CHAPTER TWELVE

Autumn Migration of North American Landbirds*

Elizabeth R. Ellwood, Amanda Gallinat, Richard B. Primack, and Trevor L. Lloyd-Evans

Abstract. Recent research has shown that bird species are responding to changes in temperature and that spring migrations are shifting earlier for many species. Much less research has examined if and how fall migrations are changing, particularly in the United States. Here, we present an analysis of fall migration for 37 species of landbirds captured over a 44-year period at Manomet Center for Conservation Sciences in Manomet, Massachusetts. In the years 1969–2012, migration cohorts of 28 species significantly declined in abundance and two increased. For 14 species, the mean dates of fall passage at Manomet changed—nine migrated later and five earlier. Over this time span, the mean temperature of the region during the months of August and September has warmed. Fall passage dates for 14 species were correlated with temperature—13 species tended to migrate later with warmer temperatures and one species migrated earlier. We also included fall plant phenology in our analyses—four bird species tended to migrate later when leaf color change is delayed. Linear mixed-effects analysis indicates that species that winter in the tropics migrate earlier in the fall than birds that winter in other areas, and single-brooded species migrate earlier in the fall than double-brooded birds. Patterns of fall migration at Manomet show relatively little correlation with comparable data reported from the banding station at Powdermill Nature Reserve in Rector, Pennsylvania, suggesting spatial variation in the responses of fall migration to a warming climate. It is evident that fall migration dates vary considerably among species and that species are responding in different ways to the changing climate.

Key Words: climate change, fall, landbirds, Manomet, Massachusetts, migration, phenology.

Phenological observations have become increasingly central to our understanding of the effects of climate change on various taxa (Walther et al. 2002, Parmesan 2006). Recent years have broken records for heat, drought, and extreme weather events throughout the United States, and many plants and animals have responded with altered phenology (Jochner et al. 2011, Wilson 2012, Ellwood et al. 2013). The majority of this research has focused on spring phenology events. A spring bias is due in large part to the burst of springtime activity that follows

cold winter weather and to the relative prevalence of historical records that exist as a result. Likewise, in observational studies it is often easier to record the presence of an organism, such as detections of a newly arrived migratory bird, as opposed to the absence of an organism or when a bird has departed on migration. Many plants and insects are now active earlier in the spring in response to warmer spring temperatures (Walther et al. 2002, Menzel et al. 2006, Parmesan 2006). Many migratory songbird species have adjusted to ecological change and arrive earlier in the spring as well (Lehikoinen et al. 2004, Gordo 2007, Van Buskirk et al. 2009). The timing of spring migrations for a smaller number of bird species has not changed or been delayed, possibly due to migratory cues that are inflexible, such as photoperiod, or are decoupled from temperate breeding areas (Both and Visser 2001, Gordo et al. 2005, Weidinger and Král 2007).

A lack of fall phenology records and investigations, especially for migratory birds, has left a gap in our understanding of the effects of climate change on phenology (Møller et al. 2010, Lehikoinen and Jaatinen 2012). Recent studies of fall migration of birds southbound from North America and Europe to their respective wintering grounds in South America and Africa have given mixed results. Most field studies have been conducted in Europe and have found that the timing of fall migration is spatially and temporally variable, and strategies differ among species (Sparks and Braslavská 2001, Cotton 2003, Jenni and Kéry 2003, Gordo and Sanz 2006, Knape et al. 2009, Hüppop and Hüppop 2011, Tøttrup et al. 2012). The few studies conducted in North America confirm these findings (MacMynowski and Root 2007, Van Buskirk et al. 2009, Smith and Paton 2011). However, species-specific pressures appear to be driving certain long-distance migrants toward earlier fall migration and short-distance migrants to later migration (Jenni and Kéry 2003, Thorup et al. 2007). Jenni and Kéry (2003) found that reproductive strategy influenced trends toward earlier or later fall migrations in Switzerland. Multiple-brooded species may have a second or third clutch following an early spring, which could delay fall migration (Møller 2007), whereas single-brooded species may simply depart after their brood has matured, essentially shifting the annual life cycle earlier in years with warmer springs (Sokolov et al. 2000, Gordo 2007). Van Buskirk et al. (2009), on the other hand, found that the number of clutches did not explain the variation among species in Pennsylvania. The authors did find evidence that migrating species are either expanding or contracting their breeding seasons, depending on the species.

The difficulty in identifying patterns may be due in part to regional variation associated with different migration routes. Migratory cohorts traveling along coastal flyways, including birds using Manomet as a stopover point, often contain a high proportion of hatch-year birds (Brooks 2008, Finnegan 2008), so the effects of climate change on migration in these coastal pathways may strongly affect recruitment of certain species. Changes in the length of the breeding season, time to molt and put on fat before departure, and changes in synchrony with fruit maturation, leaf senescence, or other plant resources may have a positive or negative impact on cohorts during migration. Bird migration times might also be affected by the timing of leaf senescence, which represents the end of the growing season, and the time of fruit maturation and the onset of insect diapause, two key food sources.

In the present study, we focused on fall migration of landbirds through the Manomet Center for Conservation Sciences in Massachusetts, where researchers have been consistently banding birds since the fall of 1969. This long-term data set from a single location provides us with long-term data to investigate the following questions:

1. How is the timing of fall migration changing over time?
2. How are dates of fall migration correlated with climate variables or life history traits of different bird species?
3. Is fall migration of birds synchronous with leaf senescence?

In addition, the proximity of Manomet to Powdermill Nature Reserve, as well as overlap in species composition, allows us to compare phenology trends to investigate the regional extent of responses to climate change.

METHODS

Banding Data

All banding data are from Manomet Center for Conservation Sciences, Manomet, Massachusetts

(41° 50′ N, 70° 30′ W), where staff and volunteers maintain 45–50 mist nets over the 7-ha coastal forested property. The data analyzed here represent initial capture dates, excluding recaptures of individuals, of 37 species of birds during fall passage between 15 August and 15 November, for the years 1969–2012 (44 years), for a total of 139,546 individual birds captured.

In some cases, captures of birds were due to natal dispersal or food-related irruptions of resident species not normally regarded as migratory, but these records were relatively rare events (e.g., Black-capped Chickadee and Tufted Titmouse). Nevertheless, southward movements can still involve large numbers of individuals, such as 28,535 Black-capped Chickadees captured during autumn over 44 years. Thirty-three of our study species were captured in every year, and the remaining four species were captured in at least 39 of the 44 years. The number of captures in a given year also serves as a proxy for migration cohort size and was used here to approximate the degree to which cohorts are increasing or decreasing in size over time (Lloyd-Evans and Atwood 2004).

Captures are highly variable from year to year, so to calculate the percentage of change in migration cohort sizes, we calculated mean number of captures for the first 5 years of data and compared that to the mean of the last 5 years. Mist net locations, quantity, and the number of hours each net was deployed were essentially unchanged for all 44 years. Preliminary analysis revealed that effort was consistent and as such was not included in further analysis. Captured birds were collected from mist nets and brought to the banding lab, where they were individually banded and identified according to the latest nomenclature (American Ornithologists' Union 1998, 2012; Chesser et al. 2012).

Climate Data

Monthly mean temperatures for the months before and during fall migration were acquired from the five weather stations closest to Manomet and based on available data at the National Climatic Data Center of the National Oceanic and Atmospheric Administration (www.ncdc. noaa.gov). Nearby stations were located in the Massachusetts towns of Brockton, East Wareham, Plymouth, Rochester, and Taunton and monthly temperatures were averaged across all stations.

Compiling data from several stations provided an average temperature for a small region instead of a single site and ensured that anomalous values from a single station would not bias the data set.

In addition to temperature, we included a 3-month running mean of the monthly North Atlantic oscillation (NAO) index from June through October as an additional weather variable. The NAO index measures atmospheric pressure differences in the North Atlantic Ocean; these pressure differences affect weather in the northeastern United States, with positive values generally associated with warmer temperatures. Also, the phase of the NAO affects the location and severity of hurricanes on the eastern coast of the United States (Elsner 2003). Data for the NAO index were taken from the Climate Prediction Center of the National Weather Service (www. cpc.ncep.noaa.gov/data/teledoc/nao.shtml).

Tree Phenology Data

To test the synchrony of fall bird migrations and fall plant phenology, we obtained data of leaf color and leaf fall from Harvard Forest, Petersham, Massachusetts, for the years 1991–2010 (O'Keefe 2000). Petersham is ~150 km northwest of Manomet, but provides a broad-scale index of regional plant phenology. The length of this time series and quality of the data make it the best available information for investigating questions of tree phenology over time in this region. The percentages of leaf color and leaf drop of two to five marked individuals of common woody species were recorded once or twice weekly. For our analysis, we calculated the mean dates for which leaf color and leaf fall each reached 90%. Birds are likely to see a lower proportion of leaf color and leaf fall on migration, but the categorical nature of the tree phenology data limited the levels of leaf color and leaf drop that could be used. The values were useful for differentiating between "early" and "late" years of fall tree phenology.

Statistical Analysis

All statistical analyses were conducted with R statistical software (www.r-project.org). We used mean fall migration date of initial captures of individually banded birds to avoid biases inherent in first or last dates due to changes in size of migratory cohorts over the 44 years (Miller-Rushing

et al. 2008a). Migration dates are often normally distributed within a year, which allowed us to use mean date as a reasonable estimate of bird stopover date. We used linear regression to determine the combination of months for which mean temperature was a significant explanatory variable for stopover dates of individual species. Our approach limited the number of candidate variables for final model selection and restricted the combinations of models that were fully tested. Results of the analysis show that the greatest number of species (14 species) responded significantly to mean August + September temperature, as determined by a significance level of $P < 0.05$. We repeated modeling for NAO where June, July, and August were significant for the greatest number of species (two species with $P < 0.05$, six species with $P < 0.10$). As such, further analyses included only

temperatures and NAO for these months. The relationship between stopover date versus year, leaf color, leaf drop, and changes in migratory cohort size over time were also determined using linear regressions.

We performed linear mixed-effects analyses to determine the relationship between mean bird stopover dates and the explanatory factors described later with the lme4 package of R (Bates et al. 2012). Fixed effects in the multivariate analysis included mean August and September temperature, June–August NAO, leaf color, leaf drop, broodedness (Ehrlich et al. 1988), wintering region, wintering habitat (Rappole et al. 1983)—as well as whether a species is a farmland breeder (Poole and Gill 2002), winters in the tropics (Ehrlich et al. 1988), or is sexually dimorphic (Sibley 2000; Table 12.1). Values for these factors

TABLE 12.1

Study species and life-history traits of migratory landbirds captured during autumn migration at Manomet, Massachusetts, 1969–2012.

Common name	Scientific name	No. years	n	Mean dep. date	Brood	Farm	Tropics	Sex. dim.	Winter hab.	Winter region
Downy Woodpecker	*Picoides pubescens*	44	789	269	1	No	No	Yes	Woods	NA
Eastern Phoebe	*Sayornis phoebe*	44	654	262	2	Yes	No	No	Dry	NA
Blue-headed Vireo	*Vireo solitarius*	44	432	280	1	No	Yes	No	Woods	CA
Red-eyed Vireo	*Vireo olivaceus*	44	3,417	265	1	No	Yes	No	Woods	SA
Blue Jay	*Cyanocitta cristata*	44	2,260	270	1	No	No	No	All	NA
Black-capped Chickadee	*Poecile atricapillus*	44	28,535	281	1	No	No	No	All	NA
Tufted Titmouse	*Baeolophus bicolor*	44	5,256	284	1	No	No	No	All	NA
Brown Creeper	*Certhia americana*	44	1,624	283	1	No	No	No	Woods	NA
Carolina Wren	*Thryothorus ludovicianus*	39	544	249	2	Yes	No	No	All	NA
Golden-crowned Kinglet	*Regulus satrapa*	44	3,007	290	2	No	No	Yes	Woods	NA
Ruby-crowned Kinglet	*Regulus calendula*	44	1,834	287	1	No	Yes	Yes	Woods	CA
Veery	*Catharus fuscescens*	44	532	256	1	No	Yes	No	Woods	SA
Swainson's Thrush	*Catharus ustulatus*	44	1,196	270	1	No	Yes	No	Woods	SA
Hermit Thrush	*Catharus guttatus*	44	1,844	294	2	No	No	No	Woods	NA
American Robin	*Turdus migratorius*	44	7,091	270	2	Yes	No	Yes	All	NA
Gray Catbird	*Dumetella carolinensis*	44	21,484	251	2	No	Yes	No	Dry	CA

TABLE 12.1 (continued)
Study species and life-history traits of migratory landbirds captured during autumn migration
at Manomet, Massachusetts, 1969–2012.

Common name	Scientific name	No. years	n	Mean dep. date	Brood	Farm	Tropics	Sex. dim.	Winter hab.	Winter region
Ovenbird	*Seiurus aurocapilla*	44	643	252	1	No	Yes	No	Woods	CA
Northern Waterthrush	*Parkesia noveboracensis*	44	900	250	1	No	Yes	No	Wet	CA
Black-and-white Warbler	*Mniotilta varia*	44	1,085	250	1	No	Yes	Yes	Woods	CA
Nashville Warbler	*Oreothlypis ruficapilla*	44	640	268	1	No	Yes	Yes	Woods	CA
Common Yellowthroat	*Geothlypis trichas*	44	2,044	256	2	Yes	Yes	Yes	Wet	CA
American Redstart	*Setophaga ruticilla*	44	3,787	254	1	No	Yes	Yes	Woods	CA
Magnolia Warbler	*Setophaga magnolia*	44	793	262	1	No	Yes	Yes	Woods	CA
Blackpoll Warbler	*Setophaga striata*	44	7,768	272	1	No	Yes	Yes	Woods	SA
Black-throated Blue Warbler	*Setophaga caerulescens*	42	649	269	2	No	Yes	Yes	Woods	CA
Myrtle Warbler	*Setophaga c. coronata*	44	20,204	293	2	No	No	Yes	All	NA
Black-throated Green Warbler	*Setophaga virens*	44	338	267	1	No	Yes	Yes	Woods	CA
Wilson's Warbler	*Cardellina pusilla*	44	855	256	1	No	Yes	Yes	Woods	CA
Yellow-breasted Chat	*Icteria virens*	44	1,099	262	2	No	Yes	Yes	Dry	CA
Eastern Towhee	*Pipilo erythrophthalmus*	44	868	273	2	No	No	Yes	Dry	NA
Song Sparrow	*Melospiza melodia*	44	2,959	272	3	Yes	No	No	Dry	NA
Swamp Sparrow	*Melospiza georgiana*	44	1,106	286	2	No	No	No	Wet	NA
White-throated Sparrow	*Zonotrichia albicollis*	44	8,298	285	1	No	No	No	All	NA
Slate-colored Junco	*Junco h. hyemalis*	44	2,205	293	2	No	No	Yes	Dry	NA
Northern Cardinal	*Cardinalis cardinalis*	44	1,646	278	2	Yes	No	Yes	All	NA
Baltimore Oriole	*Icterus galbula*	41	734	241	1	Yes	Yes	Yes	Woods	CA
American Goldfinch	*Spinus tristis*	42	426	292	1	Yes	No	Yes	Dry	NA

NOTES: Number of years refers to how many years this bird was captured in autumn over the 44-year span and n is the total number of captures over the length of the study. Mean dep. date is the mean day of year (as days past 31 December) that this species was captured in autumn at Manomet across all years. Brood is the typical number of broods that a species has in a breeding season. Farm, tropics, and sex. dim. are dichotomous variables that refer to whether a species is a farmland breeder, winters in the tropics, or exhibits sexual dichromatism. Winter hab. is the preferred habitat of species on their wintering grounds and includes the variables: "dry," which includes farmland, grassland, and other dry habitats; "woods," which includes forested areas; "wet" for wetlands; and "all" for species that can be found in a variety of terrestrial habitats. Winter region is the broadly defined region where species overwinter: NA for North America, CA for Central America, and SA for South America.

were based on typical occurrences for each species and the more conservative estimate was used if factors were variable among different regions. We conservatively assigned wintering region to each species as North, Central (including Caribbean Islands), or South America, which also served as a crude surrogate of migration distance. For wintering habitat, we designated species as wintering in one of four general habitats: woods/forest, farmland/grassland/dry habitats, wetlands, or all terrestrial habitats. The four habitats are consistent with previous publications using the same data set (Miller-Rushing et al. 2008b). Species was included as a random variable. Linear mixed-effects modeling allows for data to be input as a panel, enabling analysis of data over time, as well as with respect to the chosen variables. Akaike's information criterion (AIC) was used to assess model strength, and 22 combinations of variables were systematically tested and dropped or switched until the model with the lowest AIC was identified.

Last, we compared timing of migration at Manomet and at Powdermill Nature Reserve in Rector, Pennsylvania, by regressing slopes of change over time in species' passage dates at each location (Van Buskirk et al. 2009). The analysis included both significant and nonsignificant responses because significance values were not available for the published results of Van Buskirk et al. (2009).

RESULTS

Multivariate Results

The full multivariate model included all possible variables and traits. The strongest model, based on AIC, was the following:

Fall migration date = temperature + tropics + wintering habitat + leaf color + broodedness + captures × species

This model, therefore, is the most robust and represents the best model given all combinations of biotic and abiotic predictor variables (Table 12.2).

In this model, the relationship between fall migration of all species and temperature was positive, such that birds depart 0.43 days later for each 1°C increase in temperature (SE = 0.42, t = 1.01). Species that winter in the tropics migrate ∼ 21 days before their north temperate

TABLE 12.2
Model selection for stopover dates of migratory landbirds as a function of different environmental factors and life-history traits.

Stopover date ~	AIC	ΔAIC
a. Temperature + tropics + wintering habitat + leaf color + broodedness + captures × species	5109	0
b. Temperature + wintering region + leaf color + broodedness + captures	5122	13
c. Temperature + NAO index + wintering region + leaf color + broodedness + captures × species	5123	14
d. Temperature + NAO index + wintering region + leaf color + captures × species	5126	17
e. Temperature + tropics + leaf color + broodedness + captures × species	5127	18
f. Temperature + wintering habitat + leaf color + leaf drop + broodedness + captures × species	5128	19

counterparts. Habitat generalists that winter in "all" terrestrial habitats are the latest group of fall migrants, with species in each of the other habitats—wet, dry, and woods—migrating earlier by 4.24, 4.44, and 10.31 days, respectively. Positive relationships also exist between migration date and the date of leaf color change (β = 0.11, SE = 0.07, t = 1.51) and between migration date and broodedness (β = 1.02, SE = 5.09, t = 0.20). In other words, migration occurs earlier when leaves are changing color earlier, and in species that are more likely to have only one brood. None of the categorical explanatory variables such as wintering habitat or broodedness interacted with temperature (Tables 12.3 and 12.4).

Species Responses

The mean date of fall capture at Manomet for all species and over all years was 2 October. Baltimore Orioles (*Icterus galbula*) tended to be the first species to pass through Manomet with a mean fall migration date of 29 August (SE = 0.48, n = 734). Hermit Thrushes (*Catharus guttatus*) were generally the last to pass through, with a mean fall migration date of 21 October (SE = 0.25, n = 1844). Linear regression analyses demonstrated that 14 of the 37 species had stopover dates that have changed significantly over time (Table 12.5).

TABLE 12.3

Coefficients for the minimum AIC model explaining variation in stopover date versus temperature + tropics + wintering habitat + leaf color + broodedness + captures × species.

Variable	Estimate	SE	t value
Mean August–September temp.	0.43	0.42	1.01
Leaf color	0.11	0.07	1.51
Broodedness	0.74	5.02	0.15
Tropics	−21.46	5.90	−3.63
Winter habitat			
All: wet	4.24	12.72	0.39
All: dry	4.44	7.51	0.59
All: woods	10.31	7.08	1.51

NOTES: Positive coefficients indicate that the relationship between stopover date and the given variable was positive. For example, the relationship between stopover of all species and temperature is positive, such that birds depart 0.43 days later for each 1°C increase.

TABLE 12.4

Variance, standard deviation, and correlation among groups.

Group	Variance	Std. Dev.	Corr.
Species	165.52	12.87	
Captures	0.0004	0.02	0.095
Residual	50.45	7.10	

Nine species are now recorded with significantly later movements during fall migration, with Blackpoll Warblers (*Setophaga striata*) exhibiting the greatest delay of ~0.3 days per year (SE = 0.04, n = 7768, P < 0.001). Stopover dates of five species were significantly earlier: Black-capped Chickadees (*Poecile atricapillus*, n = 28,535), Downy Woodpeckers (*Picoides pubescens*, n = 789), Eastern Phoebes (*Sayornis phoebe*, n = 654), Gray Catbirds (*Dumetella carolinensis*, n = 21,484), and Tufted Titmice (*Baeolophus bicolor*, n = 5,256). Downy Woodpeckers had the greatest adjustment, moving 0.5 days earlier per year (SE = 0.10, P < 0.001). Twenty-three species had stopover dates that did not change significantly: 15 of these species are trending toward slightly later stopover dates, and seven toward earlier dates; one species, Swamp Sparrow (*Melospiza georgiana*), has not changed its fall stopover date (n = 1,106).

Mean August and September temperature has significantly warmed during this period at a rate of approximately 0.04°C per year (P < 0.001). Mean August and September temperature is a significant factor in the passage dates of 14 species. Thirteen species move later in warm years, with the Slate-colored Junco (*Junco h. hyemalis*) exhibiting the greatest response to temperature, migrating 3.6 days later per 1°C increase in temperature (SE = 1.14, P = 0.003). Gray Catbirds are the only 1 of 14 species to migrate earlier in warmer years, and they do so at a rate of 1.1 days earlier per 1°C increase (SE = 0.49, P = 0.04). Species with later mean migration dates also appear to be the most responsive to temperature (Figure 12.1).

The NAO index was a significant factor for timing of migration in three bird species. When the NAO index is high, Black-throated Green Warblers (*Setophaga virens*, SE = 0.91, n = 338, P = 0.003) and Tufted Titmice travel later (SE = 0.75, n = 5,256, P = 0.009), possibly because the jet stream is weaker and temperatures are above average. In contrast, Black-and-white Warblers (*Mniotilta varia*) migrate earlier when the NAO index is high (SE = 0.80, n = 1,085, P = 0.01).

Captures of 28 species have declined significantly over the 44 years of this study, reflecting a decrease in passage cohort sizes of these species. Black-capped Chickadees have declined the most at 28 fewer captures per year (P = 0.006), and declines in Myrtle Warblers (*Setophaga c. coronata*) are also substantial, with 22 fewer captures per year (P < 0.001). Annual captures of Black-capped Chickadees are now ~7% of numbers at the start of the banding program: Captures averaged 1,392 ± 808SE per year in 1969–1973 versus 102 ± 37 captures per year in 2008–2012. Myrtle Warbler captures have decreased to 17% of historic rates: 979 ± 160SE versus 172 ± 31 captures per year. Carolina Wrens (*Thryothorus ludovicianus*) and Northern Cardinals (*Cardinalis cardinalis*) are the only two species whose captures have increased significantly, both by about one capture per year (±6 and 14, respectively, both P < 0.001). Only one Carolina Wren was captured in the first 5 years of banding, but they now average 25 captures per year. Northern Cardinal captures are almost eight times greater now than they were in the past with 8 versus 62 captures per year.

Long-term changes in plant phenology over 1991–2010 were not significant for dates when at least 90% of leaves changed color (P = 0.20) or there was at least 90% leaf drop (P = 0.20). However, the relationship between leaf color

TABLE 12.5

Linear regression of captures per year versus day of season, and mean capture date versus
annual variation in environmental factors of migratory landbirds captured
during autumn migration at Manomet, Massachusetts, 1969–2012.

Common name	Captures/year	Year	Temp: Aug., Sept.	NAO: June, July, Aug.	Leaf color	Leaf drop
Downy Woodpecker	−0.53**	−0.53***	−2.76	2.57	0.38	−0.32
Eastern Phoebe	−0.01	−0.23*	−0.01	1.78	0.21	−0.83
Blue-headed Vireo	0.03	0.11	2.88**	−0.30	0.46*	0.45
Red-eyed Vireo	−2.01***	0.14**	1.90**	−0.21	0.12	0.18
Blue Jay	−1.61*	−0.02	1.54	0.86	0.59	0.75
Black-capped Chickadee	−28.10**	−0.31*	−1.28	0.57	0.55	1.30
Tufted Titmouse	1.66	−0.21**	−0.57	2.06**	0.35	0.24
Brown Creeper	−1.53***	0.07	1.56*	0.53	0.34	−0.17
Carolina Wren	0.71***	0.05	0.11	−0.06	−0.10	−0.25
Golden-crowned Kinglet	−2.49***	0.09	0.94	−0.41	0.53*	0.56*
Ruby-crowned Kinglet	−1.12***	0.08	2.00**	−0.04	0.27	0.32
Veery	−0.44**	0.11	0.42	−0.10	0.05	−0.02
Swainson's Thrush	−1.14***	0.23***	2.31*	−0.73	−0.05	0.07
Hermit Thrush	−0.44*	0.15**	2.16**	−0.56	0.12	0.14
American Robin	−5.58***	0.17	2.97*	0.21	0.29	0.93*
Gray Catbird	−4.32**	−0.16***	−1.05*	0.69	0.19	−0.07
Ovenbird	−0.37***	−0.05	0.57	1.28	0.14	0.56
Northern Waterthrush	−0.82***	0.02	1.13	0.48	0.15	0.41
Black-and-white Warbler	−1.08***	0.12	−1.09	−2.09*	−0.16	0.03
Nashville Warbler	−0.26*	0.16	0.94	−0.11	0.24	−0.13
Common Yellowthroat	−1.83***	0.21***	1.85*	−0.51	0.05	−0.15
American Redstart	−4.19***	0.11*	1.66**	−0.22	0.30*	0.25
Magnolia Warbler	−0.31**	0.13	−0.25	0.24	−0.55	0.09
Blackpoll Warbler	−10.05***	0.27***	3.25***	0.20	0.57*	0.48
Black-throated Blue Warbler	−0.02	0.09	1.66	1.00	−0.09	−0.42
Myrtle Warbler	−22.05***	0.10	2.77**	1.14	0.33	0.34
Black-throated Green Warbler	−0.15**	0.07	2.41	3.08**	−0.54	0.12
Wilson's Warbler	−0.66***	0.16*	1.36	0.73	0.05	0.09
Yellow-breasted Chat	−0.91***	−0.05	1.41	0.71	0.55	0.23
Eastern Towhee	−1.25***	0.16	1.96	1.54	0.07	−0.06
Song Sparrow	−1.72***	0.10	1.54	1.10	0.06	−0.06
Swamp Sparrow	−0.43*	0.00	0.77	0.21	0.12	−0.16
White-throated Sparrow	−1.89	0.16*	2.32*	0.06	0.13	0.17
Slate-colored Junco	−2.70***	0.18*	3.58**	0.69	0.51	0.17
Northern Cardinal	1.44***	0.03	0.96	−0.99	−0.22	−0.06

TABLE 12.5 (continued)

Linear regression of captures per year versus day of season, and mean capture date versus annual variation in environmental factors of migratory landbirds captured during autumn migration at Manomet, Massachusetts, 1969–2012.

Common name	Captures/year	Year	Temp: Aug., Sept.	NAO: June, July, Aug.	Leaf color	Leaf drop
Baltimore Oriole	−0.65**	−0.03	−1.15	−1.27	0.04	−1.07
American Goldfinch	0.03	0.16	−0.71	−3.43	−0.56	0.55

NOTES: Linear regression of captures per year versus time represent long-term changes in population cohort size over the 44-year time span; positive values indicate population increases, whereas negative values are declines. The remaining five columns display the relationship between mean capture date and each explanatory factor. Positive values indicate that stopover dates have become later in recent years, with increasing temperature, with increasing NAO index values, with later leaf color change or later leaf drop.

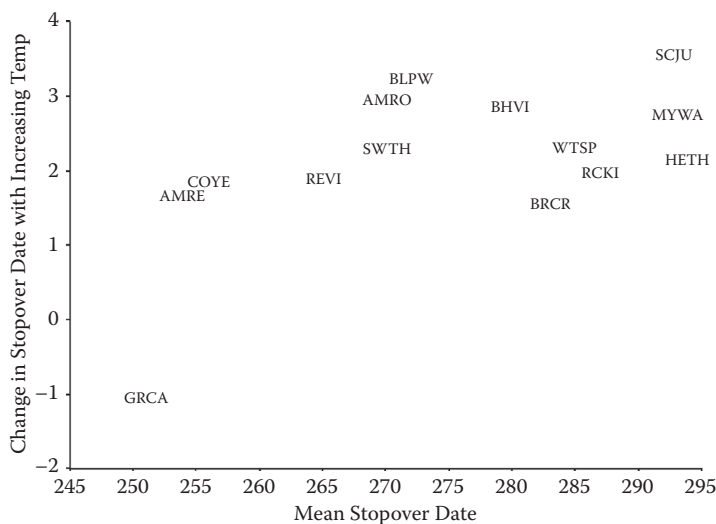Level of significance: * = P < 0.05, ** = P < 0.01, *** = P < 0.001.

Figure 12.1. The relationship between mean stopover dates and changes in stopover date with August + September temperature for species demonstrating significant changes in stopover with temperature. The x-axis represents the mean stopover date of the species over all years, and the y-axis represents the slope of stopover date and temperature, days °C^{-1}. Species abbreviations are standardized codes: BHVI (Blue-headed Vireo), REVI (Red-eyed Vireo), BRCR (Brown Creeper), RCKI (Ruby-crowned Kinglet), SWTH (Swainson's Thrush), HETH (Hermit Thrush), AMRO (American Robin), GRCA (Gray Catbird), COYE (Common Yellowthroat), AMRE (American Redstart), BLPW (Blackpoll Warbler), MYWA (Myrtle Warbler), WTSP (White-throated Sparrow), and SCJU (Slate-colored Junco).

and August–September temperatures was significant (r^2 = 0.37, P = 0.006), as is the relationship between leaf color and leaf drop (r^2 = 0.20, P = 0.045). Leaf drop was not significantly correlated with temperature (P = 0.17). When these variables of leaf color and drop were regressed with fall migration dates, four species displayed a significant positive correlation with leaf color change and two species with leaf drop; these birds migrate later when leaf color and drop occur later. Fall migration dates for Golden-crowned Kinglets (*Regulus satrapa*) were correlated positively with both leaf color (0.5 days/°C, P = 0.02) and leaf drop (0.6 days/°C, P = 0.04).

Dates of fall migration for different species did not vary based on broodedness (P = 0.28), wintering habitat (P = 0.47), whether they are farmland breeders (P = 0.30), or sexual dichromatism (P = 0.99). Species that winter in the tropics migrated an average of 18 days earlier than north temperate species (P < 0.001). Similarly, there is a significant difference in the migration dates of species based on wintering ground (P < 0.001). Species that winter in Central America migrate earliest (mean departure date = 17 September), followed by species that winter in South America (23 September), and species that remain in North America were last to migrate in fall (6 October).

Analysis of data for species captured at the banding station at Powdermill Nature Reserve (Van Buskirk et al. 2009) shows generally similar patterns to our findings at Manomet. Some species changed over time and in relation to temperature, and long-distance migrants migrated earlier in the fall than short-distance migrants. We regressed slopes of change in stopover dates over time for the same set of study species at Powdermill (date of 50% capture, Van Buskirk et al. 2009) versus slopes for mean stopover at Manomet, but responses were not related ($r^2 = 0.03$, df = 26, P = 0.39). The analysis included nonsignificant responses for Powdermill, but it is clear that species exhibit spatial variability in the timing of their fall migrations and their responses to changes in temperature. The direction and degree of change in stopover date for the same species between these two locations were not the same.

DISCUSSION

Analysis of 44 years of banding data in Manomet reveals that about one-quarter of species are migrating later in the fall now than they did in the past. An additional five species (14%) are migrating earlier in the fall than they did previously. Comparisons between sites indicate that our results are not necessarily predictive of changes elsewhere, particularly farther inland and at other locations.

Manomet has warmed significantly in recent decades; 14 species have responded to temperature changes with altered fall passage dates, nine of which are species whose fall migration dates have changed over time. Other species traits, such as wintering region, broodedness, and wintering habitat, affected the sequence of migration dates, with some groups tending to migrate earlier or later, but none of the factors affected migratory responses to warming temperatures.

Our multivariate model indicated that birds tend to migrate later in years when leaves senesced later in the season. Few studies have incorporated fall plant phenology into research on timing of bird migration. Our result could reflect the tendency of birds to migrate and leaves to change color later in warmer autumns. Alternatively, birds may utilize the visual cue of leaf color change or associated cues, such as declines in fruit and insect abundance, along with temperature and other cues as a signal to migrate in the fall. Many of the trees in this region begin changing color in mid-September, a couple of weeks before the peak of migration at Manomet, and leaf coloration could provide a cue for some species, particularly those that migrate late in the season. Furthermore, if bird migration is correlated with leaf senescence, it could provide a way to estimate fall migration through future research utilizing remote sensing imagery.

Delays in autumn passage could be due to delays in departure from the breeding grounds, decreased speed of migration, increased time spent at stopover locations, or a combination of factors (Gordo 2007). Any of these factors could result in changes in synchrony between migratory birds and their autumn food sources. However, the implications of our results for food synchrony are unclear. Information is limited regarding specific food preferences of particular birds, fall phenology of key foods, and whether food supply is a limiting factor during fall migration. We know surprisingly little about temporal variation in fruit, seed, and insect abundance or their nutritional value. In some cases, fruits are maturing earlier in response to warming temperatures (Menzel and Dose 2005). However, some insects appear to delay diapause in warm falls (Altermatt 2010, Stoeckli et al. 2012). Given the variability we found in changes in fall migration phenology, it is possible that temporal mismatches are occurring in fall, as they may be in the spring (Both et al. 2006), but the patterns are difficult to identify. Seasonal phenology of food resources used in autumn migration is an area ripe for future research.

Our results are consistent with the expectation that some species may spend more time at

breeding grounds in warmer years. Migrants of 21 bird species are captured at Manomet in the spring and fall (Miller-Rushing et al. 2008b), in sufficient numbers to examine changes in the length of time spent at breeding grounds. A comparison of spring and fall mean migration dates showed that only 1 of 21 bird species, Gray Catbirds, have significantly changed migration dates in both spring and fall.

Gray Catbirds are migrating through Manomet earlier in both seasons now than in the past. In terms of response to temperature, migration dates of only four species were correlated with temperature in the months preceding both spring and fall migration (Table 12.6). Gray Catbirds migrate earlier in both warm springs and falls. American Redstarts (*Setophaga ruticilla*), Hermit Thrushes, and White-throated Sparrows (*Zonotrichia albicollis*) respond significantly to spring and fall temperature, migrating earlier in the spring and later in the fall when the temperatures are warmer before migration; yet, the migration times of these species have not significantly changed over time. In warm years, the three species may be spending more time at breeding grounds, but the response has not been strong enough to be significant. The results must be interpreted cautiously because the spring and fall migration cohorts at Manomet are not necessarily from the same breeding populations, and the fall migration cohort contains a high proportion of first-year birds that are absent during spring migration (Brooks 2008, Finnegan 2008).

Delays in autumn passage may be indicative of changes in departures from the breeding grounds, but passage dates are driven by local temperatures for more species than were linked to the large-scale patterns of NAO. Links to local temperatures suggest that speed, stopover duration, and other events driven by local dynamics may play a more prominent role in passage than departure dates do. Future studies tracking the departures of individual breeding birds from their summer habitat to their wintering grounds could help to separate the effects of departure dates and local drivers on changing passage dates.

Last, we found that trends in fall migrations over time differed between cohorts of the same species at Manomet and Powdermill despite a relatively close geographical proximity. Our results could reflect differences in species' responses to climatic variability between the two sites. The differences between the two sites could also be influenced by differences in the breeding populations and ages of birds that pass through each location in the fall (Brooks 2008, Finnegan 2008). As a coastal site, Manomet has a higher proportion of first-year birds (71% of birds banded in 2007) than Powdermill (61% of birds banded in 2007; Brooks 2008, Finnegan 2008), and differences in age composition could influence migration timing at different sites and analytical comparisons between sites. A similar lack of correspondence for spring migration dates of birds was reported in a comparison of three sites in Massachusetts (Miller-Rushing et al. 2008c).

It is evident that the fall migration dates of birds captured at banding stations is changing over time and in response to a changing climate. To understand temporal changes in capture data from systematic bird banding stations, it is critical to determine where these birds spend their breeding season and where they overwinter, as well as the timing of departure from breeding areas and arrival at winter home ranges.

TABLE 12.6
Comparison of spring and fall migration at Manomet.

Species	Metric	Spring	Fall
Hermit Thrush	Temp	−1.69	2.16
Gray Catbird	Year	−0.12	−0.16
Gray Catbird	Temp	−1.09	−1.05
American Redstart	Temp	−1.13	1.66
White-throated Sparrow	Temp	−1.16	2.32

NOTES: Spring values are taken from Miller-Rushing et al. (2008b). The values for the metric "Year" are the slope of mean capture dates for the respective season and year, days $year^{-1}$, and for "Temp" are the slope of mean capture dates and mean temperature for the months preceding migration, days $temp^{-1}$. Only species with significant responses for both seasons are included here.

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