

STOPOVER HABITAT UTILIZATION BY MIGRATORY LANDBIRDS
WITHIN URBANIZING LANDSCAPES OF CENTRAL OHIO

DISSERTATION

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By

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ABSTRACT

For small landbirds, long-distance migration between wintering and breeding grounds involves the use of multiple stopover sites where birds must refuel to meet high energetic demands. Yet in many regions habitat fragmentation has isolated remnant forest patches for migrating birds. Urbanization may pose a considerable challenge to a migrant bird's ability to select quality habitats and regain energy reserves due to high levels of fragmentation and altered ecological processes.

I investigated habitat use and behavioral decisions of migrating Swainson's Thrushes (*Catharus ustulatus*) within an urbanizing landscape. Specifically, I examined whether differences in stopover location, energetic condition, and weather patterns influenced stopover duration. I examined both intrinsic and extrinsic influences on short-term movement rates of thrushes and total distance moved during stopover. Finally, I developed models of optimal avian migration to gain insight into how migration events influence arrival in breeding areas.

During May of 2004-2007, I caught 103 Swainson's Thrushes in a small woodlot within the metropolitan area of Columbus, Ohio and fitted each bird with a 0.66 g radio transmitter (less than 2.5% of Swainson's Thrush body weight). To simulate arrival at a stopover location, I experimentally relocated thrushes to one of seven urban forest

patches. Birds were monitored daily to quantify stopover duration (days) and fine-scale movement patterns used during foraging and site exploration. Birds showed high site tenacity with 93% remaining at the release site until migratory flight was initiated; all five birds that left release sites were located at the two smallest sites (< 4.5 ha). Mean stopover duration was 3.7 days (± 3.4 SD; range 1-12 days). Stopover duration was negatively related to the advancement of the migratory season and energetic condition at capture. Although the influence of stopover site was uninformative in explaining duration, I detected a positive relationship between distance moved by an individual and area of the stopover site. On average, birds moved 313.5 m (± 182.75 SD) during the first three days of stopover, but total distance moved was more limited in smaller patches. Modeling results highlight how migrating birds may increase their chances of reaching the breeding grounds by maintaining energetic reserves early in the migratory period while still conforming to a migratory schedule. The importance of energetic reserves and migratory timing are patterns consistent with the field data. These results indicate that Swainson's Thrush, and possibly forest interior birds, may show a degree of area sensitivity in isolated urban forest remnants, but these stopover areas in many cases can provide suitable stopover habitat and opportunities for forest interior landbirds to forage and rebuild energy stores.

DEDICATION

This dissertation is dedicated to my wife, Jordan Main, for support in
our migration to Ohio.

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CHAPTER 1

INTRODUCTION

In-depth study of avian migration extends only into the middle portion of the 20th century (Gauthreaux 1996), but interest in the seasonal movements of birds reaches back over 250 years with Linnaeus' idea that birds winter underwater (Alerstam and Hendenstrom 1998). Much of our contemporary understanding of the migratory process is driven by our inherent interest in the remarkable abilities of birds to seasonally move across diverse landscapes over great distances between wintering and breeding grounds. These studies have highlighted the abilities of birds to complete their journeys in the face of landscape barriers (oceans, deserts), extremes in weather, and physiological limitations.

With the documented decline of many populations of migratory birds (Newton 2004) it has become increasingly important to evaluate which portions of the annual cycle contribute most to population declines. There is compelling evidence that habitat fragmentation and land use change on the breeding grounds has contributed to the population declines in birds (Robbins 1979, Robinson et al. 1995). In addition, losses of tropical forests have led to declines in wintering habitat and also may contribute to population declines (Robbins et al. 1989). Because birds spend between 3-4 months

migrating each year between breeding and wintering grounds (Silllett and Holmes 2002) we must also consider how populations are influenced by events occurring during migration.

For many bird species, migration involves a long-distance movement between breeding and wintering areas, and the use of multiple stopover sites en route to replenish energy stores and rest. Long-distance migrants may travel thousands of kilometers, and these migratory movements are energetically costly and involve a high risk of mortality (Silllett and Holmes 2002). Because migrants must endure these periods of increased vulnerability, it is vital that we expand our understanding of avian migration and the specific habitat requirements of migrants during stopover periods. Such information is needed to make informed land use decisions to conserve suitable stopover habitat for migrating birds.

Recent efforts to evaluate the conservation potential of migratory stopover sites have recognized the need for maintaining habitat to meet the varying needs of birds during migration and that the value of these habitats differ across the landscape. Therefore, Mehlman et al. (2005) defined a continuum of stopover habitats conditions ranging from “fire escapes” to “convenience stores” to “full service hotels” to meet the habitat needs of forest landbirds during migration. In this perspective, the smallest habitat patches, “fire escapes”, provide only brief resting areas for migrants and do not allow for large gains in energy. At the other extreme, large blocks of forested habitat,

“full service hotels”, allow for ample rest and refueling along the migratory route.

Embedded within this perspective is the idea that there are greater densities of small, isolated stopover sites that can be useful stepping-stone stopover locations.

Isolated forest patches within urban settings have been identified as having the potential to serve as either “fire escapes” or “convenience stores” of stopover habitat (Mehlman et al. 2005). They can serve either as an emergency stopover location or, in some cases, may provide opportunities for energetic gains and function as important stopover locations. Ultimately, the factors determining utility of an urban stopover site are provisions of resting and foraging opportunities.

Areas of urban development generally have been shown to exhibit lower diversity and richness of breeding birds than undeveloped regions (Marzluff et al. 2001). This pattern appears to be attributed not only to a decrease in breeding habitat, but occurs even when the amount of habitat is comparable to areas with less development, suggesting that the changes may be driven by some specific features of urbanization (Rodewald and Bakermans 2006). Furthermore, recent evidence points to a behavioral aversion of migratory birds to breed within urban areas (Rodewald and Shustack 2008). Despite this evidence from the breeding season, urban forest patches do appear to serve as migratory stopover sites for a wide variety of birds.

Rodewald and Matthews (2005) documented migrant use of urban stopover sites during spring migration in 24 stopover sites within the Columbus, Ohio metropolitan

area. In this region, an average of 96 species was recorded per year, and of these species, greater than 50% were transient migrants. This study found that the 27 most common species of neotropical and temperate transients did not differ in abundance along an urban to rural gradient, but were more abundant within upland stopover sites than riparian sites. This is one of the only studies to quantify abundance of migrant's occurring within urban areas across multiple study sites (but see Hostetler et al. 2005 for case study example). However, surveys alone cannot address how long birds remain within urban stopover sites or if there are changes in activity and movement of birds within isolated urban forest patches.

Investigations of stopover habitat use by migrating birds should also consider how birds select habitat (Hutto 2000). Clearly birds are constantly faced with a diverse set of stopover situations. They must quickly assess the habitats available to them within their flight range (Petit 2000). The most time efficient manner for birds to select stopover habitat would be to use cues as they descend from migratory altitudes rather than directly sample potential stopover habitat (Chernetsov 2005). Within urban areas such as Columbus, Ohio, advancement of tree phenology may occur as much as one week earlier within the metropolitan region relative to the surrounding landscape (Zhang et al. 2004). This early greening of the habitat may act as an enticement to a migrant that bases its stopover decision on the visual appearance of habitat. However, once the bird lands at a stopover area within an urban forest it is unclear if the habitat will provide sufficient

resources and resting opportunities. It may either find food resources supplemented by early emergence of insects, or it may be difficult to locate resources within a fragmented landscape that is host to increased presence of avian predators (Marzluff 2007) and novel combinations of species (Alberti et al. 2003). Therefore, just because birds choose to initiate a migratory stopover within an urban area, we do not know how they may respond to the habitat and ecological changes observed within urban landscapes. For example, during migration, transient birds within Columbus, Ohio showed higher occurrence in upland forest sites than riparian forest sites. However, we do not know if birds remain in these upland forests during stopover and high abundance may not equate to high site quality (Van Horne 1983). As a result, it is difficult to evaluate the habitat suitability of urban stopover sites for migratory landbirds without exploring the behavioral responses of individual migrants to these stopover locations.

The goal of this dissertation was to expand our understanding of how isolated urban forests can serve as migratory stopover sites for neotropical migratory landbirds. In my dissertation, the following chapters address three important questions regarding migratory stopover of transient Swainson's Thrushes (*Catharus ustulatus*). First, I quantified the length of time that Swainson's Thrushes remain at stopover locations and evaluate the determinants of stopover duration. Surprisingly, stopover duration has been difficult to accurately estimate. Winker et al. (1992) suggested that Swainson's Thrushes, as well as many other species of migratory landbirds, may exhibit a migratory

strategy in which they fly by night and forage during the day, implying that they can gain enough energy in one day of foraging to continue migrating. Furthermore, estimates of stopover duration based on recapturing individuals marked at a stopover site are plagued by low recapture rates, and a recent study by Bachler and Schaub (2007) has shown that these recapture methods underestimate actual stopover duration. Therefore, I used radio telemetry to quantify stopover duration at seven urban stopover sites within the Columbus metropolitan region. The ability to follow individually marked birds allowed me to investigate both intrinsic (energetic condition at capture) and extrinsic (site influence, weather, and passage of migratory season) factors that influence stopover duration.

Next, I evaluated the movement patterns of Swainson's Thrushes by quantifying short-term movement rates and total distances moved at the same seven stopover sites. During migratory stopover, birds enter unfamiliar locations and habitats that they must use to regain energy and avoid predation. Much of our understanding of how birds use stopover habitat is limited to patterns of abundance and species richness from bird surveys or intensive mist-netting efforts where individuals are captured once. While these metrics have allowed us to understand patterns of stopover habitat use, they provide limited information on the behavioral responses of birds at stopover sites. In chapter three, I explored how energetic condition at capture influenced the fine-scale movement

rates and total distance moved by Swainson's Thrushes in different stopover locations and how site characteristics may influence use of these stopover sites.

Finally, with any migration study it is important to consider the ecological framework that is being explored. Unlike research conducted in breeding or wintering areas, migratory stopover involves the ephemeral use of habitat throughout the migratory journey. With multiple stopover events across a diverse landscape, it is essential to consider how events occurring during one portion of the migratory journey can affect migration as a whole and ultimately the bird's breeding success. Therefore, in my final chapter, I developed a dynamic programming model of optimal avian migration. This model is parameterized using information on the migratory ecology of the Swainson's Thrush. This theoretical chapter allowed me to consider migration as a whole and embed results obtained from my field research into a broader perspective of avian migration.

With heightened interest in the conservation of migratory birds throughout their annual cycle, it is becoming increasingly apparent that we must gain a better understanding of habitat requirements during migratory stopover, and the ways that stopover habitat is affected by land use change. Urban forests typically are viewed as a negative constraint for most breeding birds, but during migration, the temporary use of stopover sites within these developed regions may be important for small landbird migrants. With the expansion of urbanization worldwide, there is a great need to consider how urban-forest sites can function as stopover habitat.

CHAPTER 2

STOPOVER DURATION CHANGES WITHIN THE MIGRATORY WINDOW: THE INFLUENCE OF TIMING, ENERGY, AND WEATHER IN AN URBAN LANDSCAPE

INTRODUCTION

Birds have developed many strategies to successfully complete their annual migrations (Alerstam and Hedenstrom 1998). With few exceptions, birds cannot make their journey in a single migratory flight and must use a variety of stopover locations along their migratory route to regain energy and rest (Moore et al. 2005). While the number of stopover locations used and distance between locations depends heavily on the morphology and physiology of a particular species, for most birds migration could not be completed without suitable stopover habitat.

Stopover periods are vital to maintaining energy, and experiences during stopover may ultimately influence the reproductive success of migratory birds (Newton 2004, Smith and Moore 2003). With such importance placed on migratory stopover, it is not surprising that there is extensive evidence that stopover sites are not randomly selected (Petit 2000). The utilization of stopover habitat is likely influenced by the energetic status (Jenni and Schaub 2003) and habitat available to an individual bird (Simons et al.

2000). Once a bird has arrived at a stopover location, refueling rates can vary across habitat types (Dunn 2001), thus influencing a bird's ability to regain the energetic reserves that allow it to continue migration.

The decision of a bird to initiate stopover or resume migration is also influenced by weather conditions (Richardson 1990 and Schaub et al. 2004). European Robins (*Erithacus rubecula*) were found to remain at stopover sites longer when weather was considered poor for migration (Tsvey et al. 2007). In addition to field-based studies, theoretical models suggest the energetic advantage of migrating during favorable weather and the extra energy costs of flying during poor weather (Weber and Hedenstrom 2000). While gaining energy and maintaining migratory timing can influence a bird's readiness to depart from a stopover site, weather conditions often influence the precise date of departure.

As migrants make alternating decisions between stopover and migratory flight, they require suitable stopover opportunities along their entire migratory route. For migratory birds that utilize forest habitats during stopover, the availability of habitat varies across the region (Simons et al. 2000). In the Midwestern United States the landscape is dominated by agriculture with forests occurring in small isolated patches. In many areas, birds may be forced to use the habitat that is available to them as they

terminate a migratory flight. As a result, it is important to understand how birds utilize these inland stopover habitats and whether these isolated habitat patches can effectively support avian stopover.

In Midwestern North America, urban development constitutes another important and increasing land use (Bergen et al. 2005) that also influences birds during migration. With nearly 80% of the U.S. population classified as urban residents (United States Census Bureau 2001) and urban populations continuing to increase, the percentage of urban dominated landscapes will also increase (Hostetler and Knowles-Yanez and 2003). Understanding the impacts of urban development on animal and plant communities is being addressed for a variety of taxa (McKinney 2002). For breeding birds there is typically a decrease in diversity and richness as urbanization increases (Blair 1996, Friesen et al. 1995, Rodewald and Bakermans 2006). It might be hypothesized that during migration birds will show a similar pattern of avoidance at urban stopover sites. However, not all species follow this pattern, as demonstrated by “urban exploiters” which may prosper within urban landscapes (McKinney 2002, Rodewald and Shustack 2007). Predicting how birds respond to urbanization during migration will likely be complicated by differences in the time scale for which migrants and breeding birds occur at a location.

Rodewald and Matthews (2005) found no associations for either migrant abundance or richness along an urban to rural gradient, but the details of how birds use forest stopover habitat within urban landscapes remain unclear. In Mehlman et al.’s

(2005) evaluation of the conservation value of stopover sites, large urban remnant patches were considered unlikely to function as areas where extensive refueling could occur, but would allow migrating birds to stopover for several days and obtain some energetic resources. To evaluate the role of urban stopover sites for migratory birds, it is necessary to understand how long individuals are remaining within stopover locations.

The decision of a bird to remain at a stopover site or resume migration will depend on conditions that are both intrinsic and extrinsic to the individual migrant (Weber et al. 1998). In addition, birds are under pressure to leave stopover locations and arrive on the breeding grounds within a given time window (Newton 2004). There is likely an important trade-off between energetic gain at a stopover site and migratory timing. Thus, perturbations that influence habitat quality may limit a bird's ability to efficiently forage, resulting in changes in migratory stopover duration. Within urban landscapes changes associated with increased development may influence a bird's ability to efficiently refuel, thus, influencing stopover duration. The objectives of my study were to quantify the migratory stopover duration of Swainson's Thrushes (*Catharus ustulatus*) within a Midwestern urban landscape. Specifically, my study examined: 1) the influence of stopover location within an urban setting on stopover duration, 2) how the individual's condition at capture can affect stopover duration, and 3) how weather may influence the departure from a stopover location.

METHODS

Study Area and Experimental Relocation

Study sites were located within the Columbus metropolitan region of central Ohio and include portions of Delaware and Franklin counties. Within this area, riparian and upland forests are the two dominant habitats available to forest birds during migratory stopover (Rodewald and Matthews 2005). I selected 7 deciduous forest sites within the Scioto River watershed to examine stopover behavior of Swainson's Thrushes within the urban matrix. These forested stopover sites were selected to vary in area and the degree of urbanization within a 1-km radius of the site (Table 2.1). These metrics were digitized from digital aerial photographs or provided by the county auditors for 2002 and 2004 in Delaware and Franklin counties, respectively (Rodewald and Shustack 2008). Within a 1-km radius, quantification of urbanization within Columbus, Ohio has demonstrated an increase in buildings, roads, and mowed areas along a rural to urban gradient (Rodewald and Shustack 2008). In addition, the 1-km radius for landscape quantification corresponds to linear distances of movement during migratory stopover for European Robins (Chernetsov 2005) and Summer Tanagers (Aborn and Moore 1997).

Because migrant settlement at a site can occur before capture, I conducted an experimental relocation study to examine behavioral responses of thrushes to urban forest patches and to control for arrival of a migrant at a pre-selected stopover location. This approach allowed me to evaluate the bird's response to a new stopover situation from

settlement to departure. Birds were caught at a single location (Waterman Farm Agricultural and Natural Resources Laboratory woodlot at the Ohio State University) and moved to one of six unique stopover locations. Waterman Farm was used as the seventh site and served as a control for the relocation experiment. A Likelihood Ratio Test was used to evaluate the influence of the experimental relocation. All birds were released within 50–70 minutes of capture at a randomly selected point within each site.

Study Species

Swainson's Thrushes were used to address questions regarding the behavioral decisions of migrants at stopover sites. This species winters in South America, breeds primarily in boreal forest regions of North America, and is common during migration in Ohio (Rodewald and Matthews 2005). It is a forest interior species in both wintering and breeding areas and utilizes forests throughout its migration (Mark and Yong 2000).

Swainson's Thrushes were caught using 12 m x 3 m mist nets that were opened daily from sunrise to 10:00 am (EDT), May 1 - June 2. Captured birds were promptly removed from nets and several morphological measures were obtained; these included unflattened wing chord, tarsus length and tail length. I also weighed birds and recorded body mass to the nearest 0.01 g. Finally, the age of the bird was recorded as after-second-year, second-year, and after-hatch-year (undetermined) base on Pyle et al. (1987). Structural measurements were incorporated into one measure of energetic condition. A

principal component analysis was conducted on the correlation matrix of wing and tarsus length (Green 2001). Scores from the first principal component represented a standardized structural metric of the bird. The mass of the bird was regressed against this structural component and the residuals of this regression were used as an index of energetic condition (Green 2001). When developing a metric of energetic condition it is important to evaluate the index with an alternate measure of condition (Schulte-Hostedde et al. 2005). Fortunately, subcutaneous fat deposits in birds can be easily scored and have long been used to evaluate energetic reserves (Krementz and Pendleton 1990). I found a strong association (Spearman's $\rho = 0.7$, $P < 0.05$) between the condition index based on residuals of size-adjusted mass and categorical fat scores, supporting my use of this metric of energetic condition at capture.

Radio Telemetry

Swainson's Thrushes were fitted with 0.66 g Holohil Systems LTD BD-2 radio transmitters attached to back feathers using LashGrip eyelash cement (Kenward 2001). Mean body mass of Swainson's Thrushes was 30.56 g meaning that radios weight less than 2.5% of the bird's body mass. Although a suggested rule of thumb is that transmitter weights for small birds be kept below 3%, we must remain cognizant of potential impacts that transmitters may have on particular individuals (Millspaugh and Marzluff 2001). Radio-tags have been shown to not affect breeding over a two-year

period in Wood Thrushes (Powell et al. 1998) or return rates to breeding areas in Upland Sandpipers (Mong and Sandercock 2007), but transmitters were recently linked to negative flight performance in racing pigeons (Irvine et al. 2007). The influence of a transmitter is likely species specific, but for Swainson's Thrushes, radio telemetry has long been used to track birds during migratory flight (see Cochran et al. 1967, Wikelski et al. 2003). In addition, these birds often initiated a migratory flight within two days of attachment and were documented making repeated migratory flights (Cochran and Wikelski 2005). Therefore, I believe that transmitter weight likely had little impact on migrants during stopover but it is a potential source of bias that must be considered. In spite of the potential biases that radio weight may have, detailed information from individually tracked birds cannot be obtained by other means.

Once fitted with a transmitter, each bird was promptly transferred to one of the seven predetermined sites. Birds were monitored daily and their location, data, and time were recorded at each re-sighting event. Every effort was made to obtain at least two locations per day. If the observer could not get a signal for a transmitter the study site was traversed, spending at least 45 minutes listening for the frequency and looking for the bird. If the bird was still not located, a 1-km perimeter of the study site was driven using a car-mounted whip antenna to locate the bird. If the bird was not located, it was assumed to have initiated a migratory flight and left the study area. However, the frequency of the bird's transmitter was checked at each site for three additional days to

ensure that the bird had left the study area. The stopover duration for each bird was thus defined as the difference (in days) between the initial release and the last location.

To examine the determinants of stopover duration I used an information-theoretic approach. I used Akaike's Information Criterion with a correction for small sample size (Burnham and Anderson 2002) to rank candidate models. An a priori set of candidate models was generated using energetic condition of the bird at capture, site, day, and year to explain patterns of stopover duration. Because stopover duration consisted of count data, exhibited a left-skewed distribution, and had a variance greater than mean, I used a negative binomial distribution for analyses (White and Bennetts 1996).

Weather

Evidence for the influence of weather on migratory decisions has been established through a variety of studies (Rappole and Warner 1976, Richardson 1990, Tsvey et al. 2007). Therefore, it was necessary to evaluate the influence of weather when asking questions regarding stopover duration. I obtained hourly weather data from Don Scott Airport, which is located on the northwest side of the Columbus metropolitan region, and the closest weather station to all sites (between 1 and 10 km). I used a suite of variables to explore the determinants of migratory departure on the radio-marked birds. Variables included the date, maximum daily temperature, average daily temperature, barometric pressure, change in barometric pressure, wind direction, wind speed, and year.

To explore the influence of weather and departure decisions I used Random Forest, a robust tree-based method. This method is based on classification and regression trees, where the response variable is recursively partitioned into more homogeneous subsets based on a set of predictor variables (Cutler et al. 2007). This method has advantages to traditional linear statistical methods because it lacks distributional assumptions, avoids the issue of colinearity in the predictor set, and may contain a mix of continuous and categorical predictor variables (Prasad et al. 2006). The Random Forest methodology extends on classification and regression tree method (Breimen et al. 1984) by incorporating a bootstrapping component where a suite of classification trees was generated during model building. To model departure decisions I used a binary set of departure (1) and no departure (0) events along with the full set of predictor variables.

RESULTS

During May 2004 to 2007 I caught 128 Swainson's Thrushes. Radio transmitters were attached to 91 birds which were relocated to the seven stopover locations. Each site received between 11 and 15 birds across the four year study. Twenty-four percent of transmitters fell off the bird before it initiated a migratory flight. Despite variation in transmitter loss, I maintained a balanced sample across sites ranging from 8 to 12 individuals per site that were monitored until departure [Chadwick (9), Don Scott (9),

Highbanks (12), Lazelle (9), Rush Run (11), Waterman (8), Woodward (11)]. During the study there were three mortalities (one build strike, one predation, one unknown death).

Determinants of stopover duration

Mean stopover duration was 3.7 days (± 3.4 SD), with peak migratory activity (>50% of all captures) occurring between May 12 and May 22. There was no difference in stopover duration between translocated birds and locally released birds at Waterman Farm (Figure 2.1, $G = 6.35$, $df = 6$, $P = 0.38$).

The top six models contained virtually all of the model weight (Table 2.2), with the top two models ($\omega_{1 \text{ to } 2} = 0.62$) being indicated as the most informative in the candidate set. Date of capture (day) was the most influential variable in my candidate set, with energetic condition of the bird at capture also providing important information in describing the pattern of stopover duration. Capture date was negatively related to the stopover duration of birds at my sites ($\beta = -0.052$, ± 0.018 SE). Condition was negatively associated with stopover duration ($\beta = -0.014 \pm 0.006$ SE). Because of the weight associated with capture date, the mean coefficient of date across the top two models ($\beta = -0.05$, ± 0.02 SE) was plotted in relation to stopover duration (Figure 2.3). However, it is important to note that although the null model had a fairly high ranking, it received little support ($\Delta AICc = 4.1$). While this indicated relatively low power in the modeling effort (top model, $r^2 = 0.18$), it indicates that averaging across the season produces a pattern

similar to random. Finally, stopover duration did not show significant differences between age class ($U_{61} = 353.5$, $P = 0.11$). Further, there were no differences in the number of after-second-year and second-year birds throughout the migration period ($\chi^2 = 1.52$, $P < 0.25$).

Influence of weather on departure date

Implicit in these analyses was the assumption that the duration of stopover occurred independent of factors that would facilitate a departure event. Therefore, I explicitly examined the determinants of migratory departure. From 2004 to 2007, there were 94 unique days when radio-tagged birds were present at my study sites and they either remained in stopover or a departure event occurred. Overall model classification accuracy was 72%. Departure events were correctly classified 66% of the time and events where birds remained in stopover were correctly classified 77% of the time. The variables evaluated in the model showed variable importance in predicting departure or remaining at the stopover location (Table 2.2). For example, the occurrence of precipitation was associated with birds remaining in stopover. However, in the overall model the most informative variables (those that resulted in the greatest reduction in mean square error) were date, change in barometric pressure, and wind speed (Table 2.3). Interestingly, changes in barometric pressure and wind speed were not associated with the date of the migratory season (Spearman's $Rho = 0.04$ and -0.16 , respectively, $P >$

0.10). The influence of these top variables in predicting migratory departure can be expressed visually through partial plots of departure events (Figure 2.4), where the influence on departure for each variable is represented after averaging out the influences of the other predictors in the model.

DISCUSSION

During migratory stopover within an urban landscape a bird's decision to remain at a location or migrate was not influenced by stopover site, despite high variation in both the area of the release site and surrounding landscape characteristics. The length of time that a migratory bird remains at a stopover site has been linked to the importance of maintaining a migratory schedule, and longer stopover periods can delay arrival in breeding areas (Yong and Moore 1997). The lack of a site level influence on stopover duration suggests that birds were able to meet their stopover requirements within urban forest patches. This highlights that the short-term use of stopover sites, relative to birds breeding within these areas, may afford migrants less sensitivity to urban development. Indeed, migrant Swainson's Thrushes that were studied in a more rural setting used a wide variety of stopover habitats, from oak-dominated woodlands to floodplains (Winker et al. 1992), suggesting that the species may be able to tolerate variable stopover conditions without altering their stopover decisions.

The lack of a relationship between site characteristics and stopover duration suggests that migratory timing may play more of a role in shaping how long birds remain at stopover locations. During spring migration birds are under pressure to arrive at the breeding grounds and establish territories, and this is often assumed to influence reproductive success (Alerstam and Hedenstrom 1998, Dent et al. 2006). Swainson's Thrushes migrating through my urban study sites showed a decline in stopover duration as the season advanced. This could be because early migrants needed to stopover longer to allow for the emergence of resources as spring advances. Alternatively birds may stop for less time later in the migratory period because they are under increased pressure to reach the breeding grounds.

Energetic condition at capture also influenced stopover duration. Evidence from a variety of studies has reported important relationships between energetic condition and stopover duration (Yong and Moore 1997, Moore et al. 1995), whereas other studies have not found such associations (Bolshakov et al. 2007, Chernetsov and Mukhin 2006). If we consider the influence of date and energetic condition, it seems that migrants early in the migratory window were influenced less by their condition at capture because they could afford to remain longer at stopover sites or wait to take advantage of favorable weather conditions (Schaub et al. 2004). As the migratory season advanced at stopover sites, energetic condition at capture may have become more of an influence on stopover duration. Interestingly this pattern was not influenced by the age of the bird which was

unexpected given that Woodrey (2000) has shown that young birds may be less efficient during stopover in terms of resource acquisition and maintain lower energy stopover at than more experienced birds. Therefore, migratory Swainson's Thrushes, regardless of age, within the sites may experience increased energetic constraints as the season advances. Such a pattern would conform to heightened pressures to increase the pace of migration and to arrive at the breeding grounds at an optimal date.

One external factor that is known to influence stopover duration is the effect that weather conditions have on departure decisions (Weber and Hedenstrom 2000). Understanding how weather acts to influence migratory stopover is a very important piece to the migration puzzle because its influence on migratory behavior will vary independent of other factors. For example, the condition of an individual coupled with a temporal component may influence how long a bird remains at a given stopover location, but the weather conditions (whether advantageous or poor) can ultimately influence the precise departure date. From my model of departure decisions, I again found that date had a clear influence on departure. In addition to this temporal component, the decision to depart appears to be influenced by changes in barometric pressure and mean wind speed, which vary independently across the migratory period. Both of these variables are highly indicative of the passage of weather fronts and have been implicated in migratory behavior (Robinson 1990).

These results highlight important aspects of stopover ecology for migrant landbirds and illustrate the potential conservation value of urban stopover habitats. As other studies have shown, short-term changes in weather can influence a bird's departure decisions (Schaub et al. 2004) and this can ultimately influence migratory timing. Also, the pressures of migration may be revealed at different time periods during the migration season. If such a pattern is present, then studies addressing the importance of energetic condition must consider not only the energetic condition at arrival to different stopover locations, but also the timing of migratory passage within the study region. From a conservation perspective, the variation in stopover duration within a site was greater than the variation between the sites, and suggests that urbanization may have less of an influence on how long birds remain at a site. Mehlman et al. (2005) suggested that relatively large urban forests should provide stopover habitat where birds can rest and regain energy. In contrast, my results indicate that remnant urban forest patches of a variety of sizes may provide extended stopover opportunities for migrant landbirds.

	Chadwick Arboretum	Lazelle Woods	Woodward Park	Waterman Farm	Don Scott Airport	Rush Run Park	Highbanks Metropark
Release patch area (ha)	0.7	4.5	11.9	12.6	15.4	18.4	38.4
Road length (m)	73,532	69,084	89,869	92,874	45,534	74,771	14,605
City center (km)	5	18.56	12.08	6.6	15.08	12.46	20.86
Number of buildings	546	2265	3690	2259	439	1611	246
% Forest	5.0	2.0	6.0	6.0	6.0	32.0	54.0
% Mowed	25.0	20.0	9.0	5.0	20.0	16.0	7.0
% Agricultural	4.0	0	0	27.0	37.0	0	4.0
% Scrub/shrub	4.0	1.0	1.0	1.0	2.0	0	17.0
% Residential	0	57.0	70.0	48.0	8.0	38.0	7.0
% Paved	44.0	13.0	8.0	7.0	22.0	3.0	4.0

Table 2.1. Landscape characteristics of 7 migratory stopover sites within the Columbus metropolitan area used as release sites for experimental birds during May 2004 to 2007. Sites are represented by area (ha) of forested release patch, and landscape metrics within 1-km radius of the release location.

Model	K	Loglik	AIC	AICc	Δ AICc	ω_i
Day	3	-161.85	329.69	330.07	0	0.43
Day*Condition	5	-159.93	329.85	330.82	0.75	0.29
Condition*Day+Year*Condition	11	-152.69	327.38	332.09	2.03	0.16
Null	2	-164.99	333.98	334.17	4.10	0.06
Condition	3	-164.23	334.46	334.84	4.77	0.04
Year	5	-163.17	336.35	337.32	7.25	0.01

Table 2.2. Competing models ranked by AICc in examining the influences of day, energetic condition at capture, and year on stopover duration of Swainson's Thrushes at seven study sites in Columbus, Ohio, May 2004-2007. K is the number of parameters in the model; Loglik is log-likelihood estimate from the model, Δ AICc is the difference in AICc between the top-ranked model and the model in question; ω_i is the weight indicating the relative likelihood of the model.

Predictor variables	Mean decrease in Gini index	Variable importance	
		Remain	Depart
Day	15.67	9.78	10.66
Change in pressure	7.16	-1.96	4.19
Average wind speed	7.03	1.04	0.62
Max temperature	6.49	0.5	2.83
Station pressure	4.93	0.15	-1.58
Total precipitation	4.33	6.53	0.24
Year	1.56	-0.25	-2.31

Table 2.3. Variable importance results from the Random Forest model of migratory departure for Swainson's Thrushes at seven study sites in Central Ohio, May 2004-2007. Variable importance is based on decrease in mean Gini index in iterations were the variable was not present, and thus indicates importance of the variable. In addition to overall model drivers, the importance of variables in predicting departure or remaining at stopover site are provided.

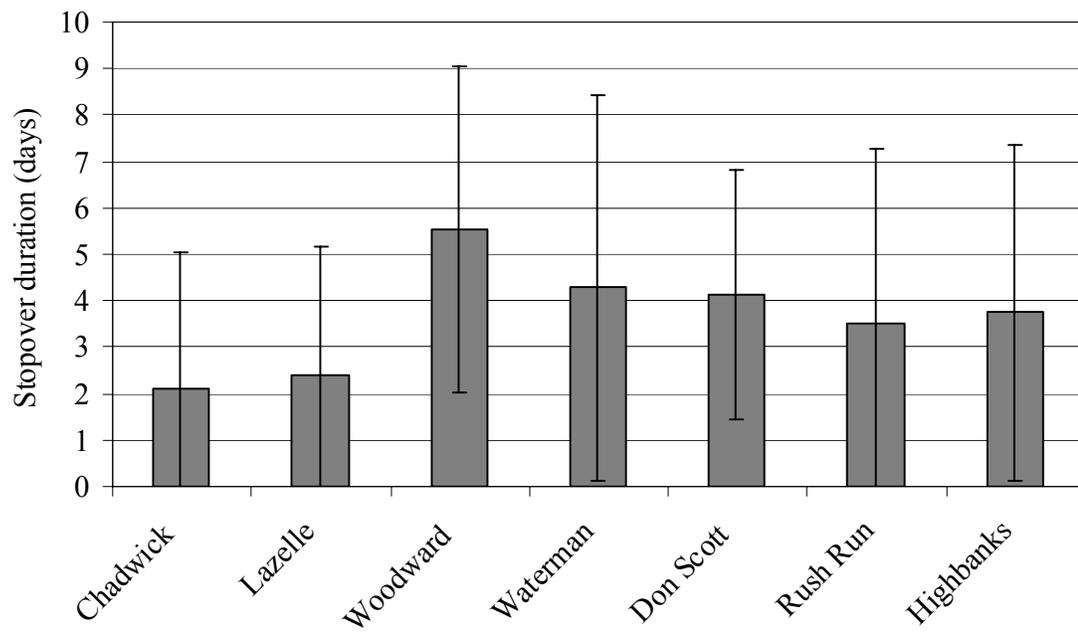


Figure 2.1. Mean stopover duration (\pm SD) for Swainson's Thrushes at seven study sites in central, Ohio, May 2004-2007. Waterman Farm represents the control site.

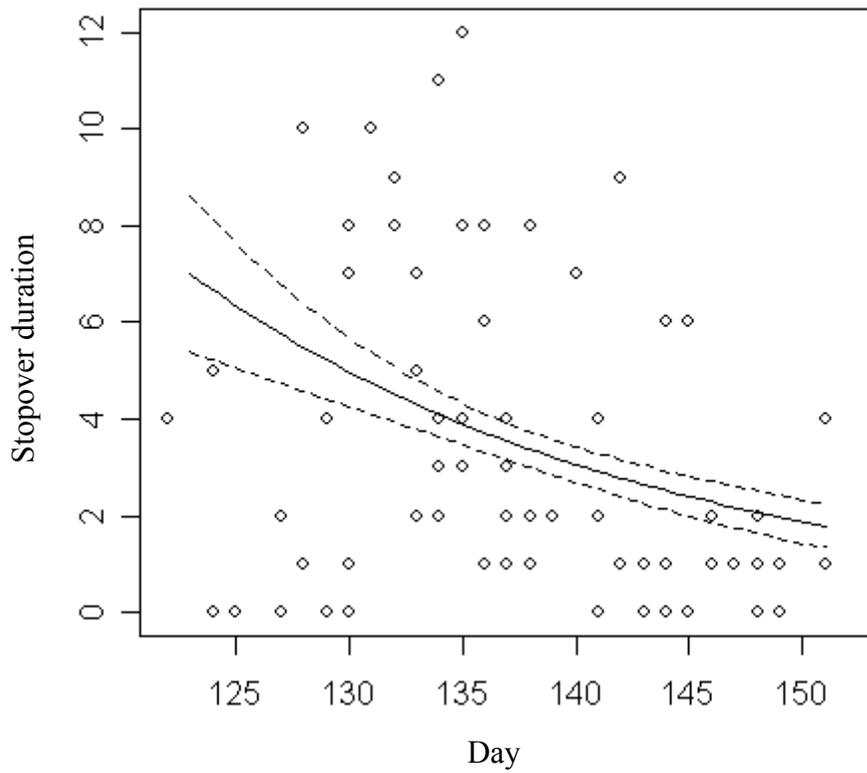


Figure 2.2. The influence of day (Julian date) on stopover duration of Swainson's Thrushes in central, Ohio, May 2004-2007. Dashed line represents the Standard Error of the model coefficient.

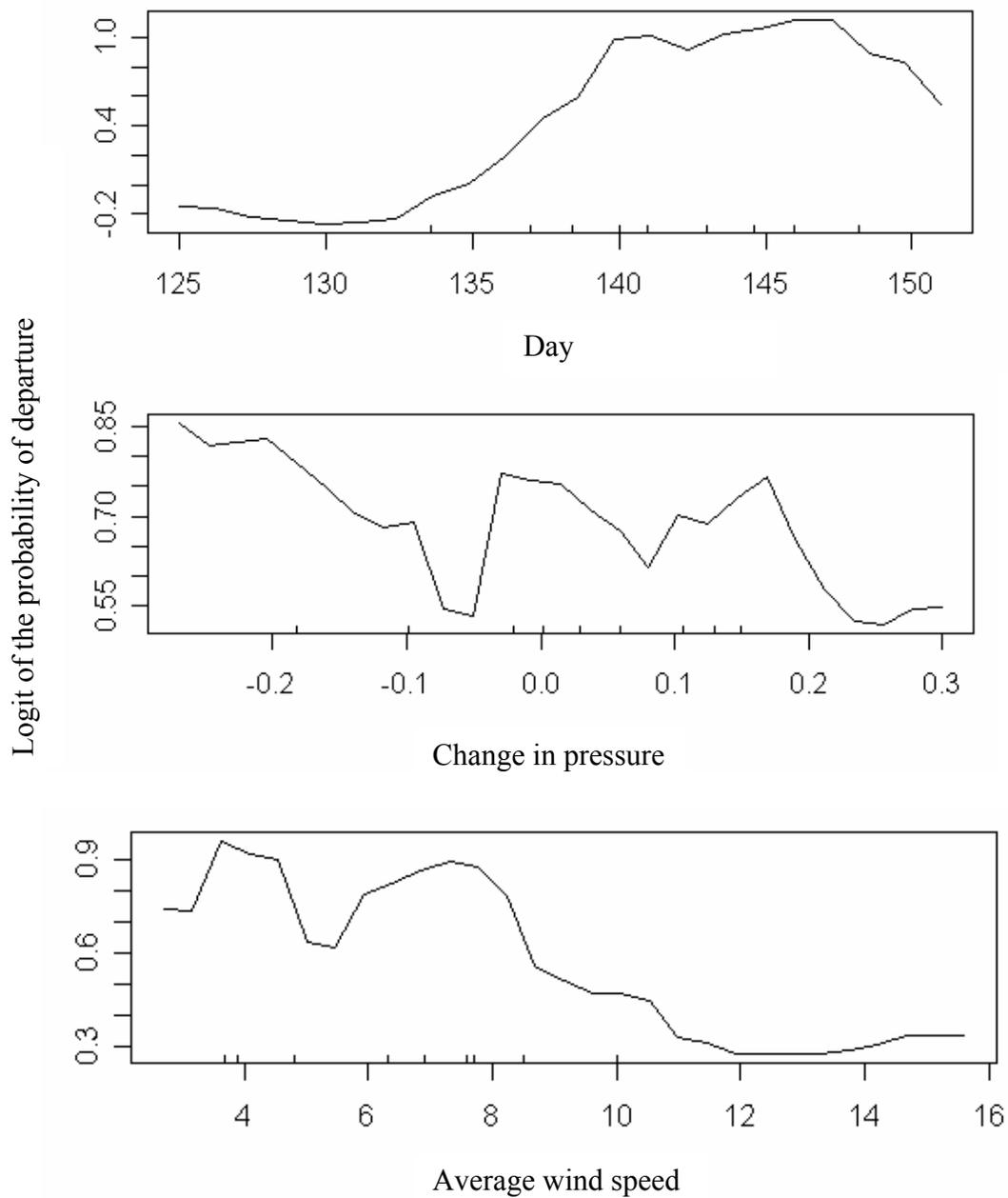


Figure 2.3. Partial plots of the influence on departure for the top three variables indicated by the Random Forest model of migratory departure in central Ohio, May 2004-2007.

CHAPTER 3

STOPOVER BEHAVIOR OF SWAINSON'S THRUSHES: MOVEMENTS WITHIN URBAN STOPOVER LOCATIONS

INTRODUCTION

During migration birds use a diverse suite of stopover habitats (Petit 2000) which are of vital importance in allowing birds to balance their high energetic turnover (Moore et al. 1995). Many migrating landbirds spend up to 90% of the migratory period resting and regaining energy at stopover sites (Hendenstrom and Alerstam 1997; Wikelski et al. 2003), making stopover habitat a key component of the migratory process (Chernetsov 2006). Fittingly, stopover ecology has recently become the focus of intensive study (Petit 2000). As our knowledge base expands, it becomes important to apply our understanding of stopover to explicitly investigate how birds respond to different stopover situations.

Because migratory birds face both energetic and time constraints during migration, there are hypothesized trade-offs with respect to foraging intensity and time spent by an individual at a stopover location (Weber et al. 1998). Birds arriving at a stopover location with depleted energetic reserves are expected to invest effort in gaining energy as fast as possible to remain on their migratory schedule. Birds with higher movement rates increase their prey encounter rate and energy gain (Hutto 1985) but also

may increase their risk of predation (Ydenberg et al. 2004). In contrast, birds that arrive at a stopover site with excess energy are expected to be able to continue their migration with little need to increase energetic stores; such birds would be able to remain relatively inactive during stopover and be less vulnerable to predation (Moore and Aborn 2000). Studies of radio-marked Summer Tanagers (*Piranga rubra*) have shown that birds with remaining fat reserves after migrating across the Gulf of Mexico remain inactive and often spend the majority of their time perched, whereas leaner birds show faster initiation of foraging behavior (Moore and Aborn 2000). European Robins (*Erithacus rubecula*), exhibit a similar energetically mediated response during stopover (Chernetsov and Mukhin 2006).

In addition to individual differences, both stopover habitat and landscape context can modify patterns of stopover use. Stopover migrant landbirds use habitat non-randomly (Petit 2000), a preference likely associated with their need to rapidly regain energy stores. After nocturnal migration, birds undergo a period of settlement within a stopover location when they select among available habitats (Chernetsov 2006). In many areas, birds appear to seek out structurally diverse habitats, where they often occur in higher abundance (Petit 2000, Rodewald and Brittingham 2004). Migrants appear to select areas that allow them to sustain a high rate of food intake because refueling rates will influence a bird's ability to resume migration (Ydenberg et al. 2004). A perception of the potential for energy gains is likely influenced by food availability within sites

(Moore et al. 1995), competition for resources (Rappole and Warner 1976 and Moore et al. 2003), and risk of predation at stopover sites (Weber et al. 1998).

Birds must make repeated stopover decisions along their migratory route and their ability to select quality habitat may be limited by the surrounding landscape (Simons et al. 2000). As small landbirds migrate across the Midwestern United States, birds that use forest stopover locations are often faced with limited availability of stopover habitat (Winker et al 1992) since much of the landscape west of the Appalachian Mountains is dominated by agriculture with only isolated forest patches (Ewert and Hamas 1996).

Urbanization is an increasingly dominant land cover type within the region (Bergen et al. 2005), and within urban landscapes migratory landbirds can be observed in a variety of stopover habitats from large areas of remnant vegetation preserved in metropolitan parks to highly altered and intensively managed recreational areas. Currently our understanding of urban stopover forest use by migrants indicates no pattern in stopover abundance across an urban to rural gradient (Rodewald and Matthews 2005). However, it remains unclear if these urban stopover sites are briefly used for emergency stopover or serve as staging areas where birds can effectively rest and regain energy (Mehlman et al. 2005). The dichotomy of available and ultimately used habitats raises intriguing questions about settlement and the process of habitat selection within highly fragmented landscapes.

My research goals were to experimentally examine site level and energetically mediated responses of migrant landbirds within urban landscapes. I use radio-telemetry to follow individually marked Swainson's Thrushes (*Catharus ustulatus*) during migratory stopover within the metropolitan region of Columbus, Ohio, USA. Specifically, my objectives were to quantify short-term movement rates and total distance moved by Swainson's Thrushes in seven forested stopover locations. This permitted me to examine how fuel reserves upon arrival can influence stopover behavior and whether these patterns are consistent across multiple sites within an urban landscape.

METHODS

Study Area and Experimental Relocation

Study sites were located within the Columbus metropolitan region of central Ohio and include portions of Delaware and Franklin counties. Within this area, riparian and upland forests are the two dominant habitats available to forest birds during migratory stopover (Rodewald and Matthews 2005). I selected 7 deciduous forest study sites within the Scioto River watershed to examine stopover behavior of Swainson's Thrushes within the urban matrix. These forested stopover sites were selected to vary in area and the degree of urbanization within a 1-km radius of the site (Table 3.1). These metrics were digitized from digital aerial photographs or provided by the county auditors for 2002 and 2004 in Delaware and Franklin counties, respectively (Rodewald and Shustack 2008).

Within a 1-km radius, quantification of urbanization within Columbus, Ohio has demonstrated an increase in buildings, roads, and mowed areas along a rural to urban gradient (Rodewald and Shustack 2008). In addition, the 1-km radius for landscape quantification corresponds to linear distances of movement for European Robins (Chernetsov 2005) and Summer Tanagers (Aborn and Moore 1997) during migratory stopover.

Because migrant settlement at a site can occur before capture, I conducted an experimental relocation study to examine behavioral responses of thrushes to urban forest patches and to control for arrival of a migrant at a pre-selected stopover location. This approach allowed me to evaluate the bird's response to a new stopover situation from settlement to departure. To do this, birds were caught at a single location (Waterman Farm Agricultural and Natural Resources Laboratory woodlot at the Ohio State University) and moved to one of six unique stopover locations. Waterman Farm was used as the seventh site and served as a control for the relocation experiment. All birds were released within 50-70 minutes of capture at a randomly selected point 20 meters from a habitat edge within each site.

Study Species

Swainson's Thrushes were used to address questions regarding the behavioral decisions of migrants at stopover sites. This species winters in South America, breeds

primarily in boreal forest regions of North America, and is common during migration in Ohio (Rodewald and Matthews 2005). It is a forest interior species in both wintering and breeding areas and utilizes forests throughout its migration (Mark and Yong 2000).

Swainson's Thrushes were caught using 12 m x 3 m mist nets that were opened daily from sunrise to 10:00 AM (EDT) from May 1 to June 2. Captured birds were promptly removed from nets and morphological measures were obtained including unflattened wing chord, tarsus length, and tail length. The birds mass was also recorded using an electronic balance (sensitivity to 0.01 g). These structural metrics were incorporated into one measure of energetic condition. A principal component analysis was conducted on the correlation matrix of wing and tarsus length (Green 2001). Scores from the first principal component represented a standardized structural metric of the bird. The mass of the individual was regressed against this structural component and the residuals of this regression were used as an index of energetic condition (Green 2001). When developing a metric of energetic condition it is important to evaluate the index with an alternate measure of condition (Schulte-Hostedde et al. 2005). Fortunately, subcutaneous fat deposits in birds can be easily scored and have long been used to evaluate energetic reserves (Krementz and Pendleton 1990). I found a strong association (Spearman's $\rho = 0.7$, $P < 0.05$) between the condition index based on residuals of size-adjusted mass and categorical fat scores, supporting my use of this metric of energetic condition at capture.

Radio Telemetry

Swainson's Thrushes were fitted with 0.66 g Holohil Systems LTD BD-2 radio transmitters attached to back feathers using LashGrip eyelash cement (Kenward 2001). Mean body mass of Swainson's Thrushes was 30.56 g meaning that radios weighed less than 2.5% of the bird's body mass. Although a suggested rule of thumb is that transmitter weight for small birds be kept below 3% of body mass, it is important to consider impacts that transmitters may have on particular individuals (Millspaugh and Marzluff 2001). The influence of a transmitter is likely species specific, but radio telemetry has long been used to track Swainson's Thrushes during migratory flight (see Cochran et al. 1967), and radio-marked birds have been observed making flights up to 800 km in one evening (Wikelski et al. 2003).

On the initial day of release birds were located on 3–4 occasions with 2-3 hours between each observation. The observer used the radio signal to locate radio-marked individuals. Once within approximately 50 m of the bird, attempts were made to obtain a visual location, while staying between 25-35 m away for the bird. If the bird's position could be determined, its location was recorded three times during a 30 min period. In addition, distance and direction from the observer to the bird were recorded along with GPS location error and distance and direction of flights observed. I also recorded the bird's height and distance to nearest habitat edge. If the position of the bird could not be precisely determined, only one location was recorded. Birds that remained on sites (i.e.,

did not migrate over night) for greater than one day were located at least twice on subsequent days, once during the morning (6:30-12:30) and once in afternoon (12:30–sunset), with locations separated by at least 4 hours. These data were collected until the bird initiated a migratory flight or the transmitter fell off the bird.

I quantified movement rate and total distance moved for each bird. Movement rate was defined as the distance moved within a 30-minute observation timeframe and averaged across the day. Total distance moved was the summed distance of successive independent locations during a three-day period. The locations used for total distance moved were recoded outside the 30-minute observation period and were at least 1 hour apart. I used an information-theoretic approach to rank candidate models (Burnham and Anderson 2002) for both movement rate and total movement distance. A set of 12 candidate models included site, energetic condition at capture, year, stopover duration (days since release), and Julian date. Model ranking was based on Akaike's Information Criterion with a correction for small sample sizes (AICc). In both cases, movement rate and total distance moved were log-transformed to conform to normality assumptions.

In addition to individually-based metrics, I considered metrics based on independent bird locations pooled for all individuals tracked within a site. While pooling across individuals resulted in increased variance, it was necessary to obtain consistency in the number of locations across sites (Table 3.2). Using the Animal Movement Extension (Hooze and Eichenlaub 1997) in ARCVIEW 3.3, I generated utilization

distributions using fixed kernel estimates with least squares validation (Marzluff et al. 2007) from bird locations within each site to quantify areas used by thrushes. I used an ANOVA to test for differences in bird locations and distance to the nearest edge for the six stopover sites; the smallest site was excluded from this comparison because it lacked a defined edge due to its small size and park-like setting. To evaluate edge avoidance at sites, I compared distance to edge for the bird locations with distance to edge for 100 random locations using pair-wise comparisons between random and bird locations with multiple Student T-tests. To correct for multiple tests, I used the methods of Benjamini and Hochberg (1995) to account for false discovery rates. Data for distance to edge were square root (+0.5) transformed to conform to normality assumptions (Zar 1999). Finally, I considered if the probability of a bird leaving the release patch, prior to initiating a migratory flight, differed across sites using Fisher's Exact Test (Zar 1999) for a 7x2 contingency table in program R (R CRAN 2004).

RESULTS

Swainson's Thrushes showed high site tenacity at stopover locations, with 93% of all birds remaining within the release patch until presumed migratory departure. In addition, only birds relocated into the smallest patches moved into the urban matrix (3 out of 8 birds at Chadwick Arboretum (37.5%) and 2 out of 10 birds at Lazelle (20%)), resulting in a significant difference in the probability leaving a patch between sites

(Fishers Exact, $P = 0.004$). Individuals that left their release patch did not return during stopover and moved between 60 and 1,000 m from the edge of the release patch.

There was considerable variation in the total area used by birds relocated to the seven stopover sites (Figure 3.1) with Swainson's Thrushes using more of the patch area in smaller sites. The pattern of patch use corresponded with significant differences between patch area and the distances of the bird locations to the nearest forest edge (Figure 3.2, $F_{5, 487} = 7.89$ $P < 0.001$). The key differences in the distance of bird locations to the habitat edge occurred between the smaller and larger study sites, with Woodward showing differences between all sites (except Lazelle) and Lazelle showing differences with Rush Run and Don Scott (Tukey post hoc test, Figure 3.2). In addition, bird locations within patches were farther from forest edges than randomly generated points for 3 of the 6 stopover sites ($P < 0.05$ Figure 3.2).

For individual responses of migrants, total distance moved during the first three days of stopover averaged 313.5 m (± 182.75 SD) and ranged from 90 to 850 meters for 59 birds with adequate data (Table 3.2). The top model in the candidate set carried 87% of the weight (Table 3.3) and incorporated a difference in intercepts based on the sites along with a negative slope reflecting the influence of the birds energetic condition at capture (condition coefficient = 0.06 ± 0.02 SE) with the overall model $r^2 = 36\%$.

Finally, there was no difference in short-term movement rates of birds between the release day and following day (Wilcox Signed Rank Test = 469, $P = 0.32$). Because

data on the release day averaged more points per bird and 12 individuals migrated after the initial day of release, I used the estimates from day one in subsequent analysis. Therefore, during the first day of release, movement rate within 30-minute observation periods averaged 32.4 m (SD = 18.57) for 55 birds (Table 3.2). Movement rate was influenced by the bird's condition at capture as well as an interaction with date of arrival and yearly variability (Table 3.4). The model with only energetic condition at capture contained 56% of the weight and was negatively related with activity ($\beta = -0.09 \pm 0.02$ SE, $F_{1,53} = 10.09$, $P = 0.002$). It is important to note that considerable variation in movement rate occurred within and between years, but the extra parameters in these models had little support as the increased predictive power was outweighed by the penalty for increased parameter estimates.

DISCUSSION

The use of stopover habitat by Swainson's Thrushes within an urbanized landscape highlights both intrinsic and extrinsic factors that can influence stopover behavior. My results indicated that thrushes in lean condition at capture had higher short-term movement rates during the first day of stopover than birds in better condition. This is consistent with Moore and Aborn's (2000) findings that lean Summer Tanagers were more active than birds with higher fat reserves. Yong and Moore (1997) found that for captive Swainson's Thrushes with unlimited access to food, the discrepancy in movement

patterns between lean and fat birds decreased with time, as lean birds accumulated more energetic reserves. These findings provide convincing evidence of an energetically mediated behavioral response by birds during stopover.

It is interesting that there was no difference in movement rates of Swainson's Thrushes in my seven stopover sites, suggesting that short-term movement rates were not adjusted to compensate for different stopover conditions and could reflect that thrushes attempt to maintain an energetic balance during stopover. This does not mean that birds only need to increase their activity to increase their energetic gains, but rather that birds showed an intrinsic behavioral response to their fuel reserves while at migratory stopover sites. However, when I considered the total distance moved by a bird during the first three days of stopover, I found that birds in smaller sites moved less than birds in larger sites. Although condition at capture still influenced total movement, leaner birds showed greater movements, a result consistent with Summer Tanagers along the Gulf of Mexico (Aborn and Moore 1997).

To interpret results for movement rate and total distance moved, we must consider the scale at which Swainson's Thrushes responded to the landscape in the study area. Stopover sites were isolated remnant forest patches within an urban matrix. Swainson's Thrushes are readily observed within urban stopover sites (Rodewald and Matthews 2005), and have been shown to initiate stopover within 50 m of housing developments (Wikelski et al. 2003). However, my results indicate that Swainson's Thrushes exhibit

site-level responses within urban stopover locations. While short-term movement rate and total distance moved are positively associated, they represent different components of behavior. The movements of a stopover migrant over a several day period likely reflect searching and settlement within a patch. On the other hand, birds with higher movement rates would likely be representative of fine-scale activities such as foraging intensity. Therefore, the differences observed when modeling short-term movement rates and total distance moved over three days correspond to the uniqueness of the two metrics and demonstrate both intrinsic and extrinsic influences on individuals during migratory stopover.

Further evidence of a site-level response during stopover was indicated by the lack of dispersal outside the release site except for a small number of thrushes relocated to the smallest stopover sites. During fall migration Swainson's Thrushes showed an avoidance of non-forested habitat (Tietz and Johnson 2007). The behavioral influences of crossing areas of unsuitable habitat have been documented during the breeding season for several forest bird species, including Black-capped Chickadees (*Poecile atricapillus*) which are more likely to travel through forests than across un-forested gaps (Belisle et al. 2002). Furthermore in a homing experiment, Black-capped Chickadee, Black-throated Blue Warbler (*Dendroica caerulescens*), and Ovenbird (*Seiurus aurocapillus*), were less likely to return to territories when relocated into a more fragmented landscape (Belisle et al. 2001). The extent to which movement patterns were constrained by the area of

isolated forest patches seemed to influence the utilization of these sites as effective stopover locations for Swainson's Thrushes. The dispersal of individuals from these smallest sites coupled with restricted movement patterns suggests a minimum threshold for stopover habitat suitability between 0.75 and 4.5 ha for Swainson's Thrushes within an urban landscape.

Within forested patches Swainson's Thrushes tended to occur farther from forest edges than randomly located points, with greatest differences occurring at the larger sites. Although Swainson's Thrushes were found in high numbers within diverse forest stopover habitats in South Dakota (Swanson et al. 2003), they are still considered a forest interior species (Mack and Yong 2000). So while they may be able to use a variety of stopover habitats, Swainson's Thrushes may show area sensitivity during stopover, a pattern that corresponds to behaviors observed during other portions of their annual cycles (Mark and Yong 2000). Moreover, it suggests that other forest bird species that exhibit edge avoidance may also be restricted during stopover within urban forest patches and other fragmented landscapes.

During migration the trade-off between energy acquisition and time spent at a stopover location must be balanced to meet short-term energy needs in the most time efficient manner as to remain on the migratory schedule (Chernetsov 2006). If the initial stopover location does not provide adequate resources then some birds may attempt local resettlement. During stopover many species of landbirds make morning flights (Bingman

1980, Moore and Aborn 2000). In many instances, these flights likely represent small-scale habitat selection to improve foraging opportunities, but these movements also require an additional time investment in searching and resettling (Chernetsov 2006). However, in urban landscapes where forest patches are more isolated by housing and other development, exploration may be costly in time and energy, and may increase predation risk. The patterns of edge avoidance, restricted movements within patches, and an apparent reluctance to move outside of the stopover patches suggests a degree of area sensitivity for Swainson's Thrushes within stopover habitats. Therefore, conserving remnant forest patches within fragmented forest systems that do not require movement into matrix habitats should enhance utilization by migratory birds. Stopover habitat selection and movements will vary according to a species' migratory strategy, habitat affinities, and energetic needs (Chernetsov and Mukhin 2006), but conservation of stopover habitats that provide adequate foraging opportunities while minimizing resettlement time should increase their value for migratory birds.

	Chadwick Arboretum	Lazelle Woods	Woodward Park	Waterman Farm	Don Scott Airport	Rush Run Park	Highbanks Metropark
Release patch area (ha)	0.7	4.5	11.9	12.6	15.4	18.4	38.4
Road length (m)	73,532	69,084	89,869	92,874	45,534	74,771	14,605
City center (km)	5	18.56	12.08	6.60	15.08	12.46	20.86
Number of buildings	546	2265	3690	2259	439	1611	246
% Forest	5.0	2.0	6.0	6.0	6.0	32.0	54.0
% Mowed	25.0	20.0	9.0	5.0	20.0	16.0	7.0
% Agricultural	4.0	0	0	27.0	37.0	0	4.0
% Scrub/shrub	4.0	1.0	1.0	1.0	2.0	0	17.0
% Residential	0	57.0	70.0	48.0	8.0	38.0	7.0
% Paved	44.0	13.0	8.0	7.0	22.0	3.0	4.0

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Table 3.1 Landscape characteristics of 7 migratory stopover sites within the Columbus metropolitan area used as release sites for experimental birds during May 2004 to 2007. Sites are represented by area (ha) of forested release patch, and landscape metrics within 1-km radius of the release location.

Study sites	Movement rate	Total distance moved	Bird locations
Chadwick Arboretum	5	6	NA
Lazelle Woods	10	6	70
Woodward Park	9	9	81
Waterman Farm	9	8	89
Don Scott Airport	5	10	89
Rush Run Park	9	10	90
Highbanks Metropark	8	10	80

Table 3.2 Sample sizes for analysis of movement rates, total distance moved, and the locations of independent points within seven study sites in Columbus, Ohio, May 2004-2007. Chadwick Arboretum did not have a defined edge, so bird locations were not used in those analyses.

Model	K	Loglik	AIC	AICc	Δ AICc	ω_i
Condition + Site	9	-32.121	82.243	85.916	0	0.87
Site	8	-35.685	87.371	90.251	4.335	0.10
Site + Year	10	-34.355	88.71	93.294	7.378	0.02
Condition * Year	4	-44.685	97.371	98.111	12.195	0.00

Table 3.3. Top-ranked models describing total distance moved by Swainson's Thrushes during the first three days of stopover in Columbus Ohio, May 2004-2007. The model that included condition at capture and site had greatest support based on ranking candidate models with AICc. K is the number of parameters in the model; Loglik is log-likelihood estimate from the model, Δ AICc is the difference in AICc between the top-ranked model and the model in question; ω_i is the weight indicating the relative likelihood of the model. Null and global models were ranked over 20 units below the top-ranked model based on Δ AICc.

Model	K	Loglik	AIC	AICc	Δ AICc	ω_i
Condition	3	-34.737	75.475	75.945	0	0.55
Condition + Date	4	-34.642	77.285	78.085	2.139	0.19
Condition + Year	5	-33.781	77.562	78.786	2.841	0.13
Condition * Year	7	-31.434	76.868	79.251	3.306	0.10
Null	2	-39.531	83.061	83.292	7.347	0.01

Table 3.4. Top-ranked models describing movement rate of Swainson's Thrushes on the initial day of release in Columbus, Ohio, May 2004-2007. Condition at capture was present in the top three models, but the highest ranked model carried 55% of the weight. K is the number of parameters in the model; Loglik is log-likelihood estimate from the model, Δ AICc is the difference in AICc between the top-ranked model and the model in question; ω_i is the weight indicating the relative likelihood of the model. The global model showed no support and the null model was greater the 7 units below the top model based on Δ AICc.

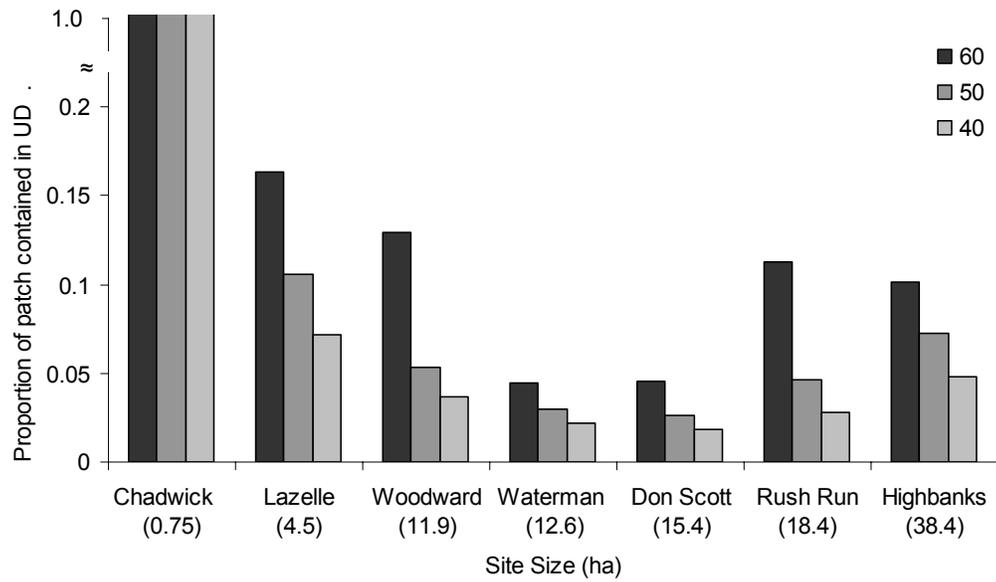


Figure 3.1. Proportion of stopover sites contained in the core area of utilization distributions (UD) of Swainson's Thrushes at 60%, 50%, 40% kernel levels in Columbus, Ohio, May 2004-2007.

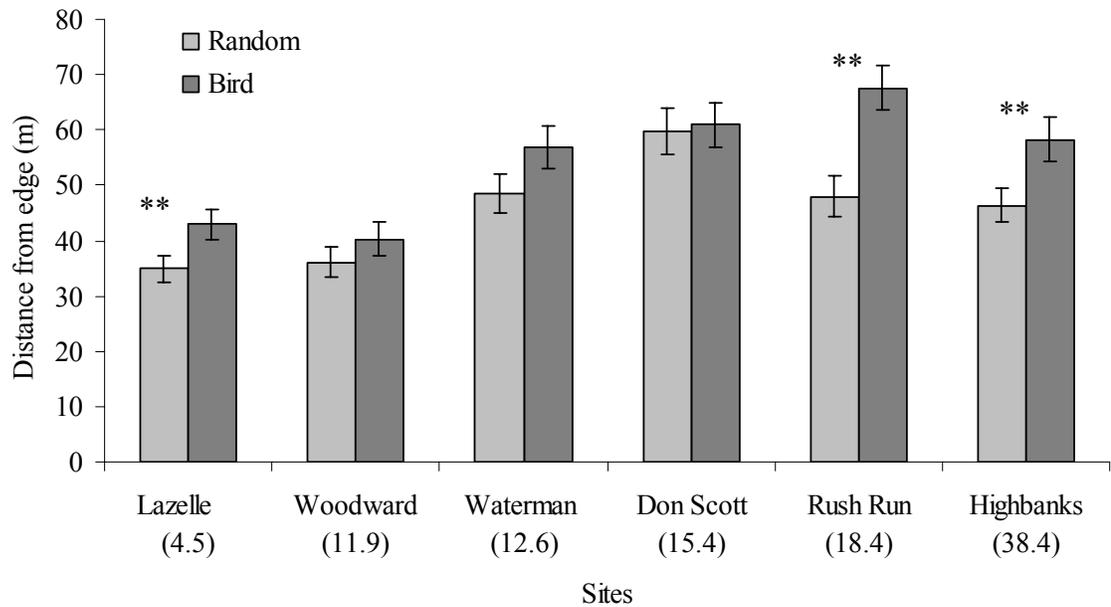


Figure 3.2. Mean distance to nearest edge for Swainson's Thrushes within six release sites (hectares (ha)) in Columbus, Ohio, May 2004-2007, and comparisons between thrush locations and randomly generated points. ** Indicates significant differences ($P < 0.05$) between random and bird locations.

CHAPTER 4

OPTIMAL MIGRATION ACROSS MULTIPLE STOPOVER EVENTS: IMPLICATIONS OF TIMING, ENERGETIC STORES, AND LOCATION

INTRODUCTION

When migrating between non-breeding and breeding areas, birds face challenges that range from continental and landscape scale processes to individual behavioral decisions concerning foraging, stopover duration, and flight duration. Not surprisingly, the study of any component of avian migration is complicated by the need to account for each factor or assume that its influence does not affect the factors being investigated. This situation is common to ecological studies, but the compressed temporal and expanded spatial scales over which long distance migration occur present unique challenges. However, through modeling and field experiments, a strong theoretical foundation of migration has been advanced to understand the processes of long distance avian migration (Alerstam and Hendenstrom1998).

Using an optimality approach, Alerstam and Lindstrom (1990) considered how, the fuel load a bird can carry, the distance an individual can fly given fuel reserves, and how fast the bird can gain fuel at a stopover site, interact to drive optimal migratory decisions under three different objective functions, time-minimization, energy-

minimization, and predator avoidance. Empirical and theoretical evidence suggest that each of these objective functions play a role in migration (Hendenstrom and Alerstam 1997, Jenni and Schaub 2003), indicating that these strategies influence multiple trade-offs that birds must balance during migration (Dent et al. 2006). For example, there is broad support for a time-minimization strategy in which birds minimize time spent migrating between wintering and breeding grounds (Weber et al. 1998, Lindstrom and Alerstam 1992). This strategy links directly to major theories describing habitat selection in breeding birds (Brown 1969, Fretwell and Lucas 1970), and specifically, that birds arriving first to breeding areas select higher quality territories (Fretwell and Lucas 1970). Energy minimization involves maintaining energy balance during migration so that individuals arrive on the breeding grounds with adequate energetic reserves, which may also have reproductive implications in the form of higher clutch size and nestling mass (Smith and Moore 2003). Finally, predation risk at stopover sites has been suggested to influence migratory decisions to use sites where high concentrations occur (Cimprich et al. 2005, Ydenberg et al. 2004). To investigate any particular component of migration, it is essential to remain cognizant of each of these influences which may impact conclusions.

One area of interest has been to understand the decisions of birds at stopover locations and how they influence the overall migratory journey. For most birds, migratory stopover is necessary to rest and regain energetic reserves (Moore et al. 1995),

but the importance of multiple suitable stopover sites increases for passerine birds due to their limited capacity to store energetic reserves. The decision of a bird to fly or to remain at a stopover site has been explored through observational study (Yong and Moore 1997), experimental trials (Danhardt and Lindstrom 2001), and modeling (Weber et al. 1998, Erni et al. 2002). However, many studies indicate conflicting determinants of migratory stopover events, ranging from strong extrinsic factors such as weather to intrinsic determinants such as a bird's energetic condition (Chernetsov and Mukhin 2006). For example, Yong and Moore (1997) found that energetic condition was negatively associated with activity of Catharus thrushes and ultimately stopover duration. Alternatively, there is evidence that poor weather conditions may encourage birds to remain at stopover sites, and that favorable conditions encourage departure (Richardson 1990). For example, Tsvey et al. (2007) found stopover duration to be positively linked to cloudy skies and headwinds. These results illustrate how trade-offs can influence decisions made during migratory stopover, and the recognition of these influences provides an opportunity to link decisions into the broader perspective of migration.

Unlike migratory shorebirds that can show high site fidelity to stopover locations, landbirds are often observed within many stopover locations. Small landbirds migrating across the continental United States encounter a landscape of patchily distributed habitat. While habitat selection at finer resolutions occurs (Aborn and Moore 1997), the act of migratory stopover is likely initiated in response to the flight range of a bird. The difference

between the selection of a stopover habitat and the initiation of a migratory stopover event corresponds to the differences in altitude at which the two events occur. During migratory flight, birds may fly at altitudes above 1 km (Bowlin et al. 2006). The ability to identify suitable habitat is compromised not only by the height at which they fly, but also by the fact that nocturnal flight restricts their visual capabilities. Therefore, the initiation of a stopover event is likely linked to weather conditions and the individual's energetic state. Swainson's Thrushes have been shown to exhibit two distinct phases of flight while aloft during migration (Bowlin et al. 2005), based on changes in wing beat frequency and heart rate during migratory flight. As a bird initiates a stopover event, wing beats and heart rate show greater variability as it descends from cruising altitude and begins to search for a stopover location. This distinction between coarse-scale stopover habitat selection and stopover initiation implies that broad front migration observed in small landbirds (Dunn 2001) is the result of the interplay between an individual's energetic reserves and weather conditions. This makes it likely that birds will utilize a diverse assortment of stopover habitats while migrating across vast areas without major ecological barriers. By increasing the potential number of stopover sites, the bird is not only faced with a decision of how intensively it should forage at a stopover site and when to leave a site, but also how far to fly given its energetic reserves.

Models of avian migration have focused on birds migrating from the wintering grounds to the breeding grounds in a limited number of migratory jumps to specific

stopover locations (Weber et al. 1998). These models have greatly advanced our understanding of concepts behind migration, but to date have not considered that small passerines use numerous stopover locations during migrations. My focus here is to better understand the decisions that birds face during multiple stopover events and explicitly examine the influence of energetic condition and migratory timing. Exploring these components can provide insight into the decisions made by small landbirds during migration and how the principles of migration theory can be utilized to explain the variable patterns observed for birds across stopover locations. To model optimal avian migration, I simulated migrant progress in daily time steps from a stopover location until arrival at a breeding location or the end of the breeding season. While the model is designed to be qualitatively relevant to characterize flight and stopover decisions of migration in long distant migrant passerines, it is specifically based on the migratory behavior of the Swainson's Thrush (*Catharus ustulatus*). This species' has been extensively studied during migration and data are available on nightly flight distance (Cochran et al. 1967), energy consumption (Wikelski et al. 2003), and migratory timing (Winker et al. 1992).

METHODS

I developed a model to evaluate the expected fitness value of decisions by an individual bird migrating toward its breeding grounds. The bird must make decisions as

to the flight distance, stopover initiation, stopover duration, and energy acquisition that will maximize its expected future fitness. Ultimately, the timing of arrival on to the breeding grounds should drive the bird's reproductive fitness. Arriving too early will result in a fitness cost as it would be too early to breed and adequate resources would likely not be available, while arrival too late will also incur a fitness penalty, as territory and breeding opportunities will decline. Furthermore, the arrival condition of a bird will also result in a fitness cost, with birds arriving in the poorest condition paying the largest cost.

Dynamic Programming Model

A dynamic programming approach (Mangel and Clark 1988, Clark and Mangle 2000) was used to model optimal stopping and starting decisions of a migrating bird, considering its energetic state, location relative to the breeding grounds, and time in the season, all of which influence the expected future fitness of the bird. For each day t ($t = 1, 2, \dots, T$, where terminal time $T = 10$), I calculated the maximum expected fitness $F(x, t, l)$ of a bird beginning day t at location l with energetic state x . Location l ranged from 1 (the starting location of the simulation) to 15 (the farthest possible breeding location). I assumed that energetic state ranged from 6 to 18, considering an energetic state below 6 to be lethal.

Terminal time: expected fitness. At terminal time T , the bird received a fitness reward, calculated as a function of its energetic state at terminal time (x_T), its location at terminal time (l_T), and the timing (t_B) of its arrival at l_T . For each of these factors, I defined a fitness multiplier function such that the terminal fitness function can be expressed as a product of the three fitness multipliers:

$$F(x, t, L) = A(x_T) * E(t_b) * B(l_T)$$

where $A(x_T)$ is the energetic-state fitness multiplier, $B(l_T)$ is the breeding location fitness multiplier, and $E(t_b)$ is the fitness multiplier associated with timing of arrival to the final breeding site.

I assumed that a bird arriving with the highest energy stores would have the highest fitness. This advantage would decrease as a step function with decreases in energetic reserves:

$$A(x_T) = \begin{cases} 1 & \text{for } x = 16 \text{ to } 18 \\ 0.9 & \text{for } 10 \leq x \leq 15 \\ 0.8 & \text{for } x_{crit} < x \leq 9 \end{cases}$$

This function implies that birds arriving on the breeding grounds will benefit from their energetic stores acquired en route, as suggested by Smith and Moore (2003).

The most influential component of the terminal fitness function considers the location of breeding, l_T . I assumed there is an optimal breeding location l_{opt} and that the closer a bird gets to this location, the higher the payoff in fitness. If the bird is too far

from this location at terminal time, breeding was not successful. For these model runs, I have assumed that $l_{opt} = 12$, and $v = 1.2$ is a parameter that specifies shape of the fitness multiplier curve:

$$B(l_T) = \begin{cases} 0 & \text{for } 1 < l_T < 8 \\ \frac{2.8}{\sqrt{2\pi v}} e^{-\frac{(l_T - l_{opt})^2}{2v^2}} & \text{for } 8 \leq l_T \leq 15 \end{cases}$$

A modeled bird either attempts to breed wherever it ends at terminal time or, if it makes it to l_{opt} at $t < T$, it can breed there when it arrives. To model the fitness effect of timing of arrival to l_{opt} , for birds that ultimately reach their breeding areas, I used a step function, with expected fitness being low for birds breeding too early, then increasing for breeding between time 3 and time 5, and falling off again until terminal time is reached:

$$E(t_b) = \begin{cases} 0.9 & \text{for } t_b < 3 \\ 1.0 & \text{for } 3 \leq t_b \leq 5 \\ 0.9 & \text{for } 5 < t_b \leq 8 \\ 0.8 & \text{for } 8 < t_b \leq T \end{cases}$$

This assumes that arrival too early to the breeding grounds would have a cost sense the bird would outpace resource availability. As time passes, the fitness advantage drops to represent the closing of the reproductive window and greater competition for resources at the breeding grounds.

Daily time steps. At each time step, the individual bird must decide whether to fly or remain at a stopover location. If the decision is to fly, then the bird must decide how far, given current energy stores. And finally, at each time step, the individual must decide how intensively to forage, given the expected gain in energy and the risk of predation. On a given day, migrants must first compare the expected future fitness from initiating a migratory flight (expected fitness = G_1) with remaining at a site (expected fitness = G_2), and choose the behavior that yields the higher expected fitness:

$$F(x, l, t) = \max \{G_1(x, l, t); G_2(x, l, t)\}$$

The value of G_1 depends on the flight distance chosen and the values of both G_1 and G_2 depend on the foraging intensity chosen by the migrant. The expected fitness of the bird that migrates from its current location, goes a distance of d_x and forages at an intensity of k , is:

$$((1 - p_k)(Fx - c(d) + y_k - S, l + d, t + 1))$$

where the migrant pays an energetic cost of flying $c(d)$ and an overnight metabolic cost S , gains y_k amount of energy from foraging, and has a risk of dying by predation of p_k . I assumed that a bird is limited by its energy reserves in how far it can travel in a single day. Thus d can take values from 1 to d_x , where d_x is the maximum daily flight distance of a bird with energy stores x . The expected fitness of the bird that stays at its current location and forages at an intensity k is:

$$(1 - p_k)F(x - S + y_k, l, t + 1)$$

Thus the complete dynamic programming equation is:

$$F(x,l,t) = \max \left\{ \begin{array}{l} \max_d \max_k \left((1 - p_k) F(x - c(d) + y_k - S, l + d, t + 1) \right) \\ \max_k \left((1 - p_k) F(x + y_k - S, l, t + 1) \right) \end{array} \right\}$$

Using backward iteration, maximum expected fitness and the migration and foraging strategies that led to maximum fitness, were calculated. Because birds encounter variable weather conditions during migration, I evaluated the optimal decision under poor, neutral, and good flying conditions by multiplying the right hand side of $G_1(x,l,t)$ by 0.8, 1, and 1.2, respectively, to arrive at the optimal choice under these conditions. Therefore, fitness would be reduced if flight occurs during poor weather, whereas the bird receives a fitness advantage for flying under favorable conditions. This assumes that birds have evolved an ability to detect weather conditions, which is reasonable given that migratory behavior is closely associated with wind, temperatures and barometric pressure (Richardson 1990).

Model parameters

I incorporated twelve parameters in the model (Table 4.1). First, the energy per time interval of a bird ranges from the minimum energy needed to survive (x_{crit}) to the maximum energetic stores (X_{MAX}). Energetic stores are derived from Wikelski et al. (2003). Noting that energy is divided by ten for modeling purposes, in the simulation it takes 18 kj to fly 8 location units. For example, Wikelski et al (2003) found that

Swainson's Thrushes requires 180kj to fly for 8 hours. The maximum distance that a bird can fly is a function of its energy stores, $d_x = x - 10$. The bird can not migrate with energy stores of 10 kj/d or lower and can fly 8 distance units with the maximum energy stores of 18 kj/d (X_{MAX}). The cost of flight is set at $1.3d_x$ with the multiplier representing the metabolic cost (kj/d) for a Swainson's Thrush during free flying migration (Wikelski et al. 2003). Foraging intensity k , is expressed in whole numbers ranging from 1 to 6. The risk of predation is a linear function (slope = 0.005) that ranges from 0.01 if foraging at the lowest intensity to 0.035 if the bird maximizes foraging opportunities. The energy gained by a foraging bird can be described as $y_k = 0.5k + 1$.

Forward simulation

Once all combinations were evaluated and the optimal decisions under all situations were calculated, I then simulated individual birds through forward iteration. I modeled 100 birds at a time for 100 replications to obtain estimates of variability. Each bird was randomly assigned an initial energy level and began the simulation at the same location. The state variables were followed through time and once the bird reached the breeding location with the highest fitness its decisions were no longer followed. Stochasticity was incorporated into two components of the model. First, foraging success was assigned based on the optimal choice, but the exact energy gain was selected from a normal distribution centered on the optimal foraging intensity with the standard deviation

equal to 0.15 times the energy expected. This was done to incorporate the likelihood that variance in food allocation will increase with foraging rate (i.e. birds foraging at a higher rate are more likely to overeat or not be able to achieve a high rate of energy gain).

Variability was also introduced in terms of weather conditions. Weather for flight can be poor, neutral, or good. Here neutral weather occurred on average 75 percent of the time with poor and favorable conditions each occurring 12.5 percent of the time.

I ran forward iterations under several alternate parameterizations to evaluate the sensitivity of my results. First, I was interested in the effect of the foraging intensity function. Therefore, I doubled the slope of foraging gain (hereafter “increased foraging reward”). Next, in order to investigate the sensitivity of the starting position of the forward simulation, I reduced the distance to the “best” breeding location by half (modeled “short distance”). In addition to simulating optimal migration with the dynamic programming model, I modeled migration where flight distance and foraging intensity were randomly assigned (hereafter “random choice”). Finally, I modeled migration where the bird maximizes both flight distance and foraging intensity, paying little attention to balancing energetic reserves (hereafter “maximum speed”).

RESULTS

Bird policy diagrams showed a high initial foraging rate that decreased with the approach of terminal time (Figure 4.1). Incorporating the influence of weather, the model

indicated that poor flying conditions resulted in the optimal decision to remain at the current stopover location, while good migratory weather promoted migratory flight (Figure 4.2). The patterns of these decisions from the dynamic programming model illustrate the influence of the parameterization of the model and are consistent with expected outcome given the terminal fitness function.

Using the optimally model I ran forward simulations to investigate how birds utilizing optimal decisions would undertake a migratory journey. Birds had the choice of stopping at 12 different locations, but on average only 4 (SE = 0.07) stopover locations were used throughout the simulation. On average 71% (SE = 0.5) of the birds arrived at the “best” breeding location by terminal time, while arrival at suitable but less desirable breeding locations occurred 4% (SE = 1.3) of the time. Average mortality was 23% (SE = 0.4) and varied according to initial energetic stores (Table 4.2). Birds in poor condition at the beginning of the simulation were more likely to be adversely affected by poor weather and increased variability in energy gain.

Energetic stores at the initiation of the simulation showed that birds possessing a variety of different energetic stores did reach the optimal breeding location by terminal time (Figure 4.3). However, individuals with higher energetic reserves arrived at the optimal breeding location faster than those in poor condition. Under deterministic parameterization (i.e. lack of variability in weather and foraging), the advantage of high energetic condition and early arrival on the breeding ground declined across temporal

increments (Figure 4.4). While there was still an advantage to arriving early and in higher condition, we see large increases from no birds arriving to nearly all arriving on the breeding grounds. Therefore, the inclusion of environmental variability tempers the extremes of the deterministic model and allows for a more realistic expectation of migratory timing.

Flight decisions also were influenced by energetic stores at each stopover location and across the entire migratory window (Figure 4.5). There was a benefit to maintaining high energetic reserves throughout the migratory period so that longer flights could be made in the event of favorable weather. At two stopover locations energetic stores increased through time and energy gains were more rapid for locations far from the breeding areas (Figure 4.6). Gains in energy can be achieved by remaining at the current location or sustained through short migratory flights. Greater gains in flight distance appear to be reserved for times when it becomes optimal to make a long flight to reach an intermediate stopover location or the final destination. This results in fewer birds using stopover locations closer to the optimal breeding location (Figure 4.7).

Random decisions resulted in little chance of a bird making it to the breeding location (Figure 4.8a). In fact under a random choice model, only 7.1% of birds reached the optimal breeding location and less than 20% of birds made it to any suitable breeding location. When birds maximized their flight distance and foraging rate there was a vast reduction in the number of birds arriving at the breeding grounds (33.1%) and decreased

influence of initial energetic stores (Figure 4.8b). These two alternative models were markedly different from the optimality results and demonstrate that decisions made by birds during migration are influenced by a variety of cues.

Sensitivity of the results were also evaluated within the optimality framework. First, it can be hypothesized that increasing foraging efficiency should eliminate the advantage that a bird might have from retaining higher energetic stores, because birds in poor condition can rapidly compensate for depleted energetic status. However, even with a doubling of the slope to the energetic gain received at each foraging decision (and no increase in predation risk) the energetic advantage remained, in part because the advantage was realized by all birds and was additive across all energetic levels (Figure 4.8c). Finally, it would be predicted that if I begin the simulation closer to the breeding grounds, more birds would be able to arrive at the optimal breeding location, and this pattern emerges under forward simulation (Figure 4.8d).

DISCUSSION

Optimality models can provide insight into many facets of biology (Mangel and Clark 1988). Indeed, much of our theoretical understanding of bird migration has been advanced through models that explore optimal strategies of migration (Alerstam and Hendenstrom 1998). Understanding the role of energetic stores in the migratory schedule of small landbirds is crucial to the understanding of migration, and my model sheds

additional light on the trade-off between a bird's condition and migratory timing. Furthermore, the model provides insight into how energetic stores not only influence a bird's decisions during migration, but also how a bird's condition may ultimately influence the likelihood of reaching the breeding grounds.

Studies addressing the influence of energetic condition on stopover duration have reported conflicting findings (Chernetsov and Mukhin 2006). For example, Yong and Moore (1997) found that the condition of a bird upon arrival at a stopover site influenced how long birds remained. However, there is equally compelling evidence suggesting that other factors (e.g. weather) determine stopover duration (Danhardt and Lindstrom 2001). Clearly, multiple factors are likely to play a role in an individual's decision, and it is necessary that we consider the context of the study and how events occurring earlier in a migratory journey are likely to influence a migrant's behavior during stopover. For example, Smith and Norment (2005) did not find an association between energetic condition and stopover activity in Swainson's Thrushes at northerly stopover sites. In contrast, Yong and Moore (2007) found that Swainson's Thrushes with lower energetic reserves were more active during foraging and less active at night along the northern coast of the Gulf of Mexico. These differences in study results were attributed to differences in stopover location (Smith and Norment 2005), but such broad scale associations are rarely explicitly addressed in research questions. This is due in part to

the fact that field research is often restricted to a few stopover locations (more typically one location), while most small passerines make many migratory flights across a broad landscape to complete their journey.

Through the simulations of optimal migration it is possible to gain unique insight into the hierarchical nature of migratory movements and how timing and energetic stores can influence arrival timing in breeding areas. Birds located farther from breeding locations benefit by foraging more intensively to increase energy stores and making shorter migratory flights since it is not possible to reach a suitable breeding location. When birds approach potential breeding locations it becomes optimal to make long flights that will allow them to arrive earlier. Therefore, modeling efforts suggest that birds farther from the breeding grounds may exhibit behavior more dependent on their energetic state than birds located closer to breeding latitudes.

It is difficult to understand how birds make decisions concerning stopover duration and flight duration, but it seems clear that input from a variety of cues is involved (Tsvey et al. 2007). The recognition of specific landscape characteristics may be one mechanism used, but this requires the ability to evaluate landscape characteristics. For nocturnal migrants, these decisions are likely made when flying at lower altitudes to enhance visual and auditory cues (Chernetsov 2006). Thus, the initiation of a stopover event (away from a major ecological barrier) may not be directly related to local habitat features but rather a function of internal mechanisms. This logic would be consistent

with that of Catry et al. (2004) which showed low site fidelity at specific stopover sites. On average, birds in my simulation utilized only one-quarter of possible stopover locations. Birds remained at stopover locations until they had stored enough energy to make a long flight or until favorable weather could facilitate more efficient migratory flight. This means that birds with higher initial energetic stores were able to reach breeding grounds earlier due to their energetic advantage, a pattern similar to the arrival of American Redstart to the breeding grounds (Smith and Moore 2003). My simulation did not evaluate variability in stopover conditions, but quality of stopover habitat has been shown to influence refueling rates (Dunn 2002). This highlights the importance of habitat specific choices that birds make once they initiate a stopover event. Furthermore, simulations of variable conditions at stopover sites indicates an increased focus on maintaining higher energetic reserves when energetic gains changed between sites (Weber et al 1998). The influence of quality stopover locations may allow for birds to make up energy deficits and illustrates the importance of quality stopover locations to migration.

My model is clearly a simplification of the complexity that has evolved in avian migration, but it provides insight that can advance our understanding of landbird migration. For example, the model indicates that stopover events should be limited to only a few locations even when the quality of stopover sites does not vary. Clearly there is great variability in the quality of stopover locations, and in many regions there has

been a reduction in the amount of suitable stopover habitat (Mehlman et al. 2005). Therefore, birds may have to (or have already) developed strategies to compensate for inconsistent availability of stopover opportunities. Furthermore, the model demonstrates that energetic stores should be gained or at least maintained at stopover sites, and that the timing of site use will be differentiated by the success of individuals at previous stopover locations. This frequent mixing of individuals with differing energetic stores may inhibit our ability to identify consistent relationships between energetic condition and stopover duration in field research. Nevertheless, the model clearly indicates an expected advantage to birds that maintain higher energetic reserves. The results suggest that birds should not migrate randomly in terms of flight distances and foraging intensities, but instead should utilize both intrinsic and external cues during migration. The results from this modeling effort provide insight that should be valuable for the development of field research to better understand the trade-offs between energy balance and timing in avian migration.

Parameters	Values	Description
X	from 6 to 18	Energetic state (kj)
X_{CRIT}	6	Minimum energy
X_{MIN}	11	Minimum energy needed to migrate
X_{MAX}	18	Maximum energy state
$D(x)$	$x-10$	Distance that a bird can fly given its energy state
K	From 1 to 6	Foraging intensity
Y_K	$0.5k+1$	Energy gain from foraging intensity
P_K	$0.005k+1$	Predation from foraging intensity
C	$1.3*D(x)$	Energy lost by flying $D(x)$
S	2	Overnight energetic cost
L	15	Maximum distance between starting location and breeding site
T	10	Total time the bird has to reach breeding ground

Table 4.1. Parameters incorporated into the dynamic programming model of optimal avian migration for a small passerine.

Initial energy	Mortality (%)	SE(%)
7	24	1.4
8	25	1.8
9	22	1.5
10	21	1.3
11	20	1.4
12	19	1.5
13	16	1.3
14	16	1.4
15	15	1.4
16	13	1.4
17	12	1.2
18	11	1

Table 4.2. Percentage of individuals that die during the simulation based on their initial energetic condition.

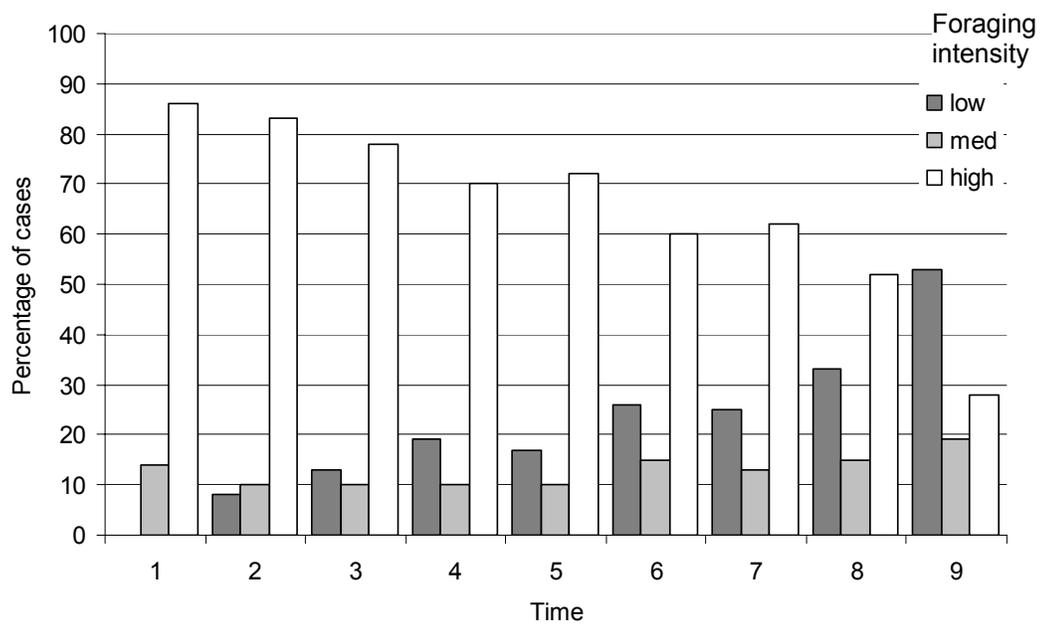


Figure 4.1. Policy diagram of optimal foraging intensities through time in any location. The six foraging intensities were classified as low (class 1 or 2), medium (3 or 4), and high (5 or 6).

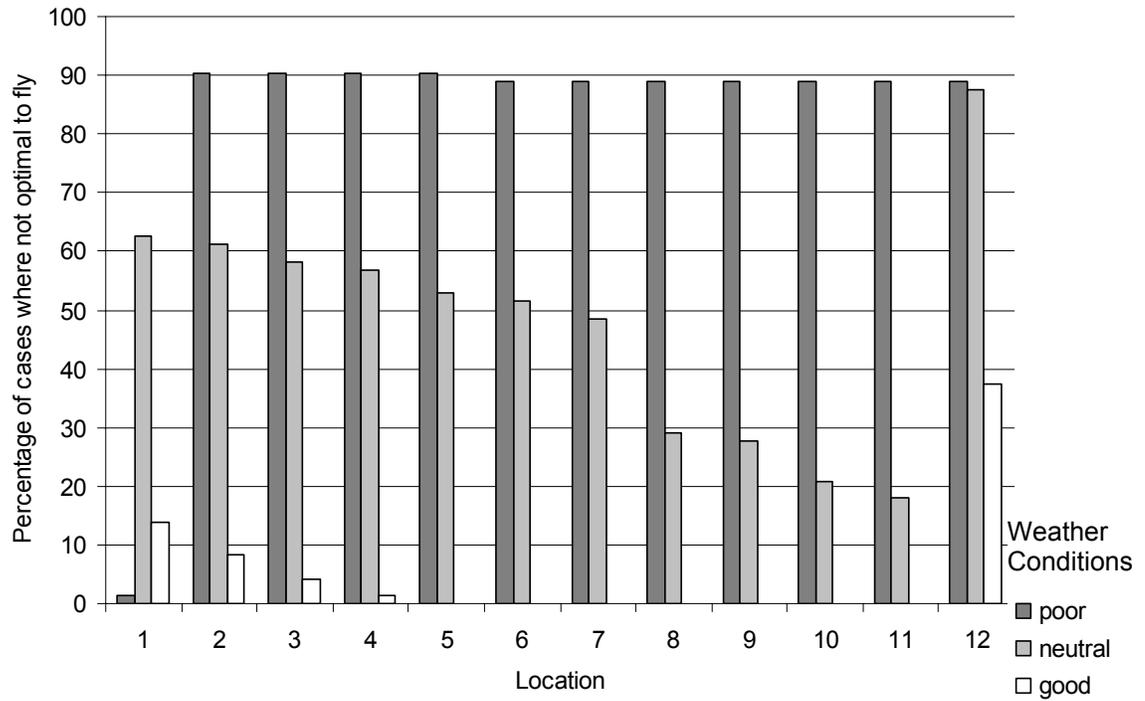


Figure 4.2. Optimal decision to remain at current stopover location under poor, neutral, and good migratory weather conditions.

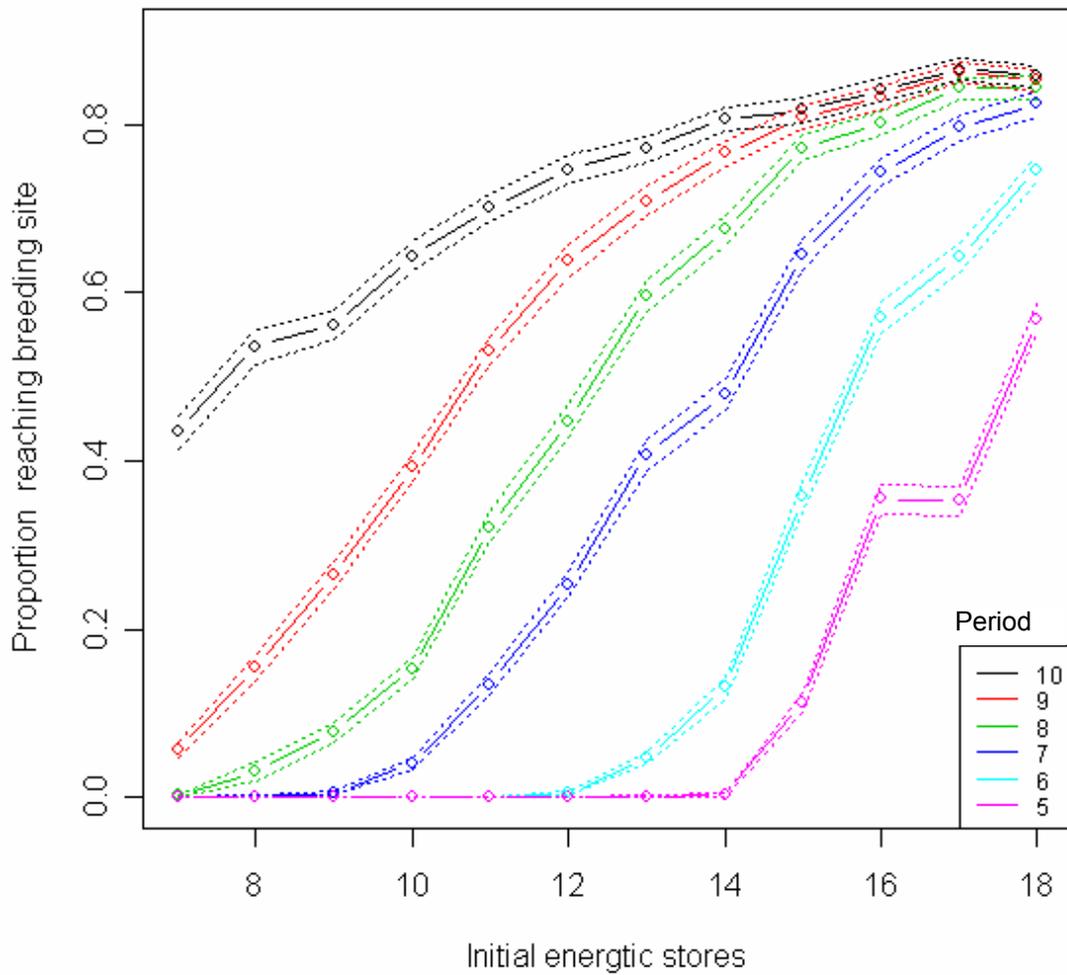


Figure 4.3. Proportion of individuals arriving at optimal breeding location through time (from terminal time 10 to time 5) based on energetic stores at the start of the simulation. Dashed lines represent standard error around the mean.

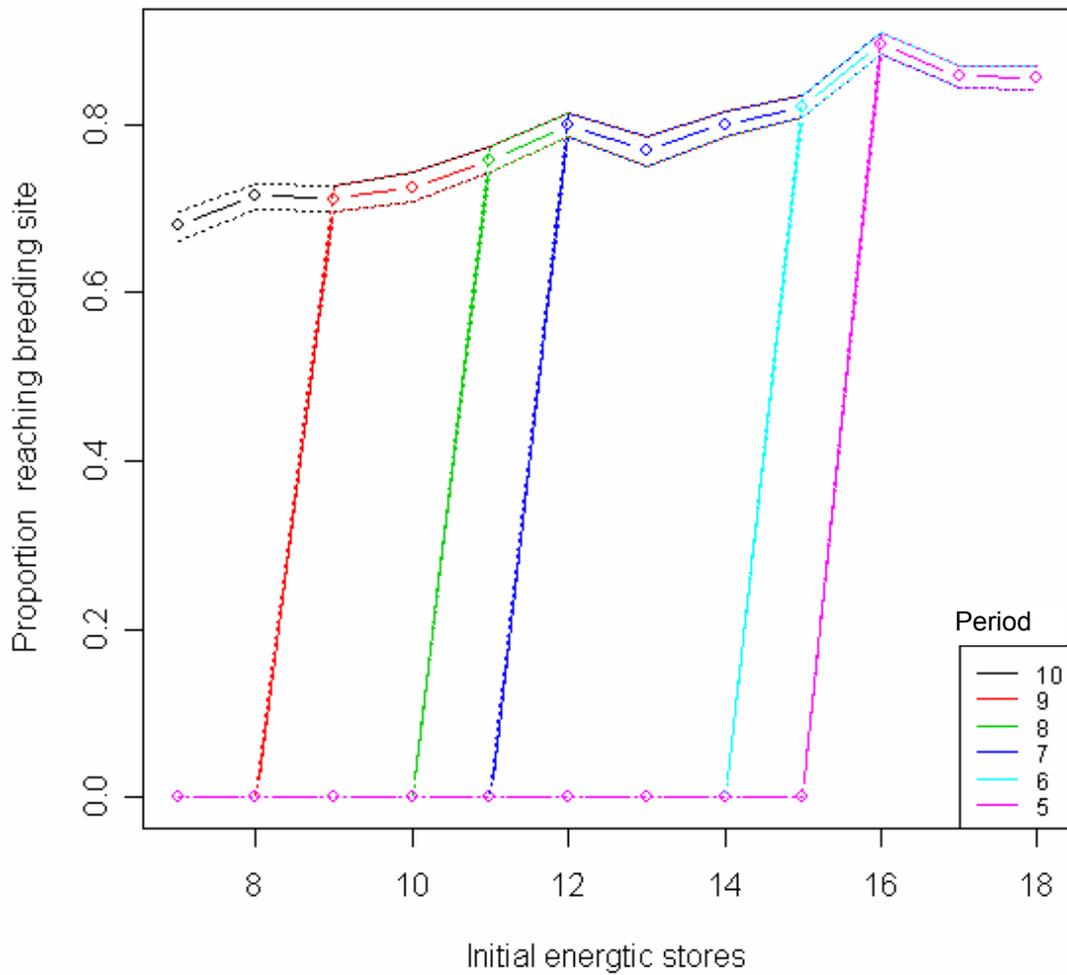


Figure 4.4. Under deterministic conditions, the proportion of individuals arriving at breeding location through time (from terminal time 10 to time 5) based on energetic stores at the start of the simulation. Dashed lines represent standard error around the mean.

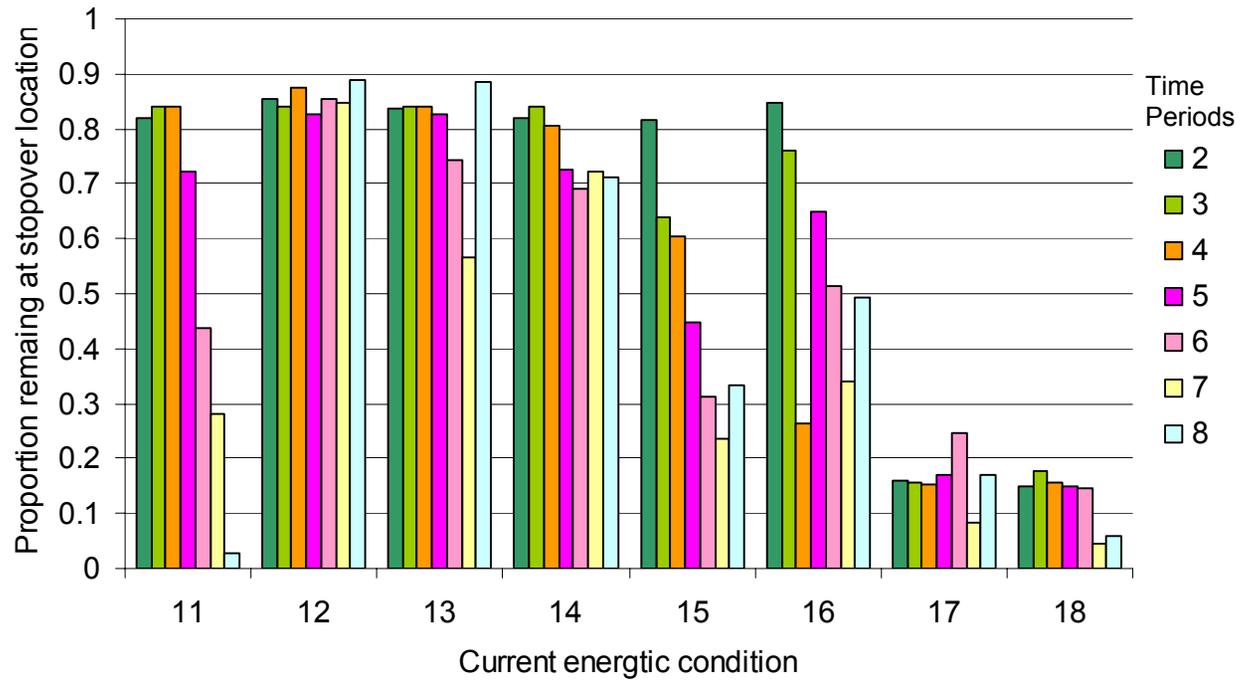


Figure 4.5. Proportion of individuals remaining at current stopover location based on current energetic status from time 2 to time 8 in the simulation.

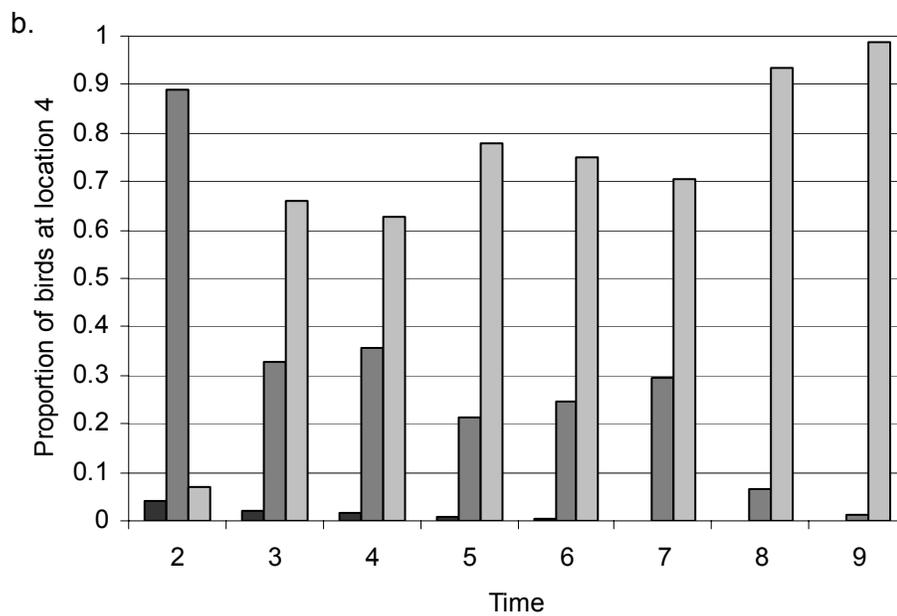
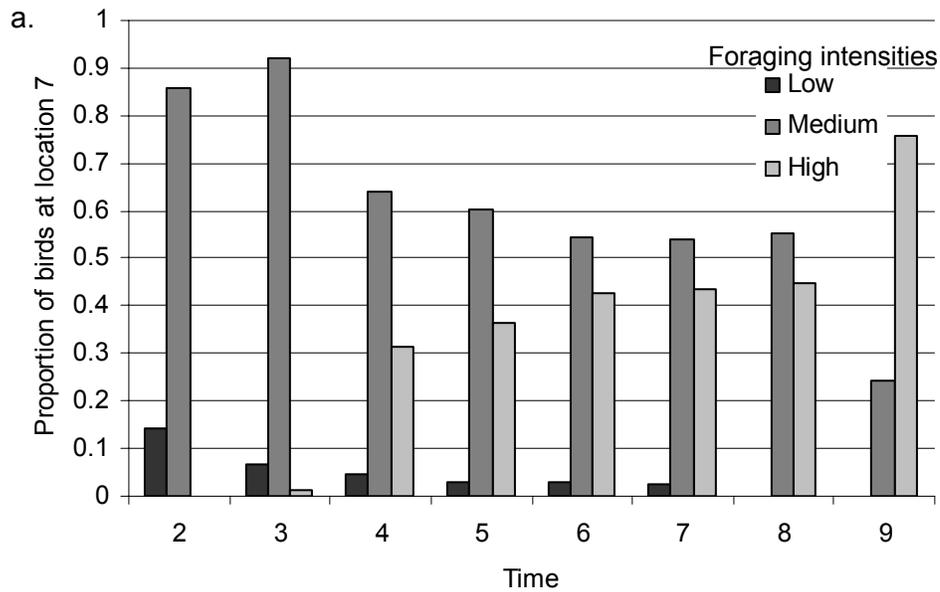


Figure 4.6. Proportion of individuals with low, medium, and high energetic stores through time at location 7 (a) and location 4 (b). The six categories of foraging intensities were classified as low (class 1 or 2), medium (3 or 4), and high (5 or 6).

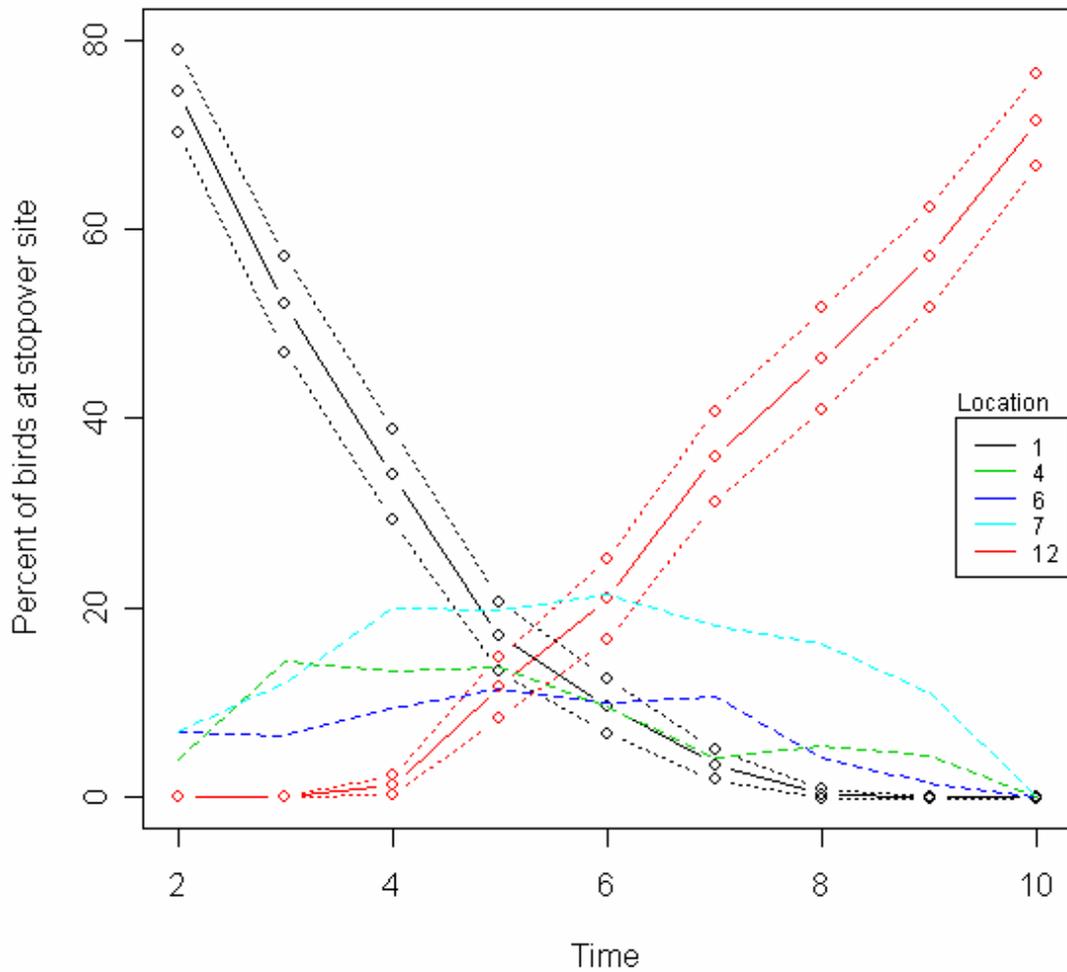


Figure 4.7. The percent of individuals occurring at a given location through time; locations include starting location (1), three intermediate stopover sites (4, 6, 7), and the “best” breeding location (12). Dashed lines around locations 1 and 12 represent standard error around the mean

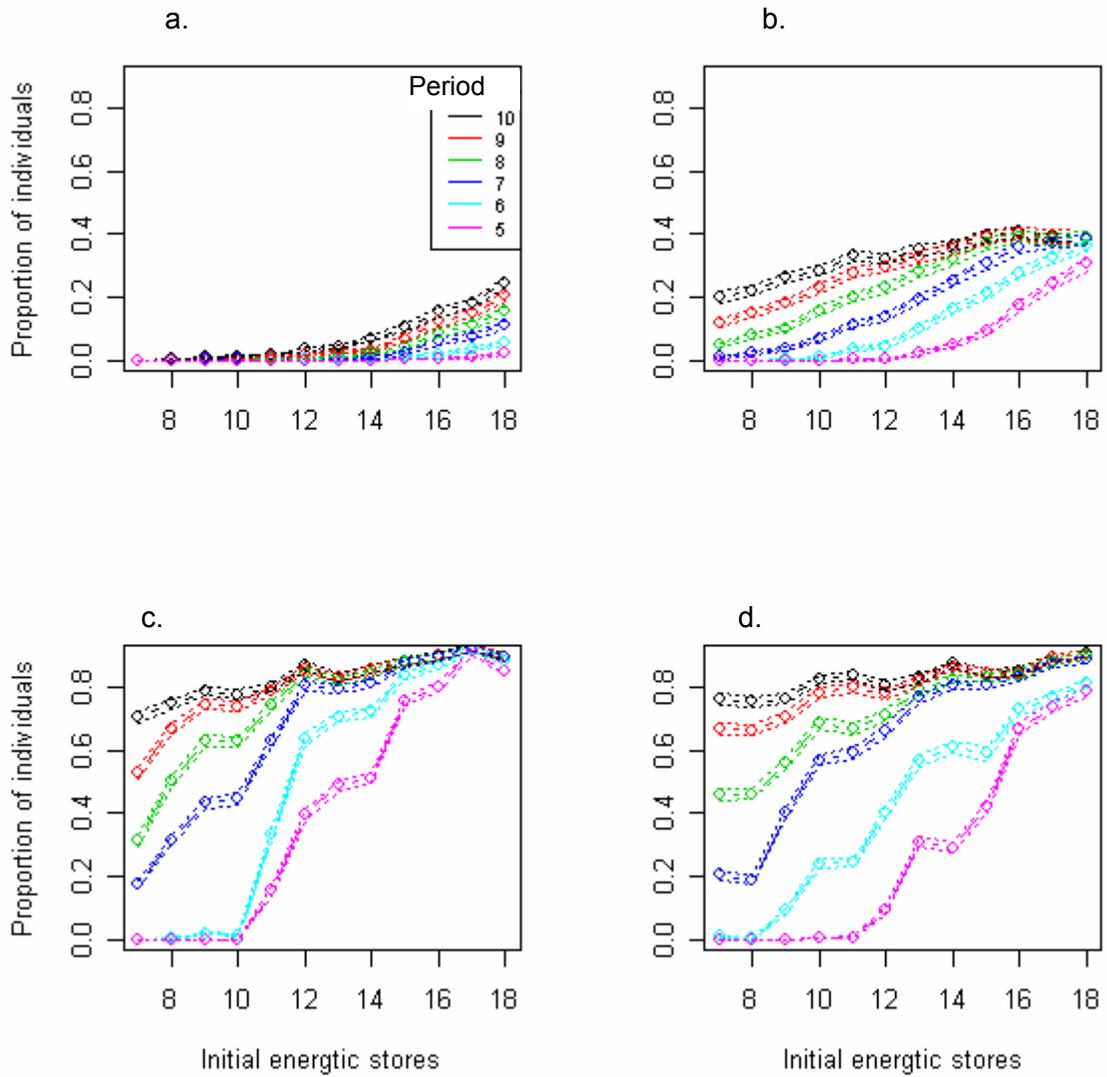


Figure 4.8. Proportion of individuals arriving at breeding location through time based on energetic stores at the start of the simulation following random choice (a), maximum flight (b), increased foraging reward (c), and shorter flight (d) models of avian migration. Dashed lines represent standard error around the mean.

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