

Matching Ephemeral Resources on Autumnal Stopover and the Potential for Mismatch*

*Brian J. Olsen, Jennifer D. McCabe, Evan M. Adams,
David P. Grunzel, and Adrienne J. Leppold*

Abstract. Climate change can alter the timing of biological events differently across members of an ecosystem, changing the nature of ecological interactions and the efficacy of evolutionary strategies. Mismatches in phenology have been reported between breeding songbirds and their food resources in north temperate ecosystems, especially for long-distance migrants and dietary specialists. Far less attention, however, has been paid to periods outside the breeding season. The success of songbird migration, like breeding, should also be determined by the degree of matching between bird and resource phenologies. Here, we tested if habitat patch use for songbirds along the migratory route was predicted by (a) habitat characteristics that varied throughout the migration season, (b) static characteristics, or (c) a combination of the two variable types. We tested for these patterns in four families of songbirds that ranged from specialists to generalists and across four stopover sites along the Gulf of Maine. Dynamic habitat characteristics alone predicted patch use in all four families better than static variables or a combination of dynamic and

static characteristics. Regardless of mean dietary niche breadth, mist net captures indicated that all four families shifted their apparent patch use throughout the season as a function of ripe fruit abundance, invertebrate biomass, vegetation defoliation, and soil moisture. The best predictors of patch use were different for short- versus long-distance migrants across the two most commonly captured families, but all species and migration strategies were sensitive to phenological changes. Our results suggest that migratory songbirds assess patch quality within a stopover site differently through time. Variation in the timing of stopover arrival thus results in different habitat selection behaviors. The potential therefore exists for timing mismatches that reduce individual fitness. We recommend that conservationists prioritize stopover habitats where landscape-scale phenological heterogeneity maintains benefits to migrants throughout the season.

Key Words: flycatchers, habitat use, phenological mismatch, sparrows, stopover behavior, vireos, warblers.

* Olsen, B. J., J. D. McCabe, E. M. Adams, D. P. Grunzel, and A. J. Leppold. 2015. Matching ephemeral resources on autumnal stopover and the potential for mismatch. Pp. 163–176 in E. M. Wood and J. L. Kellermann (editors), *Phenological synchrony and bird migration: changing climate and seasonal resources in North America*. Studies in Avian Biology (no. 47), CRC Press, Boca Raton, FL.

Temperate ecosystems are dominated by seasonal ephemera. The evolutionary success of boreal migratory birds stems in part from their ability to benefit from high-latitude summer abundance while avoiding winter scarcity. Success of migratory birds is dependent upon a match between the timing of bird behavior and the local phenology of ecological resources (Lack 1950). The fitness costs of mismatches are readily apparent on the breeding grounds of many north temperate species (Møller 1994, Sanz et al. 2003). Less attention has been paid to the potential and importance of phenological matching during migratory movements and stopover dynamics. Given the substantial energetic requirements (Berthold 1975, Blem 1980) and mortality risk experienced by songbirds during the migratory period (Lack 1968, Alerstam and Hedenström 1998, Sillett and Holmes 2002), it is reasonable to hypothesize that phenological mismatch during migratory stopover is as important as ecological conditions encountered on the breeding grounds. Here, we test for the ability of ephemeral versus static ecological resources to predict bird habitat use within four autumnal migratory stopover sites along the US coast of the Gulf of Maine.

THE CASE FOR PHENOLOGICAL MISMATCH DURING STOPOVER

On the breeding grounds, ecosystem phenology is a strong determinant of fitness for migratory birds. The timing of migratory arrival is predicted by the average timing of resources required for territory establishment and reproduction (Both 2010a). Migratory behaviors worldwide show great flexibility in timing (Sokolov et al. 1998, Marra et al. 2005, Rubolini et al. 2007), likely due to the gain in fitness achieved by matching interannual variability in local phenology. When the temporal advance or delay of breeding resources outpaces the behavioral flexibility of bird species ("mismatch": Both and Visser 2001; Both 2010a, b), birds can suffer both in terms of offspring productivity (Møller 1994, Verboven et al. 2001, Sanz et al. 2003, Both and Visser 2005, Drent 2006) or long-term species viability (McLaughlin et al. 2002, Both et al. 2006, Møller et al. 2008). On the European breeding grounds, dietary specialists—and especially insectivore specialists—appear more sensitive to phenological mismatch than dietary generalists

and long-distance migrants appear more sensitive than short-distance migrants (Both and Visser 2001, Moussus et al. 2011).

While mismatch with resources at migratory stopover sites has received less attention, the same ecological scenario may apply. As with the breeding grounds, arrival of individuals to stopover locations can be predicted by local environmental conditions (Hüppop and Hüppop 2003, Marra et al. 2005) and arrival is broadly timed to the availability of local food resources (Castro and Myers 1993, Tsipoura and Burger 1999, Lank et al. 2003, McKinney et al. 2012). Temporal mismatch can increase fitness costs by negatively impacting refueling rate or increasing stopover duration (Baker et al. 2004, Balbontín et al. 2009). For songbirds specifically, migration likely represents a majority of their annual mortality risk (Sillett and Holmes 2002, Newton 2007). Thus, mismatched timing on migratory stopover could have large consequences for individual fitness and population viability through its effect on survival, time spent migrating, and individual condition upon arrival (Lehikoinen and Sparks 2010).

Detecting Sensitivity for Phenological Mismatch on Stopover

Intra-annual habitat variation within a stopover site can be attributed broadly to three sources: static habitat structure, dynamic habitat structure, and dynamic food availability. The first two sources of variation are related to nonfood resources used by birds during migratory stopover. Static and dynamic habitat structures provide protection from predators and inclement climatic conditions, but may also provide coarse habitat cues for migrating birds unfamiliar with a specific locale. The first source of spatial variation, "static habitat structure," is unchanging throughout the migration season. This source of variation differentiates habitat patches with different plant communities such as tree- versus shrub-dominated patches or patches dominated by one shrub species over another. The second source of variation, "dynamic habitat structure," changes through time by plant defoliation, varying soil moisture throughout the migration season, or other processes. Food resources can be both static and dynamic, but for migratory species in north temperate ecosystems, food availability at the prey-species scale is almost exclusively dynamic.

Few plant species produce fruit or seeds continuously and few invertebrate species are consistently available for bird predation throughout the migration season. Further, the distributions of dynamic resources have predicted small-scale habitat selection for a few songbird species during the post-fledging period or autumnal migration (Tietz and Johnson 2007, Streby et al. 2011).

In this study, we investigated the potential for phenological mismatches to occur during migration by evaluating habitat selection within a stopover site. Specifically, we tested whether birds selected habitat patches based on static or dynamic characteristics. Temporally variable habitat use with selection for different patches at different points within a migratory season determines a taxon's risk for phenological mismatch. Taxa with temporally variable habitat use within a stopover site clearly show behavioral plasticity in the face of resource change. Behavioral plasticity itself should prevent birds from choosing a patch without adequate resources and should buffer a species from climate-change-induced resource fluctuations at a site. For taxa to be at risk of phenological mismatch, they must first match habitat use to local resource variability. Matching can become mismatched if there is a threshold beyond which behavioral plasticity can no longer adjust to temporal variation at breeding or nonbreeding sites. If matching during temporally dynamic patch use is symptomatic of behavioral plasticity at one level of temporal variability, it can also be symptomatic of a threshold in habitat variability beyond which reaction norms cannot continue to maintain benefits to individuals and lead to a mismatch. In this study, we measured matching among patches within a stopover site as small-scale patch selection (Hutto 1985). Temporal dynamics could also be at play at larger regional or subcontinental scales, especially if the relative quality of different migratory routes varies across the migration season.

Here, we examine variation in the within-stopover site, among-patch habitat use for four families of migratory songbird. We chose families that vary in their mean dietary niche breadth and possess species with varying migration distances, because these characteristics predict sensitivity to mismatch on the breeding grounds (Both and Visser 2001, Moussus et al. 2011). Our study taxa included sparrows that were generalists with a granivore to invertivore diet (F. Emberizidae,

$n = 7$ species); vireos (F. Vireonidae, $n = 3$) and warblers (F. Parulidae, $n = 19$), which were generalists with a frugivore to invertivore diet; and flycatchers (F. Tyrannidae, $n = 5$) as an invertivore specialist family (but see Parrish 1997 and Suomala et al. 2010). For each of these four families of birds, we tested (a) whether among-patch variability in habitat use was best predicted by static habitat structure, dynamic habitat structure, dynamic food availability, or any linear combination of those three sources of patch variation; and (b) whether these patterns varied for long- versus short-distance migrants within families.

METHODS

Study Area and Sampling Design

We gathered habitat-characteristic and bird-habitat-use data from 30 August to 18 October 2011 at four migratory stopover sites along the Gulf of Maine, where the dominant plant community type transitions from the northern hardwood to boreal forests. The period of observation covered the peak abundance of all groups of migratory songbirds in our region, although it did miss the beginning of migration for warblers and the end of migration for sparrows. By not sampling outside this temporal window, we lowered the probability that preferred habitats would be unoccupied merely due to low numbers of individuals.

Study sites included the two small islands of Great Duck Island (105 ha) and Metinic Island (130 ha), the southern headland of Mount Desert Island (280 km²), and the narrow peninsular headland of Petit Manan Point. The four sites are located in a series along a southwest to northeast transect. Metinic Island is the southwest site, Mount Desert Island and Great Duck Island were 10 km apart and 76 km to the northeast of Metinic, and Petit Manan Point was located 40 km farther to the northeast. Within each site, we measured bird use using mist net captures in habitats dominated by shrubs (*Alder*, *Aronia*, *Sorbus*, and *Ilex* spp.) or trees (mainly *Picea* spp., with *Abies*, *Larix*, *Betula*, *Acer*, and *Populus* spp.).

At each site, we defined a series of habitat patches that were centered on paired pitfall and hanging invertebrate traps placed in shrubs. Number of habitat patches per site ranged from one (Great Duck) to seven (Metinic) to eight (Mount Desert and Petit Manan) patches. We defined patches as

the 25-m radius circle around each invertebrate collection location and sampled these patches with one to six mist nets placed randomly with regard to the traps. Each patch was centered on one or more shrubs, but varied in the plant community across the 1.7-ha patch. Our study design standardized comparisons of invertebrate communities by sampling species only within shrub habitats and by allowing patches to vary in both static and dynamic habitat structure.

Quantifying Habitat Structure and Bird Use

We quantified habitat structure along two 4-m-wide belt transects along each side of the mist nets and averaged values across all nets within each habitat patch. Static habitat structure was then defined at the end of the migration season (October) with seven metrics: the mean, per-meter woody stem density along the center of the belt transects; the relative cover of each plant species for the shrub, tree, and herbaceous structural layers; and both the layer-specific maximum vegetation height and the modal vegetation height across all vegetative layers at each third meter along the 12-m-long transects. Relative cover was assessed based on either woody tissues only (shrub and tree layers) or final size at the end of the summer growing season (herbaceous layer). While the herbaceous layer is more dynamic than the woody structural layers in our temperate ecosystem, our single end-season measure of cover is an index for community type and does not capture the small dynamic changes in the cover of this structural layer from August to October.

We calculated the first principal components for both the relative cover measures (hereafter "cover-PC") and vegetative heights (hereafter "height-PC"), which accounted for 41% and 63% of the variance in each of the two sets of measurements, respectively. Cover-PC represents an ecological gradient from a plant community dominated by dense shrubs over a forb- and litter-dominated ground layer (low values are shrub habitat) to a more forested community with a grass-dominated ground layer and little shrub understory (high values are woodland habitat). The height-PC captures the different heights possible within each of these community types. Low values indicated a tall shrub and herbaceous layers with short trees, whereas high values indicated a short shrub and herbaceous layer with a canopy of tall trees.

We assessed dynamic habitat structure and food availability throughout the observed migratory period. Soil moisture, leaf greenness, and fruit availability were measured weekly along the two belt transects near each mist net. Soil moisture was identified as one of four categories (dry, moist but not saturated, saturated, and standing water); leaf greenness was measured as the percentage of leaves in four categories (>90% green, <90% green and <50% brown, >50% brown, and bare stems) separately for the shrub and tree structural layers, and fruit availability was measured as the relative abundance of all ripe fruit in eight broad categories (Smith and McWilliams 2009). We excluded plants in the genus *Myrica* due to unpalatability of fruit for our study species of birds (Place and Stiles 1992). We calculated a single weighted average for each of these three dynamic habitat variables per transect. We multiplied the number of samples in each category by the median value of each category's range and then summed these products. Number of samples included the percentage of leaves or fruiting plants or the raw number of soil samples. High values of the indices indicated more saturated soils, green leaves, or ripe fruits. We then calculated single values for each habitat patch by averaging the transect values within the patch.

We captured invertebrates using pitfall traps placed under shrubs and yellow cup traps hanging in shrubs at the center of each patch. All traps were filled with soapy water and deployed for 4 days at a time, and the resulting dried biomass of captured invertebrates was used as an index of availability for the habitat patch for the period from 2 days prior to 2 days subsequent to each sampling period of 8 days. We only operated invertebrate traps during periods without significant precipitation (<1 cm) to avoid collection bias due to water-filled traps. The periods of the migration cycle for which we have data, therefore, possessed more similar weather conditions than occur over the entire season, and we also avoided migrant "fall-out" conditions associated with rain events.

To assess the other dynamic habitat variables on a similar time frame, we interpolated the mean soil moisture, leaf greening, and fruit abundance variables for the median day of invertebrate sampling by assuming that the other dynamic variables changed linearly between weekly assessments. If soil moisture had been assessed during the middle of the invertebrate sampling period,

then the patch was given that value for the entire period, but if soil moisture had been assessed on the first and eighth days of the invertebrate sampling period, then the patch was assigned the soil moisture value halfway between the two samples.

We operated mist nets in suitable capture conditions and closed nets if temperatures were outside the range of 0°C–27°C, if winds were >20 km per hour, or if precipitation or fog was heavy enough for water to collect on the nets. Nets were monitored within each patch from 30 minutes before sunrise for 6 hours or until conditions deteriorated. Most species of birds captured in mist nets were from one of four families (Parulidae, Emberizidae, Vireonidae, and Tyrannidae), and we summed number of captures daily within each habitat patch (Table 10.1). We did not include Yellow-rumped Warblers (*Setophaga coronata*) to avoid overrepresentation within warblers (>66% of all warbler captures) and their preference for *Myrica* fruits, which were not included in our surveys of fruit abundance (Place and Stiles 1992, Borgmann et al. 2004).

Statistical Analysis

To test for the ability of dynamic and static habitat characteristics to predict bird habitat use, we developed a series of repeated-measures, negative-binomial, generalized linear models (Proc Genmod, SAS 9.2). We repeatedly measured daily captures in 24 habitat patches through time (366 patch-days) and used the negative binomial distribution to account for overdispersion and zero inflation in our capture data. All models included the effects of capture effort (total net hours per meters of net), stopover site (to account for site-specific capture probabilities), taxonomic family (to account for family-specific capture probabilities), and both linear and quadratic terms for the calendar day of capture nested within taxonomic family. Exploratory analysis showed that the 8-day moving averages of capture rate across all sites exhibited a quadratic relationship with Julian date nested with taxonomic family (linear term: $F_{4,8} = 63.9$, $P < 0.0001$; quadratic term: $F_{4,8} = 64.0$, $P < 0.0001$). By estimating a quadratic relationship for each family, we controlled for the broad seasonal phenology of migration within each family and thus availability to occupy patches within each site as a function of regional abundance.

We considered eight candidate variables nested within taxonomic family of birds in three categories: static habitat structure (stem density, cover-PC, and height-PC), dynamic habitat structure (soil moisture, shrub-layer leaf greenness, and tree-layer leaf greenness), and dynamic food availability (ripe fruit abundance and invertebrate biomass). We also included a quadratic term for stem density to test the possibility that intermediate values of density might be preferred by a given bird taxon. We considered quadratic terms for the remaining variables, but quadratic patterns were not supported by initial data exploration, and we dropped these terms to simplify our models. We scaled all of our candidate variables by dividing them by the mean value of each measurement across all sites and habitat patches. Likewise, we scaled our capture rates by dividing each daily capture total by the mean daily capture total for that taxonomic family across all sites. The adjustments allowed for direct comparison of parameter estimates among our candidate variables and predicted capture rates among our taxonomic families.

We then created eight separate models, including:

1. Three models that each used only the static habitat structure variables, the dynamic habitat structure variables, or the dynamic food availability variables
2. Three models that included the pairwise combinations of the three variable categories
3. The full model with all of the static and dynamic variables
4. The null model with just the five covariates

Final model selection used the quasi-likelihood under the independence model criterion corrected for parsimony (QICu; Pan 2001, Hardin and Hilbe 2007). We considered models with $\Delta\text{QICu} < 2.0$ as equivalent.

To test for the sensitivity of the final model to the migration distance of a species, we performed a phylogenetically controlled contrast by estimating the top model parameters for both a long-distance and short-distance migrant group within each family. We assessed relative migratory distance by first measuring the latitudinal distance between the centers of the breeding and non-breeding ranges for each species (Erickson et al. 2011). We then classified each species within the

TABLE 10.1
Total individuals captured and temporal range of capture (in calendar days) for four migratory stopover sites along the Gulf of Maine during the Fall of 2011.

Taxon	Individuals captured	First detection	Median detection	Last detection	Migration distance
Tyrannidae					
Eastern Phoebe	9	270	270	270	
Least Flycatcher	8	242	250	250	
Traill's (Alder or Willow) Flycatcher	45	242	244	268	
Yellow-breasted Flycatcher	8	244	244.5	268	
Vireonidae					
Blue-headed Vireo	25	268	269.5	290	
Philadelphia Vireo	4	268	269	269	
Red-eyed Vireo	187	242	268	284	
Parulidae					
American Redstart	87	242	244	291	Long
Black-and-white Warbler	16	245	258	270	Long
Black-throated Blue Warbler	14	243	270	271	Short
Black-throated Green Warbler	12	243	257.5	271	Long
Blackpoll Warbler	172	244	269	276	Long
Canada Warbler	5	244	244	244	Long
Cape May Warbler	6	245	246	247	Short
Common Yellowthroat	261	242	247	284	Short
Connecticut Warbler	6	268	272	276	Long
MacGillivray's Warbler	3	271	271	271	Short
Magnolia Warbler	28	244	268	271	Short
Mourning Warbler	3	242	242	244	Long
Nashville Warbler	29	242	269	290	Short
Northern Parula	30	242	269	274	Short
Northern Waterthrush	45	242	244	270	Long
Palm Warbler	52	242	269	284	Short
Wilson's Warbler	48	242	245	269	Long
Yellow Warbler	40	244	244	269	Long
Yellow-breasted Chat	11	269	269	274	Long
Emberizidae					
Chipping Sparrow	6	246	268.5	291	Long
Dark-eyed Junco	16	268	284	290	Short
Field Sparrow	6	292	292	292	Short
Lincoln's Sparrow	21	268	270	291	Long
Savannah Sparrow	23	242	270	271	Long
Song Sparrow	73	245	250	292	Short
Swamp Sparrow	42	245	272	284	Long
White-throated Sparrow	68	243	270	284	Short

warblers and sparrows as migrating either less or farther than the median migration distance for the family (Table 10.1). The final generalized linear model took the same form as the top-performing model, but included only captures of warblers and sparrows. We were unable to explore the effect of relative migratory distance on patch use for vireos and flycatchers due to a low number of captures among species in the short-distance category (flycatchers: $n = 17$, vireos: $n = 29$, Table 10.1).

RESULTS

Over 429 patch-capture days across 24 habitat patches and four sites, we captured 1,678 birds of 34 species in four different families: flycatchers (F. Tyrannidae), vireos (F. Vireonidae), warblers (F. Parulidae), and sparrows (F. Emberizidae, Table 10.1). Daily patch capture totals varied widely through the season by family (Figure 10.1).

Relative Patch Characteristics Vary in Space and Time

Static habitat variation among patches was greater than variation in the mean dynamic variable values among patches (Table 10.2). We transformed both principal components by adding one to make the mean one instead of zero and compared coefficients of variation for all patches. Height-PC ranged from 2.02 times higher (fruit abundance) to 12.8 times higher (shrub leaf greenness) than the dynamic variables (mean = 6.4 times higher). Similarly, cover-PC was more variable among patches than the dynamic variables, ranging from 1.90 to 12.0 times higher (mean = 6.0 times higher). Variation of the dynamic patch variables, however, was as high within patches versus among patches, indicating that patches did not change together in parallel through the season (Table 10.2). Mean within-patch variation ranged from 0.26 (tree leaf greenness) to 1.73

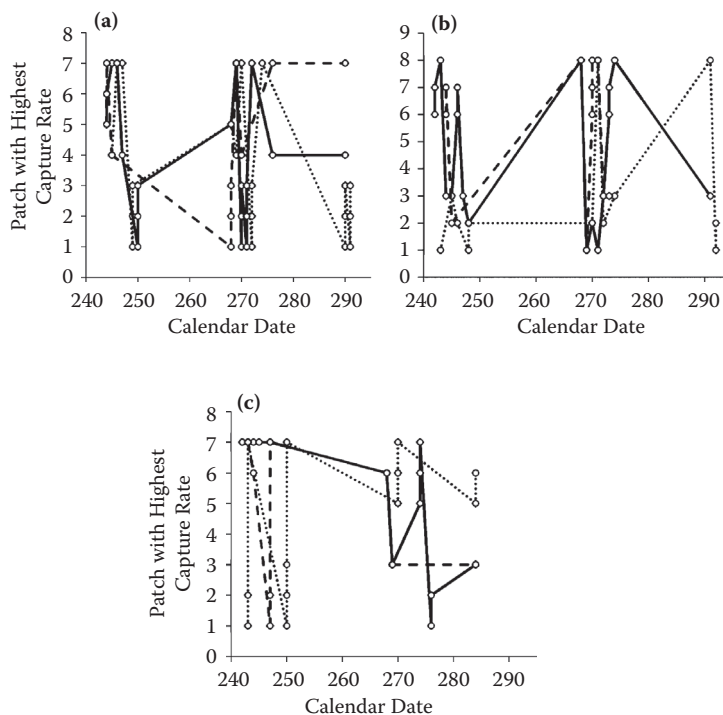


Figure 10.1. Patch capture rate (corrected for effort) variability through time for three migratory stopover sites: (a) Metinic Island, (b) Petit Manan Point, and (c) Mount Desert Island. Each point indicates the numbered patch (the number of patches ranges from eight to nine depending on the site, and number designation within each site is irrespective of patch characteristics) that achieved the highest daily capture rate (corrected for effort) at that site. Vertical lines indicate days when multiple patches achieved the highest daily capture rate, and horizontal lines indicate periods where one patch maintained the highest capture rate through time. The solid lines connect points indicating patches with the highest capture rate for warblers, the dotted lines for sparrows, and the dashed lines for vireos.

TABLE 10.2
Coefficients of variation for patch habitat characteristics
habitat variable.

	Among patches	Within patches
Ripe fruit availability	0.959	0.856
Invertebrate biomass	0.959	0.576
Tree leaf greenness	0.794	0.171
Shrub leaf greenness	0.151	0.261
Soil moisture	0.154	0.202
Height-PC	1.938	
Cover-PC	1.819	

(ripe fruit abundance) times that of among-patch variation (mean = 0.85). Shrub leaf greenness and soil moisture exhibited more within-patch than among-patch variation, while the remaining variables exhibited more among-patch than within-patch variation.

Our top-ranked model predicting family-specific variation in apparent habitat patch use included only the dynamic variables of structure and food ($w_i = 0.95$), controlling for capture effort, stopover site differences, and family-specific migration phenology (Table 10.3). This model strongly outperformed the next best model, which also included the static habitat structure ($\Delta QICu = 5.9$, $w_i = 0.05$) and the null model ($\Delta QICu = 997.6$, $w_i < 0.0001$).

Within the top model we found significant effects of fruit availability ($\chi^2 = 15.4$, $P = 0.004$), invertebrate biomass ($\chi^2 = 11.3$, $P = 0.02$), shrub leaf greenness ($\chi^2 = 10.6$, $P = 0.03$), tree leaf greenness ($\chi^2 = 15.7$, $P = 0.003$), and soil moisture ($\chi^2 = 19.6$, $P = 0.0006$). These patterns, however, varied by taxonomic family (Figure 10.2). Fruit abundance increased capture rates similarly for warblers ($\beta \pm SE = 0.42 \pm 0.09$, $Z = 4.5$, $P < 0.0001$), sparrows (0.37 ± 0.12 , $Z = 3.2$, $P = 0.001$), and vireos (0.30 ± 0.12 , $Z = 2.5$, $P = 0.01$), but was not related to captures of flycatchers ($Z = -0.29$, $P = 0.77$). Invertebrate biomass had a negative effect on capture rates of flycatchers ($\beta \pm SE = -0.35 \pm 0.12$, $Z = -3.0$, $P = 0.003$) and vireos (-0.28 ± 0.10 , $Z = -3.0$, $P = 0.003$), but no effect on warblers ($Z = -0.6$, $P = 0.58$) or sparrows ($Z = 1.3$, $P = 0.20$). Shrub leaf greenness was negatively related to captures of sparrow ($\beta \pm SE = -1.33 \pm 0.49$, $Z = -2.7$, $P = 0.007$) and flycatchers (-1.41 ± 0.64 , $Z = -2.2$, $P = 0.03$), but showed nonsignificant trends with captures of warblers ($Z = -1.8$, $P = 0.07$) and vireos ($Z = 1.9$, $P = 0.06$). Tree leaf greenness was positively related to captures of sparrows ($\beta \pm SE = 0.55 \pm 0.16$, $Z = 3.4$, $P = 0.0006$) and vireos (1.05 ± 0.28 , $Z = 3.7$, $P = 0.0002$), but had no effect on captures of warblers ($Z = 1.8$, $P = 0.07$) or flycatchers ($Z = 1.0$, $P = 0.34$). Captures of sparrows ($\beta \pm SE = 2.40 \pm 0.48$, $Z = 5.0$, $P < 0.0001$), warblers (1.30 ± 0.29 , $Z = 4.5$, $P < 0.0001$), and vireos ($\beta \pm SE = 1.63 \pm 0.69$, $Z = 2.4$, $P = 0.02$) were all

TABLE 10.3
Model selection based on QICu for eight models predicting apparent
habitat patch use as a function of different combinations of dynamic food
availability,^a static habitat structure,^b and dynamic habitat structure^c.

Model	QICu	$\Delta QICu$	w_i
Dynamic structure + dynamic food	848.8	0.0	0.95
Dynamic structure + static structure + dynamic food	854.7	5.9	0.05
Dynamic + static structure	872.6	23.8	<0.0001
Static structure + dynamic food	913.4	64.6	<0.0001
Dynamic food	914.1	65.4	<0.0001
Dynamic structure	968.3	119.5	<0.0001
Static structure	974.3	125.5	<0.0001
Null model	997.6	148.8	<0.0001

^a Fruit abundance and invertebrate biomass.

^b Vegetation height, vegetative cover, and stem density.

^c Leaf greenness and soil moisture.

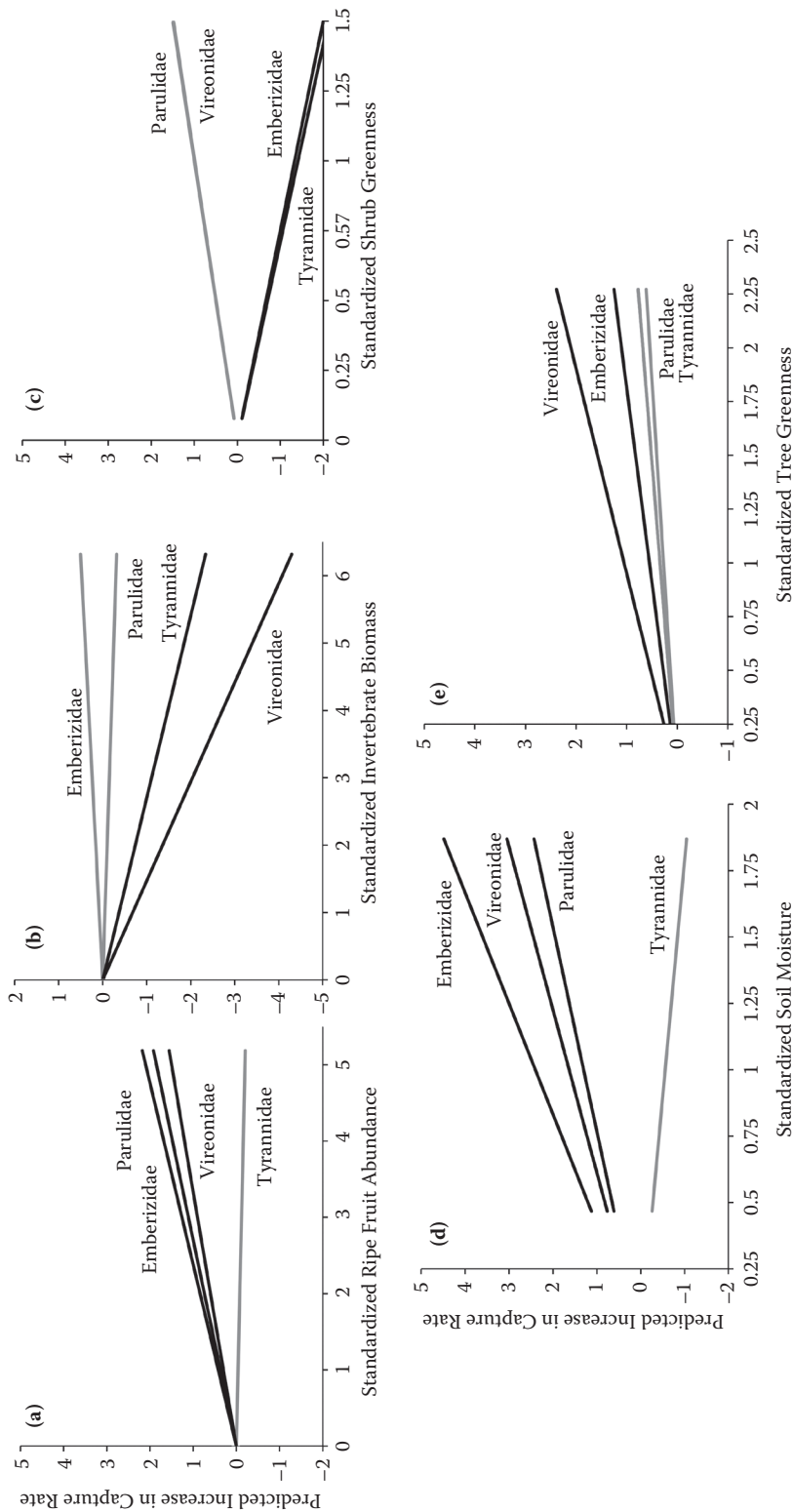


Figure 10.2. The relationships between the predicted values of daily bird captures for each of four taxonomic families and (a) ripe fruit abundance, (b) invertebrate biomass, (c) shrub leaf greenness, (d) soil moisture, and (e) tree leaf greenness within each sampled patch. Black lines are statistically significant, and gray lines are nonsignificant at $\alpha > 0.05$. All variable and predicted values were standardized for direct comparison by dividing by their means and slopes.

strongly positively related to soil moisture, but there was no relationship for this variable with captures of flycatchers ($Z = -0.9$, $P = 0.35$). Controlling for these dynamic resource effects, there were no significant differences in site use ($\chi^2 = 6.5$, $P = 0.09$).

Dynamic Habitat Importance Varies by Migration Distance

The preceding patterns varied within sparrows and warblers as a function of migration distance. Habitat use of long- and short-distance migrants was predicted by dynamic habitat attributes. Habitat use by long-distance migratory warblers (11 species) was explained only by variation in invertebrate biomass ($\beta \pm SE = -0.18 \pm 0.08$, $Z = 2.3$, $P = 0.02$). Habitat use by short-distance migratory warblers (eight species) was explained by fruit abundance ($\beta \pm SE = 0.46 \pm 0.09$, $Z = 5.3$, $P < 0.0001$), shrub leaf greenness (-1.30 ± 0.50 , $Z = -2.7$, $P = 0.008$), and soil moisture (1.84 ± 0.33 , $Z = 6.3$, $P < 0.0001$), but not by invertebrate biomass ($Z = -0.3$, $P = 0.76$).

Among sparrows, all patterns of habitat use were similar for both short- (four species) and long- (four species) distance migrants. Both groups preferred to use patches with higher fruit abundance (long-distance migrants: $\beta \pm SE = 0.48 \pm 0.15$, $Z = 3.3$, $P = 0.001$; short-distance migrants: 0.30 ± 0.10 , $Z = 3.0$, $P = 0.003$) and patches with wetter soils (long-distance: 3.13 ± 0.76 , $Z = 4.1$, $P < 0.0001$; short-distance: 2.20 ± 0.35 , $Z = 6.3$, $P < 0.0001$). Similarly, both groups preferred to use patches with more shrub defoliation (long-distance: $\beta \pm SE = 1.38 \pm 0.60$, $Z = -2.3$, $P = 0.02$; short-distance: -1.30 ± 0.50 , $Z = -2.6$, $P = 0.009$) but less tree defoliation (long-distance: 0.39 ± 0.19 , $Z = 2.1$, $P = 0.04$; short-distance: 0.91 ± 0.18 , $Z = 5.1$, $P < 0.0001$). Neither group, however, altered patch use as a function of insect biomass (long-distance: $Z = 0.7$, $P = 0.48$; short-distance: $Z = 1.5$, $P = 0.14$).

DISCUSSION

Apparent habitat patch use during autumnal migratory stopover was best explained by the variation in local resources. The model with these dynamic predictors outperformed models that included either static patch differences alone (such as woody vegetation structure and height)

or a combination of both static and dynamic habitat characteristics.

All four common families of North American songbirds were sensitive to dynamic resource changes in fruit abundance and invertebrate biomass (although direction of relationships varied), as well as soil moisture and leaf cover, and shifted their use to different patches throughout the migratory cycle at each stopover site (Figure 10.1). Thus, songbirds within each family with similar or identical ecological requirements ranked the quality of available migratory stopover patches differently as autumn progressed. Patch quality ranking, assessed by capture rates, would have remained stable within a given stopover site if high-quality patches consistently outproduced low-quality patches, or if dietary niches were broad enough to allow songbirds to meet their energetic requirements in different habitats. We can reject both of these alternatives. At a larger scale, our results suggest that the costs and benefits of a given stopover site may be temporally dynamic and that songbirds should maximize their fitness by timing their passage to match peak periods of stopover site quality. If the local phenology of fruiting and invertebrate abundance outpaces the plasticity of migrants to find adequate patches within a site, mismatches are possible that will alter the costs of migration, the relative fitness of individuals, and local population dynamics.

The Relative Taxonomic Sensitivity to Dynamic Resources

Habitat use by all four taxonomic families was predicted significantly by both food and nonfood resources, although the strength of relationships within each family varied. Not surprisingly, the importance of different food resources varied by dietary niche. Fruit abundance was positively related to apparent patch use by all but the most specialist invertivore family (flycatchers). Invertebrate biomass, on the other hand, was inversely related to apparent patch use for flycatchers and more generalist invertivores (vireos and long-distance migratory warblers), but had no effect on stopover dynamics of two groups with diets of seeds or larger fruits (short-distance migratory warblers and sparrows). Nonfood resources were also successful in predicting apparent patch use across all taxonomic families—but,

again, the patterns for each family were variable (Figure 10.2).

Nonfood resources exerted a larger effect on apparent patch use than food resources for all taxonomic families. Changes in capture rate for a given change in soil moisture and shrub or tree greenness were two to three times higher on average than a similar change in either of the food resources. Shrub leaf greenness and soil moisture were unusual as the only two variables where within-patch variation was greater than among-patch variation. Thus, even among the dynamic variables, the two variables that exhibited the greatest within-patch variation exhibited the strongest effect on bird patch use. It is clear, therefore, that the efficacy of these variables is not due simply to their ability to differentiate among patches within stopover sites.

In post hoc phylogenetic contrasts, habitat patch use was predicted by different dynamic variables for the long- versus short-distance species of migratory warblers. Patch use for long-distance migrants was related strictly to invertebrate biomass, which is not surprising since these species tend to rely on more invertebrate prey. Patch use for short-distance migrants was predicted by fruit abundance and nonfood resources. There were no apparent differences among sparrows that were comparable to the warblers, and both sparrow migratory groups behaved similarly to the short-distance warbler migrants. The range of migration distances was smaller among sparrows relative to warblers (median migration distance is 3.1 times farther for warblers), and there may not have been enough of a difference between long- and short-distance migrants to alter overall stopover strategy of sparrows. Our observation that habitat patch use in the shortest distance warbler migrants was similar to sparrows suggests that habitat patch use may be more similar among species with more similar migratory distances. More families would need investigation to support the generality of this conclusion. Patch use was predicted by dynamic habitat resources for all of the migratory groups, but we found no support for the increased sensitivity of any group over another, as has been shown among breeding birds in Europe (Both and Visser 2001, Moussus et al. 2011).

Overall, the temporal dynamics of both food and nonfood resources predicted apparent patch use, regardless of variation in the breadth of the dietary niche or migratory distance. All of the

taxa we examined shifted apparent habitat use among patches throughout the migration season, thereby exhibiting behavioral plasticity to changing ecological condition within each site. Plasticity suggests that species benefit from phenological matching and will thus likely exhibit mismatches if temporal variability outpaces their capacity for change.

Alternative Explanations

It is unclear whether any of the specific associations we report here are truly causal or whether temporal variation in these food resources is merely correlated with an unmeasured dynamic resource. Given the negative relationship between invertebrate biomass and apparent patch use by flycatchers and warblers (long-distance migrants only), we suspect the latter explanation. Our invertebrate collection methods were biased against flying insects and may reflect community trade-offs among different guilds of invertebrates, although many other such linkages are possible. The unexpected patterns are unlikely to be due to association among our predictor variables, given their weak relationships to each other (range in $r^2 = 0.002 - 0.13$; mean = 0.06).

Tree leaf greenness was positively associated with sparrow patch use, and conifer forests received the highest greenness scores later in the season when migratory sparrows were passing through our region. A strong association between sparrows and evergreen tree habitats could explain the pattern. The same cannot be said for shrub leaf greenness scores, however, as our study sites possessed no evergreen shrub species. Rare evergreen saplings were included in this layer, but the shrub layer of every patch was heavily dominated by deciduous shrubs.

Despite a lack of evidence that the measured dynamic resources were the habitat characteristics under selection by migrants, we maintain that either they are under selection or they represent an unmeasured dynamic resource. One alternative, however, is that dynamic resources performed better because migration stopover behaviors are themselves dynamic for numerous reasons unrelated to stopover site phenology, including weather, habitat quality on previous stopover sites, point of origin, and breeding season dynamics. We think bias is unlikely for two reasons:

1. All of our dynamic variables were averaged over 8-day periods. While capture rates of individual taxa can vary dramatically from day to day at a given site, our averaged dynamic habitat variables are unlikely to track the daily dynamics of migrant arrival.
2. We only used bird capture data during periods without significant precipitation because our insect collection methods precluded otherwise. Our results do not include periods with environmental conditions that cause migratory "fall-outs," when stopover site use can be over an order of magnitude higher than normal, and captures on a single day could bias an 8-day average.

Our scale of inquiry among families could be obscuring considerable variation in species- or population-level dynamics. Averaging should be more likely to decrease the importance of dynamic resources because within-family niche variation should allow different species to use a given patch for a longer period of time than a single species. We would thus predict that a species-level investigation would have shown greater sensitivity to dynamic resources than what we have shown here with taxonomic families. Two of our study families (Tyrannidae and Vireonidae) were heavily weighted by the capture rates of a single species or species complex and may perform similarly to results for individual species.

Taxonomic families would not obscure the importance of dynamic resources, however, if species within a family possessed distinct niches and migrated through a site at distinct times. What we have interpreted as differential patch use in the face of dynamic resources could simply be different niches within a family being replaced by each other over time. Given the large overlap in passage times of species within each family, however, we do not think this explanation is likely (Table 10.1). More detailed exploration into species-specific niches relative to passage time would be required to test this explanation.

The general patterns reported here, while replicated across four stopover sites within four taxonomic families, represent phenological variation within a single year. The specific relationships may vary with climatic conditions across years. Our primary conclusion—that songbirds match habitat use to temporally variable resources and therefore could experience phenological mismatch—remains even

if the matching we demonstrate here occurs only in some years. The long-standing questions are related to biological relevancy: whether future phenological changes in this region will result in a higher probability of mismatch and what degree of fitness consequences such mismatches might cause.

Incorporating Timing into Habitat Selection Theory

The current paradigm for habitat selection in migratory birds describes a hierarchical process where individuals must first select flyway, then region, then habitat patch (*sensu* Johnson 1980, Hutto 1985), but this approach is focused on spatial and not temporal scales. Timing of migration in birds has been well studied, but the objectives and conclusions of most studies have been largely removed from our understanding of habitat selection. We hope that our results here will suggest that the field needs a more formal inclusion of timing into our understanding of habitat selection in migratory animals.

Timing decisions certainly have the potential to influence habitat selection at almost any spatial scale. For instance, departure time (or even more broadly, departure season) can determine the broad route of migration (Cooke 1910, Myers et al. 1990, Delmore et al. 2012) or patterns of stopover timing (O'Reilly and Wingfield 1995). Our work here suggests that timing may also be important at the spatial scale of a stopover site. More empirical research is needed to understand how timing modifies the traditional hierarchical habitat selection model. It is widely recognized that habitat selection can influence the speed and timing of migration (Lehikoinen and Sparks 2010), but our work suggests that the timing of migration also may affect which local habitats are selected.

CONCLUSIONS

Across the four most common songbird families that migrate along the Gulf of Maine during the autumn, patterns of habitat patch use within stopover sites varied through time. The importance of particular patches to a group of birds varied through the migration season, and patch use was predicted better by within-season changes in invertebrate and fruit availability, soil moisture, and leaf greenness than by habitat characteristics that varied only spatially and not temporally. Our results suggest that songbirds may be sensitive to

changes in the resource phenology of stopover sites in ways that are similar to recently discovered sensitivities to breeding resources. Future research should explicitly test for the population and evolutionary implications of mismatch between migratory timing and stopover resource phenology. Further, the within-season variability in stopover site quality should be considered when making conservation priorities. Successful conservation actions may need to protect patches or networks of patches that maintain sufficiently high habitat quality throughout the migratory season.

ACKNOWLEDGMENTS

Data collection at Metinic Island was overseen and supported by Rebecca Holberton. Thanks to Sara Williams and the Maine Coastal Islands National Wildlife Refuge for access to, financial support of, and logistical assistance with work at Metinic Island and for sharing data collected by refuge staff at Petit Manan Point. Thanks to Bruce Connery, Bik Wheeler, and Acadia National Park for similar collaboration and support of work on Mount Desert Island and to John Anderson, the College of the Atlantic, and the Nature Conservancy for work on Great Duck Island. Last, thanks to Abe Miller-Rushing for helpful comments on an initial draft of this chapter. The project was funded by grants from the US Fish and Wildlife Service, the National Park Service, the National Institute of Food and Agriculture, and the University of Maine.

LITERATURE CITED

- Alerstam, T., and A. Hedenström. 1998. The development of bird migration theory. *Journal of Avian Biology* 29:343–369.
- Baker, A. J., P. M. González, T. Piersma, L. J. Niles, I. de L. S. do Nascimento, P. W. Atkinson, N. A. Clark, C. D. T. Minton, M. K. Peck, and G. Aarts. 2004. Rapid population decline in Red Knots: fitness consequences of decreased refueling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society of London B* 271:875–882.
- Balbontín, J., A. P. Møller, I. G. Hermosell, A. Marzal, M. Reviriego, and F. de Lope. 2009. Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird. *Journal of Animal Ecology* 78:981–989.
- Berthold, P. 1975. Migration: control and metabolic physiology. Pp. 77–128 in D. S. Farner and J. R. King (editors), *Avian biology*. Academic Press, New York, NY.
- Blem, C. R. 1980. The energetics of migration. Pp. 59–113 in S. A. Gauthreaux (editor), *Animal migration, orientation, and navigation*. Academic Press, New York, NY.
- Borgmann, K. L., S. F. Pearson, D. J. Levey, and C. H. Greenberg. 2004. Wintering Yellow-rumped Warblers (*Dendroica coronata*) track manipulated abundance of *Myrica cerifera* fruits. *Auk* 121:74–87.
- Both, C. 2010a. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. *Current Biology* 20:243–248.
- Both, C. 2010b. Food availability, mistiming, and climatic change. Pp. 129–147 in A. P. Møller, W. Fiedler, and P. Berthold (editors), *Effects of climate change on birds*. Oxford University Press, New York, NY.
- Both, C., S. Bouwhuys, C. M. Lessells, and M. E. Visser. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441:81–83.
- Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298.
- Both, C., and M. E. Visser. 2005. The effect of climate change on the correlation between avian life-history traits. *Global Change Biology* 11:1606–1613.
- Castro, G., and J. P. Myers. 1993. Shorebird predation on eggs of horseshoe crabs during spring stopover on Delaware Bay. *Auk* 110:927–930.
- Cooke, W. W. 1910. Distribution and migration of North American shorebirds. Pp. 100 in US Dept. of Agriculture, *Biological Survey Bulletin* 35.
- Delmore, K. E., J. W. Fox, and D. E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas revealed using light-level geolocators. *Proceedings of the Royal Society of London B* 279:4582–4589.
- Drent, R. H. 2006. The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. *Ardea* 94:305–322.
- Erickson, L., K. McGowan, H. Powell, M. Savoca, and C. Sedgwick. [online]. 2011. All about birds: bird guide. <<http://www.allaboutbirds.com/guide>>
- Hardin, J. W., and J. M. Hilbe. 2007. Generalized linear models and extensions. Stata Press, College Station, TX.
- Hüppop, O., and K. Hüppop. 2003. North Atlantic oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London B* 270:233–240.
- Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pp. 455–476 in M. L. Cody (editor), *Habitat selection in birds*. Academic Press, New York, NY.

- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Lack, D. L. 1950. The breeding seasons of European birds. *Ibis* 92:288–316.
- Lack, D. L. 1968. Ecological adaptations for breeding in birds. Methuen, London, UK.
- Lank, D. B., R. W. Butler, J. Ireland, and R. C. Ydenberg. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103:303–319.
- Lehikoinen, E., and T. H. Sparks. 2010. Changes in migration. Pp. 89–112 in A. P. Møller, W. Fiedler, and P. Berthold (editors), *Effects of climate change on birds*. Oxford University Press, New York, NY.
- Marra, P. P., C. M. Francis, R. S. Mulvihill, and F. R. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. *Oecologia* 142:307–315.
- McKinney, A. M., P. J. CaraDonna, D. W. Inouye, B. Barr, C. D. Bertelsen, and N. M. Waser. 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology* 93:1987–1993.
- McLaughlin, J. F., J. J. Hellmann, C. L. Boggs, and P. R. Ehrlich. 2002. Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences of the USA* 99:6070–6074.
- Møller, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* 35:115–122.
- Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences of the USA* 105:16195–16200.
- Moussus, J.-P., J. Clavel, F. Jiguet, and R. Julliard. 2011. Which are the phenologically flexible species? A case study with common passerine birds. *Oikos* 120:991–998.
- Myers, J. P., A. M. Sallaberry, E. Ortiz, G. Castro, L. G. Gordon, J. L. Maron, C. T. Schick, E. Tabilo, P. Antas, and T. Below. 1990. Migration routes of New World Sanderlings (*Calidris alba*). *Auk* 107:172–180.
- Newton, I. 2007. Weather-related mass-mortality events in migrants. *Ibis* 149:453–467.
- O'Reilly, K. M., and J. C. Wingfield. 1995. Spring and autumn migration in Arctic shorebirds: same distance, different strategies. *American Zoologist* 35:222–233.
- Pan, W. 2001. Akaike's information criterion in generalized estimating equations. *Biometrics* 57:120–125.
- Parrish, J. 1997. Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. *Condor* 99:681–697.
- Place, A. R., and E. W. Stiles. 1992. Living off the wax of the land: bayberries and Yellow-rumped Warblers. *Auk* 109:334–345.
- Rubolini, D., A. Møller, K. Rainio, and E. Lehikoinen. 2007. Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among European bird species. *Climate Research* 35:135–146.
- Sanz, J. J., J. Potti, J. Moreno, S. Merino, and O. Frias. 2003. Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Global Change Biology* 9:461–472.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Smith, A. D., and S. R. McWilliams. 2009. Protocol for the rapid assessment of fruit abundance on New England Wildlife Refuges. University of Rhode Island, Kingston, RI.
- Sokolov, L. V., M. Y. Markovets, A. P. Shapoval, and Y. G. Morozov. 1998. Long-term trends in the timing of spring migration of passerines on the Courish Spit of the Baltic Sea. *Avian Ecology and Behaviour* 1:1–21.
- Streby, H. M., S. M. Peterson, and D. E. Andersen. 2011. Invertebrate availability and vegetation characteristics explain use of nonnesting cover types by mature-forest songbirds during the postfledging period. *Journal of Field Ornithology* 82:406–414.
- Suomala, R. W., S. R. Morris, K. J. Babbitt, and T. D. Lee. 2010. Migrant songbird species distribution and habitat use during stopover on two islands in the Gulf of Maine. *Wilson Journal of Ornithology* 122:725–737.
- Tietz, J. R., and M. D. Johnson. 2007. Stopover ecology and habitat selection of juvenile Swainson's Thrushes during fall migration along the northern California coast. *Condor* 109:795–807.
- Tsipoura, N., and J. Burger. 1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor* 101:635–644.
- Verboven, N., J. M. Tinbergen, and S. Verhulst. 2001. Food, reproductive success and multiple breeding in the Great Tit, *Parus major*. *Ardea* 89:387–406.