



AN 18-YEAR STUDY OF MIGRATION AND STOPOVER ECOLOGY OF TENNESSEE
WARBLERS IN KALAMAZOO COUNTY, MICHIGAN

Author(s): SARA R. MORRIS, AMANDA S. ANDRIJEVIĆ, RYANNE SULLIVAN, RICHARD
S. KEITH, BRENDA S. KEITH and H. DAVID SHEETS

Source: *The Wilson Journal of Ornithology*, March 2013, Vol. 125, No. 1 (March 2013),
pp. 70-78

Published by: Wilson Ornithological Society

Stable URL: <https://www.jstor.org/stable/41932836>

REFERENCES

Linked references are available on JSTOR for this article:

[https://www.jstor.org/stable/41932836?seq=1&cid=pdf-
reference#references_tab_contents](https://www.jstor.org/stable/41932836?seq=1&cid=pdf-reference#references_tab_contents)

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Wilson Ornithological Society is collaborating with JSTOR to digitize, preserve and extend
access to *The Wilson Journal of Ornithology*

JSTOR

AN 18-YEAR STUDY OF MIGRATION AND STOPOVER ECOLOGY OF TENNESSEE WARBLERS IN KALAMAZOO COUNTY, MICHIGAN

SARA R. MORRIS,^{1,4} AMANDA S. ANDRIJEVIĆ,¹ RYANNE SULLIVAN,¹
RICHARD S. KEITH,² BRENDA S. KEITH,² AND H. DAVID SHEETS³

ABSTRACT.—Nearctic-neotropical passerines may spend up to one-third of the year in migration. Stopover sites have a critical role in providing migrant passerines with areas to rest and replenish fat stores. We characterized the stopover ecology of the Tennessee Warbler (*Oreothlypis peregrina*) at an inland site in Vicksburg, Michigan, using data from 4,607 warblers captured between 1990 and 2007. The recapture rate ranged from 1.6 to 12.1% annually and recaptured migrants averaged small but significant mass gains. Estimates of mass change using regression of mass on time of capture also suggested mass increases at this site. Recapture rate and mass gain estimated by regression varied significantly across the 18 years of study, although stopover length and mass change among recaptured individuals did not. Adult (after hatching year, AHY) warblers in active flight feather molt had an average lower mass and were four times more likely to be recaptured than non-molting adults. Over 95% of birds captured were hatching year (HY). The average condition and mass gains estimated by regression of HY warblers were lower than that of AHYs, but recapture rate, stopover length, and mass gains by recaptured individuals did not differ between the two age groups. The high number of captures and mass gains demonstrate the value of this site for fall migrant Tennessee Warblers. The annual differences in recapture rate and mass gains reported in this study suggest that several years of data may be needed to develop an accurate assessment of the typical use of a stopover site by migrants. Received 8 October 2008. Accepted 1 October 2012.

Key words: age-related migration, annual variation, fall migration, inland stopover, mass change, molt, *Oreothlypis peregrina*.

Nearctic-neotropical migrants spend up to a third of each year migrating, using stopover sites to rest and/or replenish their fat stores along the way (Mehlman et al. 2005). Migrants are particularly vulnerable during the migratory period, because they encounter unfamiliar habitats, increased predation risk, unpredictable food resources, and the possibility of inclement weather. Sillett and Holmes (2002) estimated that 85% of annual mortality of Black-throated Blue Warblers (*Setophaga caerulescens*) occurred during migratory periods. It is important to study the range of ecological conditions at stopover sites to protect and conserve migratory birds (Mehlman et al. 2005). Data from numerous sites allow comparison of patterns of migrant abundance and mass gains at different geographic locations and in different habitats. Both coastal and inland routes are used by passerines during migration, but most stopover studies have been at coastal sites (e.g., Moore and Kerlinger 1987, Morris et al. 1996, Bonter et al. 2007). Studies at inland sites have often been limited by low capture and/or recapture rates.

Mehlman et al. (2005) indicated the need for data on both spatial and temporal variation in stopover site use by migrants, as well as intraspecific differences in migration and stopover ecology between demographic cohorts. Few studies have examined annual differences in stopover ecology. Dunn (2000) found substantial annual variation in mass gain by Magnolia Warblers (*S. magnolia*) at Long Point, Ontario, Canada. Morris et al. (2003) described significant annual variation in the initial mass of captured birds, stopover length among females, and mass gains by both males and females in a study of the spring migration of Common Yellowthroats (*Geothlypis trichas*). Only limited information is available about potential age-related differences in stopover ecology of migrants, and this information appears to be species- and location-specific. Jones et al. (2002) studied 52 migrant species at Long Point, Ontario, Canada, and found that adults (AHY, after hatching year, hereafter used interchangeably with adult) had slightly higher mass and higher fat scores than young (HY, hatching year, hereafter used interchangeably with young), but that mean rate of mass gain did not generally differ between age classes. Woodrey and Moore (1997) studied six species during autumn migration on the coast of Alabama and reported that adults of three species were in better condition than young of the year, but that

¹ Department of Biology, Canisius College, Buffalo, NY 14208, USA.

² Kalamazoo Valley Bird Observatory, Kalamazoo Nature Center, Kalamazoo, MI 49009, USA.

³ Department of Physics, Canisius College, Buffalo, NY 14208, USA.

⁴ Corresponding author; e-mail: morriss@canisius.edu

likelihood of staying more than 1 day and rate of mass change did not differ between the two age groups for any of the six species. However, Wang et al. (1998) found that young Wilson's Warblers (*Cardellina pusilla*) had lower fat scores, higher recapture rates, and higher rates of mass gain than adults during autumn migration at an inland site in New Mexico. Studies in the Palearctic region also have found differences in stopover length (Ellegren 1991, Rguibi-Idrissi et al. 2003) and patterns of mass gain (Ellegren 1991) between young and adult migrants.

The Tennessee Warbler (*Oreothlypis peregrina*) is a widespread Nearctic-neotropical migrant with only limited information available about its migration and stopover ecology. The species' breeding range extends from southern Alaska through the boreal forests of Canada to the northernmost parts of the United States (Rimmer and McFarland 1998). Fall migration is protracted and may begin during July as adults begin moving toward non-breeding areas in southern Mexico to northwestern South America. The main fall migration routes appear to be inland (Rimmer and McFarland 1998). Tennessee Warblers are unusual in that southward migration often occurs simultaneously with prebasic flight-feather molt (Rimmer and McFarland 1998), a strategy described for only a few species of migrants (e.g., Voelker and Rohwer 1998). The impacts of this molt on migration and stopover ecology of Tennessee Warblers have not been well-documented, although if birds remain in an area to molt, their stopover ecology should be expected to differ.

Our objectives were to: (1) characterize the autumn migratory patterns and stopover ecology of Tennessee Warblers at an inland stopover site in Kalamazoo, Michigan, by recording timing of passage, condition of migrants, recapture rates, stopover lengths, and mass gains at this site; (2) examine potential annual variation in migratory patterns and stopover ecology; (3) investigate potential age-related differences in migratory patterns and stopover characteristics at this site; and (4) compare the migration timing, condition, and recapture rates of adults in active molt with those of non-molting birds to examine the molt ecology of this species during migration.

METHODS

Study Site.—We used banding data for Tennessee Warblers from 1990 to 2007 from the Pitsfield

banding station (42° 10' N, 85° 30' W) in Vicksburg, Michigan. The habitat surrounding the Pitsfield Banding Station is late successional woodland that has been maintained near the netting area. Trees have been cut near the nets to maintain a height of <10 m around the net lanes. Also, there has been an effort to control invasive species, including autumn olive (*Elaeagnus umbellata*). Native shrubs were planted in place of non-native shrubs. Habitats surrounding the banding station are mainly wooded but also have open fields, mature forest, and wetlands. Grasses, forbs, and scattered willows (*Salix* spp.) and eastern cottonwoods (*Populus deltoides*) are characteristic of the open habitat. The woodland habitat is a mix of aspen (*Populus* spp.), black locust (*Robinia pseudoacacia*), chokecherry (*Prunus virginiana*), and eastern cottonwoods. The mature forest contains mainly established black oak (*Quercus velutina*), white oak (*Q. alba*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), and black cherry (*Prunus serotina*).

Banding and Data Collection.—We captured and banded fall migrants between July and November from 1990 to 2007; we banded once a week from July to mid-August and daily from mid-August to early November during favorable weather. We operated 30 mist nets (29 12-m nets and one 6-m net, all 30-mm mesh) for 6 hrs beginning at sunrise; nets were checked at least once each hour. We banded all birds with a uniquely numbered USGS band and collected all data for both captures and recaptures. We classified age of individual Tennessee Warblers as either young (hatching year, HY) or adult (after hatching year, AHY) based primarily on skull pneumatization. Sex of young in this species cannot be reliably ascertained by external examination (Pyle 1997). We distinguished males and females only among adults. We measured wing chord to the nearest 1 mm, subcutaneous fat score (furcular fat scored from 0–5), and mass to the nearest 0.1 g for each bird. We used MAPS protocols (DeSante et al. 2008) to evaluate body molt (scored from 0 = none to 4 = heavy) and flight feather molt (none, symmetric, adventitious) for birds that were in active molt. We generally recorded when birds were in active molt, but lack of molt was only occasionally recorded; thus our sample of known birds that were not molting is lower than the actual number that were not in active molt.

Statistical Analysis.—We calculated condition index = mass*100/wing chord to standardize for body size, following Winker (1995). Recapture rate refers to the percentage of birds that were recaptured at least 1 day after initial capture in this study. We computed minimum stopover length = date of final capture minus date of initial capture for recaptured individuals following Cherry (1982) and mass change = final mass minus initial mass. We also computed percent mass change = mass change*100/initial mass.

We used SYSTAT Version 11 for all statistical tests with $\alpha = 0.05$. We compared date of capture, initial mass, wing chord, condition index, mass change of recaptured individuals, and percent mass change of recaptured individuals using two-sample *t*-tests between HY and AHY classes to investigate potential age-related differences. We compared these variables across years using one-way analysis of variance and tested for trends using linear regression on the annual averages. We also tested date of first capture and initial mass of molting and non-molting birds using two-sample *t*-tests. We used paired *t*-tests comparing initial mass to final mass to examine mass changes within an age group. We used Chi-square tests to compare recapture rates between age categories, across years, and between molting and non-molting birds. We used a Mann-Whitney *U*-test to compare minimum stopover lengths between age categories and a Kruskal-Wallis one-way analysis of variance to compare across years. Mass changes were also estimated using regression models because fewer than 5% of migrants were recaptured. We regressed mass on time of capture (hour after sunrise) with wing chord as a covariate to estimate annual rates of mass change, after testing for an interaction between wing chord and time. The interaction term was not significant in any of the 18 years, and regressions were conducted without the interaction term to provide hourly rates of mass change (the slope of the time variable). Additional general linear models were conducted with age or year as categorical variables to test for differences in mass change between ages or among years. Significance of these effects (hourly mass gain, age, and year) was based on *t*-tests of partial regression coefficients within the models.

RESULTS

We captured 4,607 Tennessee Warblers and recaptured 439 (9.4%) individuals within the

same season during the 18-year study. Annual numbers of captures ranged from 62 to 713 and annual recapture percentage ranged from 1.6 to 12.1% (Table 1). Three birds returned in subsequent years, and one was captured in 3 different years. Average mass increases among recaptured individuals were small (0.11 ± 0.54 g) but significantly different from mass at original capture ($t_{367} = 4.08$, $P < 0.001$). The average percent mass gain was significant among these individuals ($1.40 \pm 5.95\%$; $t_{367} = 4.52$, $P < 0.001$). Regression estimates of mass change also indicated significant gains at this site (mass gain rate = 0.077 ± 0.005 g/hr; $P < 0.001$). This rate translated to 0.85% gain/hr using average lean mass (9.053 ± 0.611 g, $n = 3,216$).

Comparison of Age Classes.—All but one of the warblers captured could be assigned to a specific age category allowing comparison of migration and stopover ecology between young and adult age classes. Across all years, 95.1% of individuals captured at this inland site were HY (Table 1). The percent HY varied significantly across years ($\chi^2_{17} = 56.7$, $P < 0.001$); this difference was not correlated with the total number of Tennessee Warblers captured annually (Pearson Correlation = 0.19, $P = 0.46$). The average mass of adults was 0.47 g higher than that of young (Table 2). A size-corrected condition index of the birds was significantly higher for adults. Recapture rates and stopover lengths did not differ between young and adult Tennessee Warblers, but stopover lengths varied widely and sample sizes of adults were small (Table 2). Some adults captured at this site were in active molt, and we also compared recapture rates and stopover lengths between young and adults excluding molting individuals. These tests yielded similar results of no difference in recapture rate ($\chi^2_1 = 1.85$, $P = 0.17$) or stopover length (Mann-Whitney $U = 1,786.5$, $P = 0.63$) between age classes.

Mass changes calculated from recaptured individuals and estimated by regression both indicated that young and adults gained mass at this site. Both young and adults that were recaptured at least 1 day after initial capture gained mass between captures (Table 2; HY: $t_{352} = 3.64$, $P < 0.001$; AHY: $t_{14} = 2.17$, $P = 0.048$). Regression models confirmed mass gains by both age classes (Fig. 1; HY: 0.077 ± 0.005 g/hr, $P < 0.001$; AHY: 0.101 ± 0.027 g/hr, $P < 0.001$). Mass gains calculated from recaptured individuals did not differ significantly between the two age

TABLE 1. Migration timing and stopover ecology variables for Tennessee Warblers banded in Vicksburg, Michigan, during autumn 1990 to 2007. Mean date of capture, recapture rate, and mass change estimated by regression varied significantly across years, but minimum stopover length and mass change by recaptured birds did not vary across years. * ≤0.05, ** ≤0.01, *** ≤0.001.

Year	n	Mean capture date	Hatch year %	Recapture rate % (n) ^a	Minimum stopover length ^b	Mass change recapture %	Mass change regression ^c g/hr	Mass change regression ^e %/hr
1990	155	10 September ± 11	96.1	4.5 (7)	5.1 ± 2.5	-2.8 ± 2.4*	0.067 ± 0.020**	0.71
1991	300	8 September ± 14	91.0	4.3 (13)	6.1 ± 3.1	1.2 ± 3.9	0.074 ± 0.014***	0.81
1992	62	15 September ± 12	95.2	1.6 (1)	23.0	3.1	0.094 ± 0.046*	1.03
1993	146	12 September ± 10	93.8	8.9 (13)	7.2 ± 5.3	0.2 ± 6.0	0.064 ± 0.020**	0.68
1994	151	10 September ± 10	96.7	6.6 (10)	4.3 ± 3.3	-1.6 ± 4.9	0.111 ± 0.036**	1.20
1995	259	15 September ± 11	96.1	5.4 (14)	6.1 ± 6.6	1.1 ± 9.5	0.098 ± 0.014***	1.05
1996	713	20 September ± 10	97.8	8.7 (62)	4.3 ± 3.4	1.9 ± 7.2*	0.076 ± 0.012***	0.83
1997	264	26 September ± 15	95.1	2.7 (7)	6.7 ± 6.6	0.9 ± 6.3	0.045 ± 0.027	0.50
1998	216	3 September ± 12	96.3	8.3 (18)	6.9 ± 4.6	1.0 ± 4.0	0.113 ± 0.024***	1.25
1999	196	11 September ± 12	97.5	10.2 (20)	4.4 ± 3.3	2.7 ± 3.8**	0.076 ± 0.030*	0.84
2000	135	14 September ± 12	95.6	9.6 (13)	6.3 ± 6.7	3.1 ± 6.1	0.074 ± 0.039	0.83
2001	210	11 September ± 13	96.2	10.5 (22)	4.7 ± 5.1	-0.3 ± 5.3	0.096 ± 0.021***	1.04
2002	419	13 September ± 11	96.2	9.5 (40)	6.1 ± 4.5	0.7 ± 5.6	0.123 ± 0.022***	1.37
2003	500	9 September ± 13	93.4	9.2 (46)	6.4 ± 6.1	1.7 ± 4.9*	0.093 ± 0.016***	1.04
2004	199	15 September ± 9	91.0	12.1 (24)	5.6 ± 4.6	1.5 ± 6.2	0.118 ± 0.022***	1.31
2005	406	10 September ± 11	96.1	9.1 (37)	6.6 ± 7.2	2.4 ± 6.6*	0.053 ± 0.026*	0.61
2006	184	8 September ± 11	88.6	8.7 (16)	5.9 ± 4.8	2.8 ± 7.0	0.075 ± 0.028**	0.80
2007	96	11 September ± 14	94.8	7.3 (7)	4.6 ± 2.1	2.3 ± 3.3	0.052 ± 0.035	0.50

^a Recapture rate was calculated as the percentage of individuals captured at least 1 day after initial capture. The number of individuals recaptured provides the sample size for stopover length and recapture mass gain.

^b Minimum stopover was calculated as the number of days between final capture and initial capture.

^c Mass change for recaptured migrants was calculated as percent change = (final mass minus initial mass)*100/initial mass.

^d Mass change was estimated using the slope of the regression of mass on time of capture (hour after sunrise).

^e Hourly percent gains were calculated using mass change estimates from regressions and fat free mass (average mass of all warblers with fat score = 0).

TABLE 2. Comparison of migration timing and stopover ecology of adult (AHY) and young (HY) Tennessee Warblers banded in Vicksburg, Michigan, from 1990 to 2007 (all years combined). Adults were captured earlier and in better condition (based on mass and condition index) than young. Recapture rates, stopover length, and mass change did not differ between the two age classes.

	Hatch year (HY)	After hatch year (AHY)	Test statistic	P
n	4,385	225		
Mean capture date	13 September	7 September	t _{231,9} = 4.2	<0.001
Wing chord, mm	61.9 ± 2.2	62.3 ± 2.8	t _{237,6} = 1.8	0.067
Average mass, g	9.16 ± 0.72	9.63 ± 0.90	t _{238,9} = 7.8	<0.001
Condition index ^a	14.79 ± 1.12	15.47 ± 1.36	t _{238,7} = 7.3	<0.001
Recapture rate, # ^b	8.1% (354)	6.7% (15)	χ ² ₁ = 0.6	0.44
Stopover length, d ^c	5.6 ± 4.7	8.7 ± 10.9	U = 2,874	0.59
Mass change— recaptures, g ^d	0.10 ± 0.53	0.41 ± 0.73	t _{14,6} = 1.6	0.13
Mass change— recaptures, % ^e	1.29 ± 5.82	4.47 ± 8.02	t _{14,6} = 1.5	0.15
Mass change— regression, g/hr ^f	0.077 ± 0.005	0.100 ± 0.028	F _{1,4580} = 84.9	<0.001

^a Condition index was calculated as condition = mass*100/wing chord following Winker (1995).

^b Recapture rate was calculated as the percentage of individuals captured at least 1 day after initial capture.

^c Minimum stopover was calculated as the number of days between final capture and initial capture.

^d Mass change for recaptured migrants was calculated as change = final mass minus initial mass.

^e Mass change for recaptured migrants was calculated as percent change = (final mass minus initial mass)*100/initial mass.

^f Mass change was estimated using the slope of the regression of mass on time of capture (hour after sunrise).

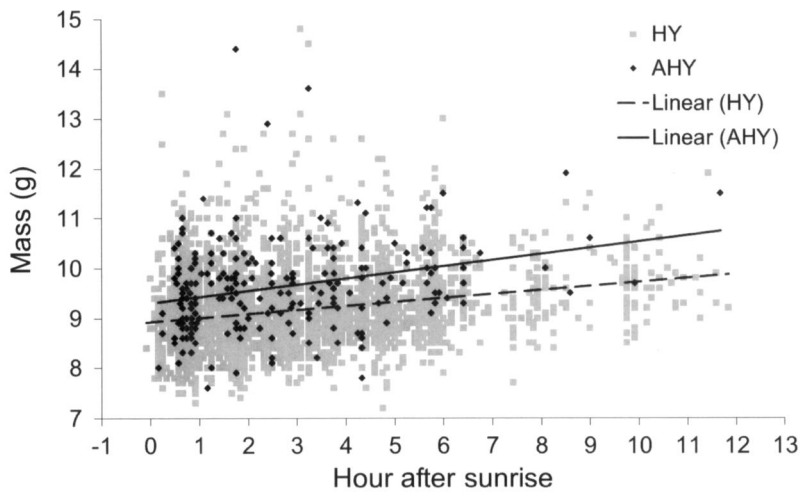


FIG. 1. Regression of mass on time of capture (hour after sunrise) suggested mass gains by both young (HY) and adult (AHY) Tennessee Warblers. Banding data from the Pitsfield banding station in Vicksburg, Michigan, were pooled between 1990 and 2007.

groups but mass gains estimated by regression were higher among adults (Table 2). We obtained the same results when we performed these tests excluding adults in active molt.

Molt.—Symmetrical flight feather molt was noted for 23 of 51 adults whose molt status was recorded. Molting birds were captured between 22 July and 20 September ($\bar{x} = 17 \text{ Aug} \pm 16.0 \text{ days}$), 5 days earlier than the average arrival date of non-molting birds ($\bar{x} = 22 \text{ Aug} \pm 22.8 \text{ days}$): this difference was not significant ($t_{47,9} = 0.954, P = 0.35$). The mass of birds undergoing flight feather molt was slightly, but significantly, lower than that of non-molting birds (molting: $9.60 \pm 0.42 \text{ g}$; non-molting: $10.15 \pm 1.11 \text{ g}$; $t_{36} = 2.39, P = 0.022$). The recapture rate of molting warblers (17.4%) was more than four times higher than the recapture rate of non-molting warblers (3.6%); this difference was not significant ($\chi^2_1 = 2.7, P = 0.099$).

Annual Variation for All Birds.—Mean date of capture varied across years ($F_{17,4593} = 61.2, P < 0.001$), ranging from 3 September in 1998 to 26 September in 1997 (Table 1); however, regression analysis did not find a trend toward earlier or later captures across years ($F_{1,17} = 0.2, P = 0.63$). Annual recapture rates also varied ($\chi^2_{17} = 36.25, P = 0.004$), and linear regression indicated they increased over time ($F_{1,16} = 10.6, P = 0.005$). Stopover length did not differ across years (Kruskal-Wallis statistic = 19.3, $P = 0.31$) even after removing 1992, a year in which we

recaptured one bird 23 days after initial capture. Average mass changes among recaptured individuals were significant in five of the 18 years of study; recaptured migrants gained mass in four of these years while migrants lost mass in the fifth. Regression models estimated that migrants experienced significant mass changes at this site during 15 of the 18 years with positive slopes in all 15 years that indicated migrants gained mass. We found no annual variation in percent mass change among recaptured individuals ($F_{17,350} = 0.80, P = 0.69$), although regression-based mass estimates indicated a significant effect of year on rate of mass gain ($F_{17,4584} = 3.97, P < 0.001$).

DISCUSSION

A key indicator of stopover habitat quality is the ability of migrants to gain mass at a site (Simons et al. 2000, Dunn 2001, Bonter et al. 2007, Smith and McWilliams 2010). Two measures of mass gains by migrant Tennessee Warblers suggest the Pitsfield site has appropriate resources to provide fuel for continued southward migration in this species. Regression models indicated significant mass gains by migrants in 15 of 18 years (Table 1). Recaptured individuals pooled across all years also experienced small but significant mass gains between first and final capture; recaptured migrants gained mass during 15 years of the study, although these gains were significant in only 4 years. The rates of mass gain we estimated from regression are similar to or

higher than those documented in other studies. Dunn (2002) reported autumn mass gains by Tennessee Warblers ranging from 0.09 to 1.21%/hr from seven migration banding sites; only two of these sites reported greater average gains than our average of 0.85%/hr. Our estimates were higher than those of Winker et al. (1992) for Tennessee Warblers, who estimated mean mass gains of 0.02 g/day from regression models and mass losses of 0.07 g/day by recaptured birds in Minnesota. Bonter et al. (2007) studied 21 fall migrant species and reported an average gain of 0.80%/hr at a stopover site south of Lake Ontario in New York; individual species' averages ranged from 0.22 to 1.58%/hr. Seewagen and Slayton (2008) reported fall mass changes ranging from -4.46 to 1.28%/hr in their study of eight species captured in a New York City park.

The capture of large numbers of migrant Tennessee Warblers each fall at the Pitsfield banding station demonstrates regular use of this area in southwestern Michigan by this species. The high number of annual captures allowed comparison of migration and stopover ecology across the years of our study. The average date of capture was generally in the second week of September. The average date of capture varied significantly across years, but it did not shift directionally, either earlier or later. Recapture rates also varied significantly across years, and were generally low, averaging only 7.6%. Autumn migration stopover recapture rates for Tennessee Warblers was 17.5% and other warbler species' recapture rates ranged from 2.9 to 22.2% on the Atlantic Coast (Morris et al. 1996). Stopover rates during spring migration on the Gulf of Mexico Coast are often more than twice that high (Moore and Kerlinger 1987). Stopover length and mass change of recaptured individuals did not differ among years despite differences in average date of capture, percentage of birds recaptured, and mass change estimated by regression. The lack of annual differences in recapture rate and stopover length may reflect low sample sizes. Differences between years suggest the need for several years of data to develop an accurate assessment of the typical use of a stopover site by migrants as noted by other authors (e.g., Morris et al. 1996, Dunn 2000, Calvert et al. 2009). Migration conditions may vary in time and a limited sample may not reflect a site's long-term use by migrants.

The extremely high proportion of young Tennessee Warblers at our inland site was unexpected as it conformed to age-related patterns

among migrant warblers at stopover sites along the Atlantic Coast where young often comprise >90% of migrants (e.g., Murray 1966, Ralph 1981, Morris et al. 1996) and was higher than most other studies of this species. Dunn and Nol (1980) found much lower percents of young Tennessee Warblers at most of their coastal, inland, and nocturnal kill sites in northeastern North America (ranging from 36.9 to 98.7%). Previous studies at Atlantic Coast stopover sites have shown much lower proportions of young among Tennessee Warblers than among most other transient warbler species in New Jersey (69.5%; Murray 1966) and southern Maine (75.5%; Morris et al. 1996), and the proportion of young on the coast was much lower than in our study. The percentage of young Tennessee Warblers in our study was higher than Tennessee Warblers (92%) and other warbler species studied in South Dakota (range = 72.7–93.8%; Dean et al. 2004) and warblers in coastal Alabama (range = 69–76%; Woodrey and Moore 1997), both mid-continental sites. The high percentage of young was initially described along the Atlantic Coast and has been called the 'coastal effect'. The coastal effect has been investigated along the Atlantic Coast (e.g., Murray 1966; Ralph 1978, 1981), the edge of the Great Lakes (Dunn and Nol 1980), and along the edge of the migratory route (Dean et al. 2004). High numbers of young have been hypothesized to reflect a tendency for this age class to migrate along the coast (or edge of the migratory route) as opposed to inland routes due to inexperience or poor navigation (Ralph 1978, 1981), a hesitance of young to fly over water or to reorient if they find themselves over water at the end of a migratory flight (Murray 1966, Dunn and Nol 1980), or because of appropriate stopover habitats at coastal sites (Dean et al. 2004). Our study site is surrounded by Lakes Superior, Michigan, Huron, and Erie, and it is possible these large lakes affect regional migration patterns by acting as ecological barriers that funnel birds, particularly young, west and east of the lakes. The proximity of Pitsfield to the southern border of the species' breeding areas may have contributed to the high percent of young; the nearest breeding populations are ~400 km north of our field site. Adult Tennessee Warblers may go through molt migration and may leave early or move rapidly south, while fledgling dispersal shortly after the breeding season and before their migration may contribute to the high proportion of hatch-year

birds during daily banding in September and October. Dunn et al. (2004) found much lower rates of young Magnolia Warbler and Yellow-rumped Warblers (*S. coronata*) at the same site in Michigan, further suggesting that Tennessee Warblers are using this site differently than other warblers.

Our study detected few age-related differences in the stopover ecology of Tennessee Warblers. Adults were on average heavier, had a higher condition index, and had higher mass gains estimated by regression than young, but we found no differences in recapture rate, stopover length, or mass gains by recaptured birds between age groups. When we excluded adults that were in active molt from the analyses, we still did not find a difference in recapture rate, stopover length, or mass gains of recaptured birds between age groups. Our results are similar to those of Woodrey and Moore (1997) who studied several species of migrants along the Alabama coast and found adults often had higher fat stores than young but did not exhibit different recapture rates or mass gains by recaptured individuals. The reported difference in mass and condition between age groups is consistent with other studies; however, the lack of differences in other variables contrasts with several existing studies of age. For example, Ellegren (1991) reported adult Blue-throats (*Luscinia svecica*) had more fat, were less likely to be recaptured, and stayed for a shorter period at a stopover site in Sweden than did young. Similarly, Wang et al. (1998) found that young fall migrant Wilson's Warblers had lower fat stores, higher recapture rates, and longer stopovers than adults in New Mexico. Young Eurasian Reed Warblers (*Acrocephalus scirpaceus*) in Morocco had longer stopovers than adults during both spring and fall, although there was no difference found in rate of body mass gain between the two age classes (Rguibi-Idrissi et al. 2003). Jones et al. (2002) found that, in many species of autumn migrants, adults were heavier, had higher fat scores, and had higher rates of mass gain than young, although many of these differences were not significant. The lack of agreement among these findings demonstrates the need for additional study of age-related differences in migration and stopover ecology from multiple species and geographic areas.

Adult Tennessee Warblers may complete their prebasic molt either in breeding areas or during fall migration (Rimmer and McFarland 1998). We

captured 23 adults in active flight feather molt on dates ranging from 22 July to 20 September, indicating molt at this northern location occurs throughout the migratory period. Average capture date of adult warblers, regardless of molt condition, was significantly earlier than average capture date of young warblers, indicating adults migrated earlier than young. These results were consistent with Carlisle et al. (2005), who found that migration among adults was earlier than young in species that used a molt-migration strategy. The mass of molting warblers was lower than that of non-molting warblers, which may reflect the energetic costs of molt and/or a lower physiological capacity for building fat stores at that time. We had a limited sample of birds scored for molt, but those that were molting were almost five times more likely to be recaptured than those that were not molting and were almost twice as likely to be recaptured as young of the year. Young are often more likely to be recaptured than adults at stopover sites (e.g., Ellegren 1991, Morris et al. 1996, Wang et al. 1998), and the higher recapture rate of molting adults may reflect the importance of stopover sites for individuals that have relatively high energetic demands during this period. Leu and Thompson (2001) reviewed the molt of neotropical migrants during migration and made a case for increasing the understanding of when and where molting occurs, especially during migration. Our study documents that some Tennessee Warblers molt at a stopover site in the north-central United States located relatively close to breeding areas.

Only three birds (0.07%) were recaptured in successive years, indicating limited fidelity to this stopover site. Low rates of fidelity to stopover sites are typical of migrant passerines (Catry et al. 2004), although Winker and Warner (1991) reported stopover site fidelity by one Tennessee Warbler in Minnesota. In their work, the particular individual was captured two to three times per season in each of 3 years and was observed in symmetrical flight feather molt each year, indicating molt migration and fidelity to a site used for molting. None of the three warblers captured between years at our site in Michigan was captured more than once in a single season and, while one of the warblers was noted to be molting during one of the captures, another was noted not to be molting during each of the 2 years it was captured. One of the birds recaptured between years was initially captured in its hatching year

when it would not have been molting. This suggests fidelity to this site by these individuals may not be related to molt.

Our results provide support for the study of migration and stopover ecology across a wide geographic area and a variety of species. Our study is one of many that have found lower mass gains by recaptured birds compared to mass gains estimated by regression, supporting regression analysis as the preferred method of estimating mass gains at most sites. Standardizing the method of reporting results (in g/hr and %/hr) will assist comparisons across sites, species, and time. Our data from an inland site support the growing body of evidence that young migrants are generally lighter and gain mass slower than adults, regardless of location. Our results of no difference in recapture rate or stopover length between age groups differed from other studies, indicating the need for additional studies to ascertain if the differences are species-specific or whether they relate to location, timing, or other variables between sites. Our work also indicates the importance of stopover sites for birds in active molt. These birds are likely to be recaptured, have long stopovers, and must meet high energetic needs in the areas where they stop. Migration banding stations are encouraged to score migrants for the presence or absence of molt, and to characterize the extent and location of molting feathers to address questions of timing, location, and stopover ecology of molting birds.

ACKNOWLEDGMENTS

We are grateful to the many staff and volunteers who helped collect data at the Pitsfield banding station for their long hours of hard work and especially to Ray Adams who started the banding program at the Kalamazoo Nature Center. We thank Canisius College and the Buffalo Ornithological Society for providing regular financial support for the Computational Ecology Research Group. ASA received funding through the CEEP program at Canisius and the Howard Hughes Medical Institute to work on this project. This manuscript benefited from constructive comments of C. E. Braun, E. H. Dunn, and C. C. Rimmer that made this a stronger paper.

LITERATURE CITED

- BONTER, D., T. M. DONOVAN, AND E. W. BROOKS. 2007. Daily mass changes in landbirds during migration stopover on the south shore of Lake Ontario. *Auk* 124:122–133.
- CALVERT, A. M., P. D. TAYLOR, AND S. WALDE. 2009. Cross-scale environmental influences on migratory stopover behavior. *Global Change Biology* 15:744–759.
- CARLISLE, J. D., G. S. KALTENECKER, AND D. L. SWANSON. 2005. Molt strategies and age differences in migration timing among autumn landbird migrants in southeastern Idaho. *Auk* 122:1070–1085.
- CATRY, P., V. ENCARNAÇÃO, A. ARAÚJO, P. FEARON, A. FEARON, M. ARMELIN, AND P. DELALOYE. 2004. Are long-distant migrant passerines faithful to their stopover sites? *Journal of Avian Biology* 35:170–181.
- CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. *Auk* 99:725–732.
- DEAN, K. L., H. A. CARLISLE, AND D. L. SWANSON. 2004. Age structure of neotropical migrants during fall migration in South Dakota: is the Northern Great Plains region an inland “coast”? *Wilson Bulletin* 116:295–303.
- DESANTE, D. F., K. M. BURTON, P. VELEZ, D. FROELICH, AND D. KASCHUBE. 2008. MAPS manual: 2008 protocol. Institute for Bird Populations, Point Reyes Station, California, USA.
- DUNN, E. H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migratory stopover. *Auk* 117:12–21.
- DUNN, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. *Journal of Field Ornithology* 72:419–432.
- DUNN, E. H. 2002. A cross-Canada comparison of mass change in birds during migration stopover. *Wilson Bulletin* 114:368–379.
- DUNN, E. H. AND E. NOL. 1980. Age-related migratory behavior of warblers. *Journal of Field Ornithology* 51:254–269.
- DUNN, E. H., D. J. T. HUSSELL, AND R. J. ADAMS. 2004. An investigation of productivity indices derived from banding of fall migrants. *Studies in Avian Biology* 29:92–96.
- ELLEGREN, H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scandinavica* 22:340–348.
- JONES, J., C. M. FRANCIS, M. DREW, S. FULLER, AND M. W. S. NG. 2002. Age-related differences in body mass and rates of mass gain of passerines during autumn migratory stopover. *Condor* 104:49–58.
- LEU, M. AND C. W. THOMPSON. 2001. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. *Biological Conservation* 106:45–56.
- MEHLMAN, D. W., S. E. MABEY, D. N. EWERT, C. DUNCAN, B. ABEL, D. CIMPRICH, R. D. SUTTER, AND M. WOODREY. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. *Auk* 122:1281–1290.
- MOORE, F. R. AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.
- MORRIS, S. R., D. W. HOLMES, AND M. E. RICHMOND. 1996. A ten-year study of the stopover patterns of migratory

- passerines during fall migration on Appledore Island, Maine. *Condor* 98:395–409.
- MORRIS, S. R., C. R. PUSATERI, AND K. A. BATTAGLIA. 2003. Spring migration and stopover ecology of Common Yellowthroats on Appledore Island, Maine. *Wilson Bulletin* 115:64–72.
- MURRAY JR., B. G. 1966. Migration of age and sex classes of passerines on the Atlantic Coast in autumn. *Auk* 83:352–360.
- PYLE, P. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, USA.
- RALPH, C. J. 1978. The disorientation and possible fate of young passerine coastal migrants. *Bird-Banding* 49:237–247.
- RALPH, C. J. 1981. Age ratios and their possible use in determining autumn routes of passerine migrants. *Wilson Bulletin* 93:164–188.
- RGUIBI-IDRISSI, H., R. JULLIARD, AND F. BAIRLEIN. 2003. Variation in the stopover duration of Reed Warblers *Acrocephalus scirpaceus* in Morocco: effects of season, age and site. *Ibis* 145:650–656.
- RIMMER, C. C. AND K. P. MCFARLAND. 1998. Tennessee Warbler (*Vermivora peregrina*). The birds of North America. Number 350.
- SEEWAGEN, C. L. AND E. J. SLAYTON. 2008. Mass changes of migratory landbirds during stopovers in a New York City park. *Wilson Journal of Ornithology* 120:296–303.
- SILLETT, S. AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- SIMONS, T. R., S. M. PEARSON, AND F. R. MOORE. 2000. Application of spatial models to the stopover ecology of trans-Gulf migrants. *Studies in Avian Biology* 20:4–14.
- SMITH, S. B. AND S. R. MCWILLIAMS. 2010. Patterns of fuel use and storage in migrating passerines in relation to fruit resources at autumn stopover sites. *Auk* 127:108–118.
- VOELKER, G. AND S. ROHWER. 1998. Contrasts in scheduling of molt and migration in eastern and western Warbling Vireos. *Auk* 115:142–155.
- WANG, Y., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *Auk* 115:829–842.
- WINKER, K. 1995. Autumn stopover on the Isthmus of Tehuantepec by woodland Nearctic-Neotropical migrants. *Auk* 112:690–700.
- WINKER, K. AND D. W. WARNER. 1991. Unprecedented stopover site fidelity in a Tennessee Warbler. *Wilson Bulletin* 103:512–514.
- WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992. Daily mass gains among woodland migrants at an inland stopover site. *Auk* 109:853–862.
- WOODREY, M. S. AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.