THE ROLE OF FOOD AVAILABILITY IN THE WINTERING ECOLOGY OF HERMIT THRUSHES (*CATHARUS GUTTATUS*)

by

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(Under the Direction of Robert J. Cooper)

ABSTRACT

The role of diet in limiting migratory birds during the non-breeding period is poorly understood in part due to the complexities of quantifying food availability and the food consumed by birds. We tracked changes in winter food availability and the diet of the short-distance migratory bird, the Hermit Thrush (*Catharus guttatus*), in a southeastern mixed hardwood-pine forest. Larger-bodied birds, predominately males, maintained territories with higher arthropod abundance and had a greater proportion of arthropods in their diet. Larger-bodied birds experienced less variation in diet and fat loads over the winter, suggesting that smaller-bodied females gain fat midwinter to cope with unpredictable and lower-quality resources. Contrary to previous research, our results suggest that arthropod density, not fruit abundance, determines territory quality, and that smaller birds are behaviorally excluded from optimal territories. Future research should determine the long-term consequences of food limitation on winter condition and impacts on breeding success and survival.

INDEX WORDS: Hermit Thrush, *Catharus guttatus*, nonbreeding season, habitat quality, food supply, fruit, arthropods, territory

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

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” (Pulliam and Millikan 1982). Although survival is certainly a prerequisite for any measure of success, we now know events in the winter that influence body condition carry over into the breeding season. Through the use of stable-isotopes as tracers of winter habitat quality, for example, American Redstarts (*Setophaga ruticilla*) leaving winter habitat later have been shown to arrive at breeding areas later and in poorer physical condition than birds that leave early (Marra et al. 1998) and have lower breeding success (Norris et al. 2004). Young American Redstarts occupying lower quality winter habitats must migrate further north to find unoccupied territories or adequate food sources for breeding as a result of their late departure (Studds et al. 2008). The role of winter in the context of the entire annual cycle has been under studied until recent years. To better understand the role of winter in driving subsequent events in the annual cycle of migratory birds, we must continue to build a basic understanding of what factors influence the physical condition of birds during the non-breeding season.

Food availability often has been shown to be the key limiting resource for birds during the nonbreeding season (Hutto 1985, Strong and Sherry 2000, Johnson and Sherry 2001, Sherry et al. 2005, Brown and Sherry 2006). Birds in the nonbreeding season often face harsh conditions that may limit access to food for some individuals. In tropical regions, drought or dry conditions may limit arthropod availability in some habitats (Dugger et al. 2004, Brown and Sherry 2006). American Redstarts are aggressively territorial in winter and sexually segregate, allowing males greater access to higher quality habitat with higher arthropod availability than that in territories occupied by females or juveniles (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000). In temperate regions, low temperatures can reduce winter arthropod abundance and increase energetic demands. The shorter days also require birds to find more food in less time. Furthermore, the potential for snowfall can make some resources unpredictable for some birds (Rogers 1987, Rogers and Smith 1993).

Several studies have addressed the mechanisms by which birds cope with changes in food availability over the non-breeding period. Ground foraging birds experience a higher risk of food limitation due to snow cover than birds in other foraging guilds and often compensate for unpredictable resources by maintaining higher fat reserves (Rogers 1987, Rogers and Smith 1993). Northern Juncos (*Junco hyemalis*) wintering in more northern latitudes maintained higher fat stores than individuals in southern populations (Rogers et al. 1993). In the tropics, Ovenbirds (*Seiurus aurocapilla*) maintained higher fat stores in areas with lower ant biomass (Strong and Sherry 2000). Non-territorial Wood Thrushes (*Hylocichla mustelina*) in Mexico maintained higher fat than their territorial conspecifics (Winker et al. 1990). Additionally, birds may take advantage of abundant food by increasing fat reserves. In one food supplementation study, several species of birds with access to supplemented food increased fat reserves (Rogers and Heath-Coss 2003). In another study of wintering Song Sparrows (*Melospiza melodia*), juvenile females increased fat stores when food was supplemented (Smith et al. 1980). In general, individuals in lower quality habitats or in unpredictable environments may maintain higher body fat stores to compensate for the potential for future limited food (Rogers 1987).

For many birds, the ability to switch diet to meet nutritional and energetic needs is crucial to maintaining condition. Diet switching occurs when preferred food types decline or become available or preferences change with changing needs (Bairlein 1996). For omnivorous songbirds, fruit is a common addition to the winter diet. Overall, fruit is considered to be nutritionally poor and insufficient alone for maintaining body mass for many birds (Levey and Karasov 1989, Long and Stouffer 2003, Pearson et al. 2003). Although fruit can be high in carbohydrates and lipids for energy, it lacks the protein and nitrogen necessary for maintaining muscle mass (Blem 1990). Fruits vary in sugar, lipids, nitrogen and other macronutrient content (Bosque and Pacheco 2000, Levey and del Rio 2001). Fruits with high lipid content can be directly incorporated into the fat reserves of birds (Podlesak and McWilliams 2007) and tend to be selected if they are easy to obtain. Despite these nutritional limitations, fruit is often abundant, easy to acquire, and may be more valuable for its energy content than its macronutrients when other sources become scarce.

Another consideration for maintaining body mass in winter is the potential effect of switching diet on physical condition. Nutritional components of food sources vary and can also influence how they are absorbed in the digestive tract. Insectivorous birds have longer gut retention times necessary for extracting macronutrients from arthropods (Levey and Karasov 1989). Large fleshy berries have a high sugar and moisture content, which is quickly assimilated and may reduce digestive efficiency if retained in the gut longer than necessary (Levey and del Rio 2001). American Robins (*Turdus migratorius*) are capable of shortening gut retention times when consuming fruit. The rapid absorption of sugars triggers digestion to move faster; however, there is a lag of several days in returning to a longer gut retention time when they switch back to insects, causing the insects to be passed before being thoroughly digested (Levey and Karasov 1992). Lipid-rich fruits require a longer gut retention time and are often consumed in greater quantities than sugary fruits by birds that are primarily insectivorous, but even these fruits are not always digested efficiently (Witmer and Van Soest 1998). In general, our understanding of how wintering birds tolerate and adjust to resources of varying quality and abundance is poor.

Assessing diet in songbirds, regardless of method, generally requires repeated observations over a broad period to determine the contribution of multiple sources of food. Observational data can be biased by the type and location of food items, habitat structure, and foraging strategy, skewing results towards more easily seen items (Rosenberg and Cooper 1990). For example, it may be more difficult to observe birds that forage higher in the canopy or in dense vegetation. Furthermore, birds eating sessile and showy fruits are easier to observe than those eating cryptic arthropods. To avoid these and other biases, diet studies have directly examined the contents of the digestive system and its remnants (White and Stiles 1990, Blake and Loiselle 1992, Servat 1993, Burger et al. 1999, Deloria-Sheffield et al. 2001, Strong et al. 2005). Directly examining stomach content is lethal and precludes repeated observations on individual birds. Forced regurgitation using emetics to examine stomach contents is invasive and has potential for injury and death (Johnson et al. 2002, Carlisle and Holberton 2006). Fecal samples provide similar results and are non-invasive to obtain; however, the contents are often degraded and difficult to identify (Rosenberg and Cooper 1990). Although the above methods provide some insight into diet, they all have problems and are limited by the frequency and timing of capture. That is, a diet sample obtained using one of the above techniques represents what the bird ate during only a few hours beforehand; inferences for longer time frames require more samples.

In the last decade, measuring stable isotope ratios has become a useful tool in identifying the source diet at varying temporal and geographic scales (Marra et al. 1998, Hobson et al. 2001, Dalerum and Angerbjorn 2005, Podlesak et al. 2005, Phillips and Eldridge 2006). In concert with other estimates, such as available food and fecal sampling, stable isotope analysis provides a composite picture of an animal's diet. Heavy stable isotopes, such as ^{13}C and ^{15}N, are naturally occurring in trace amounts and are incorporated into the tissues of plants and animals (Gannes et al. 1998). Tissues become more enriched in ^{13}C when an animal consumes food at higher trophic levels. This process of tissue enrichment, called discrimination, is due to the selection of lighter isotopes (^{12}C and ^{14}N) during physiological processes, such as metabolism, which results in the accumulation of heavier isotopes (^{13}C and ^{15}N) in tissues (Martínez del Rio and Wolf 2005, Sulzman 2007). The ratio of heavy isotopes to light isotopes (^{13}C/^{12}C and ^{15}N/^{14}N) as it deviates from a standard is represented by δ^{13}C and δ^{15}N. Such distinct signatures make it possible to estimate where similar animals are eating trophically. For example, whole blood of insectivorous bats was more enriched in ^{13}C and ^{15}N isotopes resulting in the more positive δ^{13}C and δ^{15}N signatures than the whole blood of frugivorous bats (Herrera et al. 2001). Furthermore, because tissues of the body are replaced at measurable intervals, changes in δ^{13}C and δ^{15}N signatures can be used to measure change in diet across the same interval (Thompson and Furness 1995, Dalerum and Angerbjorn 2005, Miron et al. 2006). The rate of isotopic turnover (2 half-lives) is dependent on the type of tissue being replaced and the mass of the organism and will influence the window in which one is able to estimate a diet shift. Breath, plasma, whole blood and muscle tissues have increasingly longer turnover rates (Podlesak et al. 2005). Turnover of δ^{13}C in plasma is less than one day in a small warbler and 6 days in a crow (Hobson and Clark 1993, Hobson and Bairlein 2003). In that same warbler, turnover rate in whole blood is about 10 days (Hobson and Bairlein 2003).

For Hermit Thrushes, both fruit and arthropods appear to be important for maintaining overwinter condition. Fruit abundance is positively correlated with Hermit Thrush abundance (Kwit et al. 2004, Strong et al. 2005). Additionally, the analysis of fecal samples revealed peak fruit consumption to be in January, while the presence and proportion of arthropods in fecal samples increased in late winter and spring (Strong et al. 2005), suggesting that fruit is an important food item to this species, although arthropods may also be a key limiting factor during some periods of the winter. Despite the evidence that Hermit Thrushes appear to rely heavily on fruit during the winter, captive wintering Hermit Thrushes given an unlimited supply of insects and fruit chose to consume only insects and exhibited significantly higher fat and mass gain compared with thrushes, which lost mass, that were fed only fruit (Long and Stouffer 2003). Furthermore, experimental fruit removal did not result in changes in territory size or space use (Brown and Long 2006). To explain this result, Brown and Long (2006) hypothesized that it was saturation of available habitat that 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, we cannot adequately assess the significance of the experimental reduction in overwinter fruit resources.

As the winter season progresses and temperatures fall, arthropod availability declines. Winter residents, such as the Hermit Thrush, may be forced to depend more on available fruit where arthropod biomass is limited. Although many of the previous studies were successful at linking fruit to Hermit Thrush abundance, these studies did not assess arthropod availability or measure the effects of a winter diet shift on body mass, condition or fat stores. The objective of this study was to first identify how the diet of Hermit Thrushes changes in relation to food availability over the winter. To do this we measured territory-level differences in food availability multiple times during the winter and assessed how territorial behavior influenced food acquisition. Our second objective was to document if differences in fruit and arthropods consumption occurred and if there were measurable effects on body condition. We predicted that limited food resources would result in competition for higher quality habitat, and that Hermit Thrushes would preferentially consume insects over fruit.

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CHAPTER 2

LIMITED RESOURCES DRIVE DIFFERENCES IN HABITAT OCCUPANCY DURING THE NONBREEDING SEASON IN AN OMNIVOROUS SONGBIRD.[1]

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ABSTRACT

The role of diet in limiting migratory birds during the non-breeding period is poorly understood in part due to the complexities of quantifying food availability and avian diet. We tracked overwinter changes in arthropod and fruit availability for the short-distance migratory bird, the Hermit Thrush (*Catharus guttatus*), in a southeastern mixed hardwood-pine forest. Fruit availability declined overwinter and arthropods tracked changes with temperature. Concurrently, using fecal samples and stable isotopes, we tracked diet consumption. Fruit declined in fecal samples from early to mid season and $\delta^{13}C$ and $\delta^{15}N$ isotope signatures in blood became more enriched consistent with a decline in fruit consumption and an increase in arthropod consumption. Larger-bodied birds, predominately males, maintained territories with higher arthropod abundance and had a greater proportion of arthropods in their diet. Larger-bodied birds experienced less variation in diet (as indicated by $\delta^{13}C$) and fat loads overwinter, suggesting that smaller bodied females gain fat midwinter to cope with unpredictable and lower-quality resources. These data are consistent with both a size-mediated form of dominance and sexual habitat segregation such that smaller bodied birds, largely females, are behaviorally excluded from optimal territories. Future research should focus on the long-term consequences of food limitation and size and sex-mediated dominance behavior on both within season condition of birds and on subsequent breeding success and survival.

INTRODUCTION

Food availability often has been shown to be the key limiting resource for birds during the nonbreeding season (Hutto 1985, Strong and Sherry 2000, Johnson and Sherry 2001, Sherry et al. 2005, Studds and Marra 2005, Brown and Sherry 2006). In tropical regions, the onset of dry conditions in spring typically limits arthropod availability (Dugger et al. 2004, Brown and Sherry 2006). American Redstarts, for example, are aggressively territorial in winter and sexually segregate, with males out-competing females for territories in higher quality habitat that contain greater arthropod availability (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000). Through the use of stable-isotopes as tracers of winter habitat quality, American Redstarts (*Setophaga ruticilla*) leaving winter habitat later have been shown to arrive at breeding areas later and in poorer physical condition (Marra et al. 1998) and have lower breeding success (Norris et al. 2004) than birds that leave early. The role of winter in the context of the entire annual cycle has been severely understudied until recent years. To better understand the role of winter in driving subsequent events in the annual cycle of migratory birds, we must continue to build a basic understanding of what factors can compromise and limit the physical condition of birds during the non-breeding season.

Several studies have addressed the mechanisms by which birds cope with unpredictable food availability over the non-breeding period. In temperate regions, low temperatures can reduce winter arthropod abundance and increase energetic demands. The shorter days also require birds to find more food in less time. Furthermore, the potential for snowfall can make some resources unpredictable for some birds (Rogers 1987, Rogers and Smith 1993). Ground foraging birds, such as the Northern Junco (*Junco hyemalis*), experience a higher risk of food limitation due to snow cover than birds in other foraging guilds and often compensate for unpredictable resources by maintaining higher fat reserves (Rogers 1987, Rogers and Smith 1993). In the tropics, Ovenbirds (*Seiurus aurocapilla*) maintained higher fat stores in areas with lower ant biomass (Strong and Sherry 2000). Non-territorial Wood Thrushes (*Hylocichla mustelina*) in Mexico maintained higher fat loads than territorial individuals (Winker et al.

1990). In contrast, some species of birds have been shown to increase fat reserves in the presence of supplemental food (Rogers and Heath-Coss 2003). In general, however, individuals in lower quality habitats or in unpredictable environments maintain higher body fat stores to compensate for the potential for future food limitation (Rogers 1987).

The ability to switch diets to meet nutritional and energetic needs is crucial to maintaining condition. Diet switching occurs when preferred food types decline or become available or preferences change with changing needs (Bairlein 1996). For an omnivorous songbird, fruit is a common addition to the diet in winter. Fruit, however, is considered to be nutritionally poor and insufficient for maintaining body mass (Levey and Karasov 1989, Long and Stouffer 2003, Pearson et al. 2003). Although high in carbohydrates and lipids, both necessary for energy, fruit often lacks the protein and nitrogen necessary for maintaining muscle mass (Blem 1990). Fruits vary in sugar, lipids, nitrogen and other macronutrient content and often contain secondary compounds that may limit fruit consumption (Bosque and Pacheco 2000, Levey and del Rio 2001). Despite nutritional limitations, fruit is often abundant, easy to acquire, and may be more valuable for its immediate energy content than its macronutrients when other sources become scarce.

Assessing diet and its impacts on the condition of songbirds, regardless of method, generally requires repeated observations over a broad period to determine the contribution of multiple sources of food. Observational data can be biased by the type and location of food items, habitat structure, and foraging strategy, skewing results towards more easily seen items (Rosenberg and Cooper 1990). For example, it may be more difficult to observe birds that forage higher in the canopy or lower in dense vegetation. Furthermore, birds eating sessile and showy fruits are easier to observe than those eating cryptic arthropods. To avoid this bias, diet studies have directly examined the contents of the digestive system and its remnants (White and Stiles 1990, Blake and Loiselle 1992, Servat 1993, Burger et al. 1999a, Deloria-Sheffield et al. 2001b, Strong et al. 2005). Directly examining stomach content is lethal and precludes repeated observations on individual birds. Forced regurgitation using emetics to examine stomach contents is invasive and has potential for injury and death (Johnson et al. 2002, Carlisle and Holberton 2006). Fecal samples provide similar results and are non-invasive; however, the contents are often degraded and difficult to identify (Rosenberg and Cooper 1990). Although the above methods provide some insight into diet, they all have problems and are limited by the frequency and timing of capture.

In the last decade, measuring stable isotope ratios has become a useful tool in identifying the source diet at varying temporal and geographic scales (Marra et al. 1998, Hobson et al. 2001, Dalerum and Angerbjorn 2005, Podlesak et al. 2005, Phillips and Eldridge 2006). In concert with other estimates, such as available food and fecal sampling, stable isotope analysis provides a composite picture of an animal's diet. Heavy stable isotopes, such as ^{13}C and ^{15}N, are naturally occurring in trace amounts and are incorporated into the tissues of plants and animals (Gannes et al. 1998). Tissues become more enriched in heavy isotopes when an animal consumes food at higher trophic levels. Because tissues of the body are replaced at measurable intervals, changes in $\delta^{13}C$ and $\delta^{15}N$ signatures can be used to measure change in diet across the same interval (Thompson and Furness 1995, Dalerum and Angerbjorn 2005, Miron et al. 2006).

For Hermit Thrushes, both fruit and arthropods appear to be important for maintaining overwinter condition. Fruit abundance is positively correlated with Hermit Thrush abundance (Kwit et al. 2004b, Strong et al. 2005). Additionally, the analysis of fecal samples revealed peak fruit consumption to be in January, while the presence and proportion of arthropods in fecal samples increased in late winter and spring (Strong et al. 2005). Despite evidence that Hermit Thrushes appear to rely heavily on fruit during the winter, captive wintering Hermit Thrushes given an unlimited supply of insects and fruit chose to consume only insects and exhibited significantly higher fat and mass gain compared with thrushes, which lost mass, that were fed only fruit (Long and Stouffer 2003). Furthermore, experimental fruit removal did not result in changes in territory size or space use (Brown and Long 2006). To explain this result, Brown and Long (2006) hypothesized that it was the saturation of available habitat that 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, we cannot adequately assess the significance of the experimental reduction in overwinter fruit resources.

As the non-breeding season progresses and temperatures decline, arthropod availability also declines. Winter residents, such as the Hermit Thrush, may be forced to depend more on available fruit where arthropod biomass is limited. Although many of the previous studies were successful at linking fruit to Hermit Thrush abundance, these studies did not assess arthropod availability or measure the effects of a winter diet shift on body mass, condition or fat stores. The objective of this study was to first identify how the diet of Hermit Thrushes changes in relation to food availability over the winter. To do this we measured territory-level differences in food availability multiple times during the winter and assessed how territorial behavior influenced food acquisition. Our second objective was to document if differences in fruit and arthropod consumption occurred and if there were measurable effects on body condition. We predicted that limited food resources would result in competition for higher quality habitat, and that thrushes would preferentially consume insects over fruit.

METHODS

Study System. This study was conducted 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). Research was conducted on three 5-ha plots within the preserve. The forest in these areas is primarily mixed oak species (*Quercus spp.*) and loblolly pine (*Pinus taeda*) overstory with a moderate to dense understory of waxmyrtle (*Myrica cerifera*), beautyberry (*Callicarpa americana*), farkleberry (*Vaccinium arboretum*), inkberry (*Ilex glabra*) and oak regeneration. This habitat is common along the southeastern coast and often contains a dense understory used by many species of birds, including Hermit Thrushes.

Study Species. Hermit Thrushes are a suitable species for this study because they are common and territorial on the non-breeding grounds (Brown et al. 2000, Brown et al. 2002). Their omnivorous diet and foraging behavior in winter also makes them ideal for a study of the influence of diet on overwinter condition. Also, because of their size, at 30g, they are able to carry radio transmitters to facilitate observations and recapture.

Hermit Thrushes are short-distance migrants that breed throughout the northeastern U.S., most of Canada and much of the western U.S, and winter in southeast U.S., through Mexico to Guatemala. It is the only species of *Catharus* that winters in North America, switching from a breeding diet of mainly arthropods to wintering diet heavily supplemented with fruits (Jones and Donovan 1996).

Wintering Hermit Thrushes maintain territories of less than 1 ha (minimum convex polygon), and show fidelity to these sites throughout the season. No differences in territory size were found due to age or sex (Brown et al. 2000), or between habitat types in Louisiana (Brown et al. 2002). Evidence that Hermit Thrushes are limited by resources include (1) territorial behavior, (2) home ranges that abut or slightly overlap one another, (3) the presence of non-territorial birds (floaters), and (4) quickly filled territory vacancies (Brown et al. 2000).

*Territory Estimation***.** Because Hermit Thrushes are difficult to observe, we used radio transmitters to track the movements of individuals and to map territories. Transmitters, attached in January 2005, weighed 1.5g (5% of a 30g bird) and lasted an average of 10 weeks. We attached radio transmitters (Holohil, Model BD-2, with two harness tubes) using a modified harness method with a thread looped through harness tubes and under the thighs, securing the transmitter just above the tail (Rappole and Tipton 1991). Attempts were made to recapture all individuals with transmitters for removal. Birds were tracked every other day for an average of 30 observations before recapture. Territory sizes estimated from minimum convex polygons (MCP) were plotted against the number of observations to determine the appropriate number of observations need to estimated territory size. Territory size began to plateau around 15-20 observations. In 2007, transmitters were deployed in two periods, beginning in November and January, respectively, to assess changes in territory size from early to late winter. Because of the shorter radio tracking period, we were able to reduce the transmitter weight. Transmitters used in 2007 weighed 0.75g (less that 3% of a 30g bird) and lasted an average of 4 weeks. Birds were tracked at least once a day for an average of 30 observations each before recapture. An attempt was made to place transmitters on the same birds in the second time period but we were only successful in 80% of the cases (n = 8). Territories were mapped in ArcView 3.2. Territory sizes were measured using conv_hulls_pts.avx (ArcView extension, Jeff Jenness (2006)), which creates minimum convex polygons (MCP) around point observations.

Food Availability. To estimate changing fruit availability on plots in 2005 in November, January and March**,** we established transects by randomly selecting an initial start location and select additional start locations every 50 meters along the edge of each plot. The average transect length was approximately 200m long and 2 meters wide and each plot had 4 or 5 transects. All fruiting plants in each transect were tagged and available fruit counted. For the larger shrubs, where large berry production or shrub height made a count impractical, we estimated fruit abundance by counting a representative branch and multiplying the count by the number of total branches.

During the 2007 winter season, we estimated changing fruit availability in Hermit Thrush territories in November, January and March. Territory estimates began in November (late fall), two months earlier than in 2005, allowing us to assess fruit within territories before it had been consumed. ArcView 3.2 was used to randomly select points within territory polygons to sample fruit. Random point selection was limited so that each sampling area would not overlap. Locations were flagged and all fruit in the 5m-radius was tagged and counted or estimated. Samples in 2007 were pooled to estimate changes in fruit availability across plots for comparison against 2005 availability.

In the 2007 winter season, we also estimated changing arthropod abundance in November, January and March within the same 5-meter radius area that fruit was sampled. A $0.5m^2$ area frame was placed near center of the sampling area on top of the leaf litter using methods modified from Strong and Sherry (2000). Observers spent 5 minutes searching the designated area by scanning and flipping leafs individually to mimic a foraging Hermit Thrush (Jones and Donovan 1996). We identified arthropods to Family (when possible) and Order and recorded length (mm, head to abdomen tip) to create an index (average of sample sum of arthropod lengths) of arthropod biomass.

Capture Methodology**.** In 2005, we captured birds during three periods: Early (December), Mid- (January-February) and Late (March) Winter, averaging 35 days in each period. In 2007, we added a Late Fall period in early November, with each period averaging 13 days. All Hermit Thrushes were captured using mist nets, using a combination of passive and targeted netting with a recorded playback. For passive net capture, we opened an average of 15 mist nets (12m x 3m) from ½ hour before sunrise until noon over a 3-4 day period per site. We also used playbacks of Hermit Thrush vocalizations to attract individuals to the nets. Birds were each banded with an aluminum USGS band and a unique colored band combination to facilitate subsequent identification of individual birds in the field. Birds caught early in the season were targeted for recapture during subsequent capture periods, and net effort and placement were determined by previous observations of banded and unbanded birds. Birds were released immediately after being processed.

Birds were aged and measured at the time of capture. Birds were aged using plumage characteristics, such as greater coverts and rectrix shape (Pyle 1997). Mass and furcular fat stores were measured at every capture to assess body condition. Birds were weighed to the nearest 0.1g on an electronic Ohaus balance and wing, tail and tarsus were measured using a wing ruler and an electronic caliper. We visually assessed furcular fat levels. In 2005, fat scores ranged from 0-4 (0 = no fat, 0.5 = trace, 1 = continuous thin sheet of fat, 2 = fat filling furculum and level with breast, 3 = fat bulging from furculum, 4 = any amount greater than 3). However, most birds scored below 1, and scores were insufficiently precise for analysis. In 2007, fat scores were further refined and ranged from 0-5 (0 = no fat, 1 = 5-25% full, 2 = 30-60% full, 3 = 65-95% full, 4 = 100% full, 5 = any amount greater than 4).

Several tissue samples were taken at the time of capture. Blood samples were collected for DNA sexing and stable isotope analysis. Blood (100-120µl) samples were drawn from the brachial vein into a non-heparinized capillary tube and immediately transferred to sterile vials and stored in a cooler in the field until samples could be placed in a freezer (-20°C). Blood for DNA sexing was placed on sterile card (10µl) provided by and analyzed by Avian Biotech International (Tallahassee, FL). We also collected fecal samples from the cotton bags used for holding birds or from directly beneath the 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 due to the relatively compact nature of the droppings. Additionally, the right third rectrix was plucked to induce a new feather to assess physical condition during regrowth (Grubb 1989).

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

Blood samples for stable isotope analysis were kept frozen until freeze-dried. Vials were punctured with a dissecting probe to allow moisture to escape in the vacuum of the freeze-dryer where they remained for at least 48 hours. Dried whole blood was ground into a powder using the tip of a lab spatula before it was weighed (1 ± 0.2mg) into 5 x 9mm tin capsules. Capsules were rolled and crimped and placed in a numbered cell plate and sent to the UC Davis Stable Isotope Facility (Davis, California) for stable δ^{13}C and δ^{15}N isotope analysis. Samples were analyzed using an ANCA-GSL & PDZ Europa 20-20 isotope ratio mass spectrometer. Results are presented as deviations from standard ratios (VPDB for δ^{13}C and Air for δ^{15}N).

Statistical Analyses. Changes in δ^{13}C and δ^{15}N, mass and fat were assessed using repeated-measures mixed models (PROC MIXED from SAS Institute), with models including age, sex and interaction effects with adjusted Tukey mean comparisons. We used the coefficient of variation (CV) of fat scores, mass and δ^{13}C signatures for individuals captured 3 times to compare the variability in diet and fat and mass. We used two-tailed t-tests, ANOVA and linear regression for all other tests, where appropriate.

RESULTS

Food availability. Fruit availability declined over winter (Figure 2.1a). In 2005, the January and March counts were only 2% and 1% of the November counts, respectively. In 2007, 28% and 1% of the fruit remained in January and March counts from the November count. The above percentages are from counts that were pooled for all fruit species; however, *M. cerifera* (representing 63% and 98% of fruit sampled in 2005 and 2007, respectively) declined at approximately the same rate as the pooled samples in their respective years. In 2007 we also measured spatial variability of fruit. The average fruit sample in 2007 (n = 157) yielded 3771 ± 1385 SE berries in November and declined to 1050 ± 398 SE and 42 ± 16 SE in January and March, respectively. Of the 157 samples, 68 (42%) had no fruit.

Arthropod availability in 2007 declined from November to January, but rose in March, tracking temperature change (Figure 2.1b: ANOVA, DF = 2, F = 45, $P < 0.0001$). Arthropod data were not available for 2005.

Diet of all individuals. In 2005, fruit was identified in 71% (n = 14) and 81% (n = 21) of the fecal samples in early and mid-winter and declined to 29% (n =17) of late winter samples. In 2007, fruit was found in the feces of 60% (n = 10) and 64% (n = 22) of the birds sampled in the late fall and early winter periods respectively, and then declined to 33% (n = 18) and 11% (n = 18) in mid and late-winter (Figure 2.2b). *M. cerifera* was found in two-thirds of the fecal samples containing fruit, distantly followed by *I. glabra*, *C. americana*, *V. arboretum*, and *I. vomitoria*. *M. cerifera* was identified in every sampling period in both years. Eight other unidentified species, often only represented by one sample, were found in fecal samples in 2005 and 2007. One-third of fecal samples with fruit contained multiple species. Identifiable arthropod parts (legs, mouth parts, wing fragments) were present in all but 3 of the 122 samples from 2005 and 2007.

In both years, $\delta^{13}C$ and $\delta^{15}N$ signatures in whole blood of all captured individuals changed over the winter, with no influence of age or sex (Table 2.1, Figure 2.2). In 2005, the $\delta^{15}N$ signatures in blood were more positive in the mid- and late winter periods than early winter (Table 2.1, Figure 2.2a: $F_{2,15} = 2.96$, $P = 0.08$). In 2005, $\delta^{13}C$ signatures became significantly more positive in late winter (Table 2.1, Figure 2.2b: $F_{2,15} = 30.16$, $P < 0.0001$). In 2007, $\delta^{15}N$ signatures were more positive from the early and midwinter periods, but then become more negative in late winter (Table 2.1, Figure 2.2a: $F_{3,33} = 9.1$, $P = 0.0002$). The $\delta^{13}C$ signatures in the mid- and late winter periods of 2007, were more positive than the late fall and early winter periods (Table 2.1, Figure 2.2b: $F_{3,33} = 48.98$, $P < 0.0001$). When non-recaptures were omitted from the analysis, only the $\delta^{13}C$ model changed. In addition to the strong period effect ($F_{3,31} = 59.61$, $P < 0.0001$) there was also a sex effect ($F_{1,15} = 5.57$, $P = 0.03$).

Body mass, fat stores and feather growth. These analyses include all individuals captured once as well as recaptures. Birds were at their heaviest midwinter in both years and then declined in late winter (Figure 2.3; 2005: $F_{2,16} = 10.37$, $P = 0.001$; and 2007: $F_{3,33} = 11.69$, $P < 0.0001$). Mass was not influenced by age or sex, when wing was used as a covariate, in any period in either year (Table 2.2, wing effect: 2005: $F_{1,37} = 3.5$, $P = 0.07$; and 2007: $F_{1,37} = 6.04$, $P = 0.02$). Changes in fat stores were similar to mass changes in 2007, where fat scores peaked in January (repeated measures mixed model for period, $X^2 = 9.81$, n = 86, $P = 0.02$). The rate of feather regrowth was significantly slower in feathers induced in January in both years versus feathers induced in November and December (2005: $F_{1,22} = 5.93$, $P = 0.02$; 2007: $F_{2,12} = 11.27$, $P = 0.002$). In addition to slower feather growth, some feathers failed to induce in the late winter. In 2005, all pulled feathers regrew midwinter, but one feather did not regrow in late winter. A total of 31% (5/16) of late winter feathers failed to grow at the time of recapture compared to 0% and 6% in early and mid winter of 2007, respectively.

Population Structure and Territory Estimation. We captured 81 individuals in 2005 and 2007. Males captures were 56% of all captures and was consistent between years ($X^2 = 0.36$, n = 89, $P = 0.55$). Adults comprised 67% of captured individuals, which is significantly greater than 1:1 ($t = 2.34$, n = 87, $P = 0.02$), and did not vary between years ($X^2 = 1.13$, n = 87, $P = 0.29$). Nine individuals (21%) from 2005 were recaptured or resighted in 2007. Returning birds had similar sex and age ratios as the larger population, with 55% male and 56% adults. Returning birds were captured or resighted within 50 meters of their 2005 capture location.

We mapped the movements of 30 individuals in each of 2005 and 2007 using radio transmitters. Territory sizes averaged 0.72 ± 0.3 ha (n = 24) and did not differ by age (t = 1.74, DF = 22, P = 0.10) or sex (t = 1.39, DF = 22, P = 0.18). There was no difference in territory size between years (t = 0.36, DF = 22, P = 0.72). Territories of remeasured individuals did not change from early winter to late winter (paired t-test, n = 8, t = 0.56, DF = 7, P = 0.59). Two individuals were mapped in both years and maintained similar territories. We detected four floaters (14% of radio-tracked birds), which we defined as individuals whose 90% MCP were outliers from the normal distribution of all individuals. These were excluded from calculations of territory size. Floaters (n = 4, 3 males and 2 adults) movements ranged from 1.5 to 50 ha.

Territory Relationships. We were able to measure the food abundance overwinter on the territories of nine birds in 2007. We found no relationship between territory size and fruit (Figure 2.3a: R^2 = 0.20, n = 9, P = 0.23) or arthropod density (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).

Larger birds, as measured by wing length, occupied territories with higher arthropod density (Figure 2.4a: R^2 = 0.54, n = 9, P = 0.02) and lower fruit density (R^2 = 0.57, n = 9, P = 0.02). Larger birds also had less negative δ^{13}C signatures in whole blood in early winter (Figure 2.4b: R^2 = 0.79, n = 9, P = 0.001). Less negative δ^{13}C signatures in these birds were associated with lower fruit density (R^2 = 0.65, n = 9, P = 0.009) and higher arthropod density (Figure 2.4c: R^2 = 0.37, n = 9, P = 0.08).

Recaptured Hermit Thrushes. Here, we examined the relationship between diet and condition of individuals recaptured multiple times in 2007. In midwinter, greater enrichment of ^{13}C (i.e., more positive) and ^{15}N isotopes in blood was associated with mass gains (Figure 2.5a, δ^{13}C: $R^2 = 0.53$, $n = 16$, $P = 0.002$ and δ^{15}N: $R^2 = 0.50$, $n = 16$, $P = 0.002$) and increased fat loads ($X^2 = 4.92$, $n = 16$, $P = 0.02$). More negative δ^{13}C signatures in early winter resulted in greater change in δ^{13}C signatures mid winter (Figure 2.5b: $R^2 = 0.54$, $n = 16$, $P = 0.001$). Birds that exhibited greater variability in δ^{13}C signatures overwinter also experienced greater variation of fat loads overwinter ($R^2 = 0.28$, $n = 14$, $P = 0.04$). The δ^{13}C and δ^{15}N signatures were highly correlated ($R^2 = 0.69$, $n = 16$, $P < 0.001$) in this period. Mass changes were positively correlated with changes in fat scores throughout the winter season (Nov-Dec: $X^2 = 4.41$, $n = 9$, $P = 0.04$; Dec-Jan/Feb: $X^2 = 9.01$, $n = 17$, $P = 0.003$; Jan/Feb-Mar: $X^2 = 23.46$, $n = 15$, $P < 0.0001$). There was no relationship between mass and fat changes and change in δ^{13}C and δ^{15}N isotope signatures in early or late winter. Additionally, birds that increased mass and fat in early winter typically lost the most mass and fat by late winter (mass: $R^2 = 0.28$, $n = 14$, $P = 0.05$ and fat: $R^2 = 0.34$, $n = 14$, $P = 0.03$).

Just as in the smaller subset of birds with associated food data, larger birds also had more positive δ^{13}C signatures in early winter (Figure 2.5c: $R^2 = 0.47$, $n = 16$, $P = 0.003$), and their δ^{13}C signatures were less variable overwinter (coefficient of variance: $R^2 = 0.31$, $n = 14$, $P = 0.04$). Although body size was not correlated with mass change ($R^2 = 0.0$, $n = 16$, $P = 0.92$) or δ^{13}C changes ($R^2 = 0.09$, $n = 16$, $P = 0.25$), smaller birds showed a greater increase in fat scores in midwinter ($X^2 = 4.54$, $n = 17$, $P = 0.03$) and a trend towards greater losses in fat in late winter ($X^2 = 2.43$, $n = 15$, $P = 0.1$).

DISCUSSION

Food Abundance and Diet. The rate of fruit removal at this site was similar to that of other studies in the region (McCarty et al. 2002, Kwit et al. 2004a). Fruit was depleted faster in 2005, which had cold temperatures earlier in the winter, than 2007 (Figure 2.1a, b). This finding is consistent with other studies that found fruit resources are depleted faster in colder years as arthropods decline and energetic demands increase (Kwit et al. 2004a). It is also possible that differences in removal rates could be attributed to differences in fruit sampling methods between years or differences in yearly fruit production, which were not measured. However, sampling differences cannot account for changes in consumption. Both fecal samples and $\delta^{13}C$ signatures support higher consumption of fruit midwinter in 2005 following a colder December. The majority (81%) of fecal samples in January 2005 contained fruit compared to only 33% containing fruit in January 2007. This is despite the fact that a significant quantity of fruit persisted on plants during this period. This is further anecdotal evidence that, although fruit likely provides a critical emergency resource at times of colder temperatures, arthropods, if available, are the preferred food item by Hermit Thrushes.

Changing $\delta^{13}C$ and $\delta^{15}N$ signatures overwinter demonstrated a clear shift from a fruit dominated diet in early winter to an arthropod diet in late winter. Such shifts are consistent with our data on the background availability of fruit and arthropods over the winter and with the prevalence of fruit and arthropods in fecal samples. Mean $\delta^{13}C$ signatures corresponded closely to fecal proportions for each period and year (Figure 2.2). Stable isotopes of ^{15}N, although exhibiting the same general enrichment, did not track the changes in fecal samples as was found in $\delta^{13}C$. Stable isotopes of ^{15}N became more depleted in March 2005 and March 2007 in contrast to ^{13}C isotopes which tended to become more enriched. Depletion in ^{15}N could be due to a trophic-level shift in consumption within arthropod communities. Early spring marks the emergence of different arrays of arthropod communities, such as larval lepidopterans, which are lower trophically, and therefore more isotopically depleted of ^{15}N than predatory and adult arthropods (Gannes et al. 1998, Tibbets et al. 2008).

Changes in δ^{13}C and δ^{15}N in late winter may also reflect more than changes in the consumption of arthropods. The enrichment of ^{13}C and ^{15}N in blood, suggestive of continued diet shift from fruit to arthropods, may have been dampened or masked in the late winter as a result of the fat and mass changes experienced by many birds by the end of the winter (Figure 2.4). It is likely that the levels of stable isotopes found in blood reflect a mix of internal and external sources of fat, and potentially, protein. Given this, we expect δ^{13}C signatures to be more depleted than their current diet would suggest, since we expect that fat reserve would reflect the carbon signatures of the previous fruit-dominated diet.

Body mass and fat loads were greatest mid-winter in December and January. These periods lie on either side of the shortest day of the year, and reflect mass and fat gains typical of winter fattening seen in many temperate wintering songbirds (Lehikoinen 1987, Rogers 1995), including low-latitude wintering birds (Gosler 2002, Merom et al. 2005). Not only did mass increase mid-winter in both years, but the higher mass loads in January 2005 (Figure 2.4) may have been in response to the rapid drop in temperatures experienced the previous month (Figure 2.1b). Both the higher proportion of fecal samples containing fruit and the relatively enriched ^{13}C diet (Figure 2.2b) indicated that birds were consuming more fruit as a result of this drop in temperature and the likely associated decline of arthropod availability. This is further supported by the faster depletion of fruit resources in 2005 (Figure 2.2a). Fat deposition and subsequent mass gains are common in temperate species subjected to unexpected temperature changes and changing food resources (Rogers 1987, Rogers et al. 1993, Bednekoff et al. 1994, Rogers 1995). In March, as temperature and day length increased, mass also declined significantly (Figure 2.4). It is unknown how much of this mass loss was muscle versus fat in the late winter period.

Whether or not these changes in body mass translate into compromised physical condition remains difficult to assess. One indicator of condition was the use of ptilochronology or induced feather growth. Our results suggested that feather regrowth was significantly slower in late winter, suggesting mass loss did indeed result in a decline in condition. Unfortunately, we were unable to compare feather regrowth between individuals because we could not see growth bars in many of the original feathers to standardize for body size of the Hermit Thrushes (Grubb 1989).

Territories. Once established, Hermit Thrush territories did not change overwinter and individuals returned to the same territories between years. Territory sizes of thrushes in this study were similar to those of wintering individuals in Louisiana (Brown et al. 2000, Brown et al. 2002). Also similarly, male and female Hermit Thrushes maintained neighboring territories in a variety of habitats, and both sexes were observed exhibiting aggressive behavior, such as chasing, chucking and wing-flapping (Brown et al. 2000, Brown et al. 2002). Given the annual site fidelity, and the aggressive behavior observed between neighboring individuals in the field, our data suggest that many of these birds were territorial.

Floaters in our study were present in the same proportion (14% of birds with radio transmitters) as those in Louisiana (Brown et al. 2000) and similar to proportions of floaters in Ovenbird populations in Jamaica (Brown and Long 2007). The presence of floaters is an indicator that all appropriate habitats are fully occupied and selective pressures are acting on a population (Brown 1969).

Sex ratios differed from those reported from a more southerly study on wintering Hermit Thrushes. The ratio of males to females in our study was about 1:1, but populations in Louisiana were only 25% male (Brown et al. 2000), and were consistent with latitudinal segregation described by Stouffer and Dwyer (2003). Adults made up 67% of our populations, which also differs from Brown's (2000) findings in Louisiana of 40% adults. Such patterns of sex and age segregation by latitude could be attributed to differences in habitat quality and/or the timing of migration (Cristol et al. 1999).

Territorial and recaptured individuals. Although some studies have linked Hermit Thrush abundance to fruit abundance (Kwit et al. 2004b, Strong et al. 2005), we found no relationship between territory size and fruit density. Furthermore, experimental alterations of fruit abundance in Louisiana found no effect on Hermit Thrush movements (Brown and Long 2006). The lack of a relationship between fruit abundance and territory size provides some initial support that fruit is not a limiting resource for this species despite the heavy consumption of fruit by many individuals. Rather, we argue, using data on overwinter changes in thrush body condition along with stable carbon isotope data from thrush blood, that arthropod density determines territory quality and, potentially, the subsequent success of individuals overwinter.

Several studies investigating the social systems of birds during the non-breeding season have found sex and age to be important factors in a bird's ability to acquire and maintain high quality territories (Holmes et al. 1989, Marra 2000, Marra and Holmes 2001, Latta and Faaborg 2002). Previous work with Hermit Thrushes found no other evidence of age or sexual segregation, outside of the tendency for females to winter further south than males (Brown et al. 2000, Brown et al. 2002, Stouffer and Dwyer 2003). Conversely, we found a pattern between bird size and its sex along with patterns of habitat occupancy. Specifically, larger, male birds occupied territories associated with a greater arthropod density and not surprisingly had a diet that consisted of a higher proportion of arthropods as indicated by stable isotope analysis (Figures 2.4 and 2.5). Larger birds also had less fruit on their territories, although the reason for this inverse relationship between arthropod and fruit density is unclear. Our results suggest that, in winter, behavioral dominance may be playing a role in driving patterns of habitat occupancy and that arthropods, not fruit, are the limiting resource for this species.

The simultaneous evaluation of changing stable isotopes, body mass and size, and fat loads provided us with important insights into the influence of diet on the condition trajectories of individual birds. A shift in diet to a higher proportion of arthropods was associated with an increase in midwinter mass changes. Larger diet shifts were observed in birds with a higher proportion of fruit in their diet initially (Figure 2.5a, b). Although there was no relationship between body size, diet and mass changes, smaller body-sized birds in this period tended to increase fat loads more than larger birds. Larger-bodied birds had diets that were more consistent over-winter and these birds experienced less variation in fat loads. Smaller-bodied thrushes occupying territories with higher fruit densities in early winter gained fat midwinter likely because of unpredictable and lower-quality resources (Rogers 1987, Cuthill et al. 2000). This is consistent with social dominance found in other species in the nonbreeding season, where dominant birds are better able to secure territories in higher quality habitats.

Sexual habitat segregation is well documented in many wintering species in both the new and old world. Two hypotheses have been proposed to explain this phenomenon: behavioral dominance by larger-bodied males and the alternative, habitat specialization by each sex (Marra 2000). Female redstarts that were upgraded to territories in male-dominated habitat were in better condition than females remaining in scrub, confirming that male dominance excludes females from higher-quality habitats (Marra 2000, Studds and Marra 2005). Male Cape May Warblers (*Dendroica tigrina*) were also found to exclude females from higher quality habitats and were in better physical condition at the end of the winter period (Latta and Faaborg 2002). Some data support the alternative hypothesis of habitat specialization as seen in Hooded Warblers (*Wilsonia citrina*), where females show a preference for shrubby habitats (Morton 1990, Stutchbury 1994), but more experimental work is needed to better assess the importance of this phenomenon in the wild. Regardless, habitat specialization is likely a result of sexual dominance in the birds' history, exerting selective pressures towards female preference (Morton 1990).

Fruit has long been considered to be an inadequate food source for meeting the dietary needs of many bird species. Despite the energy that fruit provides, winter fruits are often high in secondary compounds which can be toxic and may limit the amount an individual can consume over a period of time (Levey and del Rio 2001). Laboratory experiments demonstrated that American Robins (*Turdus migratorius*) limited consumption of otherwise high energy- and protein-rich fruits, even in the presence of no alternative (Levey and Karasov 1989). The reliance on a diet dominated by fruit is a risky proposition. Colder winters could result in faster depletion of fruit resources, leaving individual birds with little to supplement their already low arthropod consumption in mid to late winter. Increasing fat stores provides insurance against potential food declines but also requires longer foraging time and increases the risk of predation, due to both decreased vigilance while foraging and lowered flight performance (Witter and Cuthill 1993).

Behavioral dominance and territoriality can restrict access of subordinate individuals to higher quality resources (Gauthreaux 1978). Such intraspecific competition is likely a result of limited food availability (Terrill 1990, Sherry and Holmes 1996), which can be more of a limiting factor on the wintering than on the breeding grounds (Holmes et al. 1989, Lovette and Holmes 1995). Differential patterns of habitat occupancy caused by the behavioral dominance of larger thrushes may result in smaller subordinate individuals, often females, being relegated to poor sites, with consequences on physical condition and survival.

Conclusions and Future Directions. The stationary portion of the non-breeding season is likely a limiting period for many species of migratory songbirds. In this study, using both direct and indirect methods, we have demonstrated that arthropods form a critical component of winter diet for the Hermit Thrush during the non-breeding season. Larger-bodied and often male birds are able to acquire and defend territories with greater arthropod densities and they consume arthropods in greater proportions than fruit. In midwinter, smaller individuals lacking a stable and sufficient arthropod supply likely compensate by spending more time foraging to increase body mass, but also make themselves more susceptible to predation and starvation in severe winters.

Future research could include experimental alterations in arthropod abundance to confirm that smaller birds consume more fruit as a result of reduced arthropod availability. Possible experiments could include arthropod supplementation on territories of smaller birds and arthropod reduction on territories or larger thrushes. .Additional research could also look for evidence of behavioral dominance across habitat types and latitudes. Efforts should also focus on understanding how these events influence subsequent events in 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 trends may influence the ecology of short-distance migratory birds overwintering in temperate regions has now become essential.

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Table 2.1: Repeated measures mixed-models for $\delta^{13}C$ and $\delta^{15}N$ signatures by year for all recaptured and non-recaptured birds. Means, standard errors and Tukey comparions for period effects are presented in Figure 2.2.

	2005					2007				
		$\delta^{13}C$		$\delta^{15}N$			$\delta^{13}C$		$\delta^{15}N$	
Effect	DF	F	P	F	P	DF	F	P	F	P
Period	2,15	30.16	<.0001*	2.96	0.08	3,33	48.98	<.0001*	9.1	0.0002*
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

Table 2.2: Repeated measures mixed-models for mass by year for all recaptured and non-recaptured birds. Wing was used as a covariate to control for body size. Means, standard errors and Tukey comparions for period effects are presented in Figure 2.3.

	2005			2007		
Effect	DF	F	P	DF	F	P
Wing	1,37	3.5	0.07	1,37	6.04	0.02*
Period	2,16	10.37	0.001*	3,33	11.69	<0.0001*
Age	1,37	1.16	0.29	1,37	0.14	0.71
Sex	1,37	0.01	0.92	1,37	1.47	0.23
Period*Age	2,16	0.3	0.75	3,33	0.49	0.69
Period*Sex	2,16	1.28	0.30	3,33	0.48	0.70

FIGURE LEGEND

Figure 2.1: Food availability and temperature changes in 2005 and 2007 winters. a) Fruit decline in January to 2 and 28% of November availability in 2005 and 2007, respectively. Only 1% remains in March in both years. b) Arthropod availability (mean ± SE) declined from November to December and peaked in March, tracking changes in temperature. 2005 temperature presented for comparison.

Figure 2.2: Seasonal $\delta^{13}C$ and $\delta^{15}N$ signatures (mean ± SE) and percentage of fecal samples without fruit. Periods that differ significantly are shown with different letters, uppercase letters for 2005 and lowercases letters for 2007. No statistical comparisons are made between years. a) $\delta^{15}N$ signatures generally became more positive throughout the winter. b) $\delta^{13}C$ signatures became more positive over the winter. Proportion of fecal samples that contain only arthropods generally increase throughout the winter and track closely with $\delta^{13}C$ signatures for each period.

Figure 2.3: Mass changes (mean ± SE) over winter periods for all birds captured. Periods that differ significantly are shown with different letters, uppercase letters for 2005 and lowercases letters for 2007.

Figure 2.4: Territory-level relationships: a) Larger birds occupied territories with higher arthropod densities. b) Larger birds consume higher proportion of arthropods in early winter. c) Higher arthropods abundance is associated with higher arthropod density.

Figure 2.5: Repeated-capture relationships: a) Mass gains are associated with a greater change in diet. b) Diets with a higher proportion of fruit in early winter (more positive $\delta^{13}C$ signatures) shift towards a more arthropod-rich diet. c) Modest increases in mass in early winter, resulting larger decreases in late winter. d) Larger birds consume a larger proportion of arthropods (less negative $\delta^{13}C$ signatures) early winter.

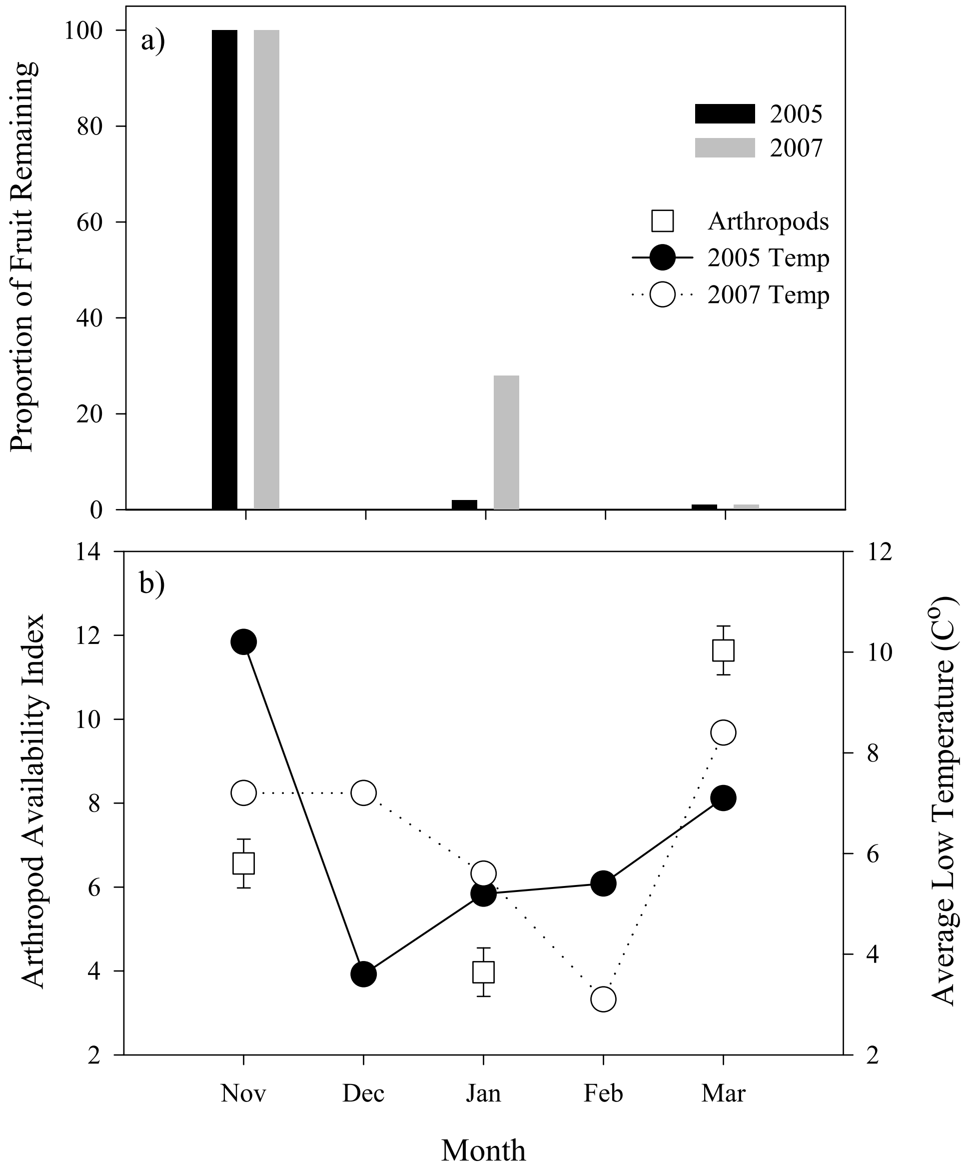

a)
Proportion of Fruit Remaining
0
20
40
60
80
100
2005
2007
Arthropods
2005 Temp
2007 Temp
b)
Arthropod Availability Index
2
4
6
8
10
12
14
Average Low Temperature (C^o)
2
4
6
8
10
12
Nov
Dec
Jan
Feb
Mar
Month

Figure 2.1.

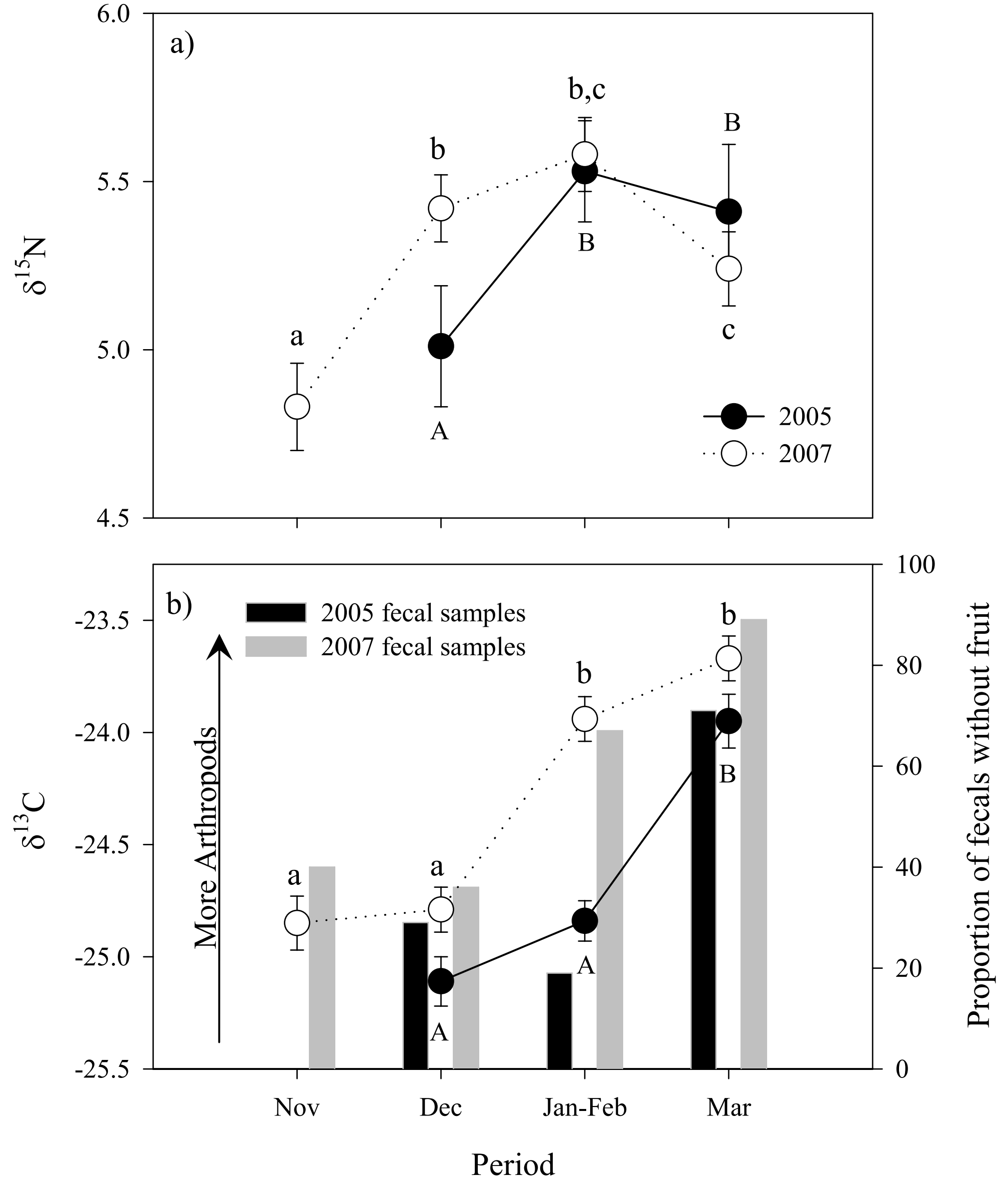
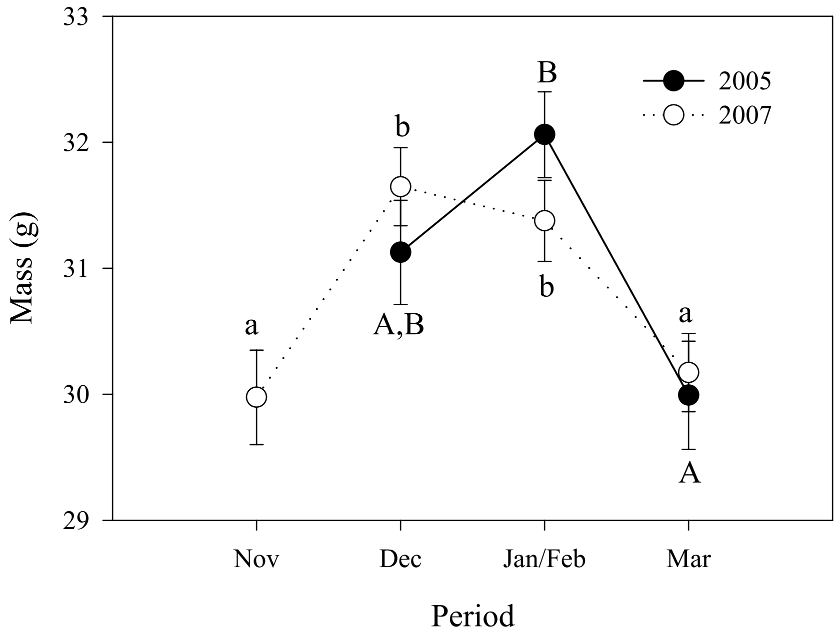

a)
6.0
5.5
5.0
4.5
$\delta^{15}N$
a
b
b,c
B
B
A
c
2005
2007
b)
2005 fecal samples
2007 fecal samples
More Arthropods
-23.5
-24.0
-24.5
-25.0
-25.5
$\delta^{13}C$
a
a
b
b
A
A
B
100
80
60
40
20
0
Proportion of fecals without fruit
Nov
Dec
Jan-Feb
Mar
Period

Figure 2.2.



33
32
31
30
29
Mass (g)
Nov
Dec
Jan/Feb
Mar
Period
2005
2007
a
b
b
a
B
A,B
A

Figure 2.3.

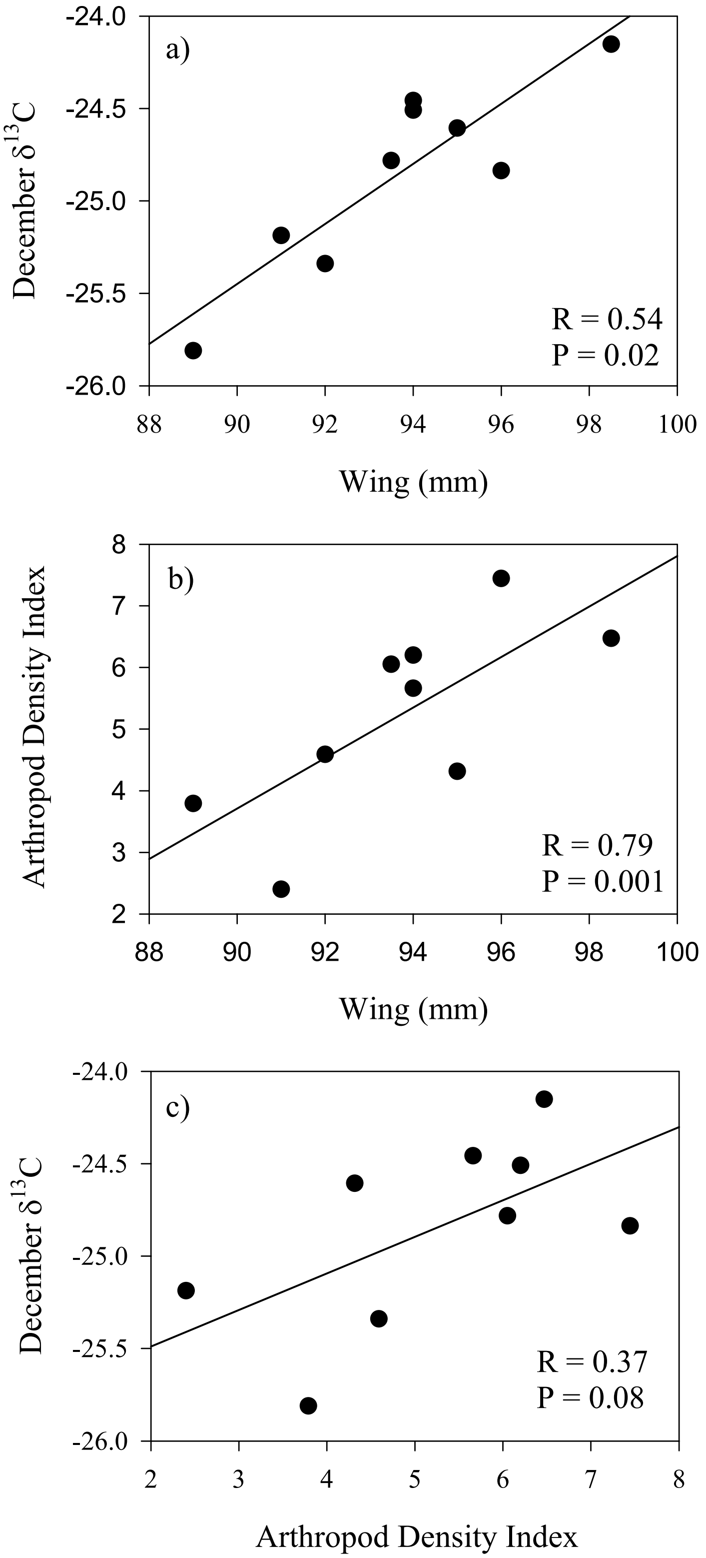

a)
December $\delta^{13}C$
-24.0
-24.5
-25.0
-25.5
-26.0
R = 0.54
P = 0.02
88
90
92
94
96
98
100
Wing (mm)
b)
Arthropod Density Index
8
7
6
5
4
3
2
R = 0.79
P = 0.001
88
90
92
94
96
98
100
Wing (mm)
c)
December $\delta^{13}C$
-24.0
-24.5
-25.0
-25.5
-26.0
R = 0.37
P = 0.08
2
3
4
5
6
7
8
Arthropod Density Index

Figure 2.4.

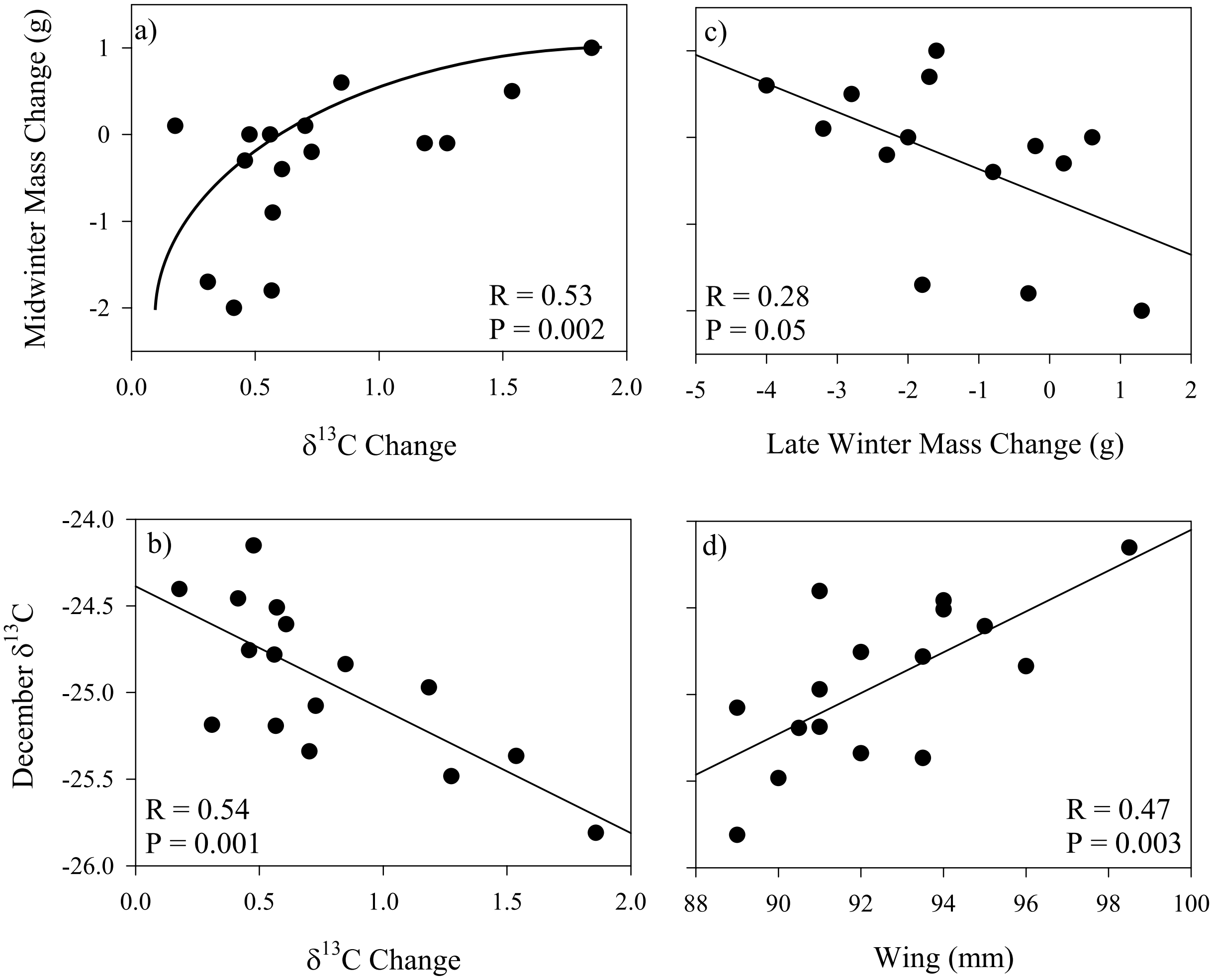

a)
Midwinter Mass Change (g)
1
0
-1
-2
R = 0.53
P = 0.002
0.0
0.5
1.0
1.5
2.0
δ13C Change
c)
R = 0.28
P = 0.05
-5
-4
-3
-2
-1
0
1
2
Late Winter Mass Change (g)
b)
December δ13C
-24.0
-24.5
-25.0
-25.5
-26.0
R = 0.54
P = 0.001
0.0
0.5
1.0
1.5
2.0
δ13C Change
d)
R = 0.47
P = 0.003
88
90
92
94
96
98
100
Wing (mm)

Figure 2.5.

CHAPTER 3

MAJOR FINDINGS & CONCLUSIONS

The stationary portion of the non-breeding season is likely a limiting period for many species of migratory songbirds. Here, I have demonstrated that arthropods are an important diet choice for Hermit Thrushes in the nonbreeding season. Larger-bodied, male birds are able to acquire and defend territories with greater arthropod densities and consumed arthropods in greater proportions to fruit. In midwinter, smaller individuals lacking a steady and sufficient arthropod supply likely compensate by spending more time foraging to increase their mass, making them more susceptible to predation or starvation in severe winters.

Although several studies have examined the wintering ecology of Hermit Thrushes, this study is the first to suggest a connection between arthropod density and behavioral dominance. No prior study had examined the importance of arthropod abundance, which was related to body size when fruit was not, on winter ecology of the species. Additionally, use of isotopes allowed us to reconstruct diet over a broader period than fecal samples could provide. Without the use of isotopes, it is likely we would have missed the advantage that larger birds had securing access to more stable food sources. Experimental alterations in arthropod abundance could confirm relationships between body size, arthropod abundance and fruit consumption.

Although I did not show that females are ultimately in poorer condition prior to migration as result of differences in habitat occupancy, the presence of a body size relationship and the nutritional superiority of an arthropod-rich diet is suggestive of an advantage to larger, dominant birds. Future research should look for evidence of behavioral dominance across habitat types and latitudes. Our study was limited to a handful of small sites with similar habitats within a managed preserve, and inferences about other habitats across the Hermit Thrushes range cannot be made. Given the latitudinal segregation of Hermit Thrushes, it is unknown if the relationship between body size and arthropod density will hold in more southerly latitudes where females predominate. Efforts should also focus on understanding how these wintering season events influence subsequent events in the breeding season. Finally, given the critical role of temperature in regulating arthropod availability, a better understanding of how future warming trends may influence the ecology of short-distance migratory birds overwintering in temperate regions has now become essential.