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# Nocturnal Activity Levels and Stopover Behavior of Spring Neotropical Migrants Along the Southern Lake Ontario Shoreline

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*The College at Brockport*

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NOCTURNAL ACTIVITY LEVELS AND STOPOVER BEHAVIOR OF SPRING  
NEOTROPICAL MIGRANTS ALONG THE SOUTHERN LAKE ONTARIO  
SHORELINE

A Thesis

Presented to the Faculty of the Department of Biological Sciences  
of the State University of New York College at Brockport  
in Partial Fulfillment for the Degree of  
Master of Science

by

Susan B. Smith

Submitted July 26, 2001

THESIS DEFENSE

SUSAN SMITH

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## ABSTRACT

The energetic condition of individual birds is thought to influence the selection and use of stopover sites during migration. Through analysis of nocturnal restlessness and stopover patterns, I investigated the relationship between physiological state (distinguished by the amount of stored fat reserves) and spring stopover behaviors of selected species of Neotropical and temperate migrants at a site along the southern shoreline of Lake Ontario. During spring 1999, there was no significant difference between the amount of nighttime locomotor activity in lean and fat *Catharus* thrushes or *Dendroica* warblers held overnight in activity cages. During spring 2000, there was no significant difference in nocturnal activity between captive lean and fat Swainson's Thrushes (*Catharus ustulatus*) or White-throated Sparrows (*Zonotrichia albicollis*).

Very few Swainson's Thrushes or White-throated Sparrows were recaptured in either 1999 or 2000, and analysis of initial capture data for these species revealed that most individuals arrived lean with depleted fat stores. There was no significant relationship between the hour after sunrise (time of day of initial capture) and mass or condition index for either species in 1999, and only White-throated Sparrows showed significant positive relationships between hour after sunrise and mass or condition index in 2000.

Habitat selectivity was determined by examining the proportion of individuals captured in the three major habitat types (field edge, early secondary, mature secondary) at this site. During spring 1999 and spring 2000, there was no significant relationship between mean energetic condition and habitat type for both species. For all initial captures combined, there was no indication of habitat selectivity for Swainson's

Thrushes in 1999 or 2000. However, there were significantly more White-throated Sparrows captured in the mature secondary habitat than in early secondary or field edge habitats in 1999, and significantly more in the early secondary habitat than in mature secondary or field edge habitats in 2000.

Flying insects were sampled in each of the three habitat types and were present throughout the spring migratory season in both 1999 and 2000. There were no significant differences in insect abundance among habitat types in 1999. Insect abundance differed significantly among habitat types in the first three weeks of sampling during spring 2000.

Based upon the results of my study, I conclude that the behavior of birds stopping at this site is not strongly influenced by their energetic condition upon arrival. Many birds at this site are near the end of their spring migration, and factors related to time constraints and pressure for early arrival at their breeding grounds may influence their behavior during stopover, resulting in a pattern of short stopover lengths, little weight gain during stopover, and no obvious difference in migratory activity between individuals in different physiological or energetic states. Differences between the results of this study and previous studies conducted along the Gulf Coast suggest that stopover behaviors and requirements are different between sites located early along the spring migratory route and sites located near the Great Lakes shorelines. However more work is needed on a broader range of longer-distance and insectivorous species in order to assess the quality and availability of stopover habitats along Great Lakes shorelines, as well as the stopover requirements and behaviors of birds near the end of spring migration.

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## INTRODUCTION

There are 361 species of Neotropical migrants (species which breed north of the Tropic of Cancer and winter south of that line), representing 38 of the 62 breeding bird families in North America (DeGraaf and Rappole 1995). Over the past few decades, many species of Neotropical migrants have declined significantly throughout much of North America (Robbins et al. 1989, Askins et al. 1990). Because Neotropical migrants represent such a large proportion of avian diversity in North America, their decline has received increasing attention in recent years.

Causes for these declines remain indeterminate, and much research has focused upon the importance of breeding and wintering habitats (Robbins et al. 1989, Terborgh 1989, Hagan et al. 1992, Bohning-Gaese et al. 1993, Rappole and McDonald 1994, DeGraaf and Rappole 1995). However, Neotropical migrants also rely upon many additional habitats during their yearly migrations to and from North American breeding grounds (Ketterson and Nolan 1982, Martin and Karr 1986, Lindstrom 1990, Moore and Simons 1992, DeGraaf and Rappole 1995). Neotropical migrants spend approximately one-quarter of their annual cycle in migration, and difficulties faced by migrants en route to breeding and wintering grounds, such as predation, habitat loss, and ability to replenish energy reserves, may significantly affect population levels (Keast 1980, Moore and Simons 1992).

Many studies of bird migration have sought to understand the complex basis of orientation and navigation in birds which migrate over long distances, and the physiology of migrants (Farner 1955; Weise 1956; Mewaldt et al. 1964; Berthold 1975, 1996; Emlen 1975). However, relatively little research has been conducted on the

“stopover ecology” of birds at sites used for resting between migratory flights during annual migrations to and from their breeding grounds. Since migration is energetically demanding and requires the utilization of stored fat reserves (Berthold 1975, Blem 1980, Alerstam 1990), most migratory landbird species are unable to complete annual migrations without recurrent resting periods to replenish energy reserves (Berthold 1975, Bairlein 1985, Biebach et al. 1986, Safreil and Lavee 1988, Moore 1991, Loria and Moore 1990, Lindstrom 1995). Thus the availability of suitable transitory habitats for resting and foraging is crucial to migrant survival during migration (Martin and Karr 1986, Moore and Simons 1992, Rappole and McDonald 1994).

Most research on stopover ecology has concentrated on describing habitat selection, replenishment of energy reserves, and duration of stay at certain sites (Cherry 1982, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Dunn et al. 1988, Moore et al. 1990, Yong et al. 1998). Very few experimental studies have looked at individual differences in selection of stopover sites and how a bird’s physiological condition upon arrival may influence its duration of stay and behaviors at these sites (but see Rappole and Warner 1976, Yong and Moore 1993, Sandberg and Moore 1996a).

Throughout the course of their annual migration, birds may occur in two different physiological states, termed by Groebbels (1928) as “*Zugstimmung*” and “*Zugdisposition*”. Birds in *Zugstimmung* are in a flying state characterized by low feeding rates and a readiness to begin and sustain migratory flight. Birds in *Zugdisposition* are in a feeding state characterized by hyperphagia and are less inclined to begin migratory flight (see Rappole 1995). During the migratory period of their

annual cycle, captive migrants display nocturnal restlessness known as "*Zugunruhe*," which persists throughout the spring migratory season (Berthold 1975, Gwinner and Czeschlik 1978). The intensity of *Zugunruhe* is heightened in birds when they are in the physiological state of *Zugstimmung* (Rappole 1995).

Rappole (1995) hypothesized that "transients alternate between the physiological states of *Zugstimmung* and *Zugdisposition* during the course of a long-distance migration." From this hypothesis, several predictions can be made: 1) A stopover site will contain an assortment of individuals in both physiological states at any given time; 2) individuals arriving with high levels of stored fat should stay for shorter periods of time, show little weight gain, and be non-selective of habitat during stopover; 3) individuals arriving with depleted fat stores should stay for longer periods of time, show net weight gains, and be selective of habitat during stopover (Rappole 1995). This suggests that within a species, individuals will show a broad range of behaviors at any given site, based upon differing stopover requirements.

Energetic condition upon arrival may be a major factor in determining the likelihood of stopover, duration of stay, mass gain, habitat selection, and behavior during stopover (Rappole and Warner 1976, Metcalfe and Furness 1984, Bairlein 1985, Moore and Kerlinger 1987, Safriel and Lavee 1988, Loria and Moore 1990). Some migrants appear to use stopover sites to increase energy reserves (Biebach et al. 1986, Moore 1991, Morris et al. 1994, Winker et al. 1992a), and energetic condition may be a significant source of variation in individual stopover behaviors (Dunn et al. 1988). Lean migrants are less likely to resume migration and often tend to stay longer than birds arriving with larger energy reserves (DeWolf 1973, Cherry 1982, Moore and Kerlinger

1987, Kuenzi et al. 1991, Sandburg and Moore 1996a). However, other studies have found that regulation of migratory behavior is strongly influenced by ecological factors (Terrill 1987) and fat deposition may be related to many other factors, such as distance of migration, sex, migratory experience, and habitat quality (Graber and Graber 1983, Ellegren 1991, Moore and Simons 1992, Yong et al. 1998, Swanson et al. 1999). This suggests that fat content may not always accurately predict stopover length (Page and Middleton 1972, Post and Brown 1976, Lyons and Haig 1995), and that lean migrants may be better off continuing migration if they will be unlikely to rebuild fat stores at a certain stopover site (Rappole and Warner 1976, Moore and Yong 1991, Moore and Simons 1992, Gwinner et al. 1995).

Most of what we do know about stopover ecology in North America deals with the Atlantic and Gulf of Mexico coastal areas (Rappole and Warner 1976; Moore and Kerlinger 1987; Kuenzi et al. 1991; Yong and Moore 1993; Lyons and Haig 1995; Morris et al. 1994, 1996; Yong and Moore 1997; Woodrey and Moore 1997). However, relatively little is known about stopovers that occur at inland sites near the end of the spring migratory route for North American passerines (but see Winker et al. 1992a, 1992b; Smith et al. 1998). Individuals of many species may gain a competitive edge by arriving earlier at their breeding grounds (Francis and Cooke 1986, Reynolds et al. 1986) and these individuals should attempt to minimize time spent in migration (Alerstam and Lindstrom 1990, Weber et al. 1994, Lindstrom 1995). While birds arriving at breeding grounds with larger fat stores may increase their reproductive success (Gundmunsson et al. 1991, Rowe et al. 1994, Sandburg 1996, Fransson and Jakobsson 1998), there may also be costs associated with increased fat levels, such as increased

vulnerability to predation, decreased flight efficiency, and later arrival at breeding grounds (Lindstrom and Alerstam 1992, Sandburg and Moore 1996a, Kullberg et al. 2000). Many migrants arriving along the Great Lakes are near the end of their spring migration and may be within a day or so of reaching their breeding grounds. For these migrants, factors such as selective pressure for early arrival at breeding grounds may be more important than replenishing energy reserves, and stopover patterns and behaviors may differ significantly from those reported at sites farther south along the migratory route.

One important area for spring stopover is located along the south shore of Lake Ontario, along the west side of Braddock Bay, Monroe County, New York. Data from a Nature Conservancy project aimed at identifying potentially important stopover habitats in the Lake Ontario lowlands has shown that migrant diversity is significantly higher along the lakeshore than in habitats farther south (Agard and Spellman 1994, Jones 1997). This suggests that birds may concentrate as they approach the lakeshore and may be relying heavily on this area in spring before they cross the lake to breeding grounds farther north. A long-term banding operation (since 1985) at the Braddock Bay Bird Observatory has shown that large numbers of Neotropical migrants use this area during spring and fall migrations (Brooks 1997a, 1997b). Recent research suggested that significant differences in energetic condition and length of stopover occurred among conspecific migrants at Braddock Bay Bird Observatory but found no significant correlation between length of stay and change in body mass or stored fat (Jones 1997). Jones (1997) also found that most individuals arrive in relatively poor condition and

continue migration after one night's stay. This suggests that individuals may be using this area differently than sites used earlier along the migratory route.

This thesis examines how an individual's energetic condition influences the use of a stopover site along Lake Ontario during spring migration. I discuss results of a two-year study focused on determining how energetic differences among individuals of several species influence behavior during stopover, specifically the development of nocturnal restlessness, potential length of stay, and habitat preferences. This study was designed to determine whether individuals at this site exist in two distinct physiological states (*Zugstimmung* and *Zugdisposition*), which can be differentiated by the amount of nighttime locomotor activity. I tested the following null hypotheses: 1) there is no significant difference in the amount of nocturnal activity between birds with higher levels of stored fat (or in better energetic condition) and birds with depleted fat stores (in poor energetic condition), and 2) there is no significant difference in habitat preference between birds with higher levels of stored fat (or in better energetic condition) and birds with depleted fat stores (in poor energetic condition). I also discuss how differences in energetic condition are influenced by capture time and date. Because habitat quality and food availability may affect a migrant's decision whether to stay at a stopover site or continue migrating (Rappole and Warner 1976, Bibby and Green 1983, Martin and Karr 1986, Moore and Kerlinger 1987, Smith et al. 1998), I also measured the relative abundance of flying insects, a likely food source for insectivorous migratory species during stopover, and I tested the following null hypothesis: There is no significant difference in insect abundance among the three major habitat types at the Braddock Bay Bird Observatory.

Results from this study are important in understanding how and why certain stopover sites are used during spring stopover. Data on individual behavioral differences at this site will increase our understanding of habitat use and physiological requirements of Neotropical migrants near their breeding grounds. This will in turn help to identify specific resource requirements for migrants near the end of their migration, and potentially aid in maintaining critical stopover areas along the Lake Ontario shoreline.

## **METHODS**

### Study Site

I conducted this study at the Braddock Bay Bird Observatory in Rochester, Monroe County, New York (43°19' N, 77°43' W; Figure 1). The observatory is contained within approximately 8 ha of privately owned property located on the west spit area of Braddock Bay, Lake Ontario. The observatory has been operated as a migratory passerine banding station since 1985. During spring 1999 (26 April-8 June) and spring 2000 (24 April-2 June), a minimum of 28 30-mm mesh mist nets were placed throughout the observatory grounds. In 1999, 22 12 m x 2.1 m nets, four 6 m x 2.1 m nets, and two double-paneled 12 m x 2.1 m aerial nets were used. In 2000, 18 12 m x 2.1 m nets, four 6 m x 2.1 m nets, and six double-paneled 12 m x 2.1 m aerial nets were used. Mist nets were situated along net lanes in field edge and secondary woodland habitats of varying successional stages. See Jones (1997) for additional habitat descriptions. Field edge habitat was composed of grasses and shrubby hedgerows dominated by goldenrod (*Solidago canadensis*), clover (*Trifolium* spp.), red osier dogwood (*Cornus*



*sericea*), tatarian honeysuckle (*Lonicera morrowii*), and willows (*Salix* spp.). Early secondary deciduous forest habitat was dominated by willow, red osier dogwood, and cottonwood (*Populus deltoides*). Mature secondary deciduous forest habitat was dominated by cottonwood, red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), and willows.

### Study Species and Morphological Data

In spring 1999, I examined two species of *Catharus* thrushes (Table 1), and three species of *Dendroica* warblers (Table 1). I examined only Swainson's thrushes (*Catharus ustulatus*) and White-throated Sparrows (*Zonotrichia albicollis*) in spring 2000. I chose these species because they are captured in relatively large numbers during the spring at Braddock Bay Bird Observatory (Brooks 1997a, 1997b), and they are not local breeders (Andrle and Carrol 1988, Levine 1998). These species were also chosen to represent long-distance Neotropical migrants (*Catharus* thrushes and *Dendroica* warblers), as well as medium-distance temperate migrants (White-throated Sparrows). Since very few White-throated Sparrows were captured in spring 1999 at Braddock Bay Bird Observatory, I examined *Dendroica* warblers, which are typically captured in abundance at the station during the spring. For *Catharus* thrushes in spring 2000, I only examined Swainson's Thrushes because very few Gray-cheeked Thrushes (*Catharus minimus*) were captured at the station. Birds were captured daily, as weather permitted, between sunrise and the eighth hour after sunrise. I recorded the date, time of capture, sex (when possible), unflattened wing chord, weight, and fat class of each individual. Sex was determined by using Pyle's (1997) descriptions for each species. Weight was measured to the nearest 0.1 gram using an Ohaus electronic balance. Fat

class was determined by measuring the amount of visible subcutaneous fat in the interclavicular region. Fat class was scored according to the six-point scale developed by Helms and Drury (1960), with fat class 0 if there is no visible fat in the interclavicular region, and fat class 5 if the interclavicular region is greatly distended and overflowing with fat. Although the amount of visible stored fat is a good indicator of fat content when between-observer variability is minimized (Krementz and Pendleton 1990), interspecific differences in body weight may be linked to differences in body size (Connell et al. 1960, Rogers and Odum 1964, Pearson 1971). Therefore, I calculated a “condition index” for each individual by dividing mass at initial capture by wing chord measurement (Connell et al. 1960, Pearson 1971, Winker 1995). This ratio adjusts the mass of each bird for its body size and provides a more accurate prediction of an individual’s energetic condition.

### Migratory Restlessness

I measured the nocturnal activity levels of selected species of *Catharus* thrushes and *Dendroica* warblers in 1999 (Table 1), and Swainson’s Thrushes and White-throated Sparrows in 2000. Yong and Moore (1993) measured the nocturnal locomotor and daytime activity levels of *Catharus* thrushes following a non-stop passage over the Gulf of Mexico of approximately 1000 km during spring migration. This study closely approximated their methods for measurement of nocturnal activity levels. I selected individuals with either very high levels of stored fat (fat class-3-5) or depleted fat stores (fat class=0) and assigned them to corresponding “fat” or “lean” groups. Birds were held outdoors in individual activity cages (30 cm x 35 cm x 38 cm) for up to 24 hr. Each cage was sheltered from wind and precipitation by plexiglass boards, which allowed

each bird to visualize the sky and daylight patterns. Each cage was also optically isolated on all sides from other cages. Each activity cage was equipped with a horizontal perch with a microswitch on either end, which was attached to an event logger (HOBO<sup>®</sup> Event Logger, Onset<sup>®</sup> Computer Corporation). The event logger recorded the number of times the bird jumped on and off the perch (activity level). Activity was recorded during the nocturnal hours (21:00-05:00 EST), and nocturnal activity levels were calculated as the number of 2-minute time periods containing activity per hour of darkness (Yong and Moore 1993).

White-throated Sparrows were fed *ad libitum* with a diet of mealworms and commercial birdseed. *Catharus* thrushes and *Dendroica* warblers were fed *ad libitum* with a diet of mealworms mixed with chick mash and fruit. Water was available at all times.

### Stopover patterns

To determine if individuals differed in behavior and use of this site based upon energetic condition, I examined several stopover characteristics of all Swainson's Thrushes and White-throated Sparrows captured in spring 1999 and spring 2000 at the Braddock Bay Bird Observatory. These analyses included all initial captures and subsequent day recaptures (any bird captured on days subsequent to their initial capture). Within each of these species, I examined within- and between-year differences in the distribution of fat class scores, mean initial mass and condition index, and mean date of initial capture. Because there were very few subsequent day recaptures, it was not possible to use mass change between first and last date of capture to determine if individuals gained weight during stopover at this site. Assuming

that birds arrive at a given stopover site before dawn (Moore et al. 1995), the mass of birds at initial capture can be a reliable method of assessing daily mass gain in non-recaptured individuals (Dunn 2000). Therefore, I examined the relationship between mass at initial capture and hour after sunrise (time of day of initial capture). I examined behavioral differences between individuals with different amounts of stored energy reserves by determining the relationships between energetic condition and hour after sunrise, and energetic condition and date of first capture.

Because availability of suitable habitat may determine how a particular site is used during stopover, and individuals using a stopover site to replenish energy reserves may be selective of habitat (Moore and Simons 1989, Rappole, 1995), I also attempted to determine if individuals stopping over at this site displayed habitat preferences upon initial capture. For each species, I compared the proportion of initial captures located in each habitat type. I also compared mean energetic condition index between habitat types to determine if lean individuals displayed different habitat preferences than fat individuals.

### Food Abundance

I measured the relative abundance of flying arthropods (Order Diptera) in the three major habitat types on the Braddock Bay Bird Observatory grounds. I placed sets of sticky boards (10 cm x 20 cm clear plastic boards coated with Tangle Trap™) at three locations approximately once weekly for 24 hr during spring 1999 (16 May-31 May) and spring 2000 (29 April-31 May). Two replicates of 4 boards were placed at each location. In each replicate, boards were placed at 0.762 m intervals to a maximum of 3.048 m above the ground. I counted the number of flying insects stuck to each board and

averaged replicates at each height. For each sampling date, the mean of all heights was used to compare insect abundance between locations.

### Statistical Analysis

I compared within-species differences in average nocturnal activity levels between lean and fat individuals with Mann-Whitney U tests (Zar 1999). The relationships between condition index and nocturnal activity level and between date of first capture and nocturnal activity level were examined using simple linear regression (Zar 1999). For species with adequate initial capture data, I compared between-year differences in average initial capture mass, average initial condition index, and average date of initial capture with two-sample t-tests. I used Chi-Square Tests to examine between-year distributions of fat class scores. I examined the relationships between hour after sunrise and mass and between hour after sunrise and condition index with simple linear regression.

I examined within-species habitat preferences using the Chi-Square Goodness-of-Fit statistic. Because nets were not distributed evenly among the three habitat types, I first calculated the proportion of nets that were located in the early secondary, mature secondary, and field edge habitats. In this calculation, I used only nets that were located in an area that was easily distinguishable as one of the three main habitat types at this site. Each 6 m net was counted as one-half net, each 12 m net was counted as one net, and each aerial net was counted as two nets. Based upon these proportions, and using the total number of initial captures for Swainson's Thrushes and White-throated Sparrows, I calculated an expected number of individuals that would be captured in each habitat type assuming equal proportions of captures among habitat

types. For each study season, I used the Chi-Square Goodness-of-Fit test to determine if the actual number of individuals initially captured in each habitat type differed from the expected number. I also examined differences in within-species habitat occurrence between individuals with different amounts of stored fat by calculating the mean energetic condition of all individuals captured in each habitat type. I then used ANOVA to compare mean values among habitat types for each year.

I performed a log base 10 transformation on the insect abundance data (Zar 1999) to minimize differences in variance among the three habitat types. Within each study season, insect abundance data was initially analyzed with a two-factor ANOVA (Zar 1999). However, there was significant interaction between sampling date and habitat type. Therefore, I compared insect abundance among habitat types on each sampling date with a one-way ANOVA (Zar 1999). I also examined total abundance within each study season by comparing the combined abundance of all habitat types on each sample date with a one-way ANOVA. When significant differences were found with ANOVA, Tukey tests were used to compare pairs of means (Zar 1999).

For all analyses, significance level was set at  $\alpha=0.05$ .

## RESULTS

### Nocturnal activity levels

For *Catharus* thrushes held in activity cages during spring 1999, the average nocturnal activity levels of the lean ( $n=5$ ) and fat ( $n=9$ ) groups did not differ significantly ( $U=34.4$ ,  $p=0.73$ ; Figure 2). Due to very low numbers of captures in 1999, I was not able to obtain a sufficient sample size for White-throated Sparrows in the activity cages. For *Dendroica* warblers (see Table 1 for selected species), average nocturnal activity levels did not differ significantly between the lean ( $n=5$ ) and fat ( $n=4$ ) groups ( $U=24.0$ ,  $p=0.90$ ; Figure 2).

During spring 2000, the average nocturnal activity levels of lean ( $n=6$ ) and fat ( $n=8$ ) Swainson's Thrushes did not differ significantly ( $U=50.0$ ,  $p=0.95$ ; Figure 3). For White-throated Sparrows the average nocturnal activity levels of the lean ( $n=7$ ) and fat ( $n=10$ ) groups did not differ significantly ( $U=46.0$ ,  $p=0.22$ ; Figure 3).

In 1999 and 2000, there was considerable variation between individuals within each experimental group (Figures 2 and 3). Although average nocturnal activity levels were not significantly different between lean and fat groups during both years, the average nocturnal activity levels were slightly higher in lean groups than in fat groups during 1999. However this reversed in 2000 and the average nocturnal activity levels were slightly higher in the fat groups.

Regression analysis revealed no significant relationship between average nocturnal activity levels and condition index for any of the experimental groups in both 1999 and 2000 (Table 2). Regression analysis was also used to compare average

nocturnal activity levels and date of capture. However, there were no significant relationships for any of the experimental groups (Table 3).

### Initial Captures

The total number of initial captures at Braddock Bay Bird Observatory was higher in spring 2000 than in spring 1999 for White-throated Sparrows and Swainson's Thrushes (Table 4). For White-throated Sparrows, the mean Julian date of initial capture was significantly earlier in spring 2000 than in spring 1999 ( $t=2.91$ ,  $df=243$ ,  $p=0.004$ , Table 5). For Swainson's Thrushes, the mean Julian date of initial capture was not significantly different between years ( $t=1.68$ ,  $df=60$ ,  $p=0.10$ , Table 5). For White-throated Sparrows, the average mass at initial capture was significantly higher in spring 2000 than in spring 1999 ( $t=5.39$ ,  $df=243$ ,  $p=0.00$ ; Table 5). Between-year comparisons also revealed a significantly higher average initial condition index in spring 2000 ( $t=5.48$ ,  $df=243$ ,  $p=0.00$ ; Table 5). For Swainson's Thrushes, between-year comparisons found no significant differences in both the average initial mass ( $t=0.74$ ,  $df=60$ ,  $p=0.46$ ; Table 5) and the average initial condition index ( $t=1.43$ ,  $df=58$ ,  $p=0.16$ ; Table 5). Subsequent day recapture rate was very low in 1999, with only one recaptured White-throated Sparrow and no recaptured Swainson's Thrushes (Table 4). In 2000, percent of recaptures rose to 3.2% in White-throated Sparrows; however, there were still no recaptured Swainson's Thrushes (Table 4).

Individuals of White-throated Sparrows and Swainson's Thrushes tended to arrive at Braddock Bay with low energy reserves. In both 1999 and 2000, many individuals had little or no visible subcutaneous fat. Most individuals had fat class scores of 0-1, very few individuals had fat class scores of 3, and few or no individuals



had fat class scores  $>3$  (Figure 4). For both species, the distribution of fat class scores was significantly different between years (WTSP:  $\chi^2=32.88$ ,  $df=3$ ,  $p=0.00$ ; SWTH:  $\chi^2=12.56$ ,  $df=3$ ,  $p=0.005$ ), with more individuals with higher fat scores in 2000 (Figure 4).

#### Daily Mass Gain

Regression analysis revealed no significant relationships between hour after sunrise and mass or condition index for White-throated Sparrows or Swainson's Thrushes in 1999 (Table 6, Figures 5 and 6). In 2000, regression analysis also showed no significant relationships between hour after sunrise and mass or condition index for Swainson's Thrushes (Table 6, Figures 5 and 6). However, among White-throated Sparrows captured in 2000, regression analysis revealed significant relationships between hour after sunrise and both mass and condition index (Table 6, Figures 5 and 6). However, low  $r^2$  values ( $r^2=0.000$ ; Table 6) do not indicate a strong relationship.

#### Habitat Selectivity

In 1999, 18 Swainson's Thrushes and 51 White-throated Sparrows were captured in nets located in one of the three main habitat types used in this study. There were no significant differences between the observed and expected numbers of Swainson's Thrushes captured in each habitat type ( $\chi^2=2.65$ ,  $df=2$ ,  $p=0.10$ , Figure 7). The observed number of White-throated Sparrows captured in each habitat type was significantly different from the expected number ( $\chi^2=21.62$ ,  $df=2$ ,  $p=0.00$ , Figure 7), and more individuals were captured in the mature secondary habitat. In 2000, 28 Swainson's Thrushes and 117 White-throated Sparrows were captured in nets located in one of the three main habitat types used in this study. There was no significant

difference in habitat occurrence in Swainson's Thrushes ( $X^2=2.55$ ,  $df=2$ ,  $p=0.11$ , Figure 7). However, there was a significant difference between observed and expected numbers of White-throated Sparrows captured in each habitat type ( $X^2=13.58$ ,  $df=2$ ,  $p=0.00$ , Figure 7), with more White-throated Sparrows captured in the early secondary habitat in 2000. Examination of differences in habitat preference between lean and fat individuals based upon fat class score was not possible because there were very few individuals with high fat class scores in both years. Therefore I compared the within-species mean energetic condition of all individuals captured in each habitat type. For Swainson's Thrushes, this analysis was not possible in 1999 because of small sample sizes in the mature secondary habitat. In 2000, there was no significant difference in mean energetic condition of Swainson's Thrushes among habitat types (ANOVA,  $F=0.98$ ,  $df=2,25$ ,  $p=0.39$ ). For White-throated Sparrows, there was no significant difference in mean energetic condition among habitat types in 1999 (ANOVA,  $F=0.50$ ,  $df=2,48$ ,  $p=0.61$ ), but in 2000, this difference approached significance (ANOVA,  $F=2.79$ ,  $df=2,114$ ,  $p=0.07$ ), with a higher average energetic condition in the early secondary habitat.

#### Insect abundance:

Flying insects (Order Diptera) were present throughout the season in both 1999 and 2000. In both years, captured insects were predominantly midges (Chironomidae) and mosquitoes (Cuclidae). In 1999, insect sampling began on 16 May and continued for three successive dates (Figure 8). For Rochester, N.Y. (NOAA, NCDC weather station, 43° 07' N, 77° 41'W) in April 1999, the average temperature (7.39° C) was normal, but the average rainfall (52.58 mm) was below normal. In May, the average

temperature ( $15.33^{\circ}\text{C}$ ) was above normal, and the average precipitation (69.09 mm) was near normal (U.S. Dept. of Commerce, NOAA Annual Climatological Summary 1999, National Climatic Data Center, Asheville, NC). This resulted in very dry habitat conditions throughout the Braddock Bay Observatory grounds during the 1999 study season. On each sampling date, there were no significant differences in insect abundance among the three major habitat types at this site (ANOVA; Table 7). In 2000, I began sampling on 29 April and continued for four successive dates (Figure 9). Weather conditions in spring 2000 were much wetter and cooler than in spring 1999. For Rochester, N. Y. (NOAA, NCDC weather station,  $43^{\circ} 07' \text{N}$ ,  $77^{\circ} 41' \text{W}$ ) in April 2000, the average temperature ( $7.28^{\circ}\text{C}$ ) was below normal, and the average precipitation (110.49 mm) was above normal. In May 2000, the average temperature ( $15.28^{\circ}\text{C}$ ) was above normal, however the average precipitation (119.38 mm) was again above normal (U.S. Dept. of Commerce, NOAA Annual Climatological Summary 2000, National Climatic Data Center, Asheville, NC). This resulted in extremely wet conditions at the Braddock Bay Bird Observatory, with extensive areas of standing water present throughout the study season. There were significant differences in insect abundance among habitat types on all sampling dates except 27 May (ANOVA,  $F=0.50$ ,  $df=2,9$ ,  $p=0.624$ ; Table 7). Insect abundance was very high on the earliest sampling date (29 April) and declined as the season progressed (Figure 9). On 29 April, insect abundance was significantly higher in the field edge habitat than in the mature secondary habitat only (Tukey Test  $p<0.05$ ; Figure 9). On 7 May, insect abundance in the field edge habitat was only significantly higher than in the early secondary habitat (Tukey Test

$p < 0.05$ ; Figure 9). On 19 May, insect abundance in the mature secondary habitat was only significantly higher than in the field edge habitat (Tukey Test  $p < 0.05$ ; Figure 9).

When ANOVA was used to examine differences between total insect abundance for all habitats combined between dates, there were significant differences in both 1999 ( $F = 11.44$ ,  $df = 2, 6$ ,  $p = 0.003$ ) and 2000 ( $F = 5.72$ ,  $df = 3, 8$ ,  $p = 0.04$ ). In 1999, insect abundance on 16 May was only significantly higher than on 22 May (Tukey Test,  $p < 0.05$ ). In 2000, total insect abundance on 29 April was only significantly higher than on 19 May and 27 May (Tukey Test,  $p < 0.05$ ).

## DISCUSSION

### Nocturnal Activity

Energetic status appeared to have little influence on the intensity of nocturnal restlessness during this study. When migrants were held overnight in activity cages, I found no significant differences in nocturnal activity levels between lean and fat individuals in both longer-distance migrants (*Catharus* thrushes and *Dendroica* warblers), and shorter-distance temperate migrants (White-throated Sparrow). This contrasts with Yong and Moore's (1993) findings in a similar study conducted along the Louisiana coastline. They found that fat migrants were significantly more active at night than migrants with depleted fat stores. Further, when they held migrants several days in activity cages, lean migrants became more active at night as they increased their levels of stored fat, indicating a distinct relationship between energetic condition and migratory behavior during stopover.

According to the *Zugstimmung/Zugdisposition* hypothesis, birds stopping at this site should occur in two distinct physiological states and display behavioral differences in stopover site use based upon their remaining levels of stored energy reserves (Rappole 1995). However analysis of nighttime locomotor activity patterns indicates that lean birds were just as likely to continue migration as birds in better energetic condition and it is possible that only *Zugstimmung* is displayed at this site. In addition, both lean and fat groups had low average nocturnal activity levels compared to Yong and Moore's (1993) findings along the Gulf Coast. Migrants that are very close to their breeding grounds upon arrival along the south shore of Lake Ontario are also ending

the migratory phase of their annual cycle. It is possible that the intensity of *Zugunruhe* also decreases regardless of energetic status upon arrival at this site.

Orientation studies conducted along the Gulf of Mexico shoreline have shown a relationship between the amount of stored fat reserves and an individual's likelihood to orient flight in a seasonally appropriate direction (Able 1977, Sandberg et al. 1991, Sandberg 1994). Sandberg and Moore (1996a) found that lean and fat Red-eyed Vireos (*Vireo olivaceus*) arriving along the Louisiana coastline during the spring displayed distinct differences in both migratory orientation and inclination to embark on migratory flight. However, these studies were conducted at a relatively early phase of spring migration following an extremely energetically demanding flight across the Gulf of Mexico. Upon arrival along the Gulf of Mexico coastline of the United States, lean migrants may be entirely fat-depleted and may have no choice but to stopover longer to regain lost mass before continuing migration. Conversely, along the Great Lakes shoreline, migrants have been traveling over land without significant barriers to migration since leaving the Gulf Coast, and may have had many opportunities to replace energy reserves en route. Thus, based upon results of this study, energetic status alone at this site does not appear to control a migrant's decision of whether to stay for more than one night or continue migration, and migrants may not need as much fat reserves when arriving along the Great Lakes shorelines as they do upon arrival along the Gulf Coast.

Differences between my study and the results from studies conducted along the Gulf of Mexico coast (Yong and Moore 1993) may be explained by two possible reasons. First, factors related to the timing of spring migration and arrival on the

breeding grounds may be heightened at my study site. White-throated Sparrows and some Swainson's Thrushes arriving along the Lake Ontario shoreline are near the end of their migration, and most are within a night's flight of their breeding destinations (Peck and James 1987, Andrie and Carrol 1988). During my study at the Braddock Bay Bird Observatory, the mean date of passage for White-throated Sparrows was 5 May in 1999 and 1 May in 2000. Male White-throated Sparrows also typically arrive at their breeding grounds in Ontario, Canada, between the last week in April through the first week in May (Kopachena and Falls 1994). The mean date of passage for Swainson's Thrushes at the Braddock Bay Bird Observatory during my study (24 May in 1999 and 20 May in 2000) is very close to the first possible egg dates (28 May) on their breeding grounds in Ontario, Canada (Peck and James 1987). This may indicate that these species are spending minimal time at this stopover site and replacing lost energy reserves may no longer be of primary importance. Lindstrom and Alerstam (1992) described a time-minimizing migration strategy that can be used to explain migrant behavior during stopover. This hypothesis predicts that birds will attempt to minimize time spent on migration in response to selective pressure for early arrival at breeding grounds. If birds are minimizing time spent on migration, the rate of refueling will not be constant throughout migration, but rather will change depending upon the quality of a given stopover site, and this could result in migrants departing from a stopover site with lower than expected fuel reserves (Lindstrom and Alerstam 1992). The similar nocturnal activity levels of lean and fat experimental birds during this study supports a time-minimization strategy for birds that are in close proximity to their breeding grounds upon arrival along the Lake Ontario shoreline.

Migrants arriving at breeding grounds with increased fat stores presumably gain fitness benefits, such as increased reproductive output, increased success during competition for nesting sites and mates, and more time dedicated to breeding activities (Wiggins et al. 1994, Sandberg and Moore 1996b). However, there may also be associated costs. If more time is devoted to restoring energy reserves during stopover, migrants will arrive later at their breeding grounds, leaving them at a disadvantage for intrasexual competition for mates and nesting sites (Sandberg and Moore 1996b). For migrants arriving at Braddock Bay Bird Observatory, these costs may outweigh the benefits of longer stopover, resulting in many birds continuing migration with low fat stores, as supported by the similarity in nocturnal activity levels between lean and fat birds during my study.

If migrants are strongly influenced by time constraints, it is possible that the intensity of *Zugunruhe* will change throughout the migratory season as potential competition for breeding territories increases. However, in 1999 and 2000 at my study site there was no significant relationship between date of capture and nocturnal activity level. One possible explanation is that any potential seasonal change in nocturnal activity level may have been obscured by sex-related or age-related differences in migrant behavior. Sex-related differences in the timing of spring migration presumably occur because males must compete to establish breeding territories (Francis and Cooke 1986). Many studies have shown sex-related differences in the timing of spring migration with males passing through stopover sites earlier than females (Chandler and Mulvahill 1990a, Yong et al. 1998, Swanson et al. 1999). For White-throated Sparrows breeding in southern Canada, males typically arrive 1-2 weeks earlier than females



(Kopachena and Falls 1994). Age-related differences in migratory timing during the fall have been attributed to lack of migratory experience in hatch-year birds and differences in fat loads and molt patterns between hatch-year and older birds (Gauthreaux 1982, Ketterson and Nolan 1982, Chandler and Mulvahill 1990b, Woodrey and Chandler 1997). However it is unclear how much these factors influenced stopover behavior at the Braddock Bay Bird Observatory during my study since many individuals of my selected study species could not be reliably sexed (Pyle 1997).

A second possible explanation for the observed differences between my results and the results of studies conducted along the Gulf of Mexico shoreline relates to the quality the Braddock Bay Bird Observatory as a spring stopover site. Successful completion of migration depends upon the quality and availability of stopover habitat for most landbird migrants (Moore and Simons 1992). Consequently, upon arrival at a particular site fat-depleted migrants may choose whether to stay or continue migration based upon the probability of regaining lost fat reserves (Rappole and Warner 1976, Kuenzi et al. 1991, Moore and Yong 1991). Therefore, birds arriving along the south shore of Lake Ontario in the spring may be responding to the availability of food resources and the amount of suitable habitat when deciding how long to stay during stopover. Gwinner et al. (1985) related the intensity of *Zugunruhe* to food availability in a study of caged Garden Warblers (*Sylvia borin*). He determined that nocturnal activity levels actually increased following nights of food deprivation and that birds were increasing the intensity of *Zugunruhe* in response to a low probability of regaining fat stores. He concluded that individual birds at stopover sites with poor food resources would behave similarly regardless of energetic condition and most would continue

migration to find a more suitable stopover site. If the Braddock Bay Bird Observatory does not provide adequate food resources, then birds should not reduce *Zugunruhe* to stay and forage, and this could explain the similar nocturnal activity levels of lean and fat individuals in this study.

During spring migration in the northern regions of the central and eastern United States, birds may encounter harsh conditions such as delayed phenological vegetative development, unpredictable temperature and weather variations, and very limited food resources (Ewart and Hamas 1995). Emerging aquatic insects, particularly chironomids, are often heavily relied upon during spring migration by many species of songbirds, especially as they approach lakeshore regions (Ewart and Hamas 1995). Smith et al. (1998) found that proximity to the Lake Huron shoreline strongly influenced vegetation development and insect abundance in the spring. They determined that Black-throated Green Warblers (*Dendroica virens*) relied heavily upon flying insects, primarily midges, early in the spring, and exhibited variation in foraging behaviors between inland and shoreline locations. Jones (1997) measured flying insect abundance along Braddock Bay on Lake Ontario and found that insect abundance was consistently higher at shoreline locations than at sites farther inland. While flying arthropods were present throughout the spring season during my study at the Braddock Bay Bird Observatory, abundance was highly variable from week to week and was strongly dependent on prevailing weather patterns and precipitation levels. Jones (1997) found that insect abundance was higher during later weeks in the spring. In contrast, during my study insect abundance was higher in the first weeks of sampling and decreased as the season progressed. However, chironomid abundance in the

spring is highly temperature-dependent (Smith et al. 1998). Higher insect abundances early in spring 1999 of my study may be attributed to the extremely dry conditions in late May, which likely resulted in fewer cuclid irruptions. In spring 2000, the early emergence of midges coincided with heavy rains early in the season. Wet conditions in April led to the early emergence of leaves, and this effect may have been intensified at my study site due to its close proximity the Lake Ontario shoreline. The highly variable availability of food resources at this site may indicate that birds arriving here in the spring encounter unpredictable resources and may search for more suitable habitats after staying for relatively short periods of time.

### Stopover Patterns

Most Swainson's Thrushes and White-throated Sparrows arrived at this site with depleted or very low fat stores. For both species, the distribution of fat class scores differed significantly between years with more individuals in higher fat classes in 2000. White-throated Sparrows also had significantly higher initial mass and condition indices in 2000. However, there were still higher proportions of lean individuals than fat individuals in both years. This is consistent with Jones' (1997) study, which examined the spring stopover patterns of several groups of Neotropical migrants at Braddock Bay Bird Observatory. He found that the majority of individuals had depleted fat reserves upon initial capture. He also found that for White-throated Sparrows the average initial mass and average initial condition index differed significantly between the two years of his study.

Many studies have found that energetic condition upon arrival influences duration of stopover and that lean birds are more likely to stay longer than fatter birds in order to

forage and increase energy reserves (Cherry 1982, Bairlein 1985, Moore and Kerlinger 1987, Kuenzi et al. 1991). However, even though the majority of Swainson's Thrushes and White-throated Sparrows captured during this study were in relatively poor energetic condition, both species had very low rates of recapture, indicating that most migrants left this site after staying only one day. Low recapture rates also suggest that migrants did not stay long enough at this site to significantly increase their energy reserves. This, in combination with the similar nocturnal activity levels of lean and fat experimental birds and the lack of a significant relationship between initial capture time and mass or condition index, supports a time-minimizing strategy for migrants at this site, where birds are unlikely to interrupt migration to replenish energy reserves. Additionally, birds may not have to stay longer than one day if they are able to find enough food during one day of foraging at this site.

Rappole (1995) predicted that the majority of individuals at a given stopover site will be in a state of *Zugstimmung*, characterized by low rates of feeding and little or no weight gain during stopover. Comparisons of hour after sunrise of initial capture and mass revealed that in 1999, both White-throated Sparrows and Swainson's Thrushes were not significantly heavier later in the day. This would tend to be more characteristic of birds in a state of *Zugstimmung* that are not actively foraging during the day. In 2000, Swainson's Thrushes did not gain weight later in the day. However, White-throated Sparrows had a positive, although weak, relationship between capture time and mass, which suggests they may have been gaining weight throughout the day. Since hour after sunrise of initial capture time was not strongly related to mass or condition index,

and there was a very low rate of recapture, it is likely that the majority of these individuals are not staying for long periods of time in order to forage and gain weight. If migrants at this site are departing after one day, it is likely that Lake Ontario is not a large enough barrier to require them to substantially increase their energy reserves before crossing. Rappole and Warner (1976) found that Northern Waterthrushes (*Seiurus noveboracensis*) in south Texas waited for a favorable combination of fat reserves and weather conditions before resuming spring migration. Thus, it is possible that migrants that do stay for more than one day at the Braddock Bay Bird Observatory are also responding to prevailing weather conditions. While inclement weather may force a migrant with sufficient fat stores to stopover an additional day, favorable weather conditions may induce a lean migrant to embark on migration despite depleted energy reserves.

The pattern of low recapture rates and lack of apparent weight gain may be common of stopover at inland sites near the end of migration. Winker et al. (1992a) studied several species of wood-warblers (Parulidae) stopping over along the St. Croix River Valley in Minnesota. During the spring, they found very low rates of recapture and several species did not show significant positive slopes between capture time and condition index. They concluded that patterns of fat deposition vary widely among woodland migrants stopping over in areas not near a significant ecological barrier. Dunn (2000) studied hourly rates of mass change in Magnolia Warblers (*Dendroica magnolia*) during spring stopover at several sites along the northern Lake Erie shoreline and found that birds captured earlier in the season lost mass or showed no net gain in mass over 24 hours. Although birds arriving later in the season showed net mass

gains, this was attributed to increased food resources later in the season, differences in arrival condition, and the fact that earlier male migrants may have increased pressure for arrival at their breeding grounds and are less likely to stay longer to replenish fat reserves.

High proportions of lean migrants at my study site may be an indication that birds are more influenced by time constraints rather than energy replenishment before reaching Braddock Bay, are in a heightened state of *Zugstimmung* prior to arrival at this site. If so, birds would be stopping over for short periods of time at sites prior to reaching Braddock Bay and would be expected to arrive here in poor energetic condition.

#### Habitat Selectivity

Rappole (1995) predicted that individuals in *Zugdisposition* would be highly selective of habitat during stopover, and individuals in *Zugstimmung* should be relatively non-selective of habitat during stopover. During this study small sample sizes prevented analysis of habitat preferences based upon fat class score; however, there was no difference in habitat use based upon energetic condition for Swainson's Thrushes and White-throated Sparrows in both years. These results suggest that lean and fat individuals are not behaving differently with regard to diurnal foraging activity and habitat selection at this site. This contrasts with results from Moore and Aborn (2000) who used telemetry to track the diurnal movements of Summer Tanagers (*Piranga rubra*) on Horn Island off the Mississippi coast and found that lean individuals moved faster and more frequently and covered longer distances than fat individuals. Additionally, they determined that lean individuals actively selected different habitats

than fat individuals. However, their study was conducted at a much earlier point along the spring migratory route, and lean birds may place a higher priority on replenishing energy reserves following a trans-Gulf flight than near the end of migration at locations like the Braddock Bay Bird Observatory.

Many studies have shown that migratory songbirds select specific habitats based upon habitat suitability and resource abundance (Bairlein 1983, Hutto 1985, Moore and Simons 1992, Moore et al. 1995, Yong et al. 1998, Moore and Aborn 2000). Yong and Finch (1997) attributed the highly selective behavior of Willow Flycatchers (*Empidonax traillii*) stopping along the Rio Grande River Basin to the increased food resources (arthropod abundance) in certain habitats. Yong et al. (1998) studied migrating Wilson's Warblers (*Wilsonia pusilla*) along the Rio Grande River in New Mexico and determined that in the spring individuals were selecting habitat based upon the availability of preferred food resources. During this study, White-throated Sparrows were more common in the mature secondary habitat in 1999. Although insect material usually makes up the majority of their diet in early May, this species is generally a vegetation gleaning ground forager during spring migration (Kopachena and Falls 1994). Flying insects (primarily midges) were available for aerial insectivores, but it is unlikely that the foliage-dwelling food items sought by this species, such as Lepidoptera larvae, were abundant early in the season before the emergence of leaves (Jones 1997). Additionally, insect abundance did not significantly differ between habitats in 1999. In 2000, White-throated Sparrows were captured more frequently in the early secondary habitat. While significant differences in flying arthropod abundance did occur on all sampling dates except 27 May, insect abundance was highest in the field edge habitat

on 29 April and 7 May, and highest in the mature secondary habitat on 19 May.

Therefore, White-throated Sparrows were most likely choosing habitat based upon factors other than insect abundance.

One possible explanation for habitat choice among White-throated Sparrows could be the likelihood of predator evasion based upon the timing of leaf phenology and habitat structure at this site. Along the Lake Ontario shoreline of New York in the spring, leaves typically do not emerge until mid-May. This means that migratory songbirds may be more vulnerable to predation in exposed and sparse areas such as the field edge habitat. They may be choosing habitat with a higher canopy, such as the mature secondary habitat, simply because it may be more difficult for common avian predators, like the Sharp-shinned Hawk (*Accipiter striatus*), to gain access to.

Schneider (1984) experimentally determined that White-throated Sparrows preferentially choose to forage near cover to reduce the risk of predation, despite decreased foraging efficiency. Both the mature secondary and early secondary habitats may provide a shrubby layer of dense vegetative cover in some areas. Therefore, it is possible that White-throated Sparrows stopping at this site are choosing habitat to best avoid the risk of predation despite the possible loss in foraging efficiency.

Kullberg et al. (2000) studied Sedge Warblers (*Acrocephalus schoenobaenus*) during fall migration in Greece and found that increasing fuel loads increased predation risk by decreasing flight velocity and take-off speed. Excessive time spent foraging during the day may also leave individuals more vulnerable to predation. For White-throated Sparrows, the costs of foraging and increased fat stores with regard to predation risk may greatly outweigh the benefits at locations like the Braddock Bay Bird



Observatory. Near the end of their spring migration, such costs of being heavy could also explain the high proportions of lean individuals at this site.

Another possible reason for the observed patterns of habitat selection in White-throated Sparrows is that some migrants appear to choose sites with certain microhabitat features similar to their breeding habitats (Parnell 1969, Ewert and Hamas 1995). White-throated Sparrows breeding in Algonquin Provincial Park, Ontario, prefer to breed in mixed coniferous forests near openings with dense vegetative cover and along forest edges (Kopachena and Falls 1994). Similar habitat structures are found at the Braddock Bay Bird Observatory, and White-throated Sparrows could simply be choosing more familiar habitat.

Swainson's Thrushes showed no habitat preferences during spring 1999 or 2000. This is consistent with Winker et al. (1992c), who found that migrating Swainson's Thrushes stopping along the St. Croix River Valley in Minnesota were widely distributed among sampled habitat types in the spring and attributed this to the high tolerance for variation in habitat structure in this species. Similarly, during my study Swainson's Thrushes also exhibited a wide range of habitat use, which appeared to be independent of insect abundance.

## CONCLUSIONS

Results of my two-year study indicate that birds arriving at the Braddock Bay Bird Observatory in different energetic condition lacked the significant behavioral differences predicted by the *Zugstimmung/Zugdisposition* hypothesis. Upon arrival at this site, most birds were in relatively poor energetic condition and displayed a pattern of short

stopover times and little weight gain. These results suggest that the stopover behaviors and requirements of spring migrants arriving along the Lake Ontario shoreline may differ from those of birds arriving along the Gulf Coast shoreline. Conclusions from studies conducted at sites used very early along the migratory route, particularly those located along the Gulf Coast shoreline, may not necessarily apply to sites further north, especially for birds within a night's flight of their breeding grounds. For birds near the end of their spring migration, time constraints and pressure to reach breeding grounds may be increased and could more strongly influence stopover behaviors than earlier along the migratory route.

Birds may be responding to habitat quality and food abundance when deciding whether to stay or continue migration upon arrival at this site during the spring. Within the Braddock Bay Bird Observatory grounds during my study, insect abundance was highly variable among habitat types throughout each season. Chironomids and cuclids often appeared in sudden irruptions, and no habitat type had consistently higher insect abundances throughout each season. This variation in insect availability indicates that the probability of regaining fat stores may be unpredictable for insectivorous species among microhabitat types along the Lake Ontario shoreline. When unpredictable food resources are combined with the threat of predation and sparse leaf cover early in the spring at the Braddock Bay Bird Observatory, lean birds may choose to continue migration across Lake Ontario after staying only one day, despite low energy reserves. The value of this area as a stopover site may therefore be highly variable during spring migration.

Results from this study indicate the importance of further research on the stopover ecology of birds near the end of spring migration. A broader investigation encompassing more species of Neotropical migrants would be useful to help identify important resources and habitats for birds near the end of their spring migratory route. Additionally, research on habitat structure and the availability of other possible food sources in early spring could help to further assess the quality of stopover sites and how they are used by migrants arriving along the southern shoreline of Lake Ontario during the spring.

**Table 1** Species of Neotropical migrants selected for experimental study during spring 1999 and spring 2000 at Braddock Bay Bird Observatory.

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1999: *Catharus*

Swainson's Thrush *Catharus ustulatus*  
Gray-cheeked Thrush *Catharus minimus*

*Dendroica*

Magnolia Warbler *Dendroica magnolia*  
Yellow-rumped Warbler *Dendroica coronata*  
Black-throated Blue Warbler *Dendroica caerulescens*

2000: *Catharus*

Swainson's Thrush *Catharus ustulatus*

*Zonotrichia*

White-throated Sparrow *Zonotrichia albicollis*

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**Table 2** Summary of regression analyses of the relationship between condition index ( $x$ ) and mean nocturnal activity level ( $y$ ) for spring 1999 and spring 2000. Equations are in the form  $y = a + bx$ , where  $b$  is the slope.

	$n$	$b$	$r^2$	$p$
<u>Spring 1999</u>				
<i>Catharus thrushes</i>	4	-13.30	0.154	0.17
<i>Dendroica warblers</i>	9	-17.00	0.048	0.57
<u>Spring 2000</u>				
<i>Catharus ustulatus</i>	14	5.10	0.001	0.90
<i>Zonotrichia albicollis</i>	17	2.80	0.002	0.86

**Table 3** Summary of regression analyses of the relationship between date of initial capture ( $x$ ) and mean nocturnal activity level ( $y$ ). Equations are in the form  $y = a + bx$ , where  $b$  is the slope.

	$n$	$b$	$r^2$	$p$
<u>Spring 1999</u>				
<i>Catharus</i> thrushes	14	-0.08750	0.10	0.26
<i>Dendroica</i> warblers	9	-0.05060	0.05	0.59
<u>Spring 2000</u>				
<i>Catharus ustulatus</i>	14	0.13300	0.01	0.72
<i>Zonotrichia albicollis</i>	17	-0.12300	0.11	0.20

**Table 4** Number of initial captures, number of subsequent day recaptures, and percent recaptured during spring 1999 and spring 2000 at Braddock Bay Bird Observatory.

SPECIES	Number of Initial Captures	Number Recaptured <sup>1</sup>	Percent Recaptured <sup>2</sup>
<u>Spring 1999</u>			
<i>Zonotrichia albicollis</i>	79	1	1.3
<i>Catharus ustulatus</i>	28	0	0.0
<u>Spring 2000</u>			
<i>Zonotrichia albicollis</i>	166	5	3.2
<i>Catharus ustulatus</i>	34	0	0.0

<sup>1</sup> Recaptures are birds that were captured on days subsequent to their initial capture at Braddock Bay Bird Observatory.

<sup>2</sup> Percent recaptured was calculated using the number of initial captures after subtracting birds that were held overnight in activity cages.

**Table 5** Mean initial mass (grams), mean initial condition index (grams/mm), and mean Julian date of initial capture of White-throated Sparrows and Swainson's Thrushes during spring 1999 and spring 2000 at Braddock Bay Bird Observatory. Julian date 122 was 1 May in 2000 and 2 May in 1999. All date, mass, and condition index values are means  $\pm$  standard deviation.

SPECIES	n	Date	Mass	Condition Index
<u>Spring 1999</u>				
<i>Zonotrichia albicollis</i>	79	125.3 $\pm$ 7.16	24.7 $\pm$ 2.28	0.348 $\pm$ 0.026
<i>Catharus ustulatus</i>	28*	144.1 $\pm$ 8.23	32.4 $\pm$ 4.55	0.340 $\pm$ 0.048
<u>Spring 2000</u>				
<i>Zonotrichia albicollis</i>	166	122.4 $\pm$ 7.36	26.4 $\pm$ 2.39	0.368 $\pm$ 0.029
<i>Catharus ustulatus</i>	34	141.1 $\pm$ 5.61	31.6 $\pm$ 3.05	0.326 $\pm$ 0.031

\*Two birds lacking wing chord measurements at initial capture were excluded from condition index analysis (n=26).



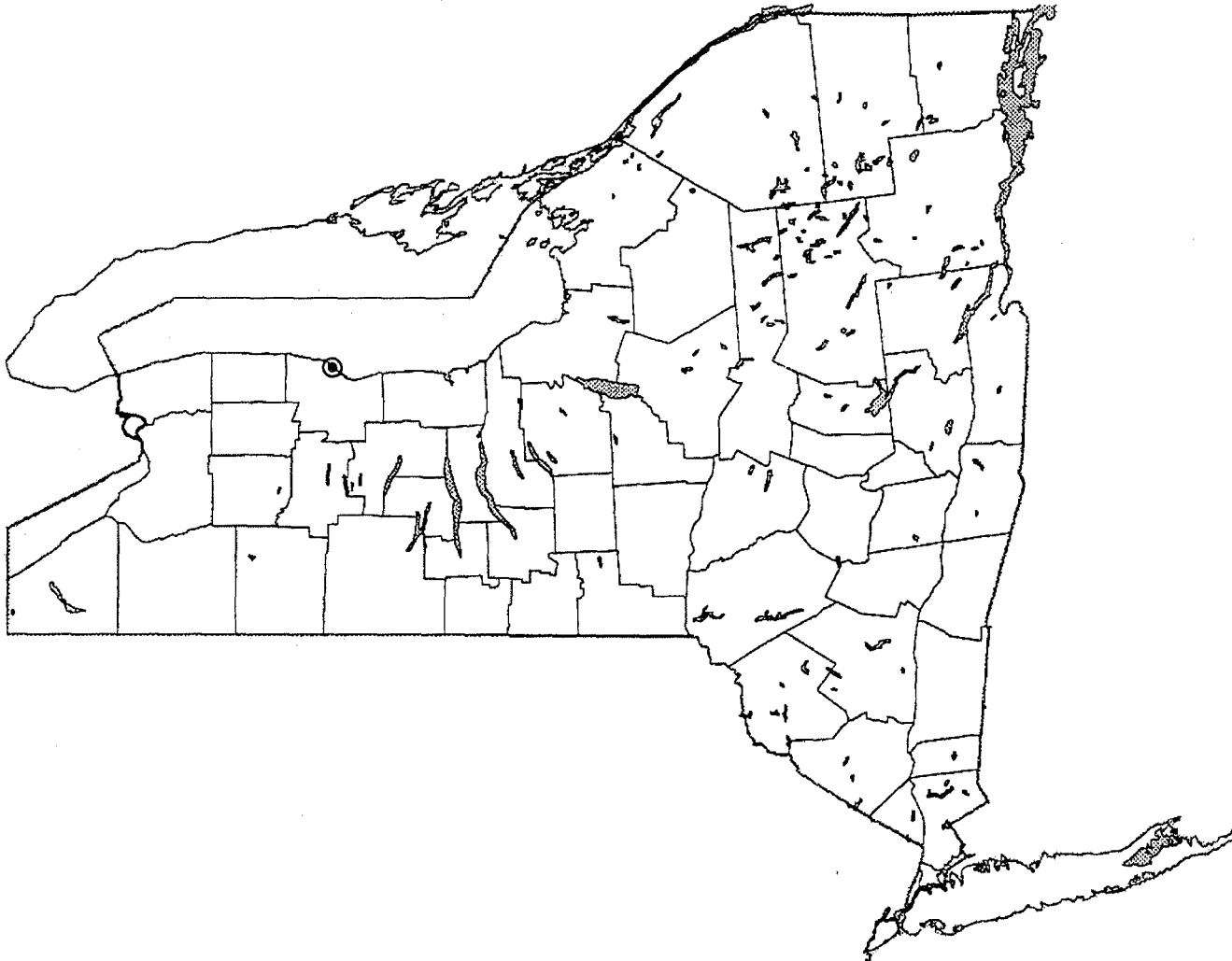
**Table 6** Summary of regression analyses of the relationship between initial capture time ( $x$ ) and mass or condition index at initial capture ( $y$ ) during spring 1999 and spring 2000 for White-throated Sparrows and Swainson's Thrushes. The equations are in the form  $y = a + bx$ , where  $b$  is the slope.

SPECIES	n	Mass			Condition index		
		$b$	$r^2$	$p$	$b$	$r^2$	$p$
<u>Spring 1999</u>							
<i>Zonotrichia albicollis</i>	79	-0.19600	0.310	0.12	-0.00023	0.000	0.88
<i>Catharus ustulatus</i>	28*	0.11100	0.002	0.83	0.00191	0.005	0.73
<u>Spring 2000</u>							
<i>Zonotrichia albicollis</i>	166	0.36200	0.110	0.00	0.00366	0.077	0.00
<i>Catharus ustulatus</i>	34	-0.05200	0.002	0.82	-0.00051	0.002	0.82

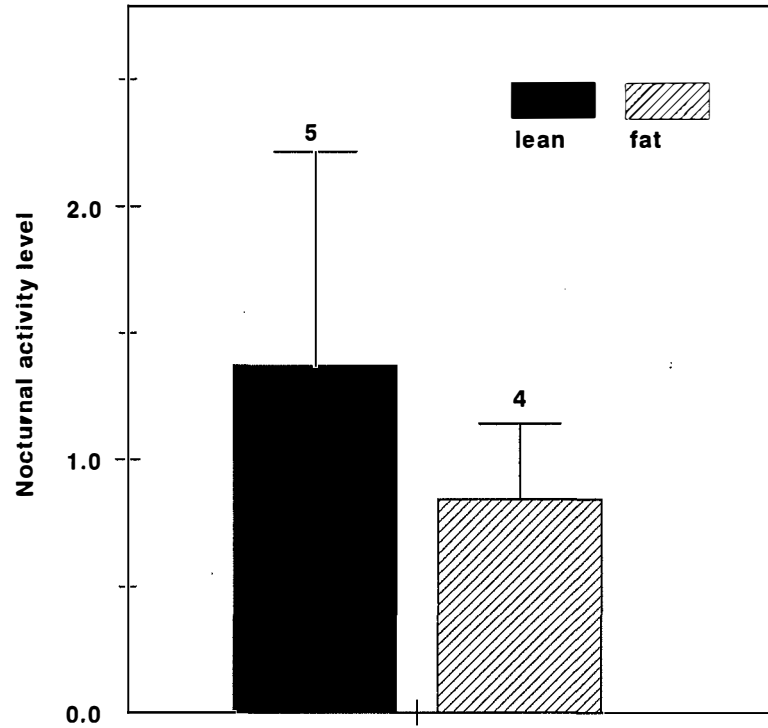
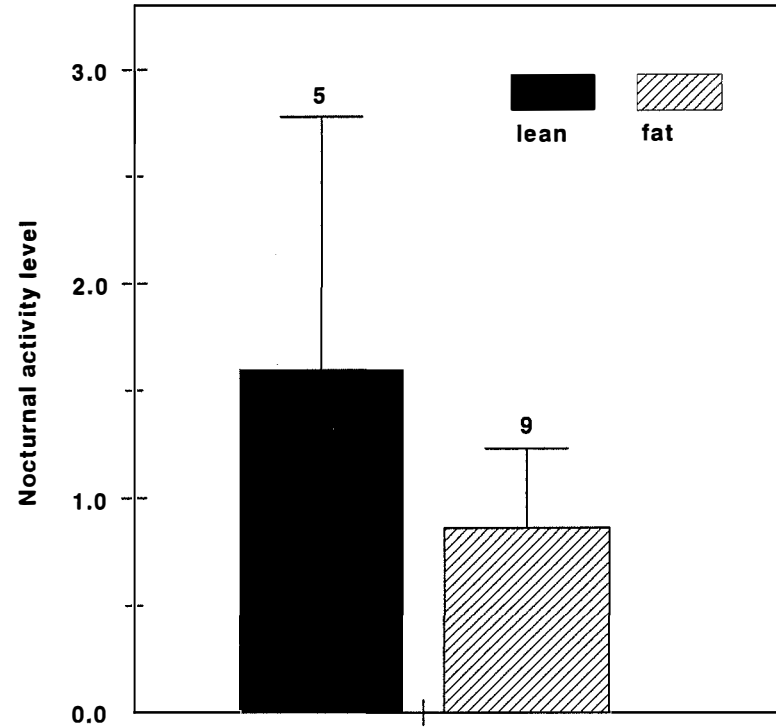
\* Two birds lacking wing chord measurements at initial capture were excluded from condition index analysis (n=26).

**Table 7** Results of ANOVA tests comparing mean insect abundance among sampling sites for each sampling date during spring 1999 and spring 2000.

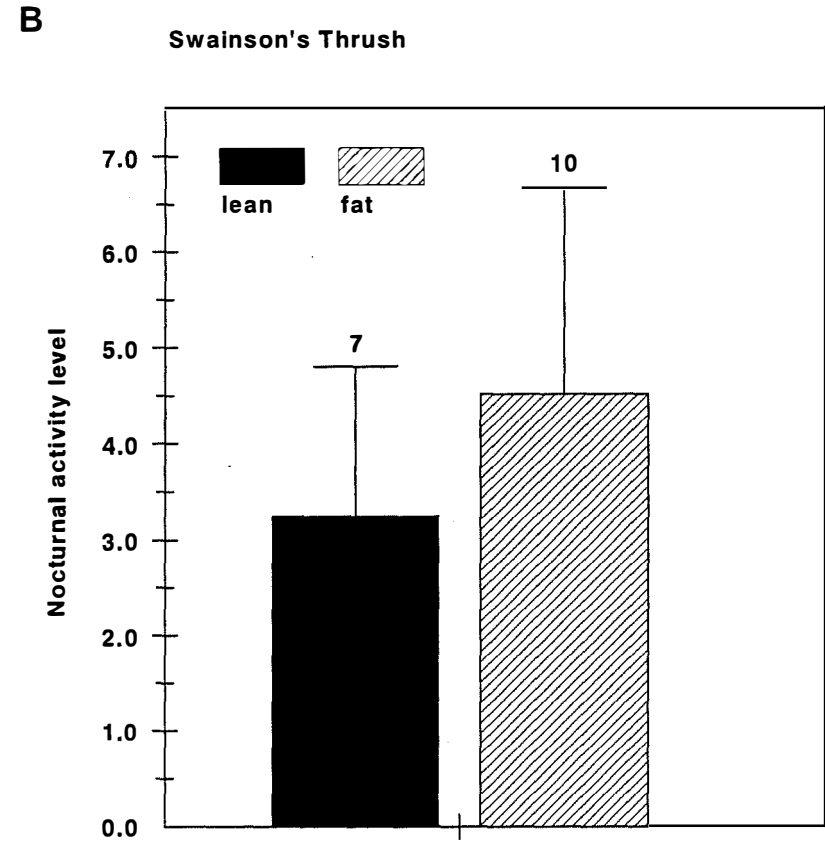
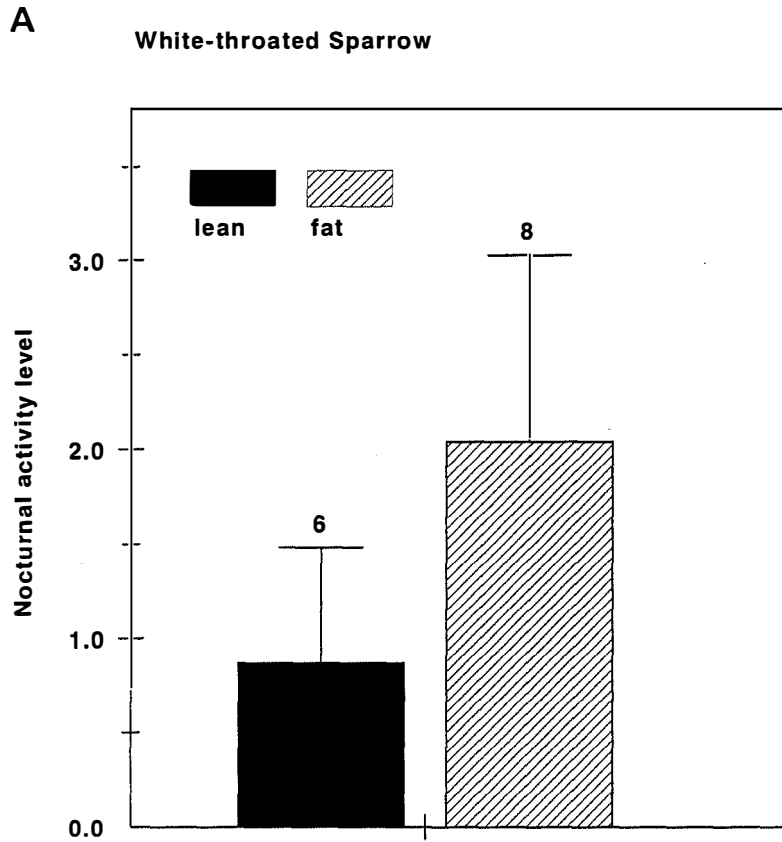
Date	<i>F</i>	<i>df</i>	<i>p</i>
<u>Spring 1999</u>			
May 16	1.54	2,9	00.266
May 22	2.41	2,9	0.145
May 30	0.19	2,9	0.830
<u>Spring 2000</u>			
April 29	12.46	2,9	0.003
May 7	6.79	2,9	0.016
May 19	5.73	2,9	0.025
May 27	0.50	2,9	0.624



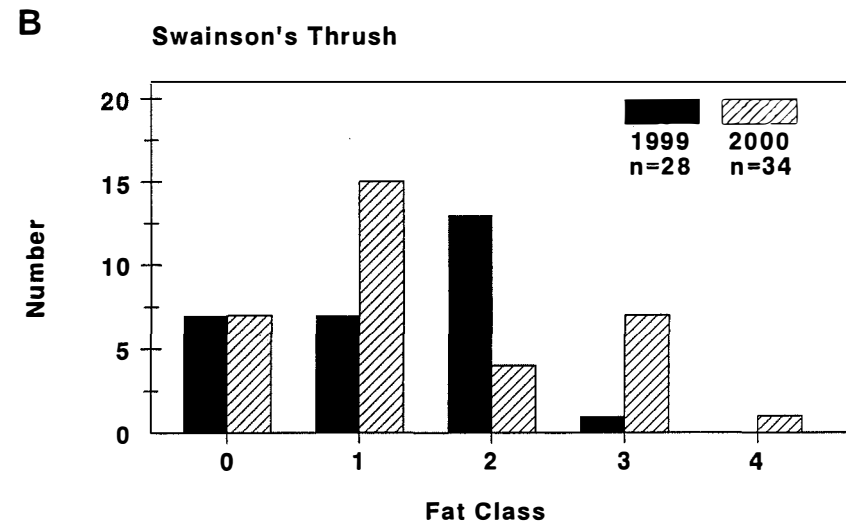
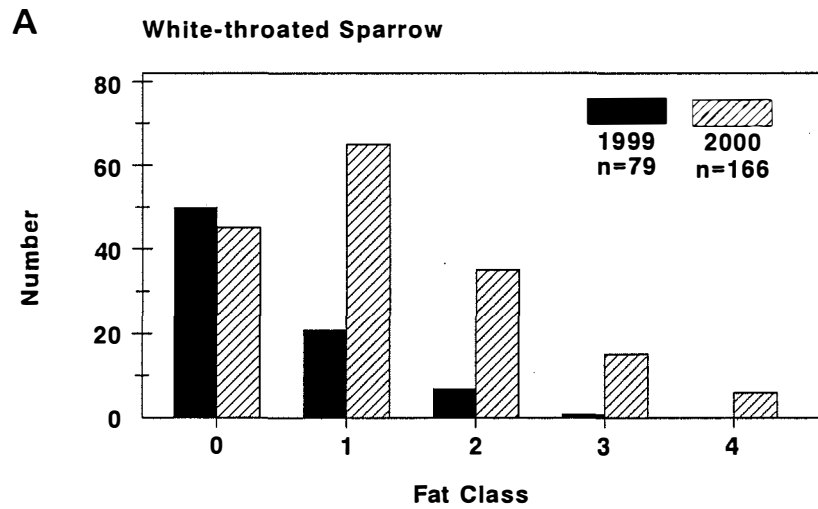
**Figure 1** Location of Braddock Bay Bird Observatory (⊙) in relation to Lake Ontario shoreline in Monroe County, New York.

**A***Dendroica* warblers**B***Catharus* thrushes

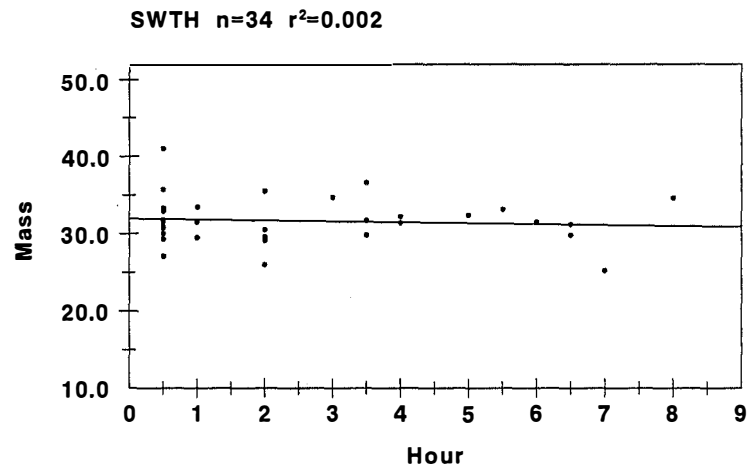
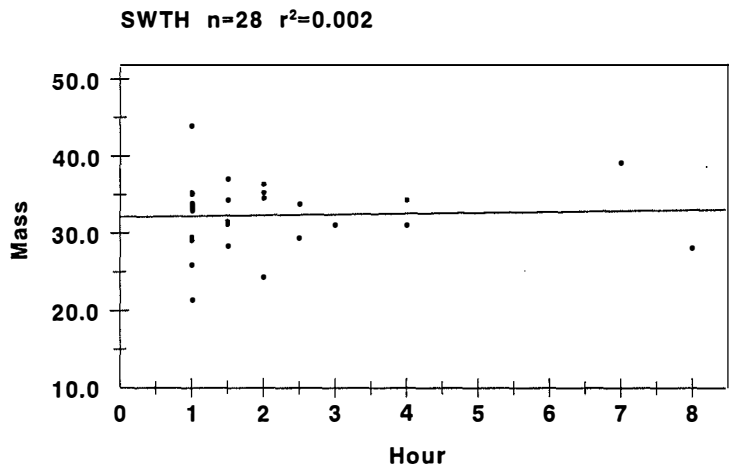
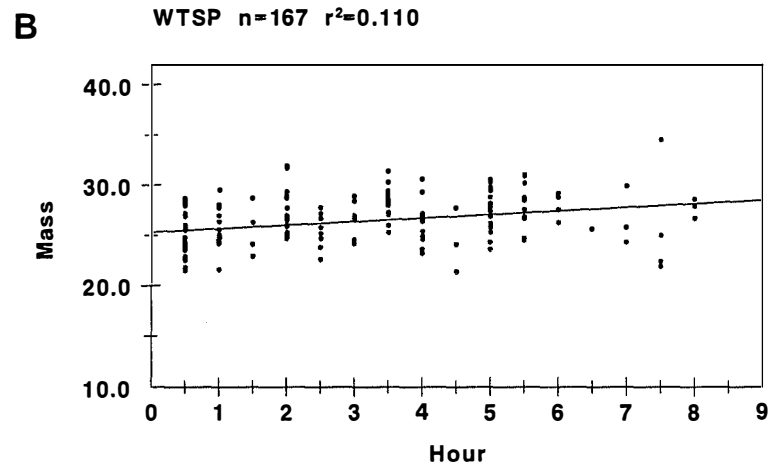
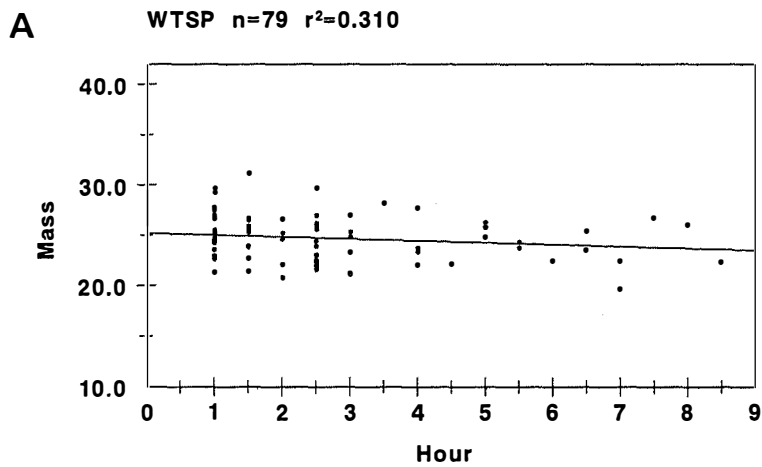
**Figure 2** Average nocturnal activity levels (+SE bars) for lean and fat *Dendroica* warblers (A) and *Catharus* thrushes (B) held in activity cages during spring 1999. Activity levels are the average number of 2-minute time periods with activity per hour of darkness. Sample sizes are given above error bars.



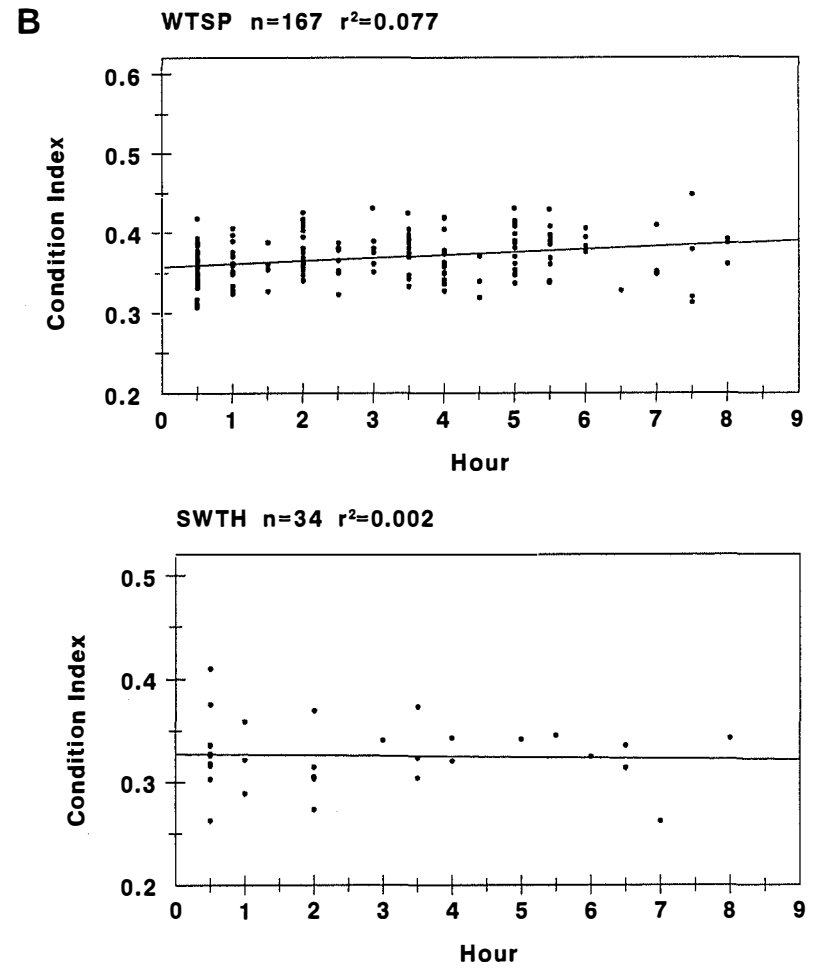
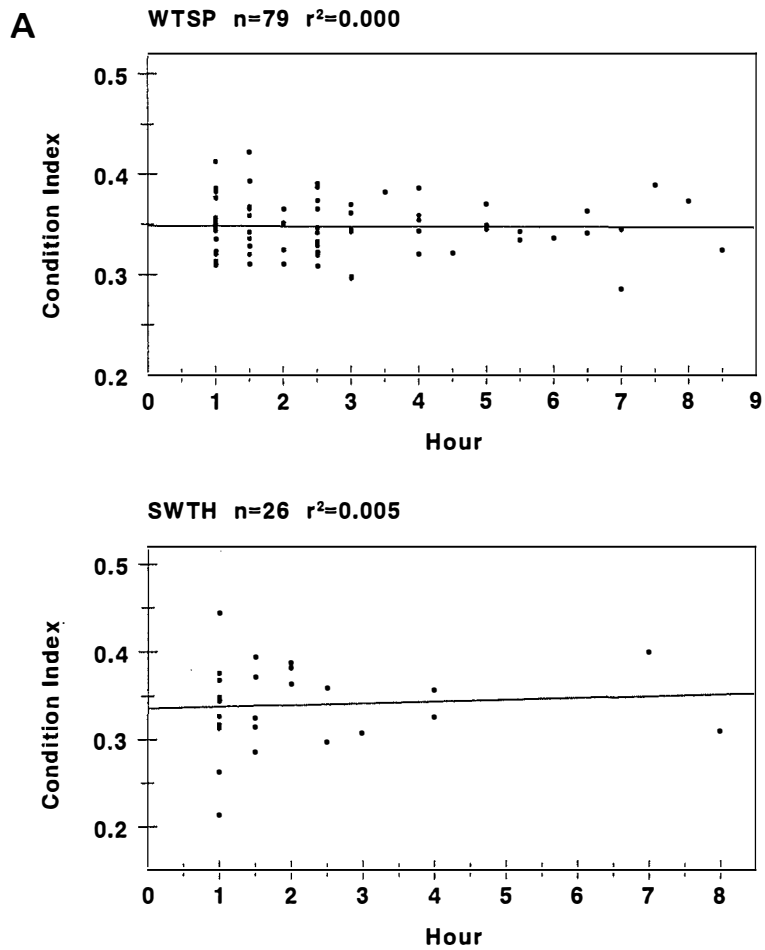
**Figure 3** Average nocturnal activity levels (+SE bars) for lean and fat White-throated Sparrows (A) and Swainson's Thrushes (B) held in activity cages during spring 2000. Activity levels are the average number of 2-minute time periods with activity per hour of darkness. Sample sizes are given above error bars.



**Figure 4** Distribution of fat class scores for White-throated Sparrows (A) and Swainson's Thrushes (B) captured during spring 1999 and spring 2000 at Braddock Bay Bird Observatory.

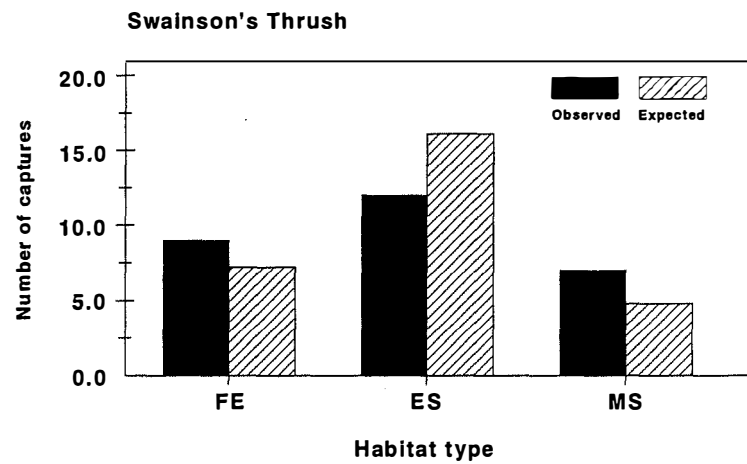
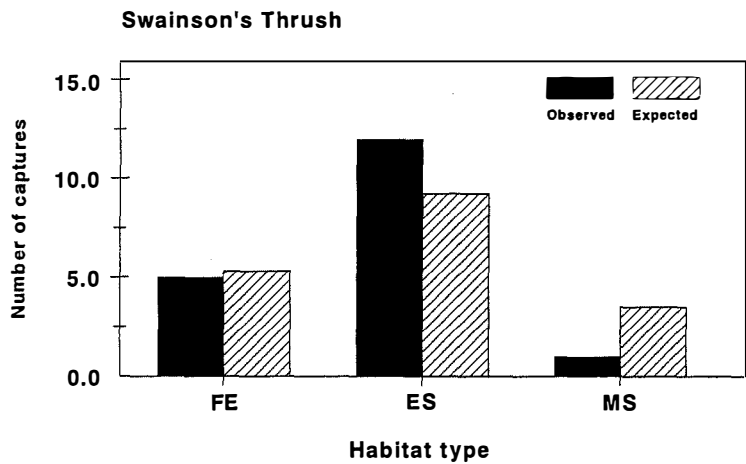
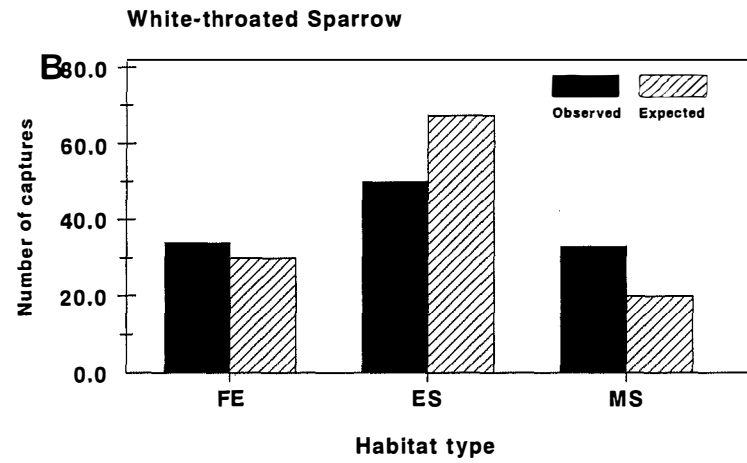
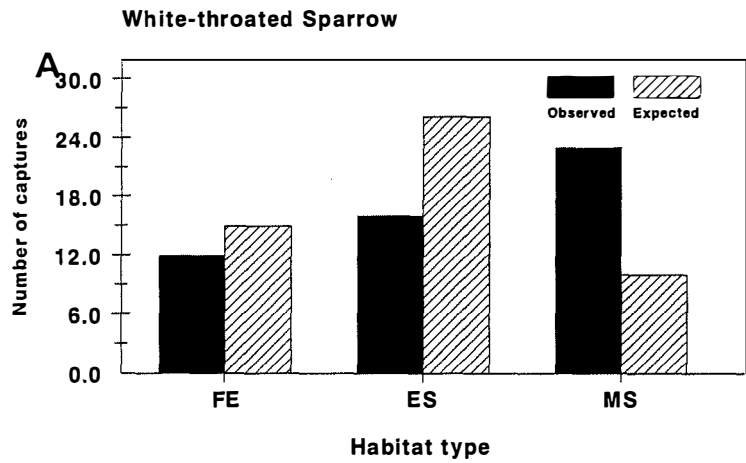


**Figure 5** Relationship between initial capture time and mass for White-throated Sparrows and Swainson's Thrushes in 1999 (A), and 2000 (B). Initial capture time is reported as the hour after sunrise.

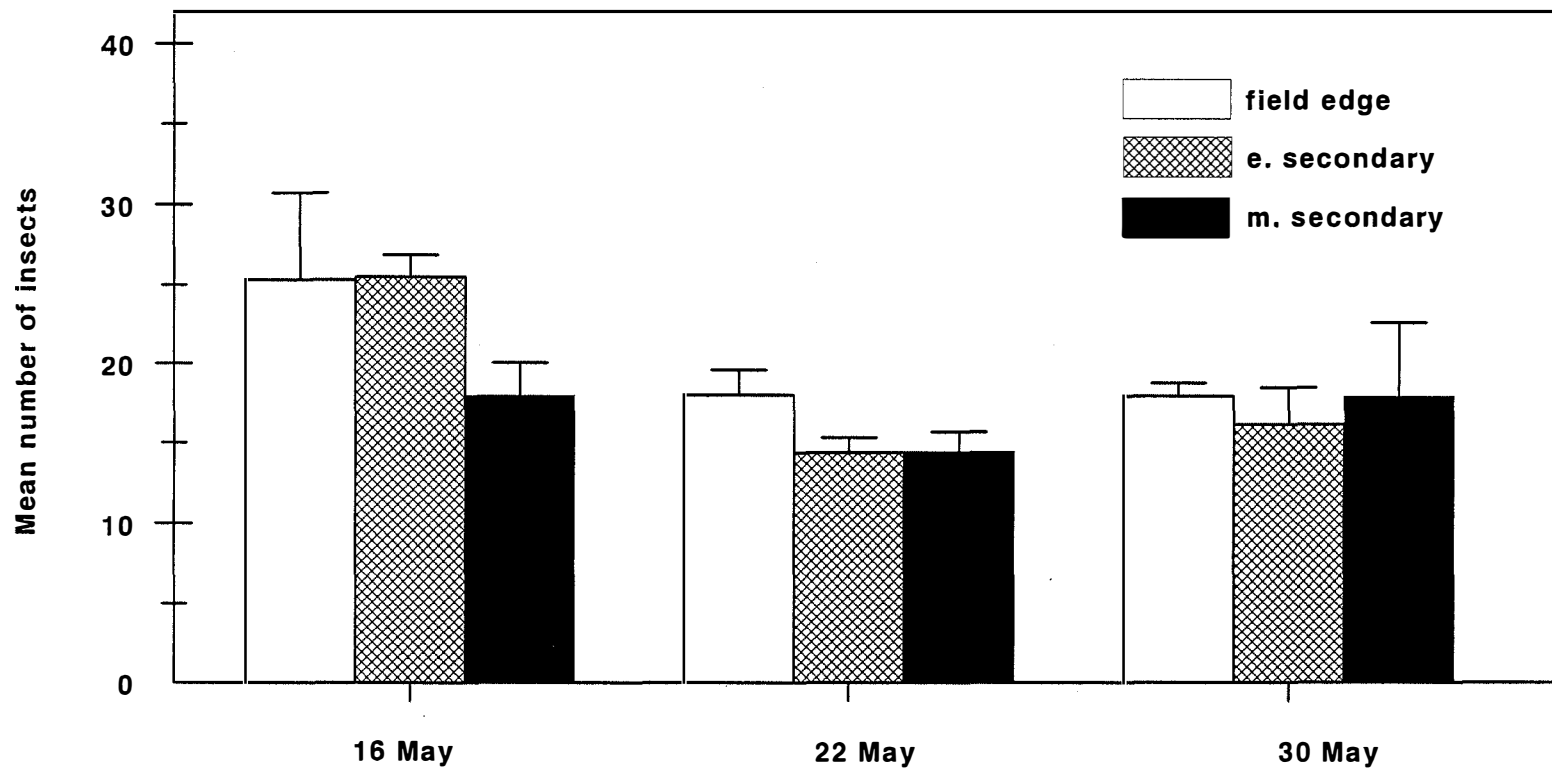


**Figure 6** Relationship between initial capture time and condition index for White-throated Sparrows and Swainson's Thrushes in 1999 (A), and 2000 (B). Initial capture time is reported as the hour after sunrise.

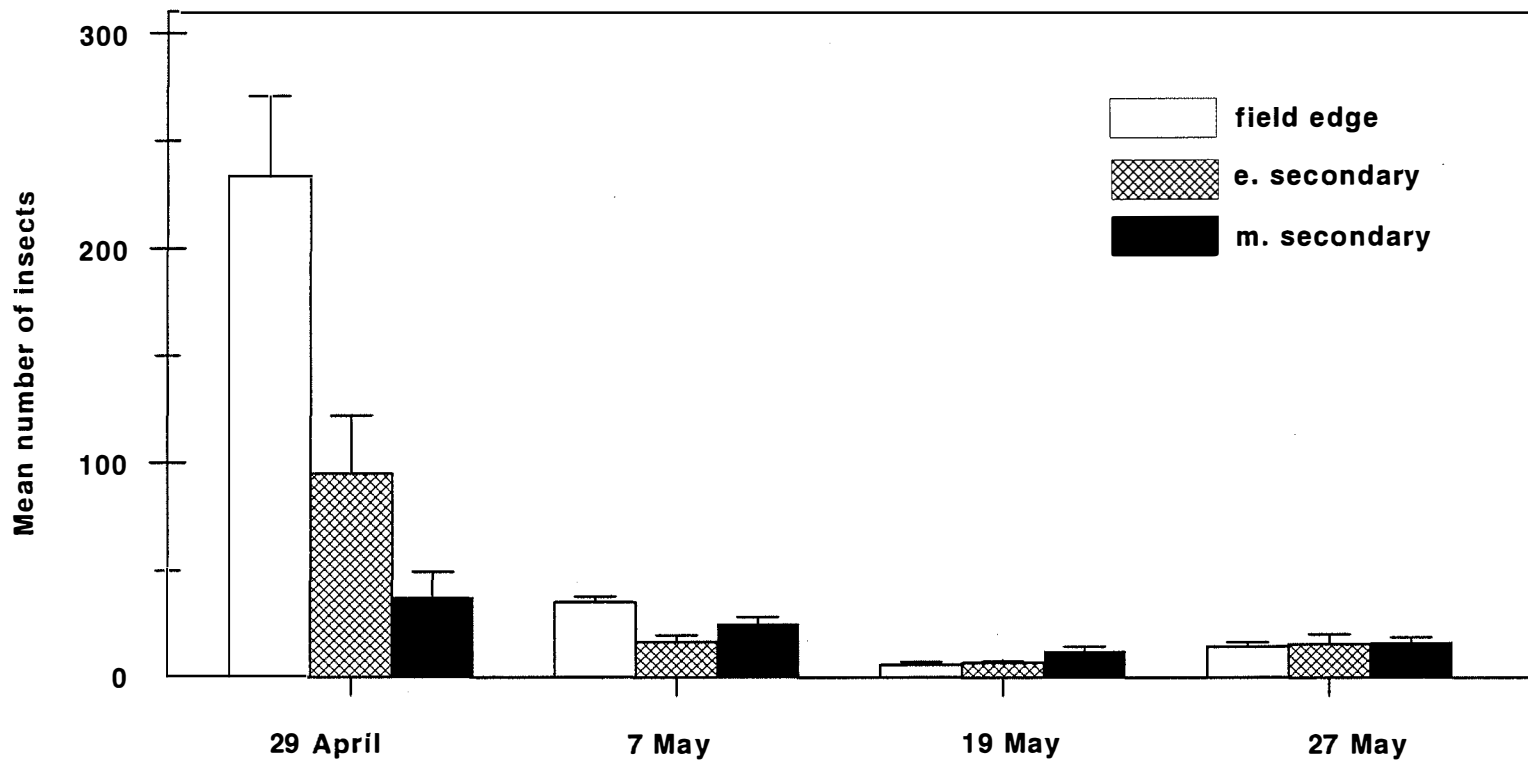




**Figure 7** Observed and expected numbers of White-throated Sparrows and Swainson's Thrushes captured in field edge (FE), early secondary (ES), and mature secondary (MS) habitats during spring 1999 (A) and spring 2000 (B) at Braddock Bay Bird Observatory.



**Figure 8** Mean number of insects (+SE bars) captured in three habitat types (field edge, early secondary, and mature secondary) during spring 1999 at Braddock Bay Bird Observatory. Values are the average of both replicates and all height intervals at each sampling location.



**Figure 9** Mean number of insects (+SE bars) captured in three habitat types (field edge, early secondary, and mature secondary) during spring 2000 at Braddock Bay Bird Observatory. Values are the average of both replicates and all height intervals at each sampling location.

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