

RESOURCE LIMITATION DRIVES PATTERNS OF HABITAT OCCUPANCY DURING THE NONBREEDING SEASON FOR AN OMNIVOROUS SONGBIRD

NORA E. DIGGS^{1,2,3}, PETER P. MARRA¹, AND ROBERT J. COOPER²

¹Smithsonian Conservation Biology Institute, Migratory Bird Center, National Zoological Park, Washington, DC 20008

²Warnell School of Forestry and Natural Resources, The University of Georgia, Athens, GA 30602

Abstract. The role of food in limiting migratory birds during the nonbreeding period is poorly understood, in part because of the complexities of quantifying food availability and diet. We tracked overwinter changes in the availability of arthropods and fruits, the primary winter foods of the Hermit Thrush (*Catharus guttatus*), a short-distance migrant. Fruit availability declined over the winter, and arthropod availability fluctuated with changing temperature. Concurrently, using fecal samples and stable isotopes, we tracked relative food consumption. In fecal samples fruit declined from early to mid season and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope signatures in blood became more enriched, consistent with a decline in fruit consumption and an increase in arthropod consumption. Larger-bodied birds, predominantly males, maintained territories in which the abundance of arthropods was higher, had a greater proportion of arthropods in their diet and less variation in $\delta^{13}\text{C}$ (indicator of a stable diet) and fat loads over the winter. In contrast, smaller-bodied birds, primarily females, gained fat midwinter in response to unpredictable and lower-quality resources. These results are consistent with both a size-mediated form of dominance and sexual habitat segregation, such that smaller-bodied birds, mainly females, may be behaviorally excluded from optimal territories. Future research should focus on the long-term consequences of food limitation in the nonbreeding season and size and sex-mediated dominance behavior on both the condition of birds within a season and on subsequent breeding success and survival.

Key words: behavioral dominance, *Catharus guttatus*, diet, habitat quality, Hermit Thrush, stable isotopes, winter.

La Limitación de Recursos Condiciona los Patrones de Ocupación de Hábitat durante la Estación No Reproductiva de un Ave Canora Omnívora

Resumen. El rol que tiene el alimento para limitar a las aves migratorias durante el periodo no reproductivo es poco conocido, en parte por las complejidades que significa cuantificar la disponibilidad de alimento y la dieta. Seguimos los cambios a lo largo del invierno de la disponibilidad de artrópodos y frutos, la principal fuente de alimentos de *Catharus guttatus*, un migrante de corta distancia. La disponibilidad de frutos disminuyó a lo largo del invierno y la disponibilidad de artrópodos fluctuó con los cambios en la temperatura. Paralelamente, usando muestras fecales e isótopos estables, seguimos el consumo relativo de alimentos. En las muestras fecales, los frutos disminuyeron desde inicios hacia mediados de la estación y las firmas de los isótopos $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ en sangre aparecieron enriquecidas, lo que fue consistente con una disminución en el consumo de frutos y un aumento en el consumo de artrópodos. Las aves con cuerpo más grande, predominantemente los machos, mantuvieron territorios en los cuales la abundancia de artrópodos fue mayor, tuvieron una mayor proporción de artrópodos en sus dietas y presentaron una menor variación en $\delta^{13}\text{C}$ (indicador de una dieta estable) y en las cargas de grasa a lo largo del invierno. En contraste, las aves con cuerpos más pequeños, principalmente las hembras, adquirieron grasa a mediados del invierno en respuesta a recursos impredecibles y de menor calidad. Estos resultados son consistentes con una forma de dominancia mediada por el tamaño y con la segregación sexual del hábitat, de modo que las aves con cuerpo más pequeño, principalmente las hembras, pueden ser excluidas por comportamiento de los territorios óptimos. Futuras investigaciones deberían enfocarse en las consecuencias de largo plazo (i) de la limitación de alimento en la estación no reproductiva y (ii) del comportamiento de dominancia mediado por el tamaño y el sexo tanto en la condición de las aves en una misma estación como en el éxito reproductivo y la supervivencia subsecuente.

INTRODUCTION

Twenty-five years ago, it was a common sentiment that “anything a bird does beyond surviving [the winter] will have little influence on its reproductive success in the spring” (Puliam and Millikan 1982). Although survival is certainly a prerequisite for any measure of success, we now know events

in the nonbreeding period (or winter) that influence body condition can carry over into the breeding season (Marra et al. 1998, Studds et al. 2008, Reudink et al. 2009). The effect of events during the winter on subsequent periods has been overlooked until recently. To better understand the role of winter events in driving subsequent events in the annual cycle of migratory birds, we must continue to build a basic understanding

Manuscript received 20 October 2009; accepted 20 April 2011.

³E-mail: diggsn@si.edu

of what factors influence the physical condition of birds during the nonbreeding season.

Food availability is known to be a key limiting resource for migratory birds during the nonbreeding season (Hutto 1985, Sherry et al. 2005, Brown and Sherry 2006), and several studies have now shown how birds cope with limited and unpredictable food availability over the winter. For example, the Dark-eyed Junco (*Junco hyemalis*), a ground forager, compensates for unpredictable resources by having higher fat reserves (Rogers 1987, Rogers and Smith 1993). In Mexico, nonterritorial Wood Thrushes (*Hylocichla mustelina*) have fat loads higher than those of territorial individuals (Winker et al. 1990). In the tropics, Ovenbirds (*Seiurus aurocapilla*) have increased fat stores in areas with lower biomass of ants, a critical food source (Strong and Sherry 2000). In general, individuals in lower-quality habitats, as defined by lower availability of higher-quality food, or in unpredictable environments prone to severe food limitation, tend to store more body fat than do conspecifics in stable or higher-quality environments (Rogers 1987).

For the Hermit Thrush (*Catharus guttatus*), both fruit and arthropods appear to be important for maintaining overwinter condition. Hermit Thrush abundance has been positively correlated with fruit abundance (Kwit et al. 2004b, Strong et al. 2005). Additionally, the analysis of fecal samples revealed fruit consumption to peak in January and the presence and proportion of arthropods in the samples to increase in late winter and spring (Strong et al. 2005). Fruit, however, is considered to be nutritionally poor and insufficient for maintaining the body mass of many omnivorous songbirds (Levey and Karasov 1989, Long and Stouffer 2003, Pearson et al. 2003). Although high in carbohydrates and lipids necessary for energy, fruit often lacks the protein and nitrogen necessary for maintaining muscle mass (Blem 1990). Despite evidence that Hermit Thrushes rely heavily on fruit during the winter, captive wintering Hermit Thrushes preparing for migration given an unlimited supply of insects and fruit chose to consume only insects and gained significantly more fat and mass than did thrushes that were fed only fruit (Long and Stouffer 2003). Although that study does not reflect the real-world availability of resources, it does demonstrate the nutritional superiority of arthropods. Furthermore, experimental removal of fruit did not result in changes in territory size or space use (Brown and Long 2006). Brown and Long (2006) hypothesized saturation of available habitat may have prevented the expansion of territories to compensate for the loss of fruit. In the absence of information on changes to body condition or survival, however, it is not possible for the significance of such experimental reductions in winter fruit resources to be assessed adequately.

The first objective of our study was to identify how the diet of the Hermit Thrush changed over the winter. Because assessing actual food consumption is difficult, our second objective was to use values of stable carbon and nitrogen isotopes derived from blood as indices of food consumption to determine if fruit and arthropod consumption varied over the winter. In the last decade, measuring stable-isotope ratios has become a useful tool

for identifying birds' diet at varying temporal and geographic scales (Hobson and Clark 1992, Podlesak et al. 2005, Phillips and Eldridge 2006). Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which are more enriched at higher trophic levels, can be used to assess relative changes in diet (Haramis et al. 2001, Podlesak et al. 2005). Hobson and Clark (1992) and Hobson and Bairlein (2003) reported the rate of turnover of carbon isotopes in whole blood for a warbler and a quail to be 6 and 11 days, respectively, so, on the basis of mass, we expected the rate for the Hermit Thrush to fall between those values.

The second objective was to measure how diet changed in relation to food availability. So, in conjunction with diet assessment, we measured site- and territory-level differences in food availability at regular intervals over the nonbreeding season. We then examined how resource use and availability influenced fat reserves and overall mass of birds through the winter. We predicted that limited resources should result in competition for higher-quality territories, as measured by food availability, and that thrushes with a higher proportion of arthropods in their diet should maintain a more stable mass through the winter.

METHODS

STUDY SYSTEM

We conducted our study on a 485-ha preserve on Spring Island, within a private residential community in Beaufort County, South Carolina (32.3° N, 80.8° W), between November and April in 2004–2005 (2005) and 2006–2007 (2007). The study area, totaling 15 ha, has an overstory primarily of mixed oak species (*Quercus* spp.) and loblolly pine (*Pinus taeda*) and a moderate to dense understory of waxmyrtle (*Myrica cerifera*), beautyberry (*Callicarpa americana*), farkleberry (*Vaccinium arboretum*), inkberry (*Ilex glabra*), and regenerating oaks. This habitat is common along the coast of the southeastern U.S. and often contains a dense understory that is used by many species of birds, including the Hermit Thrush.

STUDY SPECIES

The Hermit Thrush is short-distance migrant that breeds throughout the northeastern U.S., most of Canada and much of the western U.S. and winters from the southeastern U.S. through Mexico to Guatemala. It is the only species of *Catharus* that winters north of Mexico. It switches from a diet primarily of arthropods in the breeding season to one heavily supplemented with fruit in the nonbreeding season (Jones and Donovan 1996). Wintering Hermit Thrushes maintain territories of less than 1 ha and show fidelity to these sites throughout the season (Brown et al. 2000). In Louisiana, Brown et al. (2000, 2002) found no differences in territory size by age, sex, or habitat type.

The Hermit Thrush is well suited for this study because it is common and territorial on the nonbreeding grounds (Brown et al. 2000, 2002). Its omnivorous diet and foraging behavior in winter also makes it ideal for a study of the influence of diet on winter condition. Because Hermit Thrushes are difficult to observe, we used radio transmitters to track the movements

of individuals and to map territories. We attached radio transmitters (Holohil, Model BD-2, with two harness tubes), modifying the harness with a thread looped through harness tubes and under the thighs, securing the transmitter just above the tail (Rappole and Tipton 1991). In 2007, we attached transmitters weighing 0.75 g (less than 3% of a 30-g bird) in November and again in January because of the limited lifespan of the transmitter. We attempted to place transmitters on the same birds in January as in November but were successful with only 8 of 10. We attempted to recapture all individuals to remove transmitters. We estimated territories as minimum convex polygons in ArcView 3.2 by using the extension `conv_hulls_pts.avx` (Jenness Enterprises). We located birds at least once a day for an average of 30 observations each before recapture.

MEASURES OF FOOD AVAILABILITY

To estimate overwinter changes in fruit availability in 2005, we established random transects in 50-m increments throughout the study area, totaling 6000 m² or 4% of the area. We tagged all fruiting plants in each transect and counted fruit in November. For the larger shrubs, whose large production of berries or height made a count impractical, we estimated fruit availability by counting a representative branch and multiplying the count by the total number of branches. We repeated counts in January and March and used the differences between counts as an estimate of overwinter change in fruit availability.

During the 2007 winter season, we estimated the change in fruit availability within Hermit Thrush territories in November, January, and March. We used ArcView 3.2 and extension Random Point Generator version 1.3 (Jenness Enterprises) to randomly select non-overlapping points within territory polygons to sample fruit. Locations were flagged and all fruit in the 5-m radius was tagged and counted or estimated. In 2007 we pooled samples to estimate changes in fruit availability across plots to allow comparison with 2005 estimates of fruit availability.

In the 2007 winter season, we estimated change in arthropod availability in November, January, and March within the same 5-m radius within which we sampled fruit. Using methods modified from Strong and Sherry (2000), we placed a frame covering 0.5 m² near the center of the sampling area on top of the leaf litter. Observers spent 5 min searching within the frame by scanning and flipping leaves individually to mimic a foraging Hermit Thrush (Jones and Donovan 1996). We counted arthropods and recorded their lengths (mm, head to abdomen tip) to create an index (average of sample sum of arthropod lengths) of arthropod biomass.

CAPTURE METHOD

In 2005, we captured birds during three periods: early (December), mid (January–February), and late (March) winter, averaging 35 capture days in each period. In 2007, we added a late-fall period in early November, with each period averaging 13 days. Using a combination of passive and targeted netting with a recorded playback, we captured all Hermit Thrushes in mist nets.

We banded the birds with an aluminum U.S. Fish and Wildlife band and a unique color-band combination to permit subsequent identification of birds in the field. In addition to blanket netting, we targeted birds caught earlier in the season in subsequent capture periods. Net effort and placement were determined by previous observations of banded and unbanded birds. Birds were released immediately after being processed.

To assess body condition, at every capture of a thrush, we weighed it to the nearest 0.1 g on an electronic Ohaus balance and assessed its furcular fat. We measured the wing with a wing ruler and tail and tarsus with an electronic caliper. In 2007, we visually assessed fat levels in the furcular cavity on a subjective scale (0 = no fat, 1 = furcular cavity 5–25% full, 2 = 30–60% full, 3 = 65–95% full, 4 = 100% full, 5 = fat extending beyond cavity).

We collected blood samples for DNA sexing and stable-isotope analysis. We drew blood (100–120 µL) from the brachial vein with a needle and nonheparinized capillary tube and immediately transferred it to a sterile vial, storing it in a cooler in the field until the sample could be placed in a freezer (–20°C). Blood for DNA sexing was placed on sterile card (10 µL) provided by and analyzed by Avian Biotech International (Tallahassee, FL). We also collected fecal samples from cotton holding bags or from the ground directly beneath a captured bird in the net. Fecal samples were stored in wax envelopes and later transferred to an ethanol solution. We believe that little of the sample was lost when collected from beneath the net because of the compactness of the droppings.

DIET ASSESSMENT AND TISSUE ANALYSIS

Each fecal sample was placed into an ethanol solution and broken apart by light pressure applied with a blunt instrument (closed tweezer tips). We examined fecal samples under a dissecting microscope (Ralph et al. 1985) for insect fragments (wing scales, mandibles, appendages) and seeds that were not digested (Burger et al. 1999, Deloria-Sheffield et al. 2001).

We kept blood samples for stable-isotope analysis frozen until they were freeze-dried for 48 hr. Dried whole blood was ground into a powder with the tip of a lab spatula before it was weighed (1 ± 0.2 mg) into 5×9 -mm tin capsules. Capsules were rolled and crimped and placed in a numbered cell plate and sent to the Stable Isotope Facility of the University of California, Davis, for analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Samples were analyzed with an ANCA-GSL and PDZ Europa 20-20 isotope-ratio mass spectrometer. Results are presented as deviations from standard ratios (Vienna PeeDee Belemnite for $\delta^{13}\text{C}$ and atmospheric nitrogen for $\delta^{15}\text{N}$). This ratio is derived from: $\delta X - [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is the ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively.

STATISTICAL ANALYSES

We assessed changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with repeated-measures mixed models (PROC MIXED from SAS Institute), with models including the main effects of age, sex and, period and interaction effects between period with age and period with

sex, with adjusted Tukey mean comparisons. In these models, age and sex were between-subjects factors, and period and interactions with period were within-subjects factors. These analyses included all birds, including those captured once and those captured repeatedly. We did not combine years in mixed models because of the number of sampling periods and length of each period in the two years differed.

For the analysis of diet, mass, and fat relationships we used data for 2007 only because of the shorter sampling period needed for accurate comparisons. We compared sex and wing chord with two-sample *t*-tests for unequal variance. We used the coefficient of variation (CV) of fat scores, mass, and $\delta^{13}\text{C}$ signatures for individuals captured three times to compare the variability in diet, fat, and mass. Territory-level fruit availability was log-transformed for improved fit. We used linear regression for all continuous variables, unless otherwise stated in the results, and logistic regression (χ^2) for ordinal fat scores.

RESULTS

FOOD AVAILABILITY AND USE

Fruit availability and consumption change both within and between years. Fruit availability declined over winter (Fig. 1A).

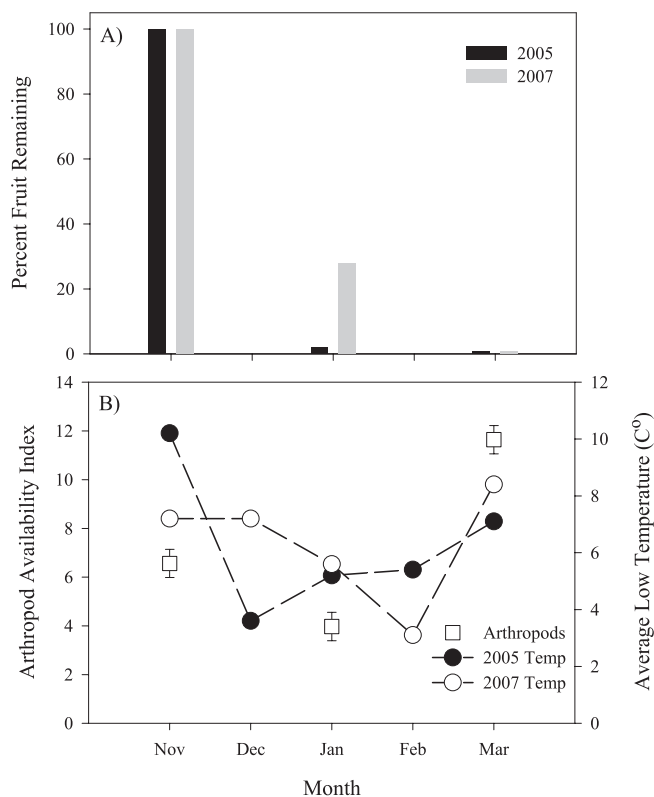


FIGURE 1. Food availability and temperature changes by year. (A) Percent fruit remaining by month and (B) changes in arthropod availability (mean \pm SE) for 2007 and corresponding changes in average monthly low temperature; 2005 temperature presented for comparison.

In 2005, fruit availability in January and March declined from November levels by 98% and 99%, respectively. In 2007, fruit availability fell from November levels by 73% by January and by 99% by March. In 2005 fruit availability declined faster than in 2007 ($\chi^2_1 = 21183, n = 716517, P < 0.001$). These percentages are from counts of all species of fruit species pooled; however, *M. cerifera*, the dominant fruit on our sites (representing 63% and 98% of fruit sampled in 2005 and 2007, respectively), declined at the same rate as the pooled samples in each year. In 2005, fruit occurred in 71% ($n = 14$) and 81% ($n = 21$) of the fecal samples in early winter (November) and mid-winter (January), respectively, and declined to 29% ($n = 17$) in late winter (March). In 2007, fruit occurred in the feces of 60% ($n = 10$) and 64% ($n = 22$) of the birds sampled in the late fall and early winter, respectively, then declined to 33% ($n = 18$) and 11% ($n = 18$) in mid and late-winter. Only in January did fruit consumption in the two years differ (Fig. 2A: $\chi^2_1 = 9.4, n = 39, P = 0.002$). We found *M. cerifera* in fecal samples during every sampling period in both years and in two-thirds of the samples containing fruit; *I. glabra*, *C. americana*, *V. arboretum*, and *I. vomitoria* were far less frequent.

Although arthropods varied in availability, they were a consistent part of the Hermit Thrushes' diet. In 2007 arthropod

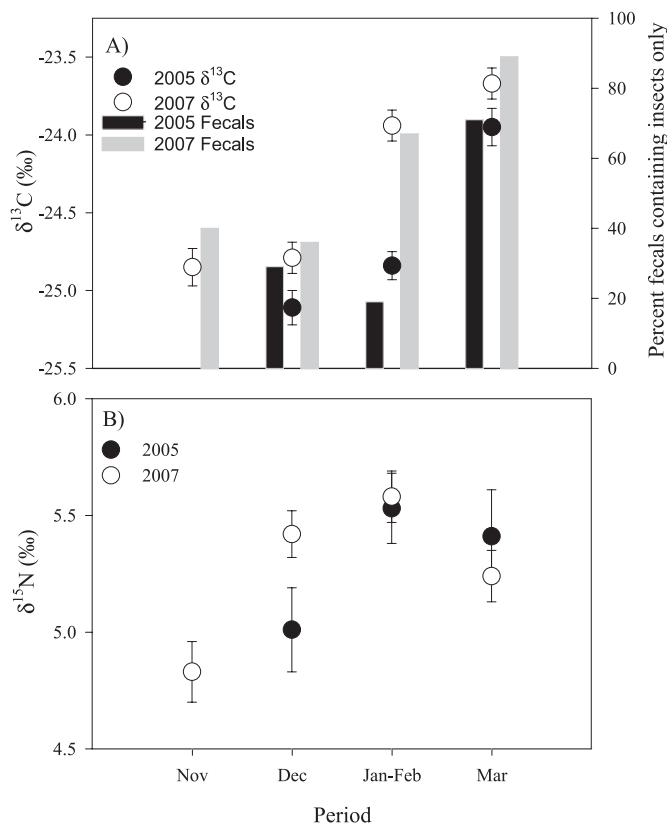


FIGURE 2. Changes in isotope signatures in whole blood (mean \pm SE) for 2005 and 2007 for (A) $\delta^{13}\text{C}$ and percent of fecal samples containing only arthropods and (B) $\delta^{15}\text{N}$.

availability declined from November to January but rose in March (Fig. 1B: $F_{2,450} = 45, P < 0.001$), consistent with temperature change. Arthropod data were not available for 2005. Identifiable arthropod parts (legs, mouth parts, wing fragments) were present in all but 3 of the 122 samples from 2005 and 2007.

We examined how isotopic signatures in whole blood changed over three (2005) and four (2007) periods for all captured birds, regardless of their territoriality. In both years, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures in whole blood of all captured individuals ($n = 81$ over both years) changed from one period to the next, with no influence of age or sex (Table 1, Fig. 2). In 2005, $\delta^{13}\text{C}$ signatures became significantly more enriched in late winter (Fig. 2A: repeated-measures mixed model, $F_{2,15} = 30.16, P < 0.001$). However, in 2007, the $\delta^{13}\text{C}$ signatures became more enriched earlier in the midwinter period (Fig. 2A: repeated-measures mixed model, $F_{3,33} = 48.98, P < 0.001$). In 2005, the $\delta^{15}\text{N}$ signatures in blood became more enriched as the winter progressed (Fig. 2B: repeated-measures mixed model, $F_{2,15} = 2.96$). In contrast, in 2007, $\delta^{15}\text{N}$ signatures became more depleted in late winter than in early and midwinter (Fig. 2B: repeated-measures mixed model, $F_{3,33} = 9.1, P < 0.001$).

TERRITORIAL BIRDS

In 2007, we measured food availability within territories of nine birds to assess how food availability correlated with consumption. We found no relationship between territory size and fruit availability ($r^2 = 0.20, n = 9, P = 0.23$) or arthropod availability ($r^2 = 0.03, n = 9, P = 0.65$). In addition, arthropod and fruit densities were inversely correlated ($r^2 = 0.60, n = 9, P = 0.01$). Birds with longer wing chords occupied territories with higher arthropod availability (Fig. 3A: $r^2 = 0.54, n = 9, P = 0.02$) and lower fruit availability ($r^2 = 0.57, n = 9, P = 0.02$). These larger birds also had whole blood that was more enriched in $\delta^{13}\text{C}$ in early winter (Fig. 3B: $r^2 = 0.79, n = 9, P = 0.001$). Larger birds were predominately male ($t_5 = 3.87, n = 9, P = 0.01$). More enriched $\delta^{13}\text{C}$ signatures were associated with lower fruit availability ($r^2 = 0.65, n = 9, P = 0.009$) and a tendency toward higher arthropod availability ($r^2 = 0.37, n = 9, P = 0.08$). The corresponding $\delta^{15}\text{N}$ relationships were not significant.

We also examined the relationship between diet, fat, and body mass of all individuals recaptured three or more times in

2007. In midwinter, greater values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in blood were associated with gains in body mass (exponential fit of mass change: Fig. 4A, $\delta^{13}\text{C}$: $r^2 = 0.53, n = 16, P = 0.002$ and $\delta^{15}\text{N}$: $r^2 = 0.50, n = 16, P = 0.002$) and increased fat loads ($\chi^2 = 4.92, n = 16, P = 0.02$). Individuals more depleted in $\delta^{13}\text{C}$ in early winter experienced a greater change in $\delta^{13}\text{C}$ by midwinter (Fig. 4B: $r^2 = 0.54, n = 16, P = 0.001$). Birds in which variation in $\delta^{13}\text{C}$ over winter was greater also varied more in fat load ($r^2 = 0.28, n = 14, P = 0.05$). Signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were highly correlated ($r^2 = 0.69, n = 16, P < 0.001$) within this period only.

Mass change was positively correlated with change in fat score over the winter (November–December: $\chi^2 = 4.41, n = 9, P = 0.04$; December–January/February: $\chi^2 = 9.01, n = 17, P = 0.003$; January/February–March: $\chi^2 = 23.46, n = 15, P < 0.0001$). There was no relationship between body mass and fat change and change in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ in early or late winter. Additionally, birds that increased in mass and fat in early winter also lost the most mass and fat by late winter (mass: $r^2 = 0.28, n = 14, P = 0.05$; fat: $r^2 = 0.34, n = 14, P = 0.03$).

When we examined all territory holders (all birds captured three or more times), wing chord was positively correlated with enrichment in $\delta^{13}\text{C}$ in early winter (Fig. 4C: $r^2 = 0.47, n = 16, P = 0.003$), and these larger Hermit Thrushes were predominately male ($t_{13,7} = 3.63, n = 16, P = 0.003$). Values of $\delta^{13}\text{C}$ in larger thrushes were also less variable over the winter (coefficient of variation: $r^2 = 0.31, n = 14, P = 0.04$). Although wing chord was not correlated with mass change ($r^2 = 0.0, n = 16, P = 0.92$) or change in $\delta^{13}\text{C}$ ($r^2 = 0.09, n = 16, P = 0.25$), fat scores of smaller birds increased more in midwinter ($\chi^2 = 4.54, n = 17, P = 0.03$) and tended toward more decline in late winter ($\chi^2 = 2.43, n = 15, P = 0.1$).

DISCUSSION

At our study site, the decline of fruit availability was similar to that reported from the region by McCarty et al. (2002) and Kwit et al. (2004b). Fruit availability declined faster in 2005, a winter of cold temperatures earlier than in 2007. This finding is consistent with other studies reporting that fruit is depleted faster in colder years as arthropod availability declines and birds’ energetic demands increase (Kwit et al. 2004a). Winter

TABLE 1. The results of repeated-measures mixed-models for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope signatures by year.

Effect	2005					2007				
	df	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$		df	$\delta^{13}\text{C}$		$\delta^{15}\text{N}$	
		F	P	F	P		F	P	F	P
Period	2,15	30.16	<0.001	2.96	0.08	3,33	48.98	<0.001	9.1	<0.001
Age	1,37	0	0.95	0.01	0.94	1,37	0.32	0.58	1.37	0.25
Sex	1,37	0.06	0.8	1	0.32	1,37	0.00	0.96	0.21	0.65
Period × age	2,15	0	0.99	1	0.39	3,33	0.94	0.43	0.34	0.79
Period × sex	2,15	1.59	0.24	0.41	0.67	3,33	0.25	0.86	1.15	0.34

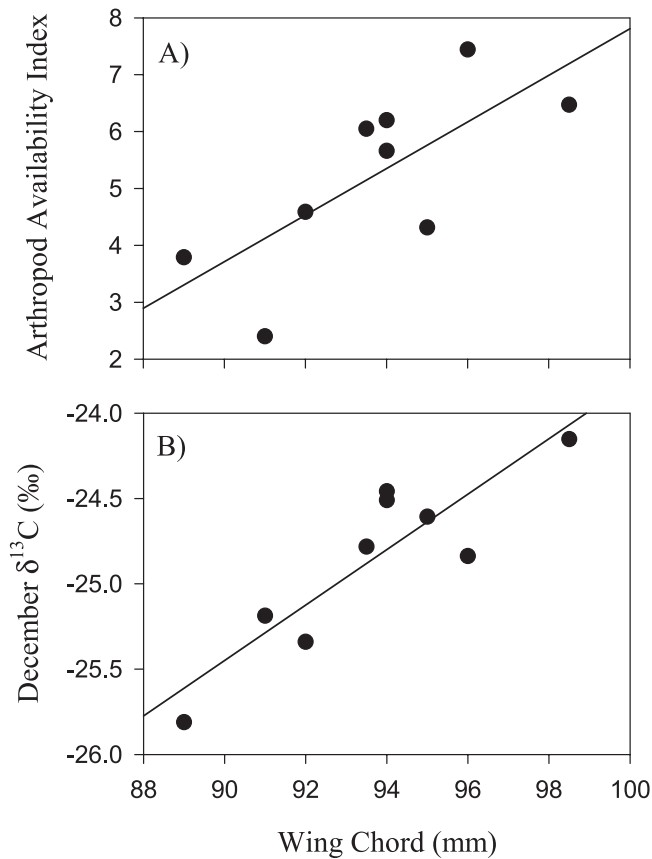


FIGURE 3. Relationships between wing chord and (A) arthropod-availability index and (B) $\delta^{13}\text{C}$ in whole blood of territorial Hermit Thrushes.

fruit, like *M. cerifera*, contains compounds that make it resistant to damage from the cold and insect (McCarty et al. 2002). It is also possible that differences in fruit-removal rates could be due to differences between the years in fruit-sampling methods, in fruit production, or consumption by other animals, including other birds, which we did not measure. Nevertheless, sampling differences cannot account for changes in consumption.

Both fecal samples and reduced values of $\delta^{13}\text{C}$ in blood suggest more consumption of fruit during an unusually cold midwinter in 2005. At that time, the majority of fecal samples contained fruit, compared to only 33% in January 2007 when temperatures were significantly warmer, even though a significant quantity of fruit was still available in midwinter 2007. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ changing over winter were consistent with our data on the background availability of fruit and arthropods and with the prevalence of fruit and arthropods in fecal samples. They independently document a shift from a fruit-dominated diet in early winter to an arthropod diet in late winter. Although $\delta^{15}\text{N}$ followed the same pattern, it did not track the change of fruit and arthropods in fecal samples as did $\delta^{13}\text{C}$. Instead, $\delta^{15}\text{N}$ became more depleted in March

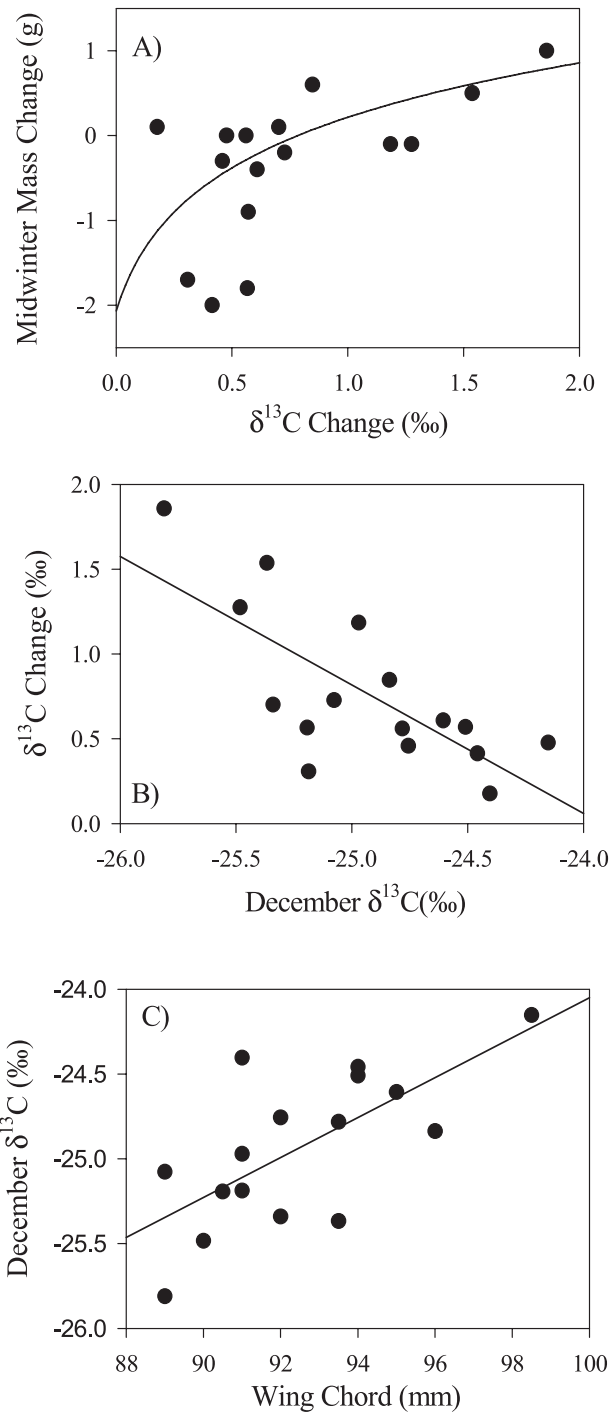


FIGURE 4. Relationships in recaptured Hermit Thrushes between (A) midwinter changes in $\delta^{13}\text{C}$ and in mass (exponential fit), (B) December $\delta^{13}\text{C}$ values and subsequent midwinter $\delta^{13}\text{C}$ change (January–December), and (C) wing chord and December $\delta^{13}\text{C}$ values.

2005 and March 2007, in contrast to $\delta^{13}\text{C}$, which tended to become more enriched.

Although Kwit et al. (2004b) and Strong et al. (2005) found that Hermit Thrushes are more abundant in

locations with abundant fruit, we found no relationship between territory size and food availability. Furthermore, experimental alterations of fruit abundance in Louisiana yielded no effect on Hermit Thrush movements (Brown and Long 2006). The role of fruit as an essential resource needs reevaluation. Because birds consuming it may accumulate toxic compounds, fruit has long been considered to be a food inadequate for meeting the dietary needs of many species (Levey and Martínez del Río 2001). This is the case for the American Robin (*Turdus migratorius*), which limits consumption of fruits otherwise high in energy and rich in protein even in the lack of an alternative (Levey and Karasov 1989). Reliance on a diet dominated by fruit therefore seems to be a risky strategy. Colder winters could result in faster depletion of fruit, leaving birds with little to supplement their consumption of arthropods, already low in mid to late winter. This is further evidence that, although fruit likely provides a critical emergency resource at times of colder temperatures, Hermit Thrushes preferentially consume arthropods when available.

The simultaneous evaluation of food availability, consumption, and over-winter changes in stable isotopes, body mass and size, and fat loads provided important insights into the influence of diet on the trajectories of individual birds' condition. We found that larger birds occupied territories with more arthropods and had a diet with a higher proportion of arthropods than did their smaller conspecifics, as indicated by stable-isotope analyses. Larger birds' diets were more consistent over the winter and their fat loads varied less. Smaller-bodied thrushes occupying territories with higher fruit densities in early winter gained fat midwinter. This is consistent with other studies in temperate regions, which have found that socially dominant birds have fat reserves lower than those of subordinates when access to food is limited (Gosler 1996, Pravosudov et al. 1999). While increasing fat stores may provide insurance against potential food shortage, it also requires more time foraging and increases the risk of predation, as a result of both decreased vigilance while foraging and lowered flight performance (Witter and Cuthill 1993, Clark and Ekman 1995).

Several studies investigating the social systems of birds during the nonbreeding season have found sex and age to be important factors in a bird's ability to acquire and maintain a high-quality territory (Holmes et al. 1989, Marra and Holmes 2001, Latta and Faaborg 2002). This behavioral dominance can restrict access of subordinate individuals to higher-quality resources when resources are limited (Gauthreaux 1978, Sherry and Holmes 1996). We argue, using data on overwinter changes in mass and fat along with diet inferred from stable carbon isotopes collected from thrush blood, that arthropod availability underlies territory quality and, potentially, the an individual's subsequent success. Different patterns of habitat occupancy caused by the behavioral dominance of larger thrushes may result in smaller and subordinate

individuals, often females, being relegated to low-quality sites that ultimately have consequences on their physical condition and survival.

USE OF ISOTOPES TO STUDY CHANGING DIET

The use of isotopes was instrumental in examining the relationships between diet and changes in body mass and fat. Sampling fruit and arthropods is time consuming and complex and often does not reflect true availability. Fecal samples can provide insights into diet but can also be biased because of varying retention time of prey items. In contrast, blood samples for isotope analysis were easy to obtain and inexpensive to analyze and provided a more precise picture of the relative contribution of multiple food sources to an omnivore's diet.

Our isotopic sampling was carefully constrained to the winter to avoid isotopic carry-over from previous seasons. Most Hermit Thrushes arrive on winter territories by October, so sampling first in late November should provide enough time for isotopic turnover and the loss of signatures associated with migration (Hobson and Clark 1992, Hobson and Bairlein 2003). This initial period is distinct from late winter because typically both fruit and arthropods are readily available. Later periods were associated with a decline in both fruit and insects that resulted in changes in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Other factors can also contribute to changes in stable isotopes over the winter and may provide an explanation for the lack of $\delta^{13}\text{C}$ relationships in late winter and why patterns found in carbon isotopes were not mirrored in nitrogen. For example, increased stress may result in the enrichment of $\delta^{15}\text{N}$ (Hobson et al. 1993, Dalerum and Angerbjörn 2005). The depletion of $\delta^{15}\text{N}$ in the late-period mixed model for 2007 could also have arisen from a trophic-level shift in consumption within arthropod communities. Early spring marks the emergence of various arthropods, such as larval lepidopterans, that are at a lower trophic level and more depleted in $\delta^{15}\text{N}$ than predatory and adult arthropods (Gannes et al. 1998, Tibbets et al. 2008). Finally, Herrera et al. (2001) reported that $\delta^{13}\text{C}$ to be more effective than $\delta^{15}\text{N}$ at measuring trophic-level differences in fruit- and arthropod-consuming species and found greater variation of $\delta^{15}\text{N}$ in blood. They suggested the problem may result from the differences between the digestibility of ^{15}N -depleted chitin and other arthropod materials (Herrera et al. 2001).

CONCLUSIONS AND FUTURE DIRECTIONS

The period of the nonbreeding season in which an individual is stationary is likely limiting for many species of migratory songbirds. In this study, we used both direct and indirect methods to demonstrate that arthropods form a critical component of the Hermit Thrush's winter diet. Larger-bodied birds, often males, are able to acquire and defend winter territories with greater arthropod densities, providing them a more consistent diet with a higher proportion of arthropods

than that of their smaller counterparts. In midwinter, smaller individuals lacking a stable and sufficient arthropod supply are likely forced to compensate by spending more time foraging to increase fat reserves but also to make themselves more susceptible to predation and starvation in severe winters.

Future research could include experimental alterations in arthropod availability to confirm that body size and behavioral dominance secondarily regulate the relative availability of fruit and arthropods. Possible experiments could include arthropod supplementation on territories of smaller birds and arthropod reduction on territories of larger thrushes. Additional research could also look for evidence of behavioral dominance across habitat types and latitudes, where sex and age ratios may differ (Gauthreaux 1978, Marra 2000). Efforts should also focus on understanding how these events influence overwinter and annual survival as well as subsequent events during the annual cycle, such as those during the breeding season (Marra et al. 1998). Finally, given the critical role of temperature in regulating arthropod availability, a better understanding of how future warming may influence the ecology of short-distance migrants wintering in temperate regions has now become essential.

ACKNOWLEDGMENTS

Funding was provided by the LowCountry Institute and supported by the Spring Island community. Chris Marsh was especially instrumental in facilitating and supporting this research. Additional funding and resources were provided by the University of Georgia's Warnell School of Forestry and Natural Resources and a Smithsonian Institution Fellowship. We thank all those who helped in the field, especially S. Conrad, S. Buck, and A. Byrd. Thanks to C. Studds, B. Ballentine, M. Reudink, B. Ryder, and R. Curry for reviews and advice.

LITERATURE CITED

- BLEM, C. R. 1990. Avian energy stores. *Current Ornithology* 7:59–113.
- BROWN, D. R., AND J. A. LONG. 2006. Experimental fruit removal does not affect territory structure of wintering Hermit Thrushes. *Journal of Field Ornithology* 77:404–408.
- BROWN, D. R., AND T. W. SHERRY. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* 149:22–32.
- BROWN, D. R., P. C. STOFFER, AND C. M. STRONG. 2000. Movement and territoriality of wintering Hermit Thrushes in southeastern Louisiana. *Wilson Bulletin* 112:347–353.
- BROWN, D. R., C. M. STRONG, AND P. C. STOFFER. 2002. Demographic effects of habitat selection by Hermit Thrushes wintering in a pine plantation landscape. *Journal of Wildlife Management* 66:407–416.
- BURGER, J. C., M. A. PATTEN, J. T. ROTENBERRY, AND R. A. REDAK. 1999. Foraging ecology of the California Gnatcatcher deduced from fecal samples. *Oecologia* 120:304–310.
- CLARK, C. W., AND J. EKMAN. 1995. Dominant and subordinate fattening strategies: a dynamic game. *Oikos* 72:205–212.
- DALERUM, F., AND A. ANGERBJORN. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia* 144:647–658.
- DELORIA-SHEFFIELD, C. M., K. F. MILLENBAH, C. I. BOCETTI, P. W. SYKES, AND C. B. KEPLER. 2001. Kirtland's Warbler diet as determined through fecal analysis. *Wilson Bulletin* 113:384–387.
- GANNES, L. Z., C. MARTÍNEZ DEL RÍO, AND P. KOCH. 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. *Comparative Biochemistry and Physiology A* 119:725–737.
- GAUTHREAUX, S. A. JR. 1978. The ecological significance of behavioral dominance, p. 17–54. *In* P. P. G. Bateson and P. H. Klopfer [EDS.], *Perspectives in ethology*. Plenum, New York.
- GOSLER, A. G. 1996. Environmental and social determinants of winter fat storage in the Great Tit *Parus major*. *Journal of Animal Ecology* 65:1–17.
- HARAMIS, G. M., D. G. JORDE, S. A. MACKO, AND J. L. WALKER. 2001. Stable-isotope analysis of Canvasback winter diet in upper Chesapeake Bay. *Auk* 118:1008–1017.
- HERRERA, L. G., K. A. HOBSON, A. MANZO, D. ESTRADA, V. SÁNCHEZ-CORDERO, AND G. MÉNDEZ. 2001. The role of fruits and insects in the nutrition of frugivorous bats: evaluating the use of stable isotope models. *Biotropica* 33:520–528.
- HOBSON, K. A., R. T. ALISKAUSKAS, AND R. G. CLARK. 1993. Stable-nitrogen isotope enrichment on avian tissues due to fasting and nutritional stress: implication for isotopic analysis of diet. *Condor* 95:388–394.
- HOBSON, K. A., AND F. BAIRLEIN. 2003. Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. *Canadian Journal of Zoology* 81:1630–1635.
- HOBSON, K. A., AND R. G. CLARK. 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor* 94:181–188.
- HOLMES, R. T., T. W. SHERRY, AND L. REITSMA. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *Condor* 91:545–561.
- HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory land birds, p. 455–476. *In* M. L. Cody [ED.], *Habitat selection in birds*. Academic Press, Orlando, FL.
- JONES, P. W., AND T. M. DONOVAN. 1996. Hermit Thrush (*Catharus guttatus*), no. 261. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Academy of Natural Sciences, Philadelphia.
- KWIT, C., D. J. LEVEY, C. H. GREENBERG, S. F. PEARSON, J. P. MCCARTY, AND S. SARGENT. 2004a. Cold temperature increases winter fruit removal rate of bird-dispersed shrub. *Oecologia* 139:30–34.
- KWIT, C., D. J. LEVEY, C. H. GREENBERG, S. F. PEARSON, J. P. MCCARTY, S. SARGENT, AND R. L. MUMME. 2004b. Fruit abundance and local distribution of wintering Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) in South Carolina. *Auk* 121:46–57.
- LATTA, S. C., AND J. FAABORG. 2002. Demographic and population responses of Cape May Warbler wintering in multiple habitats. *Ecology* 83:2502–2515.
- LEVEY, D. J., AND C. MARTÍNEZ DEL RÍO. 2001. It takes guts (and more) to eat fruit: lessons from avian nutritional ecology. *Auk* 118:819–831.
- LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106:675–686.
- LONG, J. A., AND P. C. STOFFER. 2003. Diet and preparation for spring migration in captive Hermit Thrushes (*Catharus guttatus*). *Auk* 120:323–330.
- MARRA, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11:299–308.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.

- MARRA, P. P., AND R. T. HOLMES. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk* 118:92–104.
- MCCARTY, J. P., D. J. LEVEY, C. H. GREENBERG, AND S. SARGENT. 2002. Spatial and temporal variation in fruit use by wildlife in a forested landscape. *Forest Ecology and Management* 164:277–291.
- PEARSON, S. F., D. J. LEVEY, C. H. GREENBERG, AND C. MARTÍNEZ DEL RÍO. 2003. Effects of elemental composition on the incorporation of dietary nitrogen and carbon isotopic signatures in an omnivorous songbird. *Oecologia* 135:516–523.
- PHILLIPS, D. L., AND P. M. ELDRIDGE. 2006. Estimating the timing of diet shift using stable isotopes. *Oecologia* 147:195–203.
- PODLESAK, D. W., S. R. MCWILLIAMS, AND K. A. HATCH. 2005. Stable isotopes in breath, blood, feces and feathers can indicate intra-individual changes in the diet of migratory songbirds. *Oecologia* 142:501–510.
- PRAVOSUDOV, V. V., T. C. GRUBB JR., P. F. DOHERTY JR., C. L. BRONSON, E. V. PRAVOSUDOVA, AND A. S. DOLBY. 1999. Social dominance and energy reserves in wintering woodland birds. *Condor* 101:880–884.
- PULLIAM, H. R., AND G. C. MILLIKAN. 1982. Social organization in the nonreproductive season, p. 169–197. *In* D. S. Farner, J. R. King and K. C. Parkes [EDS.], *Avian biology*, vol 6. Academic Press, Orlando, FL.
- RALPH, C. P., S. E. NAGATA, AND C. J. RALPH. 1985. Analysis of droppings to describe diets of small birds. *Journal of Field Ornithology* 56:165–174.
- RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335–337.
- REUDINK, M. W., P. P. MARRA, T. K. KYSER, P. T. BOAG, K. M. LANGIN, AND L. M. RATCLIFFE. 2009. Non-breeding season events influence sexual selection in a long-distance migratory bird. *Proceedings of the Royal Society B* 276:1619–1626.
- ROGERS, C. M. 1987. Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* 68:1051–1061.
- ROGERS, C. M., AND J. N. M. SMITH. 1993. Life-history theory in the nonbreeding period: trade-offs in avian fat reserves. *Ecology* 74:419–426.
- SHERRY, T. W., AND R. T. HOLMES. 1996. Winter habitat quality, population limitation, and conservation of neotropical–nearctic migrant birds. *Ecology* 77:36–48.
- SHERRY, T. W., M. D. JOHNSON, AND A. M. STRONG. 2005. Does winter food limit populations of migratory birds?, p. 414–425. *In* R. Greenberg and P. P. Marra [EDS.], *Birds of two worlds*. Johns Hopkins University Press, Baltimore.
- STRONG, A. M., AND T. W. SHERRY. 2000. Habitat-specific effects of food abundance on the condition of Ovenbirds wintering in Jamaica. *Journal of Animal Ecology* 69:883–895.
- STRONG, C. M., D. R. BROWN, AND P. C. STOFFER. 2005. Frugivory by wintering Hermit Thrush in Louisiana. *Southeastern Naturalist* 4:627–638.
- STUDDS, C. E., T. K. KYSER, AND P. P. MARRA. 2008. Natal dispersal driven by environmental conditions interacting across the annual cycle of a migratory songbird. *Proceedings of the National Academy of Sciences of the United States of America* 105:2929–2933.
- TIBBETS, T. M., L. A. WHEELLESS, AND C. MARTÍNEZ DEL RÍO. 2008. Isotopic enrichment without change in diet: an ontogenetic shift in $\delta^{15}\text{N}$ during insect metamorphosis. *Functional Ecology* 22:109–113.
- WINKER, K., J. H. RAPPOLE, AND M. A. RAMOS. 1990. Population dynamics of the Wood Thrush in southern Veracruz, Mexico. *Condor* 92:444–460.
- WITTER, M. S., AND I. C. CUTHILL. 1993. The ecological costs of avian fat storage. *Philosophical Transactions of the Royal Society of London B* 340:73–92.