Stopover Ecology of Neotropical Migratory Songbirds in the Northern Yucatan Peninsula, Mexico

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THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY CHARLESTON, ILLINOIS 2016 YEAR

I HEREBY RECOMMEND THAT THIS THESIS BE ACCEPTED AS FULFILLING THIS PART OF THE GRADUATE DEGREE CITED ABOVE
Stopover ecology of Neotropical migrants in the northern Yucatan Peninsula, Mexico

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Acknowledgements

I would like to thank my advisor, Jill Deppe, for giving me the opportunity to work on this project and providing guidance for me along the way. I would also like to thank the other members of my committee, Eric Bollinger, Karen Gaines, and Mike Ward. Thank you to Tony Celis-Murillo for your input and statistical help. Thank you to Rachel Bolus for helping me obtain weather data for my analysis. I also want to acknowledge the field assistance of Janelle Chojnacki, Alba Mariana Martínez González, Jonathan Ruben Nochebuena Jaramillo, Ivan Reséndiz Cruz, and Yuri Ian Macías López.

I spent many years traveling the country as a seasonal ornithologist before attending graduate school and there are many people who I worked with during those years that helped shape my career - thank you. Thank you to my family for their constant love and support. EC, AW, MT, KG – thank you for being the best girlfriends a girl could ask for. Most importantly, I could not have finished this project without the encouragement and support of Oscar Johnson. Thank you for everything.
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Introduction

Millions of songbirds annually migrate across the Gulf of Mexico during their autumn and spring migrations. Migratory songbird populations, particularly those that breed in forests of the eastern United States and Canada, have exhibited widespread declines over recent decades (Robbins 1989). The causes for these declines remain unknown, although evidence suggests that mortality rates during the migratory period are higher than any other period in the annual cycle, and may contribute to these declines (Sillett and Holmes 2002).

The act of migrating is inherently dangerous; small passerine birds flying thousands of kilometers encounter novel habitat types (Mettke-Hofmann and Greenberg 2005), competition for food resources (Moore and Yong 1991), predators (Lindstrom 1989), and inclement weather (Wiedenfeld and Wiedenfeld 1995, Newton 2007), all while needing to maintain adequate fat reserves to accomplish their long-distance flight. Understanding where migratory birds stop during their migrations and how the sites function for migrants will contribute to knowledge of full-life-cycle conservation plans, as well as providing information for conservation and management of suitable stopover areas.

The majority of research concerning stopover ecology in Neotropical migrants comes from studies along the northern coast of the Gulf of Mexico (Able 1972, Moore and Kerlinger 1987, Aborn and Moore 1997, Yong and Moore 1997, Smolinsky et al. 2013, and others). While only a few studies have investigated stopover ecology along the southern coast (Winker 1995, Deppe and Rotenberry 2005, 2008, Raymundo 2010), the Yucatan Peninsula serves as an important stopover site for birds crossing the Gulf of Mexico (Deppe and Rotenberry 2005, 2008), and understanding how birds use particular sites in this region is critical for elucidating how birds successfully complete their migrations. The first chapter of this thesis will evaluate and compare two stopover sites located in the northern Yucatan Peninsula within a conservation framework developed to prioritize stopover sites for conservation. The second chapter will use foraging behavior along with activity rates from automated radio telemetry and their relationship to
stopover behavior to understand how birds use coastal habitats at a single stopover site.
Chapter I

Full-service hotels, convenience stores or fire escapes? Evaluating function of stopover sites for Neotropical migrants in the northern Yucatan Peninsula

Abstract

Nearctic-Neotropical migratory songbirds incur the highest mortality rates during their annual migrations. Migratory songbirds use a network of stopover sites to rest, refuel, or seek refuge during times of poor weather conditions; and the time and energy expended at these sites exceeds that of migratory flight. In order to conserve stopover sites with the highest value to Neotropical migrants, a conceptual framework was developed to classify stopover sites into three functional categories based on their function for migratory landbirds, but there have been few attempts to empirically validate this framework. We evaluated the stopover site conservation framework using two protected areas hypothesized to lie at opposite ends of the framework. We use capture data and radio-tracking data to examine patterns in daily capture rates, body condition, rates of mass gain, stopover duration, and departure behavior with a focus on four species; Swainson’s Thrush (Catharus ustulatus), Red-eyed Vireo (Vireo olivaceus), Gray Catbird (Dumetella carolinensis), and Prothonotary Warbler (Protonotaria citrea). Our results indicate that variance in daily capture rates, energetic condition, and rates of mass gain are reliable metrics by which to evaluate stopover site function for migratory landbirds. In addition to these metrics, departure direction may provide additional information regarding landscape-scale stopover site use by migratory landbirds. This conservation framework should be used to facilitate stopover site conservation for
Neotropical migratory songbirds, and can be applied at sites in the United States as well as tropical regions.

Introduction

Neotropical migratory birds have exhibited widespread and alarming population declines in recent decades (Robbins et al. 1989, North American Bird Conservation Initiative 2016). The causes of these declines vary depending on the species and the locale (Wilcove and Wikelski 2008, Saino et al. 2011), although in general, their declines are attributed primarily to habitat loss and alteration (North American Bird Conservation Initiative 2016). However, migration has been identified as the period of highest mortality (Sillett and Holmes 2002), which is not surprising as the migratory period for a Neotropical migrant is inherently challenging; during these journeys, migrants encounter novel habitat types (Mettke-Hofmann and Greenberg 2005), competition for food resources (Moore and Yong 1991), predators (Lindstrom 1989), inclement weather (Wiedenfeld and Wiedenfeld 1995, Newton 2007), and risky ecological features (Deppe et al. 2015), all while needing to maintain adequate fat reserves. For birds to successfully complete their long-distance migrations they depend on a network of stopover sites along their route where they can rest, refuel, or seek refuge (Schaub and Jenni 2001, Deppe et al. 2015). Accordingly, properly managing and conserving suitable stopover sites is critical for migratory birds and a key strategy for their conservation. The task of protecting and managing stopover sites, however, is not easy. Given the limited resources available, conservation and management activities should focus on
protecting the stopover sites with the highest value for Neotropical migrants, specifically, those sites that are best able to satisfy their en-route requirements.

In practice, identifying stopover sites with the greatest value to migrants is complicated by the fact that sites vary not only in quality but also function. For example, some sites are used to refuel whereas others are used primarily for resting, such as when birds are forced to interrupt flight due to poor weather conditions. Due to differences in function, comparisons between refueling and resting sites for the purpose of establishing conservation priorities have limited value. To facilitate the prioritization of stopover sites for conservation, Mehlman and his colleagues (2005) developed a conceptual framework to classify stopover sites based on their function for migratory forest-dwelling landbirds; within each category sites can then be prioritized based on quality, or how well they satisfied migrants’ specific requirements. The framework defines three functional types – fire escapes, convenience stores, and full-service hotels – each of which plays an essential role based on how birds use them to successfully complete their migration. Consequently, conservation plans need to include all three types.

*Fire escapes* lie at one end of the continuum and are small, isolated sites embedded in an inhospitable landscape, usually along the edges of barriers. Birds use these sites to rest in emergency conditions, typically when unfavorable weather forces them to stop. Consequently, variation in capture rate is expected to be high within and among years and show a predictable relationship with weather; specifically, capture rates are predicted to be higher on days when weather conditions are unfavorable for continued migration (e.g., strong headwinds or cross
winds). Because birds are forced to interrupt flight at fire escapes regardless of energetic condition when weather is poor (Moore and Kerlinger 1987), mean body condition should be higher on days with high capture rates than low capture rates. Additionally, food resources are expected to be too low at these sites to allow birds to refuel, such that changes in body condition are likely to be negligible. Finally, because fire escapes are used primarily for resting and food resources are likely to be low, stopover durations should be short, as birds quickly resume migration.

Convenience stores lie between fire escapes and full-service hotels. They are characterized as relatively small habitat patches, like fire escapes, that are embedded in low quality landscapes. Birds with moderate energy needs are expected to use these sites to rest and replenish enough energy to complete short flights to higher quality sites; thus, body condition of birds should improve while they are at the site. Because food resources are likely less than in large contiguous habitat patches, however, birds are likely to have lower rates of mass gain and relatively short stopover durations (e.g., 1-2 days, Mehlman et al. 2005).

Full-service hotels lie at the opposite end of the continuum from fire escapes, and are characterized by large forested areas with abundant food resources, where birds can replenish fat and muscle to continue migration. Birds are expected to stay for extended periods at full-service hotels and demonstrate large improvements in body condition. While they may be used by large numbers of birds, observed densities may be lower and variance in capture rate is expected to be significantly reduced relative to fire escapes.
There have been few attempts to empirically validate the classification framework proposed by Mehlman et al. (2005), and those efforts have focused on migratory landbirds in temperate regions (e.g., Buler and Moore 2011, Buler and Dawson 2014). Although the framework was designed particularly for forest-dwelling migratory landbirds using stopover sites in eastern Canada and the United States (Mehlman et al. 2005), it should be applicable to subtropical and tropical regions as well. Our understanding of the stopover ecology of Neotropical migratory landbirds, specifically their habitat requirements and the distribution of suitable stopover sites, south of the U.S.-Mexico border is scarce (e.g., Winker et al. 1992, Deppe and Rotenberry 2005, 2008, Sanchez 2009, Bayly et al. 2012). However, our ability to successfully conserve migratory landbirds is hindered if high quality sites in each functional class are not available along birds’ entire migratory routes. The application of Mehlman et al.’s (2005) framework has the potential to significantly enhance efforts to conserve migratory birds by identifying the functional role and quality of stopover sites, thereby guiding more effective prioritization of sites for protection and development of successful management strategies for sites that are already protected.

We empirically evaluated the functional role of two protected stopover sites along the southern Gulf of Mexico in the northeastern Yucatan Peninsula – Contoy Island National Park and El Eden Ecological Reserve – following Mehlman’s et al. (2005) conceptual classification framework. Migratory landbirds encounter both sites immediately or shortly after crossing the Gulf during fall migration (Deppe et al. 2015). Based on the classification framework, we hypothesized that these sites lie
at opposite ends of the classification framework. Contoy is a 230-ha island located 33 km north-northeast of Cancun and is hypothesized to function as a fire escape. On the other hand, Eden is a 2000-ha forested reserve embedded in a largely forested landscape 45 km west of Cancun that likely functions as a full-service hotel. We used capture and radio-tracking data to examine patterns in daily capture rates, body condition, stopover duration and departure behavior with a focus on four focal species: Swainson’s Thrush (*Catharus ustulatus*), Red-eyed Vireo (*Vireo olivaceus*), Gray Catbird (*Dumetella carolinensis*), and Prothonotary Warbler (*Protonotaria citrea*).

To test our hypothesis that Contoy functions as a fire escape and Eden functions as a full-service hotel, we developed predictions about patterns in daily capture rate, body condition, and stopover behavior. First, we expected variance in daily capture rate to be greater at Contoy than Eden. Furthermore, we expected variance in capture rate at Contoy to show a predictable relationship with weather and mean physiological condition of migrants; days with high capture rate were predicted to coincide with poor weather and a higher average body condition (fat score). On the other hand, we predicted that variance in capture rates at Eden would show no discernible relationship with weather or fat. Second, we expected average fat across the season to be lower at Contoy than Eden. Although we expected the average body condition of birds on Contoy to be higher on days with high than low capture rates, the former only occur on a relatively small number of days during fall migration in the southern Gulf (Buskirk 1980, Deppe and Rotenberry 2005). On most days, when capture rates are likely to be low on Contoy, birds are expected to
have a lower average body condition. By evaluating average body condition across the season at both sites, we also aimed to gain a better understanding of the average energetic need of migrants' at each site, useful in interpreting changes in body condition. Third, we expected changes in body condition to be lower at Contoy than Eden; specifically, we expected negative or no changes in body condition at Contoy and positive changes at Eden (Winker 1995, Horton and Morris 2012, Dunn 2000, 2001). While changes in body condition are useful in understanding how birds are using different sites, when considered in the context of birds’ energetic condition, or fat reserves, upon arrival at a site, they also can provide insight into the consequences of using a site. Fourth, we predicted birds to stopover longer at Eden than Contoy, as birds were hypothesized to use Eden for refueling and Contoy primarily for resting, regardless of their fat reserves upon arrival. Finally, we evaluated departure direction of birds from the two stopover sites as a way to integrate information about the functional role and quality of each site. We expected that birds stopping at Contoy and Eden should depart toward the south or southeast if they had sufficient energetic reserves to continue their migration at the time of departure. If Contoy is used primarily for resting and offers little or no opportunity to deposit fat, then we expected most birds to head west from Contoy, toward the mainland, in search of refueling sites, unless they had sufficient fat to continue migrating in a seasonally appropriate direction, which in most cases would require an overwater flight (Sandberg and Moore 1996, Sandberg et al. 2002, Deutschlander and Muheim 2009). On the other hand, we expected Eden to be used by birds in better energetic condition, and offer refueling opportunities, allowing a higher
propor tion of birds to depart the site in a seasonally appropriate direction than at Contoy.

Methods

Field Sites

Contoy Island National Park (hereafter Contoy; 21.472186 N, -86.78889 W; Fig.1) is managed by Mexico’s National Commission for Natural Protected Areas. It is classified as an Important Bird Area by Birdlife Conservation and is a Ramsar Site (citation). The site is an ecotourism destination, although tourism is highly regulated (<200 visitors per day to a small area of the island), and a small area at the northern extent of the island is occupied seasonally (September through December) by a small, regulated fishing cooperative. The island is dominated by coastal scrub, mangroves (primary and secondary mangrove assemblages), and a small abandoned coconut plantation toward the south end of the island. The El Eden Ecological Reserve (hereafter Eden; 21.210548 N, -87.19203 W; Fig.1) is a private protected area with no tourism and limited activity by researchers that is managed by the Center for Tropical Research (Centro de Investigaciones Tropicales, CITRO) at the University of Veracruz. Eden is dominated primarily by semi-deciduous tropical rain forest, secondary semi-deciduous forest, seasonally inundated forest, and savannas.
**Data Collection**

During fall migration in 2014 (1 September to 21 November) and 2015 (28 August to 12 November) we captured and banded migratory birds at Contoy Island and Eden. We operated 10 to 16 mist nets (12m x 2.6m, 30mm mesh) at each site daily, starting at 15 minutes before sunrise and continuing for approximately 4.5 hours (weather permitting). Birds were banded with uniquely numbered metal bands, and we determined species, age and sex using criteria in Pyle (1997). We recorded mass (± 0.1 g), un-flattened wing chord (± 0.5 mm) and visual fat reserves. The amount of subcutaneous fat visible in the furcular and abdominal region was scored on a scale of 0 to 5 (Helms and Drury 1960).

**Radio-telemetry**

We attached radio-transmitters to four focal species: Swainson’s Thrush (*Catharus ustulatus*; n=27), Red-eyed Vireo (*Vireo olivaceous*; n=37), Gray Catbird (*Dumetella carolinensis*; n=24), and Prothonotary Warbler (*Protonotaria citrea*; n=16). These species are numerous at both study sites and vary in their migratory behavior and wintering locations (Petit 1999, Cimprich et al. 2000, Mack and Yong 2000, Smith et al. 2011). After initial banding and processing, we attached analog pulse transmitters (JCJC Corp or Lotek Wireless) to birds’ backs using eyelash adhesive following the methods of Raim (1978) and Smolinsky et al. (2013). Transmitters weighed between 0.66 and 0.89 g and did not exceed 6% of a bird’s body weight (range 2.0 to 5.8%); most transmitters were below 5%. The standard maximum for radio transmitters is to weigh no more than 5% of a bird’s body.
weight; however, there has been no evidence that transmitters weighing slightly more than 5% have adverse effects on birds (Barron et al. 2010).

We used automated radio telemetry systems (ARTS; Kays et al. 2011) to track birds between the time of radio-tagging and departure. Each ARTS consisted of six Yagi antennas positioned at 60° intervals connected to an automated receiving unit (ARU; JDJC Corp, IL). The ARUs continuously scanned pre-programmed frequencies and recorded signal strength, pulse width, pulse interval, and noise. In 2014 both sites had one automated receiving tower; in 2015 we added two additional ARTS to Contoy Island for a total of three receiving systems.

Departures from Contoy and Eden were indicated by an increase in signal strength as the bird gained altitude and the ARTS obtained an unobstructed signal from the bird, which was then followed by a complete loss of signal (see Smolinsky et al. 2013 for a detailed description of the departure signal patterns). We used signal strength as our primary cue for departure, but in some cases birds were located farther away from our towers and the towers could only detect changes in pulse width. In these cases, data still showed the typical increase in pulse width immediately followed by a complete loss in signal. At the same time the ARU detected an increase in signal strength and/or pulse width, we estimated the departure bearing based on the two adjacent antennas with the strongest signal strength (Smolinsky et al. 2013). Departure time was recorded as the date and hour when the departure signal reached its peak strength. We defined stopover duration as the minimum number of days a bird was at a site, as we do not know how long an
individual was present prior to capture. We considered birds departing our sites the night of capture to have a stopover for 1 day.

**Weather data**

We obtained weather data from the National Oceanic and Atmospheric Administration's North American Regional Reanalysis (NARR; measurements acquired 8 times/day) data set through Movebank's Env-DATA service (Mesinger et al. 2006, Wikelski and Kays 2014). We retrieved data for the following weather variables as they have been found to influence departure and flight behavior in other studies (Akesson and Hedenstrom 2000, Morganti et al. 2011, Deppe et al. 2015, Liu and Swanson 2015, Dossman et al. 2016): 24-hour change in percent humidity (measured as the difference from the value exactly 24 hours prior; %), 24-hour change in barometric pressure (measured as the difference from the value exactly 24 hours prior; hPa), U-wind (m/s; positive winds toward the north) and V-wind (m/s; positive winds toward the east). We retrieved interpolated weather data at 14:45 on each day prior to the morning of capture to characterize weather conditions at the time of arrival at Contoy. Data collected from a previous effort to track migratory landbirds across the Gulf of Mexico (Deppe et al. 2015) demonstrated that birds arrived or passed over Contoy Island on average at 14:45.

We obtained all weather variables at surface level. We examined relationships among weather variables and only weather variables having $|r| < 0.60$ were retained for analysis (Deppe et al. 2015).
Statistical Analysis

For our analyses of daily capture rate, we included only initial captures of nocturnal landbird migrants. We calculated a daily capture rate (DCR) as the number of migrant individuals captured per net hour per day (one net hour = one 12-m mist net open for one hour). We included all migratory landbird species captured at our sites in our analyses of daily capture rate. To compare variance in daily capture rate we used a Levene’s homogeneity of variance test. We used generalized linear models (GLiM) to evaluate the relationship between DCR and fat and weather separately at Contoy and Eden. DCR was the response variable in our models, and we included all four weather variables and the mean daily fat score across all captured individuals as predictors. As the DCR is adapted from count data, a negative binomial generalized linear mixed model (GLMM) was used to assess which variables influence the daily capture rates.

To compare birds’ energetic condition between the two sites we used a GLiM with a Poisson distribution and log link. We used fat score as the response variable and site, species, interaction between site and species, and year were included as predictor variables. We only considered the four focal species in our comparison of fat scores between the two sites, as there were many migratory species with small sample sizes, including some that were captured only at one site.

We evaluated changes in body condition of the four focal species using a regression approach. A Condition Index (CI) was calculated as mass x 100 divided by wing length. CI was calculated using a linear value of wing length instead of a cubic value, as this variation of CI has been found to be more accurate and better at
predicting fat content (Winker 1995). We used a GLiM with a Poisson distribution and log link; CI was included as the response variable and time of day (hour since sunrise), time and species interaction, and time and year interaction were included as predictor variables. Time since sunrise is included in the models to control for the effect of time on CI. We evaluated changes in CI of birds at each site separately to facilitate interpretation given the possible interactions among site, species, and year.

We evaluated stopover duration of the four focal species using a negative binomial GLiM. Stopover duration in days was the response variable, and site, species, interaction of site and species, fat score, and year were included as predictor variables. The interaction of site and species allowed species to vary their stopover duration by site.

We modeled departure directions of the four focal species as either inappropriate or appropriate, and the range of departure directions in these categories varied with species. For Red-eyed Vireos and Swainson’s Thrushes, whose wintering locations are in South America, we considered departure directions between 120° – 200° appropriate. For Prothonotary Warblers and Gray Catbirds, which may winter in Central America, we considered appropriate directions to be between 120° and 270°. Departure direction was modeled using a binomial GLiM with a logit link. The predictor variables included site, species, interaction of site and species, fat, wind variables (U and V) and year.
All statistical analyses were run in R version 3.3.1 (R Core Team 2016). We used package lme4 for the binomial regression models (Bates et al. 2015), and MASS for the negative binomial models (Venables and Ripley 2002).

**Results**

*Daily Capture Rates*

A total of 2,648 landbird migrants were captured in 6,240.64 mist-net hours. 2,165 migrants were captured in Contoy in 4,445.14 net-hours and 483 migrants at Eden in 1,795.5 net-hours. The mean daily capture rate was higher at Contoy than Eden (0.54 and 0.26, respectively). The variance in daily capture rates was significantly different between Contoy and Eden with greater fluctuations in daily capture rates at Contoy ($F_{1,165} = 12.2, p < 0.001$; Figure 2). The generalized linear models revealed no significant effects of U wind ($X^2 = 0.0, df = 1, p = 0.94$), V wind ($X^2 = 2.55, df = 1, p = 0.11$), change in humidity ($X^2 = 1.05, df = 1, p = 0.31$), change in pressure ($X^2 = 0.28, df = 1, p = 0.59$), or mean daily fat level of migrants ($X^2 = 0.15, df = 1, p = 0.69$) at Contoy. There were also no significant effects of U wind ($X^2 = 0.21, df = 1, p = 0.64$), V wind ($X^2 = 0.0, df = 1, p = 0.95$), change in humidity ($X^2 = 0.0, df = 1, p = 0.95$), change in pressure ($X^2 = 0.0, df = 1, p = 0.99$), or mean daily fat ($X^2 = 0.11, df = 1, p = 0.73$) at Eden.

*Fat*

Birds at Eden had significantly higher fat levels than birds at Contoy (1.12 and 0.85 respectively; $X^2 = 3.85, df = 1, p = 0.049$). The interaction of site and species was nearly significant ($X^2 = 7.34, df = 3, p = 0.06$), indicating that the four
focal species differed in their fat levels by site. Gray Catbirds and Swainson’s Thrushes both carried more fat at Eden than Contoy, while Red-eyed Vireos had very similar fat levels between the sites, and Prothonotary Warblers had slightly higher fat levels at Contoy (Figure 3). Year ($X^2 = 0.008, df = 1, p = 0.92$) and species ($X^2 = 2.05, df = 3, p = 0.56$) did not have a significant effect on fat level indicating that these patterns did not fluctuate inter-annually and were similar across species.

**Hourly change in body condition**

Time since sunrise had a significant effect on Condition Index at both sites. Overall, birds at Eden had higher rates of mass gain than birds at Contoy (time coefficients were 0.40 and 0.08 respectively). However, there was a significant time and species interaction at Contoy ($X^2 = 322.19, df = 3, p < 0.001$) and Eden ($X^2 = 105.83, df = 3, p < 0.001$). On Contoy, Gray Catbirds and Prothonotary Warblers showed no change in body condition over the morning, while Red-eyed Vireos showed a slight decrease and Swainson’s Thrushes showed a substantial increase while at Eden, Swainson’s Thrushes and Gray Catbirds had a larger increase in body condition than Red-eyed Vireos and especially Prothonotary Warblers, which demonstrated little change in condition (Figure 4). The interaction between time and year was not significant at Contoy ($X^2 = 2.27, df = 1, p = 0.13$) or Eden ($X^2 = 0.475, df = 1, p = 0.49$).

**Stopover length**

We determined stopover and departure behavior for 15 Gray Catbirds, 5 Prothonotary Warblers, 24 Red-eyed Vireos and 19 Swainson’s Thrushes. Overall,
site did not have a significant effect on stopover length \((X^2 = 0.08, df = 1, p = 0.79)\); stopover length averaged 3.8 days at Contoy and 4.2 days at Eden. Mean stopover was similar between species \((X^2 = 2.97, df = 3, p = 0.27)\) and did not vary across years \((X^2 = 0.0, df = 1, p = 0.30)\). Fat influenced stopover length significantly \((X^2 = 7.64, df = 1, p = 0.03)\), with birds in higher fat classes having shorter stopovers (Figure 5). The interaction between site and species was not significant \((X^2 = 7.63, df = 3, p = 0.10)\), although there was a non-significant tendency for Red-eyed Vireos to have longer stopovers at Eden while Gray Catbirds and Swainson’s Thrushes stayed longer at Contoy (Figure 6).

**Departure Direction**

The direction in which birds departed was not influenced by site \((X^2 = 0.00, df = 1, p = 0.97)\), although departure directions were affected by species \((X^2 = 7.91, df = 3, p = 0.04)\) and year \((X^2 = 4.94, df = 1, p = 0.02)\). The interaction of site and species was not significant \((X^2 = 3.07, df = 3, p = 0.38)\) indicating that species departed in similar directions between sites. A higher proportion of Red-eyed Vireos departed in a seasonally inappropriate direction, regardless of site, than the other three species (Figure 7). Thirteen of 24 (54%) Red-eyed Vireos departed in directions that were considered inappropriate for continuation of migration, whereas only 36% (7 of 19) of Swainson’s Thrushes and 20% (3 of 15) of Gray Catbirds departed in an inappropriate direction. All Prothonotary Warblers departed in appropriate directions. A higher proportion of birds departed both sites in seasonally appropriate directions in 2015 (76%) than 2014 (41%). Fat level \((X^2 = \)
0.12, \( df = 1, p = 0.73 \), U wind \( (X^2 = 0.22, df = 1, p = 0.64) \), and V wind \( (X^2 = 1.09, df = 1, p = 0.30) \) did not influence migrants' departure directions.

**Discussion**

We found mixed support for our hypothesis that Contoy functions as a fire escape, but strong support for Eden as a full-service hotel. As we predicted Eden demonstrated a low mean daily capture rate, little variance in daily capture rate with no relationship to weather or fat, high mean fat scores of birds coupled with increases in body condition, long stopovers (> 4 days), and most departures were in a seasonally appropriate direction. These findings support the hypothesis that Eden is used as a refueling site and is of high quality.

On the other hand, support for the hypothesis that Contoy functions as a fire escape was mixed. For example, mean capture rate was high on Contoy and there was significantly greater variance in daily capture rate on the island, consistent with our predictions; however, capture rate showed no predictable relationship with any of the weather variables we considered or mean daily fat score. On average, birds stopping on Contoy were leaner than those using Eden, suggesting that many birds stopping at the site have moderate energy requirements and need to replenish some fat reserves and are not solely using the site to rest. The longer stopover durations combined with the neutral and, in the case of thrushes, positive mass gains and the comparably high proportion of birds departing Contoy (relative to Eden) in a seasonally appropriate direction, suggest that birds on the island were in fact able to
satisfy their needs to rest and maintain or gain mass, particularly thrushes and catbirds.

These findings suggest that Contoy may function more like a convenience store, as it is used by birds with moderate energy needs for a combination of resting and replenishing enough energy to complete short flights to higher quality sites, such as the mainland coast. The improvement of body condition for several species at Contoy, poorer improvements in body condition on Contoy relative to Eden (full-service hotel), relatively long stopovers on Contoy (although longer than predicted by Mehlman et al. 2005) and departures primarily in seasonally appropriate directions support the hypothesis that Contoy functions as a convenience store (Mehlman et al. 2005). It also is possible that Contoy does in fact function as a fire escape, but is a high quality fire escape in that it offers at least some migrant species sufficient food resources to allow them to replenish fat, consequently, encouraging them to stay for longer periods of time and allowing them to continue migrating in a direction consistent with their intended destination. It is also possible that Contoy falls somewhere between a fire escape and a full-service hotel, as Mehlman and his colleagues (2005) point out that these categories represent only three types along a continuum and are not meant to be considered the only categories possible. While classifications may have some ambiguity, and further research may support the creation of additional categories, the framework nevertheless provided an approach for empirically assessing site function and estimating its quality that will be valuable in managing specific sites (e.g., through enhancing or preserving foraging...
opportunities, or minimizing impacts on refueling potential) as well as defining regional conservation priorities.

The lack of a relationship between daily capture rate on Contoy and any weather variables or fat, suggests birds are not being forced down by weather or poor energetic condition. This also runs contrary to other studies that have found strong relationships between unfavorable weather and high capture rates in coastal sites along the northern Gulf coast in the spring and along the southern coast in the fall (Able 1972, Buskirk 1980, Moore and Kerlinger 1987, Gauthreaux et al. 2005). It is likely that the lack of relationship between capture rate and weather is attributable to how we quantified weather conditions. We retrieved weather conditions at the surface level at the arrival location and time; however, for birds that arrived at Contoy and Eden, it is possible that weather conditions at the time and location of arrival are not indicative of conditions birds encounter over the Gulf as they cross.

While stopover duration and departure direction were not influenced by site, fat and species did play important roles in shaping stopover and departure behaviors. Like other studies, we observed a strong relationship between stopover duration and fat (Goymann et al. 2010, Cohen et al. 2014); birds captured with lower visible fat reserves stayed at both sites longer than those with higher fat reserves. The long stopover duration at Contoy and Eden suggests that both sites offer foraging opportunities and should be managed in a way to maintain or improve foraging opportunities. Our observation of significant species-level differences in stopover duration and departure behavior and likely variation in the
functional role and quality of sites among species, particularly between Red-eyed Vireos and the other species we considered, is not surprising. Red-eyed Vireos exhibited longer stopovers and a higher proportion of inappropriate departure directions than other species. Similar results were found for Red-eyed Vireos at a fall stopover site in coastal Alabama prior to crossing the Gulf of Mexico (Deppe et al. 2015). In that study, the authors compared Red-eyed Vireos to Swainson’s and Wood Thrushes and found that vireos were significantly more likely than the other two species to depart in a seasonally inappropriate direction and had longer stopover durations. These differences in stopover and departure could be due to the species foraging needs, wintering behavior or the proportional fuel loads required by the species to complete extended flights. Red-eyed Vireos consume less fruit and more insectivorous prey items during migration (Parrish 1997) and birds foraging on a higher proportion of fruit were found to gain mass at a faster rate (Parrish 1997, Bairlein 2002), suggesting that Red-eyed Vireos may need longer stopovers to compensate for their highly insectivorous diet during migration. Red-eyed Vireos are also not known to be territorial during winter (Cimprich et al. 2000) whereas Swainson’s Thrushes and Gray Catbirds are (Mack and Yong 2000, Smith et al. 2011); Red-eyed Vireos may not be under pressure to reach their wintering grounds and therefore can spend longer at stopover locations. Additionally, Red-eyed Vireos are smaller than Swainson’s Thrushes or Gray Catbirds and may require greater fat levels prior to completing extended migratory flights (i.e. to southern Central America) and require longer stopover to acquire the necessary fat levels.
The inability to clearly assign Contoy into a single category based on multiple metrics and species highlights several important considerations when applying the framework to understand stopover site function and quality, whether the goal is to prioritize multiple sites or provide management guidance for particular sites, including those that already have some degree of protected status. First, it is essential to consider multiple metrics. Second, metrics should include not only those that might provide insight into the functional role of a site, but also metrics that provide an estimate of a site’s quality, specifically, how well migrants satisfy their particular requirements at a site (i.e., if a migrant needs to replenish moderate energy supplies, is there evidence that these specific needs can be satisfied at the site). Metrics that provide insight into quality include estimates of changes in body condition, stopover duration and departure direction if they are considered in the context of bird’s needs at the particular site. Some of these metrics, like body condition, can provide information on both how the site is used and how well the site meets those needs, but again, additional data (e.g., energetic condition, or fat scores, upon arrival at a site) need to be collected to properly interpret patterns in those metrics of site quality. Third, an evaluation of site quality needs to take into account multiple species representing a range of biogeographic distributions, natural histories, energetics, and diet, among other factors. Mehlman et al. (2005) acknowledged that sites would likely vary among species, although within a broad group (e.g., migratory songbirds) there may nevertheless be some generalities that can be made about the site or particular subgroupings. Finally, consideration of departure directions in evaluating the functional role of stopover sites, when
possible, will provide information about conservation priorities at larger spatial scales by taking into account regional movements.

By better understanding the functional role and quality of these specific sites, our findings can inform effective management planning within reserve boundaries of these already protected areas. In sites that do not currently have any level of protection, such efforts can provide valuable guidance to entities tasked with identifying the most valuable sites within a landscape. Our results not only provide information about these two specific sites, but they also provide information necessary to inform management and conservation efforts at the landscape and regional levels. In our study, departure directions of birds on Conroy underscored the value of the northeastern coast of the Yucatan Peninsula for en-route migratory songbirds in the region. The stopover site framework has significant value in identifying the functional role and quality of particular sites and their relationship to the surrounding regions, and successful conservation and management efforts at individual sites may be compromised if regional planning is not considered. The application of the stopover site framework in areas south of the US-Mexico border may greatly improve our knowledge of stopover site ecology of landbird migrants.
Figure 1. Map of study site locations in the northern Yucatan Peninsula: Contoy Island National Park and El Eden Ecological Reserve in the state of Quintana Roo, Mexico.
Figure 2. Daily capture rates (DCR) of migrant species captured at two stopover sites located in the northern Yucatan Peninsula in 2014 (A) and 2015 (B). DCR is the number of landbird migrants captured per net hour per day (one net hour = one 12-m mist net open for one hour). Data are from 2,165 migrants captured in Contoy Island National Park, Mexico in 4,445.14 net-hours and 483 migrants at El Eden Ecological Reserve, Mexico in 1,795.5 net-hours. Day 240 refers to August 28th and day 320 to November 16th.
Figure 3. Mean fat score for Gray Catbird (GRCA, n = 172), Prothonotary Warbler (PROW, n = 125), Red-eyed Vireo (REVI, n = 96), and Swainson’s Thrush (SWTH, n = 52) at two stopover sites in the northern Yucatan Peninsula (Contoy Island National Park and El Eden Ecological Reserve). Data were collected during autumn migration in the years 2014 and 2015.
Figure 4. Hourly changes in condition index for (A) Gray Catbird (*Dumetella carolinensis*, *n* = 183), (B) Prothonotary Warbler (*Protonotaria citrea*, *n* = 129), (C) Red-eyed Vireo (*Vireo olivaceus*, *n* = 94), and (D) Swainson's Thrush (*Catharus ustulatus*, *n* = 52) at two stopover sites in the northern Yucatan Peninsula (Contoy Island National Park and El Eden Ecological Reserve). Condition Index (CI) was calculated as mass x 100 divided by wing length. Data were collected during autumn migration in 2014 and 2015.
Figure 5. Mean stopover length (in days) among fat scores for four focal species (Gray Catbird, n = 15; Prothonotary Warbler, n = 5; Red-eyed Vireo, n = 28; and Swainson's Thrush, n = 19) at two stopover sites in the northern Yucatan Peninsula (Contoy Island National Park and El Eden Ecological Reserve). Data were collected during autumn migration 2014 and 2015.
Figure 6. Mean stopover lengths (in days) of Gray Catbird (GRCA, $n = 15$), Prothonotary Warbler (PROW, $n = 5$), Red-eyed Vireo (REVI, $n = 28$), and Swainson’s Thrush (SWTH, $n = 19$) at two stopover sites in the northern Yucatan Peninsula (Contoy Island National Park and El Eden Ecological Reserve) during autumn migration 2014 and 2015.
Figure 7. Proportion of Gray Catbird (GRCA), Prothonotary Warbler (PROW), Red-eyed Vireo (REVI), and Swainson's Thrush (SWTH) departing in seasonally appropriate (gray) and inappropriate (black) directions from two stopover sites located in the northern Yucatan Peninsula (Contoy Island National Park and El Eden Ecological Reserve). Data were collected during autumn migration in 2014 and 2015.
Chapter II

Coastal habitat use by four species of migratory songbird at a stopover site in the Northern Yucatan Peninsula, Mexico

Abstract

Migratory songbirds use a network of stopover sites along their migratory routes to rest, refuel, and replenish lost energy reserves. In order for songbirds to quickly refuel and acquire sufficient energy for the next leg of their migration, birds must find suitable stopover sites that provide necessary food, shelter, and safety. Determining en-route habitat quality is particularly challenging, as birds use multiple unfamiliar sites distributed over thousands of miles and their energetic needs vary along the migration route. Stopover sites located along the edges of large geographic features such as the Gulf of Mexico may be especially important, as these areas serve as either the first or last stops before an overwater crossing, and these areas are threatened by population growth and sea level rise. We examined the foraging behavior (attack rate and movement rate) and used automated radio-telemetry data to examine activity rates between two primary habitats (coastal scrub and mangrove) at a stopover site located on the southern coast of the Gulf of Mexico during autumn migration for four focal songbird species; Swainson’s Thrush (Catharus ustulatus), Red-eyed Vireo (Vireo olivaceus), Gray Catbird (Dumetella carolinensis), and Prothonotary Warbler (Protonotaria citrea). We also examine the relationship between activity rates and stopover duration and departure direction. Our results indicate that each species has distinct habitat preferences; Gray Catbirds
and Swainson’s Thrushes spend more time, are more active, and displayed lower movement rates in coastal scrub, and also demonstrated a stronger positive relationship between activity rate and stopover. Prothonotary Warbler and Red-eyed Vireo demonstrated a weaker relationship between activity and stopover. Red-eyed Vireos also displayed lower movement rates in mangrove, although activity was not different between habitat types. Our data show that migratory songbirds use coastal scrub and mangrove based on species-specific differences, and all coastal habitats near ecological barriers should be preserved for migratory songbirds.

Introduction

Nearctic-Neotropical songbird migrants use a network of stopover sites to rest, refuel, and replenish lost energy reserves during their annual migrations. Migration is energetically costly and twice the amount of energy is expended during stopover than migratory flight (Bowlin et al. 2005). In order for birds to quickly refuel and acquire sufficient energy for the next leg of their migration, birds must find suitable stopover sites that provide necessary food, shelter, and safety. Determining en-route habitat quality is particularly challenging (Johnson 2007) as birds use multiple, and often unfamiliar, sites distributed over thousands of miles, spend as little as a day at a site, and their energetic needs vary along the migration route. Because of the importance of refueling at most sites and the influence of refueling rate on migration speed, previous studies have focused on estimating habitat quality of sites or habitats based on their refueling potential.
The foraging behavior of migratory birds at a stopover site provides information on the quality of the habitat as it reflects information on prey availability. As prey availability increases, and consequently habitat quality, the attack rate or the rate at which birds encounter food should also increase, as attack rates have been found to be proportional to prey availability (Johnson 2000). The increased attack rate has been used to identify higher-quality habitat on the breeding grounds (Lyons 2005) and at stopover sites (Smith et al. 2007, Rodewald and Brittingham 2007). At the same time that attack rates increase with habitat quality, it can be expected that movement rate (the number of foraging movements per unit time) will decrease (Lyons 2005, Rodewald and Brittingham 2002). As prey become more abundant, birds do not have to search as far or on as many surfaces to acquire the same amount of resources.

Other factors besides prey availability may contribute to habitat quality for en-route migratory songbirds, such as presence of predators and competition with other birds (Johnson 2007). Information on movement rates over a wider time period may provide information on how a bird uses certain habitat types. Previous studies have used manual radio-telemetry to quantify movement rates or distances moved (Aborn and Moore 1997, Cohen et al. 2014, Liu and Swanson 2015). In contrast to manual radio-telemetry, automated radio-telemetry systems (ARTS) allow researchers to continuously gather data on birds and determine daily activity levels and proportion of time spent active (Schofield 2015). Activity rates collected through ARTS are able to record activity that is not related to foraging behaviors, such as predator avoidance, turning while on a perch, or preening (Schofield 2015).
While ARTS activity rates may not be useful for assessing relative habitat quality as it also incorporates data on activities not directly related to foraging, if combined with information on stopover behavior, it may provide information useful in evaluating site quality.

Stopover sites located along the edges of large geographic features such as the Gulf of Mexico may be especially important for refueling by Neotropical migrants (Petit 2000), as these areas serve as either the first or last stops before an overwater crossing that lasts anywhere from 15-35 hours (Deppe et al. 2015). While research has focused on sites located on the northern coast of the Gulf of Mexico in spring and to a lesser extent fall, few studies have investigated stopover sites along the southern coast of the Gulf of Mexico (but see Buskirk 1980, Deppe and Rotenberry 2005, 2008). Yet the ability to refuel at these southern sites is essential for birds to successfully navigate the Gulf of Mexico. As coastal habitat is being threatened by population growth (Creel 2003) and potential sea level rise (Mendoza-González et al. 2013), it is critical to understand how different habitats function for migratory songbirds around the Gulf.

We compared attack and movement rates between two habitat types to evaluate relative habitat quality at a stopover site located on the southern coast of the Gulf of Mexico, Contoy Island (hereafter Contoy). We also evaluated the relationship of activity rate with stopover behavior, specifically stopover duration and departure directions, to better understand birds use of different habitats at Contoy. We focus on four species in this study: Red-eyed Vireo (Vireo olivaceus), Swainson’s Thrush (Catharus ustulatus), Gray Catbird (Dumetella carolinensis) and
Prothonotary Warbler (*Protonotaria citrea*). By considering foraging behavior in combination with activity and stopover behavior, we aim to gain a better understanding of habitat quality for en-route Neotropical migrants after crossing the Gulf of Mexico. Our results will inform conservation and management plans for coastal habitats, as we will gain information on which habitats species use and how they function for migratory songbirds.

**Methods**

*Field Sites and Banding*

We conducted fieldwork during fall migration in 2015 (28 August to 12 November) at Contoy Island National Park, an isolated island 33 km north-northeast of Cancún, Quintana Roo, Mexico (21.4721 N, 86.7888 W; Figure 1). Contoy is 230 ha in size, is approximately 8.3 km long, varies in width from 50 to 750 m, and is dominated by coastal scrub and mangrove habitats (Figure 1; Lillo et al. 1997). We operated 12 mist nets (12 m x 2.6 m, 30 mm mesh) daily, starting at 15 minutes before sunrise and operating for approximately 4.5 hours, weather permitting. We used four additional nets during the week of 5-9 October 2015 in order to increase the sample size of Swainson’s Thrushes for a related study, for a total of 16 mist nets during this period. Mist nets were distributed evenly between the two dominant vegetation types on the island. We banded birds with uniquely numbered metal bands, and determined species, age, and sex criteria following Pyle (1997). After initial processing, we attached 40 radio-transmitters to individuals of four focal
species, Red-eyed Vireo (n= 11), Swainson’s Thrush (n= 11), Gray Catbird (n= 13),
and Prothonotary Warbler (n= 5). These species were selected because they are
among the most numerous species at Contoy, and they differ in migratory behaviors
and wintering locations. We attached transmitters to the birds’ backs using eyelash
adhesive following the methods of Raim (1978) and Smolinsky et al. (2013).

Foraging observations

We recorded foraging observations for any individual of the focal species that
we encountered, primarily in the afternoon and early evening, but we also recorded
observations opportunistically during the morning. We used digital voice recorders
to record data, and for each individual encountered we noted date, time, species, age
(if known), frequency (if bird had received a transmitter), and habitat type. We
followed birds until we lost sight of them and recorded one sequence for each
individual encountered. If we lost sight of a bird momentarily, we recorded the time
it was lost from sight, and considered it part of the same sequence if the time was
less than 20 seconds. Additionally, if birds switched to another behavior type, such
as resting or preening, we recorded the amount of time spent in other behaviors in
order to quantify time spent foraging compared to other behaviors. The number of
times the bird attempted to forage was recorded, along with the attack and
movement type used. We categorized attack and movement types according to
(Remsen and Robinson 1990). We used five attack categories: glean, lunge, hang,
sally, and probe. Movement types were recorded as walk or hop, and two different
flight categories, short (≤ 1 m) or long (> 1 m). The total number of attacks was
summed to calculate an attack rate (number of total attacks/min) and the number of movements was used to calculate a movement rate (number of movements/min). Only observations longer than 30 seconds were included in the analysis. Relationships between habitat and attack rate and movement rate were examined with a negative binomial GLM in R using the package MASS (Venables and Ripley 2002).

**ARTS data**

We used a network of automated ratio telemetry systems to follow birds between the time of radio-tagging and departure from the site. We had three ARTS located on Contoy [Tower 1 (21.47219 N, 86.78890 W), Tower 2 (21.47139 N, 86.78958 W), Tower 3 (21.47467 N, 86.78929 W); Figure 1]. Each ARTS was equipped with six Yagi antennas positioned at 60° intervals connected to an automated receiving unit (ARU, JDJC Corp, IL). The ARUs continuously scanned pre-programmed frequencies and recorded signal strength, pulse width, pulse interval, and noise. We determined activity based on changes in signal strength between consecutive readings of a frequency and on changes in signal strength across antennas. A bird was defined as being active when the signal strength changed more than 250 decibel-milliwatts (dBm) between consecutive ARU readings, otherwise it was considered inactive (Schofield 2015). The cycle time of the ARU ranged from ≤ 1 minute to 2 minutes, depending on the number of frequencies programmed.

We used the signal strength from the three ARTS to triangulate the position of each bird each time it was detected, and determined whether the bird was located
in either coastal scrub or mangrove. Due to the location of the towers and the position of certain birds, there are some points where we were unable to determine the habitat with a high level of certainty. This primarily occurred when the bird was located in close proximity to Tower 1, so rather than discarding these points we created a third habitat category, “Other”. To calculate activity rate, we combined the activity and habitat data and determined the number of consecutive detections over which a bird was active out of all consecutive detections in each habitat. This allowed us to calculate the activity rate for each individual in each habitat type as a proportion of detections in which a bird was deemed to be active. Additionally, as the proportion of time spent in each habitat was not equal across habitat types, a weighted average was calculated by multiplying the activity rate in each habitat type by the proportion of time each bird spent in the habitat type. To avoid biases in the data due to birds resting in a habitat at night, we only used data points collected during daytime hours as defined by civil twilight.

It is not possible to know how long a bird was present at the site prior to capture, so we define stopover duration as the minimum number of days a bird was at the site. For example, we considered a bird departing the site the night of capture to have a stopover length of one day. Departure directions were categorized as seasonally inappropriate (I) or appropriate (A) based on the wintering distribution of each species. Red-eyed Vireo and Swainson’s Thrushes winter in South America (Cimprich et al. 2000, Mack and Yong 2000); therefore, we categorized departures between 120° and 210° as appropriate and all other directions as inappropriate. Gray Catbird and Prothonotary Warbler winter ranges include Central America.
(Petit 1999, Smith et al. 2011), so we considered a wider range of departure directions as appropriate, from 120° to 270°.

To evaluate the relationship between habitat type and weighted activity rate we used a generalized linear model (GLiM) with a Poisson distribution and a log link function in the package ‘stats’ in R (R Core Team 2016). We then evaluated the relationship between weighted activity rate across all habitats and stopover length with a negative binomial GLiM in R (package MASS; Venables and Ripley 2002) and departure direction with a binomial GLiM with a logit link (package stats; R Core Team 2016). Foraging behavior and activity rates were analyzed separately due to the fact that not all foraging observations were of radio-tagged individuals.

**Results**

*Attack rate*

We recorded a total of 54 foraging observations [Swainson’s Thrush (n=15), Red-eyed Vireo (n=15) and Gray Catbird (n=24)]; 10 of which were observations of birds with radio-transmitters [Red-eyed Vireo (n=3), Gray Catbird (n=1) and Swainson’s Thrush (n=1)]. A single foraging observation was recorded for a Prothonotary Warbler, and this observation was subsequently excluded from the analysis. Foraging observations ranged from 30 to 1,134 seconds (mean ± se; 246 ± 34 seconds).

Attack rates were higher in mangrove (4.0 attacks/min) than coastal scrub (1.5 attacks/min), and the influence of habitat was significant ($\chi^2 = 13.3, df = 1, p < 0.001$). Attack rates were not significantly different between species ($\chi^2 = 3.8, df = 2, p$
although Red-eyed Vireo and Swainson’s Thrushes had lower attack rates than Gray Catbird. The interaction of species and habitat was significant ($\chi^2 = 6.7$, $df = 2$, $p = 0.03$; Figure 2); Swainson’s Thrushes had significantly lower attack rates than Gray Catbird in mangrove (0.88 and 2.04 attacks/min respectively).

**Movement rate**

Movement rate was not impacted by habitat type ($\chi^2 = 1.2$, $df = 1$, $p = 0.26$) and was nearly equal in both habitats (10.1 and 9.0 movements/min in mangrove and coastal scrub, respectively). Species displayed differences in movement rates ($\chi^2 = 8.1$, $df = 2$, $p = 0.01$); Swainson’s Thrushes forage with a slower movement rate (6.8 movements/min) than Gray Catbirds (9.3 movements/min) or Red-eyed Vireos (12.3 movements/min). The interaction of species and habitat was not significant ($\chi^2 = 2.16$, $df = 2$, $p = 0.33$); indicating that species show similar movement rates between coastal scrub and mangrove. Gray Catbirds and Swainson’s Thrushes display slightly lower movement rates in coastal scrub while Red-eyed Vireos display nearly equal movement rates between both habitat types (Figure 3).

**Habitat-specific activity rates**

We determined activity and habitat use for 30 individuals using the ARTS [Gray Catbird (n=11), Red-eyed Vireo (n=9), Swainson’s Thrushes (n=6) and Prothonotary Warbler (n=4)]. A total of 30,207 habitat data points were collected over all 30 individuals. The number of points collected per bird ranged from 54 –
5,066 (mean ± se; 1,002 ± 234). The proportion of time spent in each habitat by species is shown in Figure 4.

Habitat type did not influence activity rates ($\chi^2 = 1.78, df = 2, p = 0.41$), although the mean weighted activity rates were highest in coastal scrub (0.32) compared to mangrove (0.18) or other (0.09). The interaction of habitat and species was not significant ($\chi^2 = 3.31, df = 6, p = 0.76$); indicating that species had similar activity rates among habitats. Gray Catbirds and Swainson’s Thrushes displayed higher weighted activity rates in coastal scrub, Prothonotary Warblers were more active in mangrove than coastal scrub and Red-eyed Vireos displayed nearly equal activity rates between the three habitat types (Figure 5).

**Relationship between activity rate and stopover length**

Activity rates had a nearly significant positive influence on stopover length ($\chi^2 = 2.9, df = 1, p = 0.08$; Figure 6), with birds exhibiting higher activity rates staying longer. Species showed variation in their stopover lengths; Gray Catbirds and Swainson’s Thrushes stayed longer on average (5.4 and 5.3 days, respectively) than either Prothonotary Warblers (1.7 days) or Red-eyed Vireos (2.1 days), although these differences were not significant ($\chi^2 = 2.06, df = 3, p= 0.55$). The relationship between stopover and activity rate varied among species; Gray Catbirds and Swainson’s Thrushes showed a stronger positive relationship between activity rate and stopover length whereas Prothonotary Warblers showed a slight negative relationship and Red-eyed Vireos displayed no relationship at all (Figure 7).
Although the relationship between stopover and activity varied between species, it was not significant ($\chi^2 = 4.06, df = 3, p = 0.25$).

**Relationship between activity rates and departure**

A higher proportion of birds departed in appropriate (73%) than inappropriate (26%) directions, and their respective activity rates were similar (0.68 vs. 0.72, respectively; Figure 8). Activity rates did not influence in which direction birds departed the site ($\chi^2 = 0.0, df = 1, p = 0.99$). Of the eight birds that departed in inappropriate directions, seven (88%) were Red-eyed Vireos and one (12%) was a Gray Catbird. Species did not impact the direction in which birds departed the site ($\chi^2 = 0.0, df = 3, p = 1.0$). The interaction of species and activity rates also did not influence the direction in which birds departed ($\chi^2 = 0.59, df = 3, p = 0.89$).

**Discussion**

We found differences between habitat and species in attack rates, movement rates, weighted activity rates and their relationship to stopover behavior, providing support that coastal scrub and mangrove habitats provide different levels of quality to different species. Gray Catbirds and Swainson’s Thrushes spend more time, and spend more active time in coastal scrub. Combined with these species’ lower movement rates in coastal scrub, longer stopovers, and higher rates of mass gain on Contoy (Chapter 1), this provides support that coastal scrub is a higher quality habitat for these species. On the other hand, Prothonotary Warblers and Red-eyed
Vireos spent more time and more active time in mangrove, had shorter stopovers, and less significant rates of mass gain at Contoy, indicating that mangrove may not provide as high quality resources as coastal scrub at this stopover site.

Gray Catbirds showed the highest attack rates in mangrove habitat, while Swainson’s Thrushes and Red-eyed Vireos did not show much difference between the two habitats. The higher attack rate found in mangrove compared to coastal scrub may be confounded by the prey items commonly taken in each habitat type; a higher abundance of insects have been found in mangrove habitats compared to dry forest (Rodriguez-Colon 2012), and birds foraging in mangrove habitats are likely foraging on insects. Additionally, the difference in attack rates between habitats may be attributed to differences in prey item size between habitats. If there are more insects eaten in mangroves, but they are relatively small in size, this may account for the higher attack rates found in mangrove. Moreover, the nutritional content of prey items between habitat types may contribute to the differences in attack rate; if more insects are eaten in mangrove but they contain lower levels of fats and lipids, it may take more prey items for a bird to build up the same amount of energy reserves compared to birds foraging on fruit. Fruits have higher levels of fatty acids (Bairlein 2002) and birds foraging on a higher proportion of fruits during migratory stopover have been found to gain mass at a higher rate (Parrish 1997, Bairlein 2002).

Birds overall activity rates between all habitat types on the island positively impacted birds stopover, and this relationship was much stronger for Gray Catbirds and Swainson’s Thrushes. Gray Catbirds and Swainson’s Thrushes stayed at Contoy longer than Red-eyed Vireos or Prothonotary Warblers, and they also exhibited a
stronger positive relationship between activity rate and stopover. Multiple factors could be affecting this relationship including initial energetic condition or diet preferences. Gray Catbirds and Swainson’s Thrushes had lower initial fat levels at Contoy (0.72 and 0.94, respectively) than Prothonotary Warblers (1.14) or Red-eyed Vireos (1.13), suggesting that they may need more time at the site to refuel. Furthermore, both Gray Catbirds and Swainson’s Thrushes are more frugivorous during migration (Parrish 1997) and they may have found coastal scrub habitat sufficient for rebuilding fat reserves and not just for resting.

While activity rates impacted stopover length, they did not influence in which directions birds left our site. This may be due to migrants using the site as more of a resting area rather than a stopover site to replenish lost energy reserves, although this may not be true for all species as there were species differences in departure direction. Nearly all of the birds departing in inappropriate directions were Red-eyed Vireos. Despite their lower movement rates, higher proportion of time, and higher activity rates in mangrove, the mean departure bearing for Red-eyed Vireos was 217°, roughly southwest, towards mainland Mexico. This indicates that although Red-eyed Vireos spent more active time in mangrove, they may have found the habitat quality to be poor, and departed southwest towards mainland Mexico to a different stopover site before continuing migration.

Our results highlight the importance of incorporating multiple metrics in one study in order to determine habitat quality for en-route migrants. By combining attack rates with habitat-specific activity rates, site-level activity rates, and the relationship between activity rate and stopover duration, we were better able to
understand how migratory songbirds use the different habitat types at Contoy. Additionally, as coastal habitats are becoming increasingly disturbed by development surrounding Cancún and elsewhere along the Yucatan Peninsula, our results may have important management implications. Although the habitats on Contoy may provide different functions (resting or foraging), all coastal habitats are essential for migratory songbirds along the southern coast of the Gulf of Mexico, and effective coastal habitat management and restoration plans should protect both coastal scrub and mangrove habitats.
Figure 1. Contoy Island National Park located in the northern Yucatan Peninsula. The locations of the three automated radio-telemetry systems (ARTs) are indicated by black circles. Coastal scrub is dark gray and mangrove habitat is light gray.
Figure 2. The mean attack rate (± SE) for Gray Catbirds (GRCA, n = 26), Red-eyed Vireos (REVI, n = 16), and Swainson’s Thrushes (SWTH, n = 19) in coastal scrub (CS) and mangrove (M) habitats at Contoy Island National Park during autumn migration 2015.
Figure 3. The mean movement rates (± se) of Gray Catbirds (GRCA, n = 26), Red-eyed Vireos (REVI, n = 16), and Swainson's Thrushes (SWTH, n = 19) between coastal scrub (CS) and mangrove (M) at Contoy Island National Park during autumn migration 2015.
Figure 4. The mean (± se) proportion of time spent in each coastal scrub (CS), mangrove (M) and other (O) habitats for Gray Catbirds (GRCA, n = 11), Prothonotary Warblers (PROW, n = 4), Red-eyed Vireos (REVI, n = 9), and Swainson’s Thrushes (SWTH, n = 6) as determined from ARTS data at Contoy Island National Park during autumn migration 2015.
Figure 5. The mean (± se) weighted activity rates of Gray Catbirds (GRCA, n = 11), Prothonotary Warblers (PROW, n = 4), Red-eyed Vireos (REVI, n = 9), and Swainson’s Thrushes (SWTH, n = 6) in coastal scrub (CS), mangrove (M) and other (O) habitat types at Contoy Island National Park during autumn migration 2015.
Figure 6. Stopover duration of Gray Catbirds, Prothonotary Warblers, Red-eyed Vireos, and Swainson’s Thrushes as impacted by birds’ weighted activity rates at Contoy Island National Park during autumn migration 2015. Data points are shown with the modeled relationship from a GLM with an interaction of species and activity rate.
Figure 7. Stopover duration of Gray Catbirds (light gray square), Prothonotary Warblers (light gray circle), Red-eyed Vireos (dark gray triangle), and Swainson’s Thrushes (black diamond) as impacted by birds’ weighted activity rates at Contoy Island National Park during autumn migration 2015. Data points are shown with the modeled relationship from a GLM with an interaction of species and activity rate.
Figure 8. The mean weighted activity rates (± se) for Gray Catbirds, Prothonotary Warblers, Red-eyed Vireos, and Swainson’s Thrushes departing in appropriate (A, \( n = 22 \)) and inappropriate (I, \( n = 8 \)) departure directions at Contoy Island National Park during autumn migration 2015.
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