

CHAPTER SEVEN

Climatic Extremes Influence Spring Tree Phenology and Migratory Songbird Foraging Behavior*

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Abstract. In the Upper Midwest of the United States, fire suppression has resulted in succession of savanna and forests that differ in both plant community composition and vegetation structure from their condition prior to Euro-American settlement. Furthermore, variations in weather affect spring phenological events and potentially alter synchronous relationships of migratory songbirds with their seasonal resources. Our goal here was to understand how annual variation in phenology of four tree species—northern red oak (*Quercus rubra*), eastern white oak (*Q. alba*), sugar maple (*Acer saccharum*), and red maple (*A. rubrum*)—affect foraging behavior of migratory songbirds during spring migration. Oaks currently have poor regeneration, whereas maples have good regeneration in forests in the Upper Midwest. A typical temperature regime in 2009 coupled with a record warm winter and early spring in 2010 provided a natural experiment for addressing our goal. In the spring and early summer of 2009 and 2010, we monitored migratory songbird foraging behavior and collected data on tree flowering and leaf-out phenology for 160 replicate trees of the four study species at the Kickapoo Valley Reserve in southwest Wisconsin. In 2009, 15 species of migratory wood-warbler (F. Parulidae) arrived at the stopover study area in late April and were present

until late May. Birds foraged heavily on flowering northern red oak and, to a lesser extent, on flowering eastern white oak and sugar maple. Red maple was not preferred by wood-warblers. In 2010, the arrival date and duration of stay among the 15 species of wood-warblers was similar to 2009, yet the frequency of use of the four tree species was reduced by 60%. Northern red oak, sugar maple, and red maple achieved summer condition 2 to 3 weeks earlier in 2010 than 2009, but these tree species were not preferred by the wood-warblers. Instead, eastern white oak, which flowered from early to late May, was the preferred foraging substrate in 2010. Our findings suggest that the flowering and early leaf-out phase of trees provides important resources to migrant wood-warblers that are apparently absent from trees that are more phenologically advanced. Our results also suggest that managing for heterogeneity in tree species, including early and late flowering species, as well as maintaining early successional tree species in the landscape, may be an important consideration in maintaining wood-warbler population levels under a variety of climate conditions.

Key Words: *Acer*, avian foraging, climate change, habitat selection, maple, oak, *Quercus*, tree composition, wood-warbler.

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In the Upper Midwest of the United States, land use practices have resulted in succession of savanna and forests that differs in both plant community composition and vegetation structure from their condition prior to Euro-American settlement. In the mid- to late 1800s, large swaths of forests were cleared for timber production, prairie and savannas were converted to agriculture, and settlements were established (Schulte et al. 2007, Rhemtulla et al. 2009). These land use patterns created dramatic changes in land cover, with an ecological legacy that persists today. Over the past half-century, forest cover on nonurban lands or those not in production for agriculture has been regenerating (Iverson et al. 1997, Rhemtulla et al. 2007). Fire and other natural processes were a dominant factor shaping land cover but are now largely absent from the landscape, which has led to changes in vegetation (Abrams 1992). In southern Wisconsin, shade-intolerant trees such as oak (*Quercus* spp.) have declined in dominance, while shade-tolerant species such as maple (*Acer* spp.) have increased (Rogers et al. 2008). At a regional scale and since the mid-1800s, oak-hickory was the most common deciduous forest habitat, but it has been reduced by 50%, whereas northern hardwood forests dominated by maple have increased by 60% (Rhemtulla et al. 2009). The successional changes have resulted in the homogenization of forest composition and likely affect bird habitat use during migration (Wood et al. 2012).

In addition to long-term changes in forest structure, variation in climate potentially affects synchrony between migratory birds and their seasonal resources (Strode 2003, Visser and Both 2005). Migratory birds depend on seasonal resources at stopover habitats to replenish energy stores necessary for migration and breeding season demands (Moore et al. 2005). Yet, climate change induces earlier springs, which causes shifts in phenological events such as timing of flowering or leaf-out (Richardson et al. 2006, Ellwood et al. 2013). Phenological mismatches can be problematic for migratory birds, especially long-distance migrants for which departure from the wintering grounds is primarily governed by endogenous cues such as links between hormone activity and photoperiod (Holberton and Dufty 2005) or exogenous cues such as precipitation (Studds and Marra 2011). Since the early twentieth century in the North American Midwest, timing of spring migration among wood-warblers has varied little

from year to year (Strode 2003). However, onset of plant and resource phenology, such as leaf unfolding and caterpillar emergence, has become increasingly similar at different latitudes. These phenological changes may lead to a decoupling of synchronous events in which wood-warblers have less overlap with peak resource availability. In extreme cases, decoupling of phenological events could potentially affect both individual and population-level fitness (McKinney et al. 2012).

It is unclear whether future forest conditions in the Upper Midwest will provide necessary foraging substrates for migratory songbirds in the face of predicted trends in climate change and extreme annual weather variation. Our goal was to determine whether annual variation in tree phenology could affect migratory songbird foraging behavior during spring migration and thereby to gain insight into how greater variability in weather and phenology might impact a group of bird species in decline (Holmes 2007). We focused our study on four species of oaks and maple. The two species of oak—northern red oak (*Quercus rubra*) and eastern white oak (*Q. alba*)—are moderately shade-tolerant trees with poor rates of regeneration in southern Wisconsin forests. The two species of maples—sugar maple (*A. saccharum*) and red maple (*A. rubrum*)—are shade-tolerant trees that are regenerating well. We chose the four tree species because they are indicators of homogenization in forest composition throughout the region (Nowacki and Abrams 2008), but are currently abundant in the landscape (Wood et al. 2012). We had three study objectives:

1. Climatic conditions play an important role in plant phenology (Körner and Basler 2010), and warm temperatures induce earlier budburst (Richardson et al. 2006, Fu et al. 2012). Our first objective was to quantify the magnitude of difference in late winter and spring temperatures between our two study years of 2009 and 2010.
2. Synchrony between plant phenology, an indicator of food availability, and songbird use of plants as foraging substrates during spring migration are poorly known for migratory songbirds in forests in the Upper Midwest, but are needed to predict the potential effects of environmental change. For our second objective, we explored

patterns of phenological synchrony of the flowering phenophase of the four tree species used by migratory songbirds.

3. For our third objective, we quantified foraging success of migratory songbirds on the oak and maple tree species during two years of different environmental conditions, to understand whether seasonal variation in spring phenology can alter foraging conditions for migratory songbirds.

METHODS

Study Area and Sampling Design

Our study area was the 3,468-ha Kickapoo Valley Reserve in southwestern Wisconsin (Figure 7.1). The study site is located in the unglaciated Driftless Area, which is an important stopover region for migratory songbirds en route to breeding habitat in the boreal forest (Wilson 2008). The vegetation

of the upland forest patches at the Kickapoo Valley Reserve, where the study was conducted, is dominated by dry- and southern-mesic forest (Curtis 1959). In a parallel study, we quantified the importance value of tree species in our study area, which is a measure of the availability of trees as foraging substrates for migratory birds, using the point-center quarter method (Wood et al. 2012). Common trees of the study area include northern red oak (17% relative importance value), eastern white oak (16%), sugar maple (16%), bitternut hickory (*Carya cordiformis*; 8%), American basswood (*Tilia americana*; 7%), and red maple (5%). Red maple was absent in the study area in the 1850s, but is now a common tree (Wood et al. 2012), similar to other forested areas throughout the region (Abrams 1998). We studied migratory songbird foraging behavior and tree phenology in four forest patches that ranged in size from 80 to 107 ha (Figure 7.1). We selected these patches because they were among the largest, unfragmented tracts

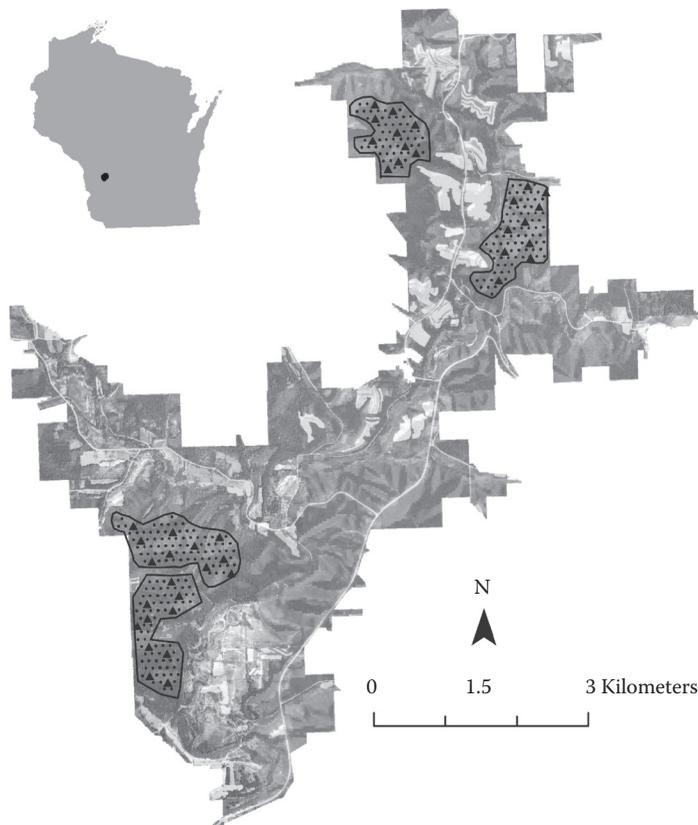


Figure 7.1. Location of the Kickapoo Valley Reserve, Wisconsin, and distribution of forested study areas (black polygons) within the reserve, with 258 lattice points superimposed. Black triangles represent randomly selected phenology-tree sampling stations.

of contiguous forest in southwest Wisconsin, representative of smaller forest patches of the region, and floristically diverse, including our four study species of deciduous trees. To select sampling locations, we digitized each forest patch in ArcGIS 9.3 (ESRI, Redlands, California, 2008) and plotted a lattice grid of points (hereafter, lattice points) separated by 100 m, with alternate rows offset by 50 m. We used each lattice point as a reference point during tree phenology and avian area-search surveys. We plotted 83, 52, 61, and 62 lattice points in the four patches for a total of 258 lattice points (Figure 7.1).

Climatic Data

To quantify differences in climatic conditions between 2009 and 2010, with a focus to inform patterns of tree phenology between years, we obtained maximum daily temperature data for the months of March, April, and May from a nearby National Oceanic and Atmospheric Administration weather station (Sparta, Wisconsin, NOAA Station ID: WI477997). The weather station was located ~15 miles north of our study area and was the closest station with climatic data. We obtained similar climatic data from 1950 to 2010 to compare long-term maximum daily temperature averages with the 2009 and 2010 data. We used maximum daily temperature during the months of March, April, and May as our weather variable of interest because tree budburst phenology is strongly influenced by late winter and early spring temperatures (Körner and Basler 2010).

Tree Phenology Measurements

To determine whether annual variation in tree phenology affects migratory songbird foraging behavior during spring migration, it was necessary to monitor tree phenology simultaneously. We randomly selected 10 lattice points within each forest patch, which were used as reference points for tree phenology measurements (Figure 7.1). At each reference point, we marked individuals from each of the four species of study trees: northern red oak, eastern white oak, red maple, and sugar maple ("phenology trees," hereafter). We selected and flagged the nearest individual of each of the four phenology trees, measured diameter at breast height (dbh) > 10 cm, and recorded GPS coordinates. We marked a total of 160 phenology trees,

with 40 in each forested patch (Figure 7.1). We later removed five phenology trees from analysis because we inadvertently included three eastern black oaks (*Q. velutina*), which are similar to northern red oak, and two bur oaks (*Q. macrocarpa*), which are similar to eastern white oak. We visited the four patches and all phenology trees on seven occasions from late April to late May in 2009 and 2010, with at least 4 days between consecutive visits. The Julian dates for our seven visits were 115, 119, 125, 132, 138, 142, and 147. We used this time interval between visits because we wanted to characterize tree phenological stages at a fine temporal scale and because the average stay for migratory birds at stopover habitats is less than 3 days (Moore and Kerlinger 1987). We revisited each phenology tree on the same Julian day in 2010 as in 2009, to control for timing of visits as a source of differences in tree phenology between years. Our sampling scheme allowed for a paired sampling design between years.

During a visit to a phenology tree, observers recorded tree phenology based on the proportion of the crown that was displaying any of the following nine tree phenophases: (1) winter condition, (2) budding, (3) bud swelling, (4) budburst, (5) young leaf, (6) mature leaf (summer condition), (7) flower emergence, (8) flowering, and (9) wilted flower. Observers stood 10 m from the base of the tree and used binoculars to carefully scan the portion of the tree crown in view before recording measurements. We collected four measurements at each tree, with one in each of the cardinal directions. The lead author trained and calibrated all observers throughout the month of April, practicing on tree species where average onset of budburst and leaf-out is similar or earlier than the phenology trees (e.g., quaking aspen, *Populus tremuloides*). We averaged the four measurements, resulting in a phenology-tree specific score for each phenophase during each visit. We further averaged data from each phenology-tree species by Julian day, throughout our study area, to understand broad phenological patterns of each tree species throughout the region.

Avian Foraging Observations

We quantified avian foraging behavior to determine whether variation in tree phenological stage affects migratory songbird tree use during spring migration. It was not possible to observe

TABLE 7.1
Scientific name, sample size of birds (n), and cumulative number of seconds of foraging observations for 15 migratory species of wood-warblers observed during spring migration in the Kickapoo Valley Reserve, Wisconsin, 2009 and 2010.

| Common name | Scientific name | n (2009) | n (2010) |
|-------------------------------------|--------------------------------|--------------------|--------------------|
| Golden-winged Warbler ^a | <i>Vermivora chrysoptera</i> | 5 ⁵⁹⁵ | 1 ⁴⁹ |
| Blue-winged Warbler ^a | <i>Vermivora cyanoptera</i> | 9 ⁴²⁴ | 2 ¹⁷⁰ |
| Tennessee Warbler | <i>Oreothlypis peregrina</i> | 53 ⁴⁶⁵⁶ | 18 ¹⁹⁰⁰ |
| Nashville Warbler ^a | <i>Oreothlypis ruficapilla</i> | 13 ¹⁰⁶³ | 8 ⁶⁰¹ |
| American Redstart ^a | <i>Setophaga ruticilla</i> | 3 ¹²¹ | 2 ⁹² |
| Northern Parula | <i>Setophaga americana</i> | 3 ³⁰⁴ | 1 ¹⁴⁰ |
| Chestnut-sided Warbler ^a | <i>Setophaga pensylvanica</i> | 6 ³⁹⁰ | 3 ⁶⁰ |
| Magnolia Warbler | <i>Setophaga magnolia</i> | 2 ¹⁷⁷ | 0 |
| Cape May Warbler | <i>Setophaga tigrina</i> | 3 ³⁷² | 0 |
| Black-throated Blue Warbler | <i>Setophaga caerulescens</i> | 1 ⁹⁷ | 0 |
| Blackburnian Warbler | <i>Setophaga fusca</i> | 19 ²⁴⁶⁰ | 3 ¹⁶⁷ |
| Yellow-rumped Warbler | <i>Setophaga coronata</i> | 13 ¹⁴⁵² | 8 ⁵²⁷ |
| Black-throated Green Warbler | <i>Setophaga virens</i> | 10 ⁶⁰³ | 10 ⁸⁹⁹ |
| Bay-breasted Warbler | <i>Setophaga castanea</i> | 2 ¹⁰³ | 0 |
| Blackpoll Warbler | <i>Setophaga striata</i> | 3 ¹³⁰ | 0 |

^a Species breeds in study area (Wisconsin Breeding Bird Atlas).

migratory songbird foraging behavior on individual phenology trees due to low frequency of use of these trees during the times we were observing them. Thus, we monitored migratory songbird foraging behavior on the phenology-tree species throughout the study area and related our observations to the study area-averaged phenology-tree measurements. We collected foraging data on 15 migratory species of Neotropical–Nearctic wood-warblers (hereafter, “wood-warblers”), which we selected because they are common at our study area and primarily use trees as foraging substrates during spring migration (Table 7.1). Wintering grounds for Yellow-rumped Warbler (*S. coronata*) are more northerly than those for the other 14 wood-warblers. We included this species in our analysis because they were commonly detected using phenology tree species along with other wood-warblers throughout our survey period. A few species were rare in our study area, such as Black-throated Blue Warblers (*S. caerulescens*). We nevertheless included rare species because they were similar to more common birds taxonomically and in their foraging habits (Whelan 2001). We grouped data from all wood-warblers to increase sample size necessary for analyses

and because our goal was to understand foraging behavior of this group of birds broadly relative to variations in annual spring tree phenology. We gathered foraging data on the same seven days on which we collected tree phenology data, which encompasses the migration period in Wisconsin for wood-warblers en route to northern breeding grounds (Temple et al. 1997). Between sunrise and 1 P.M., we performed extensive area searches of forest patches by walking on established routes designed to maximize coverage of a patch, actively searching for foraging flocks of the wood-warblers. Four trained observers collected data and rotated among forest patches with each visit in an effort to distribute observer variability as much as possible. We alternated starting points of the walking routes with each visit so that unique sections of the forest patches were visited at similar times among different visits.

After locating a flock, we followed and documented the foraging activities and movements of a wood-warbler for up to five minutes and within the boundaries of a forest patch using standardized methods (Holmes and Robinson 1981, Remsen and Robinson 1990). We often documented foraging behavior of an individual wood-warbler

in multiple phenology trees over the course of a given observation bout. We restricted our arrival, use, and synchrony analyses to observations of foraging birds made only in the first tree to guard against potential autocorrelation (Gabbe et al. 2002, Wood et al. 2012). However, we included data from all phenology trees in which foraging was observed in analyses of foraging success to gain understanding of broad patterns of wood-warbler foraging behavior among phenology trees. We recorded behavioral data with a digital recorder with a built-in timer (Sony ICD-PX720 digital voice recorder). We recorded six variables for each individual: date, time of day, species of warbler, tree species used, search effort (e.g., number of hops, walks, flights), and type of prey attack (e.g., bud glean, flower glean, leaf glean, bark glean, hover, sally, and flush-chase; Remsen and Robinson 1990). In addition to monitoring wood-warbler foraging behavior, we recorded the dominant phenophase (defined as >50% of a tree in a particular phenophase) for all trees where birds were found foraging (hereafter, “foraging trees”) to understand relationships of foraging-tree phenology and foraging behavior by wood-warblers. We collected foraging-tree phenophase measurements on a binary scale depending on the presence or absence of a dominant phenophase. We used a binary scale because determining phenophase of a tree is time intensive, and it was not possible to record conditions while simultaneously monitoring foraging behavior of wood-warblers. Once foraging data collection for a wood-warbler was concluded and a foraging-tree phenophase measurement was completed, we either moved to another wood-warbler in the immediate area—using a phenology tree, if possible—or moved back to the walking route in search of another foraging flock that was >300 m from the previous flock.

Statistical Analysis

For our first objective, we quantified differences in maximum temperatures during March, April, and May in 2009 and 2010 by calculating three paired two-sample *t*-tests, with one for each of March, April, and May, with daily maximum temperature as the response variable and year as the treatment. We also related the maximum daily temperature during March, April, and May in 2009 and 2010 with the average daily maximum temperature

from 1950 to 2010 in six additional two-sample *t*-tests (three for March, April, and May in 2009 and 2010, respectively). We checked for normality of the residuals of the dependent variables using QQ-norm plots, which revealed that no transformations were necessary. We used the critical value of $\alpha \leq 0.05$ to determine significance.

To address our second objective, we explored patterns of phenological synchrony of the flowering phenophase of the four phenology-tree species with wood-warbler foraging behavior on those trees. First, to understand wood-warbler use of the phenology trees of the study area within each sampling season, we calculated the proportion of tree use—defined as active feeding or searching by wood-warblers among the seven sampling periods—and then compared this proportional distribution in 2009 and 2010. Second, we calculated the percentage of tree crown in the flowering phenophase on phenology trees among the seven sampling periods and then compared estimates between years. We focused on the flowering phenophase because flowering is a proximate cue to the availability of food (McGrath et al. 2008) and because we commonly noticed birds using flowering trees as foraging substrate during pilot field work for our project.

Furthermore, we quantified foraging success of wood-warblers relative to phenophase of foraging trees. We constructed an attack index response variable, which is a measure of foraging success and is calculated as the ratio of the total attacks by wood-warblers, divided by total search maneuvers, scaled per minute (Wood et al. 2012). We explored differences in the attack index related to the dominant phenophase of the foraging trees (which we categorized as budburst, flowering, or mature leaf) for 2009 and 2010 combined, using a Kruskal-Wallis test, with phenophase of a foraging tree as the treatment. In a handful of cases, a particular foraging tree was categorized by a different phenology event from the three treatments we used, such as young leaves with wilted flowers. We removed these cases to ensure that phenophase categories in the analysis were distinct. Furthermore, although the timing of flowering and leaf-out is variable among the phenology trees, the phenological physiognomy is similar within oaks and maples (e.g., catkin flowers in oaks). We pooled data from the two oak species versus the two maple species to understand foraging success of wood-warblers among the two

tree groups. When Kruskal-Wallis tests were significant, we employed a nonparametric multiple comparison procedure, based on relative contrast effects, using nparcomp (Konietzschke 2011). We used a Bonferroni adjustment to the critical α value of $0.05/3 = 0.02$ to assess significance for multiple tests.

For our third objective, to determine whether variations in annual spring phenology alter foraging conditions for members of this family of birds en route to their breeding grounds, we quantified foraging success of wood-warblers, among the four study tree species, between years. To do so, we explored differences in the attack index on the phenology-tree species for 2009, 2010, and both years combined, by using a Kruskal-Wallis test, with phenology tree as the treatment. This test was similar to the previous analysis, except that we used a Bonferroni adjustment to the critical α value of $0.05/6 = 0.01$ to assess significance. We used a Wilcoxon rank sum test for 2010 data because only northern red oak and eastern white oak were used by the wood-warblers in that year. For the Wilcoxon rank sum test analysis, we used a significance threshold of $\alpha \leq 0.05$.

RESULTS

Patterns of Annual Late-Winter and Spring Temperatures

The maximum daily high temperature in 2009 was similar to the average monthly high temperature from 1950 to 2010 in March ($t_{30} = 0.46$, $P = 0.65$) and April ($t_{29} = 1.42$, $P = 0.17$), but was significantly lower in May ($t_{30} = 2.35$, $P = 0.02$; Figure 7.2). In contrast, the maximum daily high temperature in 2010 was significantly warmer than the average monthly high temperature from 1950 to 2010 in March ($t_{30} = -5.83$, $P < 0.01$) and April ($t_{29} = -3.41$, $P < 0.01$), but similar in May ($t_{30} = -0.75$, $P = 0.46$; Figure 7.2). Maximum daily temperatures were significantly warmer in 2010 than 2009 in March ($t_{30} = -5.91$, $P < 0.01$), April ($t_{29} = -3.28$, $P < 0.01$), and May ($t_{30} = -2.03$, $P = 0.05$; Figure 7.2).

Tree Phenology and Migratory Bird Synchrony

Northern red oak was the largest species in our sample of phenology trees with an average dbh of 63.8 ± 2.7 cm. Eastern white oak and sugar maple

were slightly smaller: 56.3 ± 3.2 , and 53.2 ± 2.1 cm, respectively, followed by red maple at 43.2 ± 3.1 cm. We monitored foraging behavior of 15 wood-warbler species in 2009, for a total of 216 min and 27 s (Table 7.1). In 2010, we monitored foraging behavior of 10 wood-warbler species, for a total of 79 min and 58 s. The average foraging observation was 1 min and $29 \text{ s} \pm 0.10$ in 2009, and 1 min and $21 \text{ s} \pm 0.09$ in 2010. In both years, wood-warblers used phenology trees at the stopover study area from late April (Julian day 119) until late May (Julian day 147 in 2009 and 142 in 2010; Figure 7.3). However, the frequency of bird-use of the phenology trees in the study area was 60% less in 2010 than 2009 (Figure 7.3), despite similar survey effort.

In 2009, there were apparent patterns of synchrony between wood-warbler foraging behavior and the flowering phenophase of northern red oak, eastern white oak, and, to a lesser extent, sugar maple (Figure 7.4). Red maple flowered prior to wood-warbler arrival and was not preferred by wood-warblers (Figures 7.4 and 7.5).

In 2010, northern red oak, sugar maple, and red maple flowered 2 to 3 weeks earlier than in 2009, and these tree species were not preferred by the wood-warblers (Figures 7.4 and 7.5). On the other hand, eastern white oak, which flowered from late April to mid-May in 2010, was the preferred foraging substrate in that year (Figures 7.4 and 7.5). When flowering of eastern white oaks was complete, wood-warbler use of the phenology trees subsided dramatically, which was in contrast to 2009, where birds were observed foraging among the phenology trees until late May (Figure 7.4).

In 2009 and 2010, wood-warbler foraging success was significantly greater on oak trees that were in flower, compared to trees at the budburst or mature leaf stage ($H_2 = 23.23$, $P < 0.01$; Figure 7.6). In contrast, foraging success of wood-warblers on maples did not differ among the phenological stages of budburst, flowering, or mature leaf ($H_2 = 1.49$, $P = 0.48$; Figure 7.6).

Migratory Bird Foraging Success

Foraging success differed among phenology trees within (2009: $H_3 = 16.52$, $P < 0.01$; and 2010: $W_{58} = 351.5$, $P = 0.02$) and between ($H_3 = 19.29$, $P < 0.01$; Figure 7.7) years. In 2009, average foraging success of wood-warblers was highest on northern red oak (0.34 ± 0.04), followed by eastern

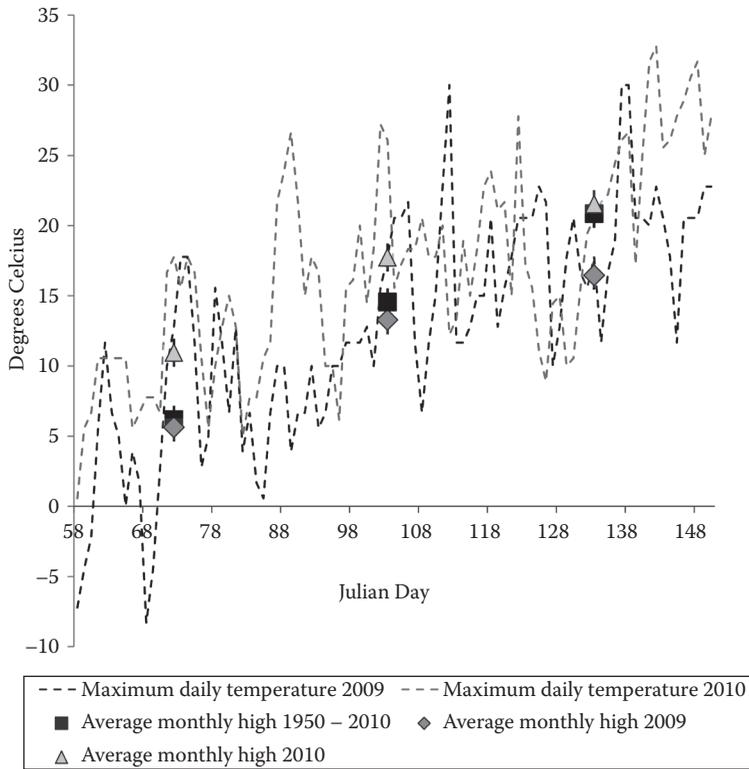


Figure 7.2. Average monthly high temperature for March, April, and May during 1950–2010 (black squares), 2009 (gray diamonds), and 2010 (gray triangles), ± 1 SE, and daily maximum high temperatures for 2009 and 2010 represented by dotted lines. Weather data obtained from NOAA Station ID: WI477997, Sparta, Wisconsin.

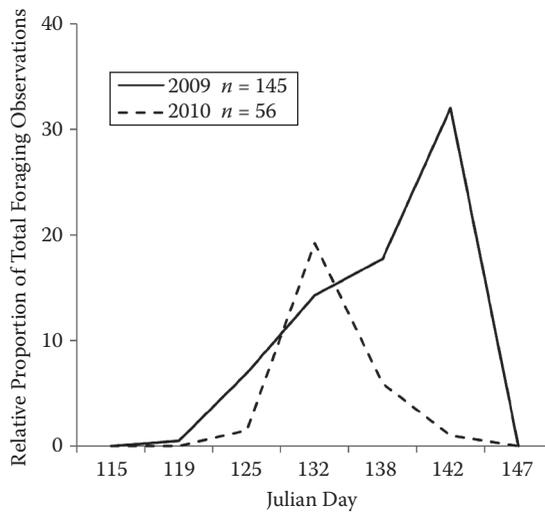


Figure 7.3. Relative number of foraging observations (number of observed foraging bouts per Julian day divided by the total for both years combined) on four tree species—*Quercus rubra*, *Q. alba*, *Acer rubrum*, and *A. saccharum*—by 15 species of wood-warblers, from 24 April to 26 May (Julian day: 115–147) at the Kickapoo Valley Reserve, Wisconsin.

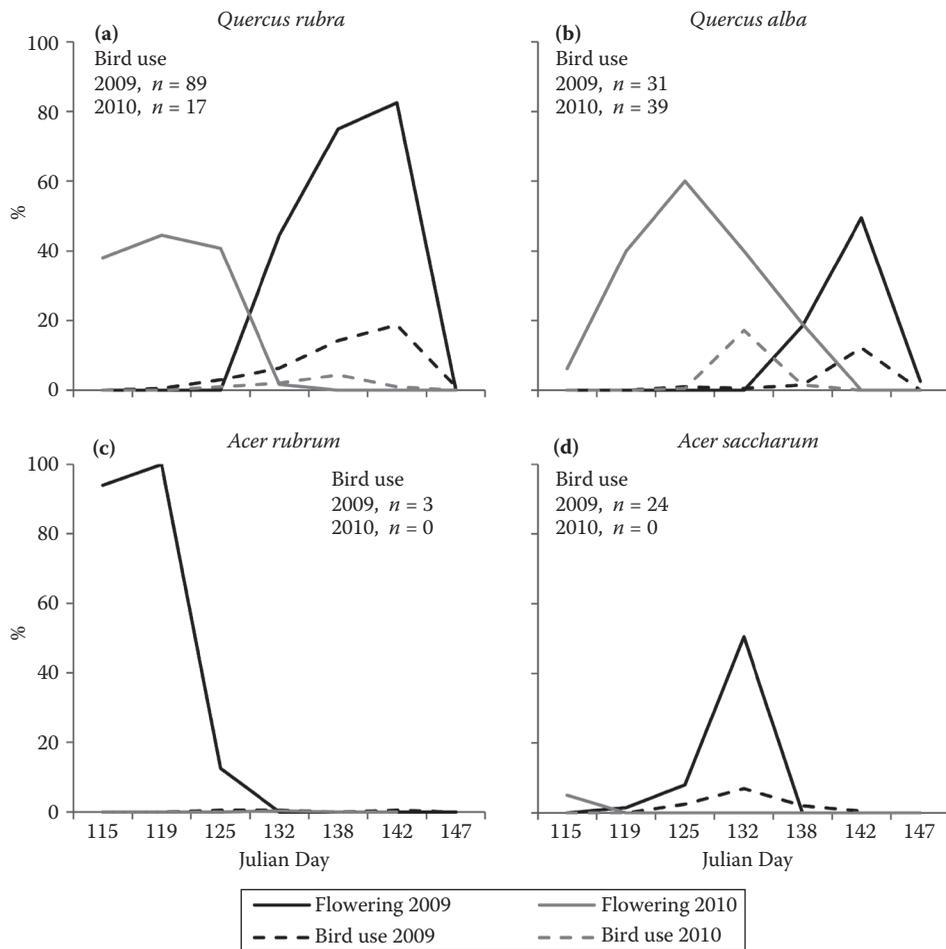


Figure 7.4. The relationship between the relative use (number of observed foraging bouts per Julian day, per tree, divided by the total foraging bouts in 2009 and 2010 combined) by 15 species of wood-warblers, and percentage of flowering of four species of trees—*Quercus rubra*, *Q. alba*, *Acer rubrum*, and *A. saccharum*—from 24 April to 26 May (Julian day: 115–147), 2009 and 2010.

white oak (0.27 ± 0.05), sugar maple (0.25 ± 0.06), and red maple (0.13 ± 0.08). Wood-warbler foraging success on northern red oak was similar to that on eastern white oak in 2009, but was significantly higher than on sugar maple (similar to eastern white oak) or red maple (Figure 7.7). In 2010, wood-warblers did not use red maple or sugar maple. Wood-warbler foraging success was highest on eastern white oak (0.38 ± 0.05), which was significantly higher than northern red oak (0.21 ± 0.05 ; Figure 7.7). When the two years were considered together, wood-warbler foraging success was highest on eastern white oak (0.34 ± 0.04), followed by northern red oak (0.32 ± 0.03), sugar maple (0.21 ± 0.06), and red maple (0.13 ± 0.08 ; Figure 7.7). Wood-warbler foraging success

on the two oak species was similar between years, yet was significantly higher than on the maple species (Figure 7.7).

DISCUSSION

Our results suggest that extreme differences in annual late-winter and spring temperatures impacted spring tree phenology, which in turn affected foraging quality of dominant trees at a stopover location in a forest in the Upper Midwest and influenced foraging behavior of wood-warblers. We found that flowering northern red oak and eastern white oak, which are both trees that are regenerating poorly in the region, are preferred as foraging substrates by

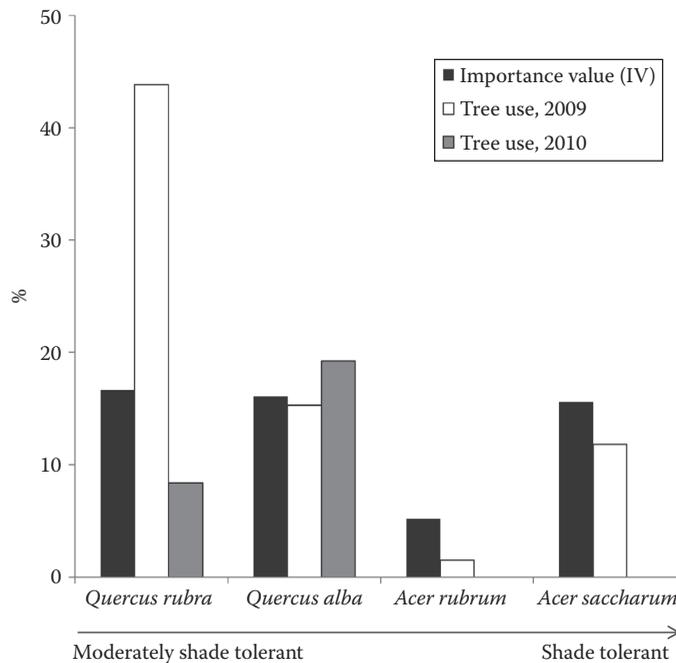


Figure 7.5. Relative importance value, which is a measure of the proportional availability of each of four tree species ordered by shade tolerance—*Quercus rubra*, *Q. alba*, *Acer rubrum*, and *A. saccharum*—as foraging substrates versus the proportion of all foraging observations by 15 species of wood-warblers on the four species of trees from 24 April to 26 May (Julian day: 115–147) at the Kickapoo Valley Reserve in 2009 and 2010. Relative use was calculated as the total number of wood-warbler observations for a tree species, in a given year, divided by the sum of all observations among the four tree species, in both study years.

wood-warblers. Eastern white oak generally flowers later in May than northern red oak throughout our study region. Therefore, if both tree species persist in this landscape, the foraging needs of spring migrant wood-warblers are likely to be met. Ensuring long-term viability of oak species is one step that can be taken to buffer the negative impacts to foraging quality of variable climate conditions. Wood-warblers also used flowering sugar maple, but red maple was rarely used. During warm springs, both species of maples are poor foraging substrates for wood-warblers. Our observations raise a conservation concern because maples are regenerating throughout forests of the Upper Midwest, with a substantial increase in red maple in particular (Abrams 1998, Wood et al. 2012).

Tree phenology is influenced by a variety of environmental cues interacting throughout the winter and spring period. Winter chilling, photoperiod, and late-winter and spring temperatures affect budburst of both early and late successional tree species (Körner and Basler 2010). For some plant species, once the winter chilling

requirement has been met, late-winter and early spring temperatures largely influence budburst (Körner and Basler 2010). For example, common lilac (*Syringa vulgaris*) is an ornamental shrub that advances budburst in warm springs (Körner and Basler 2010) and has been the subject of ongoing research on effects of climate change on spring green-up in North America (Schwartz and Reiter 2000). In New England hardwood forests, onset of sugar maple budburst is ~9 days earlier than in 1957 due to increasing spring temperatures (Richardson et al. 2006). In a controlled experiment, saplings of three temperate tree species advanced budburst with increased warming temperatures (*Betula*, *Fagus*, and *Quercus* spp.; Fu et al. 2012).

Our 2-year sample size was too low to explore relationships between spring climatic conditions and tree phenology, but our results suggest that annual variation in late-winter and spring temperatures likely affect budburst of oak and maple species. Late-winter and spring temperatures were significantly warmer in 2010 than in 2009, and the long-term average for these months appears

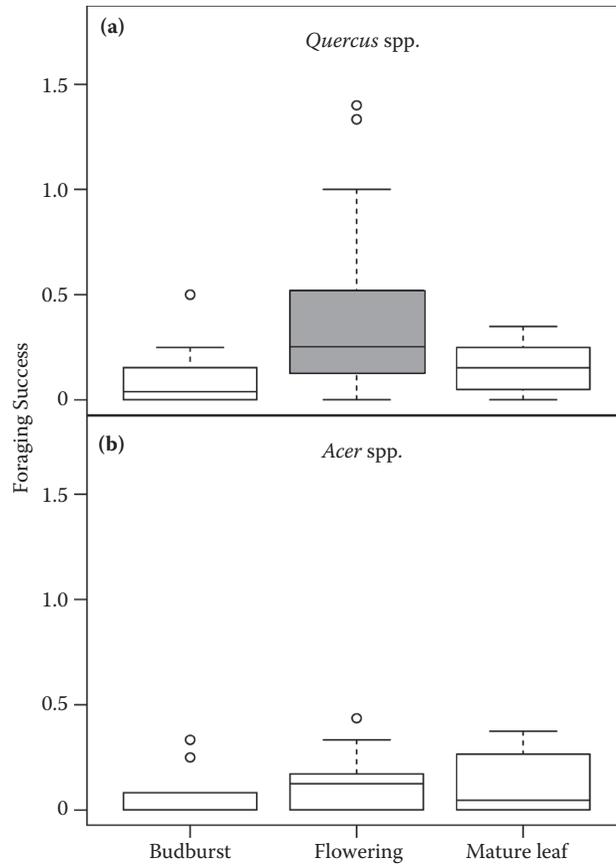


Figure 7.6. Box plots of the attack index (total attacks/total searches, per minute), a measure of foraging success, for 15 species of wood-warblers using two genera of trees (a-b), *Quercus* and *Acer*, in 2009 and 2010. Attack index is shown for three distinct phenophases: budburst, flowering, and mature leaf. Box plots with different colors differ significantly based on a Kruskal-Wallis test with nonparametric multiple comparisons procedure with a Bonferroni adjusted $P \leq 0.05/3 = 0.016$.

to be associated with a 2- to 3-week phenology advancement of the four tree species. In contrast to Körner and Basler (2010), our results suggest that, for late-successional tree species such as red maple and sugar maple, temperature appears to play a larger role in determining budburst than photoperiod. We matched Julian days in the two years of our study to control for differences in day length between years, thus allowing for direct comparisons of phenology. Photoperiod appeared to be an important factor determining spring budburst for some tree species in our study area, such as black walnut (*Juglans nigra*; pers. obs.), but was likely not as important as temperature in determining budburst of oaks and maples. Taken together, our findings suggest that warming trends and increased variability in spring temperatures (Schär et al. 2004) will likely alter

spring tree phenology and possibly resource availability, such as caterpillar emergence, for migratory bird species.

Changes in phenology are a concern because we found patterns of phenological synchrony between wood-warblers and the flowering period of northern red oak and white oak and, to a lesser extent, sugar maple. Our observations of synchrony between migratory birds and seasonal resources are similar to patterns reported elsewhere: Spring arrival of Orange-crowned Warblers (*Oreothlypis celata*) overlaps with flowering of honey mesquite found in Arizona riparian habitats (McGrath et al. 2008), Broad-tailed Hummingbird (*Selasphorus platycercus*) migration is coincident with abundance of nectar resources in Arizona pine-oak woodlands (McKinney et al. 2012), migratory landbirds concentrate in habitats

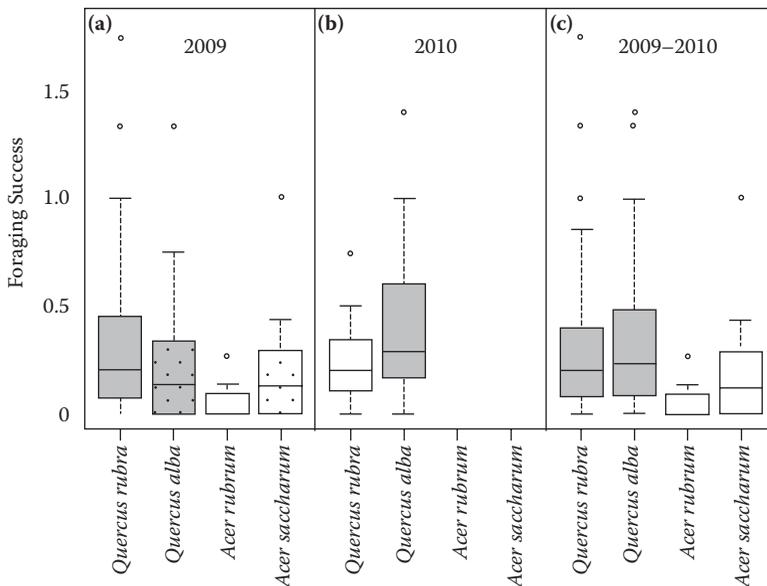


Figure 7.7. Box plots of foraging success, measured by the attack index (total attacks/total searches, per minute), for 15 species of wood-warblers using four tree species as foraging substrates during spring migration: *Quercus rubra*, *Q. alba*, *Acer rubrum*, and *A. saccharum* in (a) 2009, (b) 2010, and (c) both years combined. Box plots with different colors or patterns differ significantly based on a Kruskal-Wallis test with nonparametric multiple comparison procedures with a Bonferroni adjusted $\alpha \leq 0.05/4 = 0.013$. Data from 2010 were evaluated based on a two-way Wilcoxon rank test, $P = 0.05$.

where plants are in early leaf development in Pennsylvania suburbs and forests (Rodewald and Brittingham 2007), and wood-warbler migration corresponds with peaks in Lepidopteran availability in Illinois woodlots (Graber and Graber 1983, Strode 2009). Lepidopteran abundance on oak trees is greatest during the spring flowering and leaf-out period, prior to an increase in tree chemical defenses during the summer (Forkner et al. 2004). Maples and oaks have different levels of chemical defenses; this, in turn, likely affects the abundance of insects available as food resources to birds (Adams et al. 2009). Chemical defenses may be a possible mechanism explaining the foraging patterns we observed. We did not measure food availability among the four phenology trees throughout our study period, but our findings of higher foraging success on northern red oak and eastern white oak during flowering, rather than during budburst or mature leaf-out stages, suggests the importance of synchrony between timing of flowering and use by wood-warblers. The flowering duration of northern red oak and eastern white oak is ~three weeks throughout our study area. Thus, if tree phenology is advanced by two to three weeks, as in 2010, and wood-warblers are not able to adjust their arrival to

coincide with flowering (Strode 2003), the birds will miss the flowering phenophase and peak food availability altogether, and foraging success will likely be negatively impacted.

A plausible explanation for lower wood-warbler foraging success on northern red oak and eastern white oak trees that were in summer condition with mature leaves rather than flowering is the differences in food accessibility (Wood et al. 2012). During spring, trees undergo rapid physiognomic changes, which likely affects accessibility of food items found on flower or leaf surfaces. In 2009, we observed some use by wood-warblers of sugar maple during the flowering and emerging leaf-out period. In 2010, the majority of sugar maple achieved summer condition by April 28 (Julian day 119), which is two to three weeks earlier than peak wood-warbler migration throughout southern Wisconsin (Temple et al. 1997). We did not observe wood-warblers foraging on sugar maple in 2010. In general, leaves of shade-tolerant trees, such as sugar maple, are supported by long petioles, which support the large leaves necessary for improved light-gathering in shady conditions (Takenaka et al. 2001). To acquire food items on leaf surfaces of tree species with long leaf petioles, bird species must use energetically costly foraging

maneuvers (Whelan 2001). Under optimal foraging theory, migrating wood-warblers should forage to maximize caloric intake while minimizing energetic output and risk, and they might be predicted to avoid unsuitable foraging substrates, such as red maple or sugar maple, in summer conditions. Foraging success of migratory songbirds is negatively correlated with leaf-petiole length a measure of food accessibility that is characteristic of shade-tolerant tree species that are regenerating throughout forests in the Upper Midwest (Wood et al. 2012). In addition to red maple and sugar maple, other shade-tolerant tree species with long leaf petioles, such as American basswood, are also regenerating regionally (Wood et al. 2012). Without management for early or mid-successional tree species, forest homogenization will likely continue, resulting in lower quality stopover habitat for wood-warbler species. Our results suggest that these effects will be exacerbated in warm springs when shade-tolerant tree species will be in summer condition throughout the migratory period, creating poor-quality foraging conditions for songbird species in Upper Midwestern forests.

Our findings provide evidence that large variation in late-winter and spring temperatures likely affects tree phenology, resulting in asynchrony of migratory wood-warbler species with ephemeral tree phenological stages necessary for optimal foraging at stopover habitats. We show that this asynchrony affects foraging success and, in extreme cases, may result in deleterious effects to the condition and breeding success of individuals (McKinney et al. 2012). Migratory bird species are constantly encountering environmental variability, which affects stopover habitat quality and food resource availability (Hutto 1985). Yet, we show that the combination of forest succession and climate variability will likely continue to impact spring stopover habitat quality negatively for wood-warblers throughout the Driftless Area.

As a strategy for maintaining stopover habitat for migratory songbirds under a variety of climate conditions in forests in the Upper Midwest, we advocate for management that encourages forest tree heterogeneity. The Kickapoo Valley was historically a mesic forest island within a savanna matrix, shaped by relatively cool summer temperatures and high annual rainfall, in contrast to the surrounding oak savanna landscape (Kline and Cottam 1979). Sugar maple and white oak

historically dominated the Kickapoo Valley, and these species remain common today (Kline and Cottam 1979). Yet, the presence of red maple, which was historically an uncommon tree species in southern Wisconsin forests, as well as poor recruitment rates of oak and other early successional species, suggests a change in forest composition toward further dominance by shade-tolerant species throughout the region (Wood et al. 2012). We suggest that forest management plans for the Driftless Area and other similar forested habitats in the Upper Midwest include promoting early and late flowering species such as red and white oak, as well as trees adapted to low or moderate shade such as quaking aspen. Furthermore, we recommend carefully managing recruitment of shade-tolerant tree species, especially on south-facing slopes, and ridge tops, where these species were most likely never common (Kline and Cottam 1979).

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