INVESTIGATING LANDBIRD STOPOVER ECOLOGY AND DISTRIBUTIONS ALONG THE U.S. COAST OF THE GULF OF MEXICO

by

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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Ecology

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ABSTRACT

Every spring, billions of Nearctic-Neotropical landbird migrants travel from tropical wintering grounds in Mexico, the Caribbean, and Central and South America to temperate breeding grounds in the United States and Canada. In autumn, they reverse this journey, heading south to return to their wintering grounds. During both spring and autumn migration, individuals use stopover habitat to rest and feed between flights. Habitats along the Gulf of Mexico coast are particularly critical in providing resources, as they represent the first possible landfall in the spring after the long, nonstop flight across the Gulf and the last opportunity to refuel in autumn before crossing. However, no studies have investigated the roles that synoptic weather and winds encountered during migration play on where migrants stopover along the coast in a comprehensive manner. I used archived weather surveillance radar data to better understand the stopover ecology of landbird migrants along the U.S. coast of the Gulf of Mexico. First, I quantified the influence of broad-scale weather patterns (i.e., synoptic weather) over the Gulf of Mexico on spring stopover distributions of birds along the coast. Second, I assessed the influence of low-altitude winds aloft over the Gulf of Mexico, Atlantic Ocean, and Caribbean Sea on spring stopover patterns along the entire coast and regionally. Third, I determined whether local stopover site function and stopover duration varies from autumn to spring, using 19 sites in southern Mississippi and eastern Louisiana. Overall, I found that synoptic weather and winds encountered during migration were both important in determining where birds stopped over along the U.S. coast of the Gulf of Mexico. Synoptic weather had the strongest influence in explaining mean stopover density among predictors that included longitude, latitude, distance from the coast, and the amount of hardwood forest in the surrounding landscape. Unfavorable synoptic weather types involving conditions adverse to northward spring migration altered bird stopover distributions in terms of longitude and distance from the coast. For example, strong coastal concentrations of migrants were evident on the days following headwinds over the Gulf of Mexico. Low-altitude winds encountered during migration also influenced bird stopover density across the entire coast. In particular, strong winds from the east over the Caribbean Sea and Atlantic Ocean steered migrating birds to the northern Gulf of Mexico coast. In terms of stopover function, we found that coastal stopover sites functioned primarily as rest stops in both the autumn and spring. At more inland stopover sites, site function and migrant stopover duration both depended on seasonal food availability. In the spring, food availability was generally low, so most inland sites functioned as rest stops only; at sites with food, migrants stayed longer where food availability was higher. In autumn, food resources were greater than in spring, so most inland sites functioned as refuel sites, and birds were able to feed and leave more quickly from sites with higher amounts of available food. My results offer quantitative evidence that synoptic weather and winds aloft shape the broad-scale spatial distributions of migrants during stopover and that stopover site function varies by season. My research advances scientific understanding of the role that atmospheric conditions play in bird migration and how seasonal food availability can affect stopover site function and stopover duration; ultimately, this knowledge can be used to predict the effects of future climate change on migrating landbirds and guide conservation efforts.

Chapter 1

BROAD-SCALE SYNOPTIC WEATHER PATTERNS INFLUENCE SPRING STOPOVER DISTRIBUTIONS OF MIGRATING LANDBIRDS

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Written in the style of Ecography

1.1 Abstract

Weather patterns shape biogeographical distributions of migrating organisms at multiple scales. Long-distance bird migrants must contend with a variety of weather conditions during migration, particularly when flying across ecological barriers, yet we know relatively little about how broad-front weather patterns affect their survival, migratory routes, or stopover distributions on the ground. We used data collected by 10 weather surveillance radars during the peak of spring migration (March–May) over an 8-year period (2008–2015) to quantify the influence of synoptic weather on the densities and distributions of birds in stopover habitat. We expected daily broad-scale synoptic weather patterns to play an important role in determining stopover distributions of migrating birds after crossing the Gulf of Mexico in the spring. During the study period, migrating birds encountered eight synoptic weather types, five of which involved headwinds or frontal systems unfavorable for northward migration. After controlling for departure weather conditions, we found that the synoptic weather

birds encountered in flight over the Gulf of Mexico had more influence on mean bird stopover densities than geography or landscape composition. In particular, three of the five unfavorable synoptic weather types interacted with longitude and proximity to the coast in influencing migrant distributions. For example, migrants were concentrated in high densities in Texas and Louisiana and close to the coast on days following strong headwinds over the Gulf of Mexico. Our results offer quantitative evidence that weather conditions encountered in flight broadly affect the number and spatial distributions of birds that stopover along the northern Gulf of Mexico coast.

1.2 Introduction

Weather drives biogeographical distributions of organisms in space and time. At the broadest scale, climate (i.e., long-term average weather patterns) influences global and regional distributions of plant and animal species (Klomp 1963, Woodward 1987, Chen et al. 2011). At finer scales, severe weather events can impact local distributions of individuals and populations through movement or mortality (Parmesan et al. 2000). For example, strong storms can result in the death of migrating and roosting birds (Hall and Harvey 2007, Newton 2007, Diehl et al. 2014). Intermediate in scale to long-term climate and localized storms, synoptic weather patterns are characterized by general wind speed and direction, air pressure gradients, and frontal systems, and typically occur over a broad spatial extent for 1–2 days. Synoptic weather can affect the movement and distribution of migrating animals, from insects (Kisimoto 1976, Drake and Farrow 1988) to birds (Russell 2005) to ungulates (Kucera 1992). Yet an understanding of how animal migration is shaped by synoptic weather remains an information gap for most species and regions.

Aerial migrants that travel long distances may be particularly susceptible to the influence of synoptic weather. Accordingly, scientists have long studied the impact of weather on bird migration (e.g., Smith 1917, Lack 1960). Early accounts noted unusually early bird migration and the appearance of regionally rare birds in response to intense storms (Gunn and Crocker 1951), and reviews from past decades relate the timing and amount of bird migration to weather (e.g., Richardson 1978, 1990). Weather variation impacts the energetic cost of flight, the time budget of migrating birds, an individual's ability to maintain a preferred course, and the probability of en route mortality (Richardson 1978, Newton 2007, Shamoun-Baranes et al. 2017). Elements of weather also affect migration timing, route choices, and flight duration (La Sorte et al. 2015, Sjöberg et al. 2015). For instance, tailwinds affect flight speeds and travel distances of soaring migrants (Vansteelant et al. 2014), as well as increase the numbers of shorebirds migrating through the south Yellow Sea along the East Asian-Australasian Flyway (Ma et al. 2011). Bar-tailed godwits (*Limosa lapponica baueri*) in New Zealand also adjust their departure timing and migration schedules to maximize wind assistance (Conklin and Battley 2011).

Weather plays a well-defined role in influencing the behavior of nocturnally migrating landbirds (i.e., passerines and related species with terrestrial life histories) both in the air and on the ground at stopover sites, which comprise the habitat used between migratory flights to rest and refuel (Bulyuk and Tsvey 2006, Mateos and Arroyo 2011, Schmaljohann and Naef-Daenzer 2011, Bulyuk 2012). Winds affect the magnitude (Nisbet and Drury 1968, Able 1973, Erni et al. 2002, Wainwright et al. 2016) and speed of migration (Bloch and Bruderer 1982). Wind conditions further determine the advantages or disadvantages of compensation and drift (Alerstam 1979;

Horton et al. 2016). However, the role of weather in migration is likely best understood for departure from stopover habitats, in that birds are unlikely to continue migration when weather conditions are unfavorable (e.g., Akesson and Hedenstrom 2000, Schaub et al. 2004, Arizaga et al. 2011, Morganti et al. 2011, Deppe et al. 2015). Ultimately, the cumulative effects of individual responses to weather conditions shape migratory flyways and determine where migrating birds stop to rest and refuel (Alerstam 2001, Shamoun-Baranes et al. 2017).

However, very few studies have investigated the effects of synoptic-scale weather encountered during migration on if and where birds land after crossing an ecological barrier, such a desert or large body of water. Therefore, our objective was to answer the following questions that have yet to be addressed about the influence of weather on the terrestrial distributions of birds: 1) Does synoptic weather influence where birds stopover? 2) If so, what are the most influential synoptic weather types? 3) How long do birds remain at stopover sites in response to a synoptic weather event? 4) What combinations of lag time and synoptic weather type are most influential? We addressed these questions for nocturnal landbird migrants upon arrival across the Gulf of Mexico (GOM) en route from wintering grounds in the Caribbean and Central and South America to breeding grounds in the United States and Canada. The GOM is thought to serve as an ecological barrier (Buler and Moore 2011, Lafleur et al. 2016, Buler et al. 2017) and thus presents a unique opportunity to study weather impacts on bird migration, as migrants cannot easily evade or take shelter from weather they encounter during the nonstop 18–24-hour flight across the GOM.

Several qualitative or local-scale studies suggest that winds and weather over the GOM could influence the arrival and distributions of migratory birds along the northern GOM coast. Rappole and Ramos (1994) suggested that prevailing wind direction and the likelihood of encountering turbulence over the GOM may be the primary factors affecting migratory bird routes. Supporting this idea, Russell (2005) related large-scale synoptic weather patterns over the GOM to bird use of offshore oil and gas platforms and found that centers of offshore abundance and landfall location vary in concert with synoptic weather. For instance, on days when winds typically have a stronger easterly component over the GOM, migrants are most abundant on platforms in the far western GOM and landfall tends to be along the Texas coast, suggesting that trans-GOM migration is at least partially “steered” by synoptic-scale winds. In addition, Yaukey and Powell (2008) found numbers of some migratory bird species are higher in New Orleans, Louisiana, when a cold front is about to approach the Louisiana coast or has already passed, compared to when airflow is off the GOM or from the east. More recently, Lafleur et al. (2016) found longitudinal patterns in migrant distributions along the northern GOM coast differ between years, potentially due to variability in annual wind patterns over the GOM. Therefore, we hypothesized synoptic-scale weather patterns would interact with longitude and distance from the coast to influence stopover densities and distributions. Favorable synoptic weather conditions (e.g., tailwinds) are likely to minimize energetic costs of flight and maximize speed and, therefore, we expected birds to continue migration further inland and fewer birds to stop along the coast of the GOM under these conditions. Conversely, we expected weather types with strong headwinds or a cold front over the GOM (i.e., unfavorable conditions) to increase overall stopover density, particularly along the immediate coast and at longitudes corresponding to the locations of headwinds or fronts, because after encountering adverse flight conditions, migrants are likely to land to rest and refuel in the first available habitat (Pennycuick 1989, Russell 2005, Yaukey and Powell 2008). Here, we took a region-wide and long-term approach, incorporating the entire U.S. coast of the GOM and 8 years of data, to investigate the relationships between migratory bird stopover distributions and synoptic weather patterns during spring migration.

1.3 Material and Methods

1.3.1 Using weather surveillance radar to quantify bird stopover density

Weather surveillance radars can be used to detect birds in the airspace at the onset of nocturnal migratory flight departing from stopover sites (e.g., Buler and Diehl 2009, Buler and Moore 2011, Buler and Dawson 2014, Lafleur et al. 2016). Radar reflectivity is positively correlated with the number of birds aloft, providing an estimate of relative bird density across a landscape (Gauthreaux and Belser 1999, Diehl et al. 2003). The magnitude of radar reflectivity is calculated at the moment of mass departure, when the position of birds in the airspace is closely associated with their position on the ground; thus, radars allow for a spatially explicit assessment of the relative use of stopover sites across large geographic areas (Buler and Dawson 2014).

We calculated bird stopover density during the peak of spring migration (1 March to 31 May) during 2008–2015, using archived Level II radar data from the National Oceanic and Atmospheric Administration National Centers for Environmental Information from across approximately one-third of the U.S. coast of the GOM, comprising the area within 100-km of ten WSR-88D radar stations (Fig. 1.1). Radars collected reflectivity and radial velocity values in 5–10 min intervals and

360° sweeps of the beam at multiple elevation angles. Individual sample volumes within each sweep were 250 m in range and 0.5° in width. We used these data to measure the relative density of birds departing from stopover habitat.

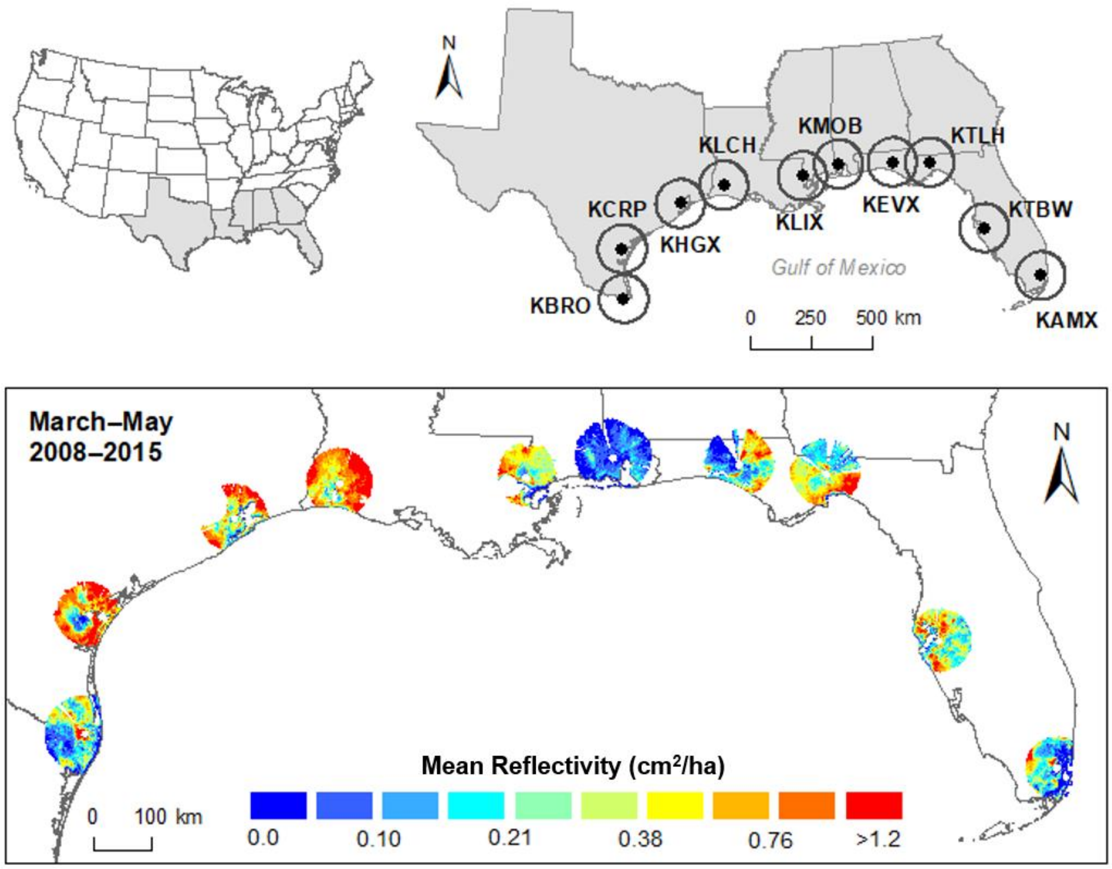


Figure 1.1: The locations and coverage of the 10 WSR-88D Doppler radars (circles represent a 100-km radius sampling area) along the northern Gulf of Mexico coast, as well as the mean stopover density measured as mean vertically-integrated reflectivity for the entire study period (March–May 2008–2015). From west to east, the radar stations are: KBRO near Brownsville, TX (25.916111 N, 97.418889 W); KCRP near Corpus Christi, TX (27.784167 N, 97.511111 W); KHGX near Houston, TX (29.471944 N, 95.079167W); KLCH near Lake Charles, LA (30.125278 N, 93.215833 W); KLIX near Slidell, LA (30.336667 N, 89.825556 W); KMOB near Mobile, AL (30.679444 N, 88.239722 W); KEVX near Pensacola, FL (30.564444 N, 85.921389 W); KTLH near Tallahassee, FL (30.397500 N, 84.328889 W); KTBW near Tampa, FL (27.705556 N, 82.401667 W); and KAMX near Miami, FL (25.611111 N, 80.412778 W).

We eliminated data collected by the radars when various sources of contamination restricted our ability to measure reflectivity from migratory birds. Following Buler and Dawson (2014), we visually screened sweeps from each night and removed nights from analysis if they contained precipitation, anomalous propagation (i.e., extreme refraction of the radar beam toward the ground), or clutter (e.g., sea breeze fronts, smoke). We used the speeds of the animals in the airspace to further eliminate nights with biological reflectivity dominated by organisms other than birds. Specifically, we combined radial velocity and North American Regional Reanalysis wind measurements (Mesinger et al. 2006, Buler and Diehl 2009, Ruth et al. 2012, Buler and Dawson 2014) and discarded nights with mean animal airspeeds of less than 5 m/s because we considered them dominated by insects (Larkin 1991, Cabrera-Cruz et al. 2013).

We calculated reflectivity within each radar sample volume at the time of daily peak departure from stopover sites for each uncontaminated, bird-dominated night (McLaren et al. 2018). We corrected for sources of measurement bias to calculate the total amount of reflectivity within a vertical column of airspace, vertically-integrated reflectivity (VIR; see Buler and Dawson 2014). The VIR was converted to units of cm^2 per hectare (Chilson et al. 2012) and served as an index of bird density. To georeference and display the radar data, we constructed polar coordinate grids with 285,120 polygons representing the two-dimensional boundaries of sample volumes within each radar domain. Within each grid, we identified individual sample volumes to be excluded from data analysis where the radar beam was partially or fully blocked by topographical features or nearby structures, the sample volume was located over open water, or there was contamination from persistent ground clutter (Buler and

Dawson 2014). Because of well-known free-tailed bat (*Tadarida brasiliensis*) roosts that showed up consistently in the region northwest of the KHGX radar, we also excluded the area around those bat roosts from analysis.

1.3.2 Classifying synoptic weather types

We used a classification scheme with eight defined synoptic-scale weather types (Fig. 1.2), adapted from Russell (2005), Muller (1977), Muller and Wax (1977), and Yocke et al. (2000), that were likely to have different impacts on migrating birds. Based on wind direction (headwinds vs. tailwinds) and frontal activity, we considered the following five synoptic weather types to be consistently unfavorable for northbound birds during spring migration: 1) Western Gulf Fronts involve a cold front oriented north-south or northeast-southeast over the western portion of the GOM or GOM coast; 2) Central Gulf Fronts involve a cold front oriented north-south in the middle of the GOM or oriented northeast-southwest across most of the GOM; 3) Eastern Gulf Fronts involve a cold front oriented north-south over the eastern portion of the GOM or GOM coast; 4) East Coast Lows involve a low-pressure system that has moved east of the Mississippi River and a cold front that has swept over the GOM and into the Atlantic Ocean; and 5) Midwest Continental Highs involve a high-pressure system centered between the Mississippi River and Rocky Mountains, so winds over the northern GOM are dominated by anticyclonic flow and surface winds flow from the northeast. During Western, Central, and Eastern Gulf Fronts, winds behind the cold front are mainly blowing from the north, while those preceding the front are blowing from the south and support northward migration. Thus, the location of the cold front determines how migrating birds are affected across the coast. During

East Coast Lows and Midwest Continental Highs, winds are consistently unfavorable, particularly along the western GOM coast.

We considered the following three synoptic weather types to be favorable for northward migration: 6) Eastern Continental Highs involve a high-pressure system located between the Mississippi River and the Atlantic Coast, so surface winds in eastern areas may be from the east, while those in western areas may be from the south; 7) Bermuda Highs involve a high-pressure system centered over the Atlantic Ocean, with surface winds over the northern GOM blowing from the south or southeast; and 8) Gulf Highs involve high pressure centered over the GOM or immediate GOM coast and are usually associated with a weak pressure gradient and slow to nonexistent winds. All three favorable synoptic weather types are particularly supportive of northward migration along the western GOM coast. A subset of days did not fit into one of the eight categories, so a ninth "Other" category was included to comprise those complex weather situations.

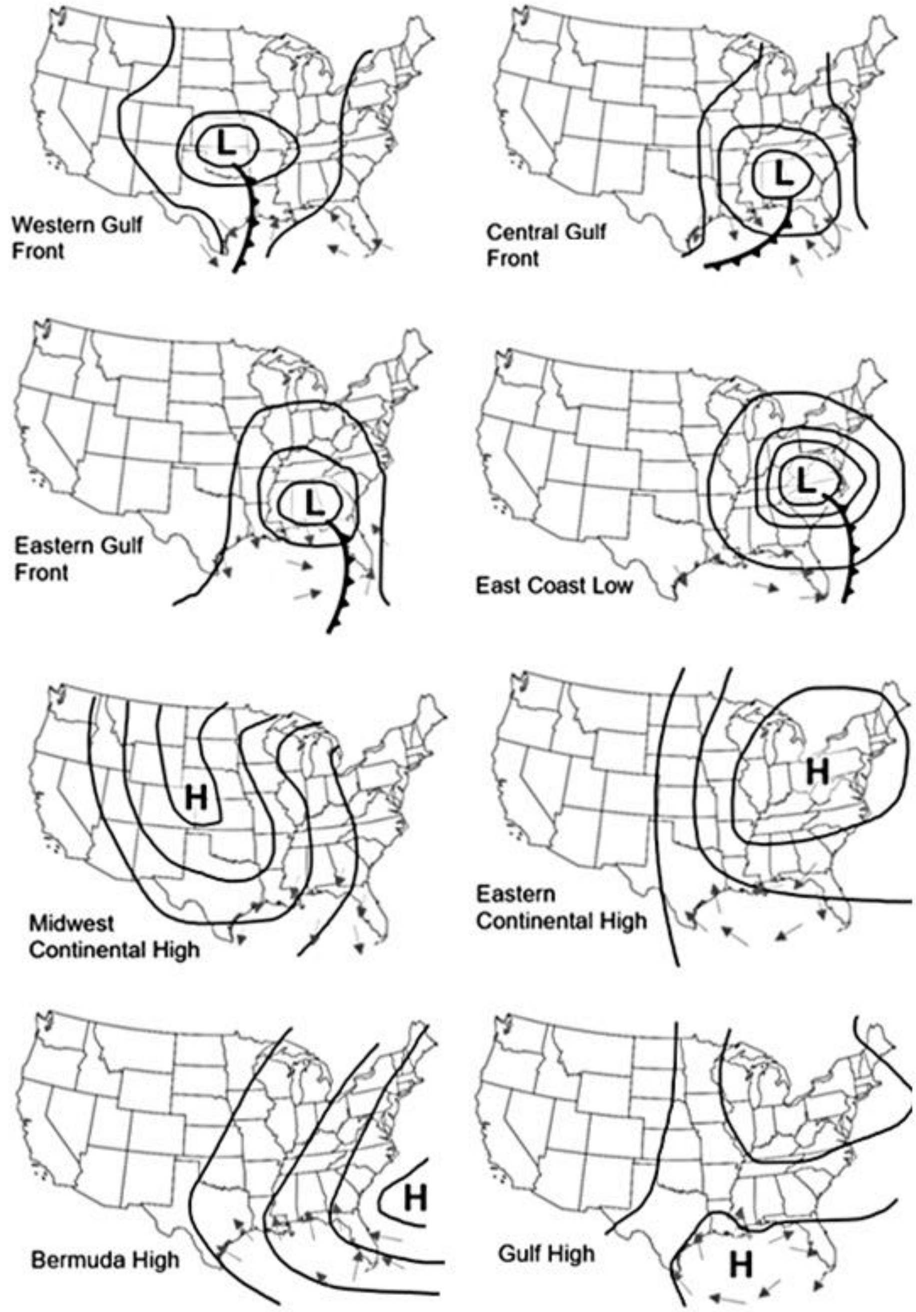

Western Gulf Front
Central Gulf Front
Eastern Gulf Front
East Coast Low
Midwest Continental High
Eastern Continental High
Bermuda High
Gulf High

Figure 1.2: Generalized diagrams of the eight defined synoptic weather types considered in this study, with labeled pressure systems ("L" = low pressure, "H" = high pressure), pressure isobars (black lines), frontal system boundaries (lines with black triangles denoting direction of movement), and general wind direction over the coast and Gulf of Mexico (indicated by the arrows).

We assigned a synoptic weather type to each of the four days preceding a sampling day, as well as the day of departure, using daily weather maps from 5:05 UTC archived by Unisys (Russell 2005); categorization was based on surface pressure contours, configurations of major high- and low-pressure systems, and wind flow patterns. For each of the 36 combinations between lag time (i.e., day after synoptic weather occurrence) and synoptic weather type, we calculated the geometric mean VIR for every sample volume of the 10 radars.

1.3.3 Determining relative influence of weather

We aggregated the overall geometric mean VIR values to a 1-km x 1-km grid that encompassed the area surrounding the 10 radars. For each grid cell, we calculated the area-weighted-mean VIR across all sample volumes within each cell. We modeled the influence of weather on mean VIR using boosted regression tree models with the package "dismo" in R (De'Ath 2007). Boosted regression trees combine statistical and machine-learning methods. They are useful for this type of analysis because they can fit complex nonlinear relationships and handle interaction effects between predictors (Elith et al. 2008). We fitted four models (Table 1.1) to determine: 1) whether synoptic weather influences where birds stopover; 2) the most influential synoptic weather types, 3) how long birds remain at stopover sites after a synoptic weather event; and 4) the most influential combinations of lag time and synoptic weather type.

Table 1.1: Description of boosted regression tree models used to understand the influence of synoptic weather on stopover density along the northern Gulf of Mexico coast.

Model	Question	Predictor Weather Variable	Levels of Predictor Weather Variables
1	Does synoptic weather influence where birds stopover?	Synoptic weather overall (1 total)	Every combination of lag time and synoptic weather type (36 total)
2	What are the most influential synoptic weather types?	Synoptic weather types (9 total)	Days after synoptic weather occurrence (4 total)
3	How long do birds remain at stopover sites in response to a synoptic weather event?	Days after synoptic weather occurrence (4 total)	Synoptic weather types (9 total)
4	What combinations of lag time and synoptic weather type are most influential?	Every combination of lag time and synoptic weather type (36 total)	Treated as dummy variables (1 or 0)

The objective of the first model was to determine the overall influence of synoptic weather, encompassing all combinations of lag time and synoptic weather type. The eight predictor variables included synoptic weather encountered during migration over the GOM, longitude, latitude, distance from the GOM coast (km), the proportion of hardwood forest within a 5-km radius (calculated using land cover data from the 2011 National Land Cover Database), relative elevation (m; ground height above sea level minus the radar antenna height above sea level), distance to the radar (m), and departure weather (i.e., synoptic weather type occurring during departure). Longitude, proximity to the coast, and amount of hardwood forest cover in the landscape were included because previous work found support for their influence on stopover density (Lafleur et al. 2016). Relative elevation and distance to the radar accounted for residual range bias in the radar data. Stopover distributions were calculated based on departure from stopover sites, so we added departure weather as a variable to control for variation in VIR due to atmospheric conditions affecting departure decisions (Arizaga et al. 2011, Andueza et al. 2013, Covino et al. 2015). Specifically, the number of migrants detected during departure could depend on wind and weather conditions at that time, such as local barometric pressure, precipitation, cloud cover, or wind speed (Dänhardt and Lindström 2001, Schaub et al. 2004, Sjöberg et al. 2015). None of the numeric predictor variables were strongly correlated ($r < 0.51$).

The second model determined the influence among synoptic weather types across days. Each synoptic weather type was included as a separate variable, with the number of days after their occurrence as the factor levels, resulting in 13 predictors. The third model assessed the relative influence among days after synoptic weather occurrence across synoptic weather types. Each day was included as a separate variable, with the synoptic weather types as the factor levels, resulting in 10 predictors. The final model distinguished which combinations of lag time and synoptic weather type were most influential and contained 43 predictors, with each combination of lag time and synoptic weather type treated as a dummy variable (i.e., a value of 1 or 0 denoting whether that combination corresponded to the inputted VIR values or not, respectively).

For each model, we used a tree complexity (i.e., the number of nodes in individual trees) of 2, learning rate of 0.75, bag fraction (i.e., the proportion of data used to train the models) of 0.5, a minimum of 1,000 trees, and a Gaussian error distribution (Elith at al. 2008). We used the “gbm.step” function within the “dismo” package, which assessed the optimal number of boosting trees using k-fold cross validation; the function calculated the average holdout residual deviance and identified the optimal number of trees at which the holdout deviance was minimized. Furthermore, to reduce spatial autocorrelation, we used a subset of grid cells that were separated by 5 km (Buler and Dawson 2014), resulting in a total subset of the same 150,696 observations for each model.

1.4 Results

1.4.1 Frequency of the synoptic weather types

Of the 736 calendar nights considered during the 2008–2015 study period, we classified 516 as uncontaminated and bird-dominated for at least one radar per night. We used an average of 15.5% of the calendar nights for each radar in each year for analysis. We assigned synoptic weather types to 711 days across the 8 years.

The frequency of the synoptic weather types varied by year (Table 1.2). Gulf and Bermuda Highs were most common, followed by Central Gulf Fronts and Eastern Continental Highs. The least common synoptic weather types were Eastern Gulf Fronts, East Coast Lows, and Midwest Continental Highs. Weather patterns during ~10% of the nights did not fit one of the eight defined synoptic weather patterns and were categorized as “Other”. Most of the synoptic weather types occurred throughout the spring, but Midwest Continental Highs did not occur in May.

Table 1.2: Annual and total frequency (and percentage of the total) of the unfavorable (Western Gulf Front, Central Gulf Front, Eastern Gulf Front, East Coast Low, Midwest Continental High) and favorable (East Continental High, Bermuda High, Gulf High) synoptic weather types within our study period (March to May 2008–2015).

Synoptic Weather Type	Year								
	2008	2009	2010	2011	2012	2013	2014	2015	Total
Western Gulf Front	8 (9)	6 (7)	3 (4)	10 (11)	7 (8)	8 (9)	10 (11)	8 (9)	60 (8)
Central Gulf Front	10 (11)	9 (11)	6 (8)	11 (12)	11 (13)	10 (11)	11 (12)	22 (24)	90 (13)
Eastern Gulf Front	4 (4)	3 (4)	3 (4)	4 (4)	4 (5)	6 (7)	8 (9)	3 (3)	35 (5)
East Coast Low	1 (1)	4 (5)	5 (6)	7 (7)	1 (1)	2 (2)	4 (4)	0 (0)	24 (3)
Midwest Continental High	5 (5)	0 (0)	4 (5)	0 (0)	1 (1)	7 (8)	2 (2)	1 (1)	20 (3)
Eastern Continental High	21 (23)	16 (19)	11 (14)	12 (13)	11 (13)	8 (9)	2 (2)	5 (5)	86 (12)
Bermuda High	16 (17)	14 (17)	15 (19)	13 (14)	9 (10)	19 (21)	21 (23)	25 (27)	132 (19)
Gulf High	8 (9)	15 (18)	26 (33)	33 (35)	37 (43)	26 (29)	27 (29)	18 (20)	190 (27)
Other	20 (22)	16 (19)	7 (9)	4 (4)	6 (7)	3 (3)	8 (9)	10 (11)	74 (10)

1.4.2 Does synoptic weather influence where birds stopover?

Although stopover densities were consistently influenced by geographic and landscape variables across models (Fig. A.1.1–A.1.4), we found that synoptic weather encountered during migration over the Gulf of Mexico had the highest relative influence, nearly 2.6 times that of the next most influential variable, longitude (Table 1.3). Among the synoptic weather types, relationships with mean VIR varied (Fig. A.2.1). The highest mean VIR along the GOM coast occurred on days following unfavorable synoptic weather types. In contrast, favorable synoptic weather types were generally associated with lower than average VIR across the study region. Synoptic weather interacted most strongly with longitude, followed by distance from the coast (Table A.2.1). Mean VIR deviated from average longitudinal patterns on days following unfavorable synoptic weather types (Fig. A.2.2); similarly, those same days were associated with distributions that differed from the standard interaction with distance from the coast (Fig. A.2.3). On days following favorable synoptic weather patterns, mean VIR was similar to average in terms of both longitude and distance from the coast.

Table 1.3: Relative influence of synoptic weather encountered during migration over the Gulf of Mexico (GOM), geography (longitude, latitude, distance from the GOM coast), landscape (proportion of hardwood forest within 5 km), and departure weather from the four boosted regression tree models. Synoptic weather variables are italicized.

Model	Predictor Variable	% Influence
Model 1[a]: Does synoptic weather influence where birds stopover?	*Synoptic weather over GOM*	*38.2*
	Longitude	14.7
	Latitude	9.5
	Proportion of hardwood forest within 5 km	6.6
	Distance from the GOM coast	5.1
	Departure weather	0.7
Model 2[b]: What are the most influential synoptic weather types?	Longitude	22.2
	Latitude	12.5
	Proportion of hardwood forest within 5 km	8.7
	Midwest Continental High	*7.5*
	Distance from the GOM coast	7.1

	East Coast Low	*7.0*
	Western Gulf Front	*2.3*
	Departure weather	1.5
	All other synoptic weather types	*<1.0 each*
Model 3[c]: How long do birds remain at stopover sites in response to a synoptic weather event?	Longitude	19.7
	Latitude	12.0
	1 day after synoptic weather occurrence	*10.3*
	Proportion of hardwood forest within 5 km	8.1
	Distance from the GOM coast	7.1
	4 days after synoptic weather occurrence	*6.3*
	3 days after synoptic weather occurrence	*3.4*
	2 days after synoptic weather occurrence	*2.6*
	Departure weather	1.6
Model 4[d]: What combinations of lag time and synoptic weather type are most influential?	Longitude	19.7
	Latitude	12.1
	Distance from the GOM coast	10.2
	Proportion of hardwood forest within 5 km	9.3
	4 days after East Coast Low	*4.5*
	1 day after Midwest Continental High	*2.5*
	1 day after Western Gulf Front	*2.4*
	3 days after Midwest Continental High	*1.9*
	1 day after East Coast Low	*1.6*
	Departure weather	1.6
	All other combinations of lag time and synoptic weather type	*<1.0 each*

[a] Percent deviance explained: 61.9; CV correlation: 0.717; No. trees: 7100
[b] Percent deviance explained: 65.2; CV correlation: 0.733; No. trees: 5900
[c] Percent deviance explained: 66.0; CV correlation: 0.735; No. trees: 7300
[d] Percent deviance explained: 65.2; CV correlation: 0.734; No. trees: 7000

1.4.3 What are the most influential synoptic weather types?

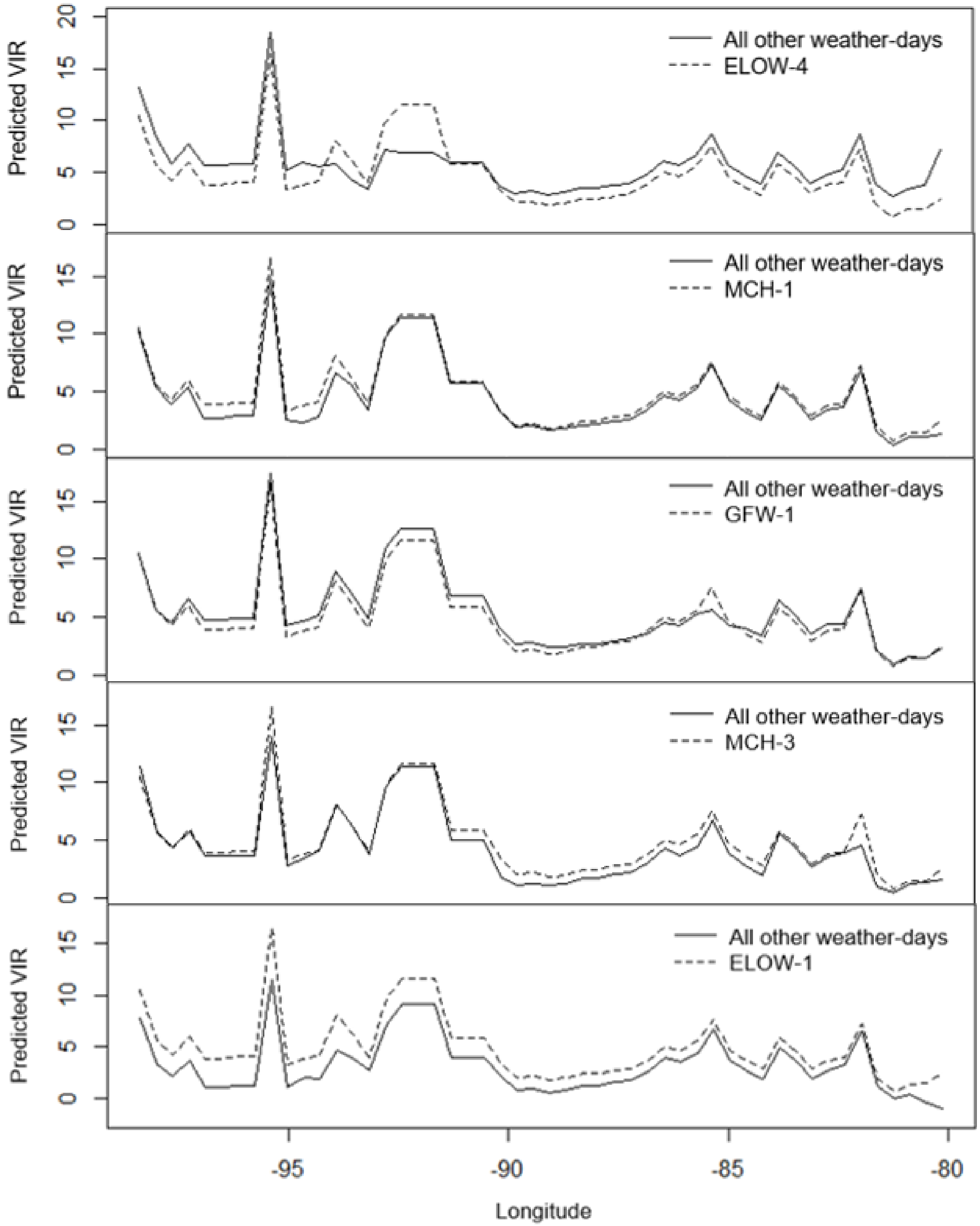
The second model allowed us to identify the most influential synoptic weather types, while controlling for departure weather conditions and the geographic and landscape variables. Comparing among the eight synoptic weather types, three with unfavorable conditions (Midwest Continental High, East Coast Low, Western Gulf Front) had the strongest relative influence (Table 1.3). The rest of the synoptic weather types had very little relative influence. Midwest Continental Highs, East Coast Lows, and Western Gulf Fronts all featured headwinds over the western GOM. Midwest Continental Highs interacted very strongly with longitude; among the four days, mean VIR was generally low across the GOM coast the following day, relatively high in Texas and Louisiana and low in Florida two days later, relatively high in Louisiana three days later, and relatively low in Texas four days later (Fig. A.3.1). East Coast Lows had the strongest interaction with longitude. The fourth day after an East Coast Low showed the lowest VIR west of -95º W and east of -90º W, but the highest VIR at -92º W (Louisiana); apart from Louisiana, the highest VIR across the GOM coast occurred the day after an East Coast Low (Fig. A.3.2). East Coast Lows also had strong interactions with the proportion of hardwood forest and distance from the coast (Fig. A.3.3). Among the other predictor variables, Western Gulf Fronts interacted most strongly with longitude. The day after a Western Gulf Front generally showed the lowest VIR, particularly west of -88º W (Fig. A.3.4). Overall, most of the eight synoptic weather types had the strongest interaction with longitude, followed by distance from the coast.

1.4.4 How long do birds remain at stopover sites in response to a synoptic weather event?

Synoptic weather had the highest influence on mean VIR the following day (Table 1.3). Of the remaining days, synoptic weather had more influence four days later than two or three days later. Synoptic weather interacted most strongly with longitude, followed by distance from the coast, in predicting mean VIR after unfavorable synoptic weather occurred. Higher than average VIR occurred along the western GOM coast the day after an East Coast Low (Louisiana and Texas) (Fig. A.4.1), while higher VIR closer to the coast and low VIR far from the coast occurred the days after a Midwest Continental High and Western Gulf Front (Fig. A.4.2). Four days after an East Coast Low, VIR was lower than average in Texas and Florida, but elevated in Louisiana (Fig. A.4.3).

1.4.5 What combinations of lag time and synoptic weather type are most influential?

Of the 36 combinations of lag time and synoptic weather type, we identified the five with the most influence, all associated with unfavorable conditions. An East Coast Low continued to influence mean VIR one and four days later, a Midwest Continental High continued to influence mean VIR one and three days later, and a Western Gulf Front influenced mean VIR the following day. The rest of the combinations of lag time and synoptic weather type had weak influence (<1.0%) on mean VIR. Of the five combinations of lag time and synoptic weather type with the greatest relative influence, most had the strongest interactions with longitude, followed by distance from the coast. Four days after an East Coast Low, VIR was lower than average west of -95º W and east of -90º W, higher than average at -92º W, and elevated beyond 80 km from the coast; in addition, coastal concentrations within 50 km of the coast were less pronounced (Fig. 1.3, 1.4). Correspondingly, our map showed mean VIR was higher than average (Fig 1.1) in the Lake Charles radar and lower than average in the Corpus Christi, Houston, Tampa, and Miami radars (Fig. 1.5). The day after an East Coast Low, VIR was higher than average along the entire GOM coast and across all distances (within 100 km) of the coast. The day after a Midwest Continental High, VIR was higher than average west of 93º W and within 20 km of the coast, but lower than average in the Corpus Christi, Lake Charles, Slidell, Mobile, Tallahassee, and Miami radars. Three days after a Midwest Continental High, VIR was higher than average east of -91º W and within 80 km of the coast. The day after a Western Gulf Front, VIR was generally lower than average across the coast except for near -85º W and lower than average beyond 15 km from the coast. The map revealed higher than average VIR values in the Pensacola radar, but generally similar or lower than average VIR in the rest of the radars.



Predicted VIR
All other weather-days
ELOW-4
All other weather-days
MCH-1
All other weather-days
GFW-1
All other weather-days
MCH-3
All other weather-days
ELOW-1
Longitude

Figure 1.3: Plots of the interactions between longitude and the five most influential combinations of lag time and synoptic weather type (weather-days) from the boosted regression tree model predicting mean vertically-integrated reflectivity, including four days after an East Coast Low (ELOW-4), the day after a Midwest Continental High (MCH-1), the day after a Western Gulf Front (GFW-1), three days after a Midwest Continental High (MCH-3), and the day after an East Coast Low (ELOW-1). The solid line represents the combined response of all the other combinations of lag time and synoptic weather type pooled.

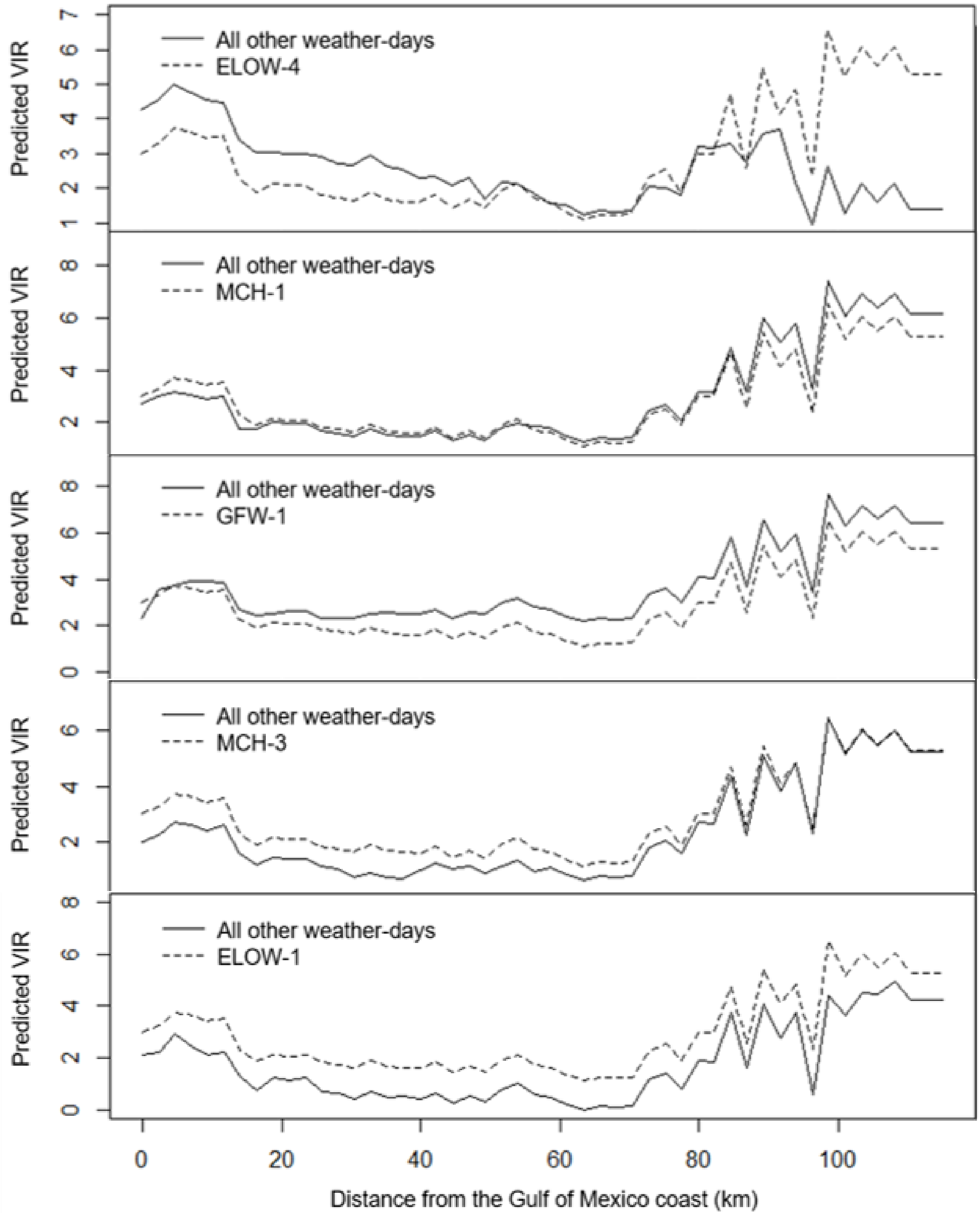
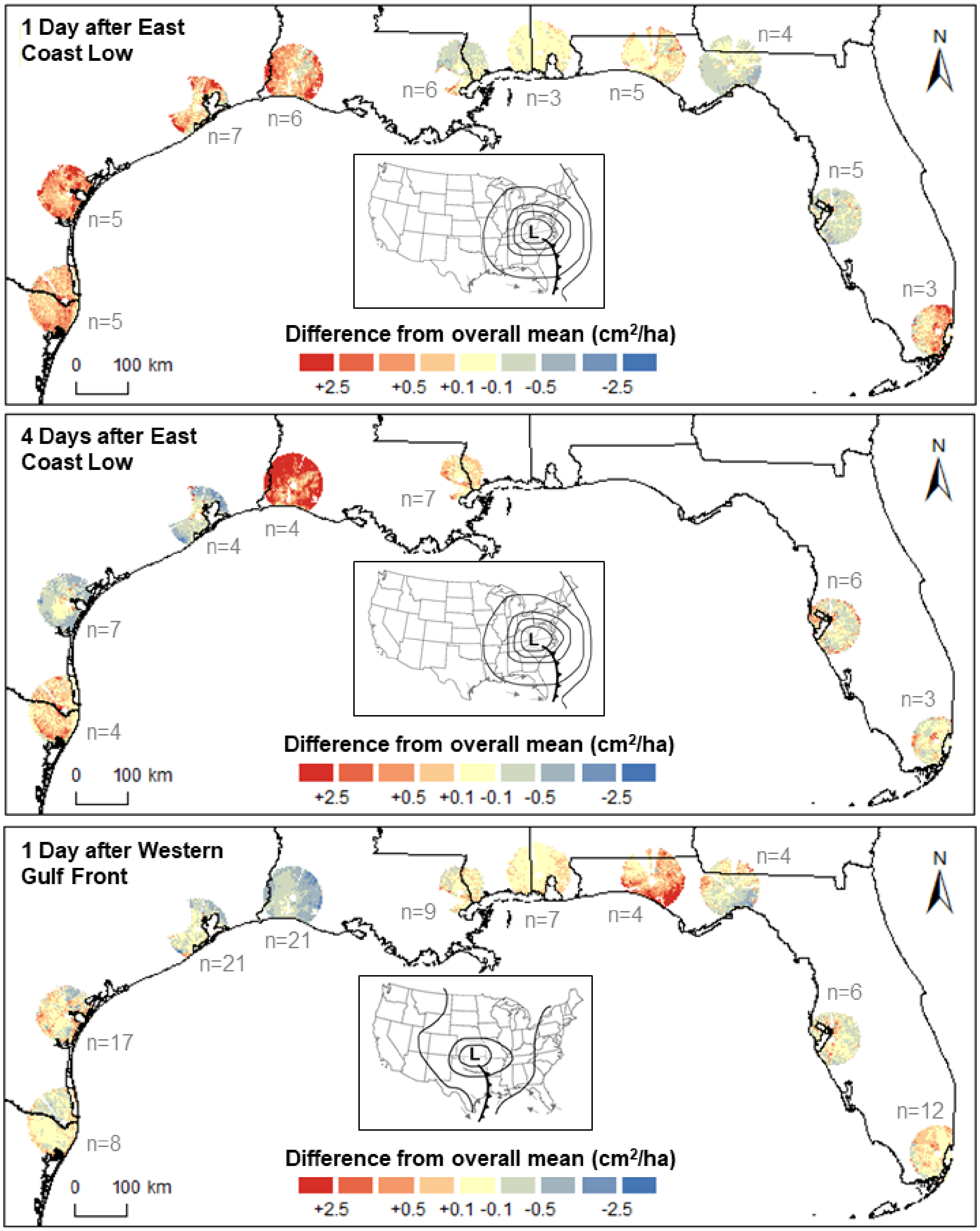

Predicted VIR
All other weather-days
ELOW-4
All other weather-days
MCH-1
All other weather-days
GFW-1
All other weather-days
MCH-3
All other weather-days
ELOW-1
Distance from the Gulf of Mexico coast (km)

Figure 1.4: Plots of the interactions between distance from the Gulf of Mexico coast and the five most influential combinations of lag time and synoptic weather type (weather-days) from the boosted regression tree model predicting mean vertically-integrated reflectivity, including four days after an East Coast Low (ELOW-4), the day after a Midwest Continental High (MCH-1), the day after a Western Gulf Front (GFW-1), three days after a Midwest Continental High (MCH-3), and the day after an East Coast Low (ELOW-1). The solid line represents the combined response of all the other combinations of lag time and synoptic weather type pooled.


1 Day after East Coast Low
n=4
n=6
n=3
n=5
n=6
n=7
n=5
n=5
n=5
n=3
Difference from overall mean (cm²/ha)
+2.5
+0.5
+0.1
-0.1
-0.5
-2.5
0
100 km
N
4 Days after East Coast Low
n=7
n=4
n=4
n=7
n=6
n=4
n=3
Difference from overall mean (cm²/ha)
+2.5
+0.5
+0.1
-0.1
-0.5
-2.5
0
100 km
N
1 Day after Western Gulf Front
n=4
n=9
n=7
n=4
n=21
n=21
n=17
n=6
n=8
n=12
Difference from overall mean (cm²/ha)
+2.5
+0.5
+0.1
-0.1
-0.5
-2.5
0
100 km
N

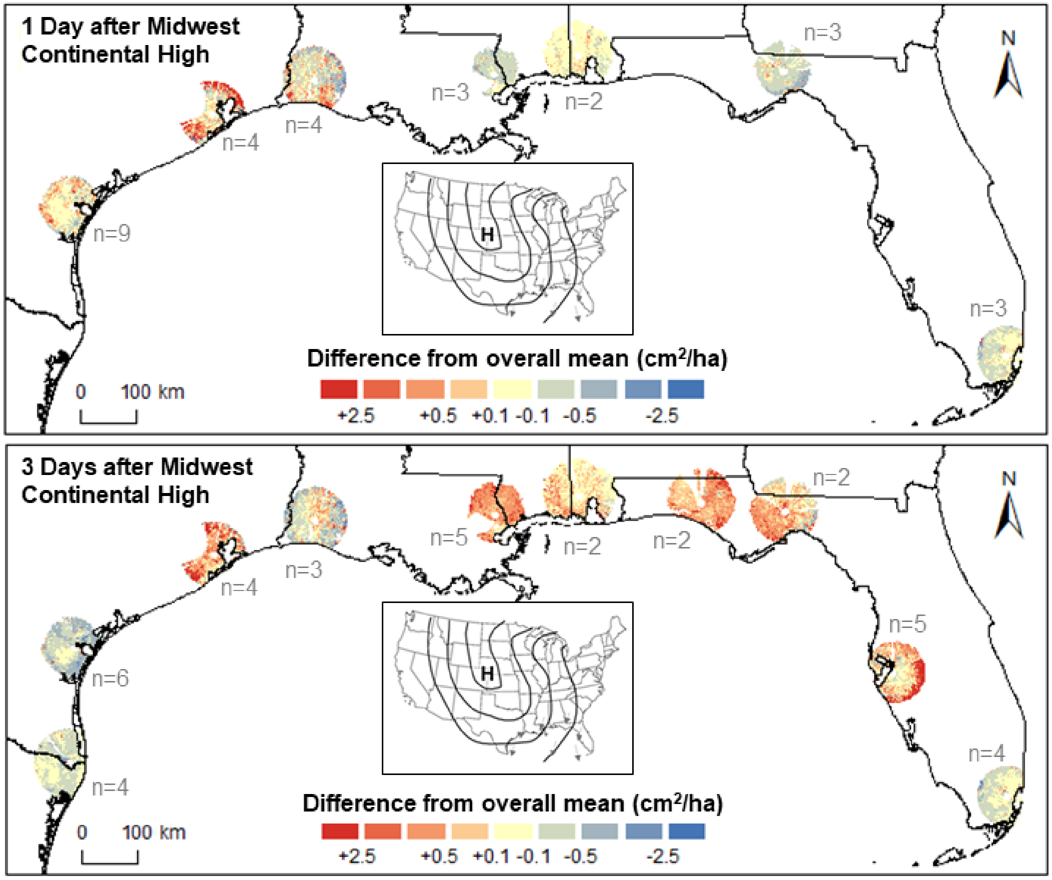


Figure 1.5: Absolute differences in mean vertically-interpolated reflectivity between the entire study period (March through May 2008–2015; see Fig. 1.1) and the five most influential combinations of lag time and synoptic weather type: one day and four days after an East Coast Low; one day after a Western Gulf Front; and one day and three days after a Midwest Continental High. The number of sampling days contributing to the mean VIR of each radar is included. Radars were excluded if there were no sampling days for that radar. The inset maps display a generalized diagram of the associated synoptic weather type (see Fig. 1.2).

1.4.6 Post-hoc analysis of sampling bias

There was natural variation in the occurrence of the eight synoptic weather patterns. Because some systems occurred more often than others, it was possible that the unequal frequency of occurrence of synoptic weather types could have biased the relative influence of individual synoptic weather types. Therefore, we randomly subsampled our data by choosing approximately 20 days of each synoptic weather type for each of the four days preceding the sampling day in a post-hoc analysis. The model set-up and parameters were identical; only the number of observations differed between the original models (n = 150,696) and the ones run with the equal sample size data (n = 139,449). Overall, the results were similar, with the exception of the relative influence of certain synoptic weather types, such as Eastern Continental High, and specific combinations of lag time and synoptic weather type (Table A.5.1), which implies the possibility for frequency bias in our original analyses.

1.5 Discussion

We found clear evidence that synoptic-scale weather over the GOM has strong influence on where birds stop after migration to the northern GOM coast. Unfavorable synoptic weather types with conditions adverse to northward migration, such as headwinds or cold fronts, were particularly influential and resulted in coastal concentrations of migrants. Indirectly, birds appeared to typically rest and refuel for one day, as the day following synoptic weather occurrence was more influential in explaining bird stopover distributions than longer lag times.

Consistent with hierarchy theory (Hutto 1985), synoptic weather had more influence on the stopover distributions of migratory landbirds along the GOM coast than any single geographic or landscape factor included in our model. The high relative influence of synoptic weather is also consistent with previous evidence of the strong influence of weather on bird migration and stopover (Richardson 1978, 1990), and supports the idea that prevailing wind patterns over the GOM influence spatiotemporal patterns in the geographic positions of migrants along the northern

GOM coast (Lafleur et al. 2016). However, because bird densities exhibit strong temporal variability from day to day and year to year (Buler et al. 2007, Buler and Dawson 2014, Lafleur et al. 2016) and weather was the only temporal variable in our models, its influence may have been elevated since it captured the dynamic temporal variability in bird distributions.

Among the eight synoptic weather types, three of the five unfavorable synoptic weather types were the most influential and exhibited strong interactions with the other predictor variables. In general, Midwest Continental Highs and East Coast Lows were associated with higher bird densities across the GOM coast, while Western Gulf Fronts were associated with lower bird densities in the western GOM coast but relatively high densities within close proximity to the coastline. All three weather types involved adverse conditions for northward migration, particularly in the western GOM region. Migrating birds encounter headwinds in the western GOM under Midwest Continental Highs and East Coast Lows. When a Western Gulf Front occurs, they must contend with the passage of a cold front in the western GOM, which is usually accompanied by storms or precipitation. Judging by the relative influence of these synoptic weather types, we suggest that adverse synoptic weather conditions may be particularly influential during migration. Other studies have indicated that headwinds, which are more energetically costly for flying, can affect orientation (Alerstam 1990), air speed of migrants (Liechti 2006), and departure for migratory flight (Akesson and Hendenström 2000, Dänhardt and Lindström 2001).

Although certain synoptic weather types were influential even up to several days after the weather occurred, synoptic weather had the strongest relative influence on bird distributions the following day. This is further evidence that migrants tend to depart quickly from stopover sites along the coast; most birds often stopover only one or two days following a trans-Gulf flight (Moore and Kerlinger 1987). However, synoptic weather also had some influence on the intensity and spatial distribution of birds in stopover habitat four days later, so certain synoptic weather types may also extend stopover for several days. Migrants that face headwinds may deplete their energy stores and that could mean that birds have to stay longer. However, four days is well within the range of time that thrushes and other migrants stopover along the GOM coast during spring migration (Moore and Kerlinger 1987, Yong and Moore 1997). Such findings are relevant because bird migrants behave in accordance with an overall migration strategy that involves minimizing time, energy, and/or predation risk (Alerstam and Lindstrom 1990). Stopover duration accounts for the majority of the time it takes to migrate, so any factor that extends the length of time at a stopover site likely also affects the timing of migration (Alerstam 1993).

Stopover distribution patterns varied for different combinations of synoptic weather type and lag time (i.e., number of days after synoptic weather occurrence). The days following two unfavorable synoptic weather types, Midwest Continental Highs and East Coast Lows, were both associated with higher stopover densities along the western GOM coast (e.g., Texas), perhaps because migrants facing headwinds landed soon after encountering the coast, while those that just faced crosswinds continued to fly inland. Another unfavorable synoptic weather type featured a front in the western GOM, which appeared to decrease stopover densities in the western radars, perhaps because migrants were either diverted by the cold front (Gauthreaux 1991) or chose not to depart from their stopover habitat that night (Richardson 1990, Liechti 2006). The days after these unfavorable synoptic weather types were also associated with pronounced coastal concentrations. These results are consistent with observations of migrants "falling out" in high densities along the immediate coastline and on offshore oil and gas platforms with the passage of cold fronts in the GOM (Richardson 1978, Russell 2005, Yaukey and Powell 2008). Furthermore, we found evidence for birds stopping over different amounts of time after encountering the same synoptic weather type. For example, after an East Coast Low occurred, most birds along the coast departed the following day but those in inland Louisiana stayed longer, perhaps because they were in high quality habitat and taking advantage of food resources.

We expected strong interactions between weather and longitude and distance from the coast. Indeed, we found interactions were generally strongest between synoptic weather type and longitude when explaining bird stopover densities, and interactions between synoptic weather type and distance from the coast were generally stronger than those with the proportion of hardwood forest. These results suggest that weather has more influence on broad-scale geographic distributions than on regional or landscape-level distributions, which is consistent with a scale-dependent framework for migrant selection of stopover sites (Hutto 1985, Moore et al. 2005). At broad spatial scales, factors like synoptic weather patterns constrain opportunities for bird migrants to select habitat (Moore and Aborn 2000). On a more limited regional scale, migrant densities tend to increase with proximity to the GOM coast (Buler et al. 2007). At landscape scales, the amount of hardwood forest cover is important in explaining stopover densities, and intrinsic habitat features are influential primarily at local or patch-level scales (Moore et al. 2005). Thus, synoptic weather interactions with longitude reveal general regions of high stopover density when considering the entire GOM coast.

Ultimately, our results potentially challenge the idea that the GOM is a difficult barrier for Nearctic-Neotropical bird migrants to cross. Many studies have referred to the GOM as an ecological barrier due to its lack of suitable habitat and vast size, which forces migrants to fly nonstop for up to 1,000 km (e.g., Moore and Kerlinger 1987, Buler and Moore 2011, Lafleur et al. 2016, Buler et al. 2017). However, we propose that the degree to which the GOM serves as an ecological barrier is weather-dependent. The most common synoptic weather types during the study period were consistently favorable for northbound birds during spring migration, providing either tailwinds or weak winds. Thus, migrating birds received wind support facilitating migration across the GOM more often than they faced headwinds. The risk of trans-Gulf migration may be high only under adverse migration conditions, including strong headwinds and storms.

Our results could be combined with future climate change projections to predict how migrating birds may be affected by changes in the frequencies of synoptic weather patterns. We have shown that synoptic weather influences stopover distributions along the GOM coast, and other studies associate the locations of migration flyways with atmospheric conditions (La Sorte et al., 2014). Lafleur et al. (2016) drew qualitative relationships between variation in annual longitudinal patterns of migrant distributions and variability in GOM wind patterns. Thus, annual variability in synoptic weather types may explain annual variability in broad-scale migrant stopover distributions. If so, shifts in the frequencies of synoptic weather types due to global climate change are likely to impact migrating landbirds and where they stopover in this region. For example, La Sorte and Fink (2016) projected changes in prevailing autumn winds encountered by transatlantic migratory birds and concluded that climate change could reduce time and energy requirements due to a decreased likelihood of encountering strong winds from the west.

There are some caveats to our results. Unequal frequencies of synoptic weather types among days may have introduced bias for individual synoptic weather types and specific combinations of lag time and synoptic weather type. Rare weather types represented by only a few samples could have had inflated influence over more frequent synoptic weather types with distribution patterns averaged over many days. In addition, there were some factors that influence bird stopover behavior and habitat use that we were unable to account for, such as variation in fuel reserves and body condition of the birds (Smolinsky et al. 2013, Deppe et al. 2015). Birds in good body condition (i.e., high fat scores and relative body mass) may depart a stopover site sooner than birds in poor condition which arrived at the same time, as the latter delays resuming migration to refuel for a longer period (Cohen et al. 2014). Beyond individual variation in stopover duration due to body condition, there could be interspecific variation if certain species reside at a stopover site for different amounts of time than others, as found by Moore and Kerlinger (1987) and Schaub and Jenni (2001a). This variation could have weakened the relationship between bird densities and weather or possibly created spurious relationships with certain combinations of lag time and synoptic weather type. Finally, because we were looking at average weather patterns across several years, rather than daily weather variation, our study was not designed to detect fine-scale spatiotemporal trends or weather conditions, such as cloud cover or wind speeds at different altitudes. Investigating the mean stopover densities from nights associated with particular combinations of lag time and synoptic weather type meant that if a distinct pattern did not consistently occur, its influence on the average would be negligible.

Our research provides novel quantitative evidence of the large-scale spatiotemporal dynamics of bird distributions associated with GOM-wide synoptic weather systems. We established the significance of the role that synoptic weather plays compared to geographic and landscape variables. Through the interactions with longitude and distance from the coast, we further presented quantitative evidence that synoptic weather affects bird stopover distributions on a broad geographic scale. Unfavorable weather types, with headwinds or cold fronts in the western GOM, interacted strongly with longitude and distance from the coast, resulting in extremes of stopover distributions, such as elevated coastal concentrations. This general phenomenon of synoptic weather influencing stopover distributions likely holds true for other regions through which birds migrate, both within North America (e.g., the northeast United States [Nisbet and Drury 1968]) and across the globe (e.g., Sweden [Akesson 1993]). Furthermore, although our study mainly targeted nocturnal landbird migrants, synoptic-scale weather patterns are not limited in their influence to just these species. In addition to having potential influence on the broad-scale distributions of diurnal migrants, such as soaring raptors or aerial insectivores, synoptic weather could have even stronger effects on organisms with weaker flying abilities, such as migratory arthropods (Drake and Farrow 1988). Ultimately, quantifying the influence of synoptic weather on stopover helps answer macro-ecological questions about species distribution patterns.

Chapter 2

BROAD-SCALE WINDS SHAPE SPRING STOPOVER DISTRIBUTIONS OF MIGRATING BIRDS ALONG AN ECOLOGICAL BARRIER

Hannah L. Clipp, Emily B. Cohen, Jaclyn A. Smolinsky, Kyle G. Horton, and Andrew Farnsworth, and Jeffrey J. Buler

Written in the style of Global Ecology and Biogeography

2.1 Abstract

Aim: Volant animal migration systems are inextricably linked to wind patterns aloft. Yet the spatiotemporal relationships between wind patterns and migration systems remain poorly explored. We took advantage of a unique large-scale dataset to measure the influence of winds aloft on the distribution and abundance of migrating birds departing from stopover habitat.

Location: We measured the influence of winds over the Gulf of Mexico, Atlantic Ocean, and Caribbean Sea on stopover distributions of northward migrating birds across the U.S. coast of the Gulf of Mexico from Texas to Florida.

Time period: March–May 2008–2015.

Major taxa studied: Nocturnally-migrating landbirds.

Methods: We used the U.S. network of weather surveillance radars to sample daily bird stopover densities across the northern Gulf of Mexico coast during spring migration. These data are systematically collected across the entire region each day and are thus uniquely suited to measuring how distributions of migrating birds change in response to wind patterns. We modeled the relative influence and interactions of 20 wind, geographic, landscape, and other variables on bird stopover density across 4 spatial extents.

Results: Even after controlling for departure conditions and other important factors, the total influence of winds aloft during migration on monthly mean stopover density was consistently high across the northern Gulf of Mexico coast. Strong winds from the south over the Gulf of Mexico and strong winds from the east over the Caribbean Sea tended to increase overall stopover densities along the coast, while strong winds from the north over the Caribbean Sea tended to decrease stopover densities. In addition, strong winds from the east over the Atlantic Ocean increased overall stopover densities within the eastern Gulf Coast region. Generally, winds from the north/south had twice the relative influence of winds from the east/west, and strong winds from the south increased stopover densities inland.

Main conclusions: Winds aloft during migration are influential in determining if and where birds stop along the northern Gulf of Mexico coast. Winds over the Atlantic Ocean and Caribbean Sea steer birds toward the Gulf Coast region and are potentially more important than winds over the Gulf of Mexico.

2.2 Introduction

Atmospheric conditions are important in shaping volant animal migration systems worldwide (Drake & Farrow, 1988; Kisimoto, 1976; Liechti, 2006; Shamoun-Baranes, Liechti, & Vansteelant, 2017), and winds aloft are particularly influential for migrating birds (Erni, Liechti, & Bruderer, 2005). When wind direction is favorable (i.e., aligned with the direction of intended migration), the magnitude of nocturnal bird migration increases (Able, 1973; Nisbet & Drury Jr, 1968; Wainwright, Stepanion, & Horton, 2016). Wind speed and direction is also related to the air speeds of migrating birds (Bloch & Bruderer, 1982) and determines whether migrating birds compensate for drift (Alerstam, 1979; Horton et al., 2016). Wind further affects the altitude of migration, as birds will concentrate at altitudes with the most favorable winds (Bruderer, 1971, 1975; Richardson, 1976). Predictable airflow patterns ultimately create freeways, detours, and tailbacks for migrants (Shamoun-Baranes et al., 2017). In addition, departure of landbirds (i.e., passerines and near-passerines with terrestrial life histories) from stopover habitat used between nocturnal flights for diurnal resting and refueling is strongly influenced by local wind conditions, with favorable winds increasing the probability of departure (e.g., Arizaga, Belda, & Barba, 2011; Covino, Holberton, & Morris, 2015; Deppe et al., 2015; Schaub, Liechti, & Jenni, 2004). Numerous studies investigate how departure decisions and flight behaviors of migratory birds relate to wind conditions (Liechti, 2006; Shamoun-Baranes et al., 2017), but there has been limited focus on how winds encountered during flight affect subsequent stopover distributions.

The effects of winds on bird migration and stopover may be even more pronounced over and around large ecological barriers, since regions of inhospitable habitat (e.g., waterbodies, deserts) force migrants to contend with wind conditions they might otherwise avoid by pausing migration and taking shelter. During spring migration, Nearctic-Neotropical bird species may fly over the Gulf of Mexico, Atlantic Ocean, and Caribbean Sea to reach their breeding grounds. The Gulf of Mexico (GOM) in particular is a significant feature in the Neotropical-Nearctic migration system that migrants navigate as they travel from wintering grounds in

Mexico, Central and South America, and Caribbean islands to temperate breeding grounds in the United States and Canada (Cohen et al., 2018). The northern coast of the GOM (hereafter GOM coast) is an important stopover region for billions of birds migrating north in the spring, as it provides critical resources (e.g., food and shelter) after the nonstop 18–24 hour flight across the GOM (Cohen et al. 2017; Moore, 1999; Rappole & Ramos, 1994; Stevenson, 1957). Bird migrants moving through this region during spring migration can be coming anywhere from Veracruz (Delmore, Fox, & Irwin, 2012) and the Yucatan Peninsula (Callo, Morton, & Stutchbury, 2013; McKinnon et al., 2014; Stutchbury et al., 2009) in Mexico to Honduras/Nicaragua in Central America (Stanley et al., 2015) and South America (Gómez et al., 2017; Heckscher et al., 2011).

Therefore, the winds that birds encounter during long flights over water (GOM and possibly the Atlantic Ocean and Caribbean Sea) are likely important in determining if and where birds stop along the coast. Under strong supporting winds (i.e., tailwinds), migrants may have enough energy stores to continue past the coast and stopover in more inland habitats, while strong opposing winds (i.e., headwinds) may cause migrants to deplete their fuel more quickly and stopover in the first habitat available. A hierarchy of factors influence if and where migrating birds stop after the flight across the GOM, and winds may be even more important than geography or landscape characteristics in determining stopover densities of birds (Moore et al., 2005). Extrinsic factors including wind and weather are most influential at the broadest spatial scale in determining whether birds stop after crossing the GOM, while factors intrinsic to habitat are more important at finer spatial scales. However, this scale-dependent approach is thought to apply mainly to trans-Gulf migrants (Moore et al., 2005). While many birds cross the GOM when migrating north (Lowery, 1946), others fly around the GOM through Mexico (Williams, 1945). Because there may be a high proportion of circum-Gulf migrants in Texas, we expect that winds aloft during migration will be less influential within the western GOM coast. Furthermore, due to proximity, we expect that winds over the GOM will have the highest influence and strongest interactions within the central GOM coast, while winds over the Atlantic Ocean will have the strongest influence on the eastern GOM coast and the least influence on the western GOM coast.

Prevailing wind direction is one of the main selective factors suggested to affect migratory routes (Horton et al., 2018; Rappole & Ramos, 1994; Shamoun-Barnes et al., 2017). There has been qualitative support for the influence of broad-scale wind on landbird migration over the GOM, including the diel timing of arrival to the northern coast (Gauthreaux, 1971) and coastal "fallouts" during unfavorable winds (Moore & Kerlinger, 1987). Although Gauthreaux et al. (2006) found little support for the influence of winds over the GOM on the distribution of migrants passing through the northern GOM coast, Lafleur et al. (2016) found qualitative support for longitudinal patterns related to annual variability in GOM wind patterns. Therefore, we expected interactions between winds from the east/west and longitude such that stopover densities would increase in the regions toward which the wind is blowing, and between winds from the north/south and distance from the coast such that coastal stopover densities would increase with winds from the north and inland stopover densities would increase with winds from the south.

Few studies have explored how winds over the GOM may explain stopover distributions along the northern GOM coast. Of those, analyses are limited in the number of years and spatial extent. A more comprehensive assessment of the influence of wind on migrating birds, including interactions with other factors, is needed. Therefore, we used a network of weather surveillance radars to measure the magnitude of bird density departing stopover habitat across the northern coast of the GOM during spring migration in relation to geographic, land cover, and wind predictors at four spatial extents (full GOM coast and western, central, and eastern GOM coast). We addressed the following questions: (1) Are broad-scale winds encountered during migration over the GOM, Atlantic Ocean, and Caribbean Sea important in determining if and where birds stop? (2) How does the overall and region-specific influence of these winds vary across the four spatial extents of the GOM coast? (3) How does wind direction and speed relate to stopover distributions? Our goal is to advance understanding of how wind influences the broad-scale stopover distributions of migrating birds along a large ecological barrier. To our knowledge, this is the first study to address the influence of winds during migration on if and where birds stopover across such a large region.

2.3 Methods

2.3.1 Study region

We defined the northern coast of the GOM as extending from Brownsville, TX, to Miami, FL, coinciding with the locations of the outermost of 10 U.S. weather surveillance radar stations (Fig 2.1). This region stretches nearly 2,000 km, from 80° W to 98° W longitude, with ground elevation ranging from sea level to 100 m. In terms of land cover, the GOM coast consists of primarily bottomland hardwood forest, pine forest, emergent herbaceous wetlands, agriculture, and shrub/scrub. However, areas along the coastline are under heavy development pressure and becoming rapidly urbanized and populated by humans (Abdollahi, Ning, & Stubblefield, 2005; Partnership for Gulf Coast Land Conservation, 2014).

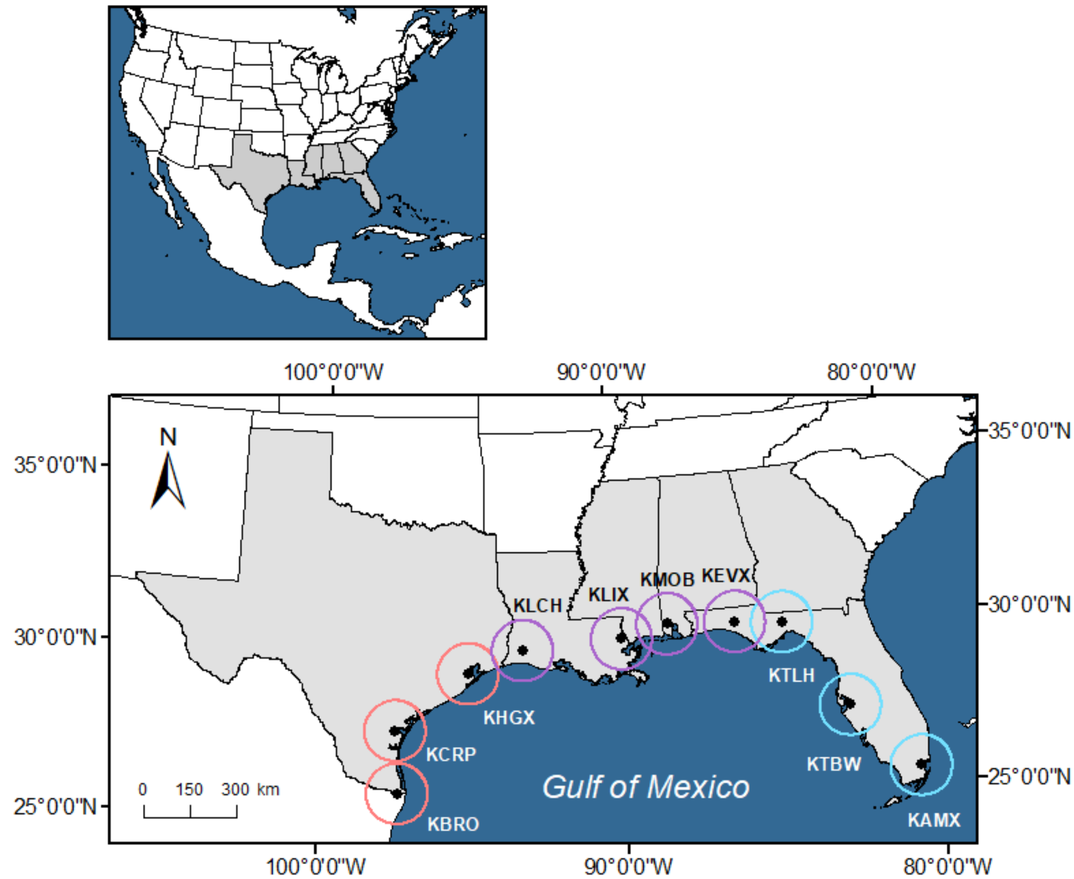


Figure 2.1: Map showing the locations and coverage of the 10 WSR-88D stations (circles forming a 100-km radius around each radar station) along the northern Gulf of Mexico coast. From left to right, the radar stations are located near Brownsville, TX (KBRO); Corpus Christi, TX (KCRP); Houston, TX (KHGX); Lake Charles, LA (KLCH); Slidell, LA (KLIX); Mobile, AL (KMOB); Pensacola, FL (KEVX); Tallahassee, FL (KTLH); Tampa, FL (KTBW); and Miami, FL (KAMX). We divided the full Gulf of Mexico coast into three regions, denoted by color: western (red; KBRO, KCRP, KHGX), central (purple; KLCH, KLIX, KMOB, KEVX), and eastern (blue; KTLH, KTBW, KAMX).

2.3.2 Radar data processing

Weather surveillance radars can detect birds in the airspace as they depart stopover sites at the onset of nocturnal migratory flight (e.g., Buler & Dawson, 2014; Buler & Diehl, 2009; Buler & Moore, 2011; Lafleur et al., 2016). Radar reflectivity is positively correlated to the number of birds aloft, providing an estimate of relative bird density across the sampling area (Diehl et al., 2003; Gauthreaux & Belser, 1999). By calculating the magnitude of reflectivity at the moment of mass departure, when the position of migrating birds in the airspace is closely associated with their position on the ground, radars allow for a spatially explicit assessment of the relative use of stopover sites across large geographic areas (Buler & Dawson, 2014). In this study, we quantified bird stopover density within 100-km radius circles centered on 10 radar stations (Fig. 2.1).

Level II radar data are collected every 5–10 min with 360° coverage at multiple tilt angles (i.e., angle of the radar beam) and archived by the National Oceanic and Atmospheric Administration National Centers for Environmental Information. The data are comprised of individual sample volumes that are 250 m in range and 0.5° in width or adjusted to those values. Following Buler and Dawson (2014), we visually screened sweeps from each night at the lowest tilt angle to eliminate nights with reflectivity from precipitation, anomalous beam refraction, or clutter (e.g., sea breeze fronts, smoke). We further excluded nights dominated by insect movements based on mean airspeeds derived from azimuthal velocity and North American Regional Reanalysis (NARR) wind measurements (Buler & Dawson, 2014; Buler & Diehl, 2009; Mesinger et al., 2006; Ruth, Diehl, & Felix, 2012).

We determined the optimal departure timing to sample the bird-dominated nights (mean airspeeds of >5 m/s; Larkin, 1991). The precise departure timing of migrating birds can vary temporally and spatially, so we used radar-specific departure timing calculated from the sun angle at the time of the maximum change in reflectivity during departure for each day (Mclaren et al., 2018). We further processed radar data to correct for several sources of measurement bias and produce values of vertically-integrated reflectivity (VIR), the total amount of reflectivity in the airspace over a specific area, in units of cm^2 per hectare (Buler & Dawson, 2014).

To georeference the radar data, we constructed polygons representing the two-dimensional boundaries of the sample volumes within each radar domain. We excluded individual sample volumes from data analysis if they were located over open water, where the radar beam was blocked by topographical features or nearby structures, or where there was contamination from persistent ground clutter (Buler & Dawson, 2014). In addition, we consistently detected prominent free-tailed bat (*Tadarida brasiliensis*) roosts in the northwest areas of the KHGX radar, so we excluded the area around identified bat roosts from analysis (Lafleur et al., 2016). We aggregated monthly mean VIR values to a 1-km x 1-km grid that encompassed the 10 radars. For each grid cell, we calculated the area-weighted-mean VIR across all sample volumes within each cell.

2.3.3 Winds aloft during migration

NARR wind data is divided into north-south (N-S) and east-west (E-W) components and measured in m/s at 29 pressure levels (hPa) every 3 hours at approximately 30-km intervals (Mesinger et al., 2006). Because Nearctic-Neotropical bird species may fly over the Gulf of Mexico, Atlantic Ocean, and Caribbean Sea during spring migration, we calculated the monthly mean values for the N-S and E-W wind components at 925 hPa (~760 m altitude) from 0:00 UTC to 6:00 UTC prior to departure from over those three waterbodies (Fig. 2.2). We chose the pressure level and timing for several reasons. First, we chose the altitude to coincide with where songbirds typically fly (500–1,000 m; Able, 1970; Kerlinger & Moore, 1989; La Sorte et al., 2015), and we used a single altitude because winds speeds were highly correlated among levels. In addition, previous work found support for a relationship between migrant distributions in the airspace and wind at a similar low altitude (500 m; Gauthreaux et al., 2006). Second, the diel timing coincides with when birds are migrating over the GOM (Buskirk, 1980). Furthermore, synoptic weather the night before departure has the strongest influence on stopover density in this region (Clipp et al., unpub. data).

Figure 2.2: Map of regions from which wind data were taken: Gulf of Mexico, Atlantic Ocean, and Caribbean Sea.

2.3.4 Additional model variables

In addition to winds aloft during migration, we considered 14 more variables pertaining to geography, landscape composition, departure conditions, corrective measures, timing, and other factors documented to affect stopover density in previous studies (Table 2.1). For instance, Lafleur et al. (2016) found that stopover density is related to longitude, proximity to the coast, and amount of hardwood forest cover in the landscape. Furthermore, several studies have shown that land cover variables, conditions during departure (e.g., Andueza, Arizaga, Belda, & Barba, 2013; Arizaga et al., 2011; Covino et al., 2015; Shamoun-Baranes et al., 2017), NDVI, and distance from bright light (McLaren et al. 2018) are also influential on stopover densities (Cohen et al., unpub. data). Finally, we included relative elevation and distance to the radar station to account for residual range bias in the radar data. Apart from timing, where year and month were assigned as factors, we calculated the numeric values of each variable for every grid cell in the 1-km x 1-km grid that encompassed our 10 radars. For all temporal data (e.g., departure conditions, NDVI), we calculated the monthly mean value. None of the numeric predictor variables were correlated ($r < 0.64$).

Table 2.1: List of predictor variables included to control for known effects on the stopover densities and distribution of migrating landbirds.

Predictor Variable	Details/Units	Data Source
Longitude	---	---
Distance from the coast	Proximity to the nearest coastline in km	---
Proportion of hardwood forest cover within 5 km	30-m resolution	2011 National Land Cover Database
Proportion of urban land cover within 5 km	30-m resolution	2011 National Land Cover Database
Proportion of agricultural land cover within 5 km	30-m resolution	2011 National Land Cover Database
Relative elevation	Ground height above sea level minus the radar antenna height above sea level in m	U.S. Geological Survey Elevation Products – 1 arc-second digital elevation model
Distance to the radar	Proximity to the nearest radar station in m	---
Mean air temperature during departure	Air surface temperature in Kelvin at 0:00 UTC	North American Regional Reanalysis

Mean north-south (N-S) wind component during departure	Meters per second at 925 hPa and 0:00 UTC	North American Regional Reanalysis
Mean east-west (E-W) wind component during departure	Meters per second at 925 hPa and 0:00 UTC	North American Regional Reanalysis
Normalized difference vegetation index (NDVI)	Available on a 16-day basis and at a spatial resolution of 250 m	Moderate Resolution Imaging Spectroradiometer vegetation index products
Distance from bright artificial light at night	Number of km from values >63 on a scale from 0 to 65	2012 Defense Meteorological Satellite Program light data
Timing (year and month)	---	---

2.3.5 Statistical methods

We modeled the influence of winds relative to the other predictor variables on monthly mean VIR using boosted regression tree models with the package "dismo" in R (De'Ath, 2007). Boosted regression trees combine machine learning methods and regression statistics. They are powerful tools because they can fit complex nonlinear relationships and handle interaction effects among predictor variables (Elith, Leathwick, & Hastie, 2008). We examined the influence of the predictor variables on monthly mean stopover densities at four spatial extents (Fig. 2.1): (1) all 10 radars across the GOM coast (hereafter full GOM coast), (2) the three radars in Texas (hereafter western GOM coast); (3) the four radars in Louisiana, Alabama, and the westernmost region of the Florida panhandle (hereafter central GOM coast); and (4) the three remaining radars in Florida (hereafter eastern GOM coast). Thus, we ran 4 models, with the log-transformed arithmetic mean VIR as the response variable. The 20 predictor variables for the models included those listed in Table 2.1, as well as the N-S and E-W wind components over the GOM, Atlantic Ocean, and Caribbean Sea during migration. For each model, we used a tree complexity (i.e., the number of nodes in individual trees) of 2, bag fraction (i.e., the proportion of data used to build the models) of 0.5, and a Gaussian error distribution (Elith et al. 2008). We adjusted the learning rate to ensure that a minimum of 1,000 trees was produced. To reduce spatial autocorrelation, we used a subset of grid cells that were separated by 5 km (Buler & Dawson 2014). This resulted in data subsets of 71,978 observations for the full GOM coast model, 22,011 observations for the western GOM coast model, 28,495 observations for the central GOM coast model, and 21,472 observations for the eastern GOM coast model. To test for patterns at different timescales, we also ran models with annual, weekly, and daily mean values. Here, we present just the monthly results because they explained the highest percent deviance.

2.4 Results

The models of monthly mean VIR explained 74.2–81.7% of the deviance (Table 2.2). Overall, winds were consistently influential in shaping if and where migratory birds stopped, although there was variation in the relative importance of individual wind components. After accounting for corrective predictor variables (i.e., distance to radar and relative elevation), the total influence of all winds aloft during migration (hereafter total wind influence) on monthly mean VIR ranged from 10.6–16.8%, greater than any single geographic, landscape, or departure condition variable within the western and eastern GOM coasts, and second only to longitude for the full and central GOM coasts (Table 2.3). Among the three sub-regions of the full GOM coast, the total wind influence was similar, though ~1.5 times higher in the eastern GOM Coast than in the central GOM coast. However, the strength of interactive effects with winds aloft during migration varied by sub-region (Tables B.1.1–B.1.4). Within the western GOM coast, winds generally interacted most strongly with distance from bright light; specifically, strong winds from the east over the GOM resulted in lower mean VIR >80 km from bright light (Fig. B.2.1). Within the central and eastern GOM coasts, the strongest interactions tended to be between winds and longitude, where stronger winds from the north or south increased or decreased the mean VIR in specific locations (Figs. B.2.2–B.2.3).

Table 2.2: Performance of boosted regression tree models with a response variable of monthly mean vertically-integrated reflectivity and wind, geographic, landscape, departure condition, and corrective predictor variables (see Table 2.1). Table values indicate the spatial extent, number of trees fitted for the final ensemble model, and proportion of total deviance explained of the training data.

Spatial Extent	Number of Trees	% Deviance Explained
Full GOM coast	6,800	74.2
Western GOM coast	5,600	78.6
Central GOM coast	4,900	81.7
Eastern GOM coast	5,400	78.7

Table 2.3: Summary table for the relative importance (%) of variables predicting monthly mean vertically-integrated reflectivity at four spatial extents (full, western, central, and eastern Gulf of Mexico coast). The top five predictor variables with the greatest relative influence for each model are in bold.

		Spatial Extent			
Category	Predictor Variable	Full	Western	Central	Eastern

Geography	Longitude	**21.2**	6.0	**29.9**	**8.5**
	Distance from the coast	**6.1**	**8.1**	4.0	**8.5**
Landscape composition	Proportion of hardwood forest cover within 5 km	4.1	5.6	2.1	4.6
	Proportion of urban land cover within 5 km	4.4	3.0	2.5	3.2
	Proportion of agricultural land cover within 5 km	3.5	5.9	1.9	4.7
Corrective	Relative elevation	3.9	3.8	2.9	**6.9**
	Distance to the radar	**14.6**	**19.0**	**14.5**	**9.8**
Departure condition	Mean air temperature during departure	4.2	5.6	3.9	**6.7**
	N-S wind component during departure	3.4	3.8	3.1	5.4
	E-W wind component during departure	4.2	3.4	3.4	5.1
Other	NDVI	**5.9**	**6.9**	**5.3**	6.6
	Distance from bright artificial light at night	5.6	**6.5**	3.6	4.6
Timing	Year	**6.5**	**8.5**	**11.0**	6.3
	Month	1.6	0.6	0.8	2.2
Winds encountered during migration	N-S wind component over the GOM	1.7	3.3	1.3	3.3
	E-W wind component over the GOM	1.3	1.4	1.1	1.4
	N-S wind component over the Atlantic Ocean	3.0	1.0	**4.6**	1.9
	E-W wind component over the Atlantic Ocean	1.1	1.1	0.7	1.5
	N-S wind component over the Caribbean Sea	2.3	**6.5**	1.5	5.9
	E-W wind component over the Caribbean Sea	1.1	1.0	1.9	2.8

Winds over the Caribbean Sea and Atlantic Ocean were more influential on monthly mean VIR than winds over the GOM. Among the three waterbodies, winds over the Atlantic Ocean were most influential on monthly mean VIR across the full (4.1%) and central (5.3%) GOM coasts and least influential within the western GOM coast (2.1%), while winds over the Caribbean Sea were most influential on mean VIR within the western (7.5%) and eastern (8.7%) GOM coasts. Winds over the GOM were most strongly related to the western and eastern GOM coasts (both 4.7%), though their relative influence was exceeded by that of winds over the Caribbean Sea. Strong winds from the south over the GOM tended to increase mean VIR within the western, central, and eastern GOM coasts; for instance, VIR along the eastern GOM coast was higher than average when winds over the GOM were blowing >2 m/s from the south (Fig. 2.3a). In contrast, strong winds from the north over the Caribbean Sea clearly decreased mean VIR across the full, eastern, and western GOM coasts (Fig 2.3b). Meanwhile, strong winds from the east over the Caribbean increased mean VIR across the full, central, and eastern GOM coasts (Fig 2.3c), and strong winds from the east over the Atlantic Ocean increased mean VIR in the eastern GOM coast (Fig 2.3d). Winds over all three waterbodies interacted most strongly with distance from bright light, longitude, and distance from the coast (Tables B.1.1–B.1.4).

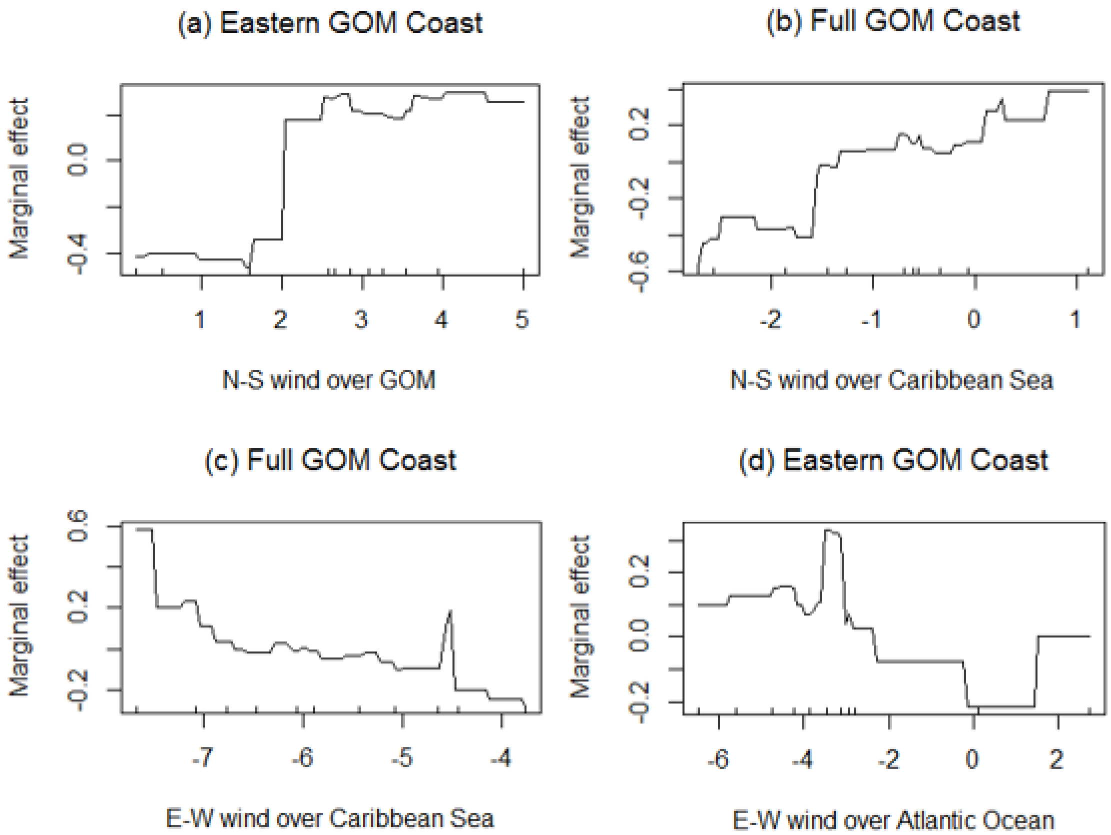


Figure 2.3: Partial dependence plots of the (a) north-south (N-S) wind component (m/s) over the Gulf of Mexico (GOM), (b) N-S wind component over the Caribbean Sea, (c) east-west (E-W) wind component over the Caribbean Sea, and (d) E-W wind component over the Atlantic Ocean, produced by boosted regression tree models explaining monthly mean vertically-integrated reflectivity (VIR) across the (a,d) eastern GOM coast and (b,c) full GOM coast, with rug plots showing the distribution of data. Negative values along the x-axis represent winds from the north or east.

N-S winds had twice the relative influence of E-W winds on monthly mean VIR across the full GOM coast and within the three sub-regions. Although the strength of interactions varied (Tables B.1.1–B.1.4), N-S and E-W winds did not clearly interact with longitude or distance from the coast, respectively. However, one of the few supported interactions was between N-S winds over the GOM and distance from the coast within the central GOM coast and showed higher mean VIR >80 km inland following stronger winds from the south (Fig. 2.4a). In addition, there were strong interactions between winds and distance from bright light. For example, mean VIR was much lower across the full GOM coast in areas >60 km from bright light following strong winds from the east (Fig 2.4b).

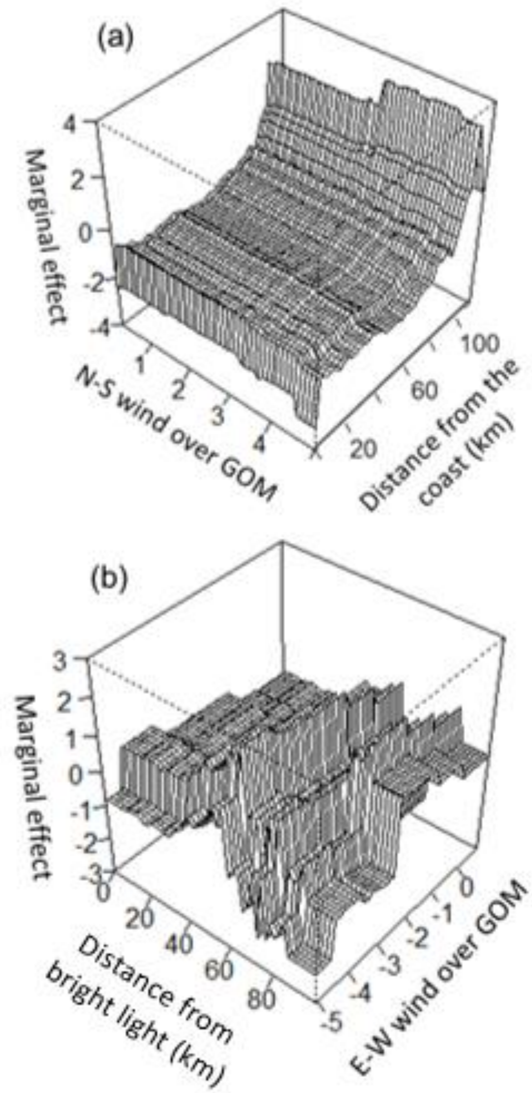


Figure 2.4: Partial dependence plots of the interactions between (a) the north-south (N-S) wind component (m/s) over the Gulf of Mexico (GOM) and distance from the coast (km) and (b) the east-west (E-W) wind component (m/s) over the GOM and distance from bright artificial light at night (km) produced by boosted regression trees predicting monthly mean vertically-integrated reflectivity (VIR) across the central and full GOM coasts, respectively.

2.5 Discussion

We related wind conditions during migratory flight to spring stopover distributions of Neotropical-Nearctic landbirds along the GOM coast. Building upon the qualitative evidence from Lafleur et al. (2016) that annual stopover distributions appear related to annual mean wind speed and heading over the GOM, we expanded the study region to the entire GOM coast and assessed the influence of wind on stopover density at multiple spatial extents. We found that winds aloft during northward migration over the GOM, Atlantic Ocean, and Caribbean Sea, particularly strong winds from the north/south, influenced where birds stopover along the GOM coast. In addition, winds over the Atlantic Ocean and Caribbean Sea had more influence on stopover densities than winds over the GOM. Thus, this study furthers our understanding of the complex relationship between winds encountered during migration over large ecological barriers and the subsequent stopover distributions of landbird migrants.

Consistent with hierarchical habitat selection theory (e.g., Hutto, 1985; Moore et al., 2005), the total relative influence of wind exceeded most geographic and landscape composition variables. This supports the idea of wind as a high-level factor that constrains habitat selection at broad geographic scales (Moore et al., 2005), with prevailing wind direction likely steering landbird migrants and shaping migratory routes (Rappole & Ramos, 1994). Longitude, distance from the coast, and NDVI had consistently high relative influence on stopover density, too. Indeed, multiple studies have connected trans-Gulf migrant distributions with longitude, another high-level factor. Gauthreaux et al. (2006) found that the mean longitude of peak arrival along the GOM coast in the spring clusters near 95° W, and Lafleur et al. (2016) found that stopover density is related to longitude, as well as to proximity to the coast. NDVI is likely positively related to suitable habitat availability and food resources (Tøttrup et al., 2008), both of which are positively related to stopover density as migrating birds appear to seek out stopover habitat with high hardwood forest composition and high arthropod density (Buler, Moore, & Woltmann, 2007; Cohen, Moore, & Fischer, 2012).

Winds aloft during migration were important across all three sub-regions of the full GOM coast, particularly in Florida. It is possible that the slightly higher influence of winds within the eastern GOM coast was due to the spatial adjacency of peninsular Florida to both the GOM and Atlantic Ocean, as well as the closest proximity to the Caribbean Sea; winds from over all three waterbodies likely played a role in stopover densities within that region. We predicted that wind would have less influence on stopover density along the western GOM coast due to the mixture of trans-Gulf and circum-Gulf migrants that pass through that region, but the relative influence of winds was similar among the three sub-regions. However, there was a difference in the strength of interactions that wind had with other predictor variables. Interactive effects between wind and longitude were strongest within the central and eastern GOM coasts, but within the western GOM coast, those interactions were weaker. Interactions between winds and longitude, as well as distance from the coast, may have been reduced if circum-Gulf migrants are intermingling with trans-Gulf migrants during departure. Many of the relationships that we expect are based on migrants' need to cross an ecological barrier, but birds who migrate around the GOM into Texas do not face the same physiological challenges (Stevenson, 1957). Because they are flying over land, circum-Gulf migrants can stopover at any time when encountering unfavorable flight conditions, such as headwinds, strong crosswinds, or precipitation.

Trans-Gulf migrants must contend with unfavorable conditions while over water. Thus, an increasing proportion of circum-Gulf migrants in a region would likely disassociate or weaken the interactive effects of winds over the GOM and geographic variables, such as longitude and distance from the coast, on stopover density.

Winds over the Atlantic Ocean and Caribbean Sea appeared to contribute to influxes of migrants to the GOM region under certain wind scenarios. For instance, strong winds from the east over the Caribbean Sea increased mean stopover density along the GOM coast. Similarly, mean stopover density within the eastern GOM coast increased when winds over the Atlantic Ocean were blowing from the east. Thus, these winds from the east may be directing migrating birds towards the GOM coast. When Lafleur et al. (2016) found unexpectedly high stopover densities in the panhandle of Florida, they proposed that migrants could be arriving in Florida via a trans-Caribbean route, when moderately strong winds blowing to the northwest steer migrants towards the eastern GOM, which is consistent with our findings. In addition, there is evidence from tracking studies that migrating landbirds do travel over the Caribbean Sea to the GOM coast, including veeries (*Catharus fuscescens*) (Heckscher et al., 2011) and common nighthawks (*Chordeiles minor*) (Ng et al. 2018) from South America.

Strong interactions between winds and geographic or landscape factors help to clarify the effects of winds on stopover distributions. We expected that wind would interact with longitude by pushing birds east or west according to the strength of the E-W component of wind speed. Additionally, we expected the N-S component of wind speed to interact with how birds are distributed in proximity to the coast, with stronger winds from the north (i.e., headwinds) causing birds to make landfall on the immediate coast. Our results indicated that wind from the north/south was consistently more influential than wind from the east/west. At a very broad scale, winds moved birds longitudinally, but in terms of interactions with longitude, we found little support for our prediction that winds from the east/west would increase stopover densities in the regions toward which the wind was blowing. In addition, because monthly means of N-S winds over the GOM were all winds from the south, we were not able to test our prediction that strong winds from the north would result in coastal concentrations (i.e. “fallouts”). However, we did find some evidence for our prediction that strong winds from the south would result in higher bird densities inland. Thus, supporting tailwinds appeared to allow migrants to bypass coastal sites and fly further inland (Liechti 2006).

Interestingly, we found very strong interactions between E-W winds over the GOM and distance from bright artificial light at night, where stopover density was much lower than average in darker areas following strong winds from the east. We propose two interpretations of this pattern: (1) when migrating birds experience stronger crosswinds, they use artificial light as beacons while aloft and concentrate landfall near brightly lit areas (LaSorte et al., 2017; McLaren et al., 2018); or (2) migrating birds are less selective under unfavorable winds and will make landfall in relatively greater density within urban areas. Furthermore, migrants leave immediately the following night from areas near bright light, possibly because they are of lower quality, whereas birds that landed away from bright light stopover for more than one day. These two alternative hypotheses should be tested in future studies, especially in conjunction with cloud cover, as we believe heavy cloud cover could increase the use of artificial light as beacons.

It is likely that other factors that we did not consider influence bird stopover density as well. Such factors could include fine-scale weather conditions, individual body condition and fuel load, and stopover duration related to food availability. Although we controlled for departure conditions, including winds and temperature, we did not account for other weather conditions, such as cloud cover. Higher cloud cover has been reported to decrease the probability of departure of migrating warblers (Liu & Swanson, 2015). There is individual variation in departure decisions due to body condition and fat reserves as well. Deppe et al. (2015) found that large fat reserves increased the likelihood of departure; another study found that lean birds remained at stopover sites longer than fat birds (Smolinsky, Diehl, Radzio, Delaney, & Moore, 2013). Finally, stopover duration may vary due to local food availability and fuel accumulation rates. Schaub et al. (2008) found that birds increasing fuel stores at intermediate rates stay longer at a stopover site than those accumulating fuel at low or high rates. As such, there may have been noise introduced into our models because we were unable to account for these other potential sources of variability.

In addition, the timing of data collection was the same for all three regions, even though migrants taking off from South and Central America likely do not reach the GOM coast at the same time as migrants taking off from Mexico or Caribbean Isles (Gómez et al., 2017; Heckscher et al., 2011). The distance from the Yucatan Peninsula, Mexico, to barrier islands in Louisiana is approximately 1,000 km, whereas the distance from the northern coast of Colombia to those same islands is more than 2 times that distance, so the disparity in arrival timing could conceivably range from several hours to nearly a full day. Thus, differences in the length of the migratory flight and thus body condition may exist among birds at the same stopover areas and affect departure decisions. Yet it was still important to include the Caribbean Sea and Atlantic Ocean as we suspect landbirds are contending with winds over both water bodies en route to the GOM coast (Lafleur et al., 2016). By including winds over the Caribbean Sea and Atlantic Ocean, we feel we have encompassed all the important wind regions that affect the Nearctic-Neotropical migrants stopping over along the GOM coast. In addition, winds on one day are correlated to some degree to winds on the following day, so our models are potentially still incorporating appropriate wind measurements.

These results can and should be combined with climate change projections to predict how migrating birds may be affected by future wind patterns. We have shown that winds over the GOM, Atlantic Ocean, and Caribbean Sea influence stopover distributions along the GOM coast, and other studies assert that the locations of migration flyways are associated with atmospheric conditions (La Sorte et al., 2014). Thus, shifts in wind patterns due to global climate change are likely to impact migrating landbirds and where they stopover in this region. For instance, La Sorte and Fink (2016) projected changes in prevailing winds for transatlantic migratory birds during the autumn and found that climate change may reduce time and energy requirements due to a decreased likelihood of encountering strong crosswinds from the west. In addition, it would be interesting to combine this wind analysis with tracking studies (e.g., GPS tags, geolocators) to examine the flight paths and stopover locations of individual birds and compare those with modeled stopover distributions.

2.6 Conclusions

Winds aloft during migration shape the spatial distributions of migrating birds stopping over when navigating a large ecological barrier. We are the first to quantify the relationship between broad-scale stopover distributions and winds encountered during migration over such a large spatial scale. Our results not only suggest that winds influence where birds stop along the entire GOM coast, but also that winds over the Caribbean Sea and Atlantic Ocean are more influential than previously thought. In addition, north/south wind components are more important than east/west wind components, and strong winds from the south over the GOM increase inland concentrations of migrants. These findings both support previous research and offer novel insights into the relationships among winds, geographic factors, landscape composition, and en-route variation in broad-scale stopover distributions of migrating birds. Our comprehensive analysis has refined scientific understanding of the many factors that shape avian stopover ecology during migration, which could be important in considering how migration systems may be affected by global environmental change.

Chapter 3

SEASONAL DIFFERENCES IN STOPOVER SITE FUNCTION FOR MIGRATING BIRDS ARE RELATED TO CHANGES IN STOPOVER DURATION AND RESOURCE AVAILABILITY

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Written in the style of The Condor: Ornithological Applications

3.1 Abstract

Most migrating birds make their journey in several long flights interspersed by periods of stopover. Sites used during stopover by migratory birds vary in their capacity (i.e. function) to meet migrants' needs to rest and refuel. A theoretical framework of discrete functional types, based in part on stopover duration at sites, was proposed by Mehlman et al. in 2005 and has provided a useful tool for researchers and conservation practitioners to categorize and identify important stopover sites for nocturnally migrating landbirds. However, no study has examined seasonal differences in the function and duration of landbird stopover across a network of sites. Our objectives were to: 1) determine the functional types of stopover sites based on radar and ground survey data collected during autumn and spring migration; 2) identify and explain any differences in the functional types of stopover sites between seasons; and 3) explain variability in stopover duration among sites and across seasons. For 19

hardwood forest sites located along the northern Gulf of Mexico coast, we calculated the ratio of arthropod prey to migrant bird “predator”, distance to the coast, proportion of hardwood forest within the surrounding landscape, and relative migrant stopover duration. We used these four variables in a cluster analysis to group the sites into discrete functional categories adapted from the Mehlman et al. framework, which included coastal rest stops, inland rest stops, and refuel sites. We found that coastal rest stops generally served the same function regardless of season, whereas the majority of refuel sites and inland rest stops changed function between seasons based on food availability. Stopover duration was best explained by a negative relationship with the prey:predator ratio in the autumn and positive relationships with the prey:predator ratio and amount of hardwood forest in the spring. Classifying stopover sites and understanding site function allows managers to assess the different needs of migrating birds and objectively prioritize sites based on their ability to facilitate migration.

3.2 Introduction

In the autumn, billions of Nearctic-Neotropical migrants travel from breeding grounds in the United States and Canada to wintering grounds in the Caribbean and Central and South America (Hayes 1995). Come spring, birds reverse this journey, departing for their summer breeding grounds. During the process of migration, energy reserves can be depleted after long periods of flight, forcing individuals to make frequent stops to rest and feed, a behavior referred to as stopover. Any site used by migratory birds during migration is considered a stopover site (Moore 2000, Mehlman et al. 2005); these sites can range from small wetlands along the coast for migrating waterbirds (e.g., waterfowl, shorebirds, waders) to vast inland forests for migrating landbirds (e.g., passerines). Some sites are used for brief respites from flying or as temporary refuges during poor weather conditions, while others are used primarily for fuel deposition to replenish energy stores (Schaub et al. 2008). Subsequently, stopover periods can range from a few hours to several days or even weeks (Seewagen et al. 2010). In general, bird migrants spend more time resting and refueling in stopover habitat than flying between sites, so stopover is the most influential factor determining a migration's total duration (Alerstam 1993, Schmaljohann 2018).

The duration and frequency of stopover can vary, based on a combination of prevailing weather, geography, an individual's physiological condition, and resource availability (Moore 2000, Schaub and Jenni 2001b). Poor weather conditions (e.g., storms, precipitation, headwinds) can cause birds to halt migration, while favorable weather (e.g., tailwinds) can conversely promote departure from stopover sites (Arizaga et al. 2011, Andueza et al. 2013, Covino et al. 2015). Departure decisions are also shaped by the geographic position of the site in relation to the next, as increasing energy stores increase emigration probabilities at sites near large ecological barriers (Schaub et al. 2008). Cohen et al. (2014) found that spring stopover duration is influenced by fuel stores, timing, and movement behavior, such that early spring migrants characterized by low fuel stores and slow movement through the landscape spend the most time at stopover sites. Goymann et al. (2010) also noted that body fat determines spring stopover duration, as lean birds stay longer at stopover sites. Similarly, Seewagen and Guglielmo (2010) found that lean birds stay longer at autumn stopover sites than fat birds. In general, migrants tend to leave sites at which they are losing fuel stores or increasing fuel stores at high rates, while they stay for a longer time at sites at which they increase fuel stores at intermediate rates (Schaub et al.

2008). Thus, stopover duration can be an indicator of migrant behavior at stopover sites.

Due to the broad range in migrant use and habitat quality of migratory stopover sites, Mehlman et al. (2005) presented a detailed theoretical framework for classifying them into three discrete functional types, based on their capacity to meet nocturnal landbird migrants' needs at a given spatiotemporal point. "Fire escape" stopover sites are used in emergency situations (e.g., poor body condition, adverse weather), have few to no food resources available, can have high predation pressure, and are often adjacent to significant barriers (e.g., large bodies of water, deserts). "Convenience store" stopover sites are locations where birds can rest for a short period of time and replenish some fat and muscle; these convenience stores are predicted to support birds between short flights to sites of higher quality or when fuel needs are moderate, but predation risks may limit stopover duration. "Full-service hotel" stopover sites are extensive areas of high-quality habitat where predation risks are low and all resources are relatively abundant and available to individuals of many species. Several studies have used this functional type framework to describe stopover sites. For example, Coffman and Waite (2011) assert that vegetated roofs in human-dominated ecosystems may act as "fire escapes" or "convenience stores" for certain bird species. Solomon (2016) used daily capture rate, body condition, and stopover behavior of migrants to evaluate the function of stopover sites for Nearctic-Neotropical migrants in the northern Yucatan Peninsula, concluding that the two study sites function as a "full-service hotel" and "convenience store." Using different methods, Schreckengost (2017) classified the stopover functional type of 45 autumn stopover sites in the mid-Atlantic and Gulf of Mexico coastal regions. Schreckengost (2017) categorized the stopover sites using cluster analysis based on migrant stopover duration and the individual site's distance to the coast, arthropod density, and amount of hardwood forest within the surrounding landscape.

Though they did not classify stopover sites, other studies examining the stopover ecology of Nearctic-Neotropical migrants acknowledge that stopover sites vary in function. Matthews and Rodewald (2010a, b) looked at the stopover duration and movements of Swainson's thrushes (*Catharus ustulatus*) in urbanizing landscapes of central Ohio. They focused on only one aspect that determines stopover function, but their results indicate that urban forest patches potentially act as "convenience stores." Ewert et al. (2006) investigated migratory bird stopover site attributes in the western Lake Erie basin and suggest that all types of stopover sites (i.e. all functional types) may be important to migrants flying through the region. In a study examining songbird responses to hurricane-disturbed habitats during spring migration, Lain et al. (2017) indicated that chenier forests located directly along the northern coast of the Gulf of Mexico serve as "fire escapes". Finally, Buler and Moore (2011) predicted that bird distributions are less influenced by the amount of forest cover in the landscape as proximity to the coast increases, based on migrants' use of "fire escapes" along the northern Gulf of Mexico coast. In addition to use within the literature, organizations such as The Nature Conservancy have already begun to incorporate the classification scheme framework into their conservation planning and efforts, including its Gulf Wings project (Duncan et al. 2005).

For trans-Gulf migrants, stopover sites along the northern coast of the Gulf of Mexico (hereafter referred to as the Gulf Coast) are critical during both autumn and spring migration for resting and feeding just before and after the nonstop 18–24 hour flight across the Gulf (Stevenson 1957, Rappole and Ramos 1994). Thus, protecting Gulf Coast stopover habitat is a priority for many bird conservation efforts, and knowledge of how those stopover sites function is valuable to conservation planners (Mehlman et al. 2005). However, few studies have empirically validated the classification framework proposed by Mehlman et al. (2005), and only two have focused on trans-Gulf migration (e.g., Schreckengost 2017, Solomon 2016). Furthermore, both of those studies determined functional types from data collected during autumn migration only. Arthropod densities, bird body condition, and migration strategies can vary between seasons. For instance, Blake and Hoppes (1986) captured higher numbers of Diptera and Coleoptera in spring compared to autumn, and other studies show that migrants exhibit higher speeds and shorter durations in the spring (Morris and Glasgow 2001, Nilsson et al. 2013). Yet to our knowledge, no research has investigated whether stopover site function varies seasonally, which could change how stopovers sites are ranked in terms of prioritization for protection and management. Before relying on stopover site functional types to guide conservation efforts, it is important to first assess whether the season affects how a stopover site functions, with particular attention to stopover duration as an indicator of migrant behavior.

Therefore, the purpose of our research was to develop a better understanding of the general function of stopover sites along the Gulf Coast by addressing this gap in our knowledge. Similar to Schreckengost (2017), we characterized stopover function based on integrated food availability, stopover duration, and geographic context. We re-named the three functional types described by Mehlman et al. (2005) to more clearly reflect and describe their function and location: 1) coastal rest stops, 2) inland rest stops, and 3) refuel sites. Coastal and inland rest stops correspond most closely to "fire escape" and "convenience store" stopover sites, respectively, while refuel sites correspond to "full-service hotel" stopover sites. Our objectives were to: 1) determine the functional types of Gulf Coast stopover sites based on weather surveillance radar and ground survey data collected during autumn and spring 2002–2004; 2) identify and explain any differences among the functional types from autumn and spring data; and 3) explain variability in stopover duration among sites and across seasons. Distance from significant barriers and landscape composition are unlikely to change from season to season, so we expected coastal rest stops to provide the same general function during both autumn and spring migration. However, we hypothesized that the role of stopover sites classified as inland rest stops and refuel sites in one season would shift between the two categories based on seasonal food availability, such that higher food availability would be associated with refuel sites.

3.3 Methods

3.3.1 Study area

We investigated stopover at 19 sites located in hardwood forest patches at varying distances from the Gulf Coast (15–70 km) where emergence of migrants from stopover sites was observable by two weather surveillance radars based in Mobile, AL, (30.679444º N, 88.239722º W) and Slidell, LA, (30.336667º N, 89.825556º W) (Figure 3.1). Our study region (i.e. southern Mississippi and eastern Louisiana) consisted of mostly forest and agricultural land cover, with intensive urban development along the coast and large swaths of bottomland hardwood forests flanking major rivers (Figure 3.2). In general, hardwood forest patches tended to be embedded in an extensive pine forest matrix. The stopover sites in this study were established previously by Buler et al. (2007). Of the 19 total sites in our study area, 16 were sampled in the autumn and 16 were sampled in the spring, with an overlap of 13 sites sampled in both seasons.

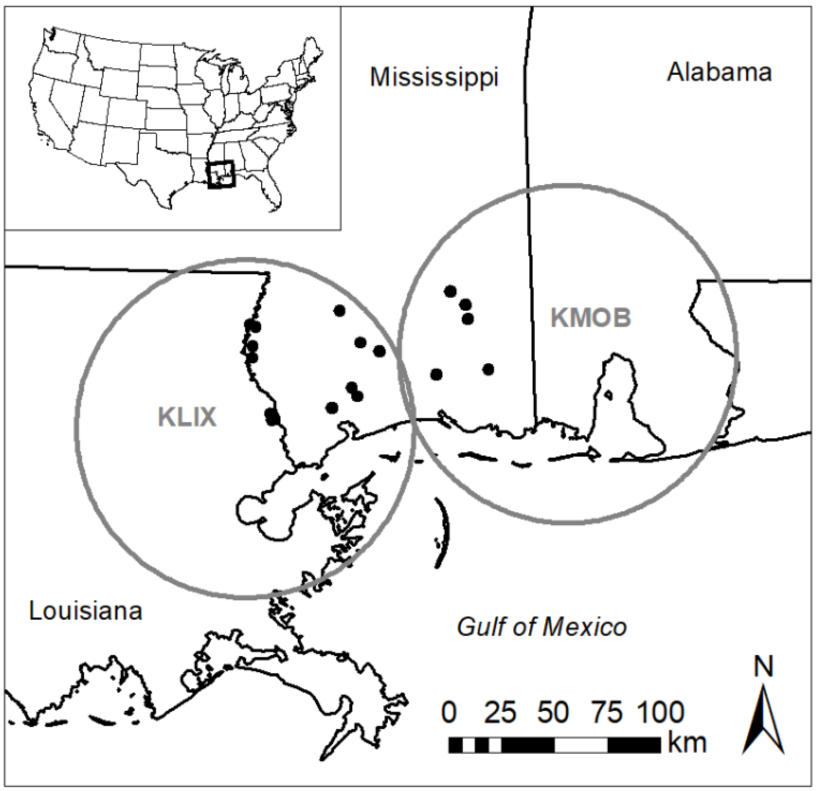

Figure 3.1: Map of locations of 19 bird transect survey sites (black points) along the northern coast of the Gulf of Mexico. Each transect was 500 m in length and positioned within an 80-km radius (gray circles) of the weather surveillance radars, KLIX and KMOB, based in Slidell, Louisiana, and Mobile, Alabama, respectively.

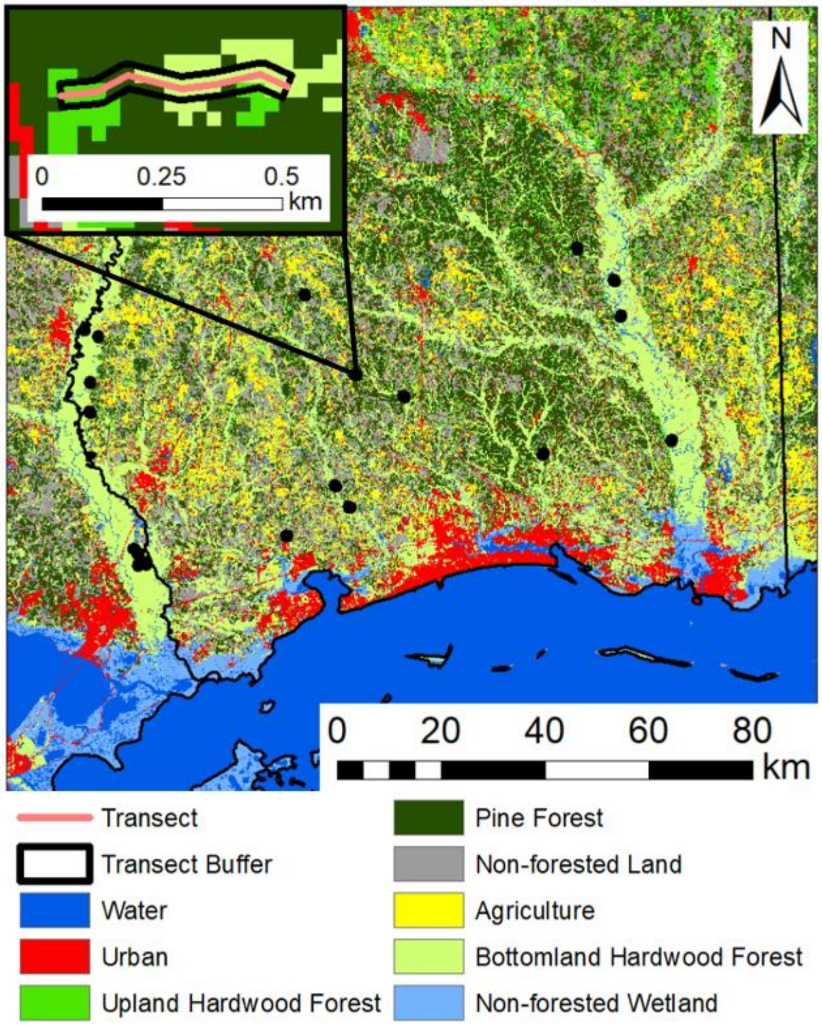

Figure 3.2: Land cover data from the 2011 National Land Cover Database for the study area along the northern coast of the Gulf of Mexico. The 19 sites with 500-m transects were located in areas with varying amounts of hardwood forest and at varying distances from the coast. Each transect was fitted with a 25-m buffer on either side (inset).

3.3.2 Data collection and processing

From mid-August to early November of 2002 and 2003 (i.e. autumn migration) and mid-March to early May of 2003 and 2004 (i.e. spring migration), distance sampling surveys for birds were conducted along 500-m transects for an average of 20 samples per season at each site (see Buler et al. 2007 for detailed methods). Observers recorded species, number of individuals, perpendicular distance from the transect (grouped in distance classes), temperature, wind (using the Beaufort scale), and sky measurements (Buler et al. 2007). We used the “unmarked” package in program R to estimate bird detection probabilities and derive nocturnal landbird migrant densities from the ground surveys (Fiske et al. 2015, R Core Team 2017). The package “unmarked” provides methods to estimate density from distance sampling of unmarked animals and incorporates covariates (Fiske and Chandler 2015). The “gdistsamp” function extends the distance sampling model of Royle et al. (2004) to estimate the probability of being available for detection. The covariates that we incorporated into the models included temperature, wind, sky measurements, and the observer. We scaled the first 3 covariates before analysis and pooled all nocturnally-migrating Nearctic-Neotropical bird species (n = 97 species) to ensure adequate sample sizes for determining detection probabilities (Schreckengost 2017). We tested candidate models of half-normal and hazard rate detection functions for each transect and calculated detection-corrected densities (birds per ha per visit) of nocturnal migrants. We chose the top models through Akaike information criterion (AIC) model selection and goodness-of-fit testing.

We calculated bird stopover densities and duration using the same approach as Schreckengost (2017). To quantify stopover densities from weather surveillance radar data, we downloaded archived Level II radar data from the National Oceanic and Atmospheric Administration National Centers for Environmental Information for our study period (the 2002–2003 autumn migration season [August 1 to October 31] and 2003–2004 spring migration season [March 1 to May 31]) at the radar stations located in Mobile, AL, and Slidell, LA. These radars collect data at regular 5–10 min intervals in 360° sweeps of the beam repeated for multiple elevation angles. Individual sample volumes have a resolution of 250 m in range and 0.5° in width. Two weather surveillance radar products provided the essential data: 1) reflectivity factor, which measures returned radio energy from objects in a sampled volume of airspace and serves as an index of relative bird density, and 2) radial velocity, which provides information on speed and direction of moving targets in the airspace (Gauthreaux and Belser 1998, Diehl et al. 2003).

We visually screened radar data from the lowest (0.5°) elevation angle using Unidata's Integrated Data Viewer (Murray et al. 2003) and eliminated sampling nights from analysis if they contained precipitation, anomalous propagation (i.e. extreme refraction toward the ground) of the radar beam, or clutter (e.g., sea breeze fronts, smoke). We distinguished nights dominated by bird activity by vector-subtracting wind speeds (obtained from archived high-resolution wind data downloaded from the North American Regional Reanalysis dataset) from ground speeds (i.e. the observed velocity of animals over the ground) to yield animal air speed. We considered all nights with mean animal airspeeds of less than 5 ms^{-1} to be dominated by insects and eliminated them from further analyses (Lafleur et al. 2017).

For each uncontaminated, bird-dominated night, we temporally-interpolated the individual reflectivity factor measures to the sun angle at the time of the maximum change in reflectivity (i.e. matching the peak departure of birds from stopover sites at the onset of nocturnal migratory flight; McLaren et al. 2018). Radar data was further processed using the w2birddensity package within the Warning Decision Support System – Integrated Information (WDSS-II) processing software developed by the

NOAA National Severe Storms Laboratory and the University of Oklahoma (Lakshmanan et al. 2007, Buler et al. 2012) to correct for several sources of measurement bias (see Buler and Dawson 2014). We vertically-integrated the reflectivity factor to incorporate the total volume of birds in the vertical column of airspace, then transformed it to reflectivity in biologically-meaningful units of cm^2 per ha (Chilson et al. 2012, Buler and Dawson 2014). To georeference radar data, we constructed polar grids with 285,120 polygon shapefiles representing the 2-dimensional boundaries of sample volumes within each radar domain. We excluded individual sample volumes from data analysis if they were located over open water, contaminated by persistent ground clutter (e.g., wind farms, airports), or in regions where the radar beam was partially or fully blocked due to topography (Buler and Dawson 2014).

We used weather surveillance radar data in combination with data from the bird ground surveys to estimate the average stopover duration of nocturnally migrating Nearctic-Neotropical bird species at each site. We plotted the 500-m transects from the ground bird surveys in a geographic information system with 25-m buffers on either side and calculated the area-weighted average reflectivity for each transect buffer. To determine an index of relative stopover duration (days per cm^2 of reflectivity), we divided the mean ground densities of nocturnal migrants (expressed as use-days) per ha by mean radar densities (cm^2 per ha) (sensu O'Neal et al. 2012). Radar-based relative stopover duration estimates are positively correlated with observed stopover duration measures based on mist-netting data (Buler et al. per. comm.).

In addition to bird surveys at each transect, invertebrates were sampled within understory vegetation once a week by standard branch-clipping (Cooper and

Whitmore 1990). Observers collected 3 branch clippings per visit from site-dominant deciduous understory plant species (e.g., American hornbeam [*Carpinus caroliniana*], witch-hazel [*Hamamelis virginiana*], and red maple [*Acer rubrum*]) and counted invertebrates. We divided the seasonal mean number of arthropods observed per gram (wet mass) of vegetation (Buler et al. 2007) by the seasonal mean daily ground densities of nocturnal migrants to yield the ratio of the number of arthropods available per bird per day (i.e. prey:predator ratio) at each site. This allowed us to control for local bird density, giving us a measure of density-independent resource availability. We also measured the distance to the Gulf Coast (km) and used the 2011 National Land Cover Database to calculate the proportion of hardwood forest cover within 5 km, following the methods of Buler et al. (2007) and Schreckengost (2017). These landscape variables have been found to influence bird stopover densities in this region (Buler et al. 2007, Lafleur et al. 2017). We log-transformed stopover duration and prey:predator ratio measures to improve normality of their distributions in our analyses.

3.3.3 Cluster analysis

We used the Partitioning Around Medoids algorithm of Reynolds et al. (2006) implemented in the package "cluster" in R (Maechler et al. 2015) to cluster the transect sites into the optimal number of stopover function groups based on 4 scaled variables: 1) distance to the Gulf Coast, 2) log of the relative stopover duration, 3) proportion of hardwood forest cover within 5 km, and 4) log of the prey:predator ratio. Data were averaged across years and analyzed separately by season. The clustering algorithm minimizes dissimilarity among members within clusters. Although the original Mehlman et al. framework proposes three functional types, we used average silhouette widths (i.e. measure of how well object fit into their assigned clusters compared to neighboring clusters) to determine the optimal number of clusters (Reynolds et al. 2006). Once the groups were formed, we assigned functional types based on interpretation of the values of clustering variables within each cluster post hoc. Sites were described by their position relative to the coast (i.e. inland vs. coastal) and by whether birds were primarily resting or refueling, which was determined by integrating the prey:predator ratio and amount of hardwood forest cover. Low food resources and/or low forest cover indicated rest stops, while high food resources and high forest cover indicated refuel sites. Stopover duration could potentially inform whether refueling took place quickly or slowly and was expected to be short at rest stops. The cluster group sizes differed and had unequal variances, so we performed Games-Howell post hoc comparison tests to determine significant differences in clustering variables among functional types (Games and Howell 1976).

3.3.4 Stopover duration modeling

Because functional types are simply classifications along a spectrum (Mehlman et al. 2005), we may be obscuring patterns by forcing stopover sites into categorical groups rather than considering them as continuous functionalities. Stopover duration sits at the core of this dynamic functionality and is more naturally considered a continuous measure. Therefore, we used generalized additive models (GAMs) to model factors explaining the variability in relative stopover duration. We used distance to the coast, proportion of hardwood forest within 5 km, and the log of the prey:predator ratio (hereafter just “prey:predator ratio”) as predictors in explaining the log of relative stopover duration (hereafter just “stopover duration”) separately by season and pooled across seasons. We used an information theoretic approach to assess the best models among a candidate set of multiple models using Akaike's information criteria (AICc) corrected for small sample sizes (Burnham and Anderson 1998). Our set of 8 models included a null model with no variables and a global model of all three variables, as well as the individual and combined predictor variables: distance to the coast only; proportion of hardwood forest within 5 km only; the prey:predator ratio only; distance to the coast and proportion of hardwood forest within 5 km; distance to the coast and the prey:predator ratio; and proportion of hardwood forest within 5 km and the prey:predator ratio. All models assumed a Gaussian error distribution and used the identity link functions. Using this model selection approach, we identified the top models with the most explanatory power (i.e. ΔAICc < 2) for each season and assessed the significance of their associated explanatory variables.

3.4 Results

3.4.1 Autumn migration

During the 2 years of autumn migration, detection-corrected estimates of daily bird use at 16 transects ranged from 0.54 to 3.59 (mean = 1.30±0.19 SE) birds per ha per day. After screening for contamination, there were 5 and 6 bird-dominated days in 2002 and 2003, respectively, from the Slidell, LA, radar and 5 and 7 bird-dominated days in 2002 and 2003, respectively, from the Mobile, AL, radar. Radar-derived bird density ranged from 0.16 to 9.11 ($\bar{x}$ = 2.71±0.68 SE) cm^2 per ha. Stopover duration ranged from 0.09 to 9.04 ($\bar{x}$ = 2.18±0.75 SE) use-days per cm^2 per ha. Arthropod density ranged from 0.83 to 3.87 ($\bar{x}$ = 1.96±0.19 SE) arthropods per gram of vegetation, and the prey:predator ratio ranged from 0.68 to 3.93 ($\bar{x}$ = 1.80±0.23 SE) arthropods per bird migrant per day. The proportion of hardwood forest cover within 5 km ranged from 0.19 to 0.88 ($\bar{x}$ = 0.57±0.06 SE), and the distance to the nearest coastline ranged from 8.46 to 56.55 ($\bar{x}$ = 33.64±4.08 SE) km.

Although we intended to form three groups a priori, the cluster analysis for autumn data resulted in a higher average silhouette width of the total data set for 2 groups rather than 3 (Table 3.1). When grouping the sites in 2 clusters, components 1 and 2 explained 87.8% of variance (Figure 3.3A). Based on the mean values of distance to the coast, stopover duration, proportion of hardwood forest cover, and the prey:predator ratio among groups, we assigned the following 2 functional types to each cluster: rest stops (n = 6) and refuel sites (n = 10). Rest stops were closer to the coast than refuel sites, had higher stopover duration values, and had lower proportions of hardwood forest cover within 5 km (Figure 3.4). These sites tended to be surrounded by agricultural land cover (Figure 3.5A). Refuel sites were farther from the coast than rest stops, had lower stopover duration values, and higher proportions of forest cover within 5 km. Most of the refuel sites were located in large patches of bottomland hardwood forest. The prey:predator ratio was not significantly different between the 2 functional groups at an alpha level of 0.05 (P = 0.06), but it tended to be higher at refuel sites.

Table 3.1: Average silhouette width values at various cluster sizes for the cluster analyses of the 19 autumn and spring stopover sites, based on distance to the Gulf Coast, relative stopover duration, proportion of hardwood forest within 5 km, and the prey:predator ratio. The highest average silhouette width value indicates the optimal number of groups.

	Average silhouette width	
Number of clusters	Autumn	Spring
2	0.392	0.416

3	0.285	0.480
4	0.225	0.479
5	0.283	0.411
6	0.363	0.319
7	0.315	0.275

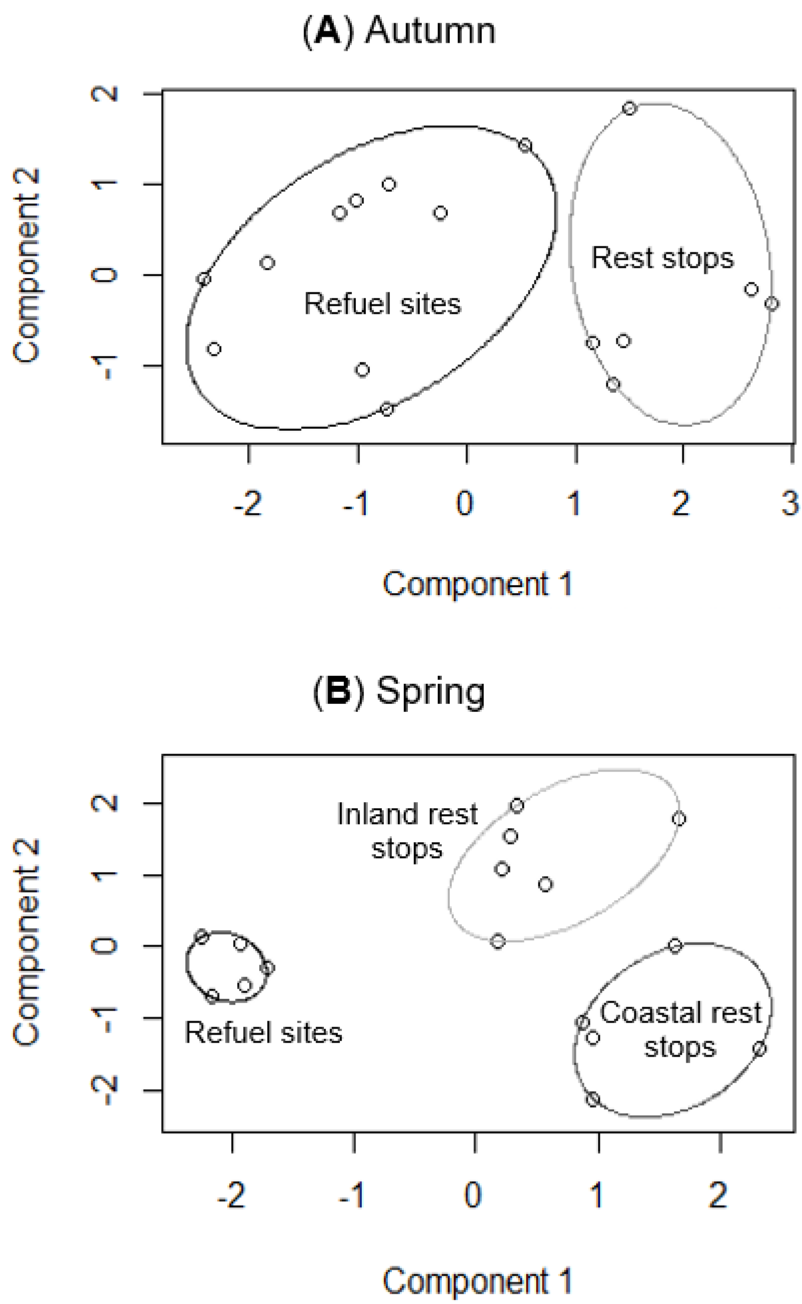

Figure 3.3: Cluster plot of 16 stopover sites from southern Mississippi and eastern Louisiana, assigned (A) based on autumn 2002–2003 data into two groups: refuel sites and rest stops; and (B) based on spring 2003–2004 data into three groups: refuel sites, inland rest stops, and coastal rest stops. Components 1 and 2 explain 87.8% and 86.8%, respectively, of the point variability.

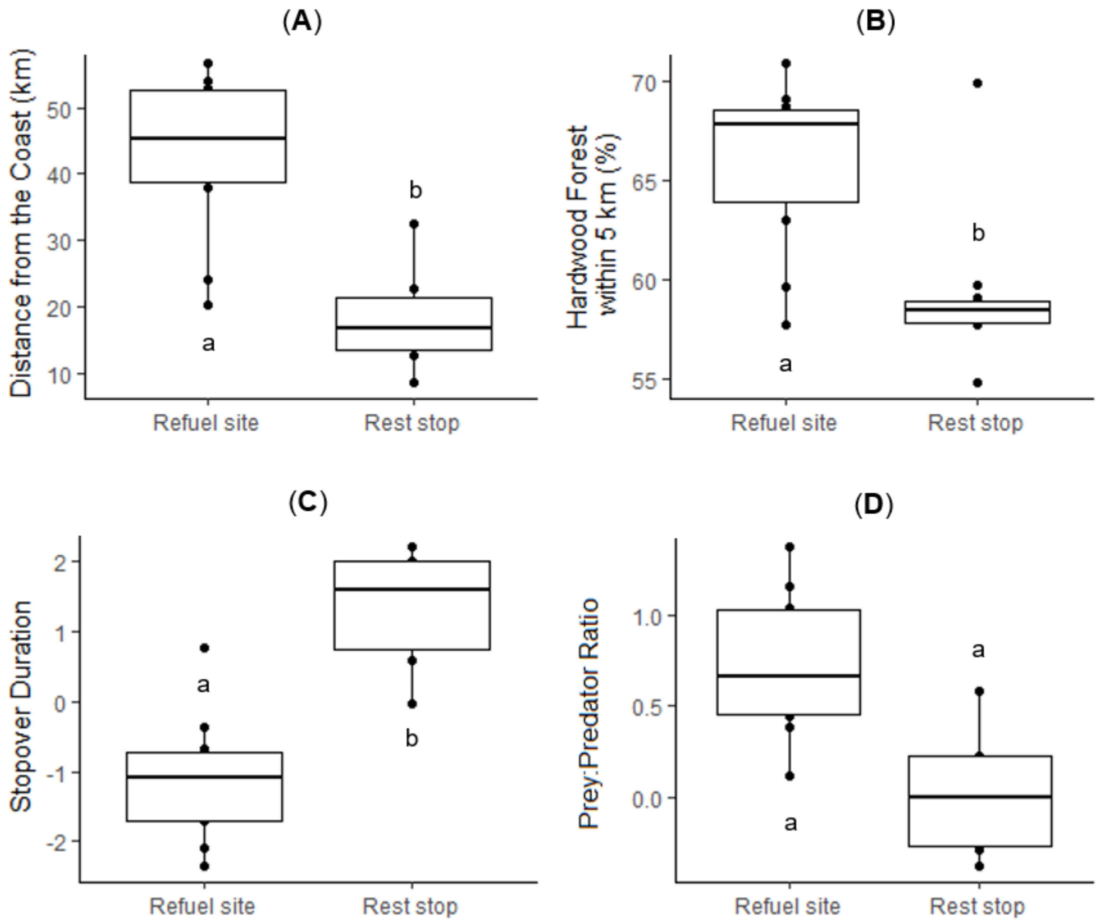

Figure 3.4: Boxplots of values of each stopover site cluster for (A) distance to the Gulf Coast, (B) proportion of hardwood forest within 5 km, (C) log of the relative stopover duration, and (D) log of the prey:predator ratio (number of arthropods per bird per day), based on autumn 2002–2003 data collected from 16 stopover sites within southern Mississippi and eastern Louisiana. Similar lower case letters denote clusters with similar values. Differences between the clusters are considered significant when $P < 0.05$.

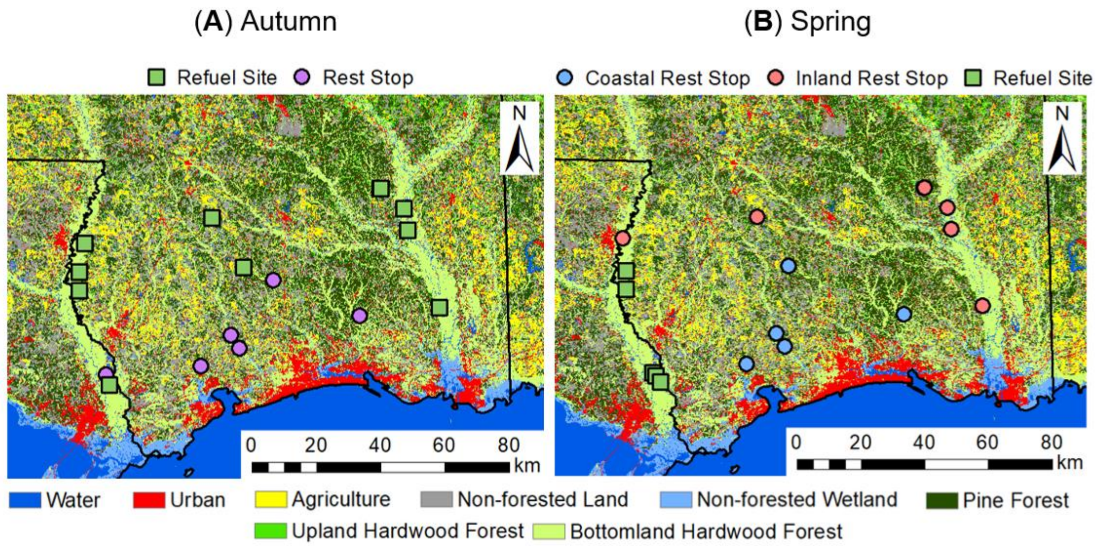

Figure 3.5: Maps of the 16 sites surveyed during (A) autumn 2002–2003 and (B) spring 2003–2004, classified by stopover functional type, which was based on proportion of hardwood forest cover within 5 km, the prey:predator ratio, distance to the Gulf Coast, and relative stopover duration. Land cover data are from the 2011 National Land Cover Database.

3.4.2 Spring migration

During 2003–2004 spring migration, detection-corrected estimates of daily bird use at 16 transects ranged from 2.10 to 8.91 (mean = 5.37±0.58 SE) birds per ha per day. After eliminating days with contamination, the Slidell, LA, radar yielded 21 and 15 bird-dominated days in 2003 and 2004, respectively, while the Mobile, AL, radar yielded 10 and 20 bird-dominated days in 2003 and 2004, respectively. Radar-derived bird density ranged from 0.72 to 3.68 ($\bar{x}$ = 1.64±0.24 SE) cm^2 per ha. Stopover duration ranged from 0.82 to 10.28 ($\bar{x}$ = 4.56±0.85 SE) use-days per cm^2 per ha. The proportion of hardwood forest cover within 5 km and the distance to the nearest coastline were similar to the autumn. Arthropod density ranged from 0.06 to 1.15 ($\bar{x}$ =

0.39±0.10 SE) arthropods per gram of vegetation, and the prey:predator ratio ranged from 0.01 to 0.17 ($\bar{x}$ = 0.06±0.01 SE) arthropods per bird per day.

The cluster analysis for spring data produced 3 optimal groups, based on components 1 and 2, which together explained 86.8% of the variance (Figure 3.3B). We again used the values of the 4 predictor variables to assign functional types to each cluster: inland rest stops (n = 6), coastal rest stops (n = 5), and refuel sites (n = 5). Inland rest stops tended to be located furthest from the coast, with relatively short stopover duration values, intermediate to high amounts of forest cover within 5 km, and low prey:predator ratios (Figure 3.6). Four of the 6 inland rest stops were located in bottomland hardwood forest within a major river floodplain (Figure 3.5B). Coastal rest stops were the closest in distance to the coast, had short stopover durations, the lowest amounts of hardwood forest cover within 5 km, and low prey:predator ratios. As with the sites classified as coastal rest stops in the autumn, these sites were within generally unfavorable landscape matrices (e.g., agriculture, pine forest). Refuel sites were intermediate distances from the coast and had the highest relative stopover duration values, proportions of hardwood forest cover within 5 km, and prey:predator ratios. These sites were all located in the bottomland hardwood forests along the major river forming the eastern Louisiana border (i.e. Pearl River).

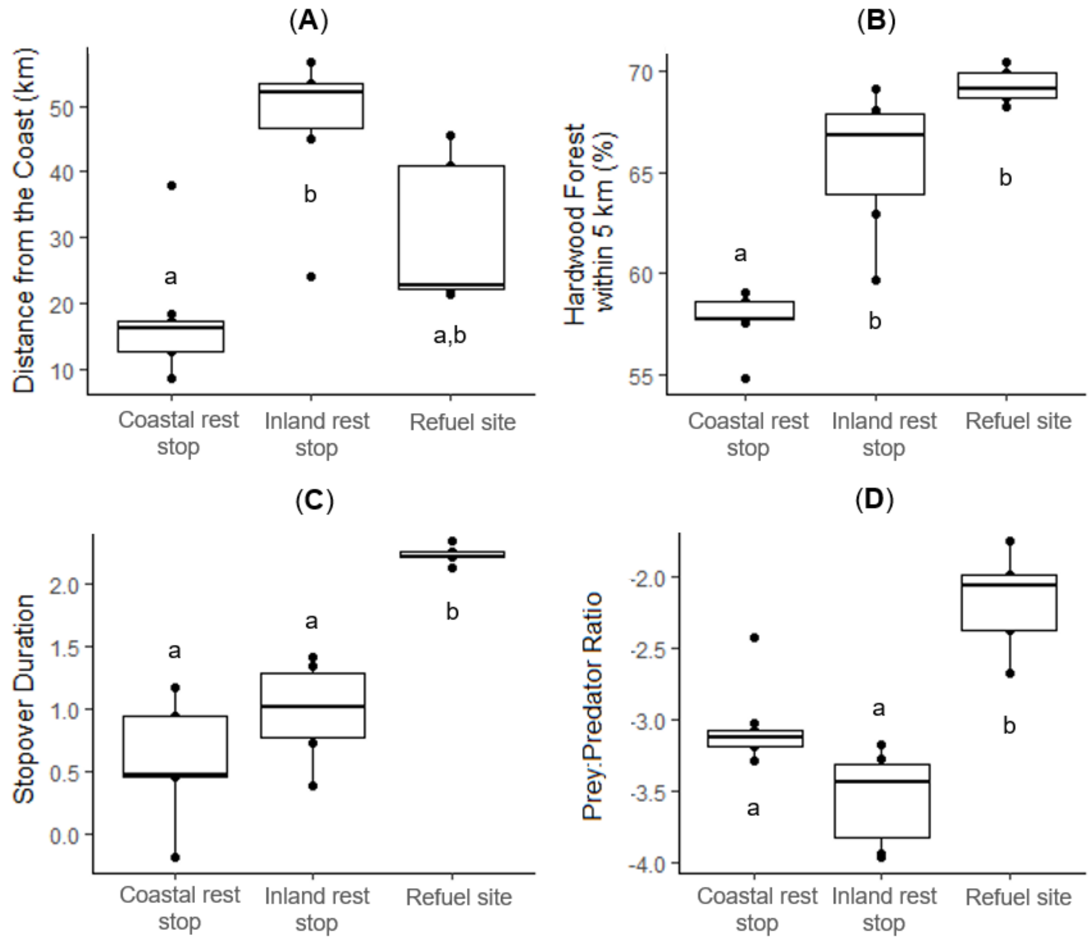

Figure 3.6: Boxplots of values of each stopover site cluster for (A) distance in km from the Gulf Coast, (B) proportion of hardwood forest within 5 km, (C) log of relative stopover duration, and (D) log of the prey:predator ratio (number of arthropods per bird per day), based on spring 2003–2004 data collected from 16 stopover sites within southern Mississippi and eastern Louisiana. Similar lower case letters denote clusters with similar values. Differences among the three clusters are considered significant when $P < 0.05$.

3.4.3 Seasonal comparison

The classification of stopover function types based on distance to the coast, stopover duration, proportion of hardwood forest cover, and the prey:predator ratio revealed that more than half of our sites varied in their relative function between seasons. In total, 6 of the 13 transect sites sampled in both the autumn and spring were assigned the same functional type for each migration season. These sites functioned as either refuel sites (n = 2) or coastal rest stops (n = 4). Meanwhile, 5 sites shifted from refuel sites in the autumn to inland rest stops in the spring, likely due to variation in stopover duration based on seasonal resource availability. Surprisingly, an additional 2 sites were classified as a refuel site in the autumn and coastal rest stop in the spring or as a rest stop in the autumn and refuel site in the spring. The site that was classified as a coastal rest stop in the spring was a slight outlier in that it was the greatest distance to the coast of the other sites in the cluster and had the lowest average silhouette width within its cluster. Similarly, the site that was classified as a rest stop in the autumn was different from the other rest stops in its cluster in that it was located in the bottomland hardwood forest along a large river.

3.4.4 Stopover duration modeling

When considering alternative models to explain stopover duration in the autumn, the top two GAM models (ΔAICc < 2) contained the proportion of hardwood forest within 5 km and the prey:predator ratio (w = 0.442) and the prey:predator ratio only (w = 0.296) as explanatory variables (Table 3.2). The first GAM explained 69.3% of the deviance and showed that stopover duration had a significant negative linear relationship (edf = 1, F = 22.605, P < 0.001) with the prey:predator ratio (Figure 3.7A). The other variable, proportion of hardwood forest within 5 km, had a weaker relationship (edf = 1, F = 4.156, P = 0.062; Figure 3.7B). The second model explained 59.5% of the deviance and also revealed a significant negative linear relationship between stopover duration and the prey:predator ratio (edf = 1, F = 20.57, P < 0.001).

In the spring, the single top model included the proportion of hardwood forest within 5 km and the prey:predator ratio as explanatory variables (w = 0.771). The GAM explained 75.5% of the deviance and revealed that there was significant positive relationship between stopover duration and both the proportion of hardwood forest within 5 km (edf = 1.393, F = 7.811, P < 0.01; Figure 3.7C) and the prey:predator ratio (edf = 1, F = 9.900, P < 0.01; Figure 3.7D). For the data pooled across seasons, the single top model included just the prey:predator ratio as an explanatory variable (w = 0.644). The GAM explained 64.0% of the deviance and showed that stopover duration had a significant curvilinear relationship with the prey:predator ratio (edf = 1.964, F = 26.02, P < 0.01; Figure 3.8).

Table 3.2: Relative support for eight alternate models explaining relative stopover duration of migrating landbirds in autumn, spring, and pooled (autumn and spring) using Akaike's information criterion corrected for small sample sizes (AICc). The *k* value, delta AICc, and AICc weight (w_i) are listed for each model.

Season	Model	*k*	ΔAICc	w_i
Autumn	Proportion of hardwood forest + prey:predator ratio	3	0.00[a]	0.442
	Prey:predator ratio	2	0.80	0.296
	Distance to the coast + prey:predator ratio	3	2.47	0.128
	Global	4	3.60	0.073
	Distance to the coast	2	4.52	0.046
	Proportion of hardwood forest + distance to the coast	3	6.98	0.013
	Null	1	12.19	0.001
	Proportion of hardwood forest	2	12.60	0.001
Spring	Proportion of hardwood forest + prey:predator ratio	3	0.00[b]	0.771
	Global	4	3.93	0.108
	Proportion of hardwood forest	2	4.35	0.088
	Proportion of hardwood forest + distance to the coast	3	7.29	0.020
	Prey:predator ratio	2	9.34	0.007
	Distance to the coast + prey:predator ratio	3	9.70	0.006
	Null	1	14.14	0.001
	Distance to the coast	2	16.47	0.000

Pooled	Prey:predator ratio	2	0.00[c]	0.644
	Distance to the coast + prey:predator ratio	3	2.78	0.160
	Proportion of hardwood forest + prey:predator ratio	3	2.79	0.160
	Global	4	5.78	0.036
	Distance to the coast	2	25.72	0.000
	Proportion of hardwood forest + distance to the coast	3	27.69	0.000
	Null	1	27.75	0.000
	Proportion of hardwood forest	2	30.21	0.000

[a] Lowest AICc = 50.3
[b] Lowest AICc = 27.7
[c] Lowest AICc = 87.8

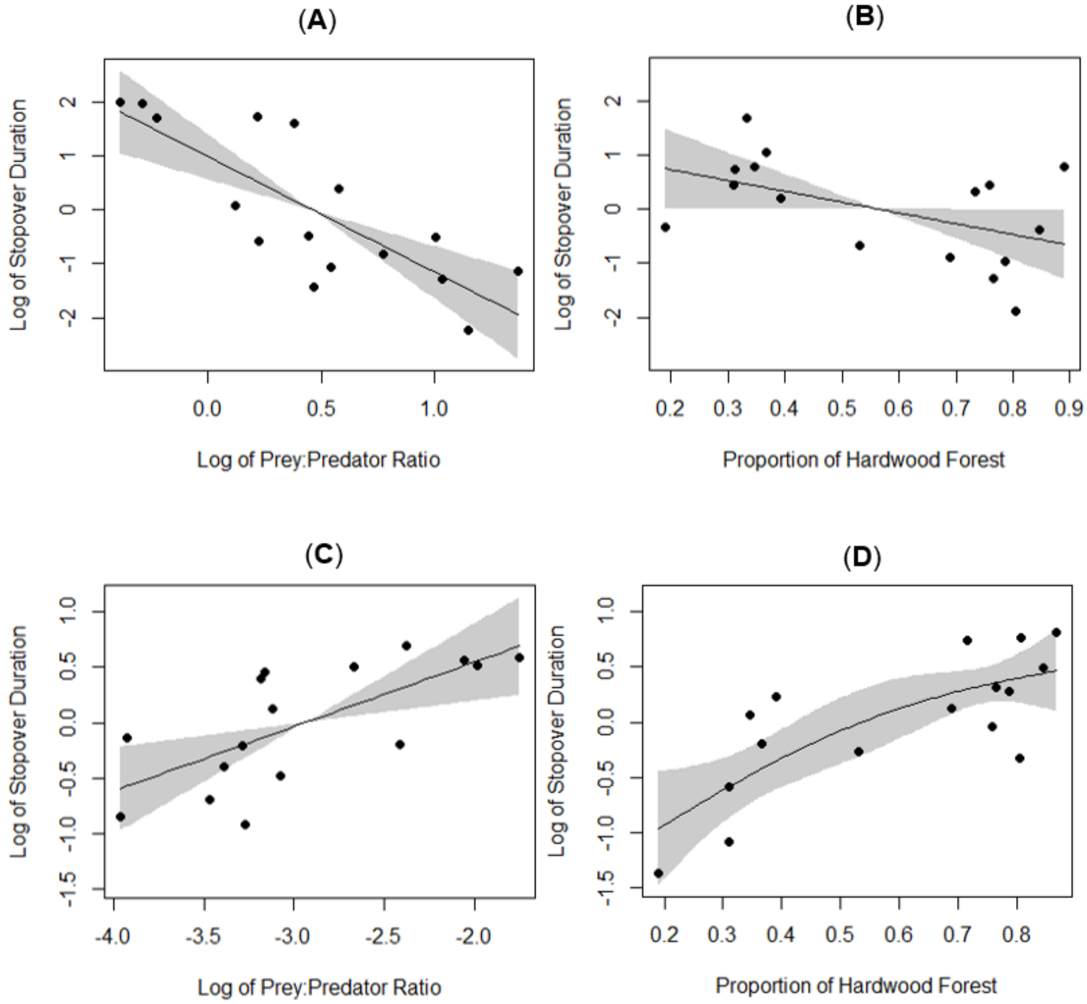

Figure 3.7: Partial response plots of generalized additive models explaining variability in the log of relative stopover duration for predictor variables in the top model during autumn (top row) and spring (bottom row). Solid lines depict mean responses with 95% confidence intervals represented by shading.

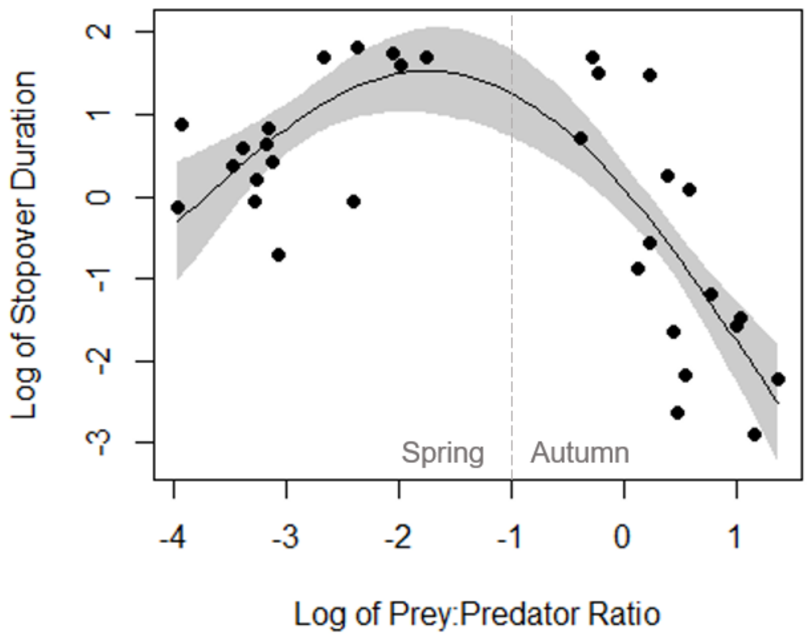

Figure 3.8: Partial response plot of the Generalized Additive Model explaining variability in the log of relative stopover duration for predictor variables in the top model for data pooled across seasons. The solid line depicts the mean response with the 95% confidence interval represented by shading.

3.5 Discussion

Our study provides the first cross-season comparison of relative stopover site function across multiple sites for migrating landbirds by integrating radar and ground observations. Sites nearest to the coast tend to serve as rest stops in both autumn and spring, while inland sites sometimes shift between their ability for migrants to refuel or rest based on relative food availability (i.e. prey:predator ratio). In the autumn, stopover sites were categorized as either rest stops or refuel sites, but in the spring, many of those refuel sites were classified as inland rest stops because they had lower prey:predator ratios relative to the sites that remained refuel sites. The relationship between stopover duration and food availability changed from negative in autumn to positive in spring but was consistent along a broader range of food availability.

In addition to shifts in stopover function, there are contextual differences between seasons. In the autumn, there may be higher numbers of migrants and thus higher competition, as both adult and hatch-year birds are moving through the same areas. In addition, these birds have likely been feeding on the way and are able to stopover more frequently compared to the spring, when adults may have just expended much of their energy reserves crossing the Gulf (Moore and Kerlinger 1987). In the spring, birds also tend to migrate more quickly because selection favors a time-minimizing strategy to maximize individual fitness by arriving early at breeding areas (Kokko 1999, Nilsson et al. 2013, Schmaljohann 2018). However, underlying behavioral motives may be similar. Migrants must refuel to either restore depleted resources in the spring or prepare for a long crossing in the autumn. For instance, fat accumulation increases when migratory birds are preparing to cross a large ecological barrier (Maggini and Bairlein 2010). Thus, the changes in functional types of stopover sites across seasons is likely not due simply to contextual differences between the seasons.

There was a large difference in the absolute and relative amounts of food resources available in each season, which likely drove shifts in stopover site functional type. Arthropod density was ~5 times higher and the prey:predator ratio was ~30 times higher in the autumn. During autumn migration, stopover duration was relatively shorter at refuel sites, which tended to have higher prey:predator ratios, compared to rest stops, which were closest to the coast. Meanwhile, in the spring, stopover duration was relatively longer at refuel sites, where the prey:predator ratio was higher, compared to both coastal and inland rest stops, which both had low prey:predator ratios. These differences were further supported by GAMs of seasonal stopover duration. In the autumn, there was a significant negative linear relationship between stopover duration and the prey:predator ratio. Meanwhile, the prey:predator ratio and proportion of hardwood forest were significant factors influencing stopover duration in the spring, exhibiting positive linear relationships. Studies have shown that insects and forest cover are also important in predicting stopover density (Buler et al. 2007, Lafleur et al. 2016).

Seasonal differences in stopover duration were likely due to relative food availability. The prey:predator ratio in the autumn was negatively related to stopover duration, possibly because food resources were so abundant in autumn that birds were able to gain mass more quickly at sites with more arthropods per bird (Caldwell et al. 1963, Morris et al. 1996, Woodrey and Moore 1997, Parrish 1997), so delaying migration to exploit high quality food resources was not necessary. Additionally, stopover durations along the coast may be extended as “naïve” juvenile birds pile up along the coast or as birds wait for good flight conditions for crossing the Gulf of Mexico (Richardson 1978, Gauthreaux et al. 2005, Buler and Moore 2011, Deppe et al. 2015). In the spring, stopover duration was longer where the prey:predator ratio was higher, presumably because energy-depleted birds spend time accumulating fuel to continue their migration where food is most available and quickly move on from areas with less food (Cohen et al. 2012, Cohen et al. 2014). When pooling data across seasons, the relationship between stopover duration and the prey:predator ratio is curvilinear; migrating birds exhibit shorter stopover duration when arthropods are either scarce or plentiful, but increase stopover duration when the prey:predator ratio is intermediate (Figure 3.8). This trend is corroborated by the findings of Schaub et al. (2008), which show that emigration probability is highest when fuel deposition rates are either low or high and lowest when they are intermediate. Thus, birds appear to move on quickly from sites with little to no food, linger at sites with intermediate amounts of food due to the time it takes to locate prey and deposit fat, and emigrate after a short time period from sites with plentiful food resources, where it takes little time to refuel.

We avoided making direct comparisons between bird densities and stopover duration between autumn and spring. One of the assumptions of distance sampling is that objects on the line are detected with certainty (i.e. 100% detection probability at distance 0). However, this assumption may have been violated in autumn when birds tend to be more cryptic in color and behavior. There was a noticeable difference in the average number of birds detected during the ground surveys, with ~4 times the numbers in the spring than in the autumn. We believe that this may be due to the increased detectability of birds in the spring, when they are often actively foraging and singing. Buler et al. (2007) mentioned that distance detection functions showed lower detectability of birds in autumn with respect to distance from transect. Thus, even with our detection-corrected estimates, we suspect our spring ground densities are inflated compared to the autumn and subsequently preclude directly comparing densities and stopover duration between the two seasons. In addition, the radar-derived densities were 1.7 times higher in the autumn than in the spring; radar provides observations that are more objective and can be seen as a more reliable sensor than observers on the ground in detecting birds. Although we hesitate to definitively state a seasonal disparity in bird densities, other studies have reported differences in these metrics between seasons. For instance, Blake and Hoppes (1986) noted higher numbers of migrants during spring migration in their study. Morris and Glasgow (2001) also found that stopover duration varied with season, possibly influenced by proximity to breeding grounds and distance from wintering grounds, as well as the presence of an ecological barrier.

There are some caveats to the results of this study. We assessed the aggregate functional type of stopover sites, which certainly varies among species and individuals. The nearly 100 nocturnal landbird migrant species that we detected have different habitat, food resource needs, and behaviors during migration. In addition, there is likely some annual variation in functional types, in addition to the seasonal variation covered in this study, which could minimize or exaggerate seasonal differences. Variation could be due to arthropod cycles, forest dynamics, land-use changes, and large-scale wind or weather patterns during migration. Finally, relative functional types may change in the face of additional data, especially from a broader spatial extent. For instance, under the classification scheme of Schreckengost (2017), who combined sites from the Gulf Coast and mid-Atlantic regions, rest stops in the Gulf Coast region classified as “coastal” in our study were classified as “inland” rest stops because the mid-Atlantic included sites much closer to the coast.

Coastal rest stops classified in this study are not entirely consistent with the description of “fire escape” stopover sites as defined by Mehlman et al. (2005). Based on the conceptual framework, stopover duration at coastal rest stops should be short because there are few to no food resources, limited cover, and likely high predator pressure. In our study, coastal rest stops had longer stopover duration values than refuel sites in the autumn. Similarly, migrants are thought to use urban stopover sites as “fire escapes” (i.e. only briefly and in times of urgency), but Seewagen et al. (2010) found that birds stopped over in these areas for several days. It is possible that birds stopping over at coastal rest stops in autumn prolong their stay because waiting for optimal wind conditions to make a trans-Gulf flight (Akesson and Hendenström 2000). In addition, it is important to recognize that while the designated coastal rest stops were closest in distance to the nearest coastline, they were not directly adjacent to the coast; therefore, it is possible that they should be classified as inland rest stops (as in Schreckengost 2017), while landscape features such as barrier islands may be more appropriately classified as coastal rest stops (Mehlman et al. 2005).

3.5.1 Conservation implications

Our results have notable management and conservation applications. Populations of migratory bird species across North America are decreasing (Robbins et al. 1989, Sauer et al. 2013). Loss and degradation of breeding habitat have traditionally drawn the most attention as causes of widespread declines (Robinson and Wilcove 1994), but threats to any portion of the annual cycle of migratory bird species can affect entire populations (Runge et al. 2014). Mortality during migration can be higher than in the breeding or wintering grounds (Sillett and Holmes 2002, Paxton et al. 2017, Rockwell et al. 2017). Researchers have increasingly acknowledged that stopover habitat plays an important role in the survival and condition of migratory birds (Hutto 1998). Protected areas and intact stopover habitats are especially critical just before and after migrants cross ecological barriers (Petit 2000). During autumn and spring migration, habitats along the northern Gulf Coast serve as critical stopover sites for >160 bird species that breed in North America and migrate across the Gulf of Mexico each year (Lafleur et al. 2016). However, much of the Gulf Coast is characterized by urban, commercial, and industrial development. Due to urban expansion and climate change, habitat loss and degradation of Gulf Coast ecosystems could increase in the near future, further reducing the amount of stopover habitat for migrating songbirds (Moore 2000, Cohen et al. 2017). Migration is the most vulnerable period in the annual cycles of many species (Newton 2006), so losses of important coastal habitat could negatively impact already declining migratory bird populations.

Identifying important stopover habitat is not a simple process. Yet classifying stopover sites allows managers to meet the different needs of migrating birds and objectively prioritize sites based on how they function in aiding birds' ability to complete migration successfully. Our results established that distance to the coast, stopover duration, proportion of hardwood forest, and the prey:predator ratio can be used to classify stopover sites, and can be further used for modeling classifications across regions to aid in conservation planning. As we demonstrate, it is important to consider both autumn and spring data, since function can vary between seasons. Faced with the prospect of losing or gaining habitat, land managers can consider stopover site functions in their cost-benefit analyses. In addition, because each functional type is valuable to migratory birds, they can identify if one is underrepresented or missing within a landscape and incorporate functional types into maps of regional stopover site connectivity. Managers might even be able to convert inland rest stops into refuel sites by managing them to produce more food resources for migrants. Classifying stopover sites as we did also enables comparisons within each functional type, rather than across types, which tends to favor the conservation of refuel sites over coastal and inland rest stops (Schreckengost 2017). We recommend that land managers compare stopover sites to others within the same category when assessing importance. As refuel sites tend to be already protected, it is particularly important to identify and conserve coastal rest stops, which could be vital in emergency situations (e.g., unfavorable winds or weather events) (Mehlman et al. 2005). In geographic areas where stopover habitat is scarce, sites that function as rest stops could mean the difference between successful migration and death.

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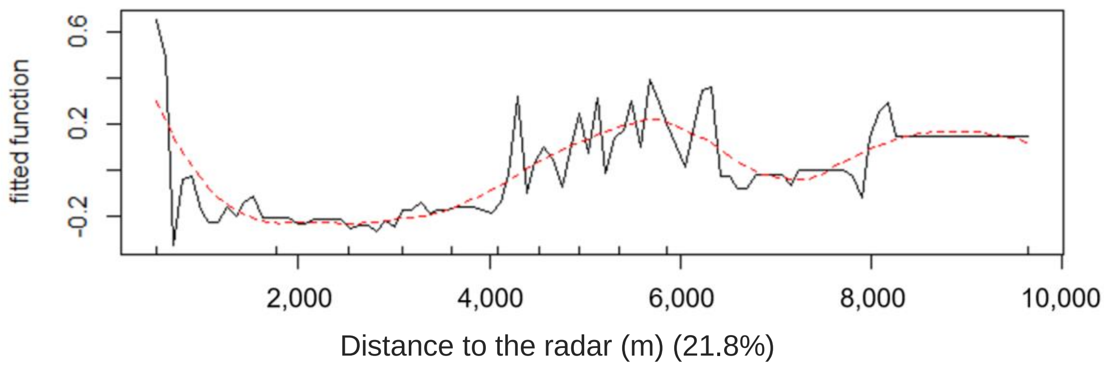
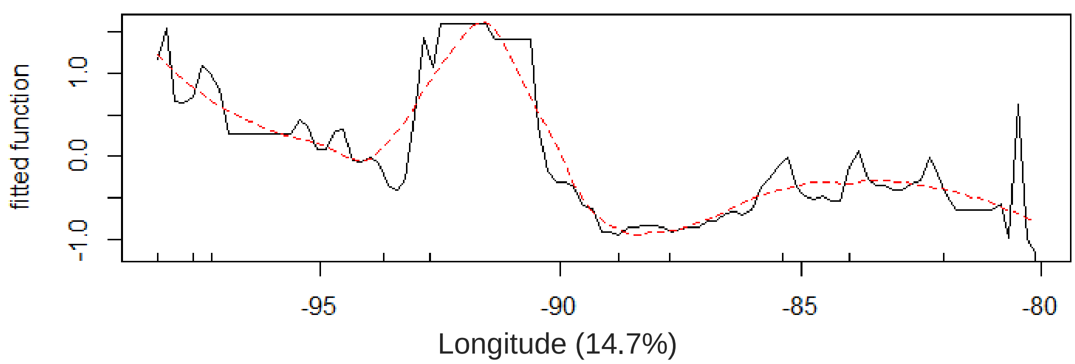
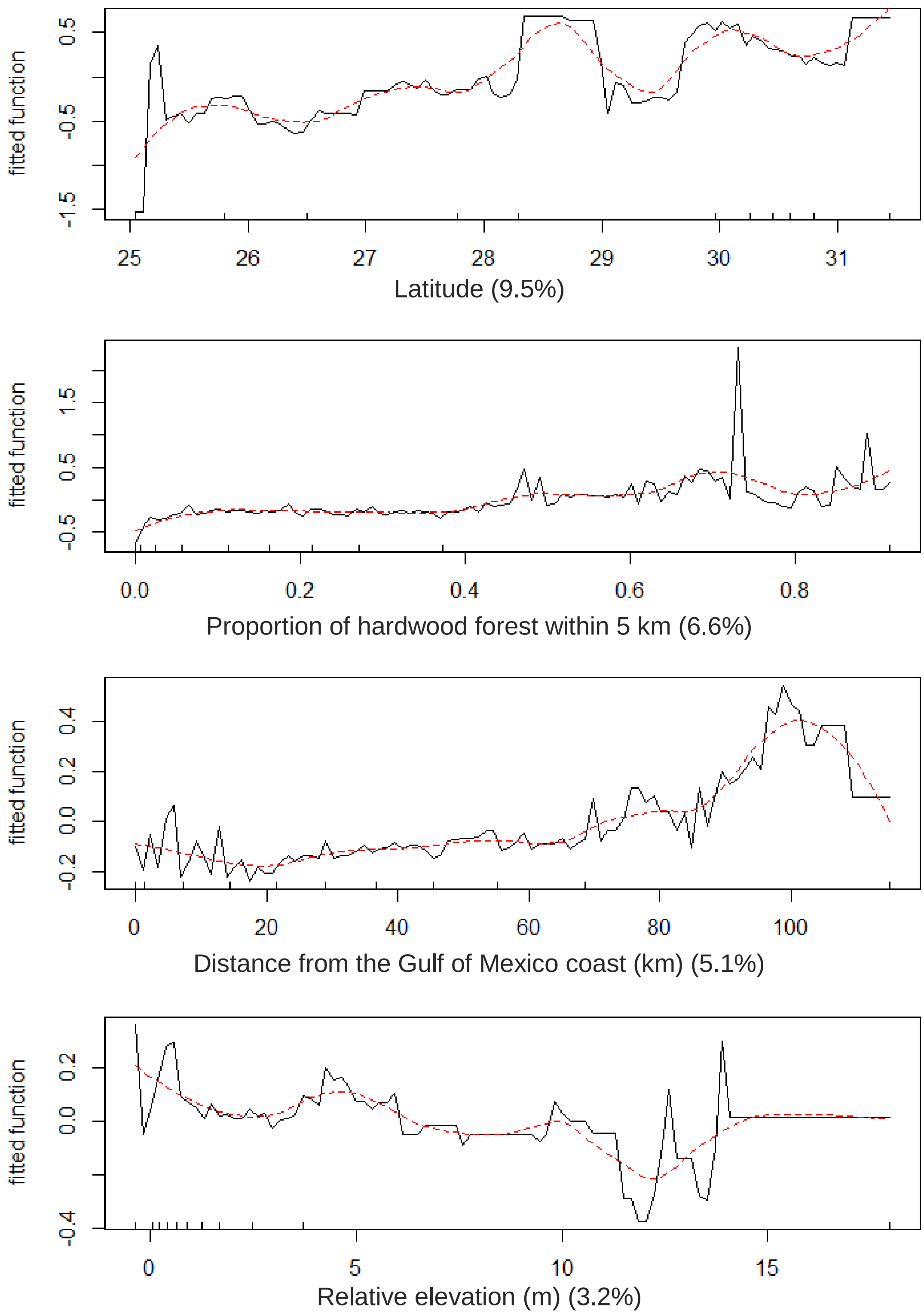
Appendix A

INFLUENCE OF SYNOPTIC WEATHER ON BIRD STOPOVER DENSITY AND DISTRIBUTIONS

A.1 Partial dependence plots of geographic, landscape, corrective, and departure weather variables for the 4 boosted regression tree models






fitted function
Latitude (9.5%)
Proportion of hardwood forest within 5 km (6.6%)
Distance from the Gulf of Mexico coast (km) (5.1%)
Relative elevation (m) (3.2%)

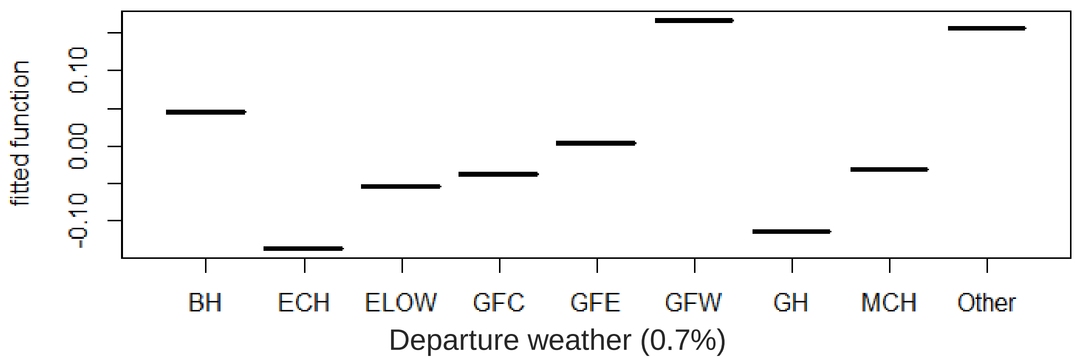
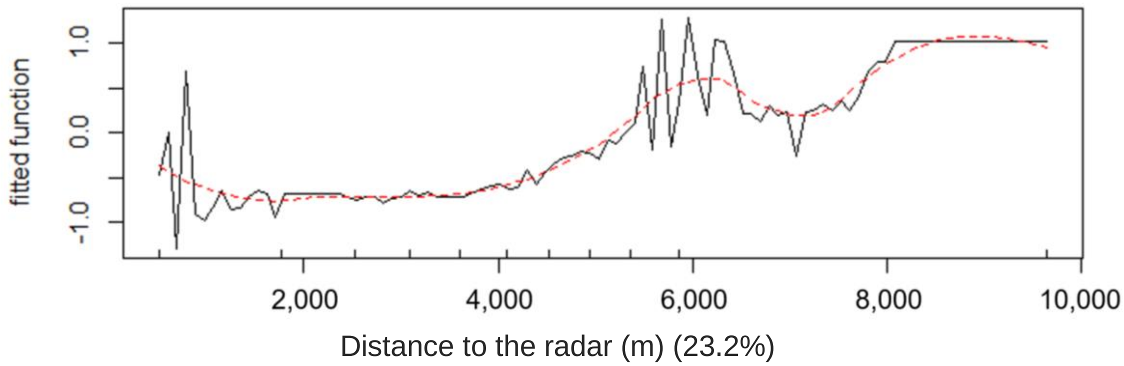
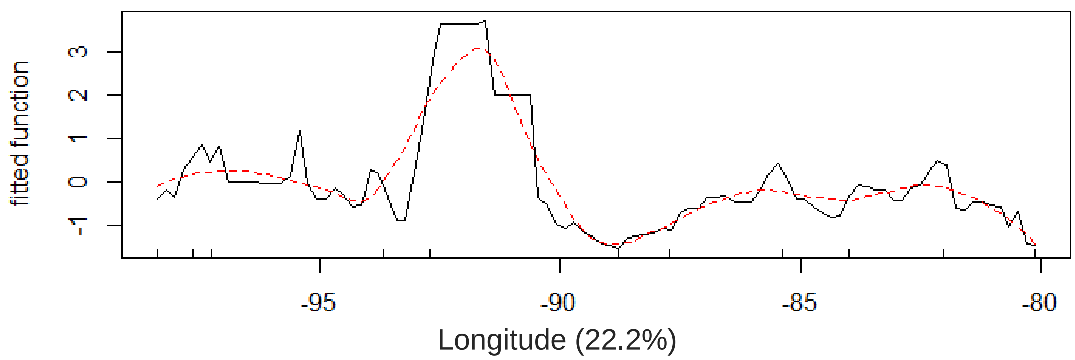
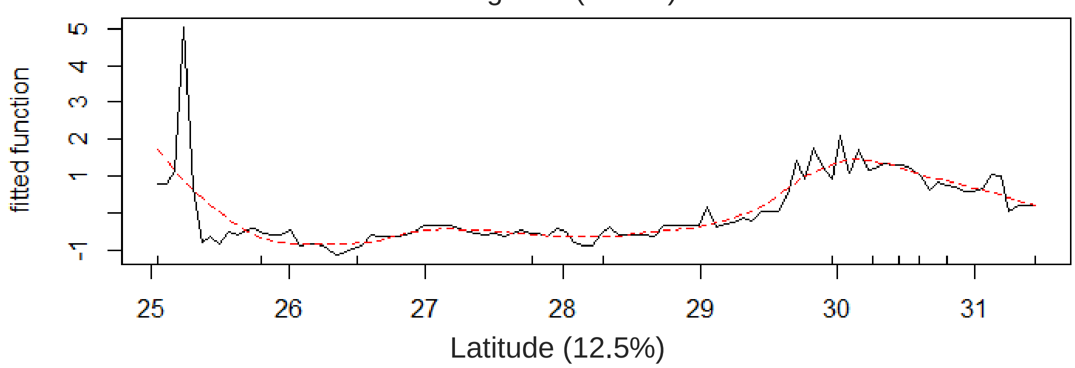


Figure A.1.1. Partial dependence plots for geographic, landscape, corrective, and departure weather predictor variables produced by the boosted regression tree model including migratory weather as a single variable with 36 levels of the combinations of lag time and synoptic weather type and mean vertically-integrated reflectivity as the response variable. The plots are ranked in order of their influence; each plot is labeled with the predictor variable and percent relative influence. The red dashed line represents the smoothed predicted response, and rug plots along the x-axis show the distribution of data. The departure weather variable includes the nine synoptic weather types (BH = Bermuda High, ECH = Eastern Continental High, ELOW = East Coast Low, GFC = Central Gulf Front, GFE = Eastern Gulf Front, GFW = Western Gulf Front, GH = Gulf High, MCH = Midwest Continental High, and Other).


fitted function
1.0
0.0
-1.0
2,000
4,000
6,000
8,000
10,000
Distance to the radar (m) (23.2%)


fitted function
3
2
1
0
-1
-95
-90
-85
-80
Longitude (22.2%)


fitted function
5
4
3
2
1
-1
25
26
27
28
29
30
31
Latitude (12.5%)

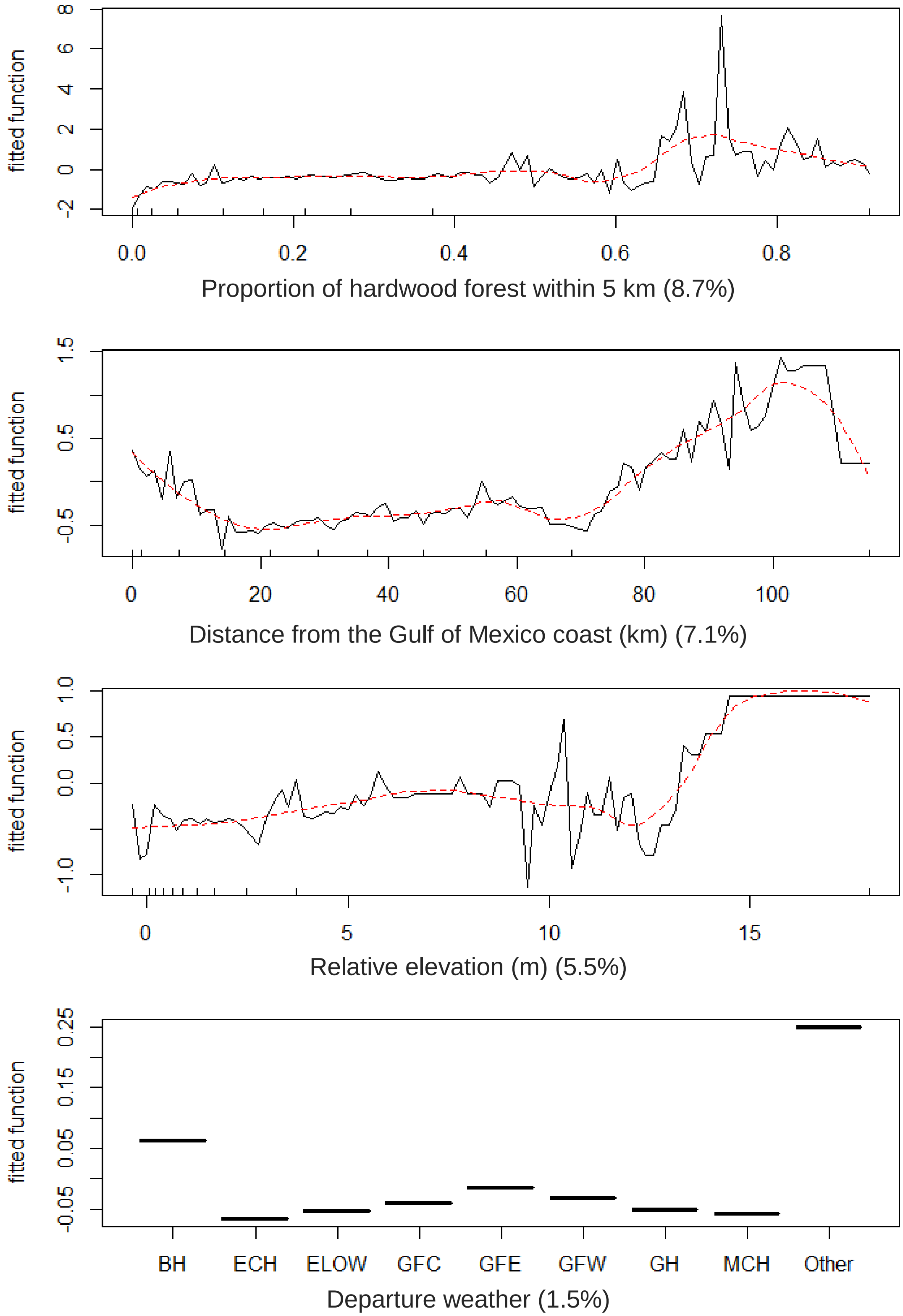
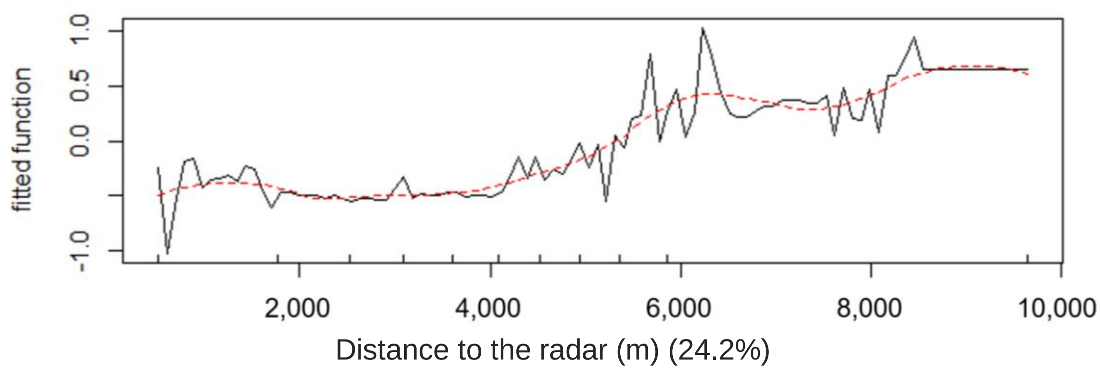
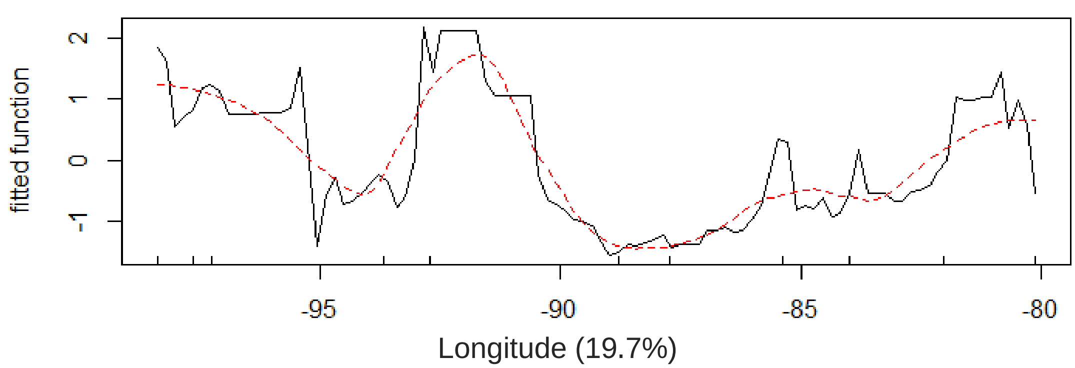
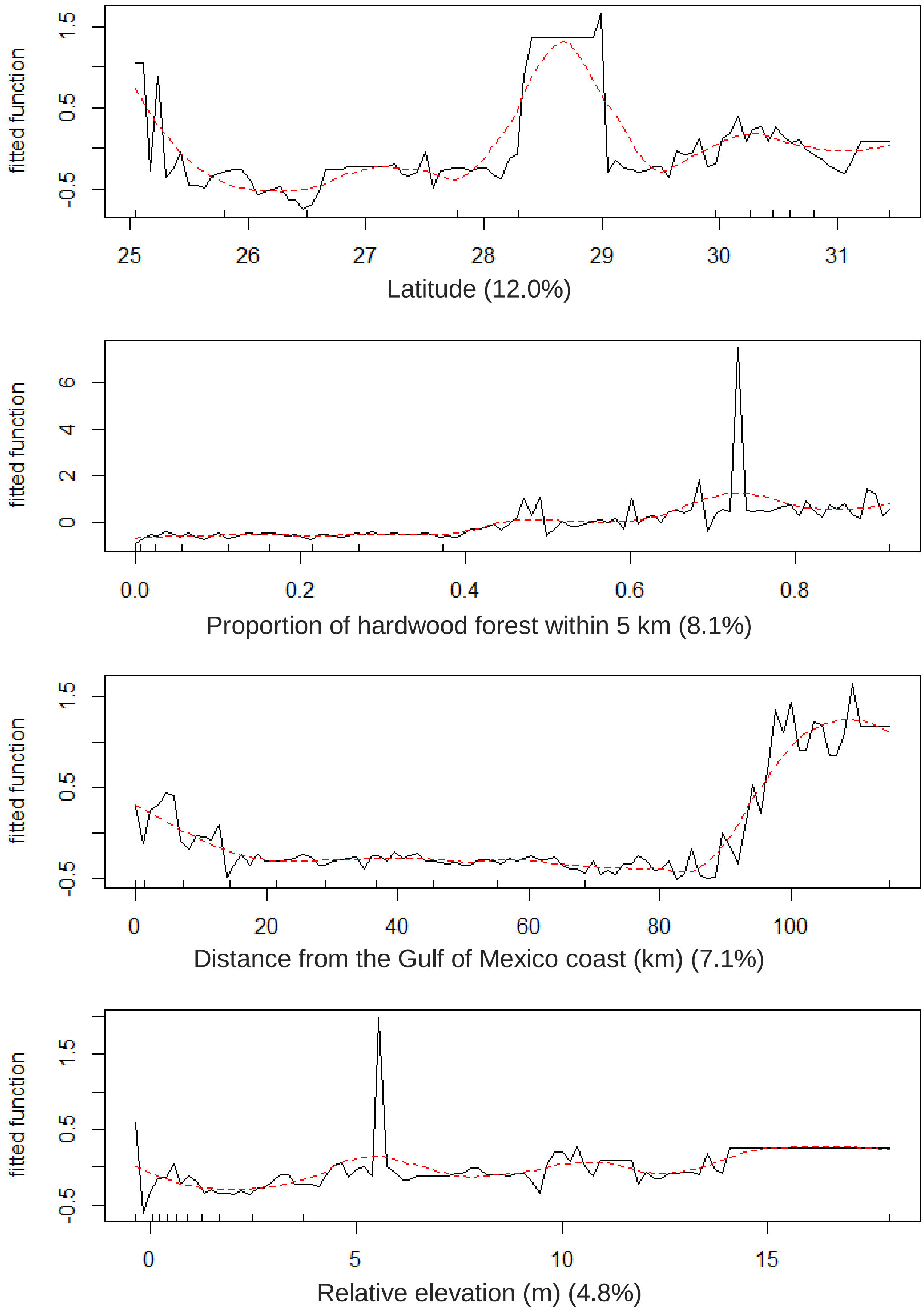

fitted function
8
6
4
2
0
-2
0.0
0.2
0.4
0.6
0.8
Proportion of hardwood forest within 5 km (8.7%)
fitted function
1.5
0.5
-0.5
0
20
40
60
80
100
Distance from the Gulf of Mexico coast (km) (7.1%)
fitted function
1.0
0.5
0.0
-1.0
0
5
10
15
Relative elevation (m) (5.5%)
fitted function
0.25
0.15
0.05
-0.05
BH
ECH
ELOW
GFC
GFE
GFW
GH
MCH
Other
Departure weather (1.5%)

Figure A.1.2. Partial dependence plots for geographic, landscape, corrective, and departure weather predictor variables produced by boosted regression tree models including each synoptic weather type added as a separate variable, with days after synoptic weather occurrence as the factor levels and mean vertically-integrated reflectivity as the response variable. The plots are ranked in order of their influence; each plot is labeled with the predictor variable and percent relative influence. The red dashed line represents the smoothed predicted response, and rug plots along the x-axis show the distribution of data. The departure weather variable includes the nine synoptic weather types (BH = Bermuda High, ECH = Eastern Continental High, ELOW = East Coast Low, GFC = Central Gulf Front, GFE = Eastern Gulf Front, GFW = Western Gulf Front, GH = Gulf High, MCH = Midwest Continental High, and Other).






fitted function
-0.5
0.5
1.5
25
26
27
28
29
30
31
Latitude (12.0%)
fitted function
0
2
4
6
0.0
0.2
0.4
0.6
0.8
Proportion of hardwood forest within 5 km (8.1%)
fitted function
-0.5
0.5
1.5
0
20
40
60
80
100
Distance from the Gulf of Mexico coast (km) (7.1%)
fitted function
-0.5
0.5
1.5
0
5
10
15
Relative elevation (m) (4.8%)

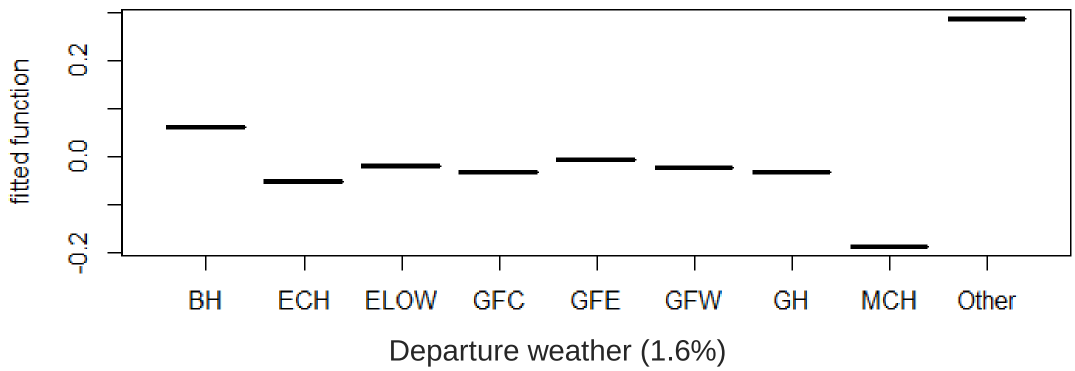
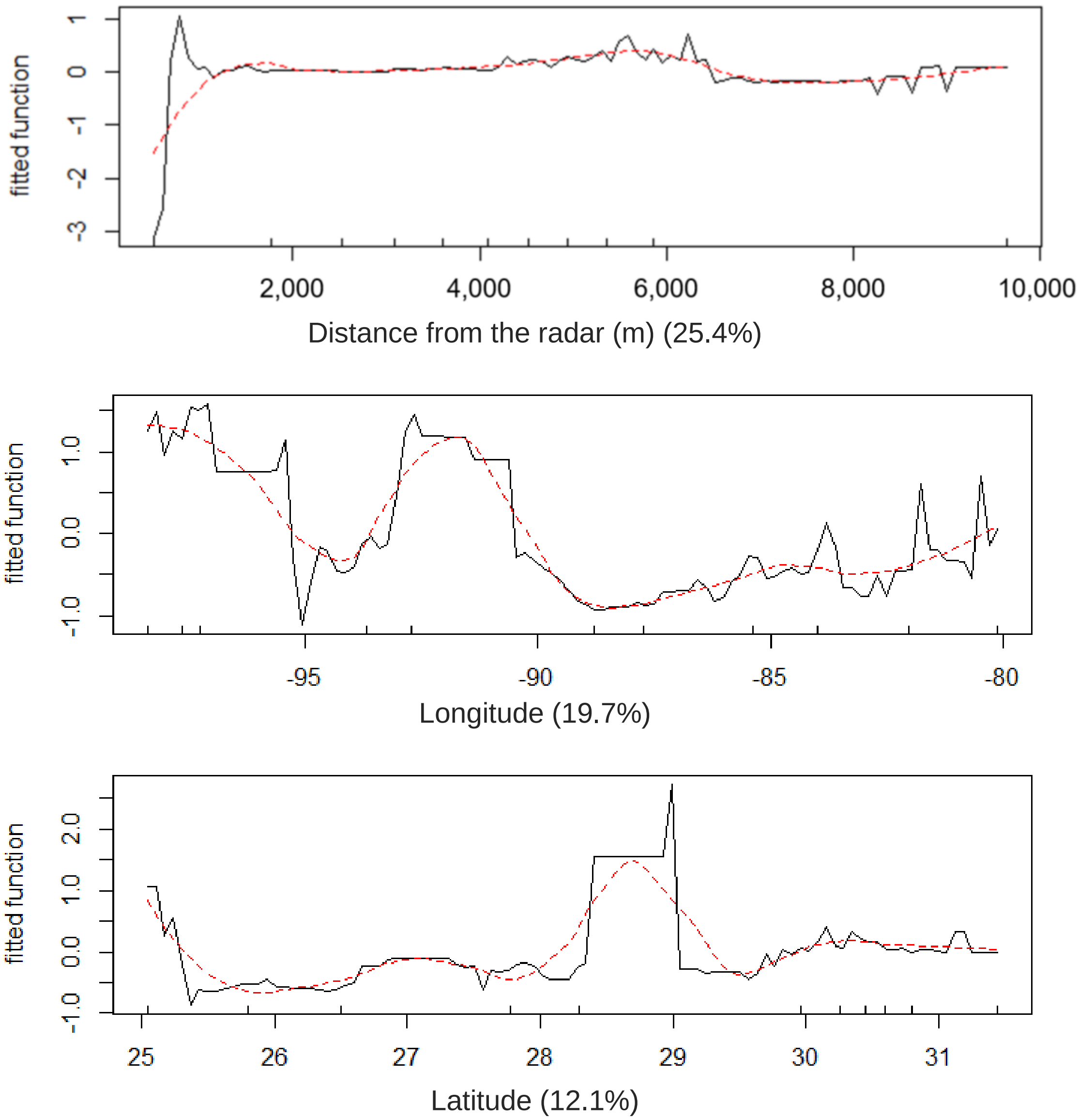


Figure A.1.3. Partial dependence plots for geographic, landscape, corrective, and departure weather predictor variables produced by boosted regression tree models including each day after synoptic weather occurrence added as a separate variable, with the synoptic weather types as the factor levels and mean vertically-integrated reflectivity as the response variable. The plots are ranked in order of their influence; each plot is labeled with the predictor variable and percent relative influence. The red dashed line represents the smoothed predicted response, and rug plots along the x-axis show the distribution of data. The departure weather variable includes the nine synoptic weather types (BH = Bermuda High, ECH = Eastern Continental High, ELOW = East Coast Low, GFC = Central Gulf Front, GFE = Eastern Gulf Front, GFW = Western Gulf Front, GH = Gulf High, MCH = Midwest Continental High, and Other).


fitted function
1
0
-1
-2
-3
2,000
4,000
6,000
8,000
10,000
Distance from the radar (m) (25.4%)
fitted function
1.0
0.0
-1.0
-95
-90
-85
-80
Longitude (19.7%)
fitted function
2.0
1.0
0.0
-1.0
25
26
27
28
29
30
31
Latitude (12.1%)

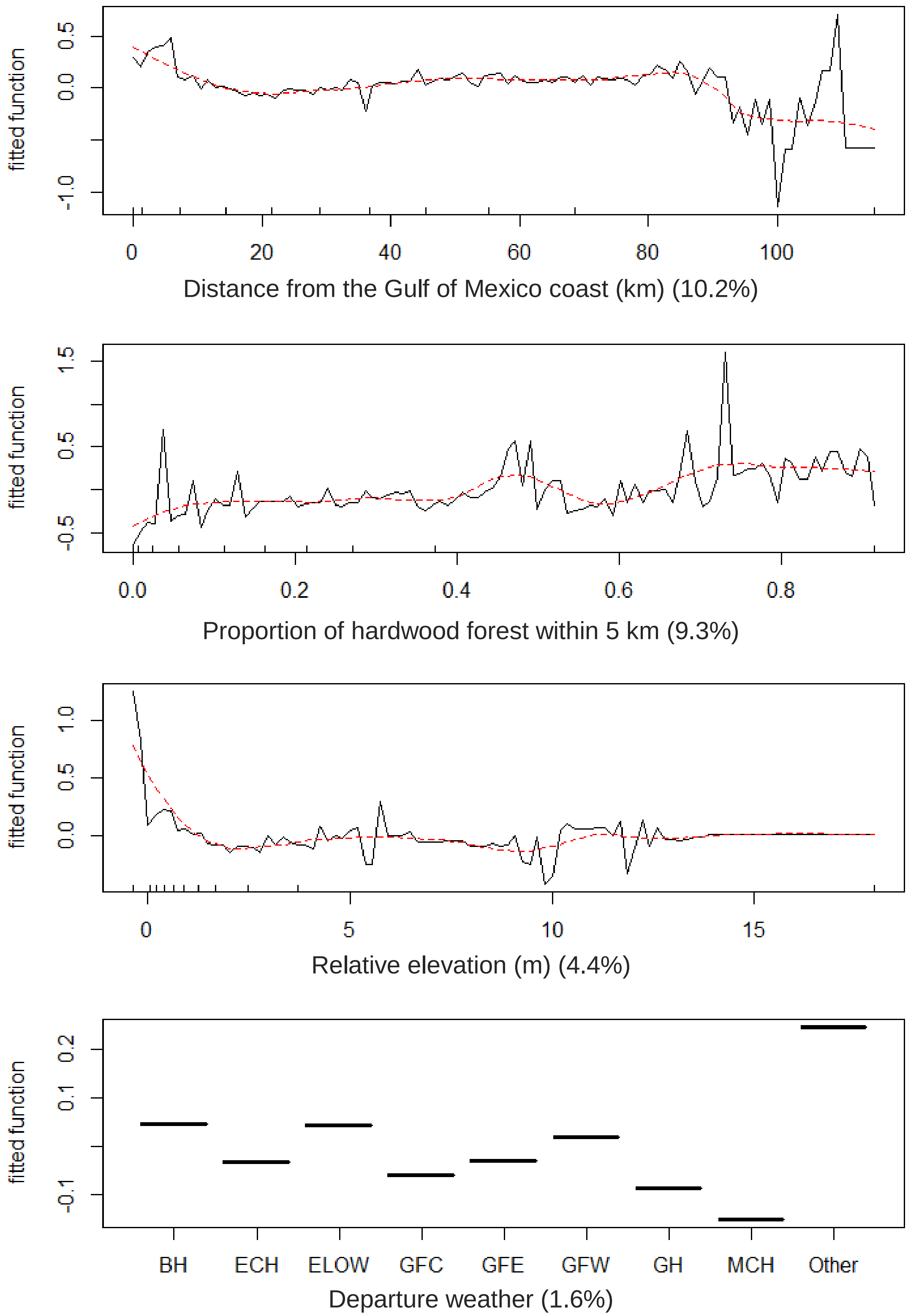

fitted function
-1.0
0.0
0.5
0
20
40
60
80
100
Distance from the Gulf of Mexico coast (km) (10.2%)
fitted function
-0.5
0.5
1.5
0.0
0.2
0.4
0.6
0.8
Proportion of hardwood forest within 5 km (9.3%)
fitted function
0.0
0.5
1.0
0
5
10
15
Relative elevation (m) (4.4%)
fitted function
-0.1
0.1
0.2
BH
ECH
ELOW
GFC
GFE
GFW
GH
MCH
Other
Departure weather (1.6%)

Figure A.1.4. Partial dependence plots for geographic, landscape, corrective, and departure weather predictor variables produced by boosted regression tree models including each combination of lag time and synoptic weather type added as a separate variable, with mean vertically-integrated reflectivity as the response variable. The plots are ranked in order of their influence; each plot is labeled with the predictor variable and percent relative influence. The red dashed line represents the smoothed predicted response, and rug plots along the x-axis show the distribution of data. The departure weather variable includes the nine synoptic weather types (BH = Bermuda High, ECH = Eastern Continental High, ELOW = East Coast Low, GFC = Central Gulf Front, GFE = Eastern Gulf Front, GFW = Western Gulf Front, GH = Gulf High, MCH = Midwest Continental High, and Other).

A.2 Partial dependence plot for synoptic weather encountered during migration over the Gulf of Mexico and interaction plots produced by the boosted regression tree model with overall synoptic weather as a single predictor variable

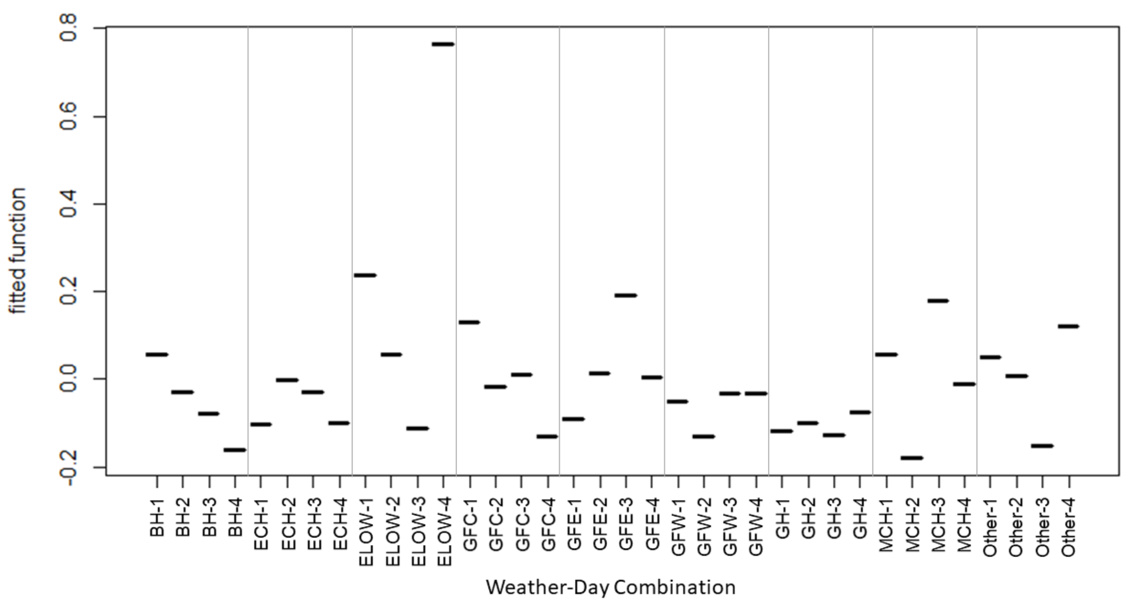


Figure A.2.1. Partial dependence plot for synoptic weather encountered during migration over the Gulf of Mexico, produced by the boosted regression tree model including overall synoptic weather as a single variable with 36 levels of the combinations of lag time (day after synoptic weather occurrence) and synoptic weather type and mean vertically-integrated reflectivity as the response variable. The synoptic weather types include Bermuda High (BH), Eastern Continental High (ECH), East Coast Low (ELOW), Central Gulf Front (GFC), Eastern Gulf Front (GFE), Western Gulf Front (GFW), Gulf High (GH), Midwest Continental High (MCH), and Other. The number after the synoptic weather type denotes the number of days after synoptic weather occurrence.

Table A.2.1. The strength of two-way interactions among predictor variables indicated by the boosted regression tree model including overall synoptic weather as a single variable with 36 levels of the combinations of lag time and synoptic weather type and mean vertically-integrated reflectivity as the response variable. Predictor variables included latitude, longitude, distance from the Gulf of Mexico coast (dist coast), departure weather, synoptic weather encountered during migration over the Gulf of Mexico, and the proportion of hardwood forest within 5 km (hardwood).

Interaction	Longitude	Dist coast	Departure weather	Synoptic weather	Hardwood
Latitude	309.6	4.2	35.8	146.2	9.0
Longitude		42.2	42.8	304.3	108.2
Dist coast			19.1	198.8	32.8
Departure weather				0.0	11.0
Synoptic weather					66.0

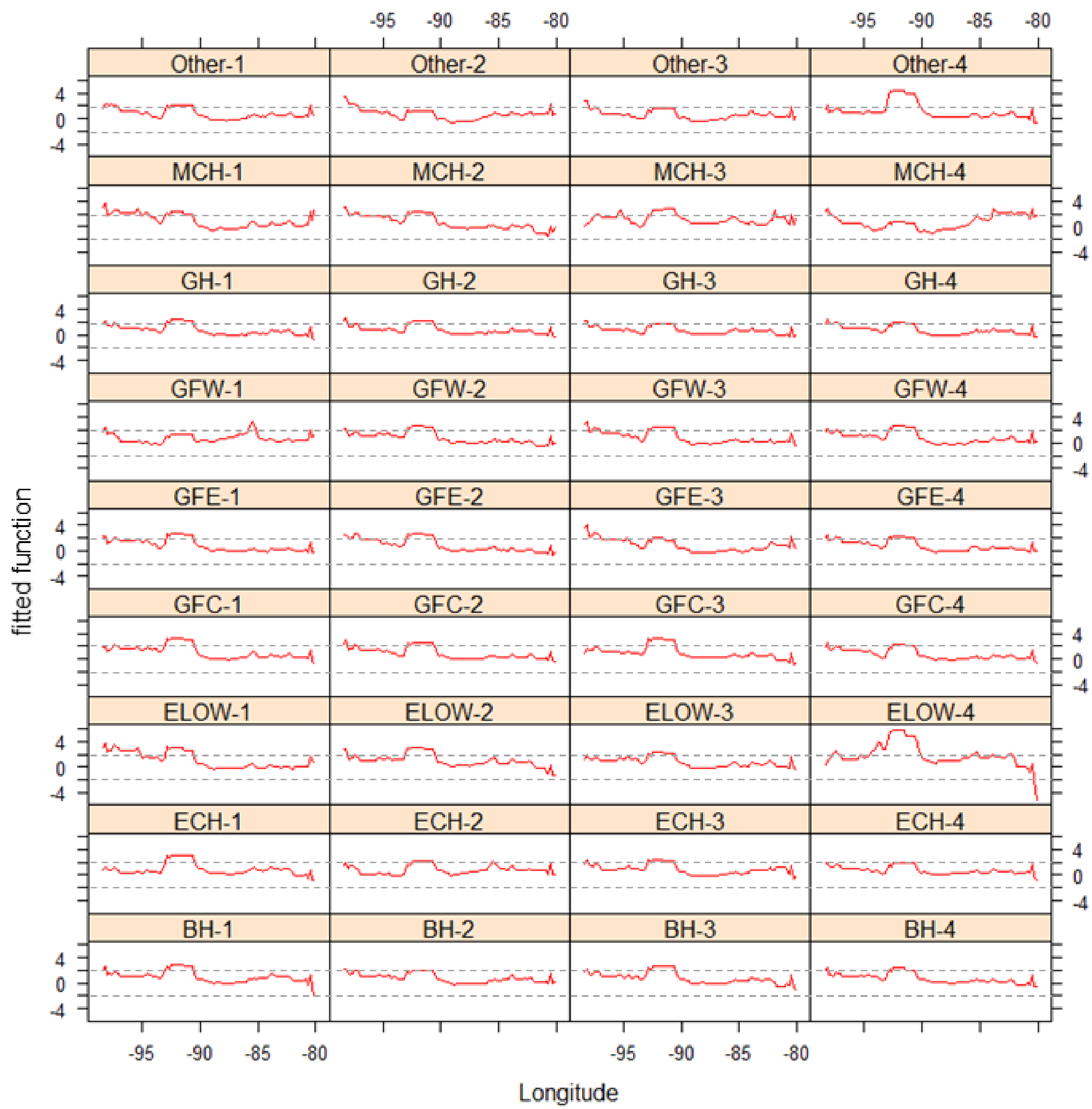


Figure A.2.2. Partial dependence interaction plot for synoptic weather and longitude, produced by the boosted regression tree model including overall synoptic weather as a single variable with 36 levels of the combinations of lag time and synoptic weather type and mean vertically-integrated reflectivity as the response variable. The synoptic weather types include Bermuda High (BH), Eastern Continental High (ECH), East Coast Low (ELOW), Central Gulf Front (GFC), Eastern Gulf Front (GFE), Western Gulf Front (GFW), Gulf High (GH), Midwest Continental High (MCH), and Other. The number after the synoptic weather type denotes the number of days after synoptic weather occurrence.

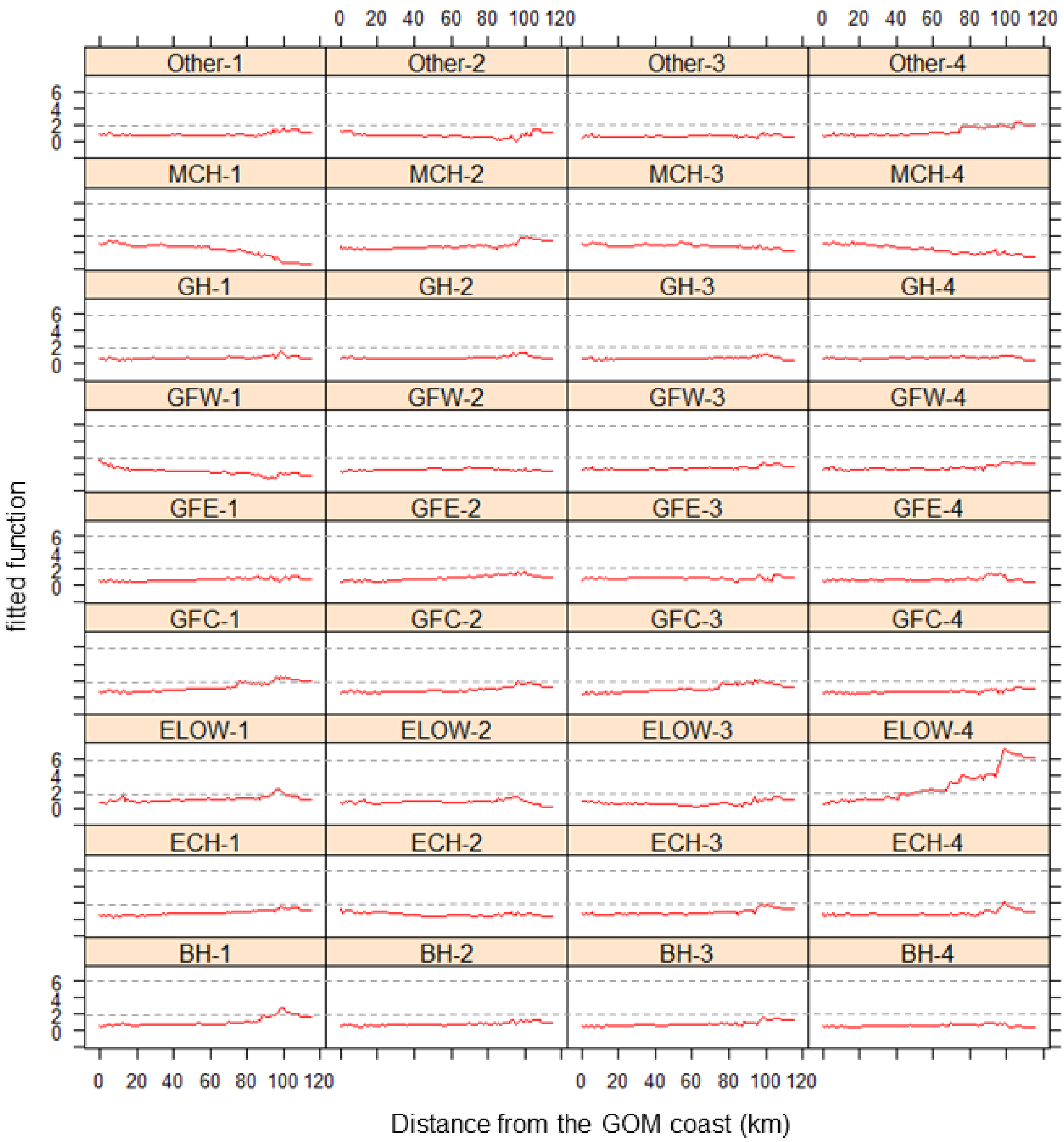


Figure A.2.3. Partial dependence interaction plot for synoptic weather and distance from the Gulf of Mexico (GOM) coast, produced by the boosted regression tree model including overall synoptic weather as a single variable with 36 levels of the combinations of lag time and synoptic weather type and mean vertically-integrated reflectivity as the response variable. The synoptic weather types include Bermuda High (BH), Eastern Continental High (ECH), East Coast Low (ELOW), Central Gulf Front (GFC), Eastern Gulf Front (GFE), Western Gulf Front (GFW), Gulf High (GH), Midwest Continental High (MCH), and Other. The number after the synoptic weather type denotes the number of days after synoptic weather occurrence.

A.3 Interaction plots produced by the boosted regression tree model including each synoptic weather type added as a separate predictor variable

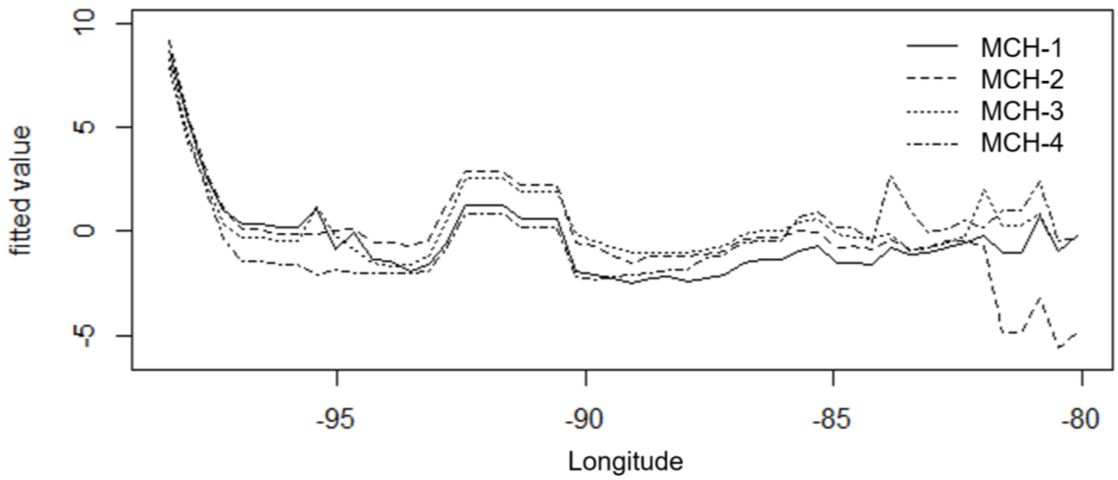


Figure A.3.1. Partial dependence interaction plots for longitude and the Midwest Continental High (MCH) weather type, produced by the boosted regression tree model including each synoptic weather type added as a separate variable, with the days (1–4) after synoptic weather occurrence as the factor levels and mean vertically-integrated reflectivity as the response variable.

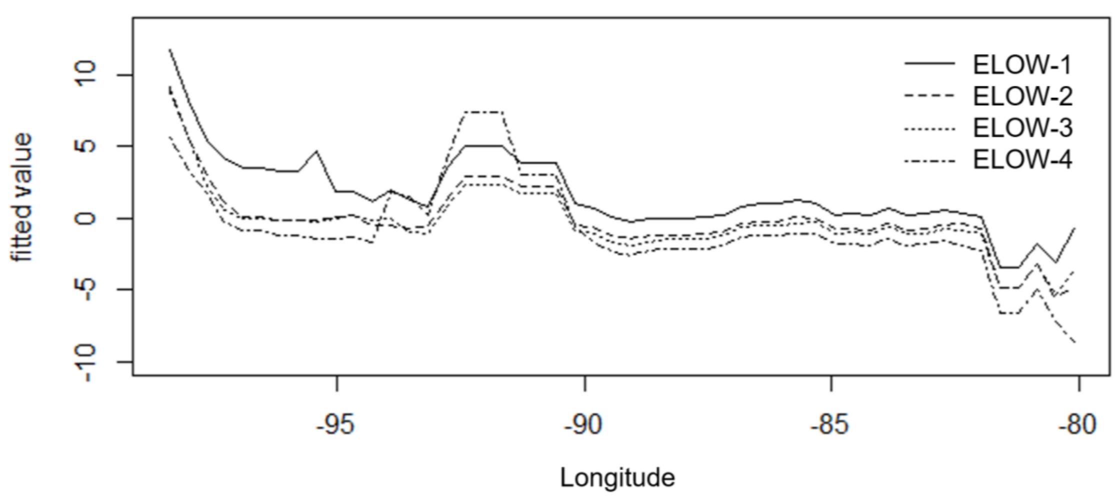


Figure A.3.2. Partial dependence interaction plots for longitude and the East Coast Low (ELOW) weather type, produced by the boosted regression tree model including each synoptic weather type added as a separate variable, with the days (1–4) after synoptic weather occurrence as the factor levels and mean vertically-integrated reflectivity as the response variable.

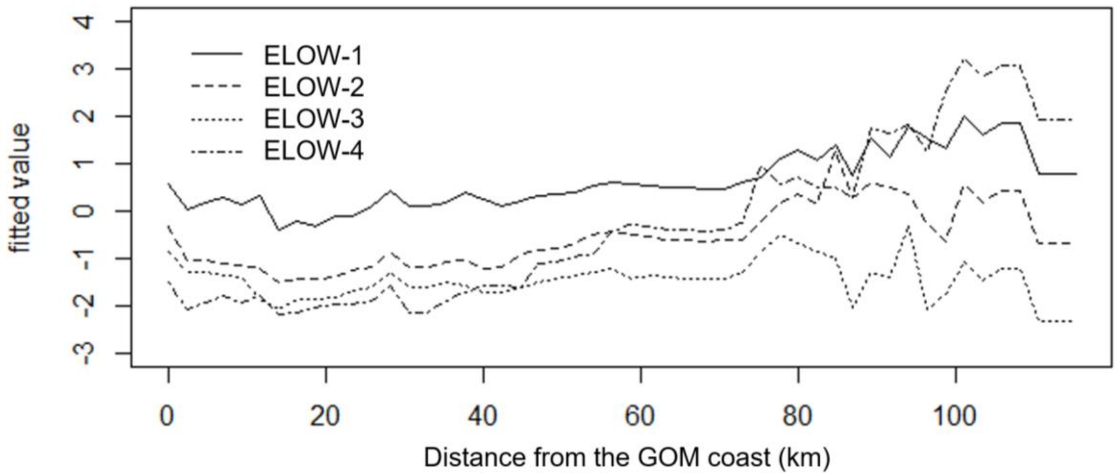


Figure A.3.3. Partial dependence interaction plots for distance from the Gulf of Mexico (GOM) coast and the East Coast Low (ELOW) weather type, produced by the boosted regression tree model including each synoptic weather type added as a separate variable, with the days (1–4) after synoptic weather occurrence as the factor levels and mean vertically-integrated reflectivity as the response variable.

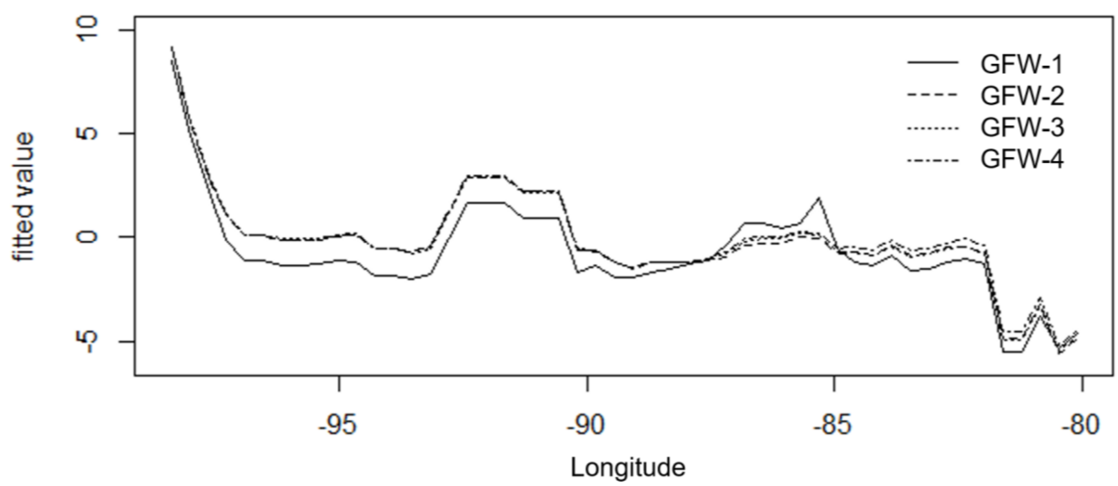


Figure A.3.4. Partial dependence interaction plots for longitude and the Western Gulf Front (GFW) weather type, produced by the boosted regression tree model including each synoptic weather type added as a separate variable, with the days (1–4) after synoptic weather occurrence as the factor levels and mean vertically-integrated reflectivity as the response variable.

A.4 Interaction plots produced by the boosted regression tree model including each day after synoptic weather occurrence added as a separate predictor variable

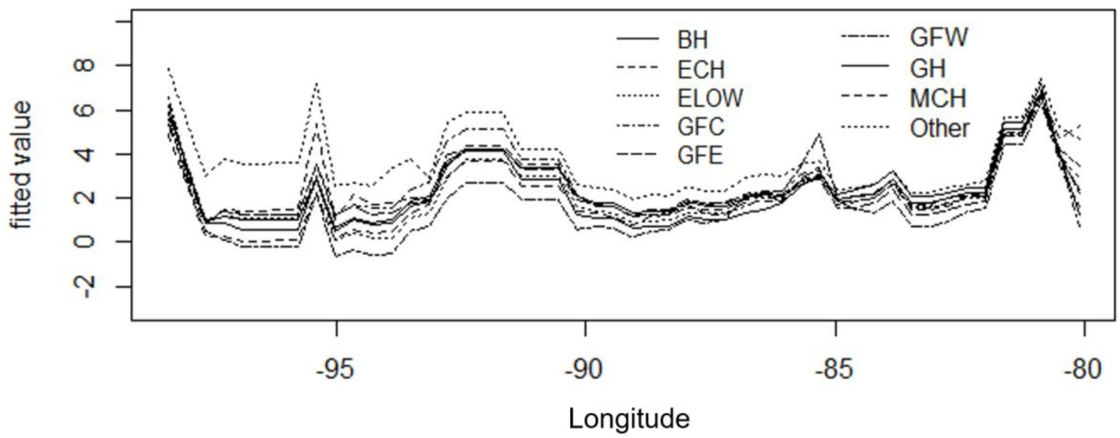


Figure A4.1. Partial dependence interaction plots for longitude and synoptic weather the day before departure, produced by the boosted regression tree model including each day after synoptic weather occurrence added as a separate variable, with the synoptic weather types as the factor levels and mean vertically-integrated reflectivity as the response variable.

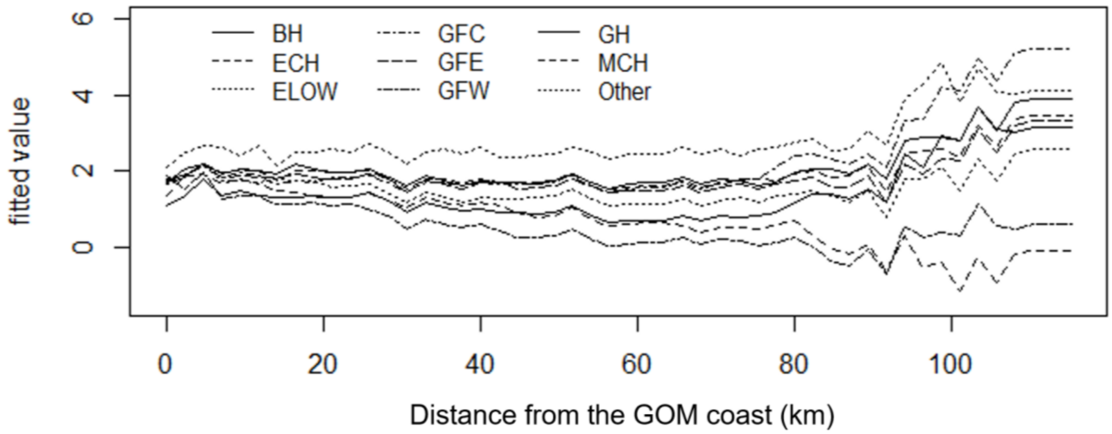


Figure A.4.2. Partial dependence interaction plots for distance from the Gulf of Mexico (GOM) coast and synoptic weather the day before departure, produced by the boosted regression tree model including each day after synoptic weather occurrence added as a separate variable, with the synoptic weather types as the factor levels and mean vertically-integrated reflectivity as the response variable.

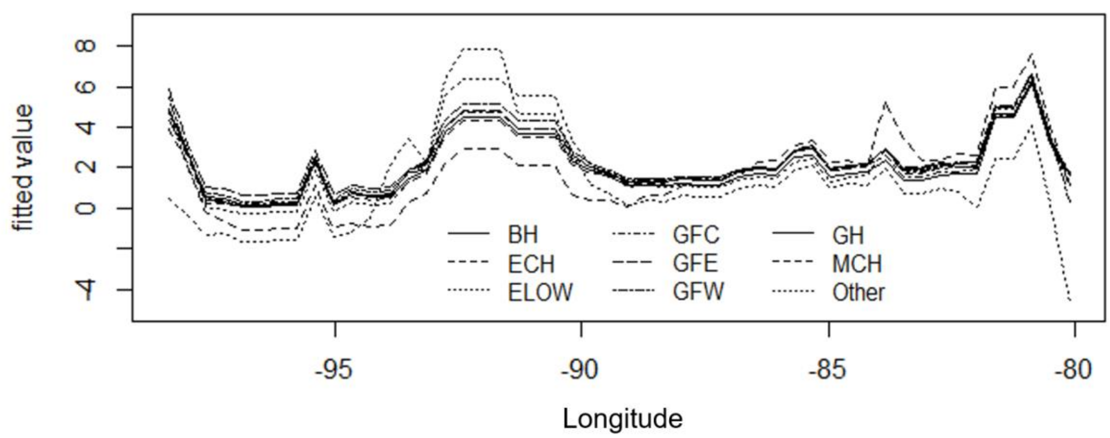


Figure A.4.3. Partial dependence interaction plots for longitude and synoptic weather four days before departure, produced by the boosted regression tree model including each day after synoptic weather occurrence added as a separate variable, with the synoptic weather types as the factor levels and mean vertically-integrated reflectivity as the response variable.

A.5 Relative percent influence from the four boosted regression tree models run with the equal sample size dataset as post-hoc analysis

Table A.5.1. Relative influence of the predictor variables from the four boosted regression tree models run with the equal sample size dataset as post-hoc analysis.

Model	Predictor Variable	% Relative Influence
Model 1[a]: Does synoptic weather influence if and where birds stopover?	Overall synoptic weather	41.4
	Longitude	13.7
	Latitude	11.4
	Proportion of hardwood forest within 5 km	6.7
	Distance from the GOM coast	4.0
	Departure weather	3.1
Model 2[b]: What are the most influential synoptic weather types?	Longitude	12.7
	Latitude	11.6
	Proportion of hardwood forest within 5 km	8.2
	Distance from the GOM coast	6.8
	Eastern Continental High	6.6
	Departure weather	5.0
	Bermuda High	2.8
	Eastern Gulf Front	1.6
	Rest of the synoptic weather types	<1.3 each
Model 3[c]: How long do birds generally remain at stopover sites after a synoptic weather event?	Longitude	14.1
	1 day after synoptic weather	12.5
	Latitude	10.6
	Proportion of hardwood forest within 5 km	6.8
	Distance from the GOM coast	6.8
	Departure weather	5.4
	2 days after synoptic weather	4.8
	3 days after synoptic weather	3.5
	4 days after synoptic weather	2.5
Model 4[d]: How long do birds stopover under specific synoptic weather types?	Longitude	14.2
	Latitude	11.7
	Distance from the GOM coast	8.4
	Proportion of hardwood forest within 5 km	8.1
	Departure weather	5.3
	1 day after East Continental High	3.2
	2 days after Bermuda High	2.6

	4 days after East Coast Low	1.2
	Rest of the combinations of lag time and synoptic weather type	<1.0 each

[a] Percent deviance explained: 47.8; CV correlation: 0.593; Final number of trees: 4300
[b] Percent deviance explained: 53.1; CV correlation: 0.640; Final number of trees: 8600
[c] Percent deviance explained: 52.1; CV correlation: 0.628; Final number of trees: 7600
[d] Percent deviance explained: 48.3; CV correlation: 0.608; Final number of trees: 3800

Appendix B

INFLUENCE OF WIND ON BIRD STOPOVER DENSITY

B.1 Interaction values between low-altitude winds aloft and other variables

Table B.1.1. Interaction sizes for interactions between wind and geographic, landscape composition, and other variables from the boosted regression tree analysis of monthly mean vertically-integrated reflectivity across the full Gulf of Mexico coast. Predictor variables listed in this table include: longitude; distance from the coast (dist coast); the proportion of hardwood forest (hardwood), agricultural land cover (agriculture), and urban land cover (urban) within 5 km; distance from bright artificial light at night (dist light); normalized difference vegetation index (NDVI); and the N-S and E-W components of the Gulf of Mexico (GOM), Atlantic Ocean (AO), and Caribbean Sea (CS). The strongest interactions for each wind variable are bolded.

	N-S wind component			E-W wind component		
Interactive variable	GOM	AO	CS	GOM	AO	CS
Longitude	**66.35**	**35.98**	**92.97**	6.38	6.08	**52.35**
Dist coast	**79.65**	4.35	**51.81**	9.26	20.32	9.95
Hardwood	2.47	11.58	12.72	16.65	4.73	8.56
Agriculture	3.55	3.51	11.69	1.82	0.62	0.74
Urban	3.04	1.57	3.43	0.11	0.67	1.28
Dist light	**57.03**	**113.82**	**136.02**	**211.77**	**417.01**	6.79
NDVI	1.42	2.65	15.30	9.48	9.10	3.91

Table B.1.2. Interaction sizes for interactions between wind and geographic, landscape composition, and other variables from the boosted regression tree analysis of monthly mean vertically-integrated reflectivity across the western Gulf of Mexico coast. Predictor variables listed in this table include: longitude; distance from the coast (dist coast); the proportion of hardwood forest (hardwood), agricultural land cover (agriculture), and urban land cover (urban) within 5 km; distance from bright artificial light at night (dist light); normalized difference vegetation index (NDVI); and the N-S and E-W components of the Gulf of Mexico (GOM), Atlantic Ocean (AO), and Caribbean Sea (CS). The strongest interactions for each wind variable are bolded.

Interactive variable	N-S wind component			E-W wind component		
	GOM	AO	CS	GOM	AO	CS
Longitude	**28.81**	2.0	**12.51**	0.14	1.7	1.62
Dist coast	5.86	4.82	**44.2**	6.87	1.09	3.76
Hardwood	0.45	**24.53**	2.58	4.8	3.09	0.48
Agriculture	1.34	7.89	0.78	0.69	1.3	0.67
Urban	0.41	1.07	2.39	0.28	0.03	0.14
Dist light	**18.03**	1.37	**14.64**	**209.9**	**79.78**	**10.68**
NDVI	2.46	1.81	8.34	0.16	0.86	0.65

Table B.1.3. Interaction sizes for interactions between wind and geographic, landscape composition, and other variables from the boosted regression tree analysis of monthly mean vertically-integrated reflectivity across the central Gulf of Mexico coast. Predictor variables listed in this table include: longitude; distance from the coast (dist coast); the proportion of hardwood forest (hardwood), agricultural land cover (agriculture), and urban land cover (urban) within 5 km; distance from bright artificial light at night (dist light); normalized difference vegetation index (NDVI); and the N-S and E-W components of the Gulf of Mexico (GOM), Atlantic Ocean (AO), and Caribbean Sea (CS). The strongest interactions for each wind variable are bolded.

Interactive variable	N-S wind component			E-W wind component		
	GOM	AO	CS	GOM	AO	CS
Longitude	**39.74**	**67.89**	**41.02**	**29.05**	4.16	**157.93**
Dist coast	**38.72**	**50.77**	8.41	2.41	2.79	**21.51**
Hardwood	1.65	14.81	2.36	12.27	0.24	0.44
Agriculture	2.35	0.23	1.42	1.91	0.07	0.77
Urban	0.56	0.60	0.19	0.24	1.16	0.53
Dist light	**34.16**	8.91	**28.30**	7.39	**40.38**	**14.59**

NDVI	14.4	1.56	1.57	0.03	1.46	1.03

Table B.1.4. Interaction sizes for interactions between wind and geographic, landscape composition, and other variables from the boosted regression tree analysis of monthly mean vertically-integrated reflectivity across the eastern Gulf of Mexico coast. Predictor variables listed in this table include: longitude; distance from the coast (dist coast); the proportion of hardwood forest (hardwood), agricultural land cover (agriculture), and urban land cover (urban) within 5 km; distance from bright artificial light at night (dist light); normalized difference vegetation index (NDVI); and the N-S and E-W components of the Gulf of Mexico (GOM), Atlantic Ocean (AO), and Caribbean Sea (CS). The strongest interactions for each wind variable are bolded.

Interactive variable	N-S wind component			E-W wind component		
	GOM	AO	CS	GOM	AO	CS
Longitude	**91.54**	**30.93**	**83.31**	**51.21**	7.71	**34.89**
Dist coast	**36.07**	5.5	**116.77**	17.94	10.27	**47.4**
Hardwood	2.51	17.02	33.6	12.82	1.94	4.53
Agriculture	1.15	0.99	4.74	4.3	4.88	2.01
Urban	2.61	2.93	5.47	0.62	1.35	0.49
Dist light	7.78	14.27	**387.49**	8.42	**120.48**	22.51
NDVI	0.43	6.94	4.49	5.82	3.19	0.64

B.2 Interaction plots between low-altitude winds aloft and other variables

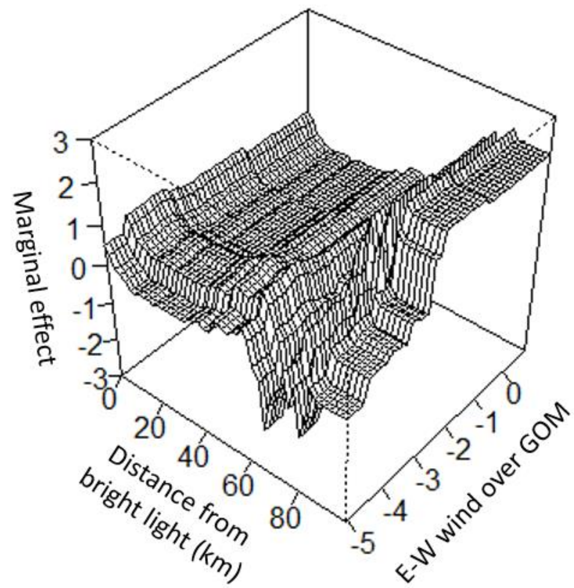


Figure B.2.1. Partial dependence plot of the interactions between the east-west (E-W) wind component (m/s) over the Gulf of Mexico (GOM) and distance from bright artificial light at night (km) produced by boosted regression trees predicting monthly mean vertically-integrated reflectivity (VIR) within the western GOM coast.

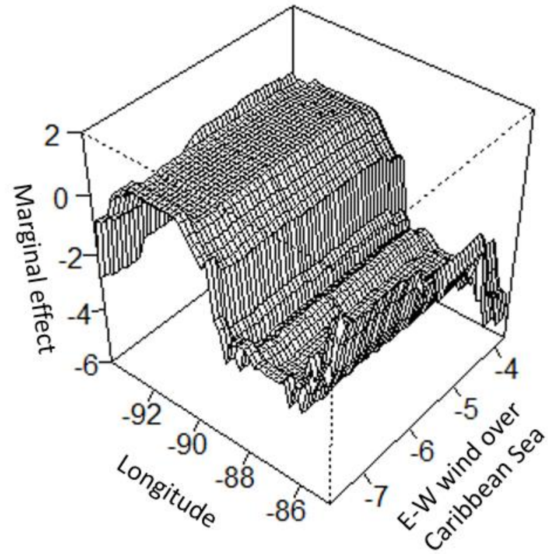


Figure B.2.2. Partial dependence plot of the interactions between the east-west (E-W) wind component (m/s) over the Caribbean Sea and longitude produced by boosted regression trees predicting monthly mean vertically-integrated reflectivity (VIR) within the central GOM coast.

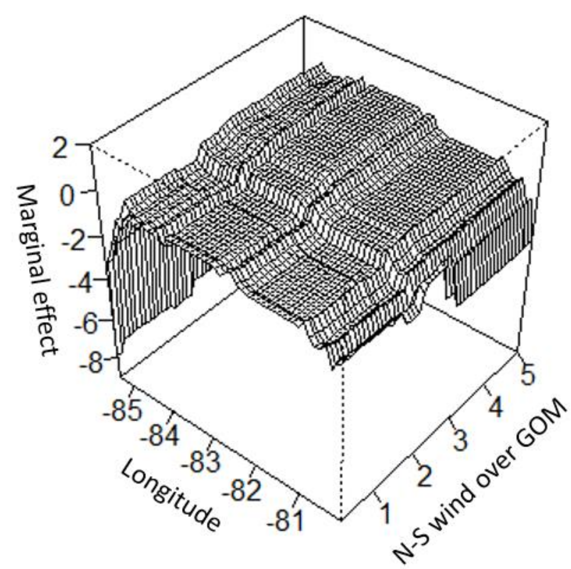


Figure B.2.3. Partial dependence plot of the interactions between the north-south (N-S) wind component (m/s) over the Gulf of Mexico (GOM) and longitude produced by boosted regression trees predicting monthly mean vertically-integrated reflectivity (VIR) within the eastern GOM coast.