AVIAN CONSERVATION & ECOLOGY

VOLUME 18, ISSUE 2, ARTICLE 7

Solomon, L. E., A. Celis-Murillo, M. P. Ward, and J. L. Deppe. 2023. Full-service hotels, convenience stores, or fire escapes? Evaluating the functional role of stopover sites for Neotropical migrants following passage across the Gulf of Mexico in autumn. Avian Conservation and Ecology 18(2):7. https://doi.org/10.5751/ACE-02150-180207

Research Paper

Full-service hotels, convenience stores, or fire escapes? Evaluating the functional role of stopover sites for Neotropical migrants following passage across the Gulf of Mexico in autumn

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ABSTRACT. Nearctic Neotropical migratory songbirds incur the highest mortality during migration. En-route, songbirds rely on a network of stopover sites to rest, refuel, and/or seek refuge during poor weather. Conservation strategies prioritize protection of sites that best meet these needs. However, the specific function of a stopover site is expected to vary in relation to factors, such as geographic location, surrounding landscape, and weather. To identify sites with the highest conservation value for migratory songbirds, a conceptual framework was independently developed to classify sites into three functional categories based on their geographic and landscape features: fire escapes, convenience stores, and full-service hotels. The few attempts to empirically validate this framework have focused on temperate stopover sites. We evaluated the framework by testing the hypothesis that a site's geographic and landscape characteristics can predict its function. We used capture and radio-tracking data at an island and mainland site in the Yucatan Peninsula, Mexico to quantify mean and variance in daily capture rate, body condition, stopover duration, and departure behavior during autumn, 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 supported our predictions that the island functions as a fire escape, providing refuge for very high numbers of birds after encountering crosswinds or headwinds over the Gulf of Mexico, and the mainland forest site serves as a full-service hotel. The framework provides valuable insight for strategic conservation planning and management of stopover sites for songbirds. We suggest future studies evaluate the framework's application to non-forest bird species. Additionally, we encourage collaborative efforts to consolidate and integrate tracking data, capture data from migration banding stations, and radar-based bird density estimates across a broad geography to test the framework's ability to inform conservation planning across species' full migratory range.

Hôtel cinq étoiles, épicerie de quartier ou sortie de secours? Évaluation du rôle fonctionnel de haltes d'oiseaux migrateurs néotropicaux suivant leur passage automnal dans le golfe du Mexique

RÉSUMÉ. La mortalité des passereaux migrateurs néotropicaux au Néarctique survient le plus souvent au cours de la migration. En cours de route, les passereaux dépendent d'un réseau de haltes pour se reposer, se ravitailler et/ou se réfugier en cas de mauvais temps. Les stratégies de conservation visent en priorité la protection des sites qui répondent le mieux à ces besoins. Cependant, la fonction spécifique d'une halte devrait varier en fonction de facteurs tels que la situation géographique, le paysage environnant et les conditions météorologiques. Afin d'identifier les haltes ayant la plus grande valeur de conservation pour les passereaux migrateurs, nous avons élaboré de façon indépendante un cadre conceptuel permettant de classer les sites en trois catégories fonctionnelles fondées sur leurs caractéristiques géographiques et paysagères : la sortie de secours, l'épicerie de quartier et l'hôtel cinq étoiles. Les quelques essais de validation empirique de ce cadre se sont concentrés sur les haltes en zones tempérées. Nous avons évalué ce cadre en testant l'hypothèse selon laquelle les caractéristiques géographiques et paysagères d'une halte peuvent prédire sa fonction. Nous avons utilisé des données de capture et de radiotélémétrie sur une île et un site continental dans la péninsule du Yucatan, au Mexique, pour calculer la moyenne et la variance du taux de capture quotidien, l'état corporel, la durée de l'escale et le comportement au moment du départ pendant l'automne, en mettant l'accent sur quatre espèces : la Grive à dos olive (*Catharus ustulatus*), le Viréo aux yeux rouges (*Vireo olivaceus*), le Moqueur chat (*Dumetella carolinensis*) et la Paruline orangée (*Protonotaria citrea*). Nos résultats confirment nos prévisions selon lesquelles l'île sert de sortie de secours, offrant un refuge à un très grand nombre d'oiseaux après avoir rencontré des vents de travers ou des vents contraires au-dessus du golfe du Mexique, et la halte forestière sur le continent sert d'hôtel cinq étoiles. Le cadre fournit des informations précieuses en vue d'une planification stratégique de la conservation et de la gestion des haltes pour les passereaux. Nous recommandons que d'autres études évaluent l'application du cadre à des espèces d'oiseaux non forestiers. En outre, nous encourageons la collaboration pour consolider et intégrer les données de suivi, les données de capture aux stations de baguage de migration et les estimations de densité d'oiseaux fondées sur les radars dans une vaste zone géographique afin de tester la capacité du cadre à contribuer à la planification de la conservation dans l'ensemble de l'aire de migration des espèces.

Key Words: *conservation; migration; site function; site quality; songbirds; stopover; Yucatan Peninsula*

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INTRODUCTION

Nearctic-Neotropical migratory birds have exhibited alarming population declines in recent decades (Askins 1995); since 1970, North America has lost 2.5 billion migratory birds (Rosenberg et al. 2019). The causes of these declines are mostly unknown, although they generally are attributed to habitat loss and alteration (Wilcove and Wikelski 2008). Migration has been identified as the period of highest mortality during the annual cycle of songbirds (Sillett and Holmes 2002, Rockwell et al. 2017), which is not surprising, because the migratory period is inherently challenging. During this time, birds encounter novel habitat types (Johnson et al. 2006), competition for food resources (Moore and Yong 1991), predators (Lindström 1989, Cimprich et al. 2005), inclement weather (Wiedenfeld and Wiedenfeld 1995), and large, inhospitable geographic features (Deppe et al. 2015), all while needing to maintain adequate energy reserves for migratory flights. The inability to deal with these challenges can have lethal consequences (Ward et al. 2018).

To complete long-distance migrations, songbirds employ a series of alternating migratory flights and stopover periods and are dependent on a network of sites along their route, where they can rest, refuel, and/or seek refuge (Gill et al. 2009, Goymann et al. 2010). Accordingly, properly protecting and managing suitable stopover sites, particularly along the edges of large geographic features, such as the Gulf of Mexico, is critical for the conservation of migratory birds (Schaub and Jenni 2001, Buler and Moore 2011, Deppe et al. 2015, Ward et al. 2018, Zenzal et al. 2021).

Given the limited availability of resources, conservation efforts for migratory birds focus on protecting the highest quality stopover sites, i.e., those that best satisfy birds' en-route requirements and promote their survival (Bayly et al. 2016). In practice, however, identifying such stopover sites or implementing management actions that improve site quality are complicated by the fact that sites vary in function, i.e., how they are used during migration (Linscott and Senner 2021). For example, some sites are used to refuel, whereas others are used primarily as refuge during poor weather or for sleeping, recovering, gathering information, or engaging in social interactions (Moore and Kerlinger 1987, Shamoun-Baranes et al. 2017, Linscott and Senner 2021). Thus, effective conservation of migratory birds requires a network of sites that satisfy these various needs during migration.

To facilitate strategic, full annual cycle conservation planning for migratory landbirds, a group of scientists and conservationists developed a conceptual framework to classify and prioritize stopover sites according to their function (Mehlman et al. 2005). The framework defines three functional types based on the ecological context of the stopover site (specifically size, landscape context, and location relative to high-risk geographic features): fire escapes, convenience stores, and full-service hotels, which lie along a continuum. Mehlman and colleagues recommended that conservation plans include all three types to ensure birds' various requirements during migration are satisfied. For maximum effectiveness, planning requires two steps: (1) classify sites based on their function, i.e., the requirement(s) they fulfill, and (2) within each functional type, prioritize the sites that best satisfy those specific requirements, i.e., those with the highest quality. Although Mehlman et al. (2005) discussed the importance of understanding a stopover site's function for the purpose of identifying the most important places to implement conservation actions, the framework can also be used to guide management actions at a given site, e.g., a protected area.

Fire escapes lie at one end of the continuum and are small, isolated sites embedded in inhospitable landscapes that present elevated risks to migrating birds, e.g., large bodies of water. They are used infrequently except in emergency conditions, when large numbers of birds are forced to interrupt flight to find refuge, e.g., when birds encounter unfavorable weather. Consequently, the number of birds at a fire escape is highly variable within and among years, but should be predictably higher on days when weather conditions are unfavorable for continued migration, e.g., strong headwinds, cross winds, or precipitation. Food resources may be insufficient for replenishing fat or muscle mass, so stopover durations for most birds are expected to be short (≤ 1 day), although higher quality fire escapes may offer some refueling opportunities (Kuenzi et al. 1991). Regardless of refueling potential, fire escapes are considered essential for migrants because of the large number of birds that use them in dire circumstances and should be protected, restored, or managed in a way that maximizes their ability to provide safe refuge to birds (Mehlman et al. 2005).

Convenience stores lie between fire escapes and full-service hotels. They are small habitat patches embedded in relatively inhospitable landscapes, e.g., urban parks, agricultural woodlots. Birds are expected to use these sites to rest for a short period (1–2 days) and sufficiently replenish energy reserves to complete short flights to sites that offer higher food availability and safer resting conditions, i.e., full-service hotels. Thus, birds' overall condition may improve slightly at convenience stores. Mehlman et al. (2005) recommended protecting, restoring, and/or managing convenience stores to meet birds' short-term needs while migrating though urban centers or large areas of intensive agriculture.

At the opposite end of the continuum from fire escapes are full-service hotels, characterized by large contiguous habitat, where birds can replenish fat and muscle and rest in preparation for their next migratory flight. Lean birds are expected to experience large improvements in body condition and stopover for a variable amount of time depending on factors like food availability. On the other hand, fat birds should depart quickly regardless of habitat quality. Mean daily capture rate at full-service hotels should be low as birds are more evenly distributed across homogeneous landscapes (in contrast with concentrated distributions in discrete habitat patches in heterogeneous landscapes; Buler and Dawson 2014), and they should have little variance in daily capture rate.

The stopover site framework for classifying sites was developed to inform conservation planning that seeks to identify the most important places to focus conservation investments (Mehlman et al. 2005). Collecting data on variables including seasonal and daily capture rates, body condition, and stopover duration that contribute to our understanding of a site's functional role are resource intensive. Consequently, these data are available for only a small fraction of the geographic range used by birds during migration, thereby limiting the use of the framework for strategic planning, although local experts are another source of information for understanding a site's specific function (Mehlman

et al. 2005). On the other hand, information on geographic location, size of a site, and landscape context are available across species' ranges with significantly less investment. Studies in other geographical regions, such as Europe (Ktitorov et al. 2008) have documented differences in function, specifically refueling, based on a stopover site's landscape context. If the functional role of a stopover site can be reliably determined based on its ecological context, then the framework can provide valuable guidance to conservation practitioners deciding where to allocate conservation efforts. Additionally, it can offer conservationists a powerful way to communicate the value of conserving and managing privately owned lands for migrating songbirds through its analogies between different functional types of stopover sites and easily understood terms.

Although some studies on the stopover ecology of migratory birds have interpreted their findings in the context of the stopover site conservation framework (Lain et al. 2017, Feldman et al. 2021), only Buler and Moore (2011) evaluated its applicability empirically, using radar data from temperate latitudes. In a subsequent study, Buler and Dawson (2014) recommended the consideration of additional sources of bird abundance to better understand site function. Studies empirically evaluating the framework at more sites, in different geographic regions, and using additional data sources, e.g., capture data and tracking data, are essential to documenting the framework's efficacy as a robust conservation tool. Furthermore, evidence shows that migratory bird species vary in their ability to negotiate the risks of geographic features, such as the Gulf of Mexico. Consequently, the relationship between geographic and landscape characteristics and the functional role of a stopover site may vary among species (Deppe et al. 2015, Zenzal et al. 2021). Before its widespread use, we need to understand the appropriate applications of the framework better. The application of this tool may be particularly valuable outside North America, where our understanding of the distribution, function, and quality of stopover sites is scarcer. Even though efforts are closing the gap (e.g., Winker 1995, Deppe and Rotenberry 2005, 2008, Bayly and Gomez 2011, Bayly et al. 2012, Gomez et al. 2014, 2017, Tonra et al. 2019), the protection and stewardship of necessary sites in this region appears to lag behind that of the United States and Canada (Cohen et al. 2017, Cárdenas-Ortiz et al. 2021).

In this study, we empirically evaluated the applicability of this conservation framework for inferring the function of two protected stopover sites in the northeastern Yucatan Peninsula in Mexico: Contoy Island National Park (hereafter "Contoy") and El Eden Ecological Reserve (hereafter "Eden"). Specifically, we assessed the hypothesis that geographic and landscape characteristics of a site can predict its function. Migratory landbirds encounter Contoy and Eden immediately or shortly after crossing the Gulf of Mexico during autumn migration (Deppe and Rotenberry 2005, Deppe et al. 2015). Contoy is a 230-ha island 15 km from the mainland, 33 km north-northeast of Cancun, Quintana Roo. Based on the definitions of the three categories in the framework, we hypothesized that this site functions as a fire escape. On the other hand, Eden is a 2000-ha forested reserve embedded in a largely forested landscape 40 km south of the Yucatan Peninsula's northern coast and 45 km west of Cancun that we expected to function as a full-service hotel. In addition, we explored whether the function of a stopover site varied among species. Neither the original framework nor subsequent studies considered species-level site use, but rather forest species collectively (Mehlman et al. 2005) or nocturnally migrating species based on radar (Buler and Moore 2011, Buler and Dawson 2014).

To test our hypothesis that geographic and landscape characteristics can predict the functional role of Contoy and Eden for migratory birds, we developed several predictions about patterns in daily capture rate (proxy for use of a site, Bolus et al. 2017), body condition upon arrival, stopover duration, and departure direction (Table 1). We used mist-netting and radio-tracking to collect data on the ecological, physiological, and behavioral characteristics of birds using the two sites. We explored variation among four focal migratory songbird species to provide additional insight into applications of the framework: Swainson's Thrush (*Catharus ustulatus*), Red-eyed Vireo (*Vireo olivaceus*), Gray Catbird (*Dumetella carolinensis*), and Prothonotary Warbler (*Protonotaria citrea*), which are known to vary in their migration ecology (Deppe and Rotenberry 2005, Deppe et al. 2015, Schofield et al. 2018, Zenzal et al. 2021). We further discuss the application of the classification framework for identifying the functional role of stopover sites, the relative quality of different sites, species-specific differences in terms of the relative value and function of sites, and further implications regarding use of the stopover classification framework to identify sites of conservation importance.

Table 1. List of predictions for Contoy Island National Park and El Eden Ecological Reserve in the northern Yucatan Peninsula, Mexico based on their role as a fire-escape and full-service hotel, respectively. The predictions were generated from the literature (Moore and Kerlinger 1987, Sandberg and Moore 1996, Schaub and Jenni 2001, Sandberg et al. 2002, Deutschander and Muheim 2009, Horton and Morris 2012).

	Contoy (fire escape)	El Eden (full-service hotel)
Daily capture rates (DCR)	Higher capture rate More variable capture rate Capture rate is higher under poor weather	Lower capture rate Less variable capture rate Capture rate does not fluctuate with weather
Mean body condition (fat score)	Leaner	Fatter
Mean stopover duration	Short stopovers	Long stopovers
Departure direction	Seasonally inappropriate	Seasonally appropriate

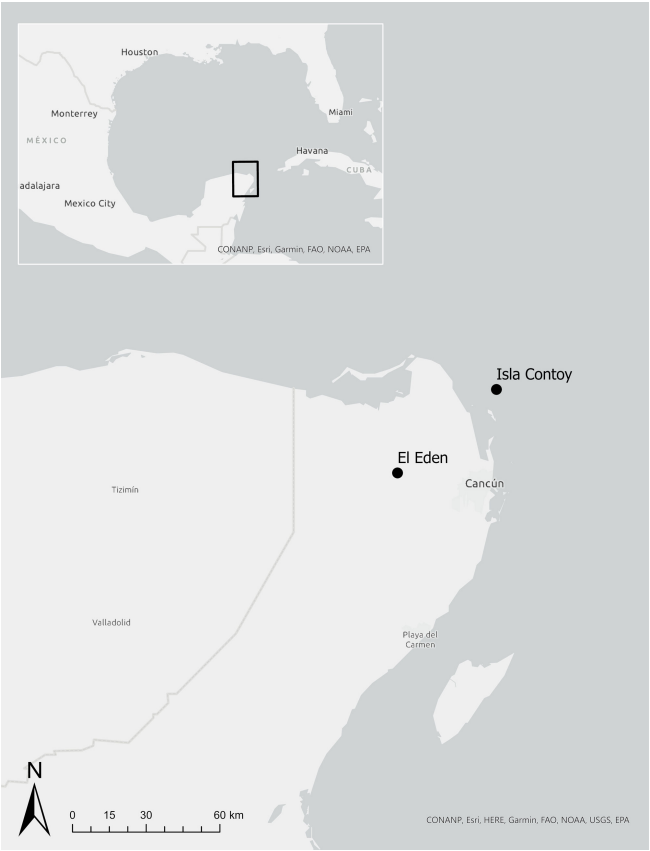
METHODS

Study sites

Contoy Island (21.4721° N, -86.7888° W; Fig. 1) is a national park managed by Mexico's National Commission of Natural Protected Areas. It is classified as an Important Bird and Biodiversity Area by BirdLife International and is designated as a Ramsar site. 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 assemblages), and a small, abandoned coconut plantation at the south end of the island. The mainland Eden site (21.2105° N, -87.1920° 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) at the University of Veracruz. Eden is dominated primarily by mature semi-deciduous tropical forest, secondary semi-deciduous forest, and seasonally inundated savannas.

Fig. 1. Study site locations in the northern Yucatan Peninsula: Contoy Island (Isla Contoy) National Park and El Eden Ecological Reserve in the state of Quintana Roo, Mexico.



Data collection

During fall migration in 2014 (1 September to 21 November) and 2015 (28 August to 10 November), we captured and banded migratory birds at Contoy and Eden. We operated 12 mist nets (12 m × 2.6 m, 30 mm mesh) daily at Eden in both years, and nets were equally distributed among the three dominant vegetation types. At Contoy, we operated 11 nets daily in 2014, with five of the nets in coastal dune and six in mangroves. In 2015, we operated 12 nets; six in each of the two vegetation types. Nets operated in both years were placed in the same locations. We opened nets 15 minutes before sunrise and operated them for approximately 4.5 hours, weather permitting. To account for variation in sampling effort, we standardized capture rates by net hour (one 12-m net operated for one hour = 1 net-hour).

Birds were banded with uniquely numbered metal bands (U.S. Geological Survey Bird Banding Lab), and we determined age and sex using criteria in Pyle (1997). We recorded visual fat reserves; the amount of subcutaneous fat visible in the furcular and abdominal region was scored on a scale of zero to five, with zero representing no visible traces of fat and five denoting fat filling the furcular area and covering the abdomen (Helms and Drury 1960).

This project was approved by the University of Illinois's Institutional Animal Care and Use Committee (IACUC 15154). Federal Banding Permits were granted by the U.S. Geological Survey's Bird Banding Lab (Permit No. 23577) and the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT).

Radiotelemetry

We attached radio-transmitters to four focal species: Swainson's Thrush (n = 27), Red-eyed Vireo (n = 38), Gray Catbird (n = 25), and Prothonotary Warbler (n = 17). These species were numerous at both study sites and vary in their migratory behavior and wintering locations (Cimprich et al. 2020, Mack and Yong 2020, Smith et al. 2020). After initial banding and processing, we attached analog pulse transmitters (JDJC Corporation or Lotek Wireless) to the backs of the birds using eyelash adhesive (Raim 1978, Smolinsky et al. 2013). Transmitters weighed 0.66–0.89 g. Most transmitters represented less than 5% of a bird's body weight and did not exceed 6% (range 2–5.8%). 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; see Schofield et al. 2018 for a detailed description) 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 Corporation). The ARUs continuously scanned pre-programmed frequencies and recorded signal strength, pulse width, pulse interval, and noise every two minutes. In 2014 both sites had one automated receiving system; in 2015 we added two additional ARTS to Contoy 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 and Zenzal et al. 2021 for a detailed description of the departure signal patterns). At the same time the ARU detected an increase in signal strength, we estimated the departure bearing based on the two adjacent antennas with the strongest signal strength (Ward and Raim 2011, Ward et al. 2018). Departure time was recorded as the date and hour when the departure signal reached its peak strength. We defined minimum stopover duration as the number of days a bird was at a site (departure date minus capture date), because the length of time an individual was present prior to capture was unknown. We considered birds departing our sites the night of capture to have made a stopover for one day.

Weather data

We obtained weather data from the National Oceanic and Atmospheric Administration's North American Regional Reanalysis (NARR) dataset with measurements acquired eight times per day via Movebank's Env-DATA service (Mesinger et al. 2006, Dodge et al. 2013). The Env-DATA service provides interpolated variables to the nearest time, location, and altitude using an inverse-distance weighted method. NARR has three-hour temporal resolution, 32-km horizontal resolution, and ~250-m vertical resolution. We included data for the following five weather variables as they have been found to influence departure and flight behavior in other studies (Åkesson and Hedenström 2000, Morganti et al. 2011, Deppe et al. 2015): 24-hour change in percent humidity (difference from the value exactly 24 hours prior; %), 24-hour change in barometric pressure (difference from the value exactly 24 hours prior; hPa), north-south winds (U-winds; m/s; positive winds toward the north), east-west crosswinds (W-winds; m/s; positive winds toward the east), and the average amount of precipitation over the Gulf. We assessed collinearity among these variables, and all had $|r| < 0.60$. We averaged these data for the previous 24 hours producing the average conditions migrants faced as they crossed the gulf. Previous research in this system suggested that on average an individual takes ~22 hours to cross the Gulf of Mexico (Deppe et al. 2015).

Statistical analysis

For our analyses of daily capture rate, we included initial captures of all landbird migrants. We calculated a daily capture rate (DCR) as the number of individuals captured per net hour per day. We used a generalized linear model (GLM) to compare mean DCR between the two sites. To evaluate the relationship between DCR and mean daily fat score, day of year, and weather, we performed separate GLMs for Contoy and Eden. We included day of year as a covariate to control for seasonal patterns in migration. We performed separate GLMs for Contoy and Eden to assess the different relationships among DCR, mean daily fat score, and weather variables that we predicted at each site. DCR was the response variable in our models, and we included all five weather variables, day of year, and mean daily fat score for all captured individuals as predictors.

To compare birds' body condition (i.e., fat scores at capture) between the two sites, we used a generalized linear model 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 as predictor variables. We only considered the four focal species in our comparison of fat scores between the two sites, because many migratory species had small sample sizes and some were captured only at one site. The interaction of site and species allowed species to vary in fat score by site. We included year as a covariate to account for differences between years.

We evaluated minimum stopover duration of radio-tagged birds of the four focal species using a negative binomial GLM with stopover duration in days as the response variable, and site, species, interaction of site and species, fat score, and year as predictor variables. The interaction of site and species allowed species to vary their stopover duration by site. We included year as a covariate to account for differences between years.

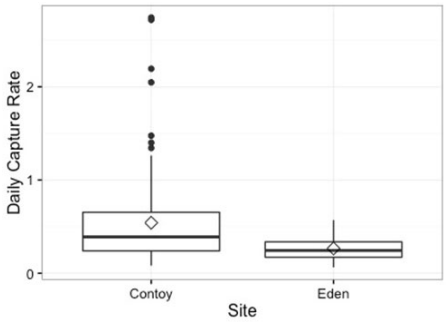
We categorized departure directions for radio-tagged birds of the four focal species as either inappropriate or appropriate, and the range of departure directions that we considered seasonally appropriate or inappropriate varied among species. For Red-eyed Vireos and Swainson's Thrushes, whose wintering locations are in South America, we considered departure directions between 120° to 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 GLM with a logit link. The predictor variables included site, species, interaction of site and species, fat, wind variables (east-west crosswinds and north-south winds), and year. All statistical analyses were run in R version 3.3.1 (R Core Development Team 2021). We used the *lme4* package (Bates et al. 2015) for the binomial models and *MASS* (Venables and Ripley 2002) for the negative binomial models.

RESULTS

Daily capture rate

A total of 2648 birds were captured in 6240.6 mist-net hours (4445.1 net hours in Contoy and 1795.5 net hours in Eden) across the two years. The mean DCR was twice as high at Contoy (0.54 ± 0.48 birds per net hour; mean ± SD) than at Eden (0.26 ± 0.13 birds per net hour; t = 5.72, df = 167, $p < 0.01$; Fig. 2). Additionally, variance in DCR was higher at Contoy (± 0.23) than Eden (± 0.02; F_1, 165 = 12.2, $p < 0.001$; Fig. 2). At Eden there was no relationship between DCR and change in humidity, change in barometric pressure, north-south winds, east-west crosswinds, surface precipitation, or day of year ($p > 0.23$). DCR was higher at Contoy on days with winds from the east (t = -2.68, $p \leq 0.01$) and out of the south (t = 2.28, $p = 0.03$). Day of year had a positive effect on DCR, i.e., as the season progressed (t = 4.16, $p < 0.01$), but there was no relationship with the other three weather variables (change in humidity, change in barometric pressure, surface temperature; $p > 0.20$) on Contoy. The mean daily fat score of captured birds at Eden and Contoy was not correlated with the weather variables ($p > 0.09$).

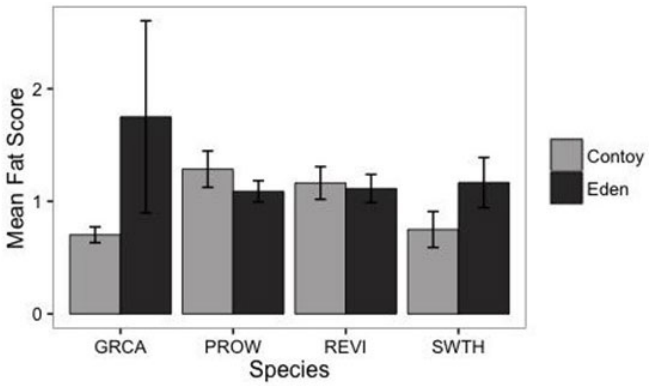
Fig. 2. Daily capture rates (DCR) of migrant species captured at two stopover sites located in the northern Yucatan Peninsula. DCR is the number of landbird migrants captured per net hour per day (one net hour = one 12-m mist net open for one hour). Data are from 2648 migrants captured in Contoy Island National Park, Mexico in 4445.1 net-hours and 483 migrants at El Eden Ecological Reserve, Mexico in 1795.5 net-hours. Within the box plot the bold horizontal line is the mean, the diamond symbol is the median, the vertical lines represent the upper and lower quartiles, and the dots are outliers.



Body condition

Birds at Eden had higher fat scores than birds at Contoy (1.12 and 0.85, respectively; $\chi^2 = 3.85$, df = 1, $p = 0.05$). The interaction of site and species was not significant ($\chi^2 = 7.34$, df = 3, $p = 0.06$), but the four focal species likely differed in their fat scores by site. Gray Catbirds and Swainson's Thrushes both carried more fat at Eden than Contoy, whereas Red-eyed Vireos had very similar fat scores between the sites, and Prothonotary Warblers had slightly higher fat scores at Contoy (Fig. 3). Year ($\chi^2 = 0.008$, df = 1, $p = 0.92$) and species ($\chi^2 = 2.05$, df = 3, $p = 0.56$) did not affect fat scores.

Fig. 3. Mean fat score for Gray Catbird (*Dumetella carolinensis*, GRCA, n = 172), Prothonotary Warbler (*Protonotaria citrea*, PROW, n = 125), Red-eyed Vireo (*Vireo olivaceus*, REVI, n = 96), and Swainson's Thrush (*Catharus ustulatus*, SWTH, n = 52) captured 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.



Stopover duration

We determined minimum stopover duration and departure behavior for 15 Gray Catbirds ($\bar{x} = 4.3$ days), 5 Prothonotary Warblers ($\bar{x} = 1.4$ days), 24 Red-eyed Vireos ($\bar{x} = 4.8$ days), and 19 Swainson's Thrushes ($\bar{x} = 3.8$ days); we were unable to calculate variables for all the individuals we radio tagged. Overall, stopover duration did not differ between sites ($\chi^2 = 0.08$, df = 1, $p = 0.79$); birds' stopover duration averaged 3.8 days at Contoy and 4.2 days at Eden. Mean stopover duration was also similar among species ($\chi^2 = 2.97$, df = 3, $p = 0.27$) and years ($\chi^2 = 0.0$, df = 1, $p = 0.30$). Fat influenced stopover duration ($\chi^2 = 7.64$, df = 1, $p = 0.03$), with fatter birds having shorter stopovers (Fig. 4). The interaction between site and species was not significant ($\chi^2 = 7.63$, df = 3, $p = 0.10$), although there was a tendency for Red-eyed Vireos to have longer stopovers at Eden whereas Gray Catbirds and Swainson's Thrushes stayed longer at Contoy (Fig. 5).

Departure direction

Site had no effect on departure direction ($\chi^2 = 0.00$, df = 1, $p = 0.97$), although departure direction differed by species ($\chi^2 = 7.91$, df = 3, $p = 0.04$) and year ($\chi^2 = 4.94$, df = 1, $p = 0.02$). There was no interaction between site and species ($\chi^2 = 3.07$, df = 3, $p = 0.38$), indicating that each species departed in a similar direction from both sites. A higher proportion of Red-eyed Vireos departed in a seasonally inappropriate direction, regardless of site, than the other three species (Fig. 6). 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 seasonally appropriate directions. A higher proportion of individuals departed from both sites in seasonally appropriate directions in 2015 (76%) than in 2014 (41%). Fat scores ($\chi^2 = 0.12$, df = 1, $p = 0.73$), north-south winds ($\chi^2 = 0.22$, df = 1, $p = 0.64$), and east-west crosswinds ($\chi^2 = 1.09$, df = 1, $p = 0.30$) did not influence departure direction.

Fig. 4. 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 in 2014 and 2015, and the data for all species were combined.

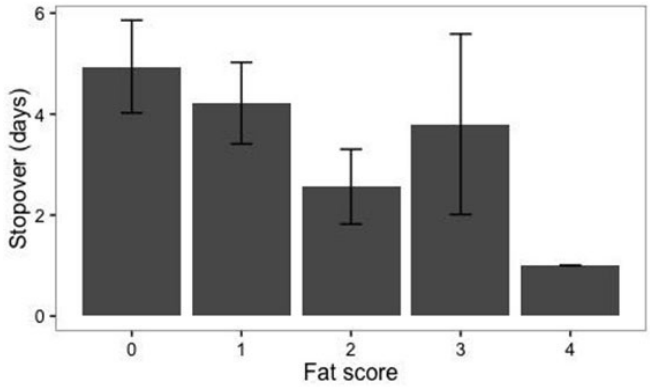


Fig. 5. Mean stopover lengths (in days) of Gray Catbird (*Dumetella carolinensis*, GRCA, n = 15), Prothonotary Warbler (*Protonotaria citrea*, PROW, n = 5), Red-eyed Vireo (*Vireo olivaceus*, REVI, n = 24), and Swainson's Thrush (*Catharus ustulatus*, SWTH, n = 19) at two stopover sites in the northern Yucatan Peninsula (Contoy Island National Park and El Eden Ecological Reserve) during 2014 and 2015 autumn migration.

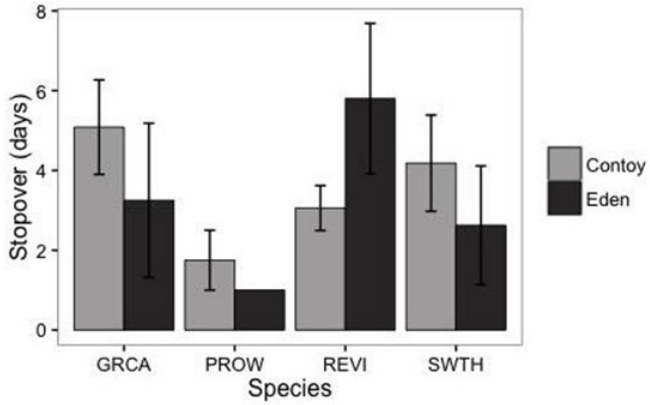
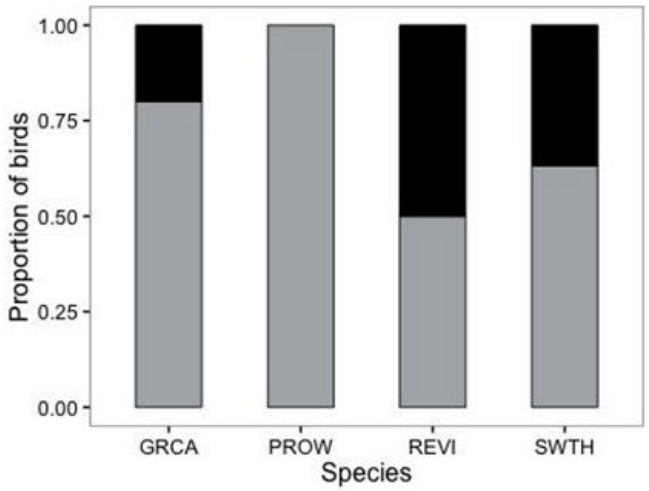


Fig. 6. Proportion of Gray Catbird (*Dumetella carolinensis*, GRCA), Prothonotary Warbler (*Protonotaria citrea*, PROW), Red-eyed Vireo (*Vireo olivaceus*, REVI), and Swainson's Thrush (*Catharus ustulatus*, SWTH) departing in seasonally appropriate (gray) and inappropriate (black) directions from two 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. Departure direction is illustrated for both sites combined, because it did not differ between them.



DISCUSSION

We found support for our hypothesis that geographic and landscape characteristics can predict the function of a stopover site (Table 2). As we predicted, Eden served as a full-service hotel: the mean and variance of DCR were low and it was not related to weather or fat, captured birds had a higher mean fat score, leaner birds had longer stopovers, and most departures were in a seasonally appropriate direction. Eden appears to be a refueling stopover site that migrants select rather than being forced to use because of inclement weather or poor body condition.

We predicted that Contoy functions as a fire escape, and patterns in DCR and body condition are consistent with this prediction. Mean and variance of DCR were higher at Contoy. In addition, weather (i.e., wind conditions) affected DCR at Contoy; DCR was higher on days when birds encountered crosswinds or headwinds over the Gulf of Mexico, indicating that Contoy functions as a place for birds to secure refuge in emergency situations. This relationship is well documented along the northern Gulf of Mexico coast in the spring and the southern coast in the fall (Able 1972, Deppe and Rotenberry 2005, Gauthreaux et al. 2006, Clipp et al. 2020). Furthermore, there was no relationship between DCR and mean daily fat score; both lean and fat birds stopped on Contoy during unfavorable weather, whereas on days following favorable weather over the Gulf of Mexico, most captured birds were lean. This result is consistent with findings along the northern Gulf of Mexico coast in the spring (Moore and Kerlinger 1987). On average across the season, birds stopping on Contoy were leaner than those using Eden.

Our predictions that stopover duration would be short on Contoy and most birds would depart the island in a seasonally inappropriate direction were not supported. On average, tagged birds stayed the same amount of time at Contoy and Eden. Fat was the primary predictor of stopover duration; at both sites, leaner birds stayed longer than fatter birds, a relationship documented in many studies (e.g., Moore and Kerlinger 1987, Goymann et al. 2010, Cohen et al. 2014). Most of the lean radio-tagged birds that stayed on the island for more than one day departed in a seasonally appropriate direction. Based on our findings, Contoy provides emergency refuge for large numbers of individuals in dire situations, the primary factor that sets fire escapes apart from convenience stores, although the island appears to be a high-quality fire escape, where birds can also refuel. Because of the complexities between stopover duration and body condition, stopover duration alone may not be a good metric for estimating the function or relative quality of a site (Van Loon et al. 2017) and needs to be considered in the context of additional variables.

Mehlman et al. (2005) developed the framework based on habitat rather than species, in part because of gaps in our understanding of species-specific stopover requirements. Driven by the urgency to identify the factors driving species population declines and the availability of new technology for tracking small songbirds, the bird conservation community is filling gaps in our understanding of the stopover ecology of species. These advances allow us to consider the applicability of the framework for individual species and design plans for their recovery. There was some evidence that the four species used Eden and Contoy differently. Red-eyed Vireos had similar fat levels at the two sites, and most individuals departed the sites in a seasonally inappropriate direction (e.g., west or north). Vireos that departed Eden and Contoy in a seasonally appropriate direction stayed multiple days (> 5 days), suggesting that they use both sites to refuel. Swainson's Thrushes, Gray Catbirds, and Prothonotary Warblers, on the other hand, tended to stay longer on the island, and most birds departed in a seasonally appropriate direction from both sites. Thrushes and catbirds captured on the island were leaner than at the mainland forest site, although warblers were fatter on the island. Overall, the migration ecology of vireos appears to differ from the other three species during autumn migration. The higher frequency of vireos departing in directions away from their winter destination relative to the other species is consistent with patterns observed for vireos in other regions. During autumn migration, Red-eyed Vireos were significantly more likely than Swainson's Thrushes and Wood Thrushes (*Hylocichla mustelina*) to depart coastal Alabama in a seasonally inappropriate direction, either retreating northward to inland bottomland hardwood forests or taking a detour around the western Gulf Coast, usually departing within a day of arrival (Deppe et al. 2015, Zenzal et al. 2021). Radio-tagged vireos had longer stopovers in bottomland hardwood forests, followed by southward departure across the Gulf (Zenzal et al. 2021). Buler and Moore (2011) considered the inland bottomland hardwood forests a full-service hotel based on radar data. Evidence from the northern Gulf of Mexico suggests vireos have more stringent intrinsic and extrinsic requirements for the next leg of their migration than larger species, such as thrushes and catbirds. Thus, vireos may make landscape level movements, consistent with movements away from stopover sites in inappropriate directions and departures during the day (rather than at sunset), to secure sufficient resources.

Table 2. Summary of support for predictions for Contoy Island National Park and El Eden Ecological Reserve in the northern Yucatan Peninsula, Mexico based on their role as a fire escape and full-service hotel, respectively. Predictions in bold were supported; the italicized predictions were supported in only some of the species; while predictions in normal font were not supported.

	Contoy (fire escape)	El Eden (full-service hotel)
Daily capture rates (DCR)	**Higher capture rate**	**Lower capture rate**
	More variable capture rate	**Less variable capture rate**
	Capture rate fluctuates with weather	**Capture rate does not fluctuate with weather**
Mean body condition (fat score)	**Leaner**	**Fatter**
Mean stopover duration	Short stopovers	**Long stopovers**
Departure direction	*Seasonally inappropriate*	***Seasonally appropriate***

The differences in stopover and departure behavior between vireos and the other three species in this study could be a result of their different foraging needs or the proportional fuel loads required by each species to complete its next migratory flight. Red-eyed Vireos consume less fruit and more insects during migration (Parrish 1997), and individuals 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. In Alabama, bottomland forests had higher insect availability than coastal areas, consistent with vireo's longer stopovers there. Higher insect abundances at Eden compared to Contoy might explain the differences in stopover duration of vireos between the sites, but this need to be tested. On the other hand, thrushes and catbirds may be able to make better use of resources, like fruit, that may be high on the island.

We investigated two sites that we predicted would be classified as a fire escape and full-service hotel; however, we did not investigate a site predicted to serve as a convenience store. In a separate study, Feldman et al. (2021) radio-tagged Red-eyed Vireos during autumn migration at Contoy (same sampling locations used in this study) and El Cuyo, Yucatan, located in the Ria Lagartos Biosphere Reserve along the northern coast of the Yucatan Peninsula. Based on its landscape and geographic features, Cuyo should function as a convenience store. The site is located on a long and narrow barrier beach dominated by coastal scrub and mangrove vegetation. It is bordered by the Gulf of Mexico to the north and an estuary to the south, with forested areas and savannas, similar to those found in Eden, approximately 4 km away. The area around El Cuyo is one of the few relatively undisturbed coastal areas in the Yucatan Peninsula, although development pressure is increasing (Deppe and Rotenberry 2008, Feldman et al. 2021). Feldman et al. (2021) found that Red-eyed Vireos had higher mass upon capture at Cuyo and, on average, longer stopover durations than on Contoy. In comparison to this study, the stopover durations of vireos at Cuyo were shorter than what we observed at Eden (full-service hotel), but longer than Contoy (fire escape). Additionally, Deppe and Rotenberry (2005) documented temporal variation in capture rates within and across years at Cuyo that was higher than we observed in this study in Eden and similar to Contoy. Although more research is needed, we suggest that the Mehlman framework can be employed in the Yucatan Peninsula and the site studied by Feldman et al. (2021) functions as a convenience store, at least for Red-eyed Vireo.

We found support for the hypothesis that landscape and geographic features of a site can predict its function; however, more research is needed to understand the broader applicability of the framework and provide more confidence to implement it in conservation decision making. We recommend additional studies across a broader geography and that consider non-forest species, including grassland birds. Additionally, studies have documented differences in migration patterns in coastal regions of the Gulf of Mexico between autumn and spring (Cohen et al. 2021), so future studies should consider variation in the function and quality of stopover sites between seasons. The accumulation of tracking data in repositories, such as Movebank and tracking networks, such as Birds Canada's Motus network offer a chance to assess the applicability of the framework across a broader geography and additional bird habitat groups using some of the metrics we considered here. Collaborative efforts that consolidate and integrate tracking with standardized capture data and radar-based estimates of bird density can provide opportunities to test the framework and develop strategic conservation plans for protecting and managing the network of stopover sites required by Nearctic-Neotropical migratory songbirds along their full migratory pathways. Although we used a relatively small number of metrics to validate predictions about the function of stopover sites, we encourage the use of additional measures, especially when the goal is to evaluate the quality of sites within a functional type or to inform management decisions of a given site, e.g., protected area. Physiological metrics, such as plasma metabolites (Guglielmo et al. 2002) may provide a more robust metric of the refueling rate of migrants at stopover sites. Behavioral observations and tracking data with high spatio-temporal resolution at stopover sites can provide information on foraging success, activity patterns (Schofield et al. 2018), resting/sleep (Linscott and Senner 2021), and predation risk (Cimprich et al. 2005) that contribute to our understanding of site function and/or quality for specific locations.

CONCLUSION

The Yucatan Peninsula represents one of the most important regions for migrating landbirds in the New World tropics (Bayly et al. 2018, Tonra et al. 2019). In our study system, fire escapes and convenience stores are essential for large numbers of individuals encountering unfavorable weather conditions during trans-gulf flights to find refuge and either maintain their condition or gain sufficient energy to continue their migration. Like much of the tropics, the Yucatan Peninsula continues to lose habitat (Céspedes-Flores and Moreno-Sanchez 2010), and the plight of migrants passing through the area will hinge on our ability to conserve and properly manage all three functional classes of stopover sites that can satisfy the diverse needs of different bird species during migration. Although stopover sites

used by a large number of individuals with low temporal variability in density may be considered no-regret conservation investments (Buler and Dawson (2014), stopover sites that are used irregularly by very high abundances of birds, characteristics of fire escapes, might yield higher returns on investment because of their ability to reduce mortality of large fractions of species' populations. The loss of habitat is not confined to large intact forests that serve as full-service hotels, but also increasing pressure from development along the coast and on nearby islands, which threaten the persistence of fire escapes and convenience stores. Although many protected areas exist in the Yucatan Peninsula, stewardship efforts to mitigate threats and provide habitat through conservation actions, like bird-friendly agriculture and bird-friendly cities (e.g., Raymundo Sanchez 2010, Partridge and Clark 2018), could improve the sustainability and quality of fire escapes and convenience stores in disturbed landscapes, ensuring that birds have a network of stopover sites that satisfy their diverse needs during migration.

Author Contributions:

L. E. S., J. L. D., A. C.-M., and M. P. W. conceived the idea, design, and experiment.
L. E. S. collected the data and conducted the research.
L. E. S., J. L. D., A. C.-M., and M. P. W. wrote the paper.
L. E. S., J. L. D., and A. C.-M. developed and designed the methods.
L. E. S., A. C.-M., and M. P. W. analyzed the data.
J. L. D. and M. P. W. contributed substantial materials, resources, or funding.

Acknowledgments:

We thank the following individuals for their assistance with field work: Janelle Chojnacki, Ivan Resendiz Cruz, Alba Mariana Martínez González, Yuri Ian Macías López, and Jonathan Nochebuena. We also thank Maria del Carmen Garcia for her support during our work in Isla Contoy National Park, Catalina Galindo for her logistical support, and the El Eden Ecological Reserve. We thank T. J. Zenzal and Ian Souza-Cole for comments on the manuscript. Funding was provided by National Science Foundation (NSF; IOS Awards 1146832, 1147096, and 1145952), Cooper Ornithological Society (Mewaldt-King Research Award), the University of Illinois - College of Agricultural, Consumer, and Environmental Sciences (ACES), Office of International Programs, and Eastern Illinois University (Research and Creativity Award). None of the funders had input into the content of the manuscript or required approval of the manuscript before submission. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U. S. Government.

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