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## Energetics and Migration in Songbirds: Two Case Studies Examining Energetic Condition and Migration at a Northern Stopover Location

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**Energetics and migration in songbirds: two case studies examining energetic condition and migration at a northern stopover location**

By

Jennalee Ann Holzschuh

A Thesis

Presented to the Faculty of the Department of Environmental Science and Biology

of the State University of New York College at Brockport

in Fulfillment for the

Degree of Master of Science

June 2014

**Department of Environmental Science and Biology**

**Thesis Defense by**

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### Part One:

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## **Abstract**

### **Energetics and migration in songbirds: two case studies examining energetic condition and migration at a northern stopover location**

Migration is an energy-intensive behavior undertaken in both spring and fall by billions of songbirds to reach distant breeding and wintering grounds. Stopover habitats, particularly those located near ecological barriers that birds must cross, provide key locations where birds can stop and refuel during migration. A bird's energetic condition affects its behavior at stopover locations; in spring, birds may accumulate energy reserves at locations *en route* to breeding grounds for tasks other than migration. This two-part study examined different aspects of the energetic condition of songbirds at a northern stopover location on the south shore of Lake Ontario. First, banding data for 12 Parulidae species were analyzed, and I found that arrival date, sex, and season explained some of the variation in the energetic condition of birds arriving at this location. My results suggest that there is possibly a reproductive advantage for spring migrants to arrive with energy reserves. Second, I found that energetic condition affects the orientation of White-throated Sparrows (*Zonotrichia albicollis*), mainly in the spring. However, like other studies of sparrows in captivity, I found bimodal orientation along the migratory axis, which makes it difficult to predict migratory orientation based on energetic condition. Both of these studies demonstrate that songbird behavior during migration is complex, variable, and worthy of further study.

**Energetics and migration in songbirds: two case studies examining energetic condition and migration at a northern stopover location**

**General Introduction**

Billions of songbirds migrate within and between continents annually. Migration is considered one of the most unpredictable and vulnerable phases of a bird's annual cycle (Sillett and Holmes 2002). To complete migration successfully, birds must use a variety of endogenous and exogenous cues to navigate accurately to seasonally appropriate locations (see Åkesson and Hedenström 2007). While the end locations of migration, breeding and wintering grounds, are important, critical locations *en route* for refueling and resting (so-called stopover habitats) can be equally, if not more, important for migrants. Locating quality stopover habitat *en route* is essential for the successful completion of migration, but much research on the stopover biology of songbirds is still needed (e.g., see Mehlman et al. 2005, Deutschlander and Beason 2014).

Given the potential consequences of mistakes during migration, there is a high selective pressure for birds to both locate stopover habitat successfully and to refuel effectively during stopover (Moore and Aborn 2000). Understanding how birds locate and use stopover habitat has important management and conservation implications because a migratory bird's energetic condition may affect both its probability of survival during migration and its reproductive success once it arrives on breeding grounds in the spring (e.g., Sandberg and Moore 1996, Drent et al. 2003).

There is evidence that both males and females can derive reproductive benefits from arriving on breeding grounds with excess energy reserves (Smith and Moore 2003, 2005, Cooper et al. 2011). Hence, the potential for migratory birds to increase fitness on the breeding grounds lends even more value to the energy reserves and nutrients that migrants accumulate *en route* and further suggests the importance of quality stopover locations.

In addition to potential spring breeding ground benefits, the energy reserves birds accumulate *en route* may also affect their stopover behaviors, such as length of stay (Cherry 1982), foraging (Loria and Moore 1990), departure decisions (Seewagen and Guglielmo 2010), and orientation (Covino and Holberton 2011). The amount of stored energy (fat) a bird has at a given stopover location can affect its orientation, particularly near a large ecological barrier (such as a body of water, desert, or mountain range); birds with inadequate energy reserves often reorient themselves away from, or parallel to, barriers to replenish energy reserves before crossing (e.g., Sandberg et al. 2002, Deutschlander and Muheim 2009). Because stopover locations near barriers can help provide migratory birds with the resources they need to cross or circumvent barriers successfully, they are especially worthy of conservation. However, many stopover locations for migrating birds, especially in coastal locations, are threatened by habitat destruction (Buler and Moore 2010). It is ineffective to conserve breeding and wintering grounds unless these vital stopover locations are also protected (Mehlman et al. 2005), and given their varied habitat requirements,

migratory species may be more vulnerable to extinction than non-migrants (Buler and Moore 2010).

This thesis has two parts, each of which focuses on a different aspect of the energetic condition of migratory birds and seeks to answer both general and specific questions about the biology of migratory birds that stop over at or near the Braddock Bay Bird Observatory (BBBO). Braddock Bay Bird Observatory is surrounded by stopover habitat that is adequate for many migrating songbirds (Bonter et al. 2007), and this site may serve as a location for songbirds to refuel either before crossing Lake Ontario in the spring or after crossing in the fall. Because BBBO is located adjacent to an ecological barrier and serves as a location for a long-term banding study, it is an ideal location to study the energetics of migratory songbirds at a northern stopover location.

The first part of this thesis uses bird banding data for 12 New World warbler (Parulidae) species to determine if arrival date, sex, and/or season explain variation in energetic condition of birds arriving at BBBO, and also to determine if patterns in condition of birds arriving at BBBO support Sandberg and Moore's (1996) breeding and insurance hypotheses. The number of Parulids that stop over at this location makes them an ideal group for my studies because most have sexually dimorphic plumage, which enables comparison of relatively large numbers of males and females. Most of these Parulids also have northerly breeding grounds and are long-distance migrants, which also makes them ideal for examining predictions of the breeding and insurance hypotheses (Sandberg and Moore 1996). The second part of

my thesis pertains to a much more specific aspect of bird migration biology: specifically, whether Zugunruhe and orientation of White-throated Sparrows (*Zonotrichia albicollis*) are affected by an individual's energetic condition. White-throated Sparrows were studied in part two because they are plentiful at this study location, are robust in captivity, and results from previous research on this species at this site (Smith and Norment 2005, Deutschlander and Muheim 2009, Muheim et al. 2009) enabled a comparison of my results to those of earlier studies. Although the focus and species of these two parts of my thesis are different, the overarching purpose of my project is to study the behavior and energetic condition of migratory songbirds at an important stopover location. Multi-scale studies conducted at stopover locations are needed, not only to provide information about migratory bird biology, but also to present further justification for stopover habitat conservation.

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**Part One: Do migratory warblers carry excess fuel reserves during migration  
for insurance or for breeding purposes?**

**Introduction**

Migration is an energetically expensive behavior that is arguably the most vulnerable period of a bird's annual cycle (Moore et al. 1990, Sillett and Holmes 2002). There is some evidence that basal metabolic rates increase considerably in migratory birds, particularly during spring migration (see Swanson 2010). To compensate for these increased metabolic demands during migration, birds must deposit adequate energy reserves to reach distant breeding and wintering grounds successfully. Some species of Neotropical, intercontinental migratory passerines are capable of accumulating fat stores of up to 50% of their body mass in preparation for or during migration (Blem 1990). The migratory journey often consists of alternating periods of oriented flight (known as *Zugunruhe*) and frequent pauses at stopover locations to rest and refuel, or *Zugdisposition* (see Ramenofsky and Wingfield 2006). To accumulate necessary fuel reserves for *Zugunruhe*, birds may expend considerable time and energy at stopover locations *en route* to seasonally appropriate destinations (e.g., Hedenström and Alerstam 1997, Wikelski et al. 2003), and accumulating fuel reserves can delay arrival on breeding grounds in the spring (Fransson and Jakobsson 1998).

Fuel reserves, however, may be important for functions other than *Zugunruhe*. Studies show that fat reserves can affect the fitness of both males and females that

arrive early on spring breeding grounds; for example, excess fat or energy reserves can be directed toward breeding activities, such as territory establishment and egg production (Ojanen 1984, Sandberg and Moore 1996, Fransson and Jakobsson 1998, Bêty et al. 2003, Smith and Moore 2003, 2005). This can lead to different patterns in energetic condition within and between species. Sandberg (1996) found that several species arrived in good energetic condition on their Scandinavian near-Arctic breeding grounds, and when both sexes arrived concurrently, females had greater fat reserves than males. However, males in some species also can arrive on breeding grounds with excess fat; for example, Fransson and Jakobsson (1998) found that male Willow Warblers (*Phylloscopus trochilus*) arrived on spring breeding grounds on Gotland Island in the Baltic Sea with relatively high fat reserves. Also, a study in the low Arctic of Canada found that both male and female Harris's Sparrows (*Zonotrichia querula*) arrived on their subarctic breeding grounds with appreciable fat reserves (Norment 1992). In contrast, there is also evidence that some passerine species do not carry excess fat reserves to northern breeding grounds and perhaps only deposit fat *en route* for daily maintenance and migration requirements. At a high-latitude site in Alaska, Benson and Winker (2005) discovered that among 16 species of songbirds, all arrived with low fat reserves in spring and about one-third of the species had greater fat reserves in the fall. Similarly, Dunn (2002) compared several stopover locations in spring and fall across Canada and found that several species of migrant songbirds had low daily mass gains and thus were not depositing excessive fat stores during migration.

Given the high degree of variability in the stopover ecology of migrating songbirds suggested by different studies and the varied ecology of migrant songbirds, patterns in the energetic condition of individual migrants likely differ among species at specific stopover locations and/or among stopover locations along a population's migratory route. An energetic surplus upon arrival on breeding grounds could be particularly beneficial for Arctic and subarctic (i.e., boreal) breeding birds, given the temporal constraints associated with breeding at high latitudes. Timing of events on the breeding grounds may affect a bird's reproductive success (e.g., Smith and Moore 2003) and subsequent departure in the autumn (Mitchell et al. 2012). Birds that arrive relatively early and in good energetic condition might be more successful at acquiring high quality territories and could breed earlier (e.g., Smith and Moore 2005, Cooper et al. 2011). Birds that depart late from northern breeding grounds may face adverse weather conditions and depleted resources at stopover locations *en route* to wintering grounds (see Newton 2006). Therefore, energetic condition coupled with the timely arrival on and subsequent departure from breeding grounds may influence a bird's fitness. In addition to the potential reproductive effects of an energy surplus, birds that arrive on stopover habitat or breeding grounds in good energetic condition would likely be better able to cope with sudden energetic demands due to unpredictable conditions (e.g., adverse weather) or resource constraints (Sandberg and Moore 1996).

To add to the body of knowledge about how birds use stopover locations and help identify key stopover sites for conservation (Donovan et al. 2002), it is useful to

study patterns in energetic condition at individual stopover locations during various stages of the migratory journey. During spring migration, birds are under selective pressure to minimize time spent at stopover locations in order to reach breeding grounds in a timely manner (Fransson and Jakobsson 1998, Dänhardt and Lindström 2001) and stopover habitat might be limiting for some songbird populations (e.g., Sillett and Holmes 2002). Stopover locations in close proximity to ecological barriers (e.g., deserts, bodies of water, and mountain ranges) are especially important, as birds often need to refuel just prior to or just after crossing the barrier (e.g., Buler and Moore 2011).

The goals of the current study were two-fold. First, I wanted to test two hypotheses about the role of energetic condition during spring migration by examining how condition varies with arrival time, sex, and season. Second, I examined birds captured at a northerly stopover location in North America during both fall and spring migration, to compare with patterns found at other locations. I investigated two hypotheses concerning the function of excess fuel and energetic condition during spring migration – the breeding performance hypothesis and the insurance hypothesis (Sandberg and Moore 1996):

1. The breeding performance hypothesis suggests that gamete production and reproductive success, particularly in females, on northern breeding grounds can be influenced by pre-stored fat that is accumulated *en route*; females arriving with more fat reserves could produce larger clutches and/or begin breeding activities earlier than females that arrive with little

or no energy reserves. Moreover, the asymmetrical energy expense of female gamete production could easily lead to sexual differences in energy acquisition, utilization, and storage while *en route* during spring migration. Sandberg and Moore (1996) predicted that females should arrive on breeding grounds with more energy reserves than males to offset some of the energetic demands of female gamete production.

2. The insurance hypothesis suggests that birds breeding at high latitudes should benefit from arriving on breeding grounds or northerly stopover locations with fat reserves because environmental conditions are harsh, and resources can be unpredictable and scarce at high latitudes in spring. Birds with stored energy reserves should be able to cope better with unpredictability, which would have fitness consequences. Because food availability and weather conditions improve with time during the spring, one prediction of this hypothesis is that birds arriving earlier in the season should have greater fat reserves relative to later birds (Sandberg and Moore 1996).

In general, both hypotheses imply that it is beneficial for birds to have energy/fat reserves in the spring. Neither of these hypotheses would predict advantages of fuel reserves during fall migration, so one expectation is that birds arrive fatter in the spring relative to the fall when they depart. While there may also be advantages to fall energy reserves, such as for long migrations, several studies suggest that fall migration occurs at a slower rate and many species may be more

likely to accumulate energy reserves as needed along their fall migratory route (e.g., Bauchinger and Klaassen 2005, Stutchbury et al. 2009).

To test these two hypotheses, I analyzed spring and fall banding data for several warbler species collected from 1999-2012 at the Braddock Bay Bird Observatory (BBBO), located along the south shore of Lake Ontario, near Rochester, NY. Although not a breeding site for most species I studied, this location is a northerly stopover site for migratory species that breed in boreal habitats. The proximity of BBBO to the boreal forest makes it a potential penultimate stopover for many Parulids. I included data for 12 Parulids in my analyses to investigate the following questions pertaining to Sandberg and Moore's (1996) hypotheses: (1) Does the energetic condition of migrant songbirds at a northerly stopover site vary predictably with factors associated with the breeding or insurance hypothesis? Particularly, does energetic condition vary with date of capture (e.g., insurance) or sex (e.g., breeding)? (2) Are there seasonal differences in energetic condition that support the prediction that birds should be fatter in the spring? My analyses should provide valuable information about songbirds that use this stopover location and will contribute to current knowledge about the stopover biology of migratory songbirds.

## **Methods**

### *Data collection:*

Braddock Bay Bird Observatory is located on the south shore of Lake Ontario near Rochester, Monroe County, New York, USA (43° 19'N, 77° 43'W). The most



direct distance across Lake Ontario at this longitude is  $\pm 75$ -80 km. The vegetation surrounding BBBO is characterized as a mix of abandoned field and early-successional land-cover types dominated by viburnum (*Viburnum* spp.), dogwood (*Cornus* spp.), honeysuckle (*Lonicera* spp.), ash (*Fraxinus* spp.) and alder (*Alnus* spp.) (Bonter et al. 2007). Much of the surrounding habitat is managed seasonally to maintain an early-successional vegetative state dominated by woody fruiting shrubs.

Songbirds were captured with 30-mm-mesh mist nets that were operated daily (weather permitting) as part of the migration monitoring protocol at BBBO. Across all years, birds were captured in the spring season from mid-April until late-May and in the fall season from late-August until mid-October. Nets were opened just prior to sunrise and operated for a minimum of 6 h/d, with net checks to remove birds at least every 30 min. The following data were recorded for each bird: time of capture, age, sex, unflattened wing chord or length (to 0.5 mm), mass (to 0.01 g), and fat score on a scale of 0-5 (Helms and Drury 1960).

#### *Data analyses:*

I selected 12 sexually dimorphic warbler species for these analyses: Black-and-white Warbler (*Mniotilta varia*), Nashville Warbler (*Oreothlypis ruficapilla*), Mourning Warbler (*Geothlypis philadelphia*), Common Yellowthroat (*Geothlypis trichas*), American Redstart (*Setophaga ruticilla*), Magnolia Warbler (*Setophaga magnolia*), Blackpoll Warbler (*Setophaga striata*), Black-throated Blue Warbler (*Setophaga caerulescens*), Yellow-rumped Warbler (*Setophaga coronata*), Black-throated Green Warbler (*Setophaga virens*), Canada Warbler (*Cardellina*

*canadensis*), and Wilson's Warbler (*Cardellina pusilla*). I compiled and analyzed data that were collected during both spring and fall from 1999 until 2012. All data were collected on the first day of capture, assumed to be the arrival day for individuals at the site if birds arrive at or before dawn (see Moore et al. 1995, Dunn 2000); data for re-captured individuals were not included in these analyses. I included only individuals that could be reliably sexed by plumage, and individuals with obvious errors in wing length or mass measurements were eliminated. Julian arrival date for all individuals was determined for each season and year. To estimate energetic condition for each individual, I used unflattened wing length and body mass to calculate the scaled mass index (SMI) of body condition for all individuals (following Peig and Green 2009). Scaled mass index enabled me to adjust the mass of all individuals to reflect what it would be if its body size (i.e., unflattened wing length) was equal to the population mean. Therefore, the SMI is a size-corrected body mass that enabled comparison of the energetic condition of individuals within the population sample for each species.

Arrival date distributions for each species were graphed by sex and season (see Appendix) to determine if there were intraspecific differences in arrival time between males and females. I used linear regression analyses to investigate the relationship between energetic condition (SMI) and arrival date for all species; each season and sex were regressed separately for each species (see Appendix). For each species, the linear regression slopes (in grams/day) and average SMI (g) of all birds with a fat score of 0 were used to calculate a daily percent change from lean mass,

similar to Dunn (2002). This allowed for comparisons among species and between sexes and seasons within my data, in addition to enabling more direct comparisons to other studies. A paired t-test was used to determine if there were significant differences in daily percent mass changes between the sexes of all species in spring.

A general linear model (GLM) was used to determine if there were differences in energetic condition between seasons and sexes for each species; I created interaction plots to elucidate specific details about the energetic condition of males and females in spring and fall. The GLM used ANCOVA to investigate if arrival date was a significant co-variant for energetic condition across seasons and sexes, and allowed me to “control” for arrival date differences between sexes and seasons when comparing condition of the sexes. I standardized arrival dates to compare both spring and fall arrival for the ANCOVAs. Median arrival date was calculated for each season by year, and the differences between individual arrival date and median date (median arrival date was equal to zero) were used for the analysis. I determined the difference between male and female median Julian arrival dates for spring and fall across all species to elucidate differences in arrival time between sexes. All data met test-appropriate assumptions before analyses were conducted. SPSS version 21 (SPSS IBM, New York, U.S.A.) and Minitab 16 (Minitab Inc., Pennsylvania, U.S.A.) were used to perform the statistical analyses.

## Results

### *Arrival date:*

Males arrived at BBBO earlier than females for all 12 species during spring migration. Magnolia Warbler, American Redstart, and Wilson's Warbler showed the smallest springtime median arrival date difference between males and females (two days), and Black-and-white Warbler had the largest difference between median arrival dates (eight days) (Table 1). During fall migration, males of five species had earlier median arrival dates than females, females had earlier median arrival dates than males for five species, and two species (Yellow-rumped Warbler and Mourning Warbler) had no difference in median arrival date between sexes (Table 1). Complete arrival distributions for all 12 species are provided in the Appendix.

ANCOVA results for all species showed significant relationships between arrival date and condition (Table 2). Regression analyses revealed that energetic condition increased with arrival date at BBBO for both males and females of all species in the spring (Table 3, Appendix). Estimates of mean daily mass change during spring migration in females ranged from 0.1% (in Magnolia Warbler) to 1.2% (in Blackpoll Warbler), while mean daily mass change for spring males ranged from 0.2% (in Magnolia Warbler and American Redstart) to 1.2% (in Blackpoll Warbler) (Table 3). Mean daily mass change did not differ significantly between males and females among all 12 species during spring migration (T-value = -1.12, P = 0.288).

For fall migrants, regression analyses showed less consistent trends with arrival date (Table 3, Appendix). Four species in the fall (Blackpoll Warbler, American Redstart, Common Yellowthroat, and Wilson's Warbler) showed patterns similar to spring (i.e., energetic condition increased with arrival date at BBBO). Mean daily mass changes for these four species ranged from 0.2% (in American Redstart, Common Yellowthroat, and Wilson's Warbler) to 0.6% (in Blackpoll Warbler) for females and from 0.2% (in American Redstart, Common Yellowthroat, and Wilson's Warbler) to 0.5% (in Blackpoll Warbler) for males (Table 3). Four other species (Nashville Warbler, Black-throated Green Warbler, Black-and-white Warbler, and Canada Warbler) showed no significant relationship between arrival date and condition (Table 3). In the remaining four species (Magnolia Warbler, Black-throated Blue Warbler, Yellow-rumped Warbler, and Mourning Warbler), one sex had a significant regression between condition and the other did not (see Table 3 for a summary of intraspecific fall differences).

*Sex:*

ANCOVA results showed significant condition differences between males and females for all species except Mourning Warbler (Table 2); interaction plots show that females of all species were in better energetic condition than males when they arrived at BBBO (Fig. 1). Across all 12 species and both seasons, females were 5.5% heavier than males. The largest mean SMI difference between sexes occurred in Blackpoll Warblers, with females averaging 2.1 g (17.9%) more than males, while the

smallest difference was among American Redstarts with females weighing 0.2 g (2.1%) more than males (Table 2).

*Season:*

Results for ANCOVA showed a significant effect of season on the energetic condition of all 12 species (Table 2). In 11 species, energetic condition was higher in the spring compared to the fall (Fig. 1). The overall SMI increase between fall and spring for these 11 species was 4.3%. The greatest seasonal increase occurred in the Blackpoll Warbler; on average, birds had a mean SMI of 16.3% more in the spring than in the fall. Black-and-white Warbler showed the opposite seasonal pattern from the 11 other species, with a mean SMI difference of -2.1% between spring and fall (Table 2).

*Interaction between sex and season:*

Although the overall trends for sex and season among all species are stated above, three species (Magnolia Warbler, Yellow-rumped Warbler, and Blackpoll Warbler) showed a significant interaction between sex and season. In Magnolia Warbler and Blackpoll Warbler, males showed a greater difference in condition between seasons than did females. Magnolia Warbler males had a mean SMI of 5.5% more in the spring than in the fall, while females had a 1.9% higher mean SMI in the spring than during fall migration. Blackpoll Warbler males had a mean SMI 21.1% greater in the spring than in the fall; in comparison, females had a 5.3% higher mean SMI in the spring than during fall migration. In contrast to Magnolia and Blackpoll

warblers, Yellow-rumped Warbler females showed a greater seasonal difference than males; females had a mean SMI that was 8.3% higher in the spring compared to fall, while males had a seasonal average SMI difference of 3.6%.

## **Discussion**

### *Energy for breeding but not insurance?*

My results support the breeding performance hypothesis (Sandberg and Moore 1996). Particularly, females of all 12 Parulids were in better energetic condition than males upon arrival at my study site during spring migration. This finding is congruent with one prediction of the breeding performance hypothesis that, given the high energy demands of egg production, females should arrive on breeding grounds with more energy reserves than males (Sandberg and Moore 1996). Those energy reserves are likely accumulated at stopover locations *en route* to breeding grounds rather than on the wintering grounds. Females begin reproductive activities shortly after arriving on breeding grounds (Ojanen 1984), which may lend additional value to any fat reserves accumulated *en route*. However, like many species of songbirds, Parulids are income breeders (Langin et al. 2006), so any benefit incurred from arriving on breeding grounds with energy reserves would likely be indirect (e.g., beginning reproductive activities earlier) rather than direct (e.g., energy directed toward egg production).

My results are complicated slightly by my finding that females are in better energetic condition than males at my study site during both spring and fall migration; therefore, this sex difference may not be fully attributed to breeding activities. However, I found that 11 of the 12 species had greater energy reserves in the spring compared to fall, which suggests that individuals of both sexes are carrying more energy reserves in the spring to potentially use for reproductive activities. This also supports Sandberg and Moore's (1996) "spring fatter" hypothesis. Male reproductive activities, including acquisition and defense of territory and singing to attract females, also require energy expenditure, and therefore, both sexes have energetic demands related to breeding. In contrast to results for most species, Black-and-white Warblers at Braddock Bay showed an inverse seasonal pattern (i.e., both males and females were fatter in the fall). Reasons for this pattern are unclear, although it has been suggested that interspecific differences in migratory behavior and foraging ecology influence energetic condition during migration (Sandberg 1996).

I found that the energetic condition of all species increased with capture (assumed arrival) date during the spring; therefore, the earliest birds to arrive at my site in the spring were in lower energetic condition relative to later arrivals for all species. My findings for this study site contradict the insurance hypothesis' prediction that earlier arrivals should carry excess fat to northern breeding grounds as insurance against inclement or unpredictable weather earlier in the season (Sandberg and Moore 1996). A possible explanation for earlier migrants arriving with lower reserves is that conditions become more favorable later in the spring season and birds



are better able to gain mass *en route* (Bonter et al. 2007, Dunn 2000). Earlier in the spring, some migrants actually lose mass at northerly stopover sites, likely due to poor resource levels and/or thermoregulatory challenges (Dunn 2000).

*Braddock Bay as a penultimate stopover site: translating my results to the breeding grounds:*

Braddock Bay is not a breeding site for most of the species I examined, but could be an ultimate or penultimate stopover location for at least some of the species. The precise breeding location (i.e., remaining migratory distance) of the Parulids that stop over at Braddock Bay is unknown and variable. For instance, Blackpoll Warblers could breed anywhere from approximately 500 km to 6500 km from BBBO. I must, therefore, be cautious about any conclusions regarding the energetic condition of birds at this stopover location compared to arrival on their breeding grounds. Braddock Bay should provide adequate resources for most migrating songbirds, but habitat quality is likely better in the fall than in the spring for warblers and other species due to the delayed spring phenology caused by proximity to Lake Ontario (Bonter et al. 2007, Smith 2013). Bonter et al. (2007) demonstrated that energetic condition varies with time of day and, like others (e.g., Dunn 2002), used regression analyses to show that many species of migrants can gain mass even in one day while stopping over near Braddock Bay. In the spring, mean hourly mass change ranged from 0.33% to 1.13% of lean mass, with an average of 0.69% for 10 warbler species included in my study. In the fall, mean hourly mass change was higher overall than in the spring, and ranged from 0.79% to 1.58%, with an average of 1.03% for seven

warbler species in my study. Interestingly, my results show that these warblers arrived at Braddock Bay in poorer condition in the fall than in spring, and for this stopover site, fall migrants in poorer condition have the opportunity to gain more mass prior to continuing migration than they would in the spring. Likewise, the lower hourly mass gains upon arrival in the spring suggest that the differences in energetic condition between males and females will probably not be offset by additional mass gain at this stopover site. Hence, these mass differences are likely carried over to the bird's next migratory location (either another stopover site or their breeding grounds).

Measurements of condition, such as SMI or fat score determined from banding data, are static measurements and do not take into account dynamic differences in energy utilization that may occur between individuals. For example, males can refuel more quickly than females (Seewagen et al. 2013). Birds assimilate energy *en route*, so it is possible that patterns in energetic condition differ between stopover sites and breeding grounds. Males, for instance, may accumulate additional energy reserves more readily than females after departing from my study site. Dunn (2002), however, compared multiple stopover locations in spring and fall across Canada and found that several species of migrant male and female songbirds had low daily mass gains and thus were not depositing excessive fat stores *en route*. Accordingly, I believe that differences in the seasonal or sex-biased patterns in energetic condition between my stopover study site and arrival on breeding grounds likely would be small, particularly in the spring when most birds are under selective pressure to reach breeding grounds quickly (e.g., Smith and Moore 2003).

*Spatial heterogeneity in energetic condition: comparisons to other sites:*

A relatively quick review of literature examining energetic condition in birds demonstrates that results vary between locations, suggesting spatial heterogeneity that could reflect population differences, latitudinal differences related to the migratory journey, or habitat-specific effects (e.g., Dunn 2000). As in my study, Sandberg (1996) found that when males and females of nine passerine species arrived synchronously on near-Arctic breeding grounds in Swedish Lapland, females carried more fat reserves than males. Another study found that female Harris's Sparrows (*Zonotrichia querula*) arrived on low-Arctic Canadian breeding grounds with more fat reserves than males (Norment 1992). Closer to my study site, American Redstart (*Setophaga ruticilla*) females arrived with more fat than males on breeding grounds in northern Michigan (Smith and Moore 2003, 2005). Interestingly, Smith and Moore (2005) also found that earlier arriving American Redstarts are in better condition than later arriving individuals, which contradicts my findings at BBBO. Not all studies, however, have found female-biased energetic condition (see Yong et al. 1998, Morris et al. 2003).

Seasonal differences also vary across study sites. Both males and females of most species that I studied arrived with significantly greater fat reserves in the spring than in the fall, which is consistent with the findings of a study that compared the fat reserves of several Parulids in New York City (Seewagen 2008). However, contrary to my findings, a study that examined 16 passerine species captured near breeding grounds in Alaska found that most species were heavier in the fall than in the spring

(Benson and Winker 2005). While it has been suggested that birds arriving at high latitudes may not carry excess fat for breeding or insurance purposes (Dunn 2002, Benson and Winker 2005, but see Norment 2002), birds captured at my northerly stopover location are consistently in better condition during spring migration, which may reflect differences in mass gain at southerly sites. Given that many passerines are in low energetic condition after they cross the Gulf of Mexico (e.g., Moore and Kerlinger 1987, Loria and Moore 1990, Kuenzi et al. 1991, Yong and Moore 1997), they must accumulate energy stores at southern latitudes on their northward journey in the spring. This suggests that there is a degree of spatial variation in energetic condition of birds during spring migration and emphasizes the need to compare further the patterns in energetic condition of migrants across North America.

*Arrival time:*

During spring at my study site, males were captured earlier in the season than females for all species that I examined, which suggests that these 12 species have differential spring migration. Males in some species depart from wintering grounds before females (Marra et al. 1998), and males that arrive early might be able to secure high-quality territory and hence increase fitness (see Sandberg and Moore 1996, Kokko 1999). Interspecific arrival timing of males and females at my site varied during fall migration, which is not surprising given that timing of fall migration is contingent upon cessation of breeding and/or molting activities (e.g., Mitchell et al. 2012). Birds migrate more quickly, and likely more urgently, in the spring than in the

fall (e.g., Yohannes et al. 2009, Schmaljohann et al. 2012), which may help explain the arrival variation at my study site during fall migration.

My findings are consistent with a study by Smith and Moore (2005), which found that migrating male American Redstarts arrived before females at a study site in northern Michigan, but birds that bred at their study site did not show arrival date differences between sexes. Other studies on several Parulidae species across North America also found that males arrived before females during spring migration, including at Prince Edward Point, Ontario (Francis and Cooke 1986), at a site in New Mexico (Yong et al. 1998), on Appledore Island, Maine (Morris et al. 2003), and at several sites across Alaska (Benson et al. 2006). My fall results are also consistent with other studies, which did not find meaningful differences between the arrival of male and female warbler species during fall migration (e.g., Yong et al. 1998, Carlisle et al. 2005).

The advantage of excess fat should not be considered without also considering arrival time differences among individuals. There is evidence, in both sexes, that high-quality individuals arrive on breeding grounds earlier (e.g., Cooper et al. 2011), and arriving early confers increased reproductive success (Smith and Moore 2003, 2005, Cooper et al. 2011). Therefore, it should be beneficial for both sexes to arrive early on breeding grounds and with excess energy reserves to offset the energetic demands of reproductive activities (e.g., Sandberg and Moore 1996). Both males and females are time-minimizers during spring migration, but males may show more time-minimization than females (Dierschke et al. 2005).

*The unknown—migratory phenotypes:*

It is worth considering that populations of migratory birds are not equal in migratory phenotype; furthermore, there may be behavioral phenotypes that I unknowingly grouped together in my analyses. For instance, Møller (1994) found that individual variation in the arrival timing of Barn Swallows (*Hirundo rustica*) was dependent on a phenotypic quality – high-quality males had longer tails and arrived earlier. Birds are under selective pressure to arrive early on breeding grounds, which may result in some phenotypes being more risk-prone than others. Therefore, perhaps some early males arrived at my study site with lower energy reserves than later arrivals because they were risking a negative trade-off by arriving earlier on breeding grounds, whereas the risk-averse phenotypes arrived later but in better condition. Differences among migratory phenotypes (e.g., risk-prone vs. risk-averse) might explain some of the variation in energetic patterns within my data, particularly at different times of the season or when birds are present at different densities (e.g., Kelly et al. 2002).

*Conclusion:*

In conclusion, I found a variety of patterns in the energetic condition of birds arriving at my study site, which show support for the breeding performance hypothesis but not the insurance hypothesis (Sandberg and Moore 1996). My findings elucidate seasonal differences in the energetic condition of 12 warbler species that used stopover habitat near BBBO. Although I found several interesting energetic condition patterns, I cannot make conclusive statements about how the

energetic condition of birds in my study affected their reproductive performance. However, given my finding that both males and females are consistently heavier during spring migration when resources are scarcer than during fall (e.g., Bonter et al. 2007), I can cautiously conclude that there is a possible reproductive advantage to arrive with excess fat reserves during spring migration.

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## Tables and Figures

Table 1. Median Julian arrival (capture) dates at Braddock Bay Bird Observatory for males and females of 12 warbler species during spring and fall migration. Difference shows female median minus male median date; a positive difference indicates that males arrived earlier than females. Complete distributions of arrival dates are provided in the Appendix.

Species	Season					
	Spring			Fall		
	<i>male</i>	<i>female</i>	<i>difference</i>	<i>male</i>	<i>female</i>	<i>difference</i>
Black-and-white Warbler	127	135	8	253	254	1
Nashville Warbler	128	135	7	263	260	-3
Mourning Warbler	143	148	5	241	241	0
Common Yellowthroat	138	143	5	255	254	-1
American Redstart	142	144	2	253	255	2
Magnolia Warbler	141	143	2	251	250	-1
Blackpoll Warbler	145	148	3	260	261	1
Black-throated Blue Warbler	134	141	7	261	263	2
Yellow-rumped Warbler	124	128	4	276	276	0
Black-throated Green Warbler	134	140	6	259	263	4
Canada Warbler	143	146	3	241	238	-3
Wilson's Warbler	144	146	2	250	249	-1

Table 2. ANCOVA results for 12 warbler species captured at Braddock Bay Bird Observatory between 1999 and 2012. Results show effect of sex and season on energetic condition with arrival date as a covariate. This table also includes the percent differences in mean energetic condition (SMI) between sexes and seasons. Energetic condition differences were determined by calculating the percent increase in female SMI compared to male for sex differences and percent increase (or decrease in Black-and-white Warblers) in spring SMI for both sexes compared to fall for seasonal differences.

Species	<i>n</i>	Sex		Season		Arrival Date	
		<i>F</i>	<i>Energetic condition difference</i>	<i>F</i>	<i>Energetic condition difference</i>	<i>F</i>	<i>P</i>
Black-and-white Warbler	571	17.19**	6.6%	4.03*	-2.1%	31.19	0.000
Nashville Warbler	1041	81.86**	4.9	73.92**	4.3	28.78	0.000
Mourning Warbler	551	1.41	2.9	5.47*	3.9	39.54	0.000
Common Yellowthroat	2650	40.56**	4.0	4.15*	1.3	118.8	0.000
American Redstart	3129	23.55**	2.1	40.09**	1.6	109.29	0.000
Magnolia Warbler***	4604	123.91**	3.2	157.44**	4.0	250.86	0.000
Blackpoll Warbler***	1189	375.31**	17.9	196.74**	16.3	83.41	0.000
Black-throated Blue Warbler	2160	268.75**	6.7	17.22**	1.8	31.66	0.000
Yellow-rumped Warbler***	2493	95.18**	6.9	117.00**	5.0	87.37	0.000
Black-throated Green Warbler	560	15.28**	3.3	19.49**	3.5	20.24	0.000
Canada Warbler	936	25.65**	5.1	1.75	1.0	19.79	0.000
Wilson's Warbler	1890	48.91**	3.0	129.82**	4.7	52.79	0.000

\*\*\*Significant interaction effect between sex and season ( $P < 0.005$ )

\* $P \leq 0.05$ , \*\* $P \leq 0.005$

Table 3. Regression analysis results by sex for arrival date vs. energetic condition of 12 warbler species captured at Braddock Bay Bird Observatory between 1999 and 2012 during both spring and fall migration. For each species, the linear regression slopes (in grams/day) and average SMI (g) of all birds with a fat score of 0 were used to calculate mean daily percent change from lean mass. Regression plots for each sex for all 12 species are shown in the Appendix.

Species	Sex					
	Female			Male		
	<i>n</i>	<i>F</i>	<i>Daily mass change</i>	<i>n</i>	<i>F</i>	<i>Daily mass change</i>
<b>Spring Migration</b>						
Black-and-white Warbler	258	18.09**	0.3%	222	30.81**	0.5%
Nashville Warbler	253	13.37**	0.3	495	51.20**	0.4
Mourning Warbler	274	16.95**	0.5	246	26.97**	0.5
Common Yellowthroat	901	41.49**	0.4	1163	95.22**	0.3
American Redstart	1333	28.70**	0.2	1393	45.76**	0.2
Magnolia Warbler	947	6.48*	0.1	1752	17.56**	0.2
Blackpoll Warbler	373	53.35**	1.2	342	52.57**	1.2
Black-throated Blue Warbler	702	22.12**	0.3	493	52.48**	0.4
Yellow-rumped Warbler	800	81.40**	0.5	1258	68.53**	0.4
Black-throated Green Warbler	100	4.35*	0.2	182	27.70**	0.3
Canada Warbler	452	13.15**	0.3	418	13.24**	0.3
Wilson's Warbler	292	10.83**	0.4	1088	57.11**	0.4
<b>Fall Migration</b>						
Black-and-white Warbler	49	2.91	0.2%	42	0.12	0.1%
Nashville Warbler	164	0.11	0.0	129	3.72	0.2
Mourning Warbler	14	7.19*	0.5	17	1.94	0.5
Common Yellowthroat	129	4.59*	0.2	456	8.12**	0.2
American Redstart	214	17.23**	0.2	189	9.02**	0.2
Magnolia Warbler	429	1.72	-0.1	1403	16.82**	0.1
Blackpoll Warbler	171	18.87**	0.6	303	26.31**	0.5
Black-throated Blue Warbler	506	26.06**	0.2	459	1.29	0.0
Yellow-rumped Warbler	226	0.1	0.0	209	7.11*	0.2
Black-throated Green Warbler	55	0.46	0.1	96	3.07	0.1
Canada Warbler	33	0.51	0.2	33	0.33	0.1
Wilson's Warbler	191	5.25*	0.2	319	13.61**	0.2

\* $P \leq 0.05$ , \*\* $P \leq 0.005$



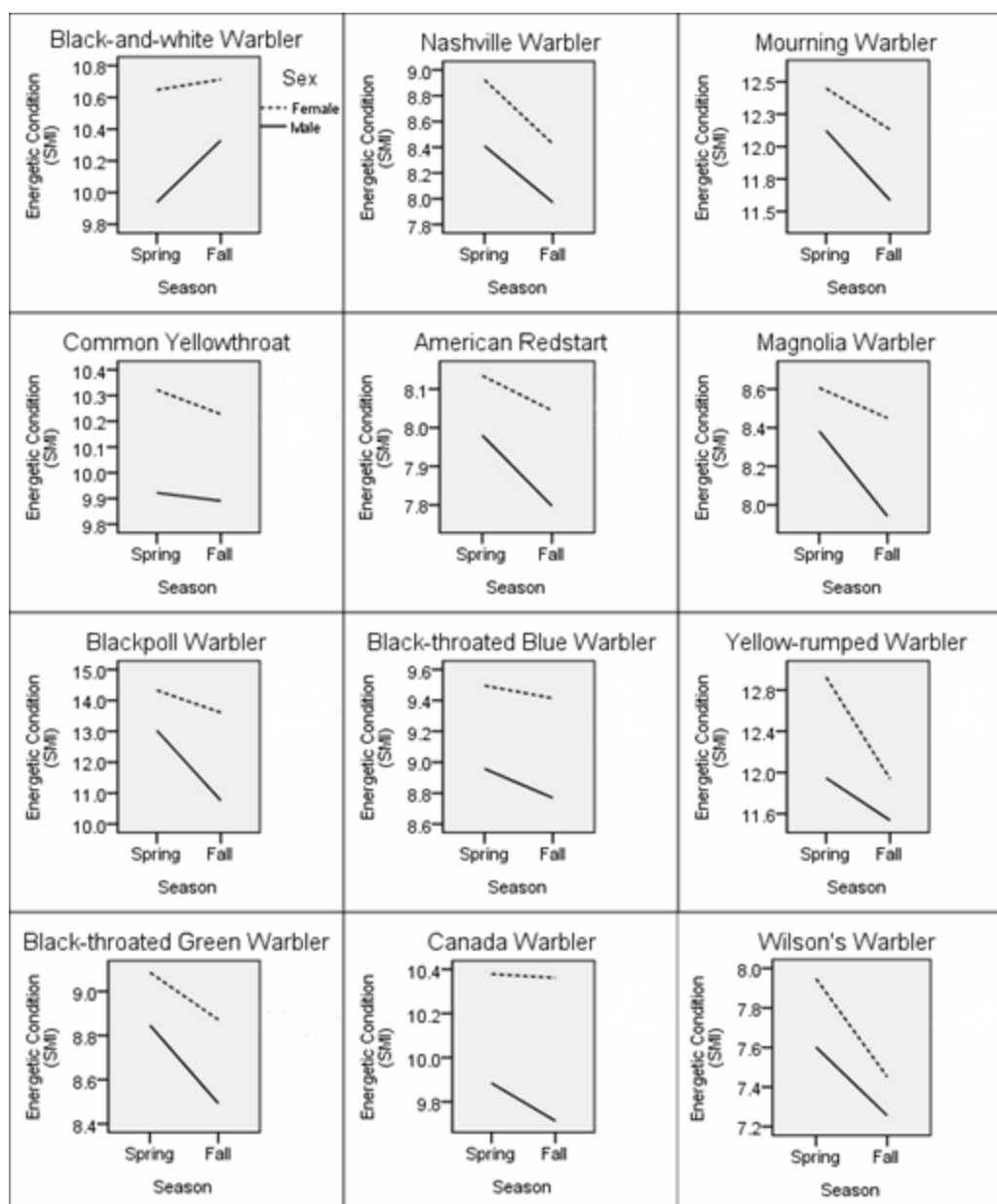


Figure 1. Interaction line plots for 12 warbler species captured at the Braddock Bay Bird Observatory showing the effect(s) of season and sex on energetic condition. SMI is reported in grams; female data are represented with a dashed line and a solid line is used for male data.

**Part Two: A longitudinal study to examine the causal relationship between energetic condition and orientation in White-throated sparrows (*Zonotrichia albicollis*)**

**Introduction**

Migration is arguably the most vulnerable and unpredictable part of a bird's annual cycle, since the preponderance of annual songbird mortality may occur during migration (Sillett and Holmes 2002). For birds to complete migration successfully they must coordinate complex environmental and physiological cues to determine accurately the timing, distance, and orientation of their movements to navigate to seasonally appropriate locations (see Åkesson and Hedenström 2007). Navigation and orientation during migration involve the integration of several exogenous cues such as skylight polarization, star patterns, angle of the sun at sunset, and information from the geomagnetic field (Muheim et al. 2006, Deutschlander and Beason 2014). However, other exogenous cues (e.g., weather conditions) and endogenous cues (e.g., energy reserves) can also influence a bird's motivation to migrate and orient appropriately (e.g., Sandberg 2003, Fusani et al. 2009).

Migratory songbirds may encounter several challenges *en route*: adverse weather conditions (Newton 2007), predators (Schmaljohann and Dierschke 2005), the need to locate resources in unfamiliar environments (see Newton 2006), depleted food resources (Kelly et al. 2002), resource competition (Moore and Yong 1991), and the need to correct for navigational errors (Ralph 1978). Many migrating birds alternate between active, orientated nocturnal flight behavior (so-called Zugunruhe)

and extended periods of feeding to replenish energy reserves, or Zugdisposition (see Ramenofsky and Wingfield 2006). Birds must deposit adequate energy stores to complete migration successfully; amazingly, long-distance intercontinental migrants can accumulate fat deposits representing up to 50% of their total body mass (Blem 1990). Stopover habitats along migratory routes provide key locations where birds can replenish these critical energy reserves, in addition to seeking respite, shelter, and/or waiting for favorable weather (e.g., Moore and Kerlinger 1987).

The amount of stored energy (i.e., fat) that a migratory bird possesses influences many behaviors during spring and fall stopover. A bird's energetic condition is a physiological constraint during migration that may affect its length of stay and departure (Cherry 1982, Winker et al. 1992, Yong and Moore 1997, Gannes 2002, Seewagen and Guglielmo 2010), rate of fat deposition and foraging behavior (Loria and Moore 1990, Schaub and Jenni 1999, Ktitorov et al. 2010), habitat and food selection (Bairlein 1985, Biebach et al. 1986, Ydenberg et al. 2002, McWilliams et al. 2004), orientation (Deutschlander and Muheim 2009), and Zugunruhe (Fusani et al. 2009, Eikenaar and Bairlein 2014). Length of stay at a given stopover location varies and is influenced by a myriad of factors. However, in general, birds spend a substantial proportion of their migratory journey at stopover locations, and songbirds can expend energy, in addition to gaining energy, during stopovers (Hedenström and Alerstam 1997). Therefore, a bird's overall migration length is constrained by how long it spends at stopover locations.

Ecological barriers to migration—areas where birds cannot stop for refueling (e.g., bodies of water, mountain ranges, and deserts)—present migrating birds with the dichotomous choice of either crossing the barrier or circumventing it (e.g., Stutchbury et al. 2009). Therefore, stopover habitat in close proximity to ecological barriers is particularly important because birds may need to replenish energy reserves urgently, either just prior to or just after crossing a barrier. When faced with a large ecological barrier, migrants in lean energetic condition may alter their migratory trajectory and reorient themselves in seasonally unexpected or even temporarily reversed directions (e.g., southward during spring migration), possibly to locate suitable habitat for refueling before continuing with migration (Alerstam 1978). Reorientation of birds in lean energetic condition occurs near aquatic ecological barriers, such as along ocean or gulf coastlines (Lindström and Alerstam 1986, Åkesson et al. 1996, Sandberg and Moore 1996a, Sandberg et al. 2002, Covino and Holberton 2011, Smolinsky et al. 2013), on island stopover locations (Fitzgerald and Taylor 2008, Schmaljohann et al. 2011), and along lakeshores (Deutschlander and Muheim 2009). Reorientation behavior near ecological barriers has been observed during free-flying experiments (e.g., Sandberg and Moore 1996a), cage experiments (e.g., Deutschlander and Muheim 2009), and a combination of both (Sandberg et al. 2002). Oftentimes, birds with low energy reserves orient themselves either away from or parallel to a barrier, while birds with adequate energy reserves continue forward migration. However, conflicting orientation behavior between birds in lean and fat energetic condition is not always observed, and a bird's migratory orientation

is likely influenced by many exogenous and endogenous factors, such as environmental conditions, resource availability, competition, stage of migratory journey, or stress (e.g., Korner-Nievergelt et al. 2002, Ilieva et al. 2012).

Although many studies show correlation between energetic condition and orientation, no published study to date was designed to test for a causal effect of energetic condition on orientation. Bäckman et al. (unpublished) conducted a repeated measures orientation experiment with Red-eyed Vireos (*Vireo olivaceus*) and found that fat loads were an important factor for orientation of individuals (see Sandberg 2003). I conducted a longitudinal (i.e., repeated measures) orientation cage experiment on White-throated Sparrows (*Zonotrichia albicollis*), a North American temperate migrant, to determine if energetic condition directly affected individual orientation at an ecological barrier. Birds were caught and tested at the Braddock Bay Bird Observatory (BBBO) on the south shore of Lake Ontario; White-throated Sparrows previously tested at this stopover location showed correlative (not direct) responses between condition, or fat levels, and seasonally-appropriate orientation (Deutschlander and Muheim 2009). I kept individual sparrows on semi-synthetic diets to manipulate their mass gain and loss, and then tested them for orientation three times: in their original condition (e.g., lean), after their condition changed on a manipulated diet (e.g., to fat from lean), and then again after they returned to their original condition (e.g., lean). I hypothesized that a change in individual energetic condition would cause a change in an individual's orientation. Specifically, when a bird was in fat energetic condition, I expected orientation in a seasonally appropriate

direction. In contrast, I expected that the same bird in lean energetic condition would either orient away from Lake Ontario or show disorientation (as in Deutschlander and Muheim 2009).

## **Methods**

### *Study site and dates:*

All experiments were conducted in the orientation laboratory at BBBO during fall of 2012 and spring of 2013. Braddock Bay Bird Observatory is located on the south shore of Lake Ontario near Rochester, Monroe County, New York, USA (43° 19'N, 77° 43'W W; total intensity of the geomagnetic field: ~54,500 nT; inclination: 70.5 deg.; declination: -12 deg.). A straight-line distance across Lake Ontario at this longitude is approximately 75 to 80 km.

### *Bird capture and processing:*

All birds were captured between 0.5 and 6 h after sunrise with 30-mm-mesh mist nets, which were operated daily (weather permitting) as part of the migration monitoring protocol at BBBO. Permits were obtained through the U.S. Fish and Wildlife Service and the New York State Department of Environmental Conservation to house birds up to 14 days for these experiments. For each bird, I recorded time of capture, age, unflattened wing length, mass (to nearest 0.01 g on a digital electronic balance), and visual subcutaneous fat estimate (where 0 = no visible fat, 1 = trace of fat visible in furcular region, 2 = furcular region lined with fat, 3 = furcular region

full and some fat on abdomen, 4 = furcular region convex and fat visible on abdomen, 5 = furcular region convex and abdomen mounded, following Helms and Drury [1960]). For testing and analyses, birds with a visual fat score of  $\geq 3$  were classified as fat, while those with a fat score of  $\leq 1$  were considered lean (similar to Deutschlander and Muheim 2009); however, due to time constraints, a small number of birds were tested with a fat score of 2. Mass and fat score were repeatedly assessed for each individual throughout the experiment (see below). Both white and tan morph individuals were used in these experiments, but due to the small number of birds tested each season, morph was not considered in my analyses. Although refueling rates may vary between morphs, body fat and lean mass do not, likely because rate differences are offset by morph-specific competitive behaviors and stopover duration (Brown et al. 2014).

*Diet and feeding:*

Birds were held indoors with minimal human disturbance at BBBO in individual bird cages (41 x 36 x 41 cm). A natural photoperiod was provided by diffuse lighting through frosted windows. All birds were given access to food and water *ad libitum* during an initial acclimation period (usually two days). Any bird that did not eat, showed signs of excessive weight loss, or that appeared lethargic during acclimation was released. After acclimation and initial testing for orientation, lean healthy birds were given *ad lib* access to food to increase their energetic condition (i.e., fat score) while fat birds were fed a restricted caloric diet (approximately 50% of their *ad lib* intake) to decrease their energetic condition.

Birds were fed a semi-synthetic diet high in carbohydrates, which simulated a seed/grain diet (Table 1) (following Smith et al. 2007). Birds were also fed a small amount of cracked corn during the acclimation period. Food consumption was continually monitored while birds were held in captivity. Bird mass and fat score were recorded daily or bi-daily.

*Orientation testing:*

Each bird was tested for orientation three times; within two days of when the bird was first caught, within two days after its energetic condition changed (e.g., from lean to fat), and again within two days after the bird returned to its original energetic condition. Prior to each test, birds were placed in an open field at sunset (when the sun was no longer visible on the horizon) for one hour in small, non-magnetic cages. This allowed birds access to natural magnetic and celestial cues, including the horizon and zenith, for internal compass calibration (following Deutschlander and Muheim 2009, Muheim et al. 2009). Testing was carried out in a building on-site, separate from where the birds were housed for feeding. The geomagnetic field properties in the open field were 54,400 nT in total intensity and 70.4° in inclination. In the testing facility, the geomagnetic field properties ranged from 51,500 to 54,500 nT in total intensity and 64.1°-69.6° in inclination. Geomagnetic field parameters were measured with a 3-axis magnetometer (model #539, Applied Physics Systems).

Orientation was assessed for approximately 60 min in round Emlen-style funnel cages (Emlen and Emlen 1966) covered in plastic window screening, which allowed visual observation of the birds from above but prevented escape. Up to six



orientation cages were placed inside a large wooden framed cube (approximately 2 m square) covered with white sheets on the top and the sides (see Fig. 1). Light was provided from outside the sheets using tungsten halogen bulbs. The lighting and white sheets created uniform illumination in the orientation testing area; therefore, during testing birds only had access to geomagnetic compass information for orientation. Lighting in the testing area was measured in multiple directions with an Ocean Optics USB2000 spectrophotometer to ensure uniformity. During testing, bird movements within the funnel cages were video-recorded with security cameras and a standard DVR (AGI Security VC-SYS-4CDIYBK provided by Leadertech USA). One camera was mounted overhead in each of two wooden frames and recorded up to six birds simultaneously (each funnel was fully visible within the video frame).

*Data analyses:*

BirdOriTrack, which was written specifically to analyze the orientation behavior of passerines, was used to analyze all video recordings (Muheim et al. 2014). The program determined bird orientation by extracting positional information from video frames and determining a bird's position relative to the center of the Emlen funnel every time the bird moved out of the center. For each test, mean direction ( $\alpha$ ), mean vector length ( $r$ ), P-value (for both unimodal and axial distributions), number of counted positions or "valid hops" ( $n$ ), and total activity levels (summed length of a bird's movement binned over 30-sec intervals relative to radius of the funnel) for both unimodal and bimodal (or axial) distributions were determined (see Fig. 2). Relative vector lengths from raw bearings and doubled-

bearings were used to determine whether individuals were oriented unimodally or bimodally, respectively (Batschelet 1981). For bimodally oriented birds, the end of the axis with the most hops was used for subsequent analyses because it likely indicated the direction birds were most oriented toward.

For each season, birds were grouped according to energetic condition (fat or lean) and corresponding test number (one, two, or three). Group orientation was tested in two ways – relative to magnetic north and relative to each bird's initial orientation (similar to Muheim et al. 2009). All initial tests (i.e., test one data) were analyzed only for orientation relative to magnetic north. Subsequent tests were analyzed for orientation relative to magnetic north and for orientation relative to each bird's initial orientation (i.e., plotted as the deflection or change in orientation from each bird's original orientation in test one). Mean vectors ( $\mu$ ) and length of mean vectors ( $r$ ) for each group (based on the orientation of all birds within groups) were analyzed for significant orientation with Raleigh's test of uniformity. As for individual orientation, group orientation was tested for both unimodality and bimodality. Additionally, a Watson's  $U^2$  test was used to determine if there were differences in orientation between fat birds and lean birds across groups. Oriana software (Kovach Computing) was used to calculate all circular statistics. I used repeated measures ANOVA to elucidate possible differences in individual activity levels and/or hops among tests (i.e., energetic condition) and between seasons. Assumptions associated with this parametric test were satisfied. SPSS version 21 (SPSS IBM, New York, U.S.A.) was used to perform these statistical analyses.

## Results

### *Condition: mass, fat, and age:*

Because most sparrows captured at BBBO during fall 2012 were in lean condition, I was only able to test birds in a lean-fat-lean testing order. The average mass for lean birds at their initial test was  $25.0 \pm 1.6$  g, while fat birds weighed an average of  $27.2 \pm 2.3$  g (roughly 9% heavier than the average initial mass), and the average mass for birds restored to original (lean) condition for their third test was  $24.2 \pm 2.3$  g (Table 2). Fat scores ranged from 0 to 2 for lean birds and from 2 to 3 for fat birds. It took birds an average of  $9 \pm 2$  days to fatten from lean condition and  $5 \pm 2$  days to lose mass before they were tested again in lean condition. All of the birds tested in fall 2012 were aged as hatch-year (HY), or birds on their first migration.

Most birds in spring 2013 were captured in fat condition, and therefore, I only tested birds with a fat-lean-fat testing order. The average mass of sparrows was  $27.3 \pm 2.3$  g during the first test. For the second and third tests (lean and fat condition, respectively), birds weighed an average of  $22.1 \pm 1.6$  g (roughly 20% less than their initial mass) and  $25.9 \pm 2.0$  g, respectively. Fat scores ranged from 3 to 4 for fat birds and from 0 to 1 for lean birds. On average, fat birds took  $8 \pm 3$  days to lean out and  $4 \pm 2$  days to fatten prior to their final orientation test. Most birds tested in spring 2013 were of unknown age, specified as after-hatch-year (AHY); six were aged second-year (SY) or birds on their first return migration.

*Orientation:*

During fall 2012, all sparrows were tested in a lean-fat-lean energetic condition sequence (see Table 3 for individual bird data and Fig. 3 for group analyses). When first tested in lean condition, the mean orientation of all lean birds was significantly bimodal, oriented along a northwest-southeast (NW-SE) axis, with mean vector of  $118^{\circ}$ - $298^{\circ}$  ( $\pm 16^{\circ}$ ,  $r = 0.514$ ,  $Z = 5.02$ ,  $P = 0.005$ ). When the birds were tested subsequently in fat condition, the group orientation relative to magnetic north was very similar to the initial test (Watson's  $U^2 = 0.092$ ,  $0.5 > p > 0.2$ ,  $df = 17, 19$ ); during test two, the group oriented bimodally along a NW-SE axis, with mean vector of  $136^{\circ}$ - $316^{\circ}$  ( $\pm 18^{\circ}$ ,  $r = 0.432$ ,  $Z = 3.17$ ,  $P = 0.04$ ). However, when the bearings were analyzed relative to initial orientation, the overall distribution of deflections from their original orientation for the group was weakly, bimodally oriented, with a mean vector of  $22^{\circ}$ - $202^{\circ}$  ( $\pm 19^{\circ}$ ,  $r = 0.421$ ,  $Z = 3.02$ ,  $P = 0.05$ ). Nine of the birds oriented in a similar direction in test one and two, while eight of the birds in test two oriented in roughly the opposite direction of their initial test.

Lastly, during the third test, when the birds were returned to a lean energetic condition, the group again oriented bimodally along a NW-SE axis relative to magnetic north ( $127^{\circ}$ - $297^{\circ} \pm 14^{\circ}$ ,  $r = 0.604$ ,  $Z = 6.94$ ,  $P = 0.0005$ ), not significantly different from the orientation in test one (Watson's  $U^2 = 0.087$ ,  $0.5 > p > 0.2$ ,  $df = 19, 19$ ). However, when the bearings were analyzed relative to initial orientation, the overall distribution of deflections from their original orientation for the group was strongly bimodal with a mean vector of  $25^{\circ}$ - $205^{\circ}$  ( $\pm 15^{\circ}$ ,  $r = 0.421$ ,  $Z = 6.17$ ,  $P <$

0.001). Nine of the birds oriented in a similar direction in tests one and three, while 10 of the birds in test three oriented roughly in the opposite direction of their initial test. Between tests two and three, about one third of the birds switched their orientation (see Table 2). In summary, the overall group orientation was NW-SE regardless of condition, but half of the individuals switched their orientation after they were fed *ad lib* and increased fat stores, and one-third changed their orientation when they were returned to a lean condition.

During spring 2013, birds were tested with a fat-lean-fat sequence (see Table 4 for individual bird data and Fig. 4 for group analyses). As during fall 2012, the distribution of bearings for birds tested in the spring was bimodally oriented along a NW-SE axis regardless of condition; mean vectors were  $131^{\circ}$ - $311^{\circ}$  ( $\pm 16^{\circ}$ ,  $r = 0.510$ ,  $Z = 4.97$ ,  $P = 0.006$ ),  $146^{\circ}$ - $326^{\circ}$  ( $\pm 20^{\circ}$ ,  $r = 0.367$ ,  $Z = 2.29$ ,  $P = 0.1$ ), and  $146^{\circ}$ - $326^{\circ}$  ( $\pm 16^{\circ}$ ,  $r = 0.534$ ,  $Z = 5.14$ ,  $P = 0.005$ ), for tests one, two, and three, respectively. When analyzed with respect to magnetic north, the overall group orientation did not change between tests one and two or tests one and three (Watson's  $U^2 = 0.057$ ,  $P > 0.05$ ,  $df = 17, 19$  and Watson's  $U^2 = 0.135$ ,  $0.2 > P > 0.1$ ,  $df = 18, 19$ ). However, when I analyzed the bearings of each individual relative to its initial orientation, a different result was apparent. In test two, when birds were tested in a lean condition, the overall distribution of bearings relative to their initial orientation did not differ significantly from random ( $r = 0.069$ ,  $Z = 0.082$ ,  $P = 0.924$ ); when birds changed from fat to lean, they randomly changed directions from their initial preferred orientation. In test three, after birds were fed *ad lib* and returned to their initial fat

condition, the overall distribution of bearings relative to their initial orientation was unimodally oriented toward their initial direction ( $352^\circ \pm 36^\circ$ ,  $r = 0.452$ ,  $Z = 3.67$ ,  $P = 0.023$ ); most birds oriented toward their initial direction after they returned to their original fat energetic condition.

#### *Activity levels:*

Traditionally in orientation tests, some estimate of the number of hops is used as a surrogate measurement of migratory activity of Zugunruhe. In BirdOriTrack, both the number of hops and an estimate of activity based on distance moved are determined for each test. Figure 5 shows a direct linear relationship between activity levels based on distance moved and number of counted hops for all birds tested in fall 2012 and spring 2013. For each season, ANOVA revealed no differences in either the number of hops or the activity levels (i.e., distance moved) for individuals among the three orientation tests (all P-values > 0.05). Additionally, I found no significant seasonal differences in either the activity levels or number of hops for tested individuals (all P-values > 0.05).

## **Discussion**

When analyzed relative to magnetic north (for an “absolute” direction), the White-throated Sparrows tested were unexpectedly well-oriented along a NW-SE axis in all tests (Figs. 3 and 4). When analyzed as a group, birds did not show seasonally appropriate **unimodal** orientation (e.g., north in the spring) or reverse orientation

based on condition, but rather showed consistent **bimodal** orientation along the correct axis for orientation regardless of condition (similar to Muheim et al. 2009, who tested this species at the same location in a similar short-term captive study – see below). Moreover, there were no differences in the amount of activity, or Zugunruhe, between seasons or among birds in different conditions. I did not expect the amount of Zugunruhe to differ among birds with different levels of energy reserves given that other studies have not found a relationship between the energetic condition of White-throated Sparrows and level of migratory restlessness at BBBO (Smith and Norment 2005, Deutschlander and Muheim 2009). My goal, however, was to determine how a change in condition affected individual orientation or Zugunruhe. Therefore, the most appropriate analysis for my longitudinal study was to examine the orientation of individuals and determine how each individual changed its orientation with condition. Accordingly, I analyzed each individual's orientation in tests two and three relative to its initial orientation in test one. Comparison of test two to test one enabled me to see how a change in condition affected orientation, while the comparison of test three to test one enabled me to see if restoring original condition resulted in a return to initial orientation.

Birds tested during spring 2013 were initially in fat condition; hence, they should have been highly motivated to migrate in a seasonally appropriate direction (e.g., Deutschlander and Muheim 2009); the bimodal NW-SE orientation of these birds is consistent with another study that held sparrows in captivity for extended periods (Muheim et al. 2009). When plotted relative to their initial orientation, it is

apparent that fat birds, after they were induced to lose fat and mass, showed random orientation during test two relative to their well-oriented “control” direction in test one (Fig. 4). This implies that birds lacked motivation to migrate or orient appropriately (despite activity levels comparable to their initial test), which might indicate dispersal behavior in lean White-throated Sparrows, as suggested by Deutschlander and Muheim (2009). After gaining fat and mass, the majority of individuals oriented in a direction similar to their initial orientation (Fig. 4), which suggests that birds’ motivation to migrate and orient in a seasonally appropriate direction returned when their fuel reserves increased. Therefore, the spring 2013 data suggest that decreasing fat mass results in less consistent individual orientation, while increasing fat mass restores a consistent orientation response. Reorientation behavior and/or lack of migratory motivation of lean birds prior to crossing an ecological barrier has been documented in many species of migratory songbirds in the fall (e.g., Lindström and Alerstam 1986, Sandberg et al. 1991, Åkesson et al. 1996, Sandberg et al. 2002, Covino and Holberton 2011) and the spring (Schmaljohann et al. 2011).

Interpretation of the fall 2012 results is slightly more complex because the birds were initially tested in lean condition – when they should be least motivated to show oriented *Zugunruhe* (Deutschlander and Muheim 2009). Surprisingly, these lean birds also were well-oriented along a NW-SE axis when initially tested, but when these birds gained mass and fat, many (about half of tested individuals) oriented opposite of their initial orientation in test one (Fig. 3). When birds were tested a third time, once again in lean condition, about half of the birds oriented opposite to their



initial orientation and the other half oriented towards their initial direction (Fig. 3); about one-third of individuals showed orientation in a different direction from the previous test (compare tests two and three in Table 3). Like the spring results, a portion of the birds tested during fall changed their orientation with energetic condition, but these results are less consistent than during spring, and I cannot exclude the alternative explanation that birds were randomly switching their orientation between ends of the preferred axis of orientation for migration.

The spring data clearly show an effect of condition on orientation, while the fall data are much less conclusive. There are several possible explanations for the differences in my results between spring and fall. First, during spring migration, birds are under selective pressure to reach breeding grounds quickly (e.g., Sandberg and Moore 1996b, Smith and Moore 2005). During the fall there is likely less selective pressure to reach winter grounds, particularly for temperate migrants, such as White-throated Sparrows, and migration occurs at a slower pace (e.g., Yohannes et al. 2009, Schmaljohann et al. 2012). Second, all birds tested in the fall were hatch-year (HY) birds with no previous migration experience (birds tested in the spring had all previously migrated). Age and inexperience might have affected the orientation responses of the birds tested in this study (as in Ralph 1978, Moore 1984, but see Korner-Nievergelt et al. 2002, Smolinsky et al. 2013). Third, the location of my test site relative to an ecological barrier (Lake Ontario) differs between seasons. In the spring, birds at Braddock Bay are faced with crossing the barrier, while in the fall birds had crossed the barrier prior to reaching my site and, therefore, reorientation is

not necessary in the fall. Sandberg and Moore (1996a) found that lean Red-eyed Vireos (*Vireo olivaceus*) oriented in a seasonally appropriate direction after crossing the Gulf of Mexico during spring migration, which could represent a situation similar to that of birds tested during the fall at Braddock Bay. Fourth, it is difficult to make direct comparisons between the fall and spring experiments because birds were not tested in the same energetic condition sequence. Initially testing birds in each season in fat condition would make my results easier to interpret because I expect birds to be most motivated to migrate in fat condition. Finally, the winter range of this species includes the study site (Falls and Kopachena 2010); therefore, it is possible that some of the individuals I studied in the fall were ceasing migration. However, overall activity levels were similar in the fall and spring, which suggests that Zugunruhe levels were similar.

It is also worth noting that White-throated Sparrows are short-distance migrants and may not need excessive fat reserves before continuing migration because they are not making long, intercontinental flights. There are well-documented differences between the migratory activities of long- and short-distance migrant species; short-distance migrants tend to demonstrate more variation in body mass and migratory activity compared to long-distance migrants (e.g., Gwinner 1972, Yong and Moore 1993). There is also evidence that distance to the next stopover location or goal can affect the departure decisions and stopover behavior of migrants. Dierschke and Delingat (2001) found that Northern Wheatears departing the North Sea island Helgoland differed in their energetic strategy based on their goal;

individuals closer to their goal departed more quickly – irrespective of energetic condition or weather – compared to birds that were farther from their destination. Likewise, Long and Stouffer (2003) found that body mass (an indicator of a bird's energetic condition) was not a good predictor of Zugunruhe in Hermit Thrushes (*Catharus guttatus*), a short-distance migrant. Energetic condition, therefore, might not be a reliable or strong predictor of migratory readiness or orientation in White-throated Sparrows and other short-distance migrants because they are not making extensive migrations. This may help explain, in conjunction with other factors, why I found variation in the orientation of the birds I tested.

There are several possible explanations for why I did not observe seasonally appropriate unimodal orientation in sparrows in fat condition. When White-throated Sparrows were tested on the day of capture at the same location along Lake Ontario under similar experimental conditions, sparrows in fat condition (fat score  $\geq 3$ ) oriented in a seasonally appropriate, unimodal direction in both spring and fall, while birds in lean condition (fat score of 0 or 1) were randomly oriented (Deutschlander and Muheim 2009). Unlike the study by Deutschlander and Muheim (2009), however, I held birds in captivity for up to 14 days, which potentially influenced the behavior of the birds I tested. A study that tested White-throated Sparrows while they were held in captivity for up to 10 days found that, very much like my study, birds were not oriented in a seasonally appropriate unimodal direction but were axially (or bimodally) oriented along the correct axis for migration even though they were in fat condition (Muheim et al. 2009). Laboratory studies on the orientation of captive

Savannah Sparrows (*Passerculus sandwichensis*) also found that the magnetic orientation of birds was consistently bimodal during fall migration (Able and Able 1993, 1995, 1996). Captivity of several nights or more appears to induce an axial orientation response in sparrows. Conducting similar experiments on a species that continues to show unimodal orientation while held in captivity would be a better model to examining the effect(s) of condition on orientation.

The artificial conditions my birds experienced in captivity, most notably fluctuations in food availability created by my experimental design, might also have affected the migratory status of birds I tested. Previous studies show a variety of conflicting results with respect to food availability and migratory readiness, or Zugunruhe. Fasting can actually increase Zugunruhe, and some studies have shown that birds have lower Zugunruhe while refueling (e.g., Korner-Nievergelt et al. 2002, Fusani and Gwinner 2004, Fusani et al. 2009, Eikenaar and Bairlein 2014). Similar to my study, Long and Stouffer (2003) found that body condition accumulated after diet supplementation did not predict the amount of Zugunruhe in Hermit Thrushes, which was contrary to the results of Yong and Moore (1993), who found increased Zugunruhe in Hermit Thrushes after they refueled. Given my study design, it is possible that individual variation in the amount of food birds consumed prior to testing affected the directedness (but not the amount) of their Zugunruhe.

I (and others) have assumed that orientation is a condition-dependent behavior that is alterable simply by changing a bird's condition, but condition and orientation may both be linked by a bird's personality (Marchetti and Zehtindjiev 2009).

Differences in the rate individuals adapt to captivity, measured by captive feeding and exploratory behavior, have a greater influence on orientation than fat levels in Sedge Warblers (*Acrocephalus schoenobaenus*), an Old World warbler and long distance migrant. Marchetti and Zehtindjiev (2009) found lean birds that ate in captivity were more likely to orient in a seasonally appropriate direction than fat birds, which suggests that conditions and behaviors in captivity may be compounded by existing individual variation in personality. Individual birds may also have different physiological traits, such as rates of fat metabolism (e.g., Eikenaar and Bairlein 2014).

Consequently, because of individual variation in physiological and psychological (i.e., personality) processes, two birds in similar energetic condition might have differing motivation to continue migration, or might respond differently to changes in condition. This might explain some of the variation in orientation I found between birds in fat and lean condition. Perhaps some of the lean birds I tested had sufficient energy reserves to continue migration, while others did not, or perhaps lean birds are more likely to have personalities associated with appropriate migratory direction than fat birds. For example, initially lean birds may be more risk-prone, and attempt migratory orientation regardless of condition, while initially fat birds may be more risk averse individuals that only attempt migratory orientation when in good condition. Additionally, the orientation of birds in Emlen cages may not always coincide with the orientation of free-flying birds, particularly if birds lack motivation

to migrate (see Nievergelt et al. 1999) and other parameters, such as weather, also affect migration initiation (see Bulyuk and Tsvey 2013).

In conclusion, my longitudinal study on White-throated Sparrows demonstrates the complexity of migration behavior at a northern stopover location and also shows the importance of considering the orientation of individuals relative to their orientation during previous tests. Although some of my results were inconsistent, I did find a change in the orientation of some individuals when their energetic condition changed, especially during spring migration. Future studies should examine the effect of energetic condition on the orientation of long-distance migrants.

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## Tables and Figures

Table 1. Semi-synthetic diet (ingredients and composition), designed to mimic a seed diet, and fed to White-throated Sparrows held at BBBO for orientation testing; approximately 63% carbohydrates, 10% protein, and 8% fat (following Smith et al. 2007).

<b>Ingredient</b>	<b>Dry Mass (%)</b>
Corn Starch	63.41
Casein <sup>a</sup>	10.31
Cellulose <sup>b</sup>	5.15
Vitamin mix <sup>c</sup>	1.03
Salt mix <sup>d</sup>	5.67
Ground silica sand	5.15
Sodium bicarbonate	1.03
Corn oil	8.25
<b>TOTAL DRY</b>	<b>100.00</b>

<sup>a</sup> USB Corporation, Cleveland, OH.

<sup>b</sup> SIGMA Chemical Corporation

<sup>c</sup> MP Biomedicals LLC, Solon, OH.

<sup>d</sup> MP Biomedicals LLC, Solon, OH.



Table 2. Data for White-throated Sparrows tested for orientation, each individual was tested three times at three different energetic conditions (e.g., fat, lean, fat) in fall 2012 and spring 2013. Fat scores and average masses reflect bird condition on night of testing; average days to change condition reflects how long birds took to fatten (*ad lib* diet) or lean (restricted diet) before testing. Visible fat was scored on a scale from 0-5.

<b>Fall 2012</b>				
n	Test condition	Fat score	Average mass (g) $\pm$ s.d.	Average #/days $\pm$ s.d. to change condition
19	Lean	0 to 2	25.0 $\pm$ 1.6	n/a
17	Fat	2 or 3	27.2 $\pm$ 2.3	9 $\pm$ 2
19	Lean	0 to 2	24.2 $\pm$ 2.3	5 $\pm$ 2
<b>Spring 2013</b>				
n	Test condition	Fat score	Average mass (g) $\pm$ s.d.	Average #/days $\pm$ s.d. to change condition
19	Fat	3 to 4	27.3 $\pm$ 2.3	n/a
17	Lean	0 to 1	22.1 $\pm$ 1.6	8 $\pm$ 3
18	Fat	3	25.9 $\pm$ 2.0	4 $\pm$ 2

Table 3. Individual orientation data for White-throated Sparrows tested three times each at three conditions (lean, fat, lean) during fall 2012. Mass and fat score reflect individual condition on night of testing. Mean direction ( $\alpha$ ) and total number of hops for each test are given for all individuals, unless the birds were inactive (hops < 35). Each individual's orientation in tests two and three relative to its orientation in test one is also included. Mean vectors for birds that were bimodally oriented during a specific test are designated with an asterisk (\*).

Bird	Test 1: Lean				Test 2: Fat					Test 3: Lean				
	Mass (g)	Fat score	$\alpha$ ( $^{\circ}$ )	No. of hops	Mass (g)	Fat score	$\alpha$ ( $^{\circ}$ )	Relative to Test one ( $^{\circ}$ )	No. of hops	Mass (g)	Fat score	$\alpha$ ( $^{\circ}$ )	Relative to Test one ( $^{\circ}$ )	No. of hops
1	22.2	0	287*	56	24.7	2	148*	230	170	24.2	1	140	222	155
2	26.6	2	107	158	27.8	3	101	186	179	27.0	2	321*	226	311
3	25.4	0	111	74	31.0	3	18	279	134	30.0	2	303	204	279
4	26.0	1	310	79	n/a	-	-	-	-	26.3	2	121	183	405
5	24.8	1	117	108	28.4	3	77	332	246	24.0	0	312*	207	143
6	24.4	1	123*	104	27.6	3	310	199	265	24.9	1	128*	17	107
7	22.4	1	79	112	26.2	3	130	63	383	22.4	1	121	54	184
8	26.4	1	321	105	29.6	3	299*	350	83	25.9	1	330	21	94
9	23.6	2	287	96	n/a	-	-	-	-	21.4	1	139	224	184
10	24.6	1	46	178	27.9	3	299*	265	97	24.5	1	98	64	117
11	24.6	1	205	144	27.9	3	230	37	222	23.7	1	195	182	203
12	25.9	1	149	114	27.1	3	179	42	54	23.7	1	208	71	79
13	25.5	1	48	163	25.0	3	162	126	125	23.6	1	109	73	128
14	26.2	1	308*	79	26.6	3	347	51	121	23.4	1	340	44	122
15	25.6	1	329*	73	26.0	3	131	174	134	23.0	1	75	118	75
16	28.7	1	338	67	30.2	3	14	48	144	25.8	1	96	130	75
17	25.3	1	100	324	29.2	3	308*	220	106	24.3	1	316*	228	75
18	22.4	1	283*	42	21.7	3	118	207	161	19.4	1	293	22	48
19	25.1	2	300	165	24.7	3	312*	24	135	21.7	1	128	200	64

Table 4. Individual orientation data for White-throated Sparrows tested three times each at three conditions (fat, lean, fat) during spring 2013; presented in the same format as Table 3.

Bird	Test 1: Fat				Test 2: Lean					Test 3: Fat				
	Mass (g)	Fat score	$\alpha$ ( $^{\circ}$ )	No. of hops	Mass (g)	Fat score	$\alpha$ ( $^{\circ}$ )	Relative to Test one ( $^{\circ}$ )	No. of hops	Mass (g)	Fat score	$\alpha$ ( $^{\circ}$ )	Relative to Test one ( $^{\circ}$ )	No. of hops
1	30.1	3	112	346	25.2	1	119	29	311	n/a	-	-	-	-
2	29.2	3	282	462	24.2	1	305	35	357	27.9	3	351	81	100
3	25.8	3	343	268	20.4	1	150*	179	125	24.2	3	151*	180	355
4	28.3	3	315*	35	22.8	0	185	242	54	28.5	3	351*	48	101
5	27.5	3	42	187	22.1	0	291	261	71	26.6	3	205	175	35
6	24.1	3	193	75	n/a	-	-	-	-	22.9	3	187	186	47
7	31.0	3	165*	320	n/a	-	-	-	-	26.2	3	151	358	296
8	26.8	3	300	102	20.3	0	323*	35	76	24.2	3	287	359	247
9	24.9	3	123	459	20.9	1	24	273	101	24.0	3	83	332	522
10	27.1	3	122*	74	23.1	1	234	124	92	25.0	3	84	334	52
11	29.4	4	307*	262	23.0	1	99	164	178	27.0	3	322	27	340
12	31.0	3	309	40	24.4	1	333	36	78	29.5	2	322*	25	131
13	26.7	3	330*	456	21.2	1	128*	170	291	28.3	3	319*	181	333
14	25.1	3	136	306	19.9	1	155	31	312	22.7	3	155	31	217
15	30.4	4	301	100	22.8	0	297	188	405	28.0	3	325*	36	123
16	25.6	3	131*	101	20.5	0	318*	199	248	26.4	3	327*	208	82
17	25.8	3	226	564	22.8	1	21	167	405	24.4	3	171*	317	428
18	26.2	3	334	275	20.5	1	353	31	57	24.9	3	289	327	126
19	24.2	3	90	74	21.8	1	29	311	115	25.5	3	308*	230	39



Figure 1. Orientation testing area (top) and video frame showing White-throated Sparrows that were video recorded and then analyzed with BirdOriTrack to determine orientation within Emlen-style cages (bottom).

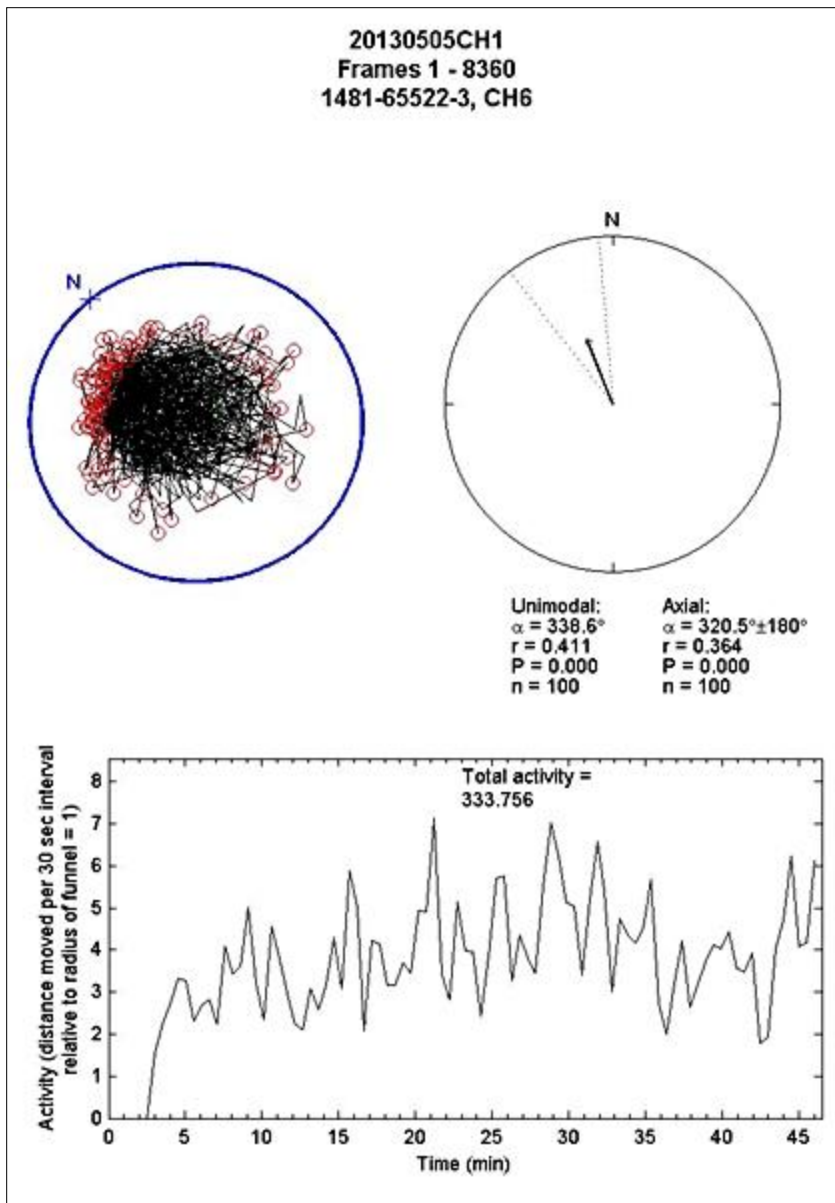


Figure 2. BirdOriTrack output for one individual bird during one orientation test, shows mean direction ( $\alpha$ ), mean vector length ( $r$ ), P-value (for both unimodal and axial distributions), number of counted positions or “valid hops” ( $n$ ), and total activity levels (summed length of a bird’s movement binned over 30 sec intervals relative to radius of funnel). Each small circle within the upper left circle plot represents a valid hop in a particular direction. The circle plot in the upper right shows the bird’s mean vector relative to magnetic north; the dotted lines on either side of the mean vector indicate the 95% confidence intervals.

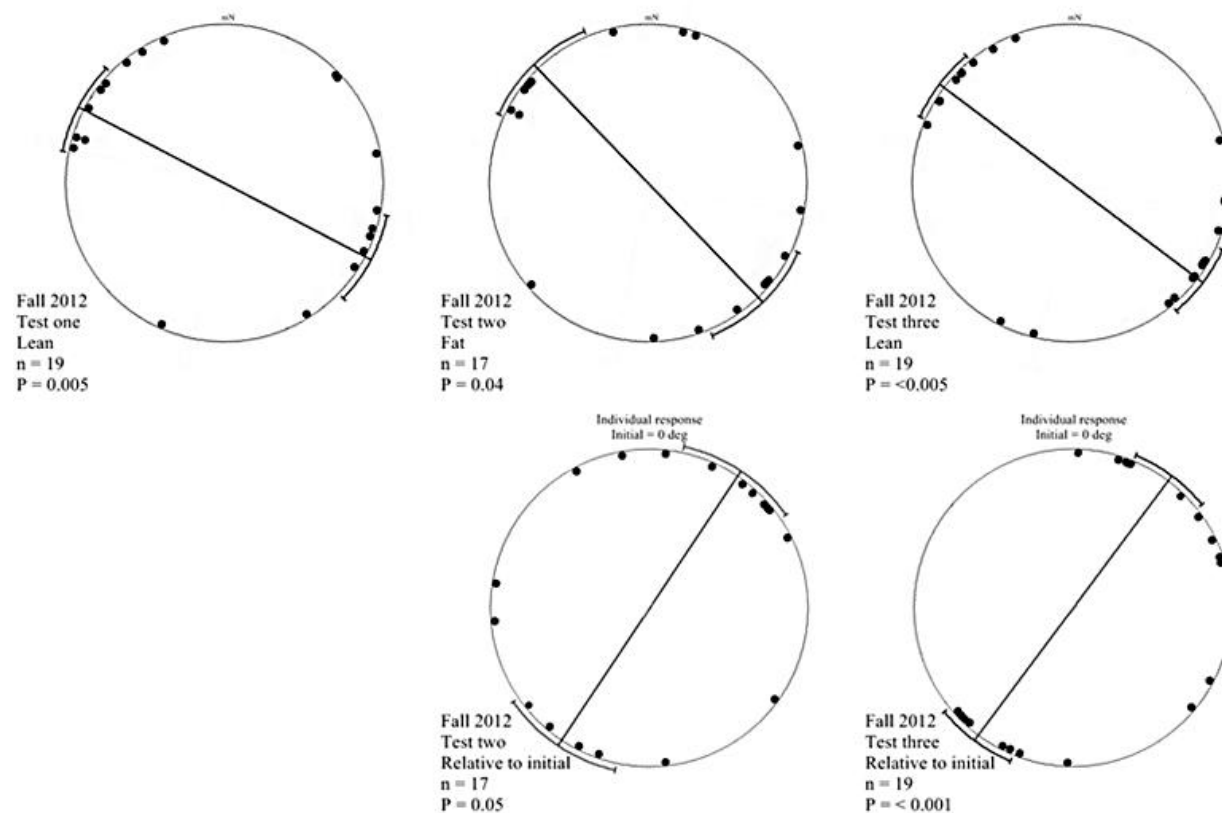


Figure 3. Orientation of White-throated Sparrows tested during fall 2012 (lean-fat-lean sequence). For each test (1, 2, and 3) data are plotted relative to magnetic North (mN = 0). For tests 2 and 3, data are also plotted relative to the initial orientation of each bird in test one (i.e., as deflections from the initial mean orientation). Each point on the circle plots represents the orientation of an individual bird (from Table 2). Lines bisecting each circle show the mean vector for all birds; brackets at the end of each line indicate the 95% confidence intervals for the mean vector. P-values are for the Rayleigh test (full statistics are reported in the text).

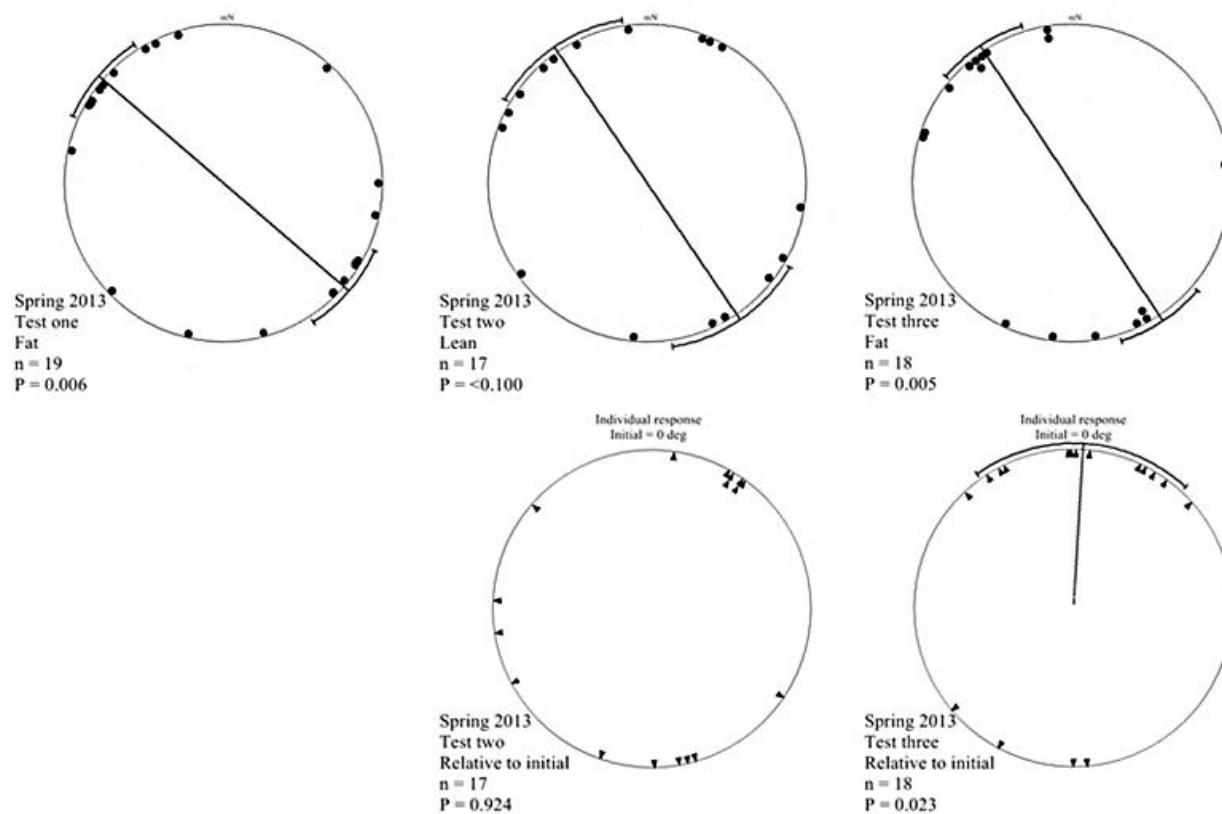


Figure 4. Orientation of White-throated Sparrows tested during spring 2013 (fat-lean-fat sequence). These data are plotted as in Figure 3, with the exception that the plots showing the orientation of birds relative to their initial orientation were not bimodally significant. Rather one distribution was not significantly different from random (so no mean vector is shown) and one distribution was unimodally oriented (shown with a unimodal mean vector and 95% confidence brackets).

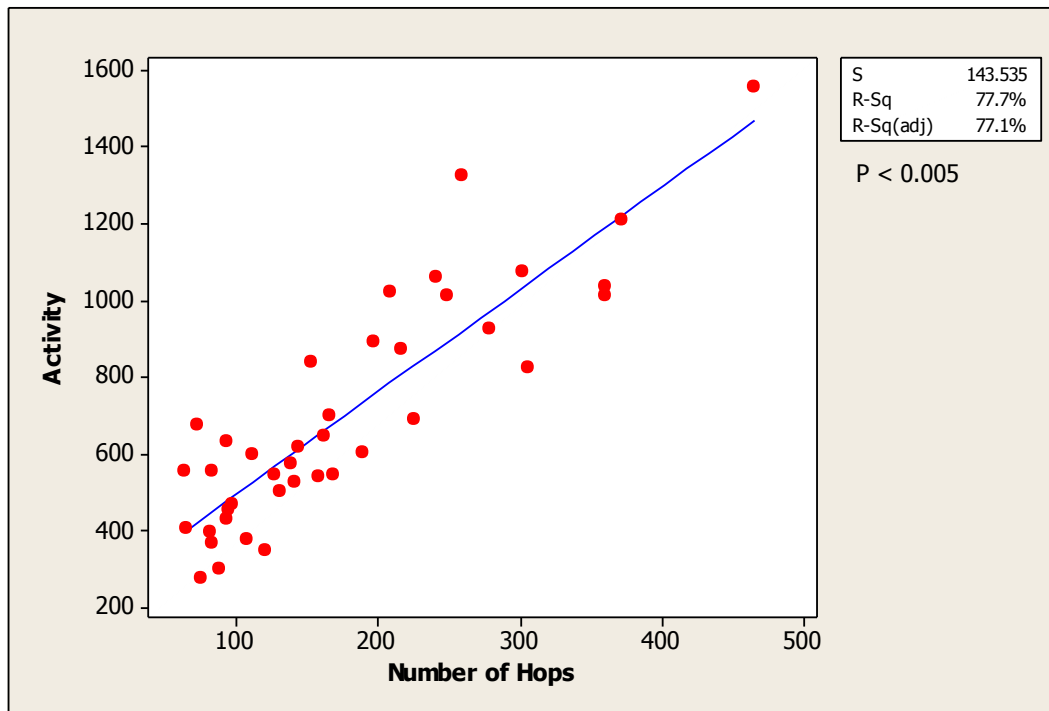
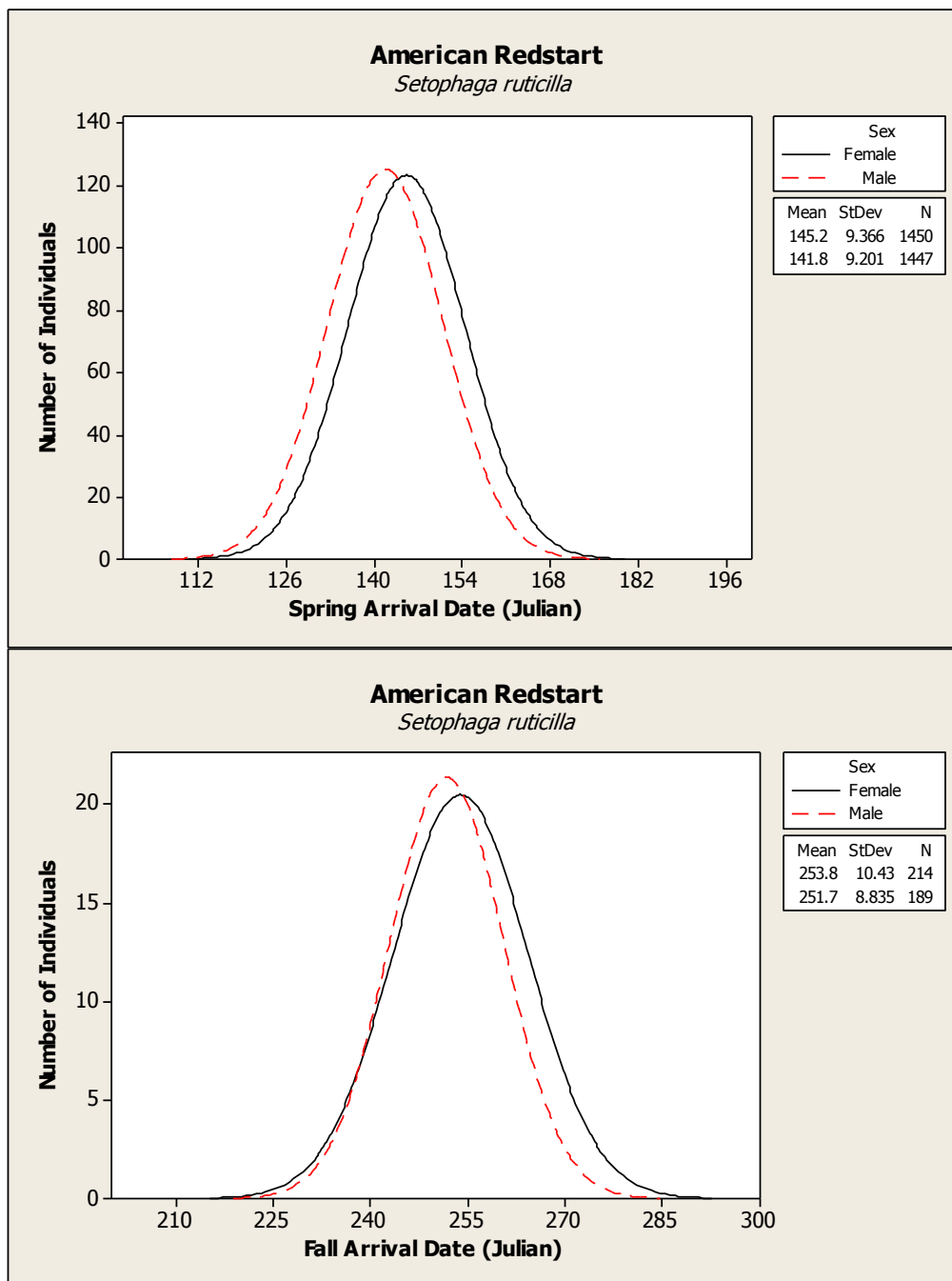


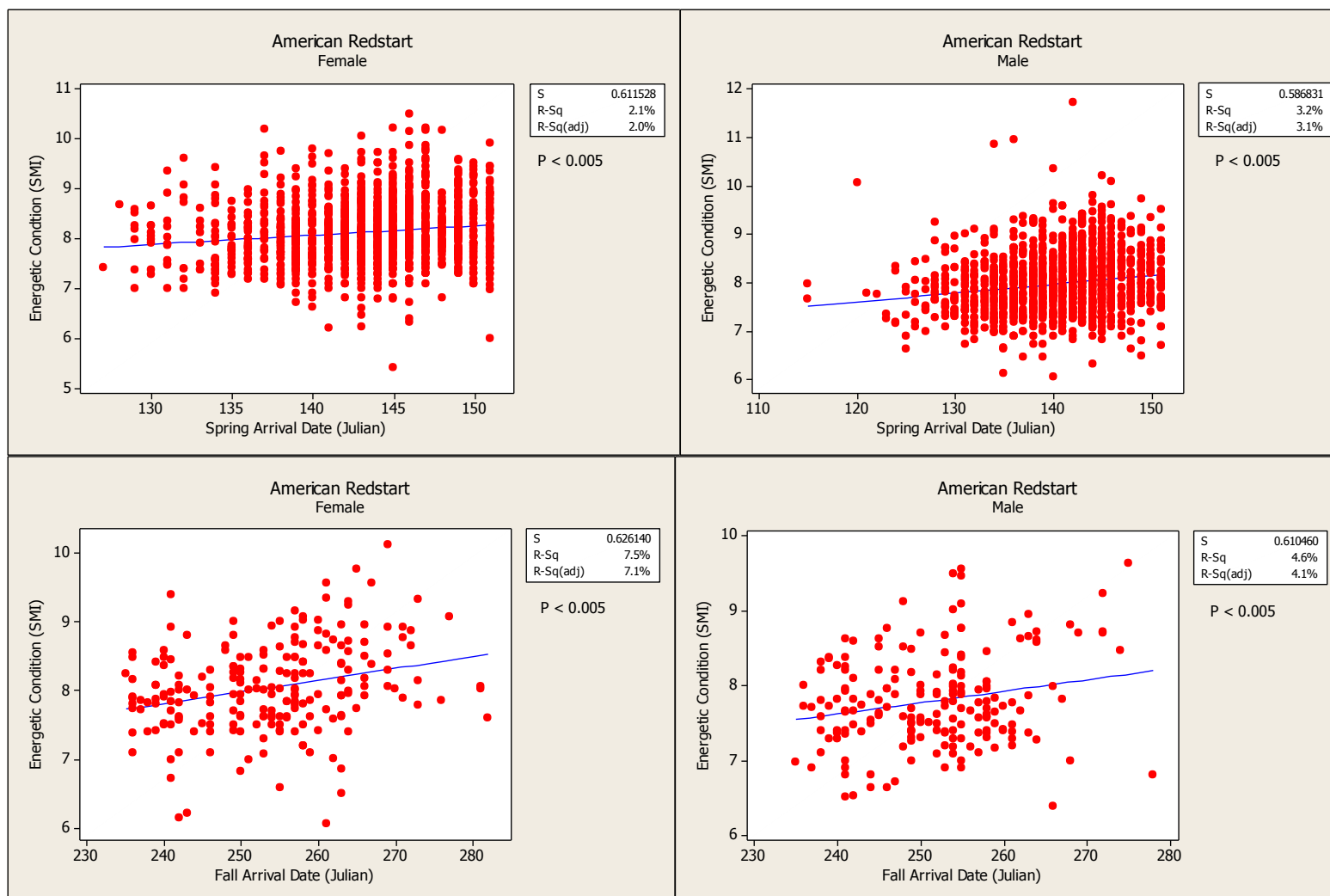
Figure 5. Relationship between mean activity levels (distance moved per 30 sec interval) and mean number of hops for all White-throated sparrows tested for orientation (three times each at three conditions) in fall 2012 and spring 2013.

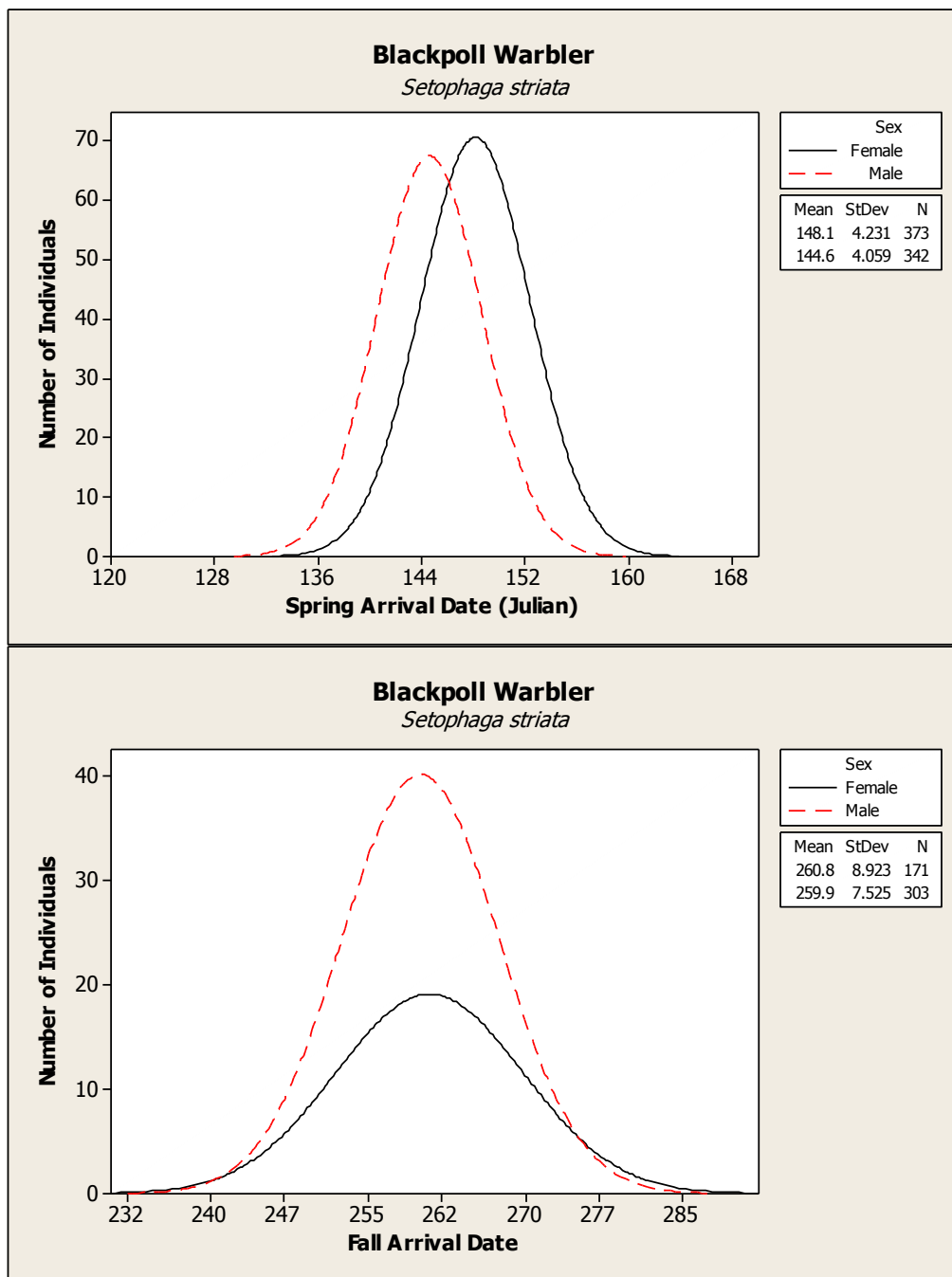


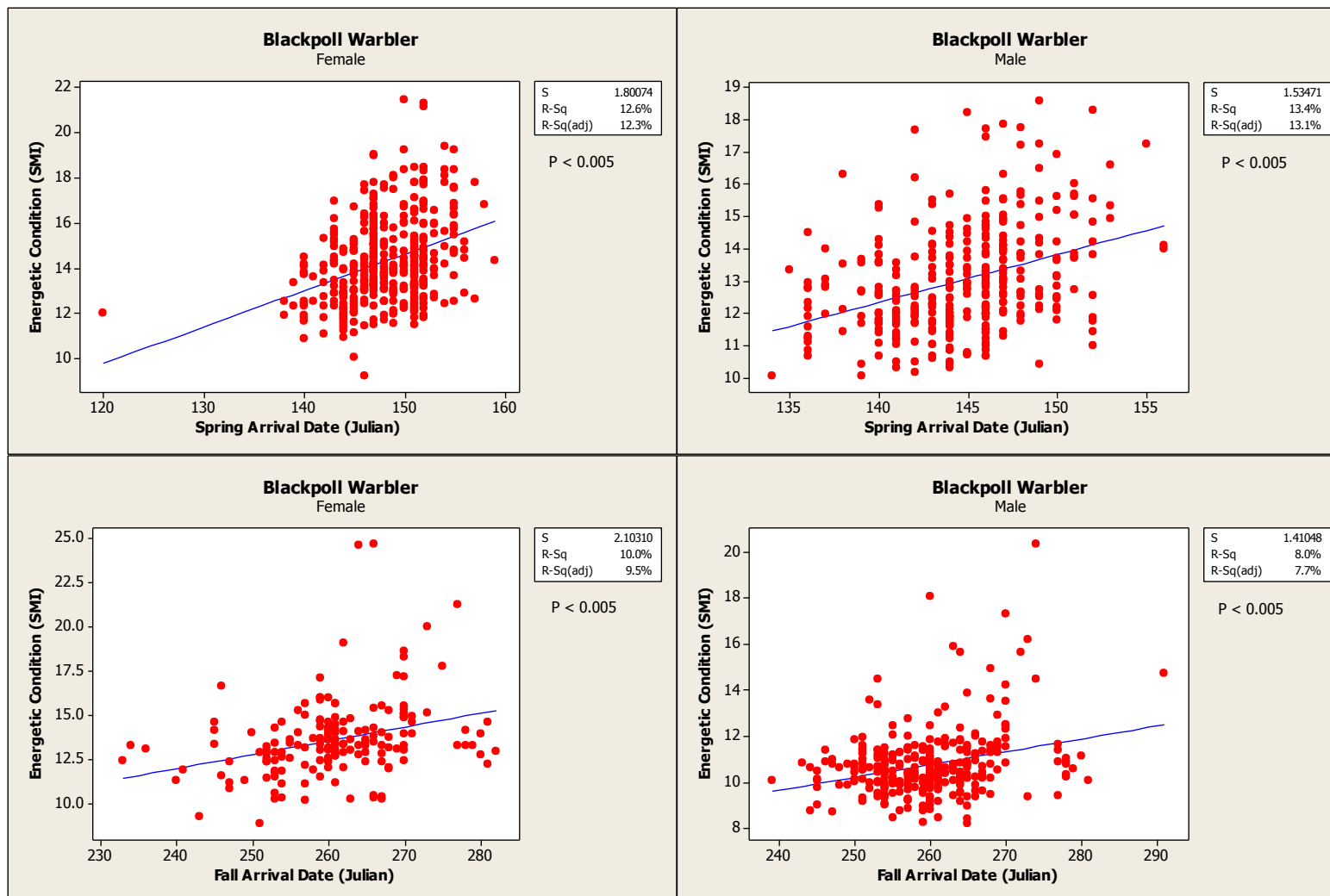
**Appendix**

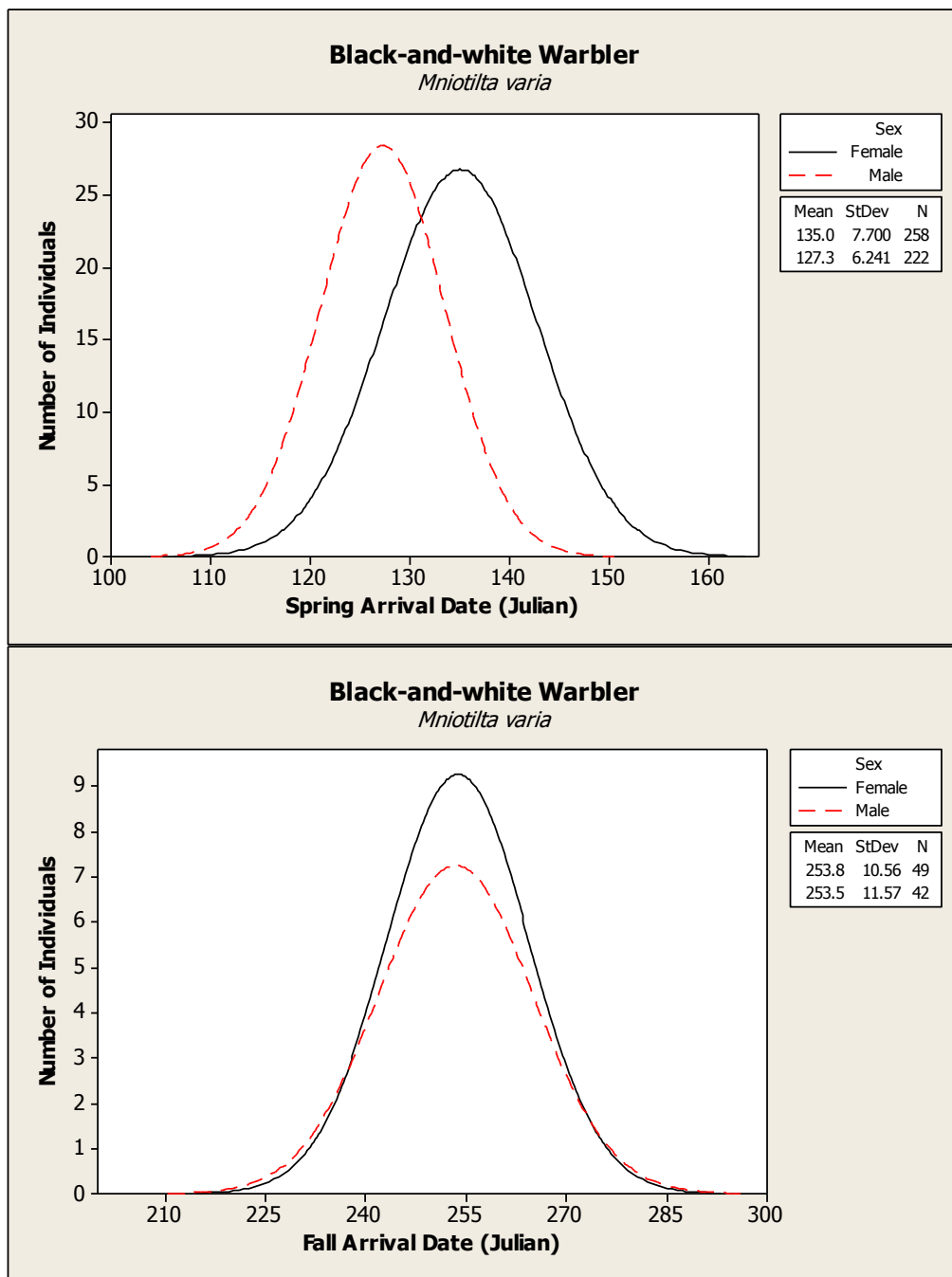
There are six figures for each of the 12 Parulidae species included in my analyses: two frequency distributions that show the number of individual males and females captured at Braddock Bay Bird Observatory (BBBO) during both spring and fall migration and four linear regressions that show the relationship between the energetic condition or SMI (g) and arrival date of males and females at BBBO during both spring and fall migration. Species are listed alphabetically.

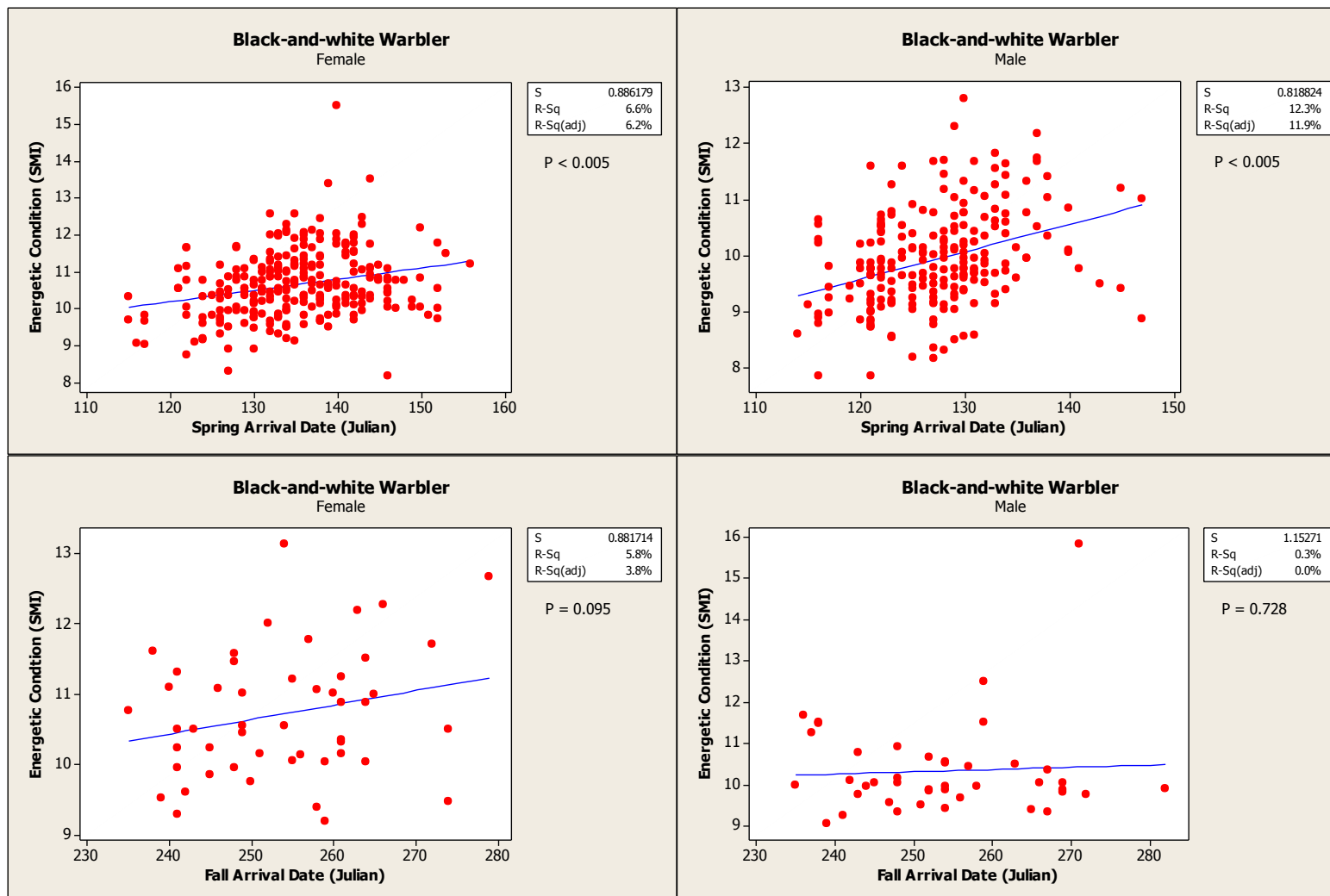
1. American Redstart (*Setophaga ruticilla*)

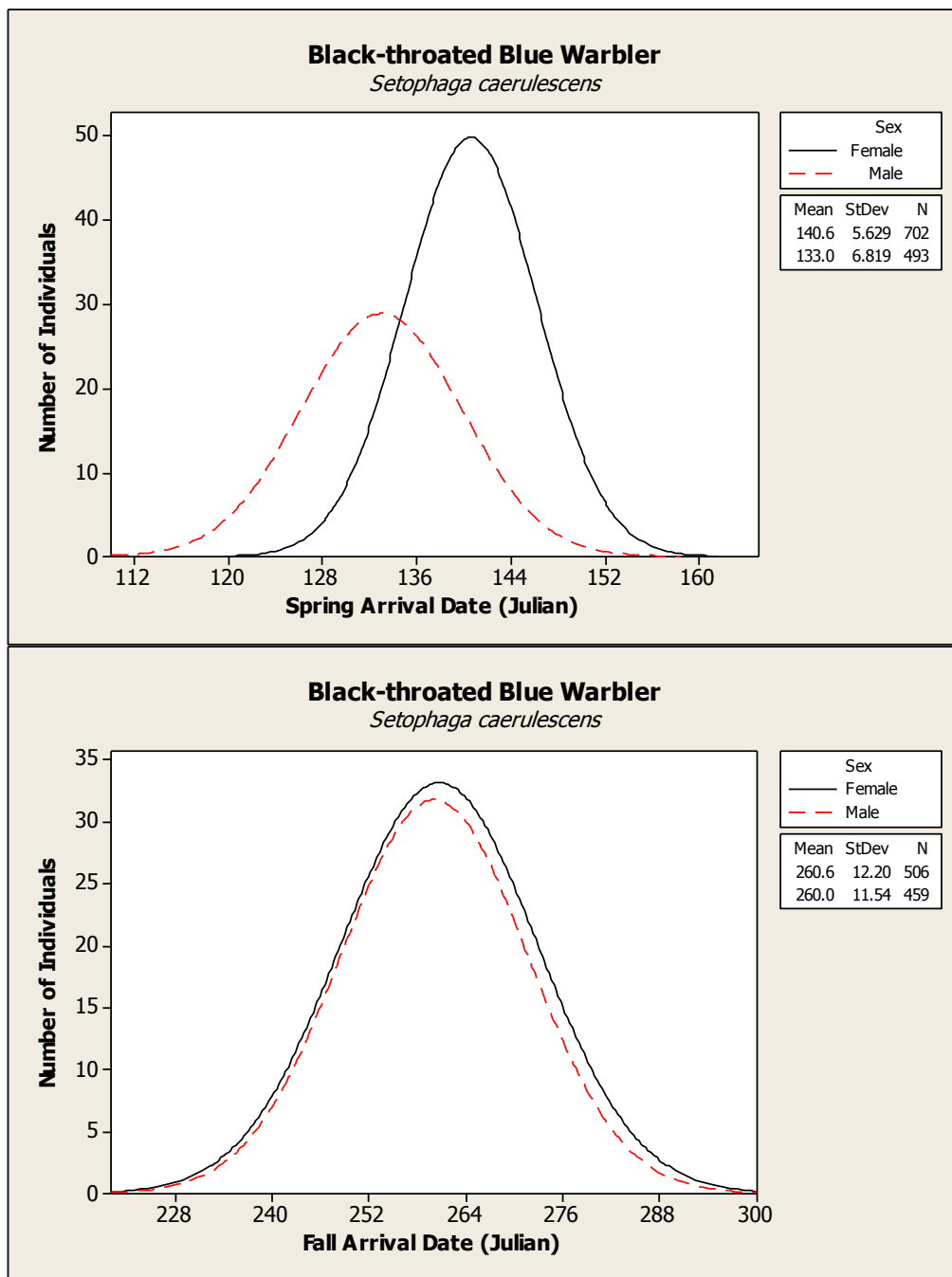


2. Blackpoll Warbler (*Setophaga striata*)

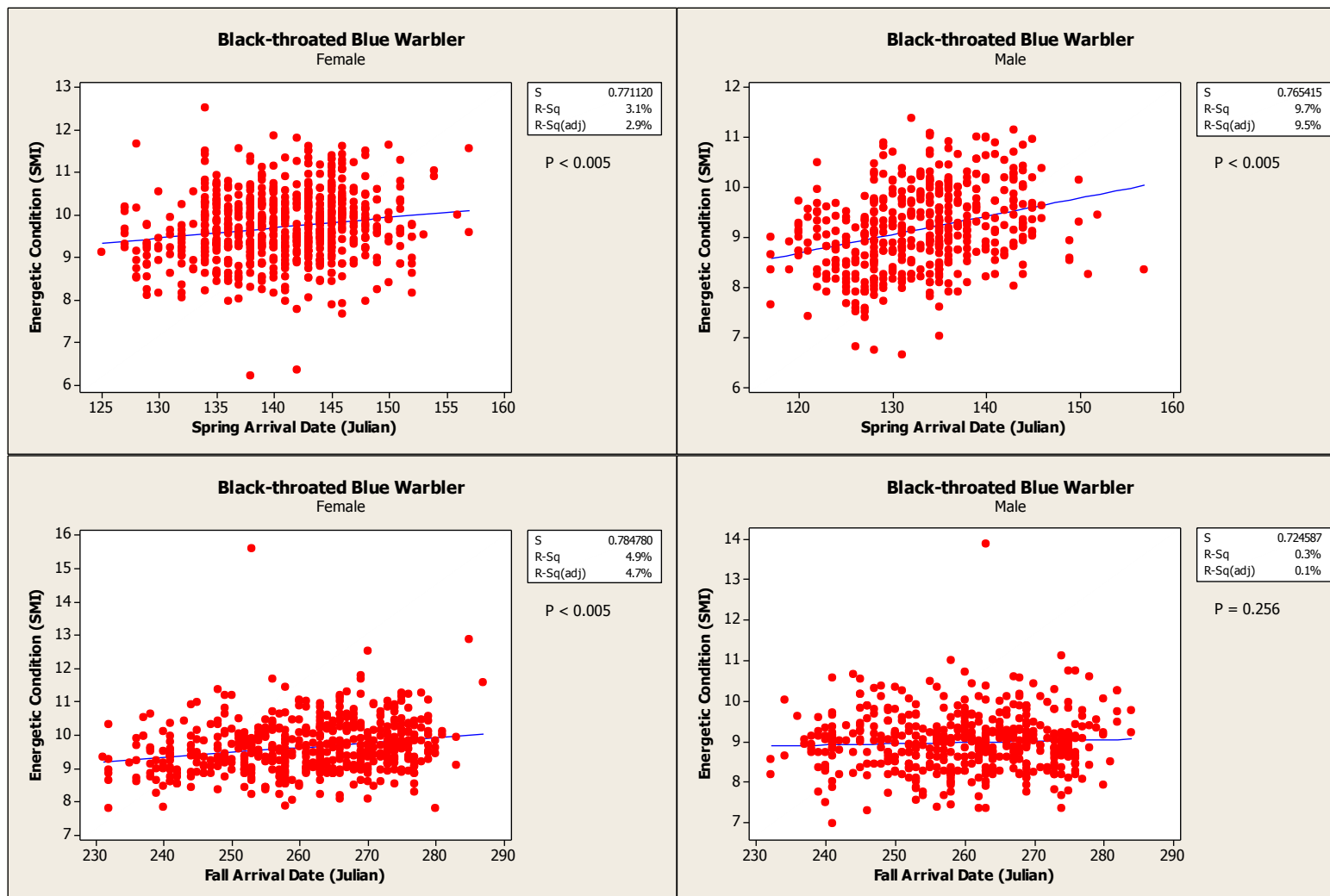


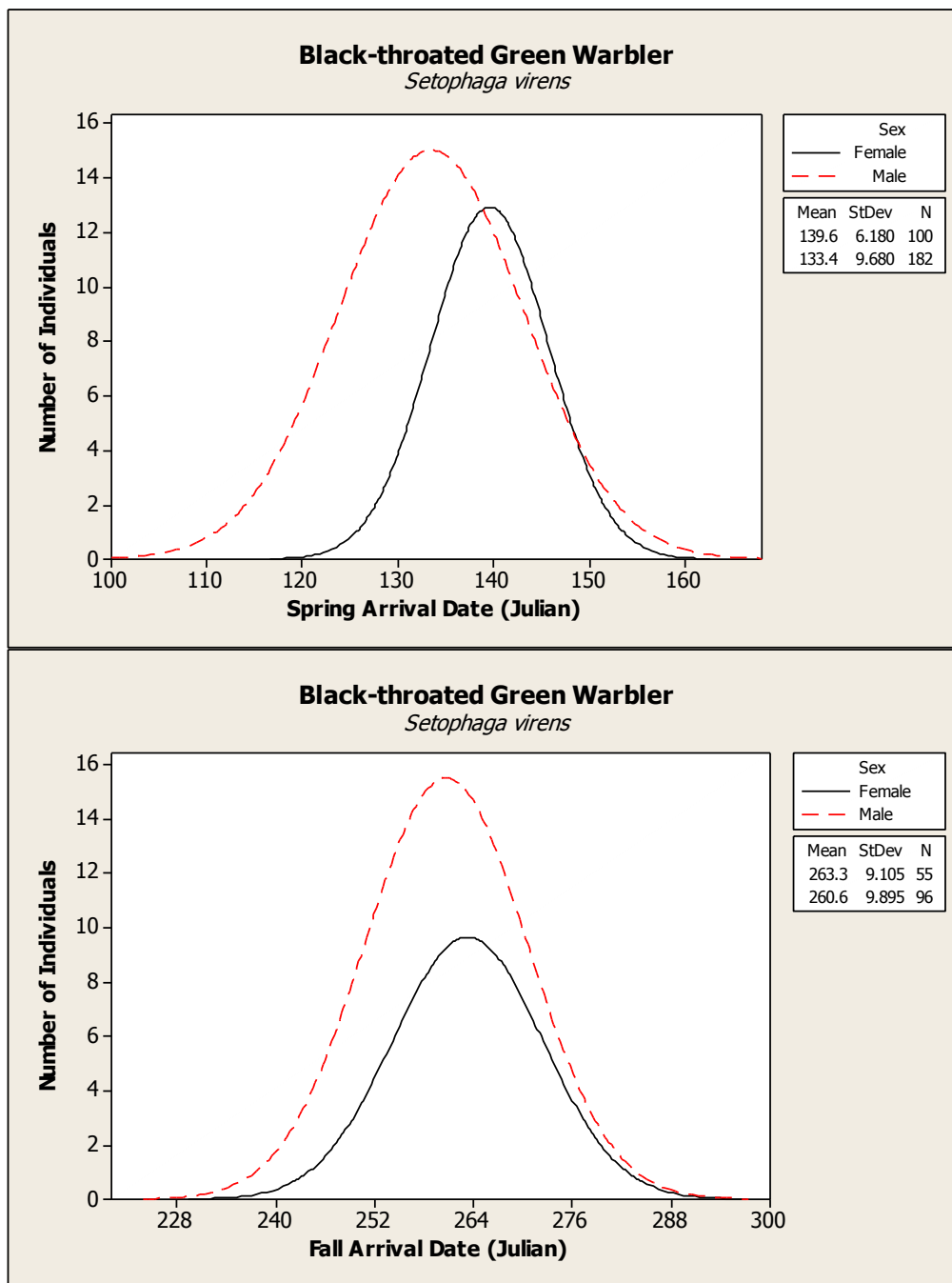
3. Black-and-white Warbler (*Mniotilta varia*)

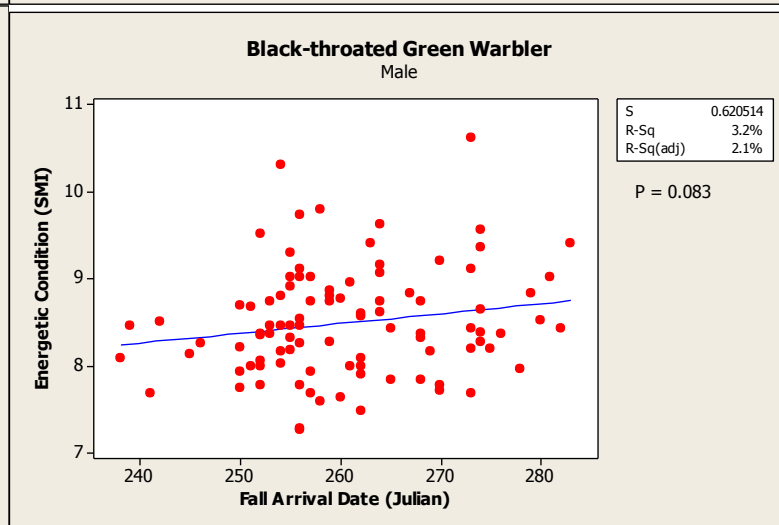
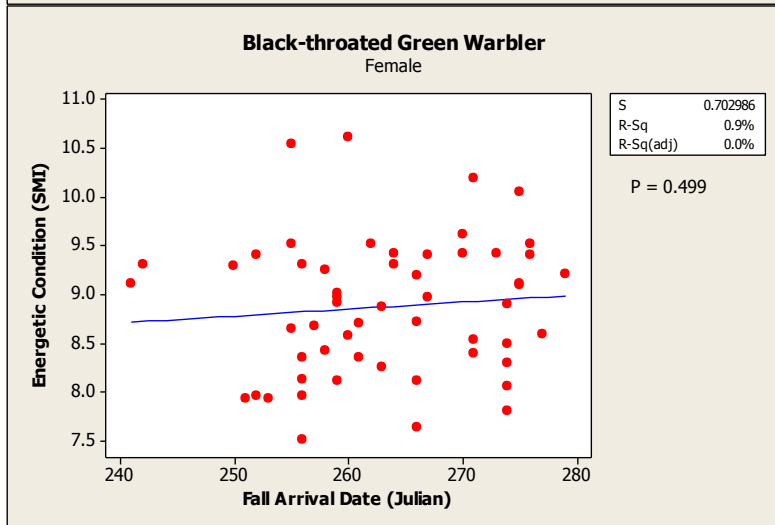
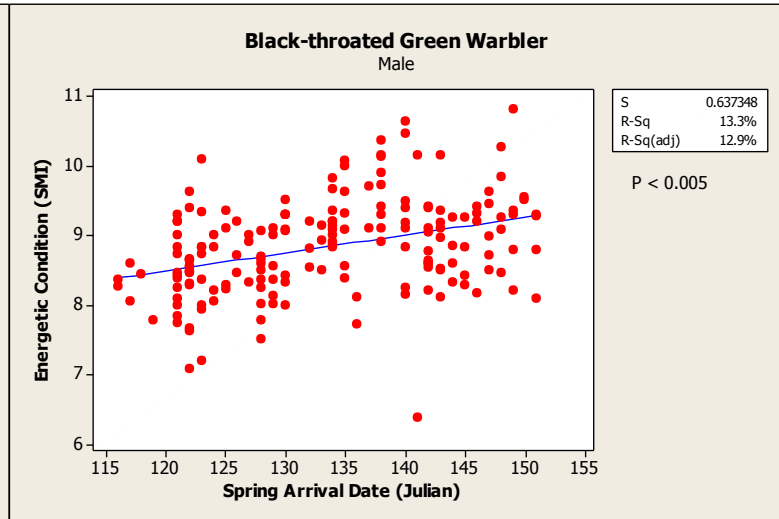
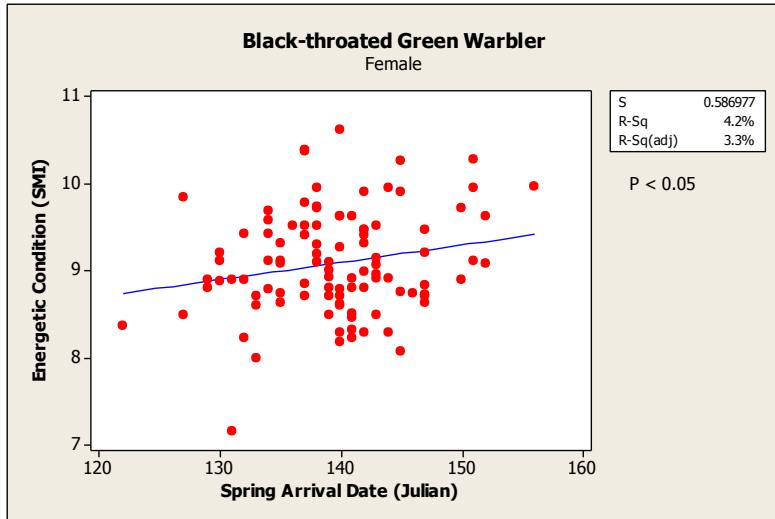


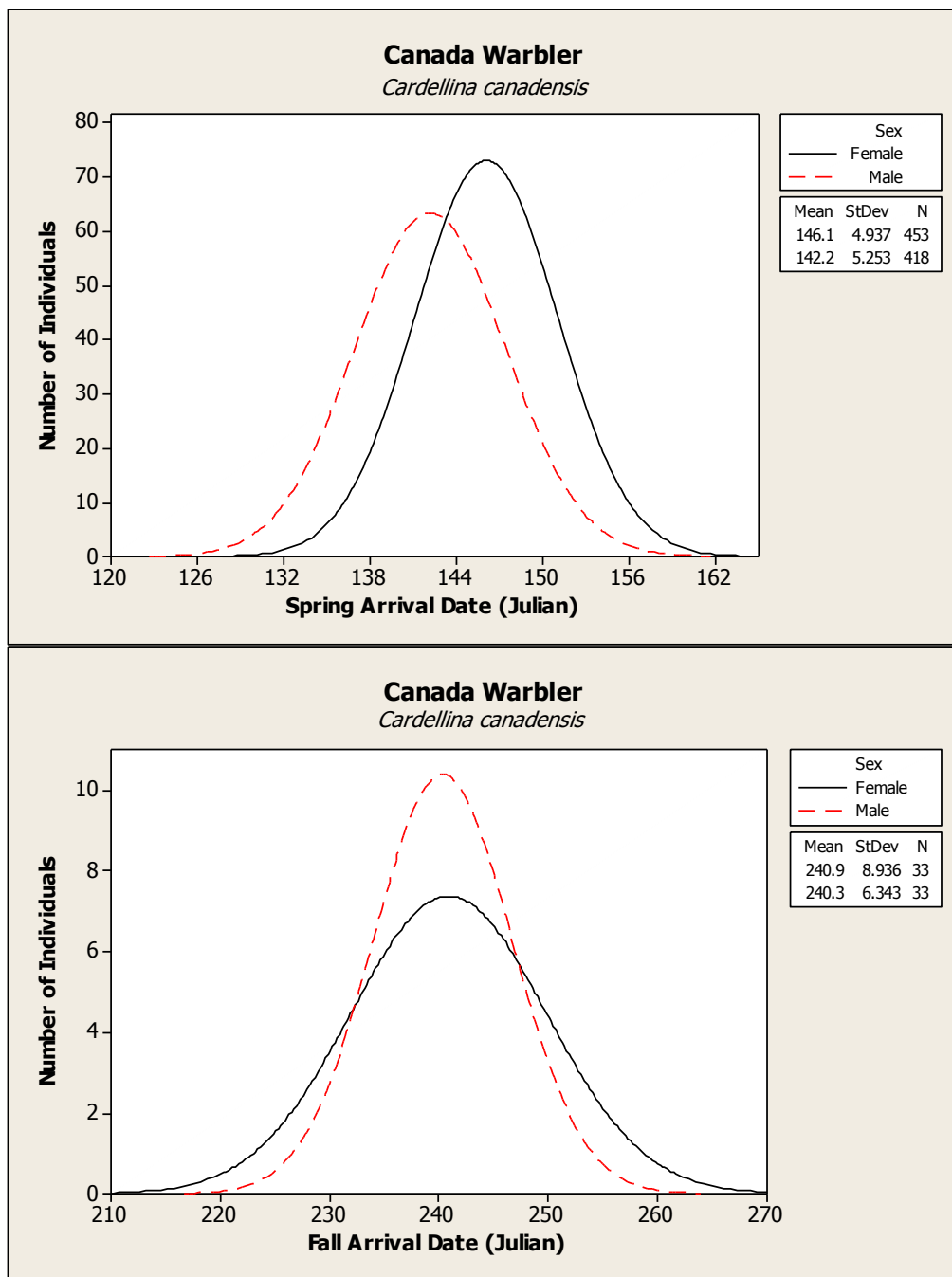
4. Black-throated Blue Warbler (*Setophaga caerulescens*)

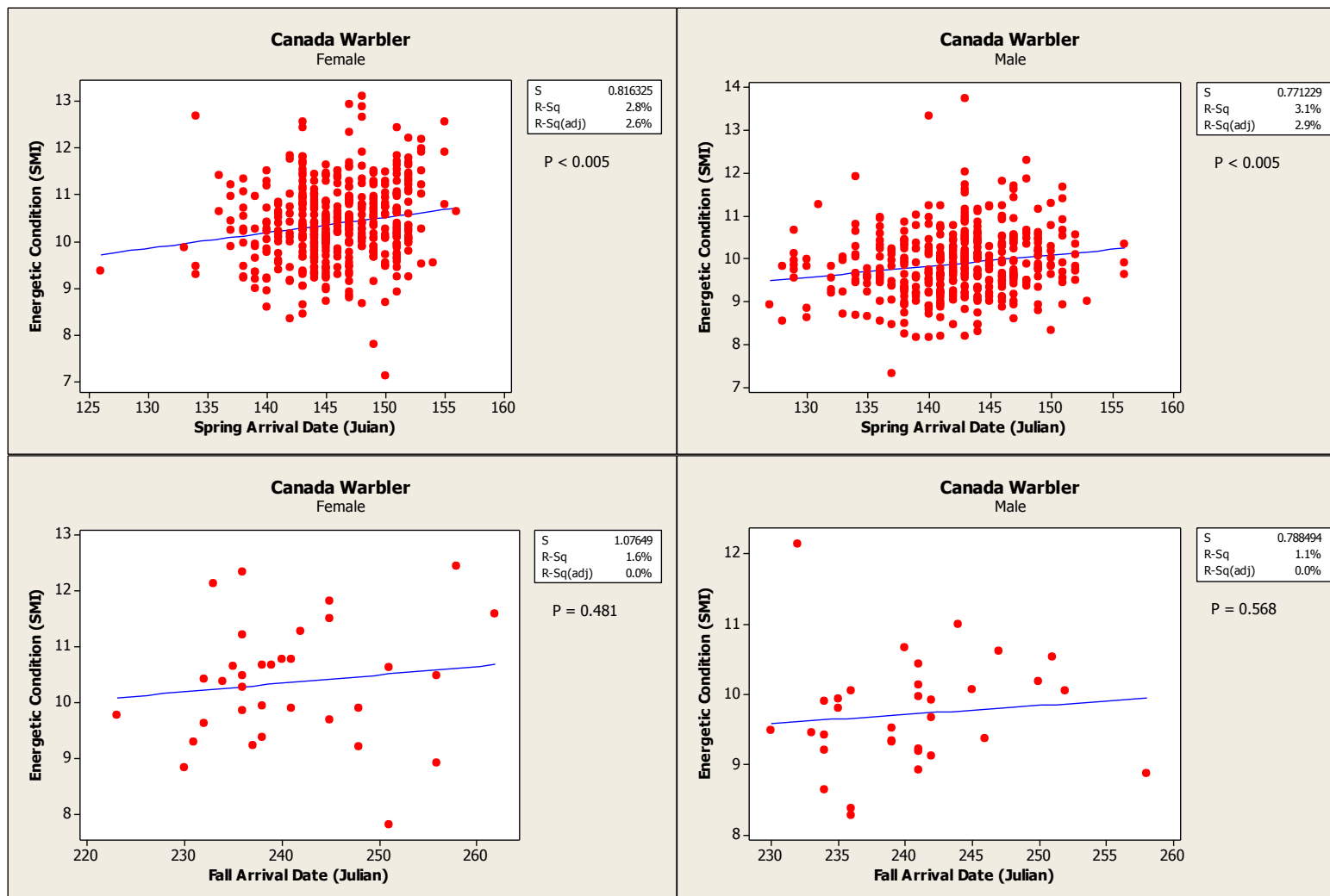


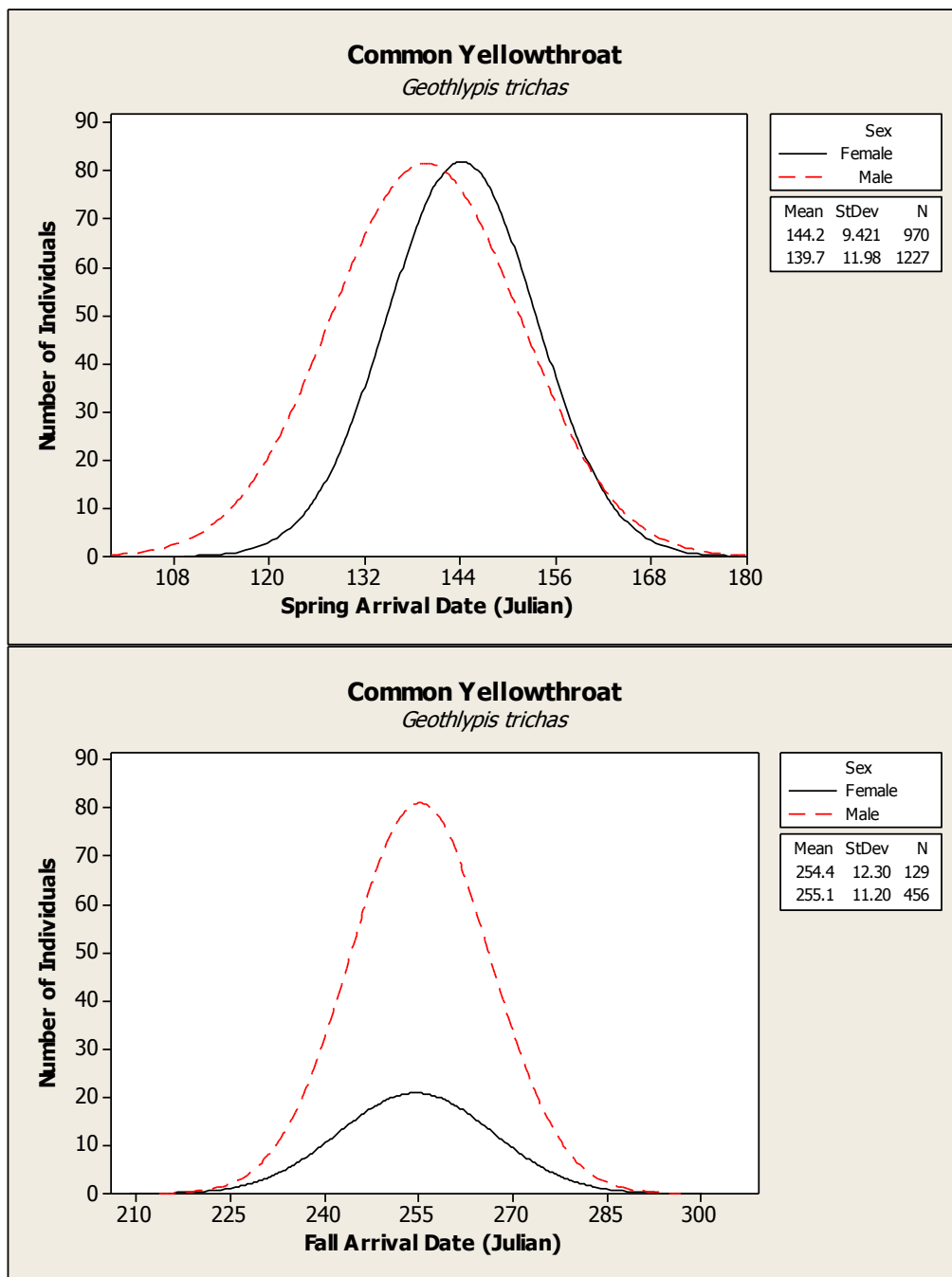


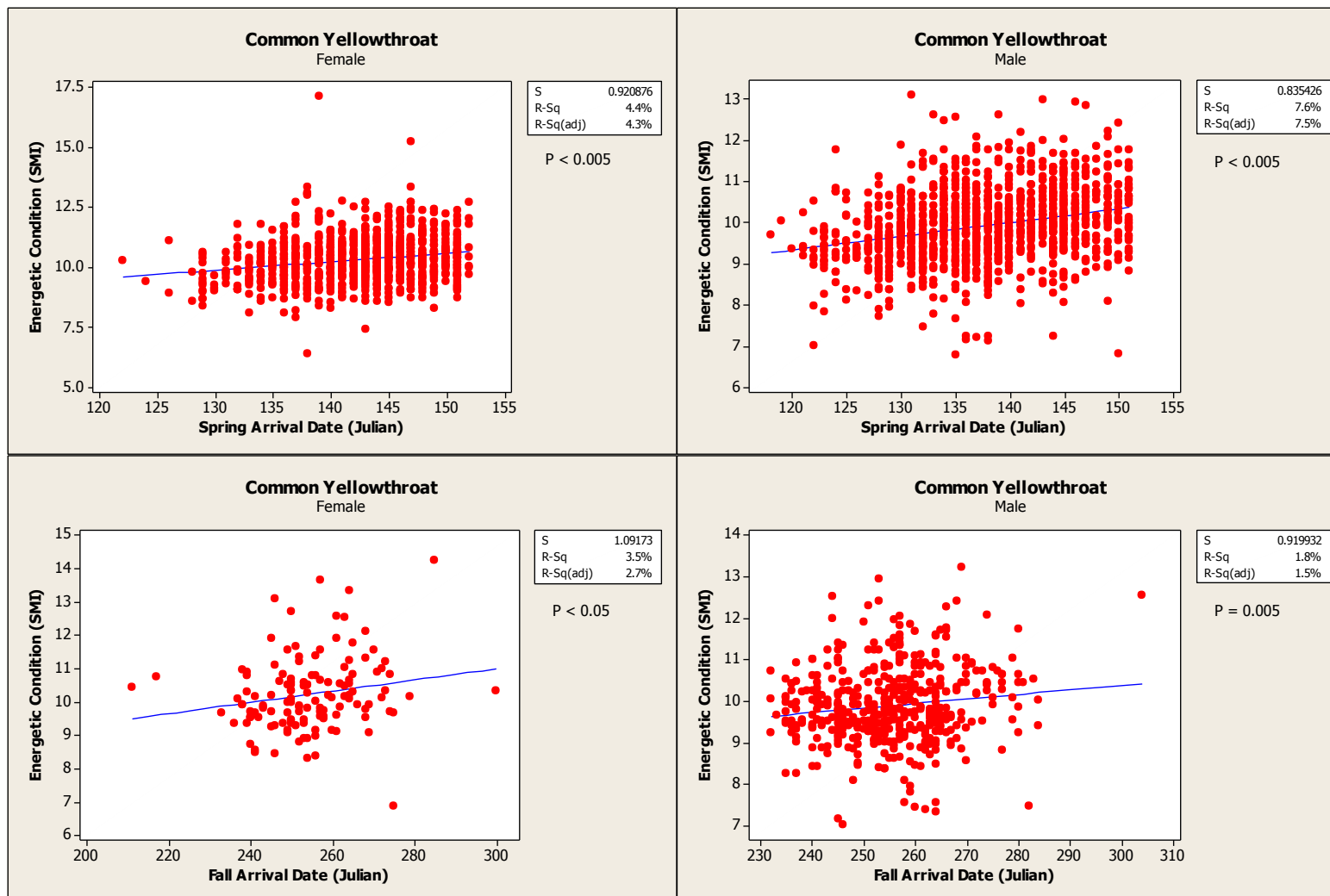
5. Black-throated Green Warbler (*Setophaga virens*)

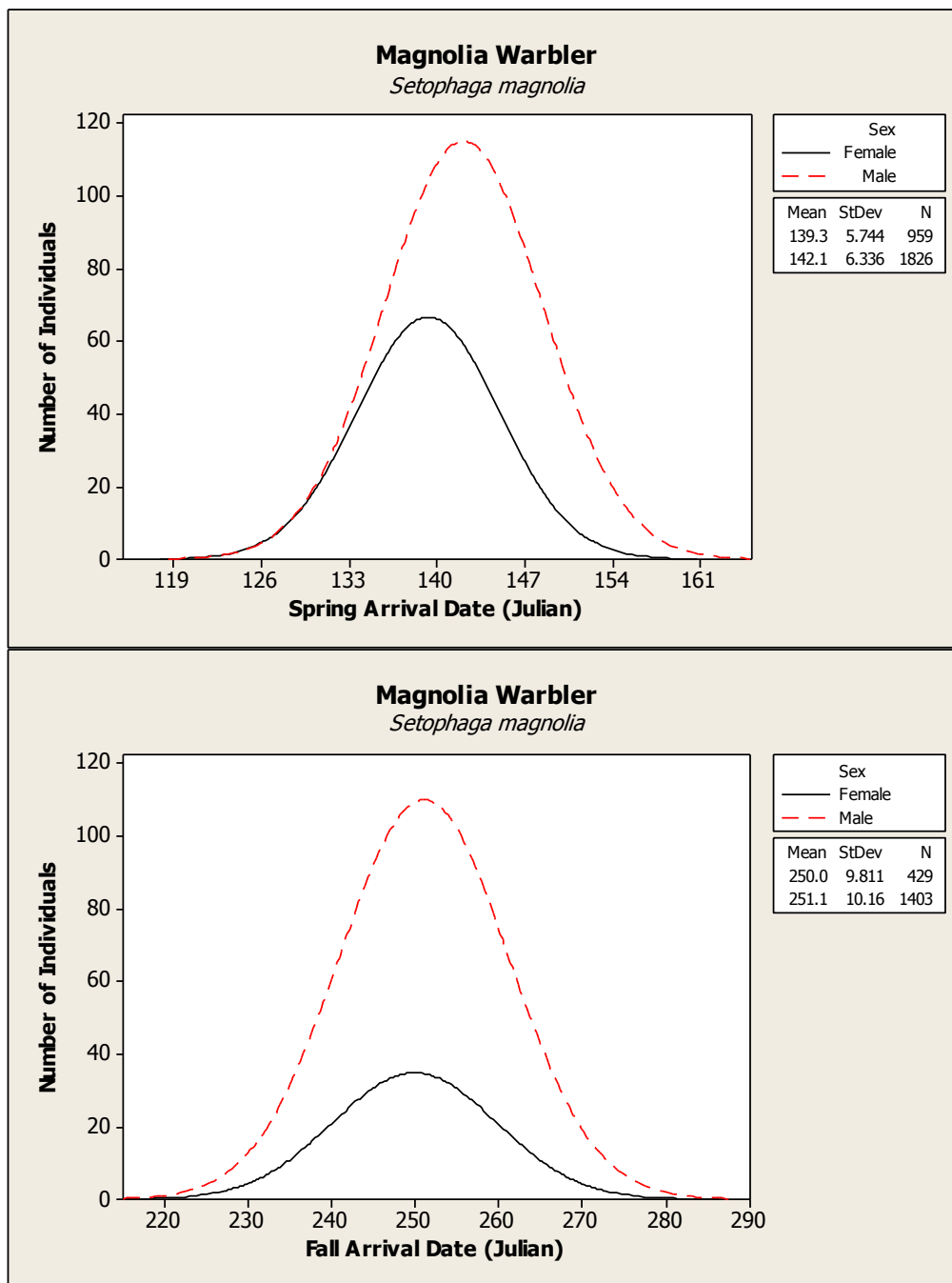


6. Canada Warbler (*Cardellina canadensis*)

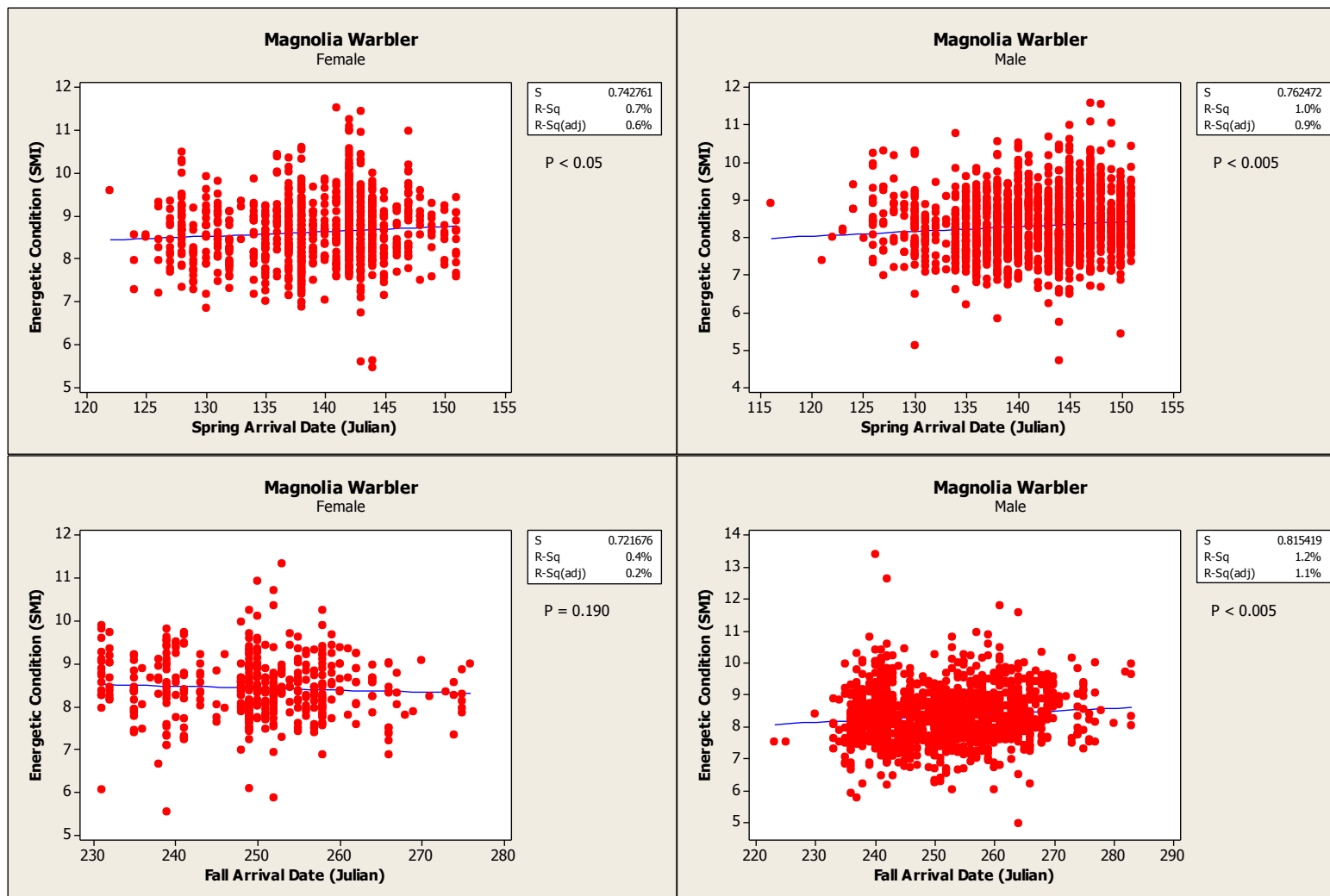


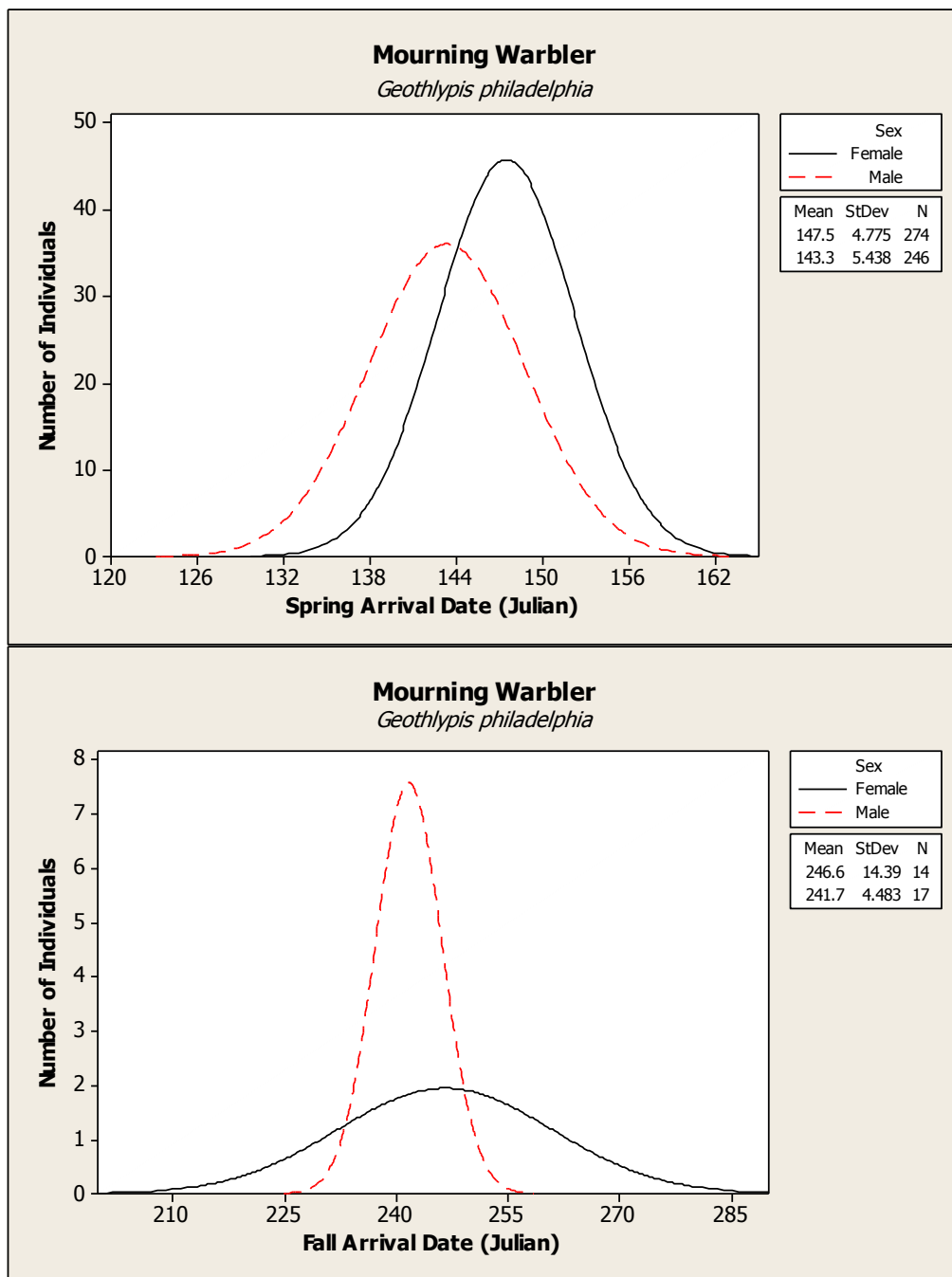
7. Common Yellowthroat (*Geothlypis trichas*)

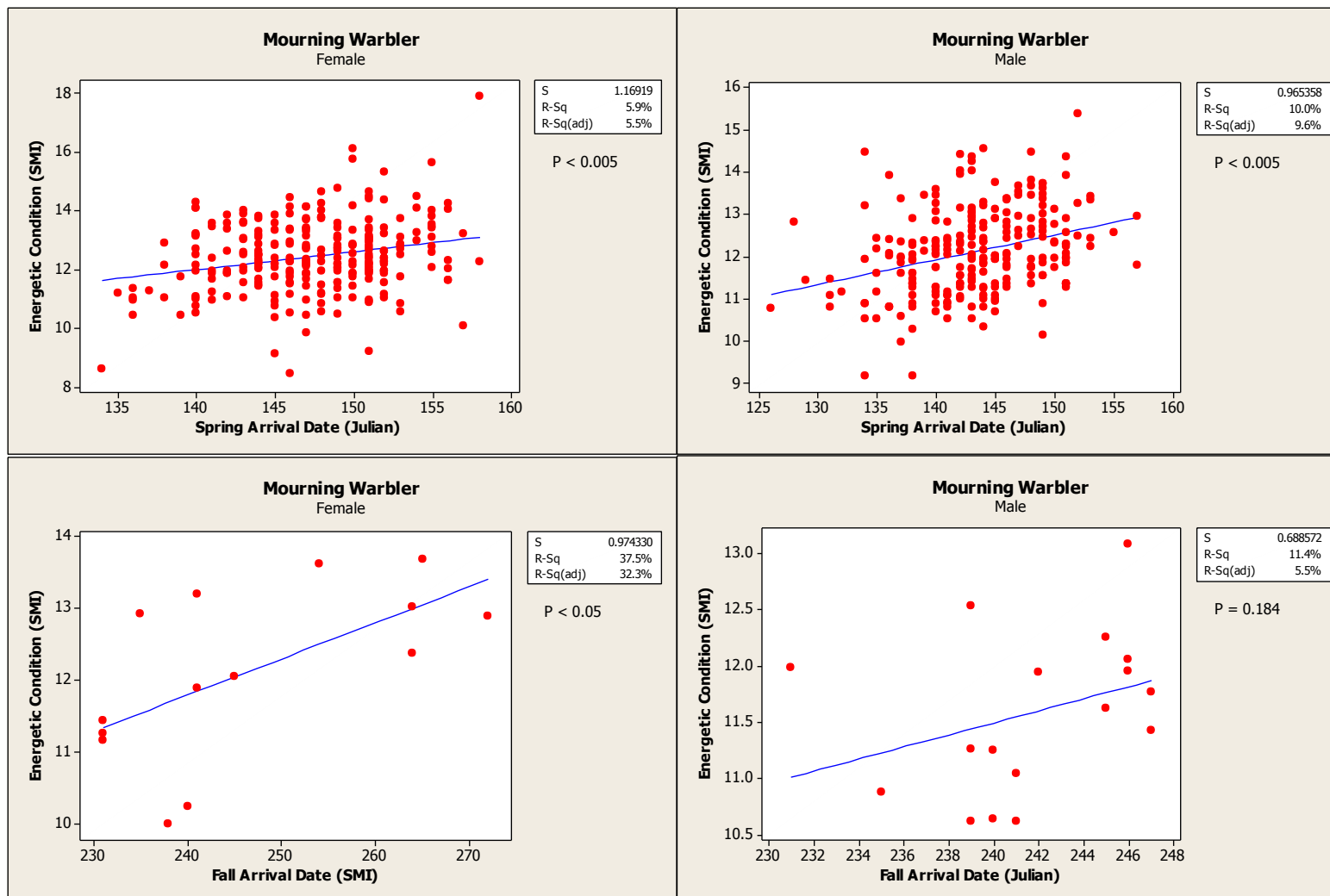


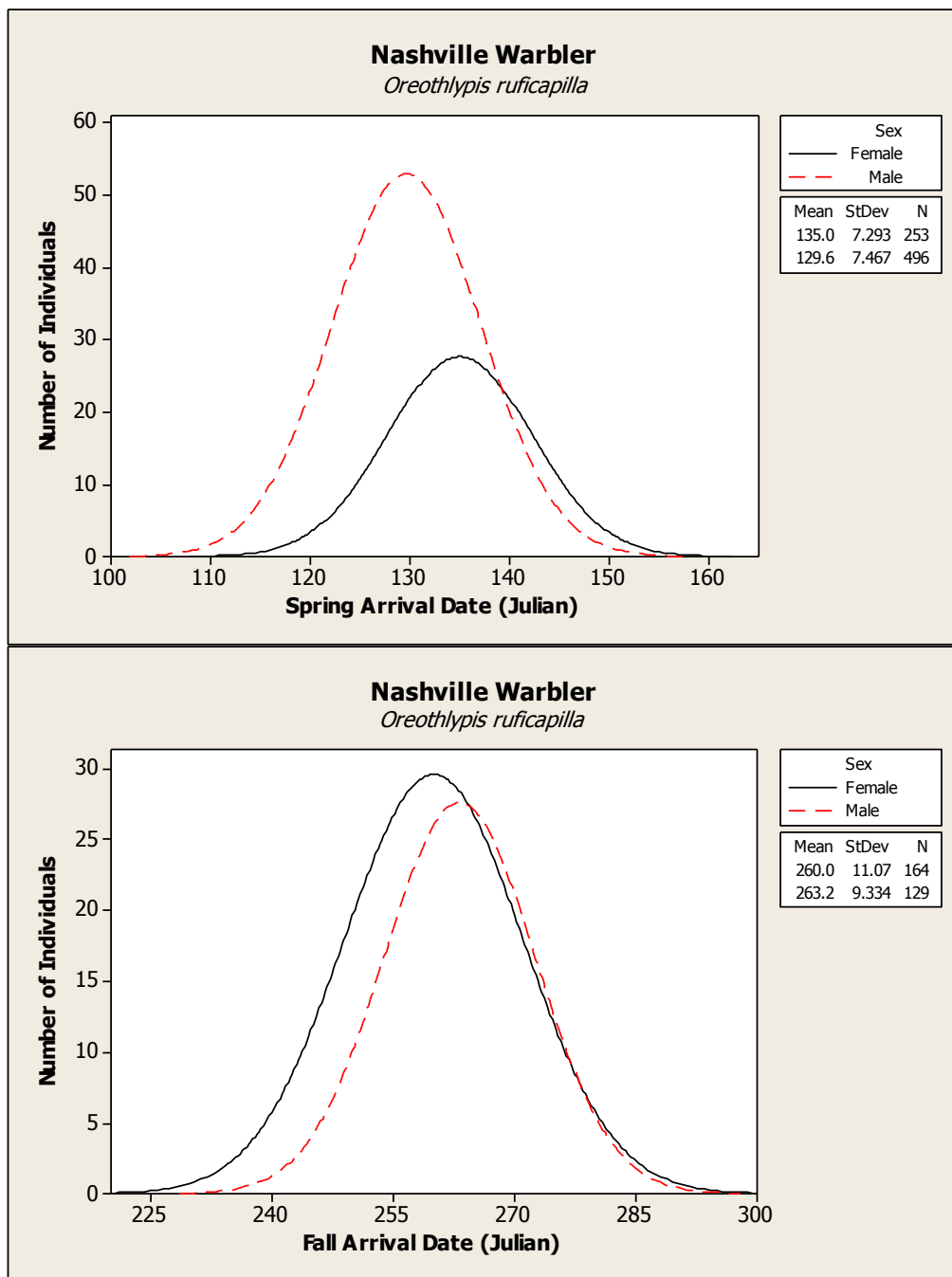
8. Magnolia Warbler (*Setophaga magnolia*)

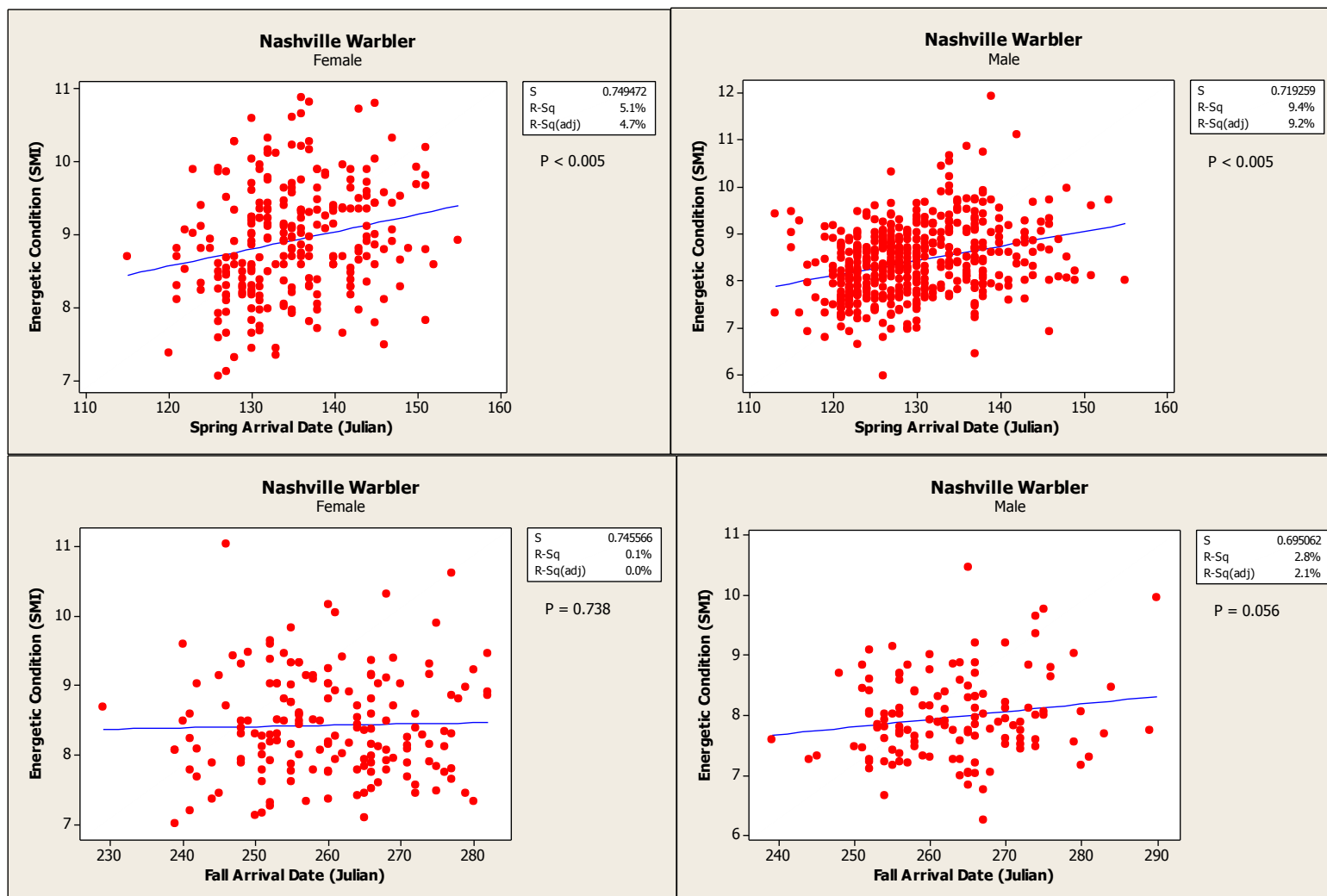


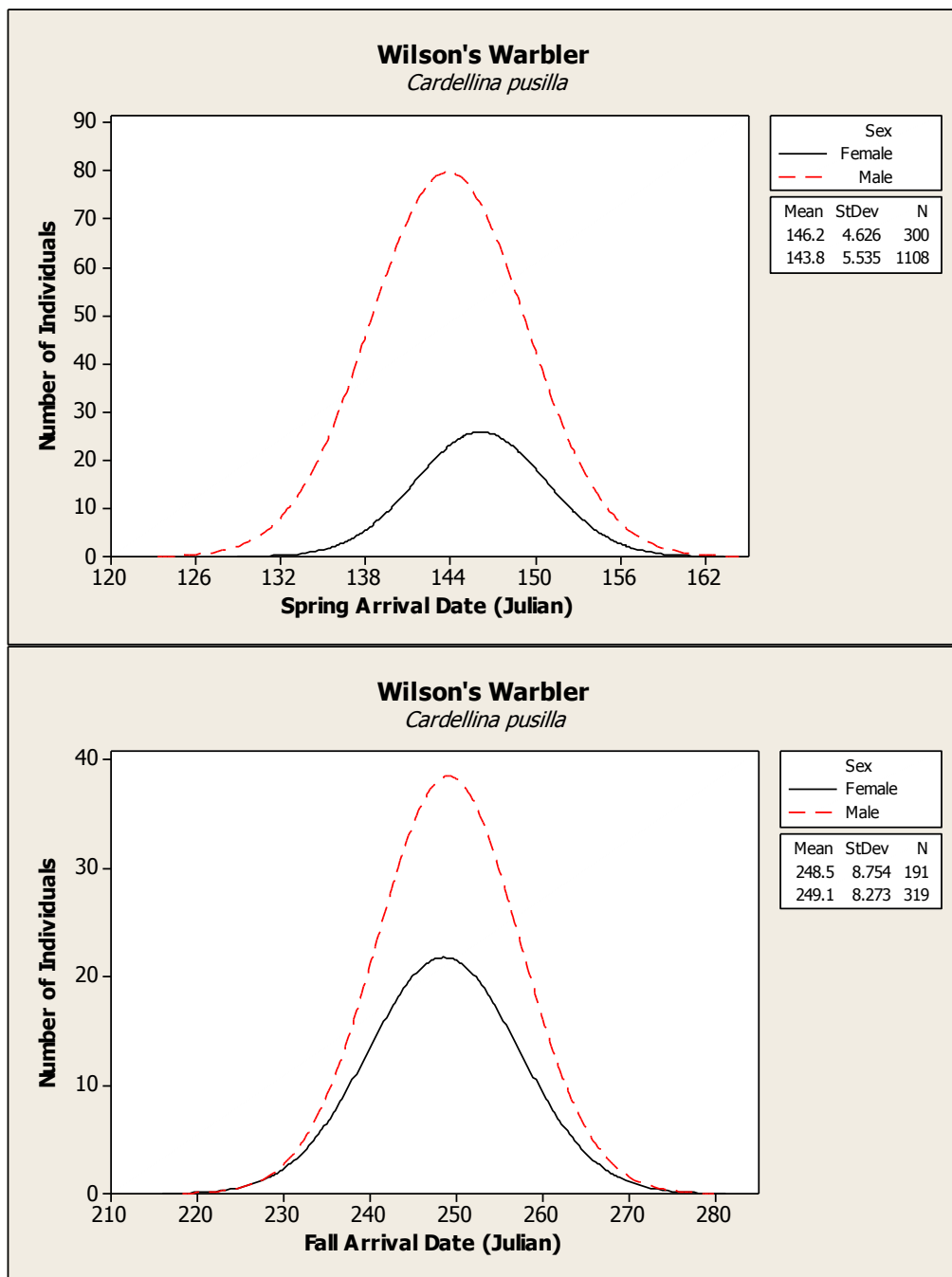


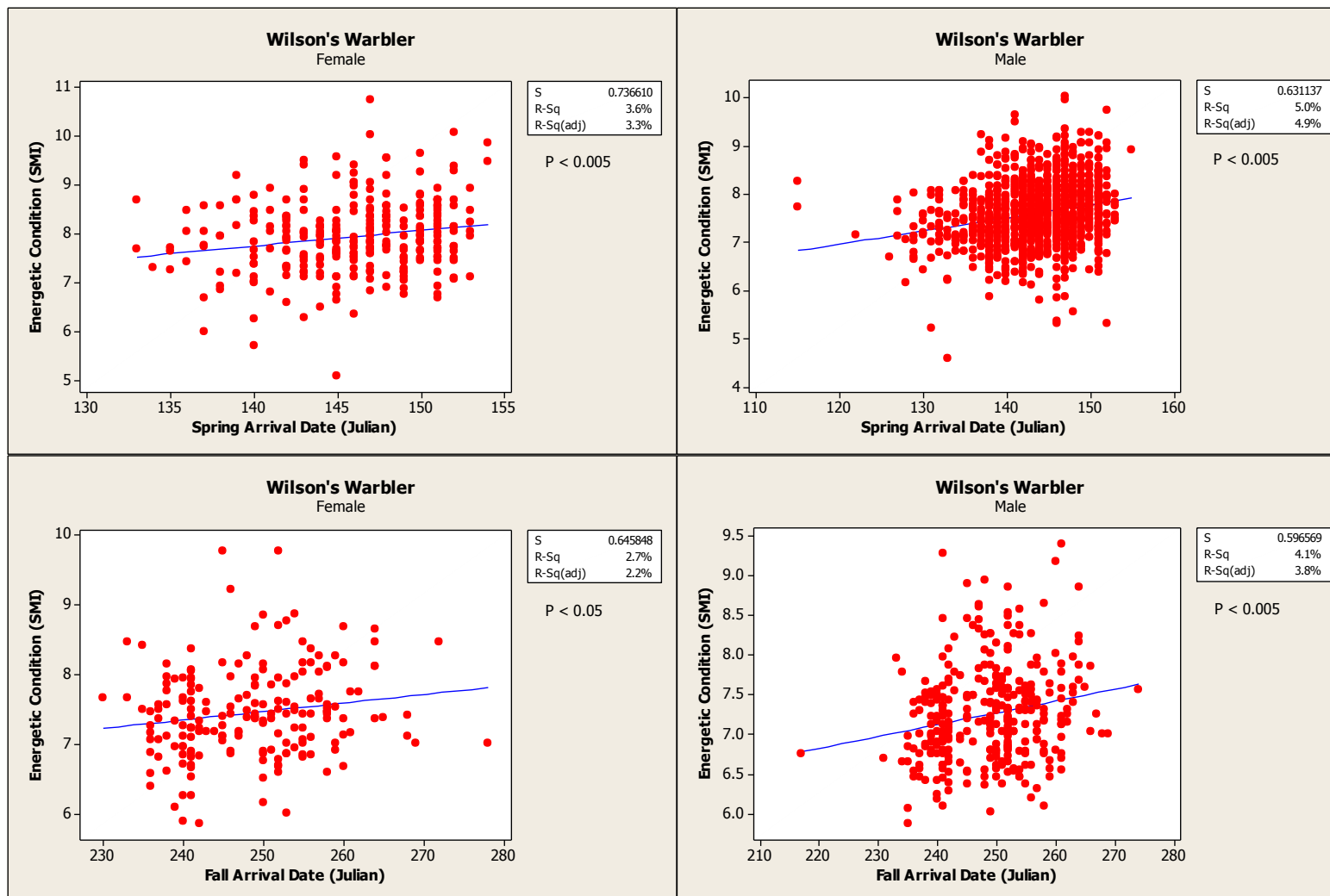
9. Mourning Warbler (*Geothlypis philadelphia*)



10. Nashville Warbler (*Oreothlypis ruficapilla*)



11. Wilson's Warbler (*Cardellina pusilla*)



12. Yellow-rumped Warbler (*Setophaga coronata*)