related to winter-specific isotope signature. Feather molt is an energetically demanding process (Leu and Thompson 2002), and growth of feathers is believed to be influenced by environmental factors, such as habitat quality and fragmentation (Yosef and Grubb 1992, Stratford and Stouffer 2001). For example, lab experiments have demonstrated that captive juvenile House Sparrows (*Passer domesticus*) provided with food *ad libitum* grew larger throat patches than those of free ranging juveniles, yet this relationship did not exist between captive and free-ranging adults (Veiga and Puerta 1996). However, throat patch size of free-ranging adult House Sparrows was correlated with physical condition regardless of age (Veiga 1993). Therefore, plumage-status of transient individuals may be a better indicator of winter habitat quality than either energetic condition or capture date, as the latter are likely more influenced by *en route* conditions such as weather and food availability. Magnolia Warblers possess black ventral streaking in alternate plumage and, males especially, have large white wing patches composed of median and greater secondary covert feathers that are broadly edged white. Although individuals within a given age and sex class showed substantial variation in the extent of these feathers replaced during the pre-alternate molt, (Figure 2.9 & 2.10) isotope value was still unrelated to plumage-status. Instead, other factors may influence the extent of molt and feather replacement. Understanding these factors is important because migrants that reach the breeding grounds in lower plumage condition may experience reduced sexual signal quality and pairing success (Norris et al. 2004b).

Although Magnolia Warblers may be negatively affected by wintering in more xeric habitats, they also may be able to improve their energetic condition during migratory stopover events. Black-throated Blue Warblers captured in the Bahamas during spring migration with more xeric $\delta^{13}\text{C}$ signatures had lower energetic condition (Bearhop et al. 2004), but these individuals were just north of their Caribbean wintering range, primarily islands of the Greater Antilles. Since these birds had probably not been engaged in extended periods of migratory flight, their energetic condition at time of capture may be more representative of their condition at their respective points of northbound departure. Nearctic-Neotropical migrant passerines cannot reach northern breeding grounds *via* one continuous migratory “leap”. Instead, migrants must rely on successive stopover periods where they can rest and refuel in between much shorter migratory flights (Moore et al. 1995). Energetic condition of individuals during migratory stopover may not be reflective of condition levels normally associated with wintering in lower quality xeric habitats.

If wintering in more xeric habitats negatively impacts Magnolia Warblers, some, perhaps many individuals may not reach their breeding grounds. Some evidence suggests that mortality is high during migration. For example, 85% of annual adult Black-throated Blue Warbler mortality is believed to occur during migration (Sillet et al. 2002) and this might explain the lack of a pattern between $\delta^{13}\text{C}$ and factors such as energetic condition. Nonetheless, I would still expect to find stopover migrants arriving in a variety of energetic conditions, as noted in northern breeding areas (e.g., Marra et al. 1998, Norris et al. 2004a). In fact, it is likely that individuals with lowered body condition simply depart tropical wintering grounds and arrive on temperate breeding grounds later than

individuals with higher body condition (Marra et al. 1998). If more xeric habitats are indeed of low quality for Magnolia Warblers, we still should expect to see a relationship between winter habitat quality and body condition, migration timing, and plumage-status despite the fact that many individuals may perish *en route*.

Little published information exists on the wintering ecology of Magnolia Warblers (Hall 1994). Additional information is needed to understand how winter habitat associations impact survival, energetic condition, migratory departure schedules, and feather molt. Establishing the quality of various tropical habitats used by Nearctic-Neotropical migrants is important for the effective conservation of these species. In addition, a better understanding of the interactions among phases in the annual cycle of Nearctic-Neotropical migratory songbirds will be useful for developing comprehensive conservation planning that spans geographic and political boundaries.

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Age and Sex Class	2004		2005	
	Capture Total	Isotope Analysis Total	Capture Total ^a	Isotope Analysis Total
After second-year Male	50	43	49	49
Second-year Male	193	178	72	69
After second-year Female	34	33	56	54
Second-year Female	58	55	76	74
Second-year Unknown	4	0	0	0
After hatch-year Male	10	0	0	0
After hatch-year Female	10	0	0	0
After hatch-year Unknown	3	0	0	0
TOTAL	362	309	253	246

^aIn 2005, birds were sexed using molecular techniques and aged using a combination of field examination and digital photographic records.

Table 2.1. Total numbers of captured Magnolia Warblers (*Dendroica magnolia*) in northwestern Ohio (2004-2005) and numbers subsequently used in stable-carbon isotope analysis of feather material.

Age and Sex Class	2004			2005		
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>
After second-year Male	-22.669	0.154	43	-22.444	0.162	49
Second-year Male	-23.055	0.086	178	-22.650	0.164	69
After second-year Female	-23.088	0.185	33	-22.588	0.153	54
Second-year Female	-23.324	0.130	55	-22.414	0.129	74

Table 2.2 Mean $\delta^{13}\text{C}$ values (SE) of alternate plumage wing covert feathers from Magnolia Warblers captured in northwestern Ohio during spring 2004 and 2005.

Dependent Variable	2004			2005		
	<i>F</i>	df	<i>P</i> -value	<i>F</i>	df	<i>P</i> -value
Body Condition	0.49	1,304	0.483	0.56	1,231	0.453
Capture Date	1.06	1,305	0.304	0.68	1,242	0.409
Plumage-status Index	—	—	—	0.20	1,220	0.656

Table 2.3. Results of general linear models testing for relationships between $\delta^{13}\text{C}$ ratios and 3 dependent variables ($\alpha < 0.05$).

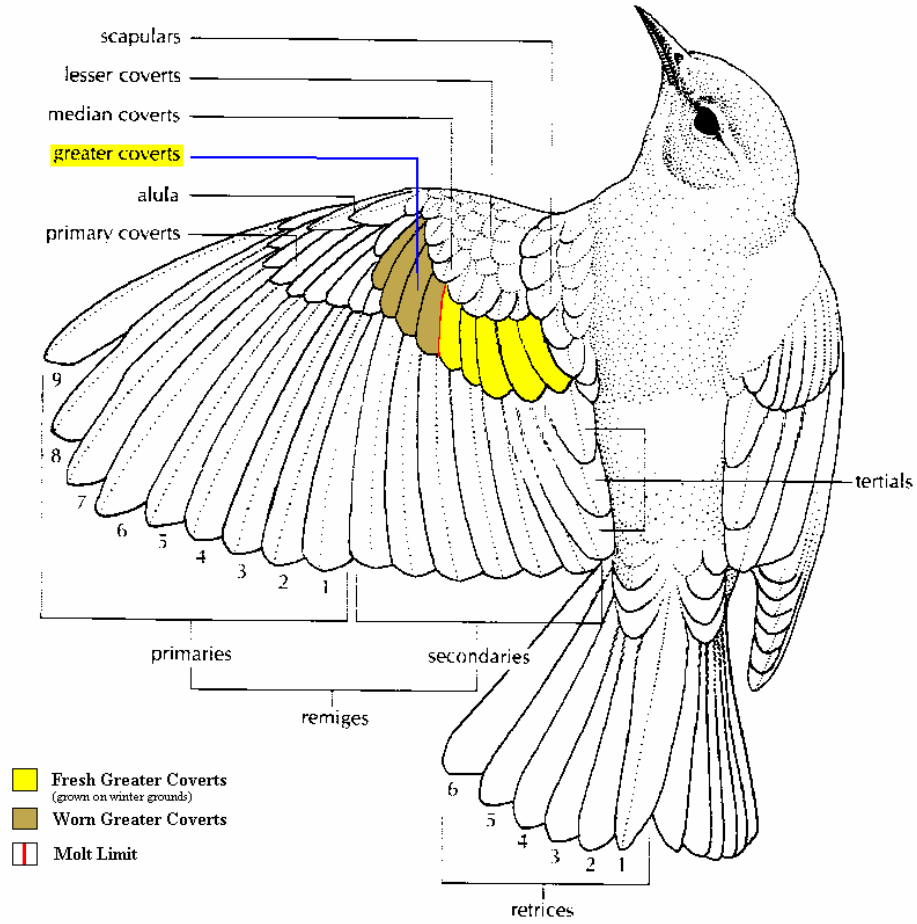


Figure 2.1. Diagram showing a hypothetical molt limit between basic plumage and alternate plumage greater secondary coverts in Magnolia Warblers. Feathers used in stable-carbon isotope analysis were alternate greater secondary coverts adjacent to the molt limit.

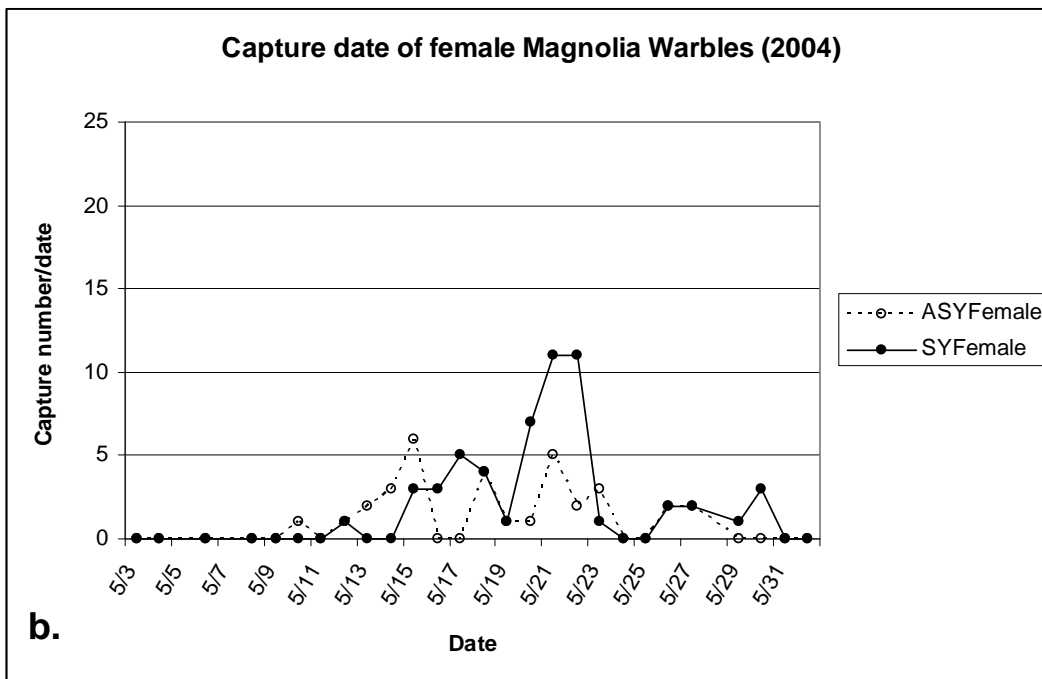
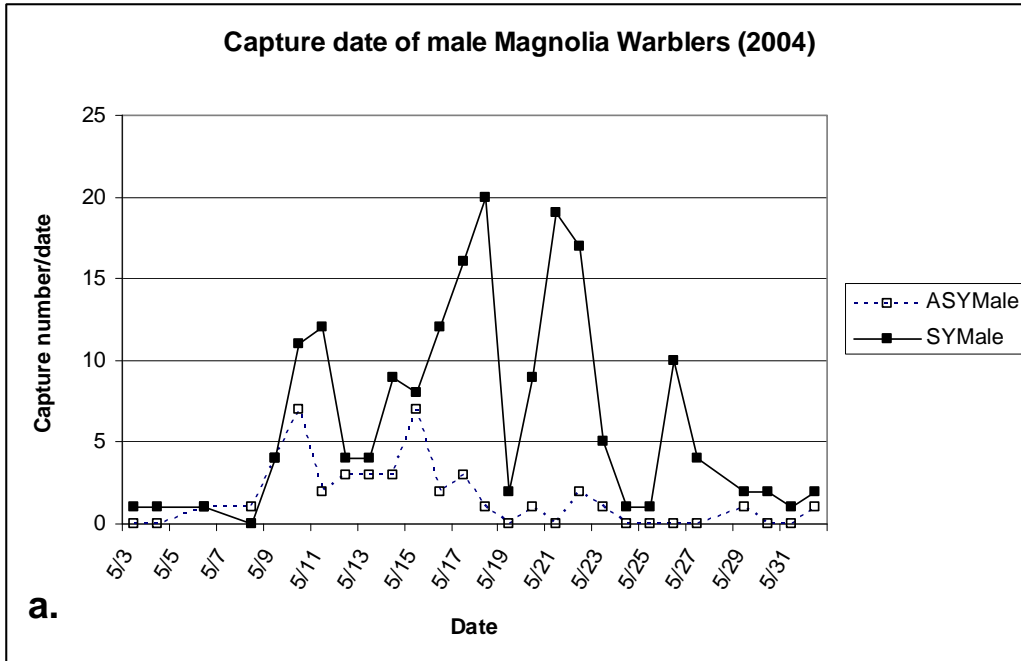


Figure 2.2. Number of male (a) and female (b) Magnolia Warbler captures in each sex class by date in northwestern Ohio, spring 2004.

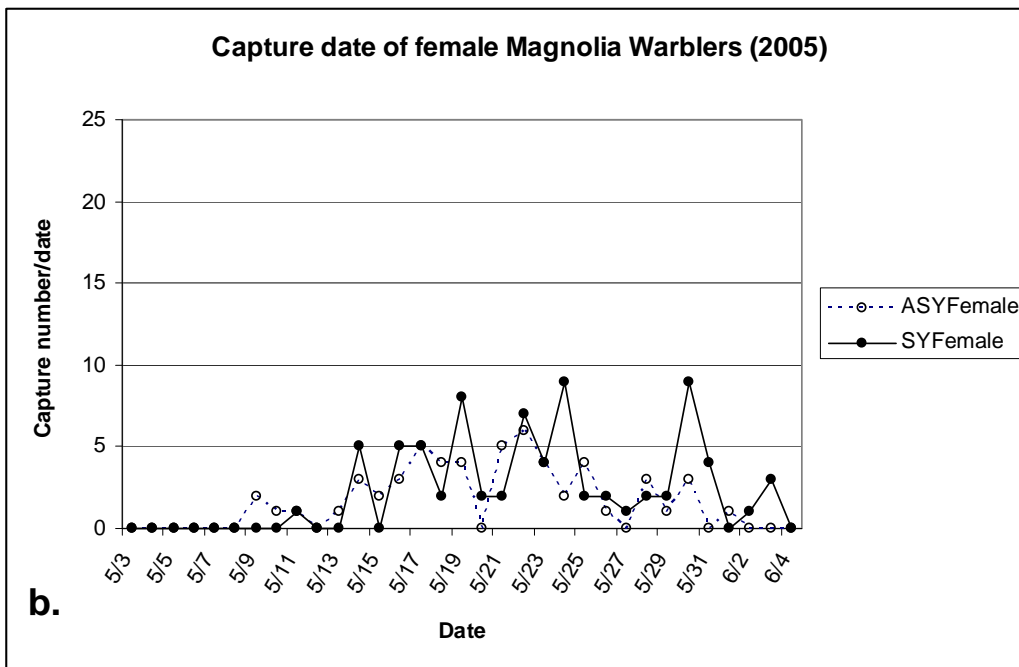
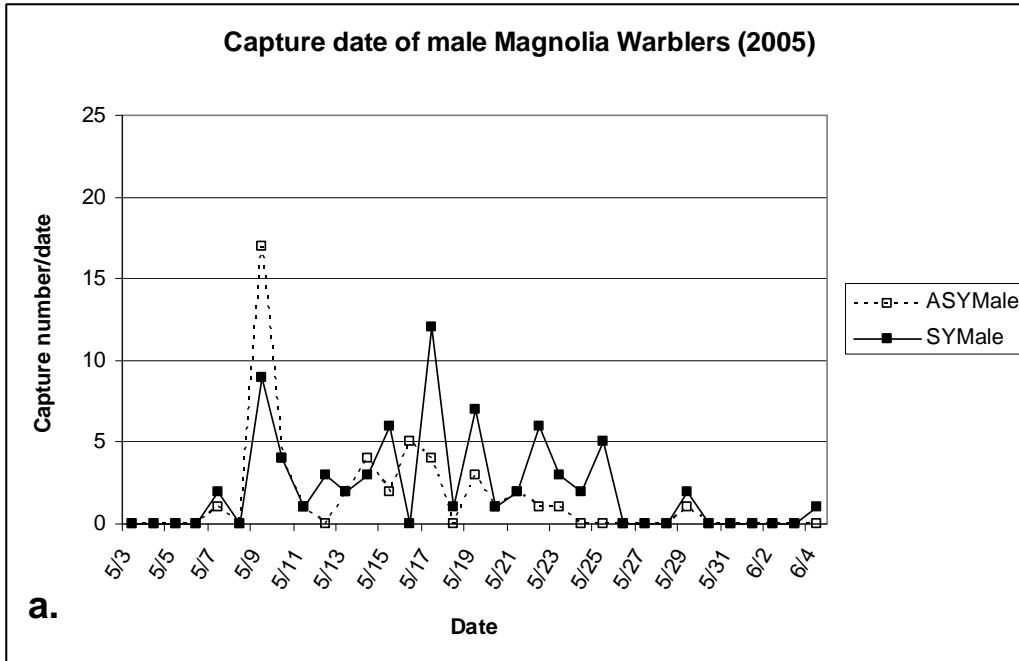


Figure 2.3. Number of male (a) and female (b) Magnolia Warbler captures in each sex class by date in northwestern Ohio, spring 2005.



Figure 2.4. Boxplots showing the range of $\delta^{13}\text{C}$ values from alternate plumage wing coverts for each age and sex class of Magnolia Warblers. Birds were captured in northwestern Ohio during spring of 2004.



Figure 2.5. Boxplots showing the range of $\delta^{13}\text{C}$ values from alternate plumage wing coverts for each age and sex class of Magnolia Warblers. Birds were captured in northwestern Ohio during spring of 2005.

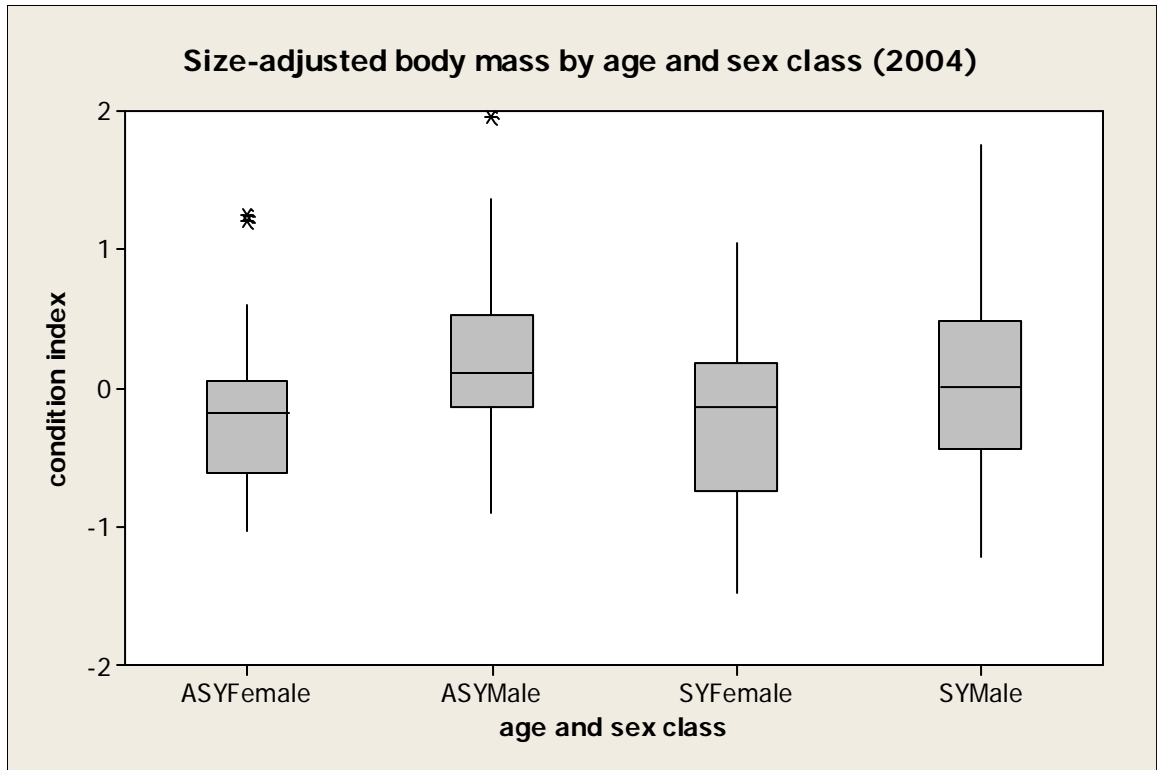


Figure 2.6. Boxplots showing the range of size-adjusted body mass index values for each age and sex class of Magnolia Warblers captured in northwestern Ohio during spring 2004.

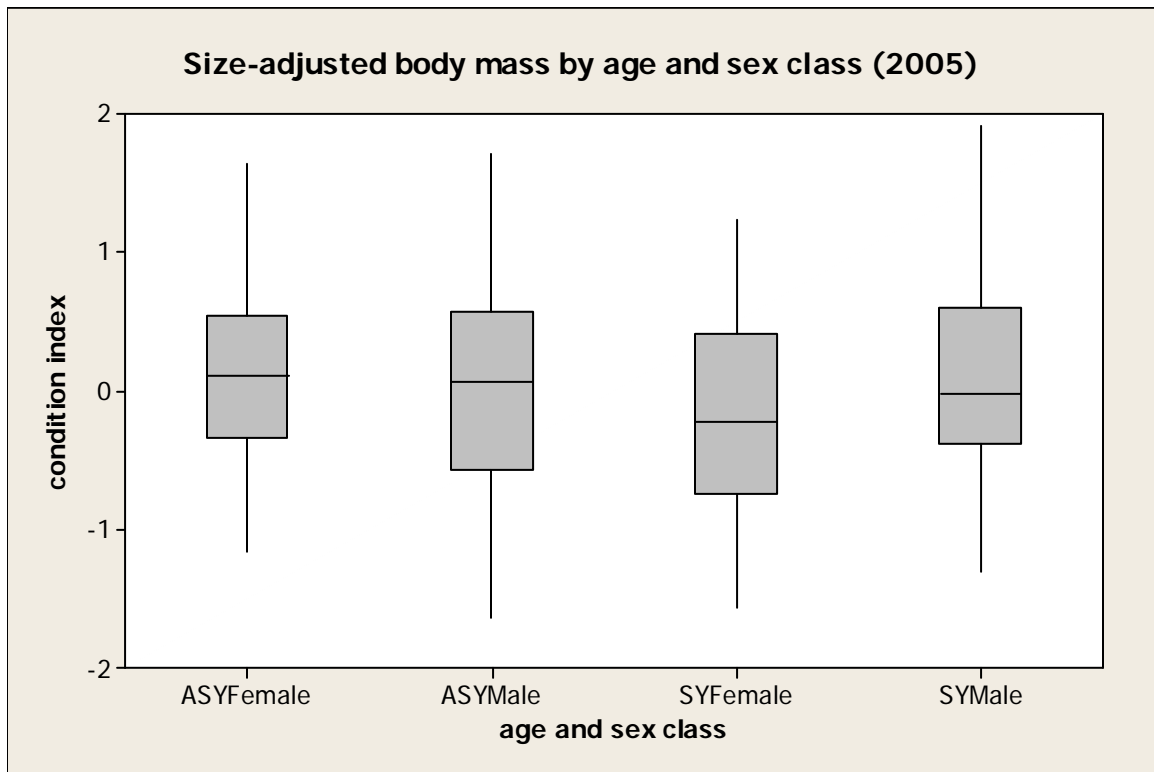


Figure 2.7. Boxplots showing the range of size-adjusted body mass index values for each age and sex class of Magnolia Warblers captured in northwestern Ohio during spring 2005.

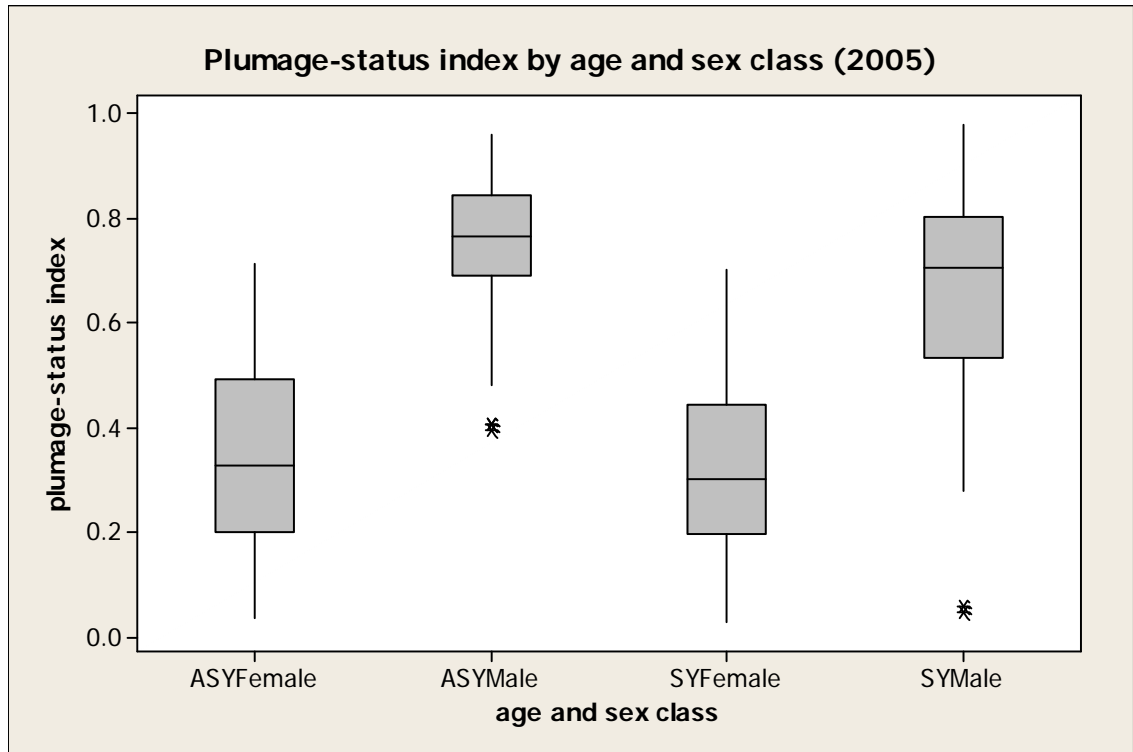


Figure 2.8. Boxplot showing the range of plumage-status index values for each age and sex class of Magnolia Warblers captured during spring 2005.



Figure 2.9. Variation in the number of replaced tertials and inner greater secondary wing coverts for two after second-year male Magnolia Warblers captured in northwestern Ohio during spring 2005.

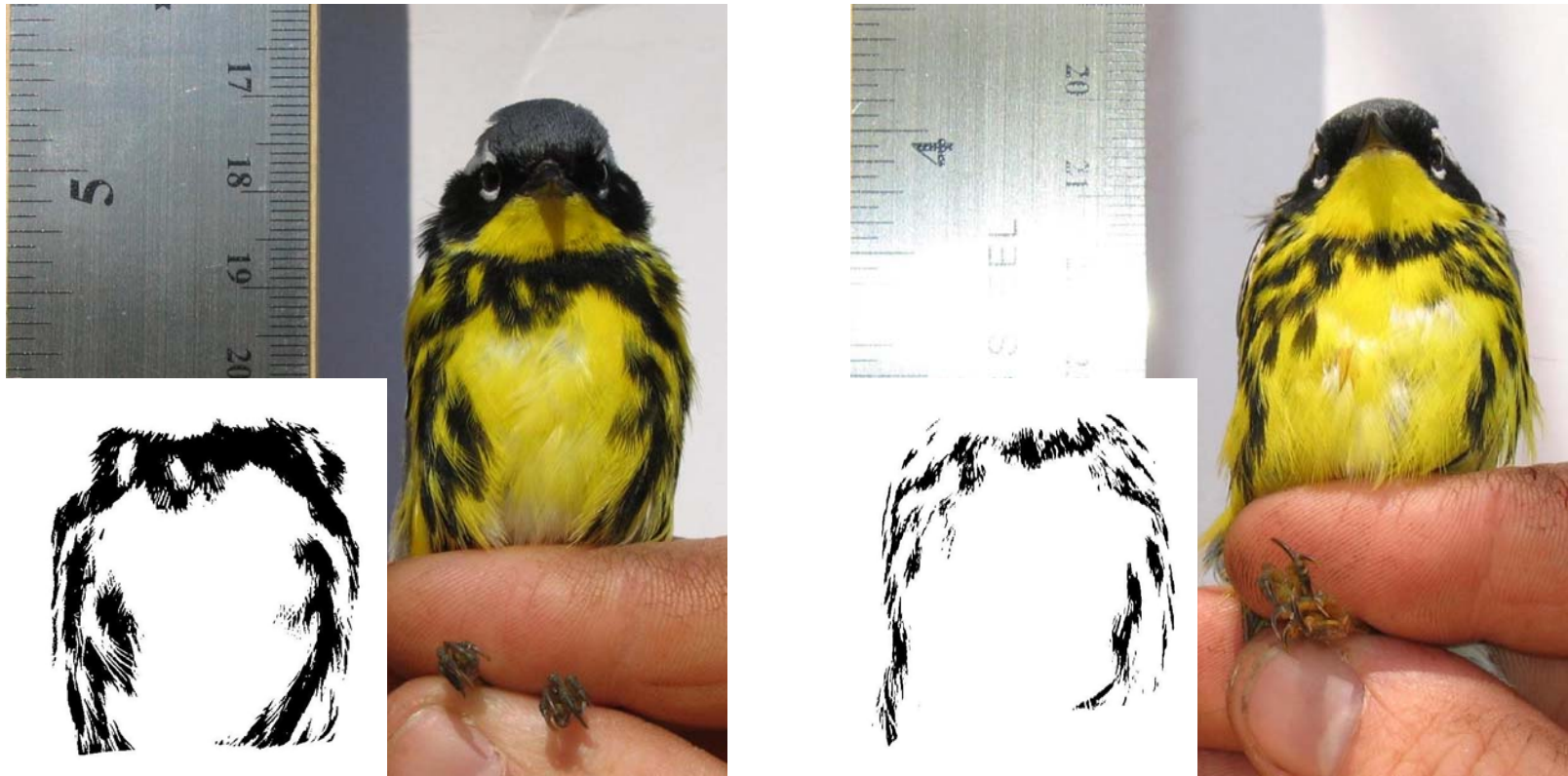


Figure 2.10. Variation in the amount of dark streaking on the underparts of two after second-year male Magnolia Warblers captured in northwestern Ohio during spring 2005.

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