Phenological Asynchrony between Migrant Songbirds and Food Resources during Early Springs*

INITIATION OF A TROPHIC CASCADE AT A STOPOVER SITE

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Abstract. This chapter compares the phenology of forest trees, caterpillars, and Neotropical–Nearctic migrant songbirds during three successive spring seasons at Trelease Woods, a 24-ha deciduous forest fragment near Urbana, Illinois, in the United States, and describes a trophic cascade in years of phenological asynchrony. I show that the phenological patterns of budbreak and leaf emergence and the occurrence of canopy caterpillars varied significantly among springs, in accordance with variation in temperature accumulation. The timing of migration of migrant songbirds through the stopover, however, did not vary among years at the community or the species levels. As a result, activity by the three trophic levels was synchronized in 2002, but unsynchronized in 2001 and 2003. In the synchronized year, mean leaf area lost to folivory was 9.3% in both bur oak (*Quercus macrocarpa*) and northern red oak (*Q. rubra*), but increased significantly to 20.5% in the year with least synchrony (2003). In the two years when black walnut (*Juglans nigra*) was included in the study, folivory increased from 1.8% in 2002 to 7.8% in 2003. Increases in folivory were likely an indirect result of trophic level asynchrony and are evidence of a trophic cascade. My findings raise concerns that more frequent early springs generated by climate change, with resulting trophic asynchrony, may affect the productivity and future composition of temperate deciduous forests, as well as the fitness of many Neotropical–Nearctic birds.

Key Words: black walnut, caterpillars, climate change, folivory, *Juglans*, migrant birds, migration, oak, phenology, *Quercus*, stopover, vireo, wood-warbler.

When Hairston et al. (1960) introduced the green-world hypothesis, they argued that producer biomass is high because predators limit herbivore populations. Top-down trophic cascades with indirect effects of predators on plants via herbivores are now the focus of numerous studies of indirect effects in communities (Pace et al. 1999, Borer et al. 2006). In many systems, trophic cascades can occur by way of phenological variance among trophic levels (Hunter

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2001, Rodríguez-Casteñeda 2013)—especially in trophic cascades in which species occupying different positions have narrow temporal windows for synchrony (Stenseth and Mysterud 2002, van Asch and Visser 2007). One such system involves migrant songbirds, their folivorous insect prey, and trees at stopover habitats in the spring.

Wood-warblers (F. Parulidae) and vireos (F. Vireonidae) are Neotropical–Nearctic migrant songbirds and are potentially vulnerable to trophic asynchrony at stopover habitats in the spring. Trophic asynchrony may arise because the birds are strongly dependent on photoperiod to time their northward movements from the tropics (Hagan et al. 1991, Breuner and Wingfield 2000, Dawson et al. 2001), while the availability of their herbivore prey (Lepidoptera) and the prey's host plants (forest trees) is linked to spring temperatures (Lysyk 1989, Hunter and Lechowicz 1992b, Lawrence et al. 1997, Ivashov et al. 2002, van Asch and Visser 2007). The timing of arrival at stopover habitats for many insectivorous songbirds has varied little over the last century (Wilson et al. 2000, Strode 2003). In early or late springs, it may be predicted that these birds could miss the peak in their food resources at stopover habitats. It also can be predicted that enough asynchrony could initiate a trophic cascade and result in increased folivory to the trees and decreased fitness for the birds.

In temperate deciduous forests, spring-feeding caterpillars emerge and feed when the nitrogen and water contents of young leaves are high (Hunter and Lechowicz 1992a). In Britain, Dury et al. (1998) found that the organic nitrogen content of leaves of pedunculate oak (*Quercus robur*) declined by 60% during the spring warm-up and leaf growth phase. Similarly, Hunter and Lechowicz (1992a) found that leaf nitrogen in the young leaves of nine species of deciduous hardwood trees in the eastern United States had declined to half of their initial levels (percentage of dry weight) after the date of a predictable temperature threshold (225°C–250°C day accumulation above a 5°C threshold).

Many spring-feeding insect herbivores have evolved spring emergence phenologies that correspond to the temperature-driven emergence of their host plant food sources (Lysyk 1989, Hunter and Lechowicz 1992b, Lawrence et al. 1997, Ivashov et al. 2002). Phenophase synchrony has been particularly well documented

for economically important insect species, especially Lepidoptera (Buse and Good 1996, Parry et al. 1998, Bryant et al. 2002). Insect herbivores in general are most dense in the spring in many forest systems (Feeny 1970, Reichle et al. 1973). Caterpillars, in particular, are at their highest densities in May in temperate deciduous forests (Kendeigh 1979), and insectivorous migrant songbirds typically arrive in these forests to rest and feed during migration.

Caterpillars are the main prey of wood-warblers and vireos during spring migration, and they account for almost 100% of the diet of some species of migratory birds (Graber et al. 1983, 1985). Previous studies have shown that forest insectivorous birds are significant population regulators of caterpillars (Holmes et al. 1979, Moore and Yong 1991), and that caterpillar-consuming birds can have both weak and strong top-down effects on forest tree growth (Marquis and Whelan 1994, Lichtenberg and Lichtenberg 2002). Indeed, predation on caterpillars by birds can reduce caterpillar abundance in saplings of forest trees by up to 50% (Marquis and Whelan 1994). Therefore, wood-warblers and vireos are likely key players in the population dynamics of spring-feeding caterpillars. However, the impact of insectivorous migrant songbirds on temperate forest ecosystems may depend on the local density of folivorous insects and the phenology of songbird migration as it relates to the phenology of their insect prey and the host plants.

Most studies to date on the leaf–caterpillar–songbird tritrophic system used understory saplings as the foraging substrate for birds and insects; only recently have researchers looked for effects in the forest canopy (Barber and Marquis 2009, Böhm et al. 2011). Most published studies also focus on a single common plant species within the study area. For example, Holmes et al. (1979) studied effects on striped maple (*Acer pensylvanicum*); Marquis and Whelan (1994), Lichtenberg and Lichtenberg (2002), and Barber and Marquis (2009) on white oak (*Quercus alba*); and Böhm et al. (2011) on pedunculate oak. Indeed, studies that focus on the understory may underestimate the impact of insectivorous birds on temperate forest ecosystems because they do not account for leaf–caterpillar–songbird interactions in the forest canopy (MacArthur 1958), where food resource levels can elicit numerical and functional responses by insectivorous birds (Morse 1978, Haney 1999)

and where most of the primary productivity occurs. Studies that focus on a single tree species as the foraging substrate may miss large impacts on tree species where insect herbivore abundance is higher and thus attracts more bird predation (Buler et al. 2007). While migrant songbirds occupy stopover habitats only briefly during the growing season (Moore et al. 1995), they occur at much higher densities than summer residents (Kendeigh 1982, Finch and Yong 2000, Rodewald and Abrams 2002), and can depress the abundance of insect prey during their short stay (Moore and Yong 1991, Barber and Marquis 2009).

A detailed study of plant–herbivore–predator relationships is especially timely in light of the accumulating evidence that climate change is uncoupling the timing of some predator species from the lower levels of the trophic system on which they depend (Harrington et al. 1999, Parmesan 2006). In this observational study, I tested the hypothesis that the phenology of budbreak, leaf expansion, and caterpillar development is linked to accumulating spring temperatures and that the spring phenology of wood-warbler and vireo migration is unlinked from these environmental cues. I predicted that the timing of wood-warbler and vireo presence at the stopover will be independent of tree and caterpillar phenology across years, whereas the phenology of trees and caterpillars will be synchronized and will vary among springs with different temperature patterns. I also tested the hypothesis that reduction of leaf area lost to folivory by spring-feeding caterpillars is indirectly mediated by migrant songbirds and depends on phenological synchrony between trophic levels. The hypothesis allows for the prediction of a trophic cascade: defoliation should be increased in years of greater phenological asynchrony among different trophic levels.

METHODS

Study Area

I conducted this study from 2001 to 2003 in Trelease Woods, a rectangular (400 m E–W by 600 m N–S) 24-ha deciduous forest fragment located 3 km northeast of Urbana, Illinois (40°09′ N, 88°10′ W). Before European settlement of east central Illinois, Trelease Woods was part of a 2,500-ha forest tract called the "Big Grove" (Miceli et al. 1977). The Trelease Woods forest

fragment has been managed as a research forest by the University of Illinois since 1917 and has been protected from human impacts. Prior to 1950, the relative basal area of trees ≥7 cm dbh (diameter at breast height) was 45% mixed hardwoods, 25% American elm (*Ulmus americana*), and 30% sugar maple (*Acer saccharum*; Boggess 1964). While diseases have reduced American elm in importance, Trelease Woods is still described as a mixed hardwood forest that maintains some characteristics of old-growth forest, including a number of large, mature oaks (Pelz and Rolfe 1977, J. Edgington, unpubl. data). The forest has no slope and is dominated by 20 tree species with a maximum canopy height of 20 to >25 m (Augspurger and Bartlett 2003). The landscape in this region is dominated by rowcrop agriculture (Illinois Department of Agriculture 2002). The Trelease Woods forest fragment is heavily used by migrant songbirds in the spring (Kendeigh 1982, Diehl 2003, Strode 2009).

Study Trees and Sampling Transects

For my first objective, I test the hypothesis that the phenology of budbreak, leaf expansion, and caterpillar development is linked to accumulating spring temperatures and the spring phenology of wood-warbler and vireo migration is unlinked from this environmental cue. The trees selected for this study occur along established bird census and tree phenology routes on both the edge and interior of the Trelease Woods forest patch. The routes include four linear 400-m transects of forest edge habitat representing each aspect (N, W, S, E) and five linear 300-m transects of forest interior habitat. The study tree species were bur oak (*Quercus macrocarpa*), northern red oak (*Q. rubra*), and black walnut (*Juglans nigra*). I selected oak and walnut trees because of their known status as preferred foraging substrates by wood-warblers and vireos in the eastern US deciduous forest in general (Holmes and Robinson 1981) and in east central Illinois in particular (Graber and Graber 1983). All three species are economically valuable forest hardwood trees (Cogliastro et al. 1990) that may indirectly benefit from predation by birds on leaf-eating caterpillars (Graber and Graber 1983, Marquis and Whelan 1994).

A total of 209 study trees were surveyed along transect lines and all were mature canopy trees of reproductive size (≥33 cm dbh) with an average canopy height of 25 m (bur oak, n = 89, northern

red oak, n = 21; black walnut, n = 99). Study trees comprised 16.3% of the total basal area of trees on transect lines (J. Edgington, unpubl. data). Of my sample, 28 bur oak, 22 northern red oak, and 27 black walnut trees were already part of a forest tree phenology study that has been ongoing in Trelease Woods since 1993 (37%, n = 77 of 209; Augspurger and Bartlett 2003).

Spring Temperature Patterns

I generated a pattern each year of spring temperature accumulation that used degree-days (DD) above 5°C (DD_5) that had accumulated since Julian day (JD) 32 (1 February) to predict the peak in number of canopy caterpillars in any given spring. I chose a base mean daily temperature of 5°C to generate the spring temperature pattern because temperatures above 5°C have been shown to drive spring development in temperate deciduous tree foliage and forest caterpillars (Hunter and Lechowicz 1992a, Parry et al. 1998). I chose JD 32 to begin the DD_5 accumulation because days with a mean temperature above 5°C in January (JD 1–31) in Urbana are uncommon (<7% of January days 1948–2003), and a consistent DD_5 accumulation in most years does not begin until after JD 31 (Illinois State Water Survey 2014). I also determined the day on which a 300 DD_5 accumulation in temperature was reached because the 300 DD_5 accumulation dates provide a thermal model for the beginning of the peak in spring caterpillar activity (Lysyk 1989, Strode 2003). I used the daily mean spring temperatures for Urbana during the 114-year period of 1889–2003 to generate a historical mean spring temperature pattern for comparison with the years of this study (National Climatic Data Center 2014).

Tree Budbreak and Leaf Growth Phenology

I recorded phenological data during the springs of 2001–2003 for each of the 77 oak and walnut study trees. I surveyed the live portion of each study tree crown with binoculars on a consistent day each week beginning before budbreak each year and ending at full leaf expansion. For detailed methods for recording tree leaf phenology data, see Augspurger and Bartlett (2003). Briefly, the date of budbreak (BB) for each individual study tree is defined as the first day on

which, through visual estimation, greater than or equal to one-third of a tree's buds have swollen so that leaf tissue can be seen between the bud scales. The date that leaf emergence (LE) begins is defined as the first day on which leaf tissue extends beyond the bud scales of more than or equal to one-third of a tree's buds. The date that leaf growth (LG) begins is defined as the day on which flattening and leaf form have occurred in more than or equal to one-third of a tree's leaves, while still miniature. The date of full leaf expansion (FE, the end of leaf growth) is defined as the first day on which more than two-thirds of a tree's leaves are deemed fully grown and no growth has occurred for two consecutive weeks of observations. The single phenological stage recorded for each individual included only the visible portion of the entire crown. Tree phenology can vary considerably within and among trees, but this study focuses on monitoring tree leaf-out among tree species to broadly understand how development varies with temperature and, in turn, how timing of leaf emergence affects caterpillar folivory and bird use of deciduous trees. Other tree phenophases such as flowering were not included in this study because only leaves were searched for caterpillars and because leaf area lost to folivory was used as evidence of a trophic cascade.

I made between- and among-year comparisons of each tree phenophase by considering the mean date by which the individuals of each species had completed each phase. I chose the completion of each phase because leaves decline in nutritional quality and acceptability to spring-feeding caterpillars during the period from the end of budbreak to the end of the leaf growth phase (Hunter and Lechowicz 1992a).

I calculated mean and standard deviation for the tree phenophases by converting the phase for each individual each week to a corresponding ordinal value similar to the five-point Likert scale (Likert 1932), in which before budbreak = 0, budbreak = 1, leaf emergence = 2, leaf growth = 3, and full leaf expansion = 4. The conversion allowed me to calculate the mean leaf phase for each tree species each week and determine the overall leaf phase (budbreak, leaf emergence, leaf growth, or full leaf expansion) during which the mean occurrence date occurred for the caterpillar community in the three study tree species in 2002 and 2003. I also calculated the cumulative proportion

of individuals observed on each survey date of each study species that had completed each leaf phenophase to compare overall budbreak and leaf development phenological patterns among years. For example, if only 2 of the 28 bur oak study trees had initiated budbreak on a given survey day, this survey day would return a proportion of 0.07 (2/28). In the next survey, if five more individual trees had initiated budbreak, the second survey would return a cumulative proportion of (2 + 5)/28 = 0.25.

Caterpillar Phenology

I recorded caterpillar abundance in the springs of 2001–2003 on 2,400 canopy leaves evenly distributed among 20 edge trees. All 20 edge trees were also part of the leaf phenology study. I based my selection of each individual in the subsample on its accessibility with a Terex TB60 telescopic boom lift with a 20-m working height. The lift maximized the number of trees that could be sampled weekly; however, its size limited sampling to the canopies of edge trees only. Only five (n = 5) of the edge northern red oak trees were accessible by the lift so I chose an equal number (n = 5) of the most easily accessed bur oak trees for the bur oak sample. The mean dbh of the oak trees was more than twice the dbh of the 13 accessible black walnut trees, so I chose the 10 most easily accessed black walnut individuals as the black walnut sample to control for basal area. The sample trees were distributed among all four forest edges (N, W, S, E).

Edge trees may be exposed to more light and wind than the interior trees of a forest habitat, and different microclimates could influence the number of insects on each tree. However, microclimate gradients in light, temperature, and humidity can extend up to 700 m into a forest patch, but the Trelease Woods forest patch was only 400 m wide (Bergès et al. 2013). Thus, the microclimate of the edge canopy of Trelease Woods is likely indistinguishable from the microclimate of the canopy in the middle of the forest habitat 200 m away. Moreover, forest fragments of the size of Trelease Woods (24 ha) are essentially all edge with respect to many community interactions (Robinson et al. 1995, Ewers et al. 2007).

Methods for estimating caterpillar abundance and determining sampling effort were based in large part on a similar study of trophic cascades in bird–caterpillar–white oaks (*Q. alba*; Marquis and Whelan 1994). Sampling units were 30 leaves and total sampling effort per season was 2,700 leaves. Before budbreak in 2001, I located and tagged four branches in the upper half of the crown of each sample tree. I only selected branches that were easily accessed and similar in architecture. Beginning with leaf growth in 2001, but with budbreak in 2002 and 2003, I searched branches at least weekly for caterpillars. Using the terminal bud as a starting point, I searched all surfaces of only the first 30 buds, leaves, or a combination of the two. I also searched the length of branch that included those leaves. I recorded the length of each caterpillar to the nearest millimeter. I held all leaves with rolled sections up to the light to detect any dark caterpillar image visible through the thin, young foliage, and the length of the image was measured. Based on lengths, I estimated biomass using a length–mass regression across species (y = 0.0314 + 0.0042x + 0.0005x^2, r = 0.91, P (x) < 0.0001, P (x^2) < 0.0001; J. Graber, unpubl. data). Length is related to biomass of invertebrates, but the biomass calculations account for additional size differences among Lepidoptera larvae, thus providing a better indication of their quality as food resources for migratory birds.

In 2003, I conducted an additional study to determine the phenology of the end of the larval phase of spring-feeding forest caterpillars and capture the timing of when caterpillars are ready to pupate on the ground. Beginning soon after budbreak, I made daily counts of caterpillars descending from the trees to pupate in leaf litter that were caught in two drop traps beneath each of seven trees and represented species monitored in canopy populations of caterpillars (Varley et al. 1974, Hunter et al. 1997).

I generated three phenological patterns for caterpillars. The first pattern was the population density of caterpillars (caterpillars per 2,400 leaves) each week (Holmes et al. 1979, Martel and Mauffette 1997). The second pattern was the mean occurrence date for caterpillar observations each year. For the final phenological pattern, I calculated the cumulative proportion of all caterpillars counted for the spring season for each survey period. The method allowed me to compare the caterpillar phenological patterns to the leaf phase phenological patterns described earlier.

Migratory Songbird Phenology

I conducted daily foraging observations and tallies of foraging songbirds, except during inclement weather. I recorded all wood-warblers and Red-eyed Vireos (*Vireo olivaceus*—hereafter, migratory songbirds) detected on edge and interior transects. Beginning on JD 91 (1 April) each year, I began surveying birds using the Trelease Woods habitat and identified and recorded the number of migratory songbirds foraging in mid-canopy and canopy trees within a fixed transect width (20 m of the forest edge transect and within 20 m of either side of each interior transect). Thus, the sampling unit was the total number of migratory songbirds detected using oak and walnut trees per 9.4 ha per day. I located birds by sight and sound, and used binoculars to identify their species. I began each census 30 min after sunrise because the focal species of migratory songbirds are nocturnal migrants, ended their flights before sunrise, and then used the day's first light to find habitats for foraging and roosting (Wiedner et al. 1992, Moore and Aborn 2000). All transects were visited on each census day. Similarly to the leaf development and caterpillar phenology patterns described before, I generated two phenological patterns for migratory songbirds: mean occurrence date each year and the cumulative proportion of each species of migratory songbird counted in the study trees for each survey day.

I also analyzed spring survey records dating from 1903 to determine the mean date of the peak in combined wood-warbler and vireo species richness (WV peak) and to gain a historical perspective on the timing of wood-warbler and vireo migration through Urbana, Illinois. The WV peak is used here as a proxy for the peak in total numbers of wood-warblers and vireos at the stopover site during migration (Rotenberry and Chandler 1999). The date indicates when potential predation pressure by Neotropical–Nearctic migrant songbirds on forest caterpillars is likely to be greatest (Graber and Graber 1983). Use of the WV peak does not take into account early migrants like the Yellow-rumped Warbler (*Setophaga coronata*), when early migrants are feeding on arthropods other than caterpillars (Strode 2009). Bird survey records are stored in the library archives at the University of Illinois at Urbana-Champaign, and further details of how I collected and used these data can be found in Strode (2003).

Folivory

For my second objective, I tested the hypothesis that the reduction of leaf area lost to folivory by spring-feeding caterpillars is indirectly mediated by migrant songbirds, which depend on phenological synchrony between trophic levels. To test this hypothesis, I measured folivory by spring-feeding caterpillars in the same 20 edge trees where I studied for caterpillar abundance. I flagged two branches in the upper half of the crown of each tree before budbreak. I chose branches that were easily accessible by the boom lift and not used for the caterpillar abundance study. In 2001, my sampling did not include the black walnut study trees because an herbicide overspray from an adjacent agricultural field along the east-facing edge of Trelease Woods caused the leaves on most of the black walnut trees to grow abnormally. The abnormal growth in 2001 prevented me from using a leaf shape–leaf area allometric relationship for estimating folivory.

The wood-warbler and vireo migration season usually ended around JD 151 (31 May). Each year, I collected 15 leaves from each oak branch (n = 30 leaves per tree, n = 150 each for both oak species; Lowman 1985) and 30 leaflets from each black walnut branch (n = 600 for walnut, except during 2001). The larger sample size for black walnut leaflets was necessary to reflect the fact that the largest northern red oak and bur oak leaves are greater in leaf area (pooled $\bar{x}$ = 123 cm^2) than the largest black walnut leaflets ($\bar{x}$ = 18 cm^2; P. Strode, unpubl. data). For oak leaf selection on each branch, I removed the longest leaf, as determined by inspection, in each of 15 terminal leaf clusters (Feeny 1970). The longest leaves are assumed to have been the first to emerge in early spring and to have been exposed to folivory for the longest time (Reichle et al. 1973). It was necessary to sample some leaf clusters twice when there were fewer than 15 clusters on the branch. For black walnut leaf selection, I first selected the five longest leaves. With numbering beginning at the petiole of each leaf, I removed one leaflet at each position from five to nine where the leaflets on black walnut are largest. I collected leaves in the morning, placed them in plastic bags, and transported them to a laboratory for leaf area measurements made later that day. Plastic bags minimized water loss and any change in leaf size.

I recorded leaf length (oaks) and leaflet length and width (black walnut) to the nearest millimeter. I used a leaf area meter (Li-Cor area meter, model 3100, LI-COR, Inc., Lincoln, Nebraska) to determine the observed area of each leaf and leaflet (Lichtenberg and Lichtenberg 2002). On the same day that I collected leaves for folivory measurements, I also collected a series of undamaged leaves from the same branches that were used as substitutes for length measurements when too much area was missing from the study leaves for length to be determined. To predict the expected area (y) from the length (x) for the study leaves of bur oak and northern red oak, I used regression equations that were generated from length (independent variable) and area (response variable) measurements of 150 additional undamaged leaves of each species (bur oak: $r = 0.98$, $y = 0.2238x^{2.1545}$, $P < 0.001$; northern red oak: $r = 0.98$, $y = 0.1706x^{2.2549}$, $P < 0.001$; Linit et al. 1986). For black walnut, I generated a regression equation that predicted area (y, response variable) from the log product of length multiplied by width (x, independent variable) from measurements of 150 leaflets ($r = 0.97$, $y = 18.873 - 39.241x + 26.409x^2$, P (x) < 0.0001, P (x^2) < 0.0001). I collected all leaves and leaflets used to generate these allometric relationships at the end of the leaf growth stage in 2001 (bur oak and northern red oak) and 2002 (black walnut) and samples represented a nearly complete range of leaf sizes present in each tree.

Statistical Analysis

I calculated mean completion dates for each tree phase (budbreak, leaf emergence, leaf growth) for each of the three study tree species for each spring in the 3 years of the study. I considered the effects of the temperature pattern each spring on the phenology of each phase for each tree species separately, using paired t-tests (Sokal and Rohlf 1995). I also pooled tree species to generate an overall pattern.

I used the Kolmogorov-Smirnov (K-S) goodness-of-fit test (Zar 1999, Yin et al. 2005) to test the null hypotheses that the spring temperature patterns among years (generated by the DD_5 accumulation) were statistically indistinguishable. The K-S test returns a test statistic (D) that is a measure of the maximum difference between the cumulative proportions of two patterns. I compared each test statistic to a critical value for D (D_{crit}), based on each sample size and a rejection level of $\alpha \leq 0.05$.

I used mean occurrence dates during the spring sampling period each year for caterpillars and migratory songbirds to detect differences in phenology between years. Mean dates have been shown to be accurate estimators of phenological shifts (Moussus et al. 2010). Mean occurrence date calculations were weighted by the counts of caterpillars or migratory songbirds on each day a survey was taken. I used t-tests to analyze the mean occurrence dates for caterpillars between years (2002 and 2003) in the three tree species and the mean occurrence dates for migratory songbirds between paired years (2001–2003). I also separately analyzed mean occurrence dates for migratory songbird species where the total number of birds counted within a species was ≥10 individuals. In all cases, I tested the null hypothesis that the mean occurrence dates for all comparisons were statistically indistinguishable.

I used the leaf phase Likert score means to determine the leaf phase during which the number of spring-feeding caterpillars peaked in each of the three tree species in 2002 and 2003. I used one-way analysis of variance (ANOVA) to test the null hypothesis that the mean leaf phase during which caterpillars peaked did not vary among years.

Last, I used the response variable of proportion leaf area missing per leaf to analyze the levels of folivory in the canopy. I square root transformed the data to improve normality and then tested for differences within species among years and among species within years in leaf area lost to folivory with ANOVA. Differences between years were analyzed with paired t-tests. ANOVA and t-tests were considered significant at a rejection level of $\alpha \leq 0.05$.

RESULTS

Spring Temperature Patterns

The DD_5 accumulation patterns for the springs of 2001, 2002, and 2003 were distinctive (Figure 6.1). The 2002 pattern closely matched the average pattern generated by the 114-year mean, while the 2001 and 2003 patterns were earlier than the 114-year mean pattern for most of each spring season. In all 3 years, the DD_5 accumulations had
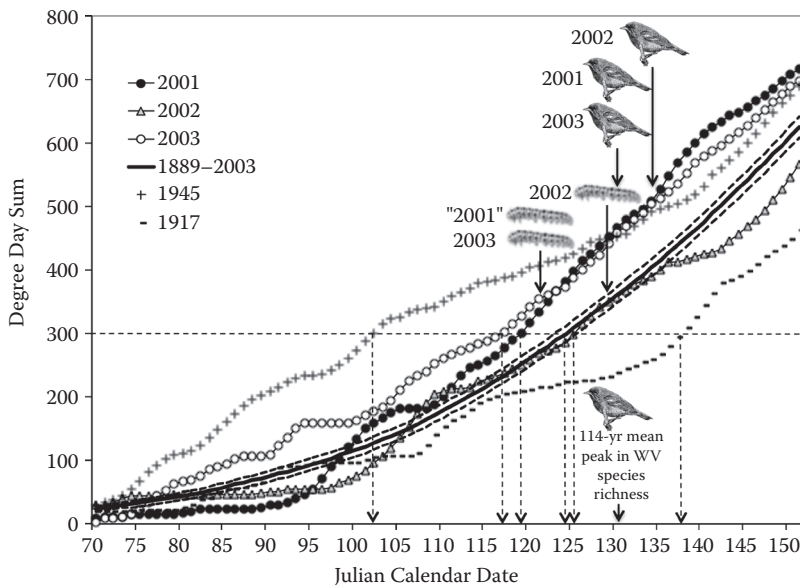
Figure 6.1. Spring temperature pattern as generated by accumulating degree-days (DD, base 5°C) for the three spring seasons of 2001–2003, the 114-year mean (dashed line—95% CI) for the years 1889–2003, and the earliest (1945) and latest (1917) springs at Urbana, Illinois. Horizontal dashed line indicates an accumulation of 300 DD_5. Caterpillar and bird images with years and vertical solid lines indicate mean occurrence dates during the spring seasons when data were recorded. Mean occurrence date for caterpillars (2002) was inferred from a thermal developmental model for cater-pillars. Vertical dashed lines with arrows indicate the date by which 300 DD_5 had accumulated for each year and the 114-year mean.

begun by JD 73. From this date to the end of the migration season (JD 151), K-S tests showed that all three spring temperature patterns were significantly different from each other (2001 vs. 2003: $D = 0.218$, $P = 0.049$; 2001 vs. 2002: $D = 0.256$, $P = 0.012$; 2002 vs. 2003: $D = 0.244$, $P = 0.020$). Degree-days in 2003 accumulated most rapidly for most of the season, 2002 degree-days accumulated most slowly, and 2001 was intermediate. Overall, 2003 DD sums preceded 2002 sums by 5 to 14 days through the end of the spring season and ran 7 to 12 days ahead of the 114-year mean (Figure 6.1).

Tree Budbreak and Leaf Growth Phenology

Taken together, each phase of leaf development for bur oak, northern red oak, and black walnut reflected the observed differences in the temperature patterns (Table 6.1). Compared to mean completion dates for 2002, the budbreak phase of leaf development for the three tree species was earlier by 3 days in 2001 ($t = -5.87$, df = 76, $P < 0.001$; paired t-tests, Table 6.1) and 5 days in 2003 ($t = 10.09$, df = 76, $P < 0.001$). Compared to

2002, the leaf emergence phase was also earlier (5 and 7 days, respectively) in 2001 ($t = -11.22$, df = 76, $P < 0.001$) and 2003 ($t = 12.99$, df = 76, $P < 0.001$). In 2003, the mean completion date of the leaf growth phase was 4 days earlier than in 2001 ($t = 10.36$, df = 76, $P < 0.001$). The mean completion date of the leaf growth phase was the same in 2001 and 2002 ($t = -0.52$, df = 76, $P = 0.60$). For all three tree species, mean completion date for budbreak, leaf emergence, and leaf growth was significantly earlier (paired t-tests, df = 27, 21, and 26 for bur oak, northern red oak, and black walnut, respectively, $P < 0.05$) in 2001 and 2003 compared to 2002 (Table 6.1). However, in 2001, the earlier mean leaf growth completion date for black walnut was statistically indistin-guishable from the 2002 date ($t = 1.55$, df = 26, $P = 0.13$).

Caterpillar Phenology

Caterpillar phenology reflected the annual dif-ferences among temperature patterns. In 2002, the total number of caterpillars on 2,400 canopy leaves of the three study tree species peaked at

TABLE 6.1

*Summary of mean completion dates (Julian calendar day) for three phenophases of Bur Oak
(*Quercus macrocarpa*), Northern Red Oak (*Quercus rubra*), and Black Walnut (*Juglans nigra*)
during three spring seasons at Trelease Woods, Urbana, Illinois.*

Species	Budbreak			Leaf emergence			Leaf growth		
	2001	2002	2003	2001	2002	2003	2001	2002	2003
All trees	111[a]	114[b]	**109**[c]	124[a]	129[b]	**122**[c]	149[a]	149[a]	**145**[b]
Bur oak	112[a]	114[b]	**108**[c]	123[a]	129[b]	**119**[c]	147[a]	145[b]	**139**[c]
Northern red oak	**111**[a]	115[b]	113[a]	**121**[a]	124[b]	122[a]	142[a]	144[b]	**141**[a]
Black walnut	111[a]	112[b]	**107**[c]	128[a]	132[b]	**125**[c]	156[a]	157[a]	**154**[b]

NOTES: Mean dates within phenophases and species with different superscript letters (a, b, c) are different at P = 0.05 (paired t-tests). Bold entries indicate earliest mean completion dates among years for each phase by species.

15 individuals on JD 131 (366 DD$_5$), with a mean occurrence date of JD 128 and an estimated mean biomass per caterpillar of 0.11 g ($\pm$0.005, n = 66). The timing of the 2002 mean occurrence date of caterpillars was 3 days later than the 114-year Urbana mean date (JD 125) of a 300 DD$_5$ accumulation (coefficient of variation (CV) = 0.06; Figure 6.1) when thermal models estimate the peak in abundance of forest caterpillars. In 2003, the total number of caterpillars peaked on JD 117 (302 DD$_5$) at 23 individuals, 14 days earlier than 2002, with a mean occurrence date of JD 122 and 0.13 ($\pm$0.005) g of estimated mean biomass per caterpillar (n = 95). Comparisons of mean occurrence dates between 2002 (JD 130) and 2003 (JD 125) were nonsignificant for caterpillars in northern red oak (t-test, t = 1.56, df = 27, P = 0.13) and between 2002 (JD 124) and 2003 (JD 121) for black walnut trees (t = 1.06, df = 48, P = 0.30). However, in bur oak trees, the mean occurrence date of JD 123 in 2003 came significantly earlier than the mean occurrence date of JD 129 for 2002 (t = 2.24, df = 44, P = 0.03). The 6-day difference in mean occurrence date between 2002 (JD 128) and 2003 (JD 122) for the entire caterpillar community sample was also significant (t = 2.99, df = 101, P = 0.003).

In 2002 and 2003, the peak of caterpillar activity, as determined by the mean occurrence date, occurred during the leaf emergence phase in all three tree species searched, but with considerable variability among tree species within years and between years within tree species. Analysis of variance revealed that the mean leaf phase during which caterpillar populations peaked varied by tree species in both 2002 ($F_{2,74} = 28.3$, P < 0.001) and 2003 ($F_{2,74} = 17.1$, P < 0.001). The t-tests showed that the mean leaf phase during which caterpillar populations peaked was significantly different between 2002 and 2003 for bur oak (t = 2.5, df = 54, P = 0.02), but not for northern red oak (t = 1.9, df = 35, P = 0.07) or black walnut (t = 0.46, df = 50, P = 0.64).

In 2003, caterpillars began appearing in the drop traps on JD 119. By JD 128, more than half (56%) of the total caterpillars captured by the end of songbird migration (JD 149) had been recorded (n = 49; mostly Hymenoptera, Geometridae, Noctuidae, and Tortricidae; P. K. Strode, unpubl. data). The last caterpillar was recorded on JD 139.

Migratory Songbird Phenology

I counted totals of 241 (27 species), 234 (25 species), and 428 (24 species) foliage-gleaning migratory songbirds, respectively, each migration season (2001–2003) in the three study tree species along the edge and in the interior of Trelease Woods. Five species of birds had adequate counts each year for analyses by species ($\geq$10; Table 6.2). The migration phenology each spring for the entire community of these birds, as determined by mean occurrence date, varied with year (ANOVA: $F_{2,898} = 30.2$, P < 0.001). The effect of year on mean occurrence date for songbird migration phenology was due primarily to a significantly later mean occurrence date in 2001 (JD 134) compared to 2002 (JD 129, t = 5.9, df = 465, P < 0.001) and 2003 (JD 129, t = 7.7, df = 516, P < 0.001; Figure 6.1). Mean

TABLE 6.2

Summary and comparative statistics[a] for all neotropical–nearctic migrant songbirds and the five species with large enough sample sizes for analysis (n ≥ 10) counted in Bur Oak, Northern Red Oak, and Black Walnut Trees during the Spring seasons of 2001–2003 at Trelease Woods, Urbana, Illinois.

Species	n	First appearance date			Mean occurrence date			ANOVA F (df)	Student's t (df)		
		2001	2002	2003	2001	2002	2003	All years	2001 vs. 2002	2001 vs. 2003	2002 vs. 2003
All birds	903	117	106	**104**	134	**129**	129	**30.15 (2,898)**	**5.93 (465)**	**7.73 (516)**	0.74 (465)
American Redstart	80	131	130	**128**	140	137	**135**	**8.60 (2,77)**	1.63 (30)	**3.38 (25)**	1.93 (22)
Black-throated-Green Warbler	81	117	**112**	118	131	133	**128**	2.22 (2,78)	0.67 (23)	1.33 (40)	1.65 (17)
Palm Warbler	88	122	**109**	113	126	**124**	126	0.72 (2,85)	1.20 (31)	0.33 (65)	0.94 (33)
Red-eyed Vireo	63	131	127	**122**	140	**138**	139	0.60 (2,60)	1.03 (39)	0.79 (42)	0.27 (38)
Yellow-rumped Warbler	157	117	106	**104**	125	121	**119**	**5.09 (2,154)**	**2.80 (39)**	**4.55 (31)**	1.68 (132)

NOTES: First appearance and mean occurrence dates are Julian calendar days and bold entries are the earliest dates for each species among years. Individual species (with species code) were the American Redstart (AMRE), *Setophaga ruticilla*; Black-throated Green Warbler (BTGW), *Setophaga virens*; Palm Warbler (PAWA), *Setophaga palmarum*; Red-eyed Vireo (REVI), *Vireo olivaceus*; and Yellow-rumped Warbler (YRWA), *Setophaga coronata*. First appearance dates for "All birds" determined by YRWA arrival because YRWA were always first to arrive. First appearance dates in oak and walnut trees are not to be confused with first arrival dates at Trelease Woods. Bolded ANOVA and t-test results indicate significance at α ≤ 0.05.

[a] ANOVA and t-tests for mean occurrence dates for all years and between pairs of years.

occurrence dates for 2002 and 2003 were both JD 129 (t = 0.74, df = 465, P = 0.46).

Five species of migratory songbirds had an adequate number of detections for phenological comparisons (≥10, Table 6.2). The songbird species (with species code) were the American Redstart (AMRE, *S. ruticilla*), Black-throated Green Warbler (BTGW, *S. virens*), Palm Warbler (PAWA, *S. palmarum*), Red-eyed Vireo (REVI, *Vireo olivaceus*), and Yellow-rumped Warbler (YRWA, *S. coronata*). Only the American Redstart and the Yellow-rumped Warbler showed shifts in mean occurrence date in at least one year-to-year t-test comparison. The mean occurrence date for the American Redstart in 2003 (JD 135) was significantly earlier than in 2001 (JD 140, t = 3.38, df = 25, P = 0.002). The mean occurrence date for the Yellow-rumped Warbler in 2001 (JD 125) was significantly later than in 2002 (JD 121, t = 2.80, df = 39, P = 0.008) and 2003 (JD 119, t = 4.55, df = 31, P < 0.001). Taken as a whole, none of the mean occurrence dates reflected the annual differences between temperature patterns with any consistency (Table 6.2; Figure 6.1).

The peak in species richness for wood-warblers and Red-eyed Vireos (WV peak) occurred on JD 133, 128, and 129 in 2001, 2002, and 2003, respectively. Analysis of the historical migration records from 1903 to 2003 placed the mean WV peak on JD 131 (11 May, n = 75 years, SD = 4 days, CV = 0.030; Figure 6.1). The date coincides within 6 days (JD 125) of the 114-year mean peak date (1889–2003) for caterpillar availability in the forest canopy, as predicted by the 300 DD$_5$ thermal model explained previously.

Trophic Level Synchrony

The general temporal patterns of leaf development, numbers of caterpillars, and numbers of birds each year were distinctive (Figure 6.2). All three trophic levels were synchronized in 2002 (Figure 6.2b) but asynchrony was detected between the first two trophic levels and the migratory songbirds in 2001 and 2003 (Figure 6.2a, c). In 2002, half of all study trees had completed the leaf emergence phase and half of all caterpillars had been recorded by JD 125; half of all migratory songbirds had arrived at the stopover by JD 128 (Figure 6.3b). In 2001, half of all study trees had completed the leaf emergence phase and, based on the 300 DD thermal developmental model,
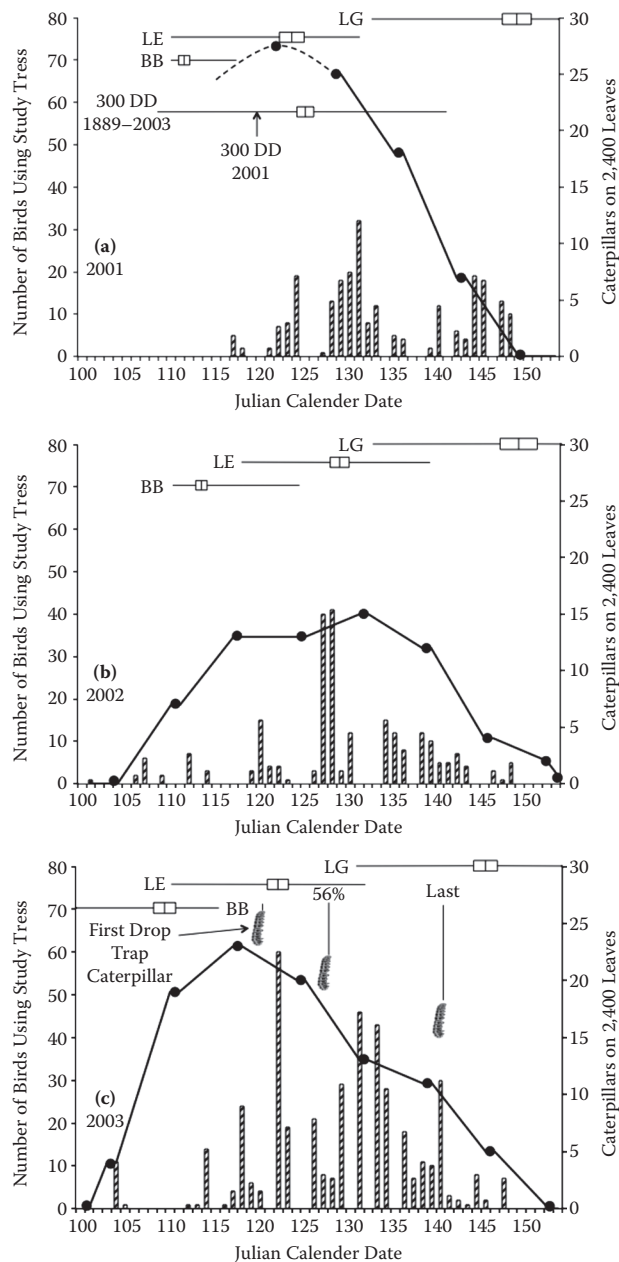
Figure 6.2. Summaries for three trophic phenophases for the spring seasons of (a) 2001, (b) 2002, and (c) 2003 at Trelease Woods, Urbana, Illinois. Hatched bars (primary y-axis) are the number of wood warblers and vireos observed using bur oak, northern red oak, and black walnut study trees in 9.4 ha of transect area; solid line (secondary y-axis) is the number of caterpillars observed on 2,400 edge canopy leaves of five bur oak, five northern red oak, and 10 black walnut trees. Dashed line in (a) indicates the peak in caterpillar activity predicted by a degree-day model (see "Methods"). In (a), 300 DD box and whisker plot indicates the mean, 95% CI, and range for the date of a 300 degree-day accumulation for the years of 1889–2003; upward arrow indicates the Julian date (119) of a 300 DD accumulation in 2001. In (c), suspended caterpillar images indicate the dates on which proportions of 0.07 (first caterpillar), 0.56, and 1.0 (last caterpillar) of the total caterpillars collected in drop traps were recorded. Box and whisker plots in (a)–(c) indicate mean completion date, 95% CI, and range for bud break (BB), leaf emergence (LE), and leaf growth (LG) phases of the study trees (see "Methods" for sample sizes). The single-day high abundance of birds on JD 122 in 2003 was driven by the arrival of Yellow-rumped Warblers (*Setophaga coronata*) and is not representative of seasonal peaks in wood-warbler and vireo migration.
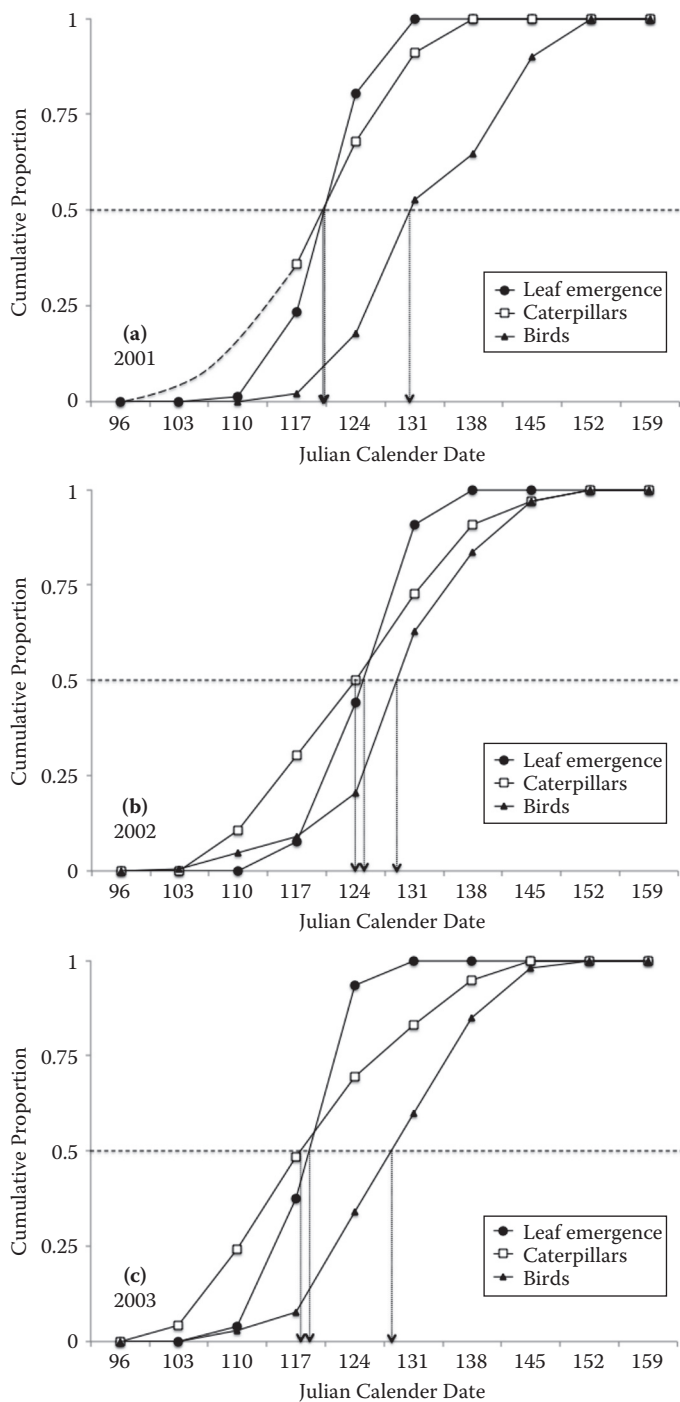
Figure 6.3. Timing of each trophic level during three springs (a–c) at Trelease Woods, Urbana, Illinois. Seasonal variation is shown for the cumulative proportion of bur oak, northern red oak, and black walnut trees (n = 77) that had completed the leaf emergence phase (leaf emergence), the number of caterpillars observed on 2,400 leaves in the canopies of a sample of the study trees (n = 20 trees, caterpillars), and the number of migratory songbirds observed in the study trees (birds). Vertical lines with arrows point to the dates on which 0.5 of each trophic level event had occurred. The curved dashed line in (a) is based on a thermal developmental model for caterpillars.
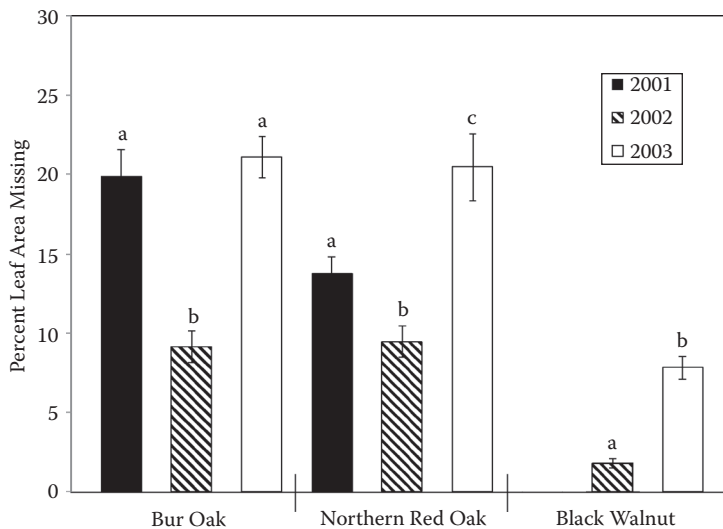
Figure 6.4. Mean percent area lost to folivory (±1 SE) on individual leaves in bur oak, northern red oak, and black walnut at the end of the three spring seasons at Trelease Woods, Urbana, Illinois. ANOVA indicates differences exist among years within species and among species within years ($P < 0.05$). Different small letters indicate significant differences within species between years as determined by post-hoc t-tests ($P < 0.05$).

half of all caterpillars would likely have been recorded by JD 120. However, the date by which half of all migratory songbirds had arrived at the stopover was 11 days later on JD 131 (Figure 6.3a). In 2003, half of all study trees had completed the leaf emergence phase and half of all caterpillars had been recorded by JD 118, while the date by which half of all migratory songbirds had arrived at the stopover was also 11 days later on JD 129 (Figure 6.3c).

Folivory

Folivory was the lowest for all three tree study species in 2002, the year with least asynchrony (Figure 6.4). Analysis of variance showed that the mean percentage leaf area lost to folivory varied significantly among years for bur oak ($F_{2,447} = 31.89$, $P < 0.001$) and northern red oak ($F_{2,447} = 10.78$, $P < 0.001$). Folivory in black walnut was significantly greater in 2003 (7.8%) than in 2002 (1.8%) according to a paired t-test ($t = 7.78$, df $= 812$, $P < 0.001$). Within year and among species comparisons also showed variation for 2002 ($F_{2,897} = 77.22$, $P < 0.001$) and 2003 ($F_{2,897} = 68.19$, $P < 0.001$), the 2 years in which black walnut was included in the folivory study. Folivory levels in bur oak were statistically indistinguishable for 2001 and 2003 (19.9% and 21.1%,

respectively; paired t-test, $t = 0.56$, df $= 298$, $P = 0.58$). However, these folivory levels were an increase of >100% from levels quantified in 2002 (9.1%) and both differences from 2002 were significant (2001: $t = 5.45$, df $= 298$, $P < 0.001$; 2003: $t = 7.27$, df $= 298$, $P < 0.001$). The 3-year pattern of folivory in northern red oak matched the pattern of bur oak. While folivory in northern red oak in 2001 (13.7%) was less than that of bur oak, folivory levels in northern red oak nearly matched those of bur oak in 2002 (9.5%) and 2003 (20.5%). All three levels of folivory in northern red oak were statistically distinct from each other as revealed by paired t-tests (2001 vs. 2002: $t = 2.78$, df $= 298$, $P < 0.001$; 2001 vs. 2003: $t = 2.63$, df $= 298$, $P < 0.001$; 2002 vs. 2003: $t = 4.28$, df $= 298$, $P < 0.001$).

DISCUSSION

The results from my 3-year study support the hypothesis that the communitywide timing and pattern of wood-warbler and vireo spring migration were unlinked from variable spring temperatures at a migratory stopover site in the midwestern United States. However, the timing of the caterpillar food resources upon which these birds depend for refueling at the stopover site does track seasonal variation in spring temperature.

Indeed, the number of caterpillars in the forest canopy of the three study tree species (bur oak, northern red oak, and black walnut) was predicted by accumulating spring temperatures, with the spring peak (mean occurrence date) for available caterpillars occurring earlier in the early springs of 2001 and 2003. Timing of budbreak, leaf emergence, and leaf growth in the study tree species also varied with the temperature pattern and all phases were completed earlier in either 2001 or 2003. Caterpillar activity was generally linked to the leaf emergence phase of forest tree phenology. Yet, because the arrival of Neotropical migrants did not vary between years, the top-down predation pressure of the migratory songbirds was less in 2001 and 2003 than in 2002. As a result, these findings suggest that a trophic cascade occurs in warm years when tree and caterpillar phenology becomes decoupled from migratory songbird stopover habitat use.

The most likely hypothesis that explains the lack of a behavioral response to variation in temperature at this temperate site by the migrant songbird community is that most of these species are long-distance migrants that are physiologically linked to day length, which controls their early spring departure from the tropics (Hagan et al. 1991, Breuner and Wingfield 2000, Dawson et al. 2001). The 6-day difference between the mean WV peak date at Urbana for 1903–2003 and the 114-year predicted mean peak of available caterpillars is notable. Selection for the photoperiodic response mechanism may have been driven in large part by the overlap of the birds' northward movements with the "green wave" of spring foliage development and the availability of food resources (Schwartz 1998). Overlap may have occurred historically in enough years to maintain fitness. The small coefficient of variation in the date of the WV peak (0.03) compared to that of the 114-year mean date of 300 DD_5 (0.06) in this study suggests that many of these species are traveling through the Illinois stopover location at similar times year after year, as well as farther north (Strode 2003). Songbirds must arrive at northern breeding grounds with time to select and defend optimal breeding territory and produce young (Coppack and Both 2002, Goodenough et al. 2010). However, photoperiod may be less of a determinant for migration timing in years of low food availability in late winter on the non-breeding grounds. For example, Studds and Marra

(2011) showed that drought years produced low food resources in March in the wintering grounds and that American Redstarts delayed the start of northward spring migration 3–5 days as a result.

The patterns for the three trophic levels (trees, caterpillars, birds) show an overlap in 2002 among the leaf emergence phase, the activity peak and mean occurrence date for caterpillars, and the peak in abundance of foliage-gleaning birds and a mismatch in 2001 and 2003. As a likely result of trophic synchrony in 2002, mean levels of folivory on leaves of bur oaks and northern red oaks (<10% for both) was within the 2%–15% range reported for temperate broad-leaved forest systems (Mattson and Addy 1975, Schowalter et al. 1986, Coley and Barone 1996) and close to the level of 10.6% (3-year range: 7.4%–12.4%) reported by Bray (1964) from two oak stands in southern Ontario, Canada. The level of 10.6% was recorded in the presence of actively foraging foliage-gleaning birds (Bray 1964). Mean folivory in black walnut (1.8%) in 2002 was comparable to levels reported in other temperate forests (Gosz et al. 1972), but was considerably less than in oaks. Lower leaf consumption in black walnut may have been influenced by the presence of a secondary metabolite (juglone) in the leaves, which is toxic to some species of Lepidoptera (Piskorski et al. 2011).

Leaf area loss can be expected to continue in the forest canopy after the end of the spring season as summer-feeding folivorous insects become active. Yet, most of the leaf damage in the canopy of temperate deciduous forests occurs in the spring when caterpillars are most numerous and leaf consumption rates are highest on young leaves (leaf area per unit time; Reichle et al. 1973). In addition, spring-feeding caterpillars consume disproportionately more leaf tissue when feeding on buds and small leaves than on fully grown leaves, which decreases the photosynthetic potential of individual leaves (Schowalter et al. 1986, Strong et al. 2000).

In 2002–2003, peak caterpillar activity was synchronized with forest tree leaf emergence. The link was likely a product of the narrow developmental window of opportunity for spring-feeding caterpillars before leaves decline in nutritional quality during the leaf growth phase (Hunter and Lechowicz 1992a, Hunter 1993, Lawrence et al. 1997, Dury et al. 1998). The phenologies of the lower two trophic levels, however, were

significantly advanced in 2003 versus 2002, and both events in 2003 occurred well in advance of the mean occurrence date and main peak in abundance of foliage-gleaning birds. The drop in number of caterpillars in the canopy in 2003 before the main pulse of migrant songbirds may have been caused by two additional factors:

1. Early migrants like Yellow-rumped Warblers may have consumed the caterpillars and depressed their number.

2. Caterpillars that had their development advanced by the early spring warmth and available food were completing the larval stage early and descending from the trees to pupate in the soil while birds were still arriving.

Indeed, the drop-trap data indicated that more than half (56%) of all caterpillars collected in the drop traps in 2003 had been collected before the main pulse of bird migration (Figure 6.2). The advances in the timing of tree leaf-out and caterpillar activity were statistically significant, but whether or not these shifts—with the lack of a response by the birds—were biologically significant enough to generate a trophic cascade is the more important ecological question.

Leaf area consumed by herbivorous insects was significantly greater in 2003 compared to 2002 for all three tree species that were monitored (Figure 6.4), a difference that provides support for the hypothesis that asynchrony between trophic levels can elicit a trophic cascade. Peak numbers of caterpillars on 2,400 canopy leaves ($n = 15$) and the total caterpillars counted in the season ($n = 66$) were lower in 2002 compared to 2003 ($n = 23$ and 95, respectively). The mean biomass per caterpillar was 15% lower in 2002 (0.11 g) than in 2003 (0.13 g), so the observed 100% increase in folivory in 2003 was most likely a consequence of a trophic asynchrony between the caterpillars and their predators. The density of caterpillar-eating birds may have been too low during the peak in caterpillar activity to depress their number effectively and thus reduce their consumptive impact in the canopy. A similar effect on the trophic cascade has been generated empirically in a deciduous forest of Pyrenean oak (*Quercus pyrenaica*) in Spain. Sanz (2001) experimentally manipulated the density of foliage-gleaning insectivorous birds in two similar forest plots and, in the plot with a lower bird density, he showed a significant increase in caterpillar density with an increase in leaf area lost to folivory.

The peak in caterpillar activity for 2001 predicted by the caterpillar DD_5 model also shows asynchrony between the birds and their food resources (Figures 6.2a–6.3a). As a possible consequence, the level of folivory in bur oak was significantly higher in 2001 than in 2002 and similar to the 2003 level, and the significant increase in folivory in northern red oak in 2001 compared to 2002 was consistent with that of the bur oak.

Reviews and meta-analyses have shown that trophic cascades often reduce damage to plants and consequences for forest ecosystems as a result of trophic asynchrony can be considerable (Halaj and Wise 2001, Mäntylä et al. 2011, this study). Low levels of defoliation (~10%) have little effect on forest tree growth (Marquis and Whelan 1994) or fitness (Schowalter et al. 1986, Hochwender et al. 2003), and most of the nitrogen freed from leaves consumed by defoliating insects ends up back in the soil through production of frass (Lovett et al. 2002). However, high levels of defoliation (>15%), especially on young leaves, can dramatically reduce tree fitness by way of significant increases in fruit abortion (Schowalter et al. 1986, Hochwender et al. 2003) and subsequent regeneration failure of some species. Oak regeneration failure has occurred during the last 150 years throughout the US Midwest (Abrams and Downs 1990, McCarthy et al. 2001), with a considerable shift from oak and hickory (*Carya* spp.) dominance to sugar maple dominance in forest habitats in Illinois (Miceli et al. 1977, Shotola et al. 1992, Cowell and Jackson 2002, Zaczek et al. 2002). If early springs that generate trophic mismatches similar to the patterns observed in this study become more frequent and more pronounced in the future, with no change in the relative abundance of caterpillars among tree species or resulting folivory levels, mismatches can be expected to drive changes in forest composition by promoting reduced forest growth and disrupting natural patterns of succession and regeneration.

The trophic mismatch also presents consequences for Neotropical–Nearctic songbirds that depend on the caterpillar food resources present at forest stopover habitats as birds move north to their breeding grounds in the spring (Graber and Graber 1983). In general, years with asynchrony can alter trophic cascades in terrestrial ecosystems (Hunter and Price 1992). In Europe, clutch sizes

of some tit species vary with the density of winter moth larvae (*Operophtera brumata*), a common insect defoliator of oaks (Buse et al. 1999). The bottom-up effect can also be sexually selective. In migrant songbirds, adult males migrate earlier than females (Francis and Cooke 1986) and juveniles (Woodrey and Moore 1997, Stewart et al. 2002). Adult males are therefore at an advantage in early springs, whereas juveniles and females arrive at stopover habitats to rest and refuel when food resources are low—an age-class and sex disadvantage. Some species also migrate earlier than others and therefore are at an advantage in early springs.

In an earlier study, Strode (2003) found that the timing of spring, as indicated by a 300 DD accumulation, has not advanced in east central Illinois, where the current study was conducted. However, at higher latitudes in the upper US Midwest, climate change has promoted statistically significant trends toward earlier springs over the last 90 years, with no adjustment in the timing of migration for many species of long-distance migrants (Strode 2003). Climate models predict this warming of the upper latitudes to continue (Intergovernmental Panel on Climate Change 2007). Moreover, late winter drought conditions at the nonbreeding grounds of many Neotropical–Nearctic migrant songbirds have become more severe and variable with unpredictable food resources, constraining the photoperiodic response that initiates spring migration (Studds and Marra 2011). If later migrants do not advance the timing of their northward movements to match a changing climate, the relative abundance of Neotropical–Nearctic migrant songbird species may change, with some species becoming more common and others becoming more rare (Jones et al. 2003). There simply may not be enough variation among individuals in their photoperiodic response for populations of many migrating birds to evolve and adjust to earlier springs in the northern latitudes brought on by climate change. Indeed, declines in migrant birds due to phenological mistiming have already been documented among populations in Asia (Lee et al. 2011), Europe (Both et al. 2006, Møller et al. 2008), and North America (Anders and Post 2006).

It is unclear what effects changes in the relative abundance of species may have at population, community, and ecosystem levels of organization and interaction. Many species of Neotropical–Nearctic migrant songbirds have already been affected by habitat loss, degradation, and fragmentation (Robinson et al. 1995, Holmes and Sherry 2001, Parker et al. 2005). Songbird species impacted by habitat loss and, especially, late spring migrants may find it difficult to maintain viable populations in the future.

ACKNOWLEDGMENTS

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