

REPORT

STOPOVER ECOLOGY OF NEARCTIC-NEOTROPICAL LANDBIRD MIGRANTS
WITHIN AN URBAN COASTAL LANDSCAPE

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Executive Summary

1. Migratory landbirds stopover in urban landscapes along the immediate coast of the Gulf of Mexico during spring migration, yet little is known about the value of these habitats as stopover sites for migrants.
2. We measured migrant densities and fattening rates within coastal woodlots surrounded by urbanization to analyze extent of use of these habitats and to assess migrant performance.
3. Migrants were more concentrated in smaller forested patches and during afternoon surveys. Higher migrant densities late in the day suggest that migrants may be transient through coastal habitats.
4. Fattening rates as evidenced by circulating plasma triglyceride levels varied across coastal habitats, and trends at some sites suggested that competitive pressure may influence triglyceride levels.
5. Variation in triglyceride levels existed among foraging guilds, notably with higher fattening rates in understory foragers in larger forested patches.
6. Future work in similar landscapes with higher sample sizes and with analysis of other plasma metabolites may provide specific information regarding migrant refueling performance in a given landscape.
7. Future work may also incorporate migrant densities and refueling potential into the spatially explicit individual-based model of Cohen et al. (2013) for understanding quality of urbanized coastal habitats as stopover sites for landbirds.

Introduction

Habitat urbanization, fragmentation, and isolation negatively impact ecological communities across taxa (Marzluff et al. 2001, McKinney 2002). Human land use changes are responsible for massive ecosystem transformations, and it has been suggested that the degree of human-induced alteration of worldwide biological processes is sufficient to justify a new classification of geologic time known as the “Anthropocene” (Ellis 2011). Current and future projections of habitat change and urbanization effects show continued degradation with significant implications for conservation (Fahrig and Merriam 1994, McDonald et al. 2008). Migratory birds may be particularly vulnerable to large scale land change as they rely on many habitats over wide geographic ranges to accommodate their variable year round breeding, wintering, and stopover habitat needs (Greenberg and Marra 2005, Moore 2000). In addition, birds in urban environments at any phase of the annual cycle are directly exposed to the many mortality risks associated with anthropogenic presence including, but not limited to, structural collisions, predation by domesticated animals such as cats, and pollution (Erickson et al. 2005).

Most investigations of population limitation among migratory birds, including those addressing effects of habitat fragmentation and urbanization, focus primarily on breeding and wintering areas (Moore et al. 1995, Moore 2000). During non-migratory periods, long distance migrants show negative responses to urbanization in the form of both edge and area effects with forest area being one of the most important predictors of bird occurrence and abundance (Askins et al. 1987, Friesen et al. 1995, Moore and Hooper 1975, Whitcomb et al. 1981). Most species exhibit tendencies to avoid using small habitat patches and establishing territories near edges of forested areas (Freemark et al. 1993, Keyser et al. 1998, Lee et al. 2002, Lindell et al. 2007, Parker et al. 2005). For most forest-dwelling birds, likelihood of occurrence increases as patch area increases and is usually positively correlated with distance from edge of forested area. Edge effects may be particularly severe in a heavily urbanized landscape when potentially useable habitat may be directly bordered by harsh matrix characterized by impervious surfaces and large expanses devoid of resources (Keyser 2002). For example, effects on birds of residential development surrounding remnant forested patches include decreases in both diversity and abundance with increasing adjacent development and, specifically, with number of houses near remnant patches of various sizes (Friesen et al. 1995, Germaine et al. 1998, Miller et al. 2003).

Studies during migration highlight the importance of landscape context for habitat use by birds in spring, showing that use urban forests as stopover sites and that migrant densities are correlated positively with amount of surrounding forested cover and negatively correlated with surrounding building area (Ktitorov et al. 2008, Pennington et al. 2008). However, large gaps remain in our understanding of effects of habitat fragmentation on en route individuals. While weather surveillance radar reveals that urbanized areas are used by migrants during stopover (Buler and Moore 2011), complimentary ground-based examination of individuals within stopover habitat patches embedded in urban areas is critical to understanding performance of migrants during stopover in that environment. The urban landscape within the Mobile, AL (KMOB) radar surveillance area provides an ideal setting for study of en route migrants stopping in a heavily developed coastal area immediately following trans-Gulf flight when migrants may be energetically compromised.

Migrants often arrive along the Gulf coast in “waves” with large numbers of birds distributed among limited coastal habitats (Moore and Kerlinger 1987). Therefore, smaller, isolated woodlots may concentrate migrants into higher densities than in larger patches (see Diehl 2003). Investigation of differences in resources potentially available to migrants across stopover sites is integral to understanding migrant behavior, including refueling performance. As most landbird migrants are omnivorous during passage, characterization of the arthropod communities within stopover sites provides an estimate of prey available to migrants. Evidence suggests that urbanization may negatively impact arthropod diversity and abundance, and studies show positive correlations between arthropod abundance and forested patch size (Burke and Nol 1998, Denys and Schmidt 1998, Gibb and Hochuli 2002). Thus, determination of both migrant and arthropod densities within fragmented stopover habitats is necessary for insight to migrant distributions and refueling success with implications for quality of each patch during stopover.

En route migrants must utilize and maintain energy stores efficiently to maximize speed of migration and achieve an optimal travel scheme (Alerstam and Hedenstrom 1998). Therefore, fuel deposition rates may be considered a currency of success during migration, particularly following trans-Gulf flight when migrants must replenish depleted energy stores. Blood plasma metabolite levels are highly correlated with changes in body mass, and measurement of circulating metabolite concentrations (particularly triglycerides) is an effective method for assessing site-specific refueling performance by capturing birds once (Acevedo-Seaman et al. 2006, Guglielmo et al. 2002, Guglielmo 2005, Schaub and Jenni 2001). Plasma triglyceride concentrations are associated with feeding and fat deposition; therefore, measuring triglyceride levels provides an opportunity to look at refueling performances at sites of different size within an urbanized landscape.

Two recent studies show that birds in more advanced stages of their spring migratory journeys (i.e., at stopping sites farther north and often closer to breeding grounds) refuel in heavily urbanized stopover environments (Seewagen and Slayton 2008, Seewagen et al. 2011). However, it may be erroneous to assume that these findings apply at stopover sites adjacent to ecological barriers where energetic reserves upon arrival are often depleted. During stopover on the northern coast of the Gulf of Mexico, distribution patterns suggest that migratory birds select hardwood forest (Buler et al. 2007), and rates of mass gain show positive correlations with amount of forested cover in the landscape (Ktitorov et al. 2008, Rodewald and Brittingham 2007). Whereas evidence suggests that larger forested patches provide more suitable habitat than smaller isolated patches for most long distance migrants, en route migrant-habitat associations within highly fragmented, urbanized landscapes are poorly understood, particularly during initial stopover when birds are energetically constrained and opportunity for habitat selection is limited (Moore et al. 1995). The objective of this study was to investigate the behavioral and physiological responses of migrating birds stopping over in human-dominated landscapes along the Mississippi coast during the most energetically constrained time of the annual cycle.

Methods

Study Area

Replicated pairs of forested study sites that differ in size along the same latitude were established within a highly developed region of the Mississippi coast. Two similarly sized, large tracts of forest are paired with two small isolated forested patches embedded within residential settings (Figure 1). Two larger sites include the Davis Bayou Area (DAV) of the Gulf Islands National Seashore near the city of Ocean Springs (N 30° 23' 31.1706", W 88° 47' 27.495") and Shepard State Park (SHE) near the city of Gautier (N 30° 22' 31.317", W 88° 37' 57.1224"). Small sites include a woodlot of approximately one acre in size at Hellmers Lane (HEL) in Ocean Springs, Mississippi, (N 30° 24' 26.463", W 88° 49' 27.9834") with access provided by the Land Trust for the Mississippi Coastal Plain and an approximately one acre woodlot known as "Don's Woods" (DON) at Buena Vista Street in Pascagoula, Mississippi, (N 30° 20' 51.486", W 88° 33' 4.3122") with access provided by private landowners. On the western side of the study region, the large site, DAV, is paired with the small woodlot HEL, and the remaining two sites, SHE and DON, are paired ~ 17 km to the east.

We characterized vegetative structure within each patch by sampling horizontal cover, community composition, canopy density, and ground cover using James and Shugart (1970) circular plots, a horizontal cover board (Nudds 1977), and Daubenmire quadrats (Daubenmire 1959). Abundant tree species at all sites included water oak (*Quercus nigra*), live oak (*Quercus virginiana*), loblolly pine (*Pinus taeda*), slash pine (*Pinus elliottii*), sweetgum (*Liquidambar styraciflua*), southern magnolia (*Magnolia grandiflora*), sweetbay magnolia (*Magnolia virginiana*), and Chinese tallow (*Sapium sebifera*). Dominant shrub and ground species included gallberry (*Ilex glabra*), yaupon (*Ilex vomitoria*), Japanese climbing fern (*Lygodium japonicum*), trumpet creeper (*Campsis radicans*), *Rhus* spp., Muscadine vine (*Vitis rotundifolia*), and common greenbrier (*Smilax rotundifolia*). Average overstory density was >85% at all sites (Table 1). Average maximum canopy height was slightly lower at the two small sites, while average shrub layer height was consistent across all sites. Average horizontal cover was slightly lower at the two eastern-most study sites. Average percent of ground covered in leaf litter was ≥75% at all sites except DON where ground cover was frequently grass.

Table 1. Measurements of vegetation including canopy height/density, tree size (diameter at breast height), shrub layer height, and horizontal cover (means ± SE).

Site	Mean canopy height (ft)	Mean shrub layer height (m)	Mean percent canopy closure	Mean tree dbh (cm)	Mean percent horizontal cover
HEL	62.3 ± 5.78	2.67 ± 0.44	86.21 ± 1.46	20.17 ± 2.29	72.72
DAV	82 ± 8.08	2.58 ± 0.30	90.50 ± 1.18	17.28 ± 1.43	87.98
DON	59.3 ± 0.67	2.33 ± 0.33	88.76 ± 1.59	18.28 ± 1.54	67.2
SHE	78 ± 4.16	2.83 ± 0.44	91.23 ± 0.63	22.92 ± 1.15	63.78

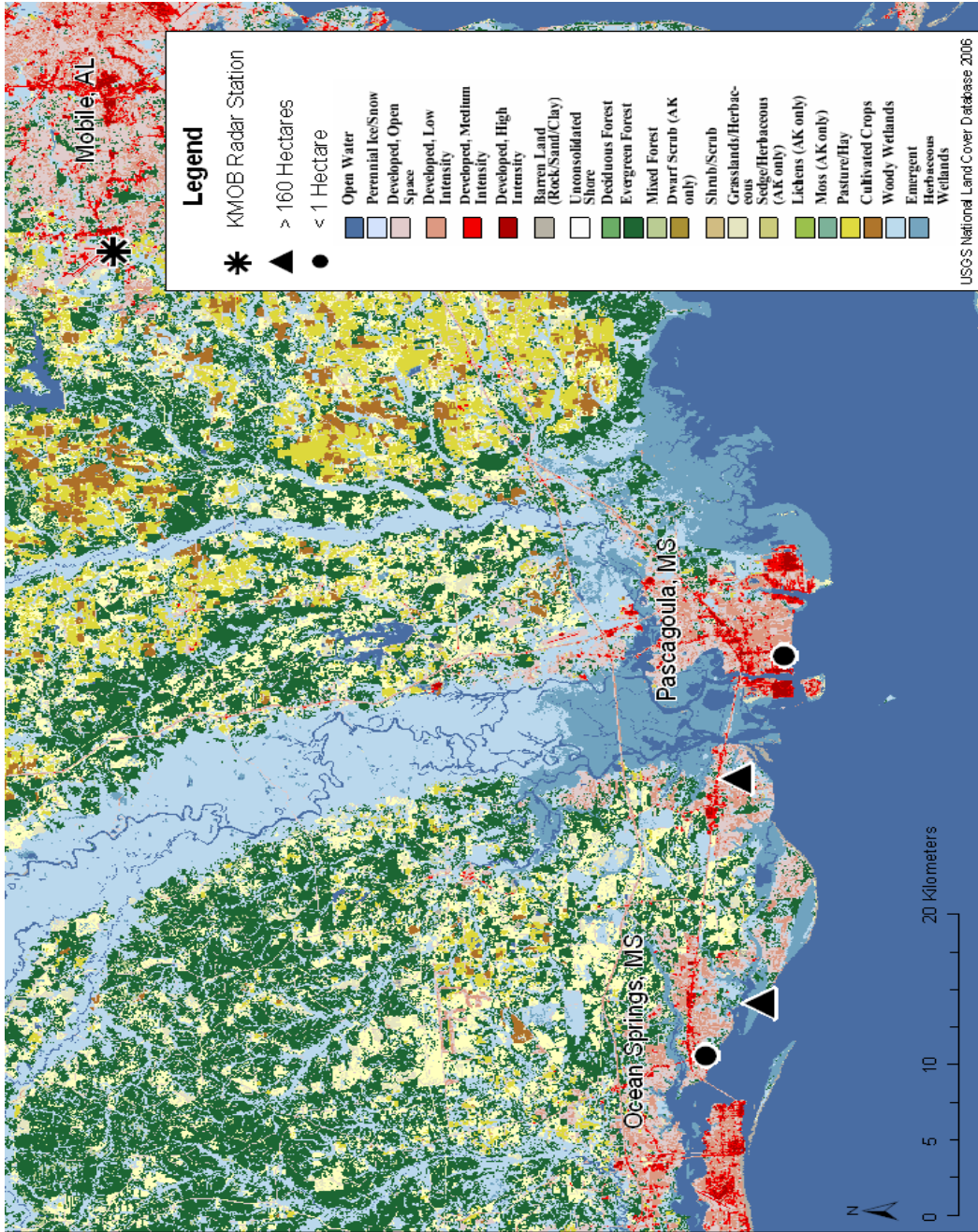


Figure 1. Study area with land cover classifications as established by the United State Geological Survey National Land Cover Dataset.

Landscape composition and configuration

Land cover data were used to quantitatively measure landscape composition and configuration of the four study sites and to examine spatial and structural differences that may contribute to extrinsic value of stopover locations to migrants. A 1 kilometer area surrounding each of the four study sites was designated using ArcMap™ 10.1 (ESRI 2011). For information on land cover categories across the study area, we accessed the 2006 National Land Cover Database (NLCD2006) which is a 16-class land cover scheme provided by the United States Geological Survey in raster format at a 30 meter resolution. We clipped this base raster to each of the study site buffers to limit the landscape analysis to those four sites, and converted the four raster files to a format compatible with the program FRAGSTATS 4.1 (McGarigal et. al 2002). An 8-neighbor rule was used during FRAGSTATS analysis to provide a more detailed examination of landscape configuration. Whereas edge habitat is typically characterized 100 meters into a forested patch for breeding migrants, evidence suggests that migrants during stopover utilize habitats further from the patch interior for foraging (Rodewald 2001, Rodewald and Brittingham 2004). Therefore, a fixed edge depth of 30 m was used for all patches. Six class-level metrics were selected based on ecological significance to Neotropical migratory birds and to avoid redundancy between metrics (Flather and Sauer 1996). Units and descriptions of each metric are shown in Table 3.2, and descriptions of each land cover class are shown in Appendix A, Table 1. For this analysis, land cover types in the four subdivisions representing varying development intensity were lumped into one “developed” cover class, and those classes representing different forest types were lumped into one “forest” cover class.

Table 3.2. Metrics analyzed for characterization of landscape composition and configuration at each site.

Metric	Unit	Description
Percentage of Landscape	Percent	Measures proportion of landscape occupied by patches of given class type
Area-weighted Mean Radius of Gyration	Meters	Measures extent of patches of given class type; expresses landscape continuity or average traversability within given class type
Area-weighted Mean Core Area	Hectares	Expresses area of the landscape occupied by core areas (with edge distance of 30 m) of given class type; quantifies amount of patch interior of each class type
Area-weighted Mean Euclidean Nearest-Neighbor Distance	Meters	Quantifies patch isolation; measures average distance of patches of given class type to other patches of that type
Patch Cohesion Index	None	Measures physical connectedness of class type across the landscape
Percentage of Like Adjacencies	Percent	Calculates class type aggregation or contagion; may be considered as an index of class type fragmentation

Resource quantification

Arthropods were sampled across the spatiotemporal extent of migration at each study site as a measure of food abundance. Arthropod sampling was conducted via branch clippings (Cooper and Whitmore 1990) once per week for seven weeks. One 8-12" branch was clipped from plants of two species (*Ilex vomitoria* and *Quercus spp.* - chosen for their ubiquity across all sites) at six points within each site. One branch was clipped from each species at each sampling point for a total of 12 branches per site per sampling period. Branches were clipped into a clear plastic zipping bag, and household insecticide (Raid® brand) was sprayed inside the bag after clipping and prior to sealing. Insecticide was applied inside the bag using one depression of the nozzle, and the bag was sealed immediately. Sealed sample bags were carried away from the study site where they were opened, and immobilized arthropods were identified to order. Length of each detected arthropod was measured to the nearest millimeter.

Vegetative material from each clipping was weighed using an electronic scale. Using the length-weight regression equation described by Rogers et al. (1976) for North American arthropods, arthropod length was used to determine arthropod biomass in each branch sample, and density of arthropods in each clipping was calculated as biomass (mg) per gram of clipped vegetation. A zero-altered negative binomial model with logit link (hurdle function of R package pscl) was used to test for effect of sampling week, habitat patch size, and year on arthropod densities (Zurr et al. 2009). A significance level of $p < 0.05$ was used for all statistical tests.

Leaf litter surveys were also conducted once per week for seven weeks at three locations at each study site. The observer knelt in front of a 0.25m² quadrat placed over leaf litter and counted all arthropods observed within the quadrat boundaries for 3 minutes. A clear hand ruler was used to estimate length of each detected arthropod. Arthropod lengths were used in a length-weight regression equation (see above) to determine total arthropod biomass detected during each sampling period. Arthropod densities were log transformed to meet the assumptions of normality, and analysis of variance (ANOVA) was conducted to analyze differences in leaf litter arthropod communities across the study area with factors including study site and date of sample. Tukey's HSD test was performed to analyze post-hoc differences across sites.

Migrant densities

Transect surveys were conducted at all sites throughout migration to determine migrant densities. Transect surveys are an efficient and effective method for quickly determining relative differences in bird populations across sites with potential for high replication of each census (Conner and Dickson 1980). At each smaller site, transect lines equaling a total of 300 m were established, while at each larger site, 500 m of transect line were established. Surveys were conducted every day from mid-March to mid-May (with the exception of severe weather days) in the morning and afternoon with morning surveys beginning 15 minutes after sunrise and ending no later than 1000 and afternoon surveys beginning after 1500 and concluding before sunset. During the 2011 season, one observer conducted all surveys so that each site was surveyed twice per day every other day. During the 2012 season, two surveyors conducted surveys so that every site was surveyed twice per day every day. Survey lines were flagged in 25 m increments, and the surveyor

maintained a constant pace along the transect line of 1 km/h. All birds encountered by sight and/or sound within 25 m of each side of the transect line were recorded. Data recorded for each detected individual included: lateral distance from transect line in 5 m increments, distance along transect line in 25 m increments, and method of detection (sight or sound). First territorial/nesting dates for species known to breed in southern Mississippi were identified from Birds of North America (BNA) species accounts (Poole, 2005), and any individuals of those species detected after said date were eliminated from analysis to ensure that tested birds were migratory individuals. Detection probabilities for spring migrants within 25m of a transect line in Mississippi forests have been shown to equal 1.0; therefore, adjustments of migrants densities due to variation in detection probability were not necessary (Buler et al. 2007). A zero-altered poisson model with logit link (hurdle function of R package pscl) was used in statistical analysis (Zuur et al. 2009).

Strip transects with distance sampling are typically considered an effective and efficient method for accurately estimating bird densities; however, the method relies on assumptions that all individuals along the line are detected and that bird behavior is not influenced by observers (Thompson 2002). Despite efforts to minimize violation of these assumptions, it has been suggested that 100% detection is rare (Hutto and Mosconi 1981). Therefore, it should be noted that, although spring migrant detection probability was found to be 1.0 at sites further inland in Mississippi (Buler et al. 2007), detection probabilities may differ in coastal habitats and between species in coastal habitats. In this study, surveyors maintained constant pacing with minimal disturbance to habitat patches; nonetheless, birds may have responded to observers by demonstrating avoidance behavior resulting in lack of detection or repeated detection of individuals during transect surveys. Survey results were standardized across sites of varying sizes by analyzing densities of migrants in terms of number of birds per hectare, and survey areas were representative of the overall study sites. Still, a larger proportion of the habitat patch was surveyed at small sites, and this must be considered when drawing conclusions from density estimates and comparing estimates across study sites of varying sizes (Watson 2008).

Predator to prey ratio

Ratios of bird to arthropod density provide a measure of relative competitive pressure which may influence refueling potential for migrants during stopover (Moore and Wang 1991). Arthropod densities measured via branch clippings and migrant densities measured via transect surveys were used to calculate a relative predator to prey ratio when migrants were present. Surveys with zero migrants were eliminated from this analysis, and only surveys from days when arthropod branch clippings were taken and one day before and after that clipping date were used so that prey values were temporally close to predator values. We divided number of migrants per hectare during each survey by total arthropod mass (mg) per gram of clipped vegetation for that sampling date to obtain a relative predator to prey ratio when migrants were present for each survey. Because these ratios were not normally distributed, we performed a Wilcoxon test to analyze differences in ratios at small and large sites.

Fuel deposition

Birds from multiple foraging guilds were captured using four-shelf nylon mist nets of either 12 or 6 meters in length and 2.6 meters in height to obtain blood samples for

metabolite profiling. 10 – 12 mist nets were run daily from mid-March through mid-May of 2011 at Hellmer's Lane, Shepard State Park, and Don's Woods and of 2012 at these three sites with the addition of Davis Bayou. Nets were operated from sunrise until approximately 5 hours after sunrise. Upon capture, standard morphometric measurements were taken, and amounts of muscle and subcutaneous fat were scored for each bird. Fat storage was scored by visually assessing subcutaneous fats and scoring fat levels along a 0-5 numeric scale (Helms and Drury 1960). Birds were banded with a U.S. Fish & Wildlife Service aluminum leg band and released after blood sampling. First territorial/nesting dates for species known to breed in southern Mississippi were identified from BNA accounts (Poole 2005), and any individuals of those species captured after said date were eliminated from analysis to ensure that tested birds were migratory individuals. Cycling metabolites are known to deteriorate and lose potential to reflect a particular feeding event within 20 minutes (Guglielmo et al. 2005, Zajac et al. 2006). Therefore, time between net checks was no more than 15 minutes to increase likelihood of detecting metabolite profiles associated with recent foraging activity within each site. Blood was taken from each migrant via brachial vein by puncturing with a 26 gauge needle. Blood was kept cool in capillary tubes until return to processing facilities on the afternoon of the capture day. Plasma was separated from red blood cells using a microhematocrit centrifuge rotor spun at 12,000 rpm for approximately 10 minutes. Plasma was extracted from capillary tubes using a Hamilton syringe and relocated to a microcentrifuge tube in which it was frozen at -80°C until analysis using endpoint assay kits (as described in Guglielmo 2002 and Guglielmo 2005). Free glycerol was subtracted from triglyceride values to determine true circulating triglyceride levels. Final triglyceride values were log transformed to meet the assumptions of normality. Analysis of variance was conducted to determine differences in triglyceride levels with capture site, year, and condition as factors. Effect of habitat patch size on triglyceride levels was also analyzed after separating species into foraging groups (listed in Table 2). Conclusions from metabolite profiling should be drawn with caution due to low sample sizes and grouping of multiple species for final analysis. Ideally, triglyceride analyses would involve higher sample sizes from a representative focal species at all sites, but logistical constraints prevented such circumstances in my study.

Principal component analysis was conducted using size-corrected mass (mass divided by wing chord), fat score, and muscle score to obtain a summarized condition score to examine effect of body condition on variation in triglyceride levels. The first PCA axis (the only axis with an eigenvalue greater than 1) explained over 40% of the total variation; therefore, this principal component score for each individual was used in all further triglyceride analyses (Table 3). Additionally, analysis of variance was conducted to examine differences in this condition index across sites.

Table 2. Foraging group classification for each species captured. Groupings are based roughly on groups of Barrow et al. (2000).

Foraging group	Species
Canopy	American Redstart
	Black-and-white Warbler
	Eastern Wood-Pewee
	Great Crested Flycatcher
	Magnolia Warbler
	Northern Parula
	Orchard Oriole
	Prothonotary Warbler
	Red-eyed Vireo
	Rose-breasted Grosbeak
	Summer Tanager
	Worm-eating Warbler
	Yellow-billed Cuckoo
Understory	Hooded Warbler
	Indigo Bunting
	Painted Bunting
	Yellow-breasted Chat
Ground	Grey-cheeked Thrush
	Louisiana Waterthrush
	Northern Waterthrush
	Ovenbird
	Swainson's Thrush
	Veery
	Wood Thrush

Table 3. Results of principal component analysis for body condition using size-corrected mass, fat score, and muscle score as variables.

	PC1	PC2	PC3
Eigenvalue	1.2181	0.9964	0.7854
Proportion of variance explained	0.4061	0.3321	0.2618
Cumulative proportion	0.4061	0.7382	1.000
Loading			
Corrected mass	0.7813	2.21015	-0.5794
Fat score	1.8765	-0.03731	1.5193
Muscle score	1.7238	-0.96117	-1.3913

Results

Landscape composition and configuration

Land cover classes that dominated all four study areas included developed (open space and low, medium, and high intensity), forested (evergreen, deciduous, mixed, and woody wetland), and emergent herbaceous wetland. Other land cover classes present, but occupying small percentages of the landscape at all sites, included barren land, shrub/scrub, grassland/herbaceous, and pasture/hay. These classes were excluded from presentation of results to facilitate easier interpretation of most relevant land cover classes. High intensity development was present at all study sites except DAV. Higher proportions of the landscape were occupied by developed land cover classes at the two smaller sites than at the two larger sites (Figure 2). Between the two smaller study sites, the landscape at HEL was made up of a higher percentage of forested land cover classes than DON. Between the two larger study sites, SHE had a higher percentage of developed land cover classes, while DAV had higher percentages of both forested land cover classes and emergent herbaceous wetland. Among all study sites, DAV had the highest proportion of emergent herbaceous wetland. At all sites, area-weighted mean radius of gyration of developed classes was higher than that of forested land cover classes, indicating that developed classes were more extensive across all four landscapes (Figure 3). Area-weighted mean core area was lowest for forested land cover classes and highest for developed land cover classes at all sites indicating that most forested area at all sites could qualify as edge habitat (Figure 4). Cohesion of forested patches was higher at large sites than at small sites but was lower than that of developed patches at all sites (Figure 5). Percentage of like adjacencies was higher in developed classes than forested classes at all sites (Figure 6). Area-weighted mean Euclidean nearest neighbor distance was lowest between patches of developed land cover classes and was highest for forested classes at both small sites (Figure 7). Patch cohesion index, percentage of like adjacencies, and area-weighted mean Euclidean nearest neighbor distance indicate that developed classes were more aggregated across the landscape at all sites and that forested patches were less physically connected.

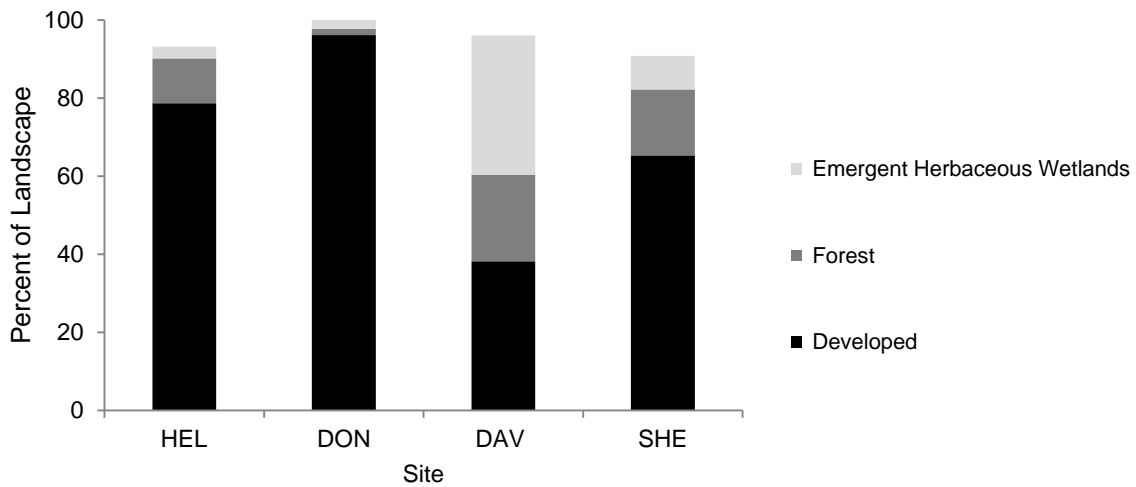


Figure 2. Proportion of 1km landscape surrounding each study site occupied by three major land cover classes.

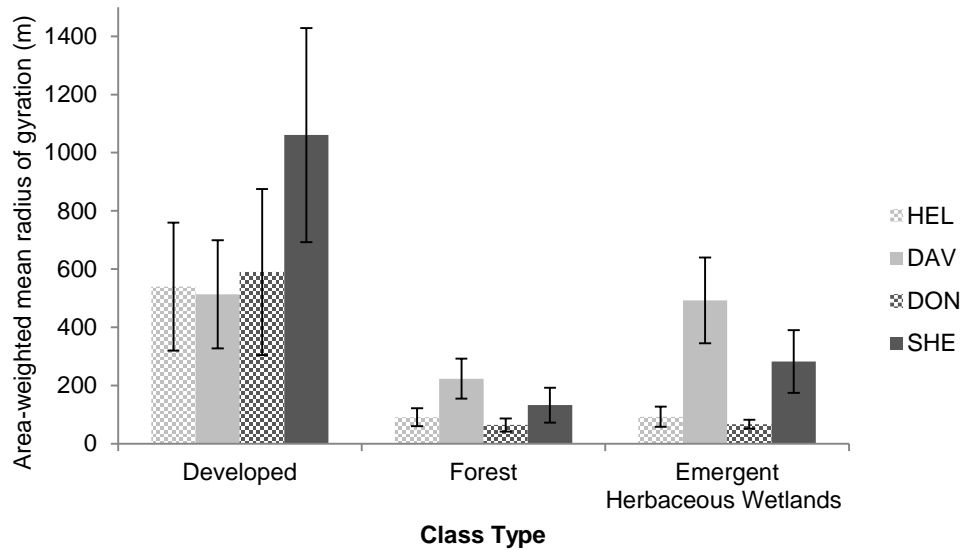


Figure 3. Area-weighted mean radius of gyration (m) of patches in each land cover class at each site. Solid bars represent large sites; patterned bars represent small sites. Error bars represent standard deviation.

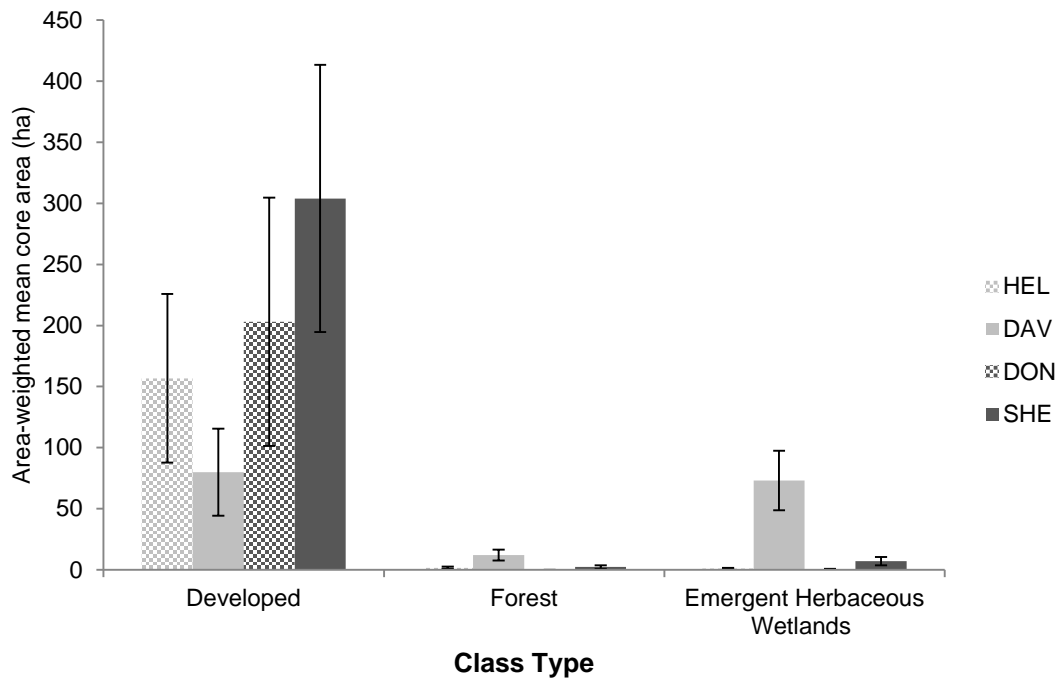


Figure 4. Area-weighted mean core area (ha) when edge depth = 30 m of all patches in each land cover class at each site. Solid bars represent large sites. Patterned bars represent small sites. Error bars represent standard deviation.

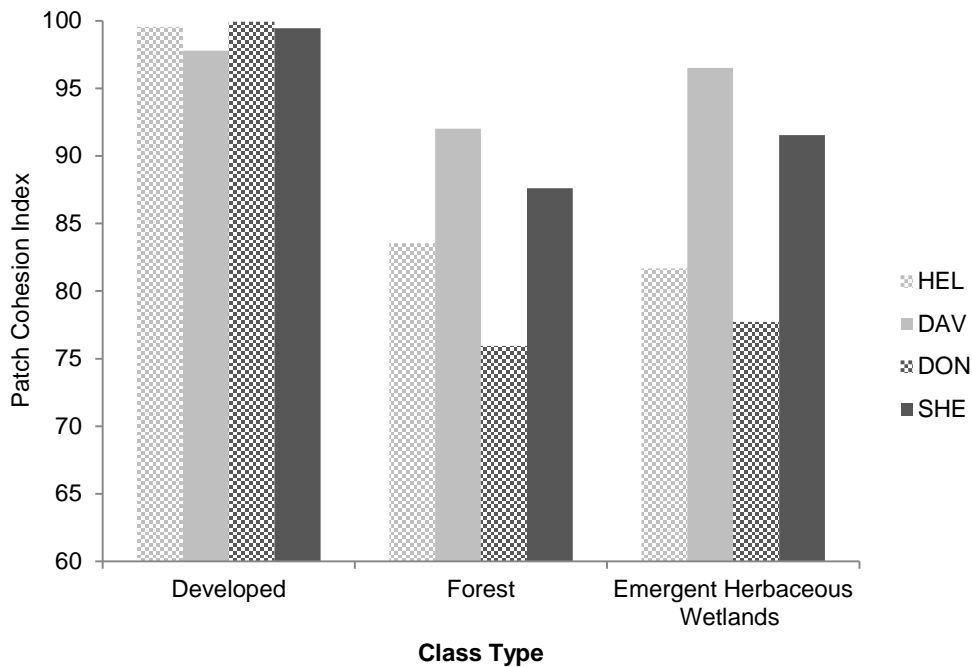


Figure 5. Patch cohesion index of patches of each land cover class at each site. Solid bars represent large sites. Patterned bars represent small sites.

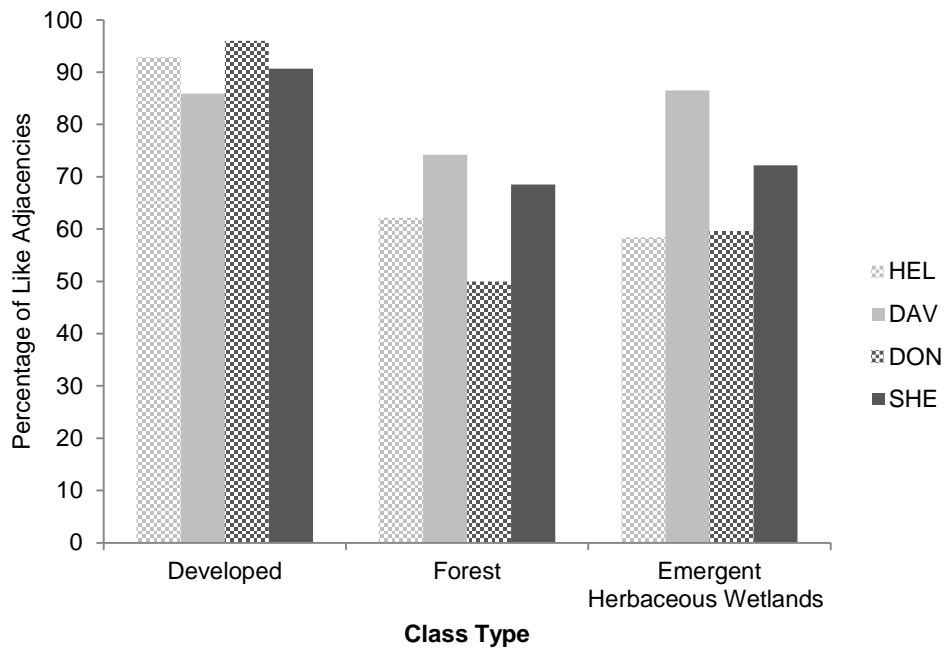


Figure 6. Percentage of like adjacencies of patches of each land cover class at each site. Solid bars represent large sites. Patterned bars represent small sites.

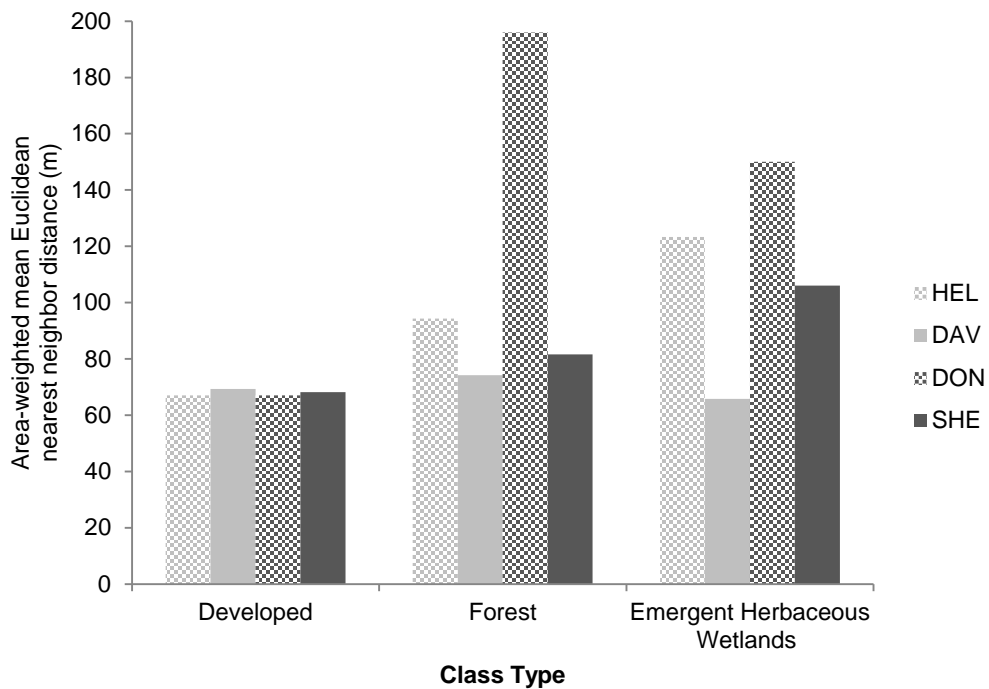


Figure 7. Area-weighted mean Euclidean nearest neighbor distance (m) for all patches of each land cover class at each site. Solid bars represent large sites. Patterned bars represent small sites.

Resource abundance

Sampling with two methods throughout migration provided insight to the arthropod communities within these habitat patches and characterized habitat quality by way of potential food abundance for en route migrants at each site. More samples with zero arthropods were found at large sites, and while there was no significant effect of habitat patch size ($\chi^2 = 1.95$, $df = 1$, $p = 0.1626$), variation in arthropod density was evident across sites. When arthropods were detected, arthropod biomass was highest at the eastern large site, Shepard State Park, and lowest at the western large site, Davis Bayou (Figure 8). Variation in arthropod densities measured from branch clippings showed a significant effect of sampling week ($\chi^2 = 15.2$, $df = 6$, $p = 0.019$), but no significant effect of sampling year ($\chi^2 = 0.169$, $df = 1$, $p = 0.681$). While there appeared to be a spike in arthropod biomass during the third sampling week at two sites (HEL and SHE), arthropod abundances detected from branch clippings generally fluctuated temporally (Figure 9).

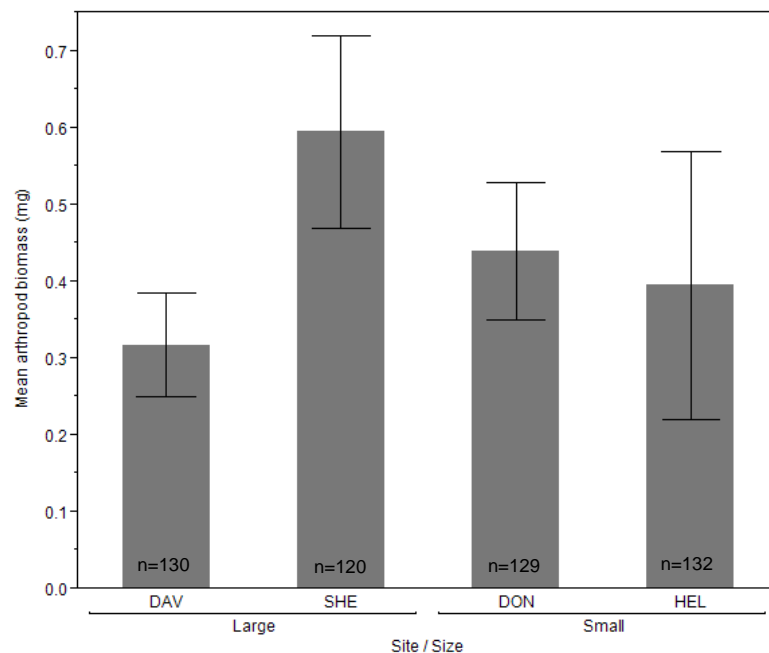


Figure 8. Arthropod biomass (mg) per gram of vegetation in branch clippings at each study site. Sample sizes on each bar represent total number of branch clippings from both sampling years at each site. Error bars represent standard error.

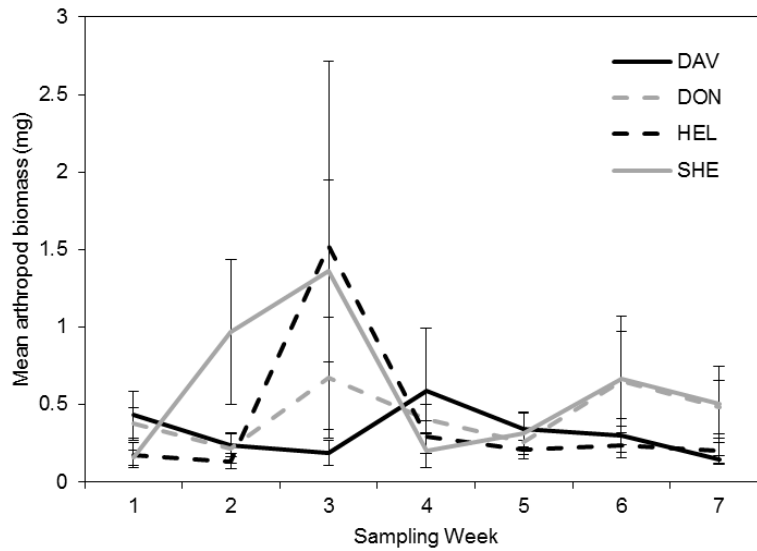


Figure 9. Mean arthropod biomass (mg) per gram of vegetation in branch clippings from each sampling week. Dashed lines represent small sites, while solid lines represent large sites. Bars represent standard error.

Results of ANOVA for differences in leaf litter arthropod densities showed a significant effect of both date ($F = 27.67$, $df = 7$, $p < 0.0001$) and habitat patch size ($F = 4.6782$, $df = 3$, $p = 0.0047$). Average arthropod biomass differed significantly between the two large sites and between the large and small sites within the eastern end of the study area (Figure 10). Like arthropod abundances detected in branch clippings, leaf litter arthropod biomass fluctuated temporally; however, at all sites, there were general positive correlations between arthropod biomass and time of season (Figure 11).

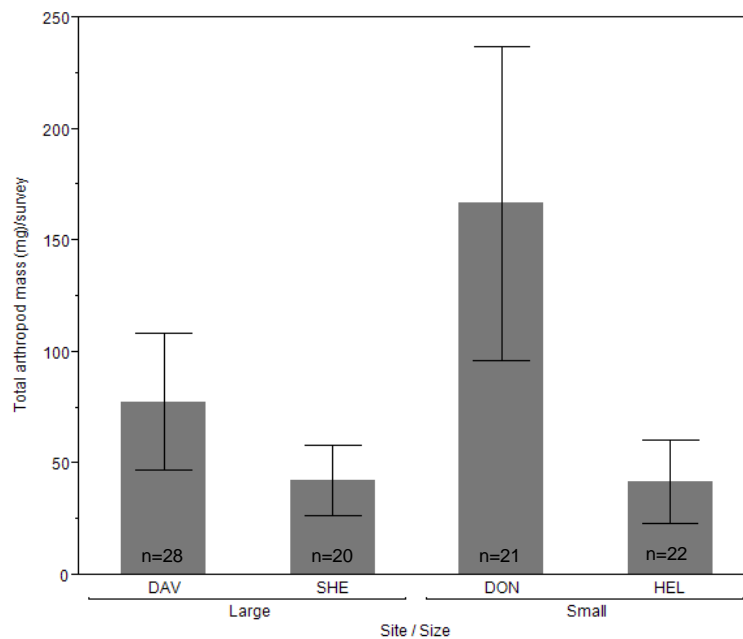


Figure 10. Mean arthropod biomass (mg) per leaf litter survey period at each site. Error bars were constructed using one standard error from the mean.

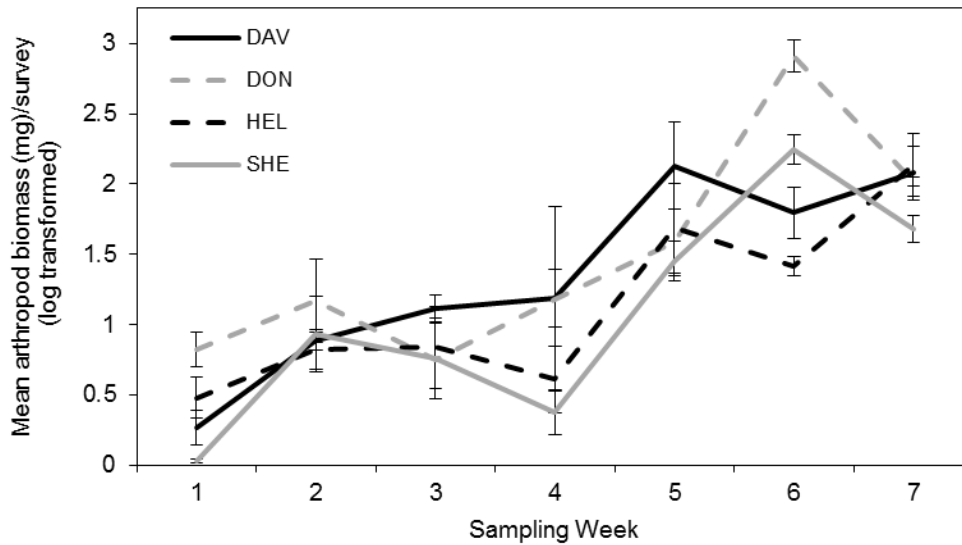


Figure 11. Mean leaf litter arthropod biomass (mg) per survey period in each sampling week. Solid lines represent large sites while dashed lines represent small sites. Bars represent standard error.

Migrant densities

More birds were detected per hectare at small sites in both site pairs. Tests for differences in migrant densities showed a highly significant effect of time of day of survey (morning vs. afternoon; $\chi^2 = 15.275$, $df = 1$, $p < 0.0001$), and a marginally significant effect of habitat patch size ($\chi^2 = 3.644$, $df = 1$, $p = 0.056$). There was no effect of year on migrant densities ($\chi^2 = 0.2775$, $df = 1$, $p = 0.598$). When migrants were detected, more birds were detected at smaller sites. At all sites, fewer birds were detected during morning surveys than during afternoon surveys (Figure 12). Surveys with zero migrant detections occurred more frequently in the morning and at small sites. During both years, there were multiple afternoons in which considerably more migrants were present than other days across the season. In these cases, more birds were present during afternoon surveys than on previous morning surveys in 2011 and on previous and subsequent morning surveys in 2012 (Table 4). These incidents suggest arrivals of waves of migrants in the afternoon with departure of those before the following morning's survey indicating potential transience of most migrants through coastal habitats.

Table 4. Migrants per hectare on afternoons with high densities relative to surrounding morning surveys and relative to other days throughout the season.

Site	Date	Time of Day	Migrants per hectare
DON	03/31/2011	AM	1.3
	03/31/2011	PM	5.3
HEL	04/21/2011	AM	0
	04/21/2011	PM	5.3
DON	04/28/2011	AM	1.3
	04/28/2011	PM	5.3
DON	04/26/2012	AM	0
	04/26/2012	PM	6.7
	04/27/2012	AM	0
HEL	04/26/2012	AM	0
	04/26/2012	PM	4
	04/27/2012	AM	0.7
SHE	04/26/2012	AM	0
	04/26/2012	PM	5.2
	04/27/2012	AM	0.8
DAV	04/27/2012	AM	0
	04/27/2012	PM	3.6
	04/28/2012	AM	0

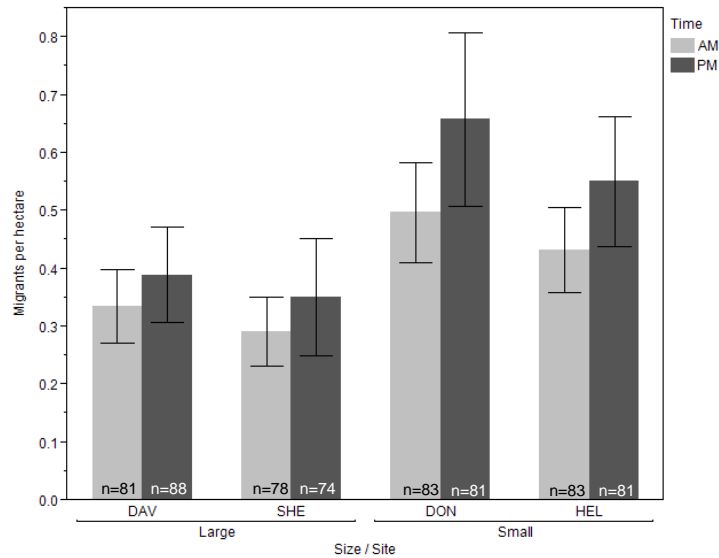


Figure 12. Mean number of migrants per hectare on transect surveys. Error bars represent standard error.

To examine transience of migrants through coastal stopover habitats, 2012 survey results when migrants were present in the afternoon were used to calculate difference in number of migrants detected on one afternoon survey from the following morning survey. This value was made relative across survey days by dividing that difference by the afternoon value from each pair of surveys. A relative value greater than zero would indicate that more birds were detected in the afternoon, a negative value would indicate that more birds were detected on morning surveys, and a zero value would indicate that equal numbers of migrants were present on both morning and afternoon surveys. Relative differences did not meet assumptions of normality; therefore, Wilcoxon signed rank tests were performed to test that relative differences in number of migrants from afternoons to the following mornings were greater than zero. Average relative differences were significantly greater than zero at small sites ($W=137.5$, $df=36$, $p=0.0011$) and marginally significant at large sites ($W=68.0$, $df=32$, $p=0.0671$) indicating that fewer birds were detected on morning surveys than surveys the previous afternoon (Figure 13).

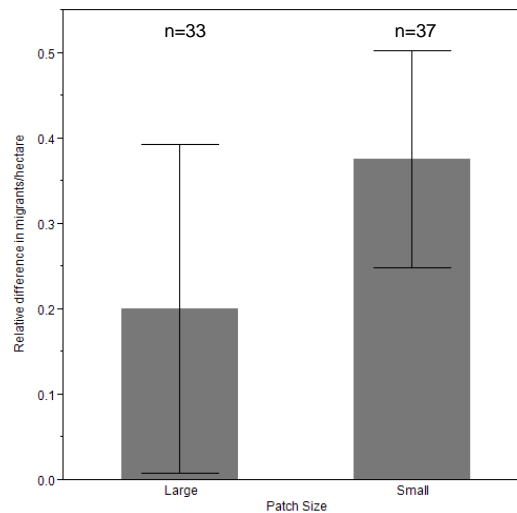


Figure 13. Mean relative difference in number of migrants ((PM-AM)/PM). Error bars represent standard error.

Predator to prey ratio

Calculation of predator to prey ratio provided a general measure of arthropod biomass present when migrants were present during surveys. Relative predator to prey ratio for each survey when migrants were present (number of migrants per hectare/total arthropod biomass (mg) per gram of vegetation on survey day) was higher at small sites than at large sites (Figure 14). Wilcoxon tests showed no significant difference in ratios between the two small sites ($\chi^2=0.4603$, $df=1$, $p=0.4975$) or the two large sites ($\chi^2=1.0426$, $df=1$, $p=0.3072$). When grouped, differences in ratios between the two large and two small sites were not significant ($\chi^2=2.2280$, $df=1$, $p=0.1355$).

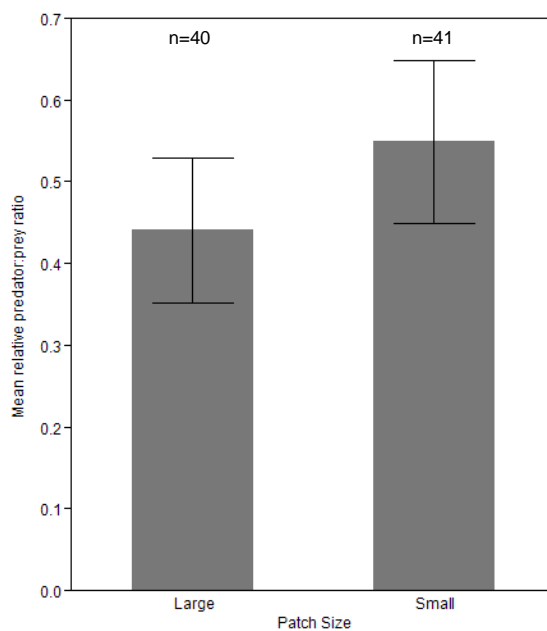


Figure 14. Mean relative predator to prey ratios (number of migrants per hectare/total arthropod biomass (mg) per gram of vegetation for given survey day) when migrants were present at large and small sites. Error bars were constructed using 1 standard error from the mean.

Fuel deposition

101 individuals of 24 species were sampled for triglyceride analysis in total. Sample sizes per species, site, and year are shown in Tables 4 and 5. Hours of netting effort at each site are shown in Table 6. Migrants of every fat score class were captured at both large and small sites (Figure 15). Most birds had fat scores above 0 indicating arrival with some fuel reserves, though > 45% of the birds that stopped along the coast were classified as 0 or 1 fat score regardless of size of site. There were significant differences in condition index among sites in 2011 ($F = 4.3012$, $df = 2$, $p = 0.0175$) but not in 2012 ($F=0.4882$, $df=3$, $p=0.6933$) (Figure 16). In 2011, condition index at DON was significantly lower than that at HEL, but condition indices at neither DON nor HEL were significantly different from that at SHE. In both 2011 and 2012, mean condition indices were lowest for birds captured at DON. That said, condition indices did not differ significantly between the two large sites or between the large sites and either of the small sites. For migrants sampled in 2011, triglyceride values were highest for birds sampled at HEL (small western site) and lowest for birds sampled at DON (small eastern site) (Figure 17). There were no significant effects of condition ($F = 0.1018$, $df = 1$, $p = 0.7508$) or capture time ($F = 2.1621$, $df = 1$, $p = 0.1469$) on circulating triglyceride levels, and there were no significant differences across study sites ($F = 1.1816$, $df = 2$, $p = 0.3141$). For migrants sampled in 2012, highest triglyceride values were detected at Shepard State Park (large eastern site), while lowest triglyceride values were detected at Davis Bayou (large western site). There were, again, no significant effects of condition ($F = 0.0934$, $df = 1$, $p = 0.7641$) or capture time ($F = 3.9340$, $df = 1$, $p = 0.0659$). Unlike 2011, there were, however, significant differences across study sites ($F = 4.8892$, $df = 3$, $p = 0.0145$). Tukey's HSD post-hoc tests revealed significant differences between the large and small sites within the western side of the study area with higher triglyceride levels at the smaller

site. The two eastern sites did not differ from one another or from either of the sites on the western side of the study area. For study sites with triglyceride data from both sampling years (SHE and DON), triglyceride values were lower at small sites in both years. Predator to prey ratios within this site pair showed the opposite relationship in that ratios were higher at small sites in both years (Figure 18).

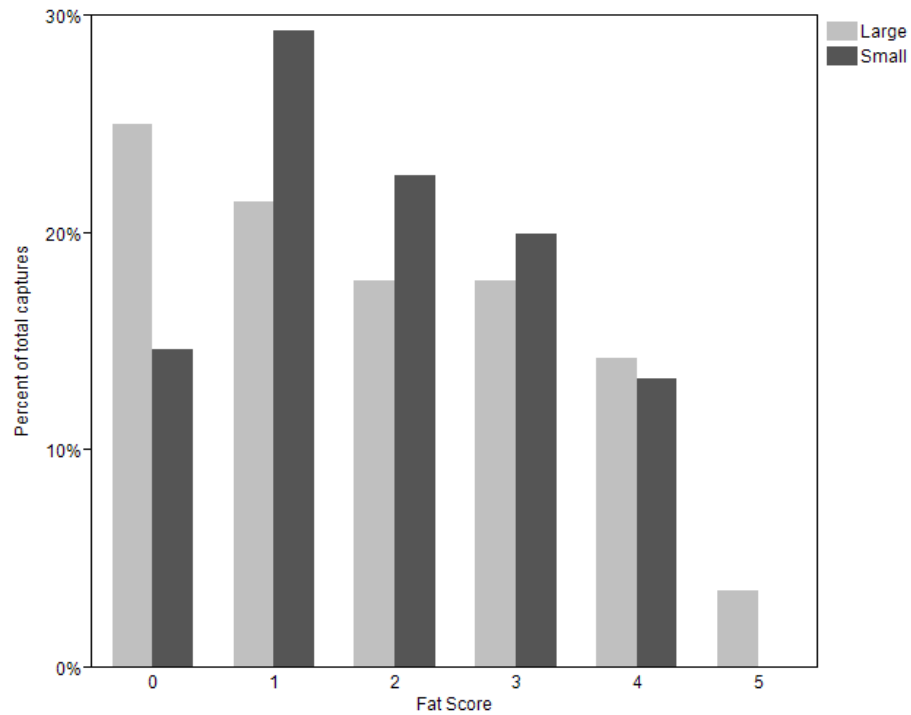


Figure 15. Fat scores of migrants (proportion of individuals in each fat class) captured in 2011 and 2012 at large and small sites.

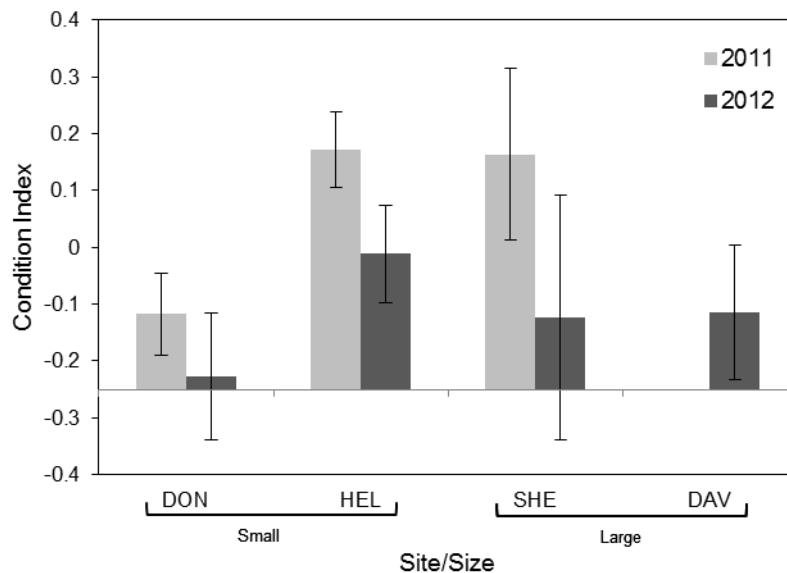


Figure 16. Average condition index of birds captured at each site during 2011 and 2012. Error bars represent standard error. Samples sizes are same as those shown in Figure 31.

Table 4. Number of birds of each species at each site sampled for triglyceride analysis in 2011.

Species	Site	n
American Redstart	HEL	1
	SHE	1
Eastern Wood Pewee	HEL	1
Hooded Warbler	DON	3
Great Crested Flycatcher	HEL	1
	DON	1
Grey-cheeked Thrush	HEL	5
	DON	1
Indigo Bunting	DON	3
Louisiana Waterthrush	DON	3
Magnolia Warbler	HEL	1
	DON	1
Northern Parula	HEL	1
Northern Waterthrush	HEL	1
	DON	2
Orchard Oriole	HEL	2
	DON	1
Ovenbird	HEL	2
	DON	3
	SHE	3
Painted Bunting	DON	2
Prothonotary Warbler	HEL	1
	DON	3
Red-eyed Vireo	HEL	1
	DON	1
	SHE	4
Rose-breasted Grosbeak	DON	1
Summer Tanager	HEL	1
	SHE	1
Swainson's Thrush	HEL	1
	DON	1
Veery	HEL	2
Wood Thrush	DON	6
Worm-eating Warbler	DON	2
	SHE	1
Yellow-breasted Chat	HEL	2
	DON	2
Yellow-billed Cuckoo	SHE	1

Table 5. Number of birds of each species at each site sampled for triglyceride analysis in 2012.

Species	Site	n
American Redstart	HEL	1
Black-and-white Warbler	HEL	1
Hooded Warbler	DON	1
	SHE	2
	DAV	1
Great Crested Flycatcher	DAV	2
Grey-cheeked Thrush	SHE	1
Indigo Bunting	DON	1
	DAV	1
	DAV	1
Louisiana Waterthrush	DAV	1
Northern Waterthrush	HEL	1
Orchard Oriole	DON	1
Ovenbird	HEL	2
	DON	1
	SHE	1
	DAV	1
Rose-breasted Grosbeak	HEL	1
Summer Tanager	HEL	1
Swainson's Thrush	HEL	3
	DAV	1
	DAV	1
Veery	HEL	1
	DON	1
	DAV	1
	DAV	1
Wood Thrush	DAV	2
Worm-eating Warbler	DAV	1

Table 6. Hours of mistnetting effort at each site during each sampling year.

Site	Year	Net Hours
HEL	2011	404
	2012	208
DAV	2012	1122
	DON	2011
	2012	63
SHE	2011	598
	2012	97

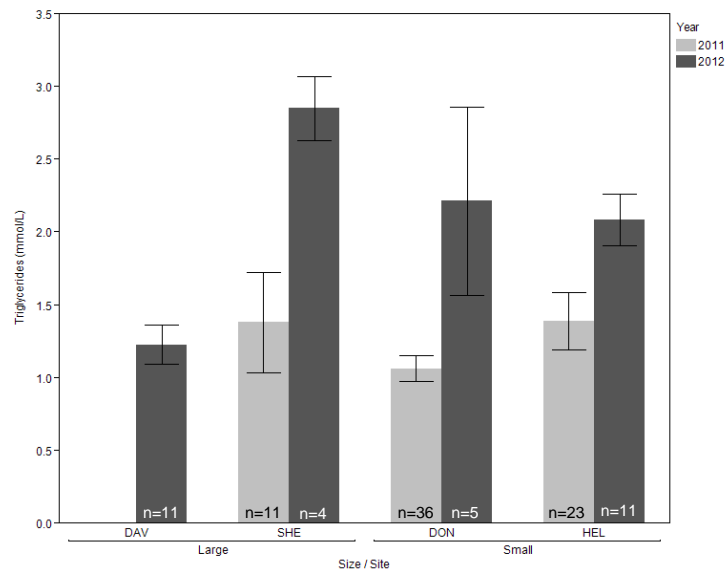


Figure 17. Triglycerides (mmol/L) of migrants captured in 2011 and 2012. Error bars were constructed using one standard error from the mean.

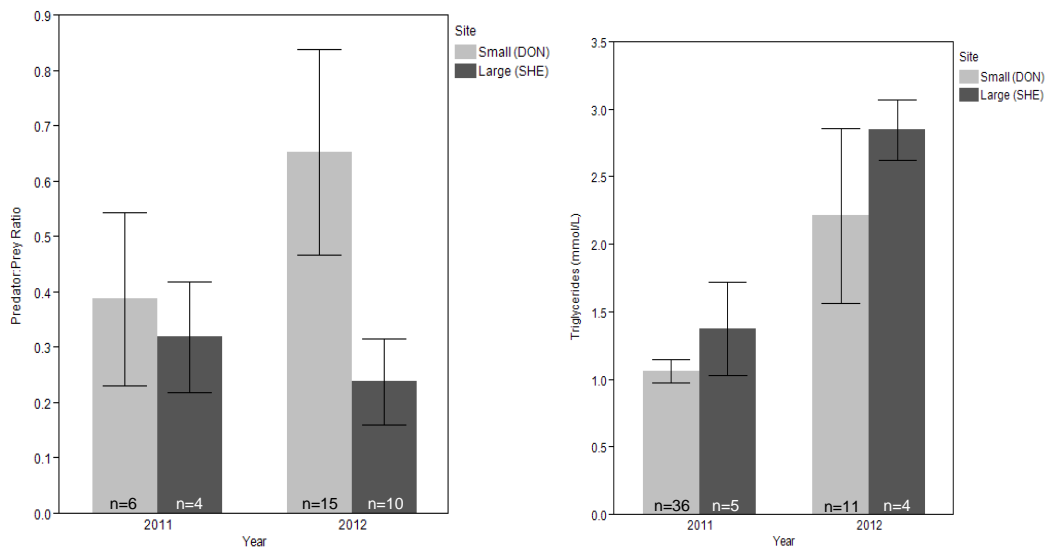


Figure 18. Triglycerides (mmol/L) of migrants and predator to prey ratios at eastern pair of study sites. Error bars were constructed using one standard error from the mean.

Triglyceride levels of understory and ground foragers were lower at small sites, whereas canopy foragers showed higher triglycerides at small sites (Figure 19). Analysis of triglyceride levels after separation into foraging group revealed an interactive effect of foraging group and patch size ($F=4.9873$, $df=2$, $p=0.0087$), but no effect of size ($F=1.9650$, $df=1$, $p=0.1642$) or foraging group ($F=0.7163$, $df=2$, $p=0.4912$) alone. Tukey's HSD post-hoc analysis revealed no significant differences among groups or patch sizes. However, individual Student's t-tests for differences between patch sizes within each foraging group suggested a significant difference between sizes in canopy foragers ($t=2.096591$, $df=34$,

$p=0.0435$), but no significant differences between sizes in understory foragers ($t=-7.80873$, $df=16$, $p=0.0893$) or ground foragers ($t=-1.32893$, $df=45$, $p=0.1906$).

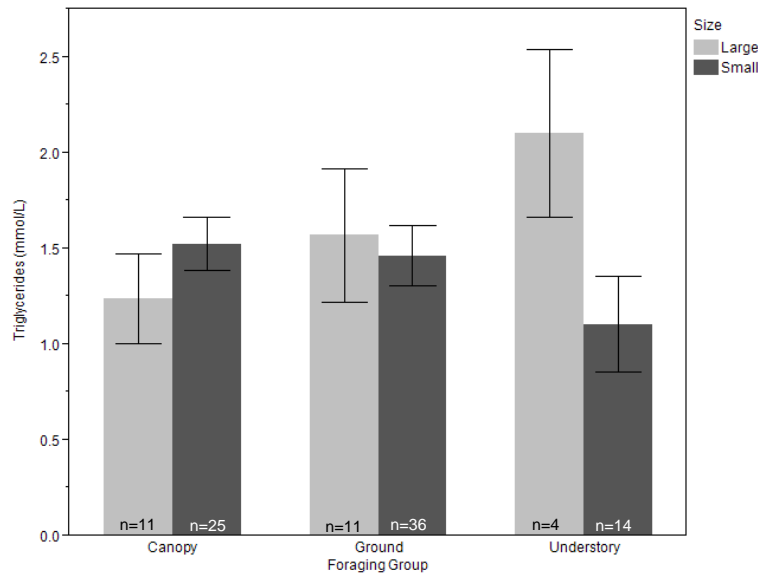


Figure 19. Triglycerides (mmol/L) of migrants captured in each foraging group. Error bars were constructed using one standard error from the mean.

Discussion

Migrants stopover in urbanized habitats along the Mississippi Gulf Coast, and they do so in both relatively large forested patches and small (<1 hectare) forested fragments. Although migrants have been shown to remain in heavily urbanized habitat patches and exhibit exploratory movements (Seewagen et al. 2010), many migrants did not remain in these coastal woodlots for extended periods as evidenced by higher migrant densities during afternoon surveys than morning surveys at all sites. Given the constraints imposed by migration schedules and the energetic condition of captured migrants, we suspect that the majority of stopping migrants in this landscape are transients; that is, birds making a short, immediate stop to rest after crossing the Gulf of Mexico with the primary goal of continuing northward (Buler and Moore 2011, Chernetsov 2012). Upon arrival along the northern coast of the GOM, migrants often in depleted energetic condition distribute themselves across limited habitats in which they have little information about habitat quality (Moore and Kerlinger 1987, Moore et al. 1990). Transient migrants likely depart quickly from these habitats after they rest, rehydrate, and/or determine that surroundings are resource-poor in relation to energetic needs (Beibach 1985, Rappole and Warner 1976, Leberg et al. 1996, Sandberg and Moore 1996).

Movements of migrants after departing the habitat patches surveyed in this study are unknown. Migrants arriving in this unfamiliar landscape may exhibit localized movements to familiarize themselves with the area and to sample nearby resources, or depending on energetic condition, may depart the urban coastal zone entirely in longer distance nocturnal flights for continued migration. Previous work suggests that habitat patch-level effects impact movements of en route migrants in both urban and non-urban environments, and those movements vary with energetic condition upon arrival, time since arrival, and with

habitat quality (Cohen et al. 2012, Matthews and Rodewald 2010). Future investigation of subsequent movements to other habitat patches in this heterogeneous landscape using telemetry may reveal the effects of finer scale spatial processes on habitat selection after migrants have had the opportunity to rest and assess their environment. Additionally, identification of movement patterns of individuals of known energetic condition within and away from these habitat patches would shed light on the quality of this landscape for migrating birds (Moore and Aborn 2000, Simons et al. 2000).

More birds were concentrated per unit area at small forested fragments than at large patches. Analysis of landscape composition and configuration showed differences in area surrounding small patches, including higher overall proportions of development, lower extent of forested patches surrounding small sites, and higher distances between forested patches surrounding small sites. These nuances in landscapes surrounding each of the four study sites may shed light on processes responsible for distribution of migrants across available habitat patches at arrival along the coast at larger spatial scales. This concentration effect in smaller, more isolated patches with fewer resources is consistent with the proximity and interception models relating position of migrants over a landscape and orientation and size of patches within that landscape to habitat patch use (Diehl 2003) and with non-ideal distributions in the face of limited knowledge of surroundings as described by Shochat et al. (2002). The crowding effect may be especially evident in coastal settings after migrants have crossed an ecological barrier and arrive with limited overall habitat, minimal cues to habitat quality, little energetic flexibility, and pressure to arrive quickly to breeding grounds.

Crowding of migrants into smaller forest fragments may come at a cost. Higher bird densities during migration result in increased competition which may reduce opportunity for a migrant to replenish depleted energy stores (Moore and Yong 1991, Moore et al. 2003). Measurement of food resources with direct relation to number of migrants present in stopover habitats provides insight to relative competition may influence stopover duration, successful refueling, and subsequent movements of migrants within or out of a habitat patch (Greenberg 1986, Moore and Yong 1991). In this study, predator to prey ratios suggest that differences in competitive pressure may exist across coastal stopover habitats and may be higher at smaller habitat patches, supporting the idea of crowding of migrants into smaller patches and potentially impacting efficient fuel deposition.

Variation in triglyceride levels indicates potential differences in refueling of migrants across stopover sites (particularly in 2012). Triglyceride values at all sites fell within the range of values detected for migrants further north at sites in Canada and at heavily urbanized stopover sites in New York City forests, and triglyceride values in the New York study were considered adequate for refueling (Guglielmo et al. 2005, Seewagen et al. 2011). While there was no consistent trend in differences between large and small habitat patches, triglyceride values were lower at the large site than the small site within the eastern half of the study area. Additionally, the relationship between predator to prey ratio and triglyceride levels within the eastern pair of study sites during both sampling years may suggest that competitive pressure influences refueling performance of migrants. These findings, along with aforementioned conclusions regarding migrant densities and distribution across sites, identify variation in migrant refueling performance at forested patches within urban coastal settings and may highlight the importance of even the smallest isolated woodlots as suitable refueling sites for migrating birds.

Arthropod surveys revealed differences in densities of resources for migrants across sites and within different foraging guilds, but, as was the case in triglyceride analyses, there was no consistent trend indicating that patch size affected resource abundance. While there was no difference between large and small habitat patches in understory arthropod densities, understory arthropod abundance in the coastal habitat patches sampled in this study was less than that found in branch clippings from forested habitats further inland along the Pascagoula and Pearl River basins during spring migrations of 2003 and 2004 (Buler et al. 2007). Leaf litter arthropod abundance, on the other hand, was higher in the present study than at inland sites. Differences in arthropod densities between large and small study sites and between patches of the same size (most evident from leaf litter surveys at the two large patches) suggest that variation in arthropod abundances attributable to factors other than forested woodlot size may be expected across this coastal landscape. Fluctuations in arthropod densities throughout the course of the season detected in both sampling methods may be due to variation in effectiveness of sampling with local weather (e.g., wind) and due to phenological differences between taxonomic groups (Booij et al. 1995). Opportunities for refueling along the immediate coast may, therefore, vary with time of arrival, fine-scale arrival location, and species-specific foraging habits.

Migrant-habitat associations during stopover near an ecological barrier are complex and less predictable than during wintering or breeding periods. In coastal Mississippi, the challenge of explaining this system is further complicated by the lack of understanding of migrant behavior and distribution in an urban landscape. Regardless, results of this study reveal that coastal woodlots embedded in heavily urbanized settings likely provide valuable opportunities for temporary resting by en route migrants after crossing the Gulf of Mexico and before continuing to stopover further inland. Moreover, for those migrants that remain to stopover, coastal forests may provide refueling opportunities comparable to those provided by sites further inland. Coastal habitats may therefore be considered critical primary refueling sites due to the emergency energetic situation faced by some migrants at landfall after costly flight across the Gulf of Mexico. Strategies for conserving declining Nearctic-Neotropical migrant populations should designate coastal woodlots as valuable refuges for en route migrants and should ideally promote preservation of remaining forested habitat within widespread urban environments along the immediate coast.

Conservation Implications

The attempt to understand migrant-habitat relations in an urban landscape is complicated by uncertainty surrounding migrant population limitation and the void in understanding of urban ecosystems. The coast of the Gulf of Mexico is a highly heterogeneous landscape, and measuring landscape composition and configuration as demonstrated here provides a quantitative look at habitats through which stopping migrants may be moving. This process is important and valuable for understanding migrant use of heavily urbanized, fragmented environments where migrant distributions and movements may be complex and unpredictable. This study reveals that migrants utilize this landscape after gulf crossing and that refueling rates along the coast may be comparable to those at stopover sites further inland.

While larger sample sizes from focal species would provide a more thorough look at refueling performance of migrants in these habitats, this study provides estimated overall

fattening rates as indicated by triglyceride levels of landbirds stopping over in urbanized coastal areas, likely shortly after completing trans-Gulf flight. Knowledge of these fattening rates allows for better understanding of stopover ecology within human dominated landscapes and provides a foundation for answering questions surrounding impacts of habitat change on stopover success. For example, the spatially explicit individual-based model (IBM) of Cohen et al. (2013) is a tool for assessing value of different landscapes and their features for migrating songbirds. While there is currently no density component of the IBM, future work could involve adding a density factor in conjunction with fattening rates to analyze refueling performance in the face of competition and other environmental or social factors. Addition of a density component to modeling effort will be particularly valuable for coastal habitats where migrant densities are often high. Densities detected on both transect surveys and from radar observations may be integrated for ranking of habitat patches in the IBM, including an estimate of potential competitive pressure to the model's analysis of refueling. While we cannot currently determine how triglyceride levels recorded in this study are tied to actual mass change, they may be used to inform the IBM for understanding refueling potential in similar urbanized landscapes. With known triglyceride values in urbanized habitat patches of various sizes, the model may reveal changes in refueling performance of migrants as they move through heterogeneous urban landscapes and may provide insight to overall success of varying stopover events in coastal settings.

We recommend investigating migrant-habitat relations in a heterogeneous landscape using a top-down approach, i.e., from a broad, regional perspective to a more narrowly focused ground-based study of individual migratory birds during stopover. To examine spring migrant distributions along the Gulf of Mexico coast, we analyzed weather surveillance radar data from Tallahassee, Florida, to Corpus Christi, Texas during four spring migrations (report to follow). Those observations revealed that migrants stop in urban habitats across the entire coast of the Gulf of Mexico, and their densities are likely higher at more western locations (i.e., Louisiana and east Texas) than at sites surveyed in this study. Understanding of broad scale spatial and temporal coastal habitat use provides a foundation for asking finer scale questions at the level of stopover habitat patch or individual migratory bird. This multi-scaled approach to investigation of migrant population dynamics may be the most necessary and effective method for informing conservation planning and designing habitat management strategies (Buler et al. 2011).

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