

# An Examination of Spring Migration Timing in Songbirds

**Anne Haas\***

Department of Biology  
Lake Forest College  
Lake Forest, Illinois 60045

## Summary

It is well established that male songbirds arrive at the breeding grounds before females in spring, presumably to gain an intrasexual advantage by claiming better quality territories, and therefore mates. However, the mechanism by which males precede females is not fully understood. Three hypotheses have been proposed to explain the earlier arrival of males: (1) males winter farther north than females, therefore migrating a shorter distance, (2) males initiate migration earlier than females, and (3) males migrate more quickly than females. This study tests the "males migrate faster" hypothesis for four species of plumage-sexable wood warblers. Five years of banding data collected at a stopover site north of Chicago, as well as data collected from four banding sites in Mississippi and Louisiana, reveal that the mean difference in arrival date between males and females does not increase as the migration progresses northward from the gulf coast to Chicago. Condition index and fat score data at an Illinois stopover site show no significant difference between the sexes at time of arrival at the stopover site, suggesting that males are not making fewer and/or shorter stopovers during migration. Furthermore, males and females at the same stopover site show no significant difference in the effect of temperature and wind speed on weather-dependent migratory flight decision rules. These three pieces of evidence suggest that males do not migrate more quickly than females. Therefore, males must either winter farther north, migrate earlier, or both.

**Key Words:** Neotropical-Nearctic migration, differential migration, migration speed, wood warblers, migration timing, sexual dimorphism

## Introduction

Latitudinal migration is best described as an optimization strategy that allows migrants to feast on the abundant summer resources of the temperate and arctic zones while avoiding the cold and barren conditions of high latitude winters. Timing is of utmost importance in taking full advantage of these benefits and minimizing associated risks. Arrival date on the breeding grounds is a strong determinant of reproductive success in songbirds, particularly for territorial males whose quality of mate decreases significantly with time (Lozano et al. 1996). At the same time, migration is a metabolically demanding process and limited food sources *en route* or a premature arrival at the breeding site could lead to starvation. Thus,

food abundance both *en route* and on the northern breeding grounds, Neotropical-Nearctic migrants must use limited information to predict the northern food flush from their winter home in the tropics several thousand kilometers away. Second, they face a challenge of risk management. Should a migrant risk battling cold, harsh weather conditions and limited food resources to get there first? The answer may not be the same across species, sexes, or individuals. Thus, a constant struggle exists within each individual to balance expected costs and benefits in a way that achieves the highest fitness possible.

Despite the challenges of migration, male songbirds manage to arrive on the breeding grounds significantly earlier than females each spring. This thesis examines spring migration timing in songbirds, including this well-known and widespread phenomenon, through discussions of current literature and original research. Chapter One is a broad literature review of factors governing the timing of migration, including factors affecting departure from the wintering grounds, the importance of timing on the breeding grounds, and sex-related constraints on arrival date and reproductive timing.

Chapter Two presents original research into the possible mechanisms that allow males to arrive at the breeding grounds first. Five years of mistnetting data is used to test the "males migrate faster" hypothesis for four species of plumage-sexable warblers migrating through northeastern Illinois. This section is presented in the form of a manuscript intended for publication in the ornithological journal, *The Auk*.

## *Timing of spring migration in songbirds*

The following literature review examines factors affecting the timing of spring migration in North American songbirds. Songbirds cope with the challenges of migration using a variety of cues, and balancing constraints to best time their spring migration. I begin with a discussion of factors affecting migratory departure timing, including internal and environmental initiation cues, pre-migratory fueling, and sexual segregation on the wintering grounds. I then examine the importance of timing on the breeding grounds for each sex, and conclude with a discussion of current and potential impacts of global warming on spring migration timing.

## *Initiation of migration*

Many aspects of avian migration are endogenously controlled, including the onset of pre-migratory behaviors and departure timing (Jenni and Schaub 2003). Circannual rhythms are at the root of avian migratory and reproductive scheduling. It has been suggested that the role of circannual rhythms is so great that, free from external influences, birds will experience changes associated with migration and breeding condition in a predictable annual cycle with only slight variation over time (Gwinner 1977). While endogenous controls set broad guidelines for migratory timing, they are probably not sufficient; external cues determine when departure should occur within a general, endogenously-controlled timeframe (Jenni and

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migrants face two large problems in timing their spring migration. First, if migratory departure is constrained by

Schaub 2003). Therefore, control of annual cycles involves strong interplay between internal and external cues, which together trigger neural and hormonal responses (Farner 1978), and indicate that the time is right to initiate important changes in behavior and/or physiology (Jacobs and Wingfield 2000).

In order to properly time migration, migrants require reliable information about the onset of spring and summer. Photoperiod is the primary external cue governing the onset of migratory behavior and breeding condition (Jacobs and Wingfield 2000, Jenni and Schaub 2003, Ramenofsky et al. 2003). Farner (1978) suggests that birds must utilize a circadian mechanism capable of "measuring" day length. This mechanism likely regulates a daily photosensitive phase. When day light extends into this predetermined phase, the early stages of gonadal development are triggered, and the bird enters into the condition of migratory restlessness, or *Zugunruhe*, during which migration is initiated. Farner (1980) found timing of gonadal development and migratory preparation to be dependent on day length; by manipulating day-night cycles, he could make their timing deviate to some degree. Furthermore, *Zugunruhe* did not occur in White-crowned Sparrows (*Zonotrichia leucophrys*) held in an artificial environment of short days for more than two years (Farner 1978).

Photoperiod may work independently, or in conjunction with additional environmental cues. A number of supplementary cues are thought to accelerate or inhibit a migrant's response to photoperiod. According to Jacobs and Wingfield (2000), synchronizing cues monitor an individual's response to photoperiod based on its status within its population. In other words, migratory timing may be dependent on both interspecific and intraspecific competition, as well as predation risk, all of which may slow down migratory departure by limiting fuel deposition rate. Finally, modifying cues, such as unpredictable major weather events or predator encounters, may cause stress, altering birds' responses to the initial predictive and supplementary cues which, under normal circumstances, determine migratory timing.

It is not obvious whether and how response to environmental cues regulates genetically based features of migration. The mechanisms by which non-photoperiodic environmental cues adjust birds' internal biological clocks remain one of the great enigmas of avian biology (Farner 1978). Furthermore, the use and weight of each environmental cue in determining migratory timing varies across species and environments. For example, while arctic birds with short breeding seasons appear to rely heavily on one cue while ignoring others, birds with longer breeding seasons vary more in timing and onset of migration and appear to use several environmental cues, which work in synchrony to predict and determine appropriate timing of reproductive development and migration (Jacobs and Wingfield 2000).

#### *Pre-migratory fueling and timing*

Once cues are received indicating that spring migration is imminent, migrants undergo a number of physiological and behavioral changes associated with acquiring fuel stores necessary for migration. Such stores may serve not only as fuel, but as a safety net; energy expenditure may exceed energy intake during migration and/or energy intake may not be possible for

long periods of time (Farner 1978). In some cases, energy stores may equal as much as half of the bird's total body mass (Sandberg and Moore 1996), although this number is generally closer to 10-25% (Berthold 2001). Fat is the primary form of energy storage used for migration because it is the most energy-dense tissue available to birds. Although proteins are also involved (Klaassen et al. 2000, Lindstrom 2003), protein is a relatively heavy fuel in comparison to lipids (Gannes 2001) so carrying greater amounts may mean greater flight costs. Pre-migratory weight gain is achieved by hyperphagia, or the act of eating more than is needed to maintain current body mass. Hyperphagia involves an increase in time spent foraging, a decrease in energy expenditure, and/or a change in diet. Because differences in fat composition have been shown to affect songbird exercise performance (Pierce and McWilliams 2005), and small birds increase their reliance on fatty acids during long distance migration, it seems logical that passerines should choose foods containing high-energy fats just prior to departure.

Pre-migratory diet switching is widespread, but its extent is not fully understood and likely varies between species. Incorporating fruit into the diet may decrease time spent foraging, thereby decreasing energy loss and predation risk (Parrish 2000). Also, it may boost fat gain prior to migration while providing important nutrients (Gannes 2001). Wood Thrushes (*Hylocichla mustelina*), for example, are thought to change to a high-energy plant and berry diet in autumn before migrating south to wintering grounds (Conway et al. 1994). Conversely, Hermit Thrushes (*Catharus guttatus*) in southeastern Louisiana switch from a highly frugivorous diet in winter to an exclusively arthropod diet come springtime (Long and Stouffer 2003). Birds consuming only arthropods gained mass, but did not initiate migration earlier. Mass gain may have been the result of muscle protein accumulation, rather than fat gain. As short distance migrants, Hermit Thrushes probably rely less on fat reserves than do longer-distance migrants (Long and Stouffer 2003).

Fuel deposition rate may be an important determinant of departure date. If so, food availability, time available for foraging, and interactions with competitors or predators, may delay migratory initiation by limiting fuel acquisition rate (Lindstrom 2003). Evidence linking fuel supply and departure date shows inconsistency between species, possibly the result of species-related variations in migratory fueling strategy. Although Marra et al. (1993) found that initiation date of spring migration was related to body condition in American Redstarts (*Setophaga ruticilla*), several studies have shown migratory restlessness to occur even in individuals with restricted diets and/or that did not fatten (Long and Stouffer 2003). Also, migratory restlessness, which occurs throughout the migratory period, was not significantly greater in fat Swainson's Thrushes (*Catharus ustulatus*) or White-throated Sparrows (*Zonotrichia albicollis*) than in thin birds (Smith and Norment 2005).

Thrushes and warblers may use different strategies for acquiring migratory fuel. While thrushes rely on energy stored in tissues to power migration, warblers may require frequent feeding at stopover sites *en route*, just prior to departure (Larsen 2007). Fat capital may allow birds to outrun the spring phenology, beating income based migrants whose departure from

the wintering grounds may be delayed, while migratory speed is limited by food abundance *en route*.

#### *Wintering segregation by sex*

Many species have been shown to segregate on the wintering grounds which could have immense effects on timing of migration either by altering the migration distance for some members of the population, or by affecting condition, which can affect departure come springtime. Sexual segregation during winter is common among songbirds; Hooded warblers (*Wilsonia citrina*), American Redstarts, Ruby-crowned Kinglets (*Regulus calendula*), and Black-throated Blue Warblers (*Dendroica caerulescens*) have all shown differences in habitat preference, with males preferring tall forests, and females using shrub and/or field habitats (Morton 1990, Wunderle 1992, Parrish and Sherry 1994, Humple et al. 2001). Both sexes establish territories on the wintering grounds in the tropics (Morton 1990), which are defended with visual displays and vocalizations, and by chasing intruders (Holmes et al. 1989). Dominant males may exclude females and younger males from their preferred territories. Marra et al. (1993) observed this behavior in American Redstarts; as males were experimentally removed from mutually acceptable habitats, females moved in to replace them.

If wintering habitat quality differs between the sexes, segregation may increase sex-related inequity in condition prior to migration, allowing males to depart sooner and get to the breeding grounds earlier than females. Wintering quality may differ between the sexes in terms of habitat vegetation, seasonal stability, predation, and food abundance. For example, male-dominated mangrove habitats in Jamaica had a more abundant insect supply than female-dominated shrub habitat (Parrish and Sherry 1994). Male American Redstarts in mangroves lost less mass over winter, and showed higher rates of annual survival than individuals of both sexes in shrub habitat (Marra and Holmes 2001). Parrish and Sherry (1994) found more birds remaining in shrub habitats than in mangrove habitats in spring, suggesting that individuals in higher quality habitats do initiate migration earlier than do their counterparts in inferior habitats.

In addition to wintering segregation by habitat, sex-based latitudinal segregation has been well documented in more than 50 Old World and New World migrant species (Cristol et al. 1999). Until recently, there was very little evidence for latitudinal segregation occurring in species wintering in tropical regions. However, Komar et al. (2005) found significant latitudinal segregation in nine of 45 Neotropical-Nearctic migratory bird species, suggesting that latitudinal segregation, like habitat segregation, may be a factor in sex-related differential timing in at least some Neotropical-Nearctic migrants.

Sexual segregation on the wintering grounds may have evolved as a result of different selective pressures; in the case of both habitat and latitudinal segregation, the dominant sex (usually males) lowers migratory costs. Because males preferentially benefit from an early arrival on the breeding grounds, they may prefer to winter in areas with more constant and/or more abundant food sources. This would allow for an earlier spring departure, and/or a shorter migratory distance to and from the breeding grounds, thereby

enabling them to get there first while avoiding the costs associated with an earlier spring migration.

#### *Timing en route*

Once migration is initiated, environmental conditions continue to weigh heavily on a migrant's progress. Most songbirds are nocturnal migrants, traveling by night and spending their days resting and/or refueling at stopover sites along the migratory route. It has been shown that stopover duration, rather than actual flight speed, is the greatest determinant of overall rate of migration (Schwilch and Jenni 2001). Therefore, factors affecting departure decisions at stopover sites may be integral in determining overall migratory timing and arrival on the breeding grounds.

There is significant evidence that conditions aloft and on the ground determine if and when a migrant will depart, both from the wintering grounds and from stopover sites *en route*. For example, it has been shown that departing birds select for wind condition. Flight costs can be drastically increased or decreased by wind speed (Liechti 2006). Additionally, wind direction may be important; a tail-wind is likely beneficial, if not necessary, for migrants to cross large barriers, such as the Gulf of Mexico (Liechti 2006), a journey made by most Neotropical-Nearctic migrants. Although it is still not clear just how migrants determine wind condition from the ground, weak winds tend to encourage take-offs, while strong winds discourage it, often resulting in a backup of migrants awaiting improved conditions (Liechti 2006). Cochran and Wikelski (2005) used radio telemetry to show that Swainson's Thrushes and Hermit Thrushes did not depart a central Illinois stopover site unless wind speeds were at or below 10 km/hr.

Temperature also affects the departure decisions of spring migrants. In fact, temperature was as important as wind in determining the departure decisions of Cochran and Wikelski's (2005) thrushes; migrants stayed grounded below 21°C. Bueter et al. (2006) also noted an earlier arrival of migrants in warmer years at a stopover site north of Chicago. Unlike wind, which affects only flight efficiency, temperature may influence migratory flight decisions both directly and indirectly. Flight costs account for a large portion of energy expenditure during migration. Because temperature can affect the relative cost of flight versus thermoregulation at the stopover site (Bowlin et al. 2005), it may act as a direct cue indicating whether or not a migrant should fly or stay grounded. Alternatively, migratory speed may be limited by spring resource phenology as migrants progress northward, with temperature acting as an indirect cue, predicting future food abundance so that a migrant does not outrun its food supply farther north.

#### *Timing on the breeding grounds*

##### *The importance of timing on reproductive success*

Proper timing on the breeding grounds is essential for songbird reproductive success. Nesting success has been shown to decrease across the season, with smaller clutch sizes and lower fledgling survival with later clutch initiation date (Rowe et al. 1994, Brown and Brown 1999). Because reproductive success clearly decreases with time, it is difficult to say why some

parent birds delay laying. It has been shown that clutches laid at the average date actually yield fewer surviving offspring than the earliest laid nests (Daan et al. 1986), suggesting that energy requirements for egg production prevent the majority of females from laying at the most advantageous times. Daan et al. (1986) found significant evidence that food supplementation advances laying date and increases clutch size in seven species of passerines, providing additional support for the role of nutrients in the pre-laying environment in timing. If constrained by food availability in early spring, females must lay as close as possible to the optimal date after having collected the nutrients necessary for egg formation. Therefore, a tradeoff likely exists where parent birds can either delay laying until the female is in better condition or lay earlier when the female is in poorer condition, leaving time for a possible second brood before the season is over.

Alternatively, the bloom of resources in early spring may not act as a direct constraint on laying, but as a cue for predicting the food availability of the most critical time period, later in the season when nestlings must be fed. For birds breeding in temperate and arctic zones, offspring survival is heavily dependent on their being born when food is abundant (Daan et al. 1986). Therefore, the typical decrease in reproductive success observed across the season may be the result of a decrease in food abundance; parent birds must dedicate more time and energy to feeding their young, who, in turn, are less likely to survive. This increase in parental cost and decrease in offspring value may explain the observed decrease in clutch size with time (Rowe et al. 1994). However, despite observing an increase in overall annual reproductive success with earlier laying dates, Brown and Brown (1999) found no evidence that food availability actually does decrease with time in southwestern Nebraska, and instead attributed a seasonal decrease in Barn Swallow (*Hirundo rustica*) offspring survival and increased nest failure to greater ectoparasitic swallow bug (*Oeciacus vicarius*) abundance later in summer. This study demonstrates that a number of environmental factors beyond food availability may contribute to the well established decline in reproductive success later in the summer.

Despite the benefits of an early arrival on the breeding grounds, migrants cannot continually advance arrival time because of associated risks and costs. Neotropical-Nearctic migrants undergo an exceptionally demanding long distance migration from wintering grounds in Central and South America, across the Gulf of Mexico, and north to temperate breeding grounds. The movement of birds across the Gulf of Mexico, alone, involves a non-stop, 18-25 hour flight covering more than 1,000 km (Moore and Simons 1992). Mortality *en route* is likely high as migrants face unknown environments and compete for limited resources while avoiding predation and coping with unpredictable weather conditions (Sillert and Holmes 2002). These challenges are greater earlier in spring when migrants face colder temperatures, harsher weather conditions, limited shelter and protection from predators, and lower food availability. As a result, arrival date on the breeding grounds is heavily dependent on the tradeoff between the fitness benefits of an early arrival versus the additional costs and risks associated with early migration.

#### *Sex-related constraints on timing*

It is well established that male songbirds arrive on the breeding grounds before females in spring migration. (e.g., Francis and Cooke 1986, Otahal 1995, Yong et al. 1998, Morris et al. 2003). This fact suggests a sex-related difference in the relative costs and benefits of early migration, wherein the costs of a late arrival and/or benefits of an early arrival are greater for males than for females. In most species, males compete amongst themselves to establish territories, the quality of which will determine the rank of mate. This could be explained by intrasexual competition for breeding territories. Lozano et al. (1996) found that earlier arriving male American Redstarts faced less competition for resources, established superior breeding territories, and were able to exploit a longer breeding season, while late-arriving males were less likely to find a mate or nest.

Earlier arrival dates are expected to occur in the sex whose reproductive success is dependent on competition at the breeding site (Kokko 1999). Whereas males are selected to arrive as early as food and weather conditions allow, females, who invest great amounts of energy in egg laying, may benefit from arriving closer to the time when they can successfully breed, and in better physiological condition (Francis and Cooke 1986). Females arriving on the breeding grounds with remaining fat stores experience increased reproductive success as measured by clutch size, egg volume, and nestling mass (Smith and Moore 2003).

The fact that females arrive before males in species displaying reverse dimorphism demonstrates the role of breeding site competition as a driving force in the evolution of migratory timing. In both Red-necked (*Phalaropus lobatus*) and Wilson's Phalaropes (*Phalaropus tricolor*), females compete vigorously for access to males (Reynolds et al. 1986). If the species which competes for mates on the breeding ground is selected to get their first, females would be expected to arrive before males. Reynolds et al. (1986) showed that females of both species did, in fact, precede males to the breeding grounds, suggesting that, in these species, a female's reproductive success is enhanced more by getting there first and obtaining the best mate possible, than by delaying arrival to get to the breeding site in better physiological condition.

The importance of arrival condition on reproductive success may be somewhat dependent on breeding strategy. Drent and Daan (1980) first introduced the concept of "capital" versus "income" breeding strategies. They hypothesized that capital breeders rely heavily on fuel stores gathered *en route*, prior to arrival at the breeding grounds, to provide energy for laying and other reproductive activities. Income breeders, on the other hand, consume the nutrients involved in laying just prior to nest establishment at the breeding site. Although small passerines have been shown to arrive with migratory fat stores remaining, they are unlikely to be full capital breeders (Sandberg and Moore 1996). In any case, fuel stores used for long distance flight lack the proteins necessary for egg production and likely contribute very little to the laying process (Klaassen 2003). Also, they would be unlikely to provide adequate energy to produce an entire clutch. Despite these facts, there is significant evidence that female parental condition is an important factor in determining laying date, clutch size, and fledgling quality (Rowe et al. 1994, Smith and

Moore 2003). Fuel stores can act as a safety net upon arrival in the case of inclement weather or unforeseen food shortages. Because less time must be spent foraging for survival, more time can be dedicated to reproductive activities such as territory establishment, nest building, mate selection, and the collection of nutrients needed for egg laying (Sandberg and Moore 1996). If residual stores provide even a small portion of necessary reproduction-related nutrients, the benefits of arriving with fat stores intact will be greater for females than for males.

#### *Climate change and migratory timing*

The impact of global warming on biodiversity has become a central biological research paradigm as worldwide temperatures have increased 0.30°C-0.60°C since the late nineteenth century (Murphy-Klassen et al. 2005). Such changes may have serious implications for North American migratory songbirds by modifying species ranges and/or temperature-dependent behaviors, including reproductive and migratory timing.

With gradual warming, temperate and arctic vegetation and arthropod population peaks have advanced (Visser et al. 1998). Such a change in phenology could result in mistimed reproduction in which birds fail to breed when food availability is greatest (Both et al. 2006). For example, in a study of Great Tits (*Parus major*), warmer springs brought earlier caterpillar peaks, but hatching date remained unchanged. As a result, chicks hatched when food supplies were suboptimal (Visser et al. 1998). On the other hand, laying date has been shown to advance in some species; Hessel (2003) predicted that an increase of 5°C in May temperature could result in an advance of seven days in median laying date in Tree Swallows (*Tachycineta bicolor*) in southern Ontario. Crick et al. (1997) found that 20 of 65 study species initiated clutches significantly earlier over 25 years in Britain, with laying date advancing an average of nine days with increasing temperatures over the study period.

Despite observed advances in laying date, there is little evidence that such adjustments will be sufficient to avoid climate change-related population declines. Although, Pied Flycatchers (*Ficedula hypoleuca*) have advanced laying date an average of 10 days over the past 20 years, a significant portion of the population currently lays too late to exploit the peak in caterpillar abundance (Both and Visser 2003). Both et al. (2006) provide direct evidence of population declines resulting from insufficient change in breeding response to earlier caterpillar peaks. Population declines were significantly greater in those areas where food peaks were earliest (Both et al. 2006).

Limited advancement of laying date could be explained by several constraints. For example, temperature and other environmental factors act as constraints on breeding timing; insectivorous Tree Swallows laid earlier and heavier eggs, and shortened incubation period with greater insect abundance, which, in turn, is affected by climate-related conditions such as temperature and precipitation levels (Nooker et al. 2005). If phenology of food prior to laying advances to a lesser degree than do food peaks later in the summer, females may be forced to lay later, when nutrients important to laying are available. Global warming could create serious challenges if females are unable to advance laying date so that chicks are born at the peak of food abundance.

Alternatively, adaptation to climate change may be constrained by migratory timing. Although a recent trend toward earlier spring arrival on the breeding grounds has already been noted in a number of studies, significant regional and between-species variation in advancement ability clearly exists (See Table 1). In Mountain Bluebirds (*Sialia currucoides*) and Tree Swallows, forty years of data show a trend towards earlier arrivals with warmer summers in Alberta, Canada (Lane and Pearman 2003). Twenty-seven of 97 species in a 63 year study in Delta Marsh, Manitoba showed altered arrival dates, with most arriving earlier over time (Murphy-Klassen et al. 2005). Wilson et al. (2000) compared spring arrival dates from 1899-1911 with those from 1994-1997 in 80 migratory species in Maine; sixty-nine percent of species that showed significant trends over time arrived later at the end of the twentieth century, when temperatures were higher.

The above studies indicate that even closely related species respond differently to climate change (Table 1). Some of this variation may be the result of differences in the relative importance of temperature and photoperiod as predictors of migratory departure on the wintering grounds. Therefore, by analyzing species' responses to climate change over time, we may be able to make inferences about the role and relative importance of various external cues on migratory initiation and timing. If migratory timing is directed exclusively by endogenous controls or by non-temperature-dependent environmental cues like photoperiod, it may be difficult, if not impossible, for migrants to adjust their migration timing to exploit earlier spring food phenology. The families *Tyrannidae* and *Vireonidae* do not appear to arrive earlier on the breeding grounds (Table 2). As a result, species within these families may be especially vulnerable to global climate change. Alternatively, migrants relying heavily on temperature as a migratory cue should be able to adjust to climate change, advancing their arrival date and exploiting the advanced peaks in arthropod abundance.

Even without adjusting their timing, migratory birds may adapt to climate change by expanding their breeding range northward (Table 1), where global warming produces a resource flush at the time to which they are already accustomed. Such shifts have been observed by Root et al. (2003) in a wide variety of species, including birds. Furthermore, northern margins of breeding ranges have progressed significantly northward in a number of North American bird species over past decades; distributions were expanded northward an average of 2.35 km/year over an approximately twenty-six year study period (Hitch and Leberg 2007). A similar pattern was observed by Thomas and Lennon (1999) in Great Britain. Such shifts may negatively affect species if those on whom they depend are not capable of equally rapid distribution shifts (Hitch and Leberg 2007).

Measuring the current response to, and future implications of, climate change is a complex and difficult task. The effect of global warming on reproductive timing needs further attention. While trends toward earlier spring migration and clutch initiation have been recorded in some species, significant regional and between-species variation clearly exists. Species of the family *Emberizidae*, for example, show no clear pattern of response to climate

change; only some species have arrived earlier on the breeding grounds with increasing global temperatures. Furthermore, while American Redstarts, Wilson's Warblers (*Wilsonia pusilla*), and Tennessee Warblers (*Vermivora peregrine*) have been shown to advance arrival date, the majority of North American warblers

(family: *Parulidae*) have not. Continued observations of species' responses to climate change over time may provide further insight into the role and relative importance of various external cues governing migratory preparation and timing.

**Table 1. Change in spring arrival time on the breeding grounds and breeding range in North American songbirds as a result of climate change.**

Species	Spring Arrival	Northward Shift	Region	Source
<b>Tyrannidae</b>				
Alder Flycatcher	no		Maine	Wilson et al. 2000
Eastern Bluebird	no		Maine	Wilson et al. 2000
Eastern Kingbird	no		Manitoba, Canada	Murphy-Klassen et al. 2005
Eastern Phoebe	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Eastern Wood-pewee	no		Maine	Wilson et al. 2000
Great-crested Flycatcher	no		Maine	Wilson et al. 2000
Least Flycatcher	no		Maine, Manitoba, Canada	Wilson et al./Murphy-Klassen et al. 2005
Olive-sided Flycatcher	no		Maine	Wilson et al. 2000
Western Kingbird	no		Manitoba, Canada	Murphy-Klassen et al. 2005
Yellow-bellied Flycatcher	no		Maine	Wilson et al. 2000
<b>Vireonidae</b>				
Blue-headed Vireo	no		Maine	Wilson et al. 2000
Philadelphia Vireo	no		Maine	Wilson et al. 2000
Red-eyed Vireo	no		Maine	Wilson et al. 2000
Warbling Vireo	no		Maine	Wilson et al. 2000
White-eyed Vireo		no	Central and Eastern US	Hitch and Leberg 2007
<b>Hirundinidae</b>				
Bank Swallow	no		Maine	Wilson et al. 2000
Barn Swallow	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Cliff Swallow	no		Maine	Wilson et al. 2000
Purple Martin	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Tree Swallow	yes		Alberta, Canada	Lane and Pearman 2003
	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
<b>Paridae</b>				
Black-capped Chickadee		no	Central and Eastern US	Hitch and Leberg 2007
Boreal Chickadee		no	Central and Eastern US	Hitch and Leberg 2007
Carolina Chickadee		yes	Central and Eastern US	Hitch and Leberg 2007
Tufted Titmouse		no	Central and Eastern US	Hitch and Leberg 2007
<b>Cirrhidae</b>				
Brown Creeper	no		Manitoba, Canada	Murphy-Klassen et al. 2005
<b>Troglodytidae</b>				
Bewick's Wren		no	Central and Eastern US	Hitch and Leberg 2007
Species	Spring Arrival	Northward Shift	Region	Source
<b>Troglodytidae</b>				
House Wren	no		Manitoba, Canada	Murphy-Klassen et al. 2005
Marsh Wren	no		Manitoba, Canada	Murphy-Klassen et al. 2005

Winter Wren	no		Maine	Wilson et al. 2000
<b>Regulidae</b>				
Ruby-crowned Kinglet	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
	no		Maine	Wilson et al. 2000
<b>Turdidae</b>				
American Robin	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
	no		Maine	Wilson et al. 2000
Hermit Thrush	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
	no		Maine	Wilson et al. 2000
Mountain Bluebird	yes		Alberta, Canada	Lane and Pearman 2003
Swainson's Thrush		yes	Central and Eastern US	Hitch and Leberg 2007
Veery	no		Maine	Wilson et al. 2000
<b>Mimidae</b>				
Brown Thrasher	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Gray Catbird	no		Manitoba, Canada	Murphy-Klassen et al. 2005
<b>Parulidae</b>				
American Redstart	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Bay-breasted Warbler	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Black-and-white Warbler	no		Maine	Wilson et al. 2000
Blackburnian Warbler	no		Maine	Wilson et al. 2000
Blackpoll Warbler	no		Maine	Wilson et al. 2000
Black-throated-green Warbler	no		Maine	Wilson et al. 2000
Blue-winged Warbler		yes	Central and Eastern US	Hitch and Leberg 2007
Cape May Warbler		no	Central and Eastern US	Hitch and Leberg 2007
Cerulean Warbler		no	Central and Eastern US	Hitch and Leberg 2007
Chestnut-sided Warbler	no		Maine	Wilson et al. 2000
Common Yellowthroat	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Golden-winged Warbler		yes	Central and Eastern US	Hitch and Leberg 2007
Hooded Warbler		yes	Central and Eastern US	Hitch and Leberg 2007
Kentucky Warbler		yes	Central and Eastern US	Hitch and Leberg 2007
Louisiana Waterthrush		no	Central and Eastern US	Hitch and Leberg 2007
Magnolia Warbler	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Mourning Warbler	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Nashville Warbler	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Northern Parula	no		Maine	Wilson et al. 2000
Northern Waterthrush	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Ovenbird	no		Maine	Wilson et al. 2000
Palm Warbler	no		Manitoba, Canada	Murphy-Klassen et al. 2005
Pine Warbler	no		Maine	Wilson et al. 2000
Prairie Warbler		no	Central and Eastern US	Hitch and Leberg 2007
Swainson's Warbler		no	Central and Eastern US	Hitch and Leberg 2007
Tennessee Warbler	yes	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
<b>Species</b>	<b>Spring Arrival</b>	<b>Northward Shift</b>	<b>Region</b>	<b>Source</b>
<b>Parulidae</b>				
Wilson's Warbler	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Worm-eating Warbler		no	Central and Eastern US	Hitch and Leberg 2007
Yellow-breasted Chat		no	Central and Eastern US	Hitch and Leberg 2007

Yellow Warbler	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Yellow-rumped Warbler	no	no	Manitoba, Canada, Maine; Central and Eastern US	Murphy-Klassen et al. 2005, Wilson et al. 2000; Hitch and Leberg 2007
Yellow-throated Warbler		no	Central and Eastern US	Hitch and Leberg 2007
<b>Thraupidae</b>				
Summer Tanager		yes	Central and Eastern US	Hitch and Leberg 2007
Scarlet Tanager	no		Maine	Wilson et al. 2000
<b>Emberizidae</b>				
American Tree Sparrow	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Bachman's Sparrow		no	Central and Eastern US	Hitch and Leberg 2007
Chipping Sparrow	no		Maine	Wilson et al. 2000
Clay-colored Sparrow	no		Manitoba, Canada	Murphy-Klassen et al. 2005
Dark-eyed Junco	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Field Sparrow	no		Maine	Wilson et al. 2000
Fox Sparrow	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Lincoln's Sparrow		no	Central and Eastern US	Hitch and Leberg 2007
Savannah Sparrow	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Song Sparrow	no		Manitoba, Canada/Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Swamp Sparrow	no	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
Vesper Sparrow	no	no	Manitoba, Canada, Maine; Central and Eastern US	Murphy-Klassen et al. 2005, Wilson et al. 2000; Hitch and Leberg 2007
White-throated Sparrow	yes	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
	no		Manitoba, Canada	Murphy-Klassen et al. 2005
<b>Cardinalidae</b>				
Indigo Bunting	yes		Maine	Wilson et al. 2000
Painted Bunting		no	Central and Eastern US	Hitch and Leberg 2007
Rose-breasted Grosbeak	yes	no	Maine; Central and Eastern US	Wilson et al. 2000; Hitch and Leberg 2007
<b>Icteridae</b>				
Baltimore Oriole	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
	no		Maine	Wilson et al. 2000
Bobolink	no		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Boat-tailed Grackle		no	Central and Eastern US	Hitch and Leberg 2007
Brown-headed Cowbird	no		Manitoba, Canada	Murphy-Klassen et al. 2005
Common Grackle	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Great-tailed Grackle		yes	Central and Eastern US	Hitch and Leberg 2007
Red-winged Blackbird	yes		Manitoba, Canada, Maine	Murphy-Klassen et al. 2005, Wilson et al. 2000
Western Meadowlark	yes		Manitoba, Canada	Murphy-Klassen et al. 2005
Yellow-headed Blackbird	no		Manitoba, Canada	Murphy-Klassen et al. 2005
<b>Fringillidae</b>				
Pine Siskin		no	Central and Eastern US	Hitch and Leberg 2007
Purple Finch	yes	no	Manitoba, Canada; Central and Eastern US	Murphy-Klassen et al. 2005; Hitch and Leberg 2007
White-winged Crossbill		no	Central and Eastern US	Hitch and Leberg 2007

**Table 2. Summary of North American songbird families showing earlier arrival dates and/or northern shifts in response to climate change.**

Family	Species arriving earlier	Species not arriving earlier	Species shifting north	Species not shifting north
<i>Tyrannidae</i>	0	10		
<i>Vireonidae</i>	0	4	0	1



<i>Hirundinidae</i>	1	5		
<i>Paridae</i>			1	3
<i>Cirrhidae</i>	0	1		
<i>Troglodytidae</i>	0	3	0	1
<i>Regulidae</i>	1	1		
<i>Turdidae</i>	3	3	1	0
<i>Mimidae</i>	1	1		
<i>Parulidae</i>	3	18	4	15
<i>Thraupidae</i>	0	1	1	0
<i>Emberizidae</i>	4	8	0	5
<i>Cardinalidae</i>	2	0	0	2
<i>Icteridae</i>	4	4	1	1
<i>Fringillidae</i>	1	0	0	3

#### *Sexual Uniformity in Spring Migration Speed in Four North American Warblers*

In most migrant songbirds, males are known to arrive on the breeding grounds before females in spring, to establish and defend territories which will secure them the highest quality mate (Francis and Cooke 1986, Otahal 1995, Yong et al. 1998, Morris et al. 2003). While sex-related differences in arrival date are clear, the mechanism by which males achieve this early arrival is still poorly understood. Three non-mutually exclusive hypotheses have been proposed (Chandler and Mulvihill 1990).

The first hypothesis suggests that males winter farther north than females, and therefore migrate a shorter distance, arriving first on the breeding ground. Latitudinal segregation on the wintering grounds has been well-documented in more than 50 New World and Old World migrant species (Cristol et al. 1999), and in eight additional Neotropical-Nearctic songbirds (Komar et al. 2005).

The second hypothesis suggests that an earlier onset of migration may allow males to precede females to the breeding grounds. If wintering habitat quality differs between the sexes, segregation may increase sex-related inequity in condition prior to migration, allowing males to depart sooner and get to the breeding grounds earlier than females. These two hypotheses are not mutually exclusive; although sexual segregation was observed in wintering Hermit Thrushes (*Catharus guttatus*) in the eastern United States and northeastern Mexico, Stouffer and Dwyer (2003) noted that males passed through Chicago an average of 20 days before females in spring migration, concluding that differential wintering, itself, was inadequate in explaining such a large discrepancy in male and female arrival date.

The third hypothesis suggests that males migrate more quickly than females. Previous studies comparing rate of migration between the sexes are few and contradictory. A study by Yong et al. (1998) examining stopover behavior of migratory Wilson's Warblers in New Mexico lends support to the idea of a sex-related difference in migration rate; males were recaptured less frequently and gained mass at a greater rate than females at a stopover site. However, similar studies of Common Yellowthroats on Appledore Island, ME (Morris et al. 2003), and of Wilson's Warblers at San Francisco Bay, CA (Otahal 1995), have produced conflicting results.

This study examines "the males migrate faster" hypothesis in four species of plumage-sexable warblers: American Redstart (*Setophaga ruticilla*), Canada Warbler (*Wilsonia pusilla*), Common Yellowthroat (*Geothlypis trichas*), and Mourning Warbler (*Oporornis philadelphia*). We test this hypothesis in three distinct ways: 1) we compare the mean difference in arrival date between males and females at an Illinois stopover site and four stopover sites on the gulf coast, 2) we compare physiological condition of males and females at an Illinois stopover site, and 3) we compare male and female weather-related migratory flight decision rules. If males migrate more quickly than females, we predict that they should: 1) gain ground on females between the gulf coast and an Illinois stopover site, 2) arrive in worse physiological condition at an Illinois stopover site, and 3) apply less conservative weather-related migratory flight decision rules.

#### **Experimental Procedures**

##### *Mistnetting procedure*

This study was conducted in the Shaw Woods portion of the Skokie River Nature Preserve in Lake Forest, Illinois, approximately 48 km north of Chicago. The study site has been described in detail by Gordon et al. (2002) and Bueter et al. (2006). Twelve standard, 33 mm mesh, 12 m mist nets were opened before sunrise and checked on the hour, for 5 h each morning on most days throughout the month of May from 2002-2006 (13 days in 2002, 20 days in 2003, 21 days in 2004, 24 days in 2005, 27 days in 2006). Captured birds were removed, placed in a breathable cloth bag, and brought to a central banding station where date and time of capture were recorded in addition to weight, unflattened wing chord, and a visible fat score of 0-2 (as described below). Sex was determined by plumage, when possible, using Pyle (1997) and Sibley (2000). Before release, new captures were banded with individually numbered, aluminum bands issued by the U.S. Bird Banding Laboratory.

Seventeen years (1987-2004) of banding data were collected at four sites along the Gulf of Mexico coast, including East Ship Island and Horn Island, both barrier islands off the coast of Mississippi, and Peveto Woods and Johnson's Bayou, both coastal

woodlands in Cameron Parish, Louisiana. Recaptures and birds which could not be confidently sexed were excluded from the study.

#### *Arrival date at stopover sites*

In order to confirm the well established pattern of males arriving before females at our study site in northeastern Illinois, mean May arrival dates were determined for both sexes for each of the four study species. A *t*-test was used to compare mean arrival date between the sexes.

To determine if males were gaining ground on females between the gulf coast and Illinois, we compared mean difference in arrival between males and females at the two sites. An arrival score was assigned to each individual, representing arrival date in days after 23 March, the date at which birds began arriving at gulf coast sites. Because of small sample sizes of Canada and Mourning Warblers at sites on the gulf coast, only American Redstarts and Common Yellowthroats were used in this portion of the study. A mean difference in arrival between males and females was determined for both species at each site. Gulf sites were pooled. An ANOVA was used to determine the effects of sex, site, and sex by site interaction on arrival date.

#### *Physiological condition at an Illinois stopover site*

A visible fat score of 0-2 was assigned to each bird upon capture where 0 indicates no fat (furcular hollow, vent, and wing pits empty), 1 indicates some visible fat, and 2 indicates heavy fat (furcular hollow, vent, and wing pits full and bulging). We also use condition index as a size-corrected measurement of weight, calculated here as (mass/wing chord) x 100 (Winker 1995). Mass was determined using a 25 g or 100 g spring scale (2002-2005), or an electronic scale (2006). A mean fat score and mean condition index values were determined for males and females for each of the four study species. Condition index and fat score means were compared between the sexes with *t*-tests.

#### *Weather-related migratory flight decisions*

We used multiple linear regression analysis to analyze the number of new captures at our northeastern Illinois study site each day as a function of weather in Urbana, Illinois, 277 km to the south, the previous evening. We collected data on daily high temperature and wind speed at 1953 hours CST from Willard airport in Urbana (<http://www.atmos.uiuc.edu/weather/>). We performed separate multiple linear regressions for each sex, pooling the four species. Male and female responses were compared with a *t*-test.

All statistical procedures were run using JMP IN, version 5.1 (SAS institute, 2003).

## **Results**

#### *Stopover arrival date*

Males preceded females at our Illinois site, arriving anywhere from 3.00 (+/- 0.80) days before females in Mourning Warblers to 5.19 (+/- 0.77) days before females in Common Yellowthroats (Fig. 1). In our Gulf-

coast-Illinois arrival date comparison, sex and site were significant factors in determining arrival date; males arrived before females at both sites, as expected (Table 3). The sex by site interaction was not significant in either species; mean difference in arrival between the sexes was not dependent on site.

#### *Physiological condition at arrival*

As shown in Figure 3, males and females arrived in northeastern Illinois with almost identical condition indexes in all four of the study species (*t*-tests, American Redstart *P*= 0.4865, Canada Warbler *P*= 0.9215, Common Yellowthroat *P*= 0.5675, Mourning Warbler *P*= 0.4206). Fat score was also statistically indistinguishable between the sexes (*t*-tests, American Redstart *P*= 0.3842, Canada Warbler *P*= 0.1540, Common Yellowthroat *P*= 0.7010, Mourning Warbler *P*= 0.5316).

#### *Weather-related migratory flight decisions*

Males and females follow similar weather-dependent migratory flight decision rules. Multiple linear regression analysis for each sex produced statistically significant models, with a significant positive effect of previous day temperature in Urbana, but no significant effect of previous evening wind speed or temperature by wind speed interaction on number of new captures at the Illinois site in either sex (Table 4). There was no sex-related difference in response to temperature, wind or temperature by wind interaction (*t*-test, *P*> 0.50).

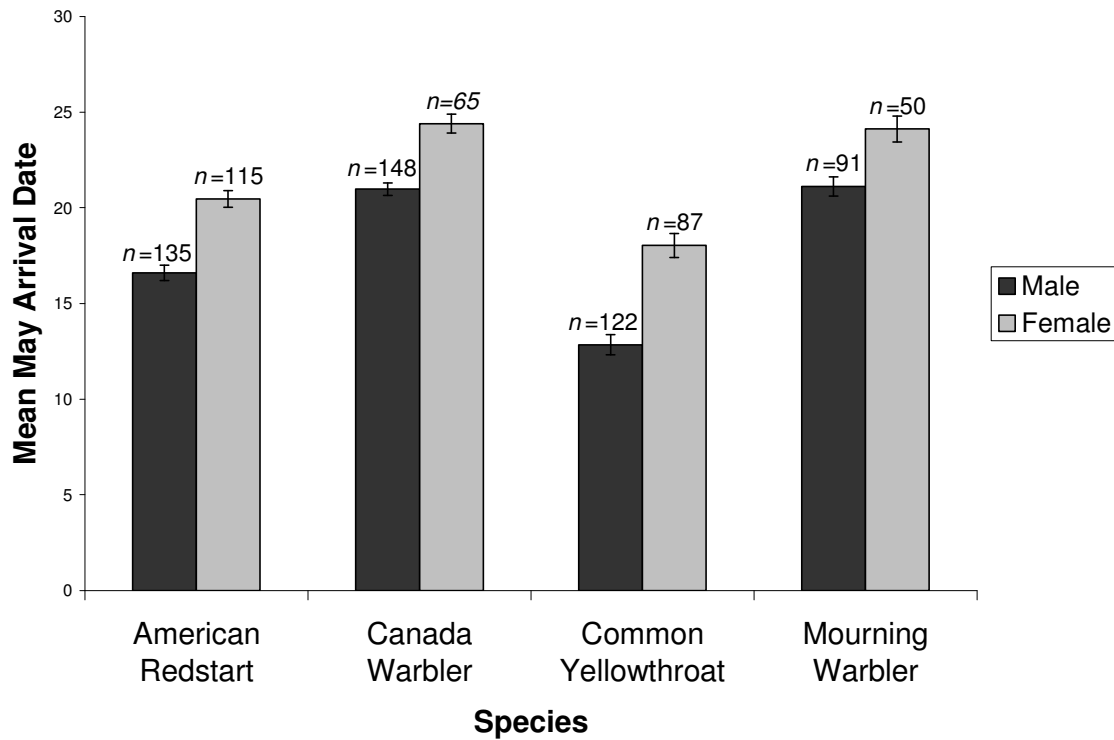
## **Discussion**

This study presents three independent pieces of evidence suggesting that males do not migrate more quickly than females. If the "males migrate faster" hypothesis was true, we would expect the difference in arrival date between the sexes to increase as the migration progressed northward, with males gaining ground on females between the gulf coast and northern Illinois. The lack of significant sex by site effect in our arrival date regression model indicates that males and females are migrating at comparable speeds between the gulf coast and northeastern Illinois (Table 3).

The fact that males and females arrive at our Illinois study site in almost identical condition suggests that they are carrying similar fuel loads (see Fig. 3). If males migrated more quickly than females, we would expect them to make fewer and/or shorter stopovers *en route* (Schwilch and Jenni 2001). As a result, males should experience a greater net fuel loss overall, assuming equal foraging ability between the sexes, and should arrive in Illinois in poorer physiological condition than females. Our findings suggest that rate of migration is similar between the sexes.

Finally, if males were migrating more quickly than females, we would expect them to apply less conservative weather-related migratory flight decision rules. We found no significant sex-related difference in the effects of temperature, or temperature and wind speed interaction on migrants' flight departure decisions (Table 4), suggesting that males and females are equally conservative when making migratory flight departure decisions based on the weather.

**Figure 1.** Mean May arrival dates of all newly captured birds at a northeastern Illinois stopover site from 2002-2006 are shown with SE bars by sex and species. Males arrived significantly earlier than females in all four of the study species (*t*-tests, American Redstart *P*< 0.0001; Canada Warbler *P*< 0.0001; Common Yellowthroat, *P*< 0.0001; Mourning Warbler *P*= 0.0005).



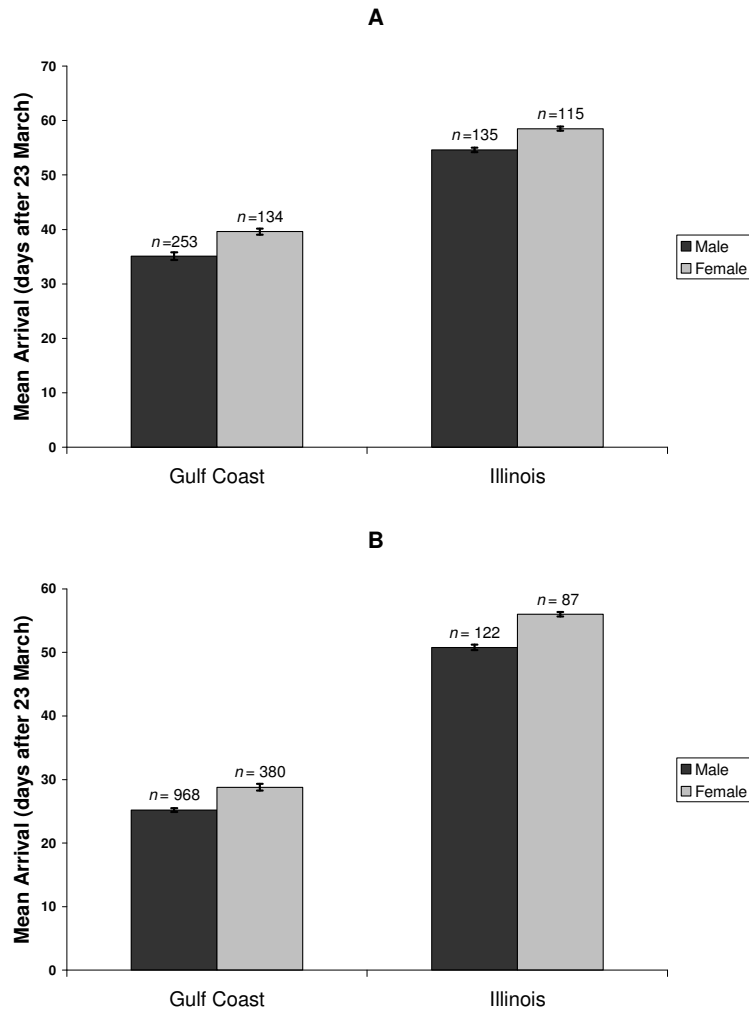
**Table 3.** Effect of sex, site, and sex by site interaction on arrival date at an Illinois stopover site (2002-2006) and stopover sites on the gulf coast (1987-2004). The overall model was significant in both species (American Redstarts,  $P < 0.0001$ ; Common Yellowthroats,  $P < 0.001$ ).  $P$ -values from the ANOVA are shown for each individual effect.

	<i>P</i> -value from ANOVA	
	American Redstarts	Common Yellowthroats
<b>SEX</b>	< 0.0001	< 0.0001
<b>SITE</b>	< 0.0001	< 0.0001
<b>SEX*SITE</b>	0.6335	0.2661

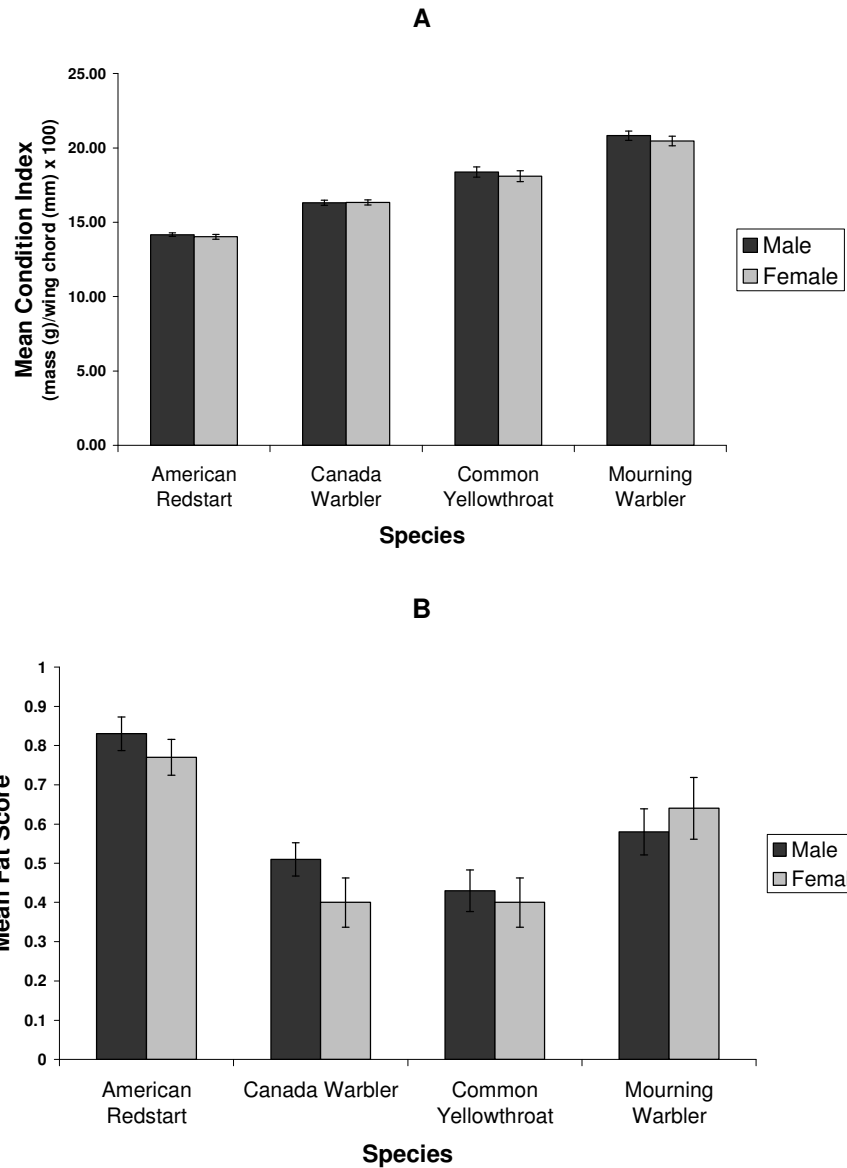
**Table 4.** Multiple linear regression of new arrivals at an Illinois stopover site (2002-2006) as a function of daily high temperature and wind speed at 1953 hours CST in Urbana, IL the previous day. The overall model was significant in both sexes (males,  $P = 0.0490$ ; females,  $P = 0.0253$ ). Sex comparison columns report  $t$ -tests comparing male and female parameter estimates from these models.

Male	Female	Sex Comparison
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	Parameter Estimate	P-value	Parameter Estimate	P-value	t-value	P-value
Temperature	0.2059	0.0240	0.1871	0.0144	0.2503	>0.50
Wind Speed	0.1300	0.2206	0.1637	0.0664	0.3707	>0.50
Temperature*Wind Speed	0.0299	0.1039	0.0189	0.2183	0.7237	0.5



**Figure 2.** Mean arrival date ( $\pm$  SE) is shown by sex at four banding sites on the gulf coast (1987-2004) and a stopover site in Illinois (2002-2006) in American Redstarts (A) and Common Yellowthroats (B). Mean arrival date is represented on the Y axes as the number of days after 23 March, the date at which migrants began arriving on the gulf coast. Males arrived before females in both species, at both sites (Illinois, see Fig. 1, Gulf coast t-tests, American Redstart,  $P < 0.0001$ ; Common Yellowthroat,  $P < 0.0001$ ).



**Figure 3.** Mean condition index ( $\pm$  SE) and fat score ( $\pm$  SE) for each of the study species at an Illinois spring stopover site (2002-2006). Values for males and females are statistically very similar for both variables and for all four study species (t-tests,  $p > 0.05$ ). Sample sizes are the same as in Figure 1.

Our results are consistent with observations by Otahal (1995) of Wilson's Warblers passing through San Francisco Bay, CA and Morris et al. (2003) of Common Yellowthroats on Appledore Island, ME, both of which found similar rates of mass gain and lengths of stay between the sexes at their respective stopover sites. However, a contradictory study by Yong et al. (1998) of Wilson's Warblers in New Mexico found lower recapture rates and higher mass gain among males, suggesting that males are bulking up more quickly and spending less time at stopovers than females, presumably in order to get to the breeding grounds first. This may suggest variation in migratory strategy between species and/or across regions.

If males are not migrating more quickly than females, either wintering farther north, initiating migration earlier, or a combination of the two should account for the earlier arrival of males on the breeding grounds in the four species studied. While many New World and Old World species have been shown to segregate on the wintering grounds (Cristol et al. 1999), very little evidence exists for latitudinal segregation occurring in species wintering in Neotropical regions. However, Komar et al. (2005) found significant latitudinal segregation in nine of 45 Neotropical-Nearctic migrants examined, suggesting that latitudinal segregation may be a factor in sex-related differential timing in at least some species.

If wintering ground quality differs between the sexes, inequity in condition prior to migration may allow males to depart sooner, getting to the breeding grounds first. Marra and Holmes (2001) showed that male American Redstarts in mangroves lost less mass over winter and showed higher annual survival than both sexes in shrub habitat. Furthermore, the number of birds remaining in female-biased shrub habitat was greater come springtime than in male-dominated mangroves, suggesting that individuals in higher quality wintering habitats may, in fact, initiate migration sooner. Of my study species, wintering habitat segregation by sex has only been observed in the American Redstart (Parrish and Sherry 1994, Marra et al. 1993, Marra and Holmes 2001). Further studies are needed on the wintering habits of wood warblers in order to determine the degree to which segregation occurs on the wintering grounds.

It has been difficult to demonstrate that latitudinal wintering segregation, itself, can explain large differences in arrival time between the sexes. For example, male Ruby-crowned Kinglets pass through southeastern South Dakota and male Dark-eyed Juncos pass through eastern New York more in advance of females than would be expected based on sexual habitat segregation on the wintering grounds alone (Swanson et al. 1999, Chandler and Mulvihill 1990). Few others have studied initiation date, beyond presenting it as a possible means of early male arrival. Long and Stouffer (2003), however, saw no significant difference in male and female initiation date in captive Hermit Thrushes, although sample sizes were small.

The sexual uniformity in migration speed in wood warblers is perplexing given the sexual dimorphism in arrival date. Condition upon arrival at the breeding grounds is generally assumed to be more important in females who must undergo the energetically-demanding process of egg-laying. However, the observed sexual uniformity in migration speed may indicate that males, like females, benefit from arriving on the breeding grounds in good physical condition. Remaining stores can act as a safety net in the case of inclement weather or unforeseen food shortages. Furthermore, if less time is spent foraging for survival, more time can be devoted to male reproductive activities such as territory establishment and defense, nest building, and sperm production (Smith and Moore 2003). If this hypothesis was correct, males might not benefit from sacrificing physiological condition for migration speed any more than would females. Therefore, they may employ an alternative method to get to the breeding grounds first, for example, by altering distance and/or onset of migration.

The fact that females arrive before males in species displaying "reverse" sexual dimorphism suggests that intrasexual competition for mates and/or territories, rather than resource constraints associated with egg-laying, is the driving force in the evolution of migratory timing. In both Red-necked (*Phalaropus lobatus*) and Wilson's Phalaropes (*Phalaropus tricolor*), females compete vigorously for access to males. Reynolds et al. (1986) showed that females of both species preceded males to the breeding grounds, suggesting that in these species, females can increase their reproductive success more by getting their first and obtaining the best the best mate possible, than by delaying arrival to conserve resources for egg-laying.

An alternative explanation for the observed uniformity in migration speed is that the physiological demands and constraints that govern migration are

strong enough to overwhelm any sexually dimorphic pressure for the territorial sex (in this case males) to get to the breeding grounds first. It is well known that migration is energetically expensive. Several studies have demonstrated the usefulness of plasma metabolites as indicators of mass gain and physiological condition of migrants, which may provide clues as to energy use during migration (e.g., Guglielmo et al. 2002, Cerasale and Guglielmo 2006, Seaman et al. 2006). Plasma metabolite studies and further development of other methods, such as wind tunnel experiments (Klaassen et al. 2000) and radio telemetry (Wikelski et al. 2003), may provide further insight into migrant physiology and the idea of migration as a marathon that cannot be rushed. This knowledge is essential to fully understanding the ecological and evolutionary constraints which govern migration.

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