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Scale-dependent habitat use by fall migratory birds: vegetation architecture, floristics, and geographic consistency

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SCALE-DEPENDENT HABITAT USE BY FALL MIGRATORY BIRDS: VEGETATION STRUCTURE, FLORISTICS, AND GEOGRAPHY

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Abstract. Animal habitat selection is a central focus of ecology and conservation biology. Understanding habitat associations in migratory animals is particularly complicated because individuals have variable habitat requirements during the annual cycle, across their geographic range, along migratory routes, and at multiple spatial scales. We studied habitat associations of 16 fall Nearctic–Neotropical migratory land birds at two spatial scales at a stopover site along the northern Yucatan coast to examine scale-dependent habitat use, identify proximate cues shaping birds' distributions, and evaluate similarities in habitat use between our tropical stopover site and temperate sites. We addressed scale-dependent habitat associations in two ways, by (1) quantifying species' distributions among and within broad vegetation types and (2) comparing migrants' associations with architectural gradients between the two spatial scales. We also evaluated the relative importance of vegetation architecture and floristics in explaining migrants' distributions within broad coastal vegetation types.

Bird species were nonrandomly distributed among broad- and fine-scale vegetation types, and patterns of habitat use varied between the two scales. Moreover, birds had different preferences for vegetation architecture at the two scales, which may reflect trade-offs between competing demands and/or reduced variation in vegetation at the small scale in our study. These findings illustrate the manner in which spatial scale and range of vegetation variation influence perceptions of animal–habitat associations. Within broad coastal vegetation types birds refined their distributions in relation to architectural and floristic attributes, which provided them with redundant and/or complementary information regarding the distribution of suitable habitat. We suggest that the relative importance of architecture and floristics is likely scale-dependent. Habitat use at our site was similar to that observed at temperate stopover sites for almost all species, indicating that habitat affinities are maintained along the migratory route for these eastern populations despite latitudinal changes in environmental factors. We highlight examples of similar patterns observed in other migratory and nonmigratory animals to illustrate the generality of these patterns beyond en route land birds and our tropical site. We also indicate where we expect to see differences and outline areas of research that merit greater attention in order to advance our understanding of animal habitat selection.

Key words: coastal vegetation; fall migration; forest; geographic variation; habitat associations; land birds; plant species composition; scale-dependent habitat use; stopover ecology; tropics; vegetation architecture; Yucatan Peninsula.

Introduction

Describing patterns in animal species' habitat use and identifying the underlying processes shaping those patterns is a central focus of ecology. However, understanding habitat use is complicated by the hierarchical, scale-dependent nature of habitat selection, in which different factors and processes operate at different spatial scales to shape species' distributions (Johnson 1980, Hutto 1985a, George and Zack 2001, Moore et al. 2005b). Animals ranging from insects and

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reptiles to mammals and birds exhibit scale-dependent patterns in habitat use across regional, landscape, macrohabitat, and microhabitat scales (e.g., McIntyre 1997, Saab 1999, Compton et al. 2002, Keinath and Hayward 2003, D'Eon and Serrouya 2005, Row and Blouin-Demers 2006). For animals that undergo migratory movements, understanding habitat use and selection is further complicated by seasonal and geographical changes in habitat associations that reflect animals' responses to temporal and spatial variation in environmental conditions and resources, as well as temporal changes in animals' physiological and ecological requirements (Brower and Malcolm 1991, Rappole 1995, Dingle 1996, Fleming 2004, Nabhan 2004, Dingle and Drake 2007).

Nearctic–Neotropical migratory land birds lie at one end of a continuum with respect to spatiotemporal

complexity in animal habitat selection and provide a model system for examining scale-dependent, geographical, and seasonal patterns in habitat use. By virtue of their high mobility and remarkable navigational capacity, long-distance migratory land birds have evolved the ability to exploit habitats in disparate ecosystems separated by thousands of kilometers; they select breeding habitat at seasonally productive temperate and boreal latitudes, winter habitat at tropical latitudes with mild climates, and stopover habitat along fall and spring migratory routes where they can refuel, rest, molt, and/or find refuge from inclement weather and predators. En route, migrants traverse large geographic areas over a relatively brief period of time, repeatedly selecting habitat at different stopover sites. Like other migratory animals, such as the monarch butterfly (*Danaus plexippus*), baleen whales, and marine turtles, long-distance migratory birds have broad scientific and public appeal, and recent declines reported for many migratory bird populations have stirred concern, bringing interest in the ecology of migration in this taxonomic group to the forefront (e.g., Terborgh 1989, Hagan and Johnston 1992).

Vegetation architecture is an important factor shaping animal species' habitat associations (Wiens and Rotenberry 1981, Parmenter et al. 1989, Law and Chidel 2002, Bertolino 2006). Physiognomy, the physical structure of the vegetation, provides information regarding the availability of resting/roosting/perch sites and shelter against abiotic conditions and predators, and it influences the efficiency with which animals move through the environment to escape predators and search for, locate, and acquire food resources (Hilden 1965, Robinson and Holmes 1982, 1984, Pounds 1988, Boonman et al. 1998, Vanhooydonck et al. 2000). Plant species composition also plays a role in shaping animal distributions, as plant species directly and indirectly influence the abundance and type of resources available to individuals (Holmes and Robinson 1981, Rotenberry 1985, Brower and Malcolm 1991, Fleming et al. 1993, Barrow et al. 2000). Of course, it is reasonable to expect that some combination of vegetation architecture and plant species composition is important, either because they convey different information regarding the distribution of resources and conditions or because they are correlated, which occurs when plant species with unique structures are present in the environment. In the former case architecture and floristics offer complementary information regarding the distribution of suitable habitat, whereas in the latter they might provide redundant information. In light of the high turnover in plant species composition between temperate and tropical latitudes along the migratory routes of Nearctic–Neotropical migratory land birds, birds' unfamiliarity with stopover sites (particularly young birds making their first migration) and species' ecomorphological constraints, vegetation architecture may provide a more reliable cue to migrants regarding the distribution of suitable habitat at stopover sites than does plant species composition. For migratory birds, which experience time and/or energy constraints during migration, architecture may enable individuals to rapidly assess habitat quality upon arrival at a stopover site. Here, we test the hypothesis that distributions of migratory land bird species are more closely associated with vegetation architecture than plant species composition during migration.

A wave of research over the past two decades has enhanced our understanding of bird species' habitat associations during migration (e.g., Hutto 1985b, Moore et al. 1990, Yong et al. 1998, Rodewald and Brittingham 2004). With few exceptions (e.g., Martin 1985, Winker 1995, Ruelas Inzunza et al. 2005), studies explicitly examining stopover habitat selection by en route Nearctic–Neotropical migrants have been conducted almost entirely at temperate latitudes. However, plant species, food resources, competitors, predators, abiotic conditions, and threats to birds and their habitats differ between temperate and tropical latitudes, and our current understanding of ecological patterns during migration of this taxonomic group does not account for this variation. Thus, one of our goals is to assess how robust our understanding of land bird species' stopover habitat requirements is, based on temperate studies.

The majority of stopover habitat selection studies also have concentrated on a single ecological or spatial scale (although see Sapir et al. 2004). Here we take a hierarchical, scale-dependent approach to understanding how land birds are distributed among and within broad vegetation types at a tropical coastal stopover site in the northern Yucatan Peninsula during fall migration and the cues that birds use in deciding where to settle at each scale. By doing so, we demonstrate how subtle differences in scale influence our perception of habitat use. We address scale-dependent habitat associations in two ways: (1) by quantifying species' distributions across broad- and fine-scale vegetation types and (2) by comparing migrants' associations with architectural attributes between the two spatial and ecological scales. We also evaluate the relative importance of vegetation architecture and plant species composition in explaining migratory bird distributions at a fine scale within broad coastal vegetation types. An examination of species' associations with architecture at the two scales and an assessment of the relative importance of architecture and floristics provides insight into the cues that birds use when deciding where to settle to satisfy their physiological and ecological demands during migration.

Each fall the Yucatan Peninsula provides stopover sites for multitudes of southbound Nearctic–Neotropical migratory land birds that traverse the Gulf of Mexico or the eastern Caribbean Sea (Paynter 1953, Buskirk 1980, Howell 1989, Mills and Rogers 1990). Coastal regions of the Peninsula as well as barrier beaches and islands provide the first available landfall for these birds and offer important stopover habitat

where they can satisfy their en route demands, particularly immature birds completing their first over-water migratory flight and individuals arriving in poor energetic condition. Due to their proximity to ecological barriers such as the Gulf of Mexico, coastal sites may play a disproportionate role in determining the successful completion of migration relative to stopover sites located away from such barriers.

Here we evaluate five questions regarding habitat use by fall trans-Gulf migratory land birds along the northern coast of the Yucatan Peninsula to improve our understanding of en route habitat selection at different ecological and spatial scales, to generate robust patterns of habitat use applicable to stopover sites beyond those studied at temperate latitudes, and to gain further insight into the proximate factors shaping species' stopover habitat associations at small ecological and spatial scales. (1) What broad coastal and interior vegetation types do land bird species use in the northern Yucatan Peninsula during fall migration? (2) How do birds distribute themselves within coastal scrub and mangrove vegetation on a barrier beach? In other words, do species respond to fine-scale variation within these two broad vegetation types? (3) Is vegetation architecture a better predictor of migrant species' distributions than plant species composition at a fine ecological and spatial scale within coastal scrub and mangrove? (4) Do species demonstrate the same relationship with architectural attributes at both broad and fine vegetation scales? (5) Is habitat use similar between our tropical stopover site along the northern Yucatan coast and temperate stopover sites in Canada and the United States?

In discussing our results we highlight examples of similar patterns observed in birds during nonmigratory periods of the annual cycle, as well as other migratory and nonmigratory animals, to illustrate the generality of these patterns beyond en route land birds and our tropical stopover site. We also indicate where we expect to see differences from the patterns we observed in our study and outline several areas of research that we think merit greater attention in order to advance our understanding of animal habitat selection in general and stopover habitat selection in particular.

METHODS

Study area

We studied 16 species of fall trans-Gulf migratory land birds in coastal and interior vegetation types near El Cuyo (21°30′48″ N; 87°40′35″ W; see Appendix A for map) in the eastern region of the Ría Lagartos Biosphere Reserve (hereafter referred to as the Reserve), located along the northern coast of the Yucatan Peninsula in northeastern Yucatan, Mexico. The Reserve covers 74 km of the peninsula's northern coastline, and a barrier beach dominated by coastal dune scrub and mangrove extends almost the entire length of the Reserve (Carabias Lillo et al. 1999). The barrier beach is 0.05–

2.20 km wide and is separated from the mainland by a coastal lagoon that varies in width from 0.08 to 4.90 km. The eastern region of the Reserve surveyed in our study extends inland ~9 km and includes interior vegetation types, such as semi-evergreen forest, seasonally inundated deciduous forest, and pasture. We surveyed migrants during fall migration in 2001 (12 August to 6 November), 2002 (4 August to 16 November), and 2003 (6 August to 27 November).

Migratory land birds

The migratory birds that we studied in Yucatan breed in Canada and the eastern United States, winter in southern Mexico and Central and South America, and cross the Gulf of Mexico during migration (Deppe and Rotenberry 2005). The species represent a diverse range of diets, foraging behaviors, and microhabitat guilds at our site (Deppe and Rotenberry 2005; J. L. Deppe, unpublished data). Most of the bird species we studied are insectivores, but several species are omnivores and consume nectar (the Tennessee Warbler and the Northern Parula; see Appendix H for scientific names) or fruit (the White-eyed Vireo and the Gray Catbird) in addition to insects. The Gray Catbird, the Tennessee Warbler, the Palm Warbler, the Common Yellowthroat, the Hooded Warbler, and the American Redstart are active in the understory and glean arthropod prey from the foliage of shrubs and saplings, although the American Redstart and the Hooded Warbler also catch aerial insects in the understory. The White-eyed Vireo, the Northern Parula, and the Magnolia Warbler are most active in the overhead canopy, where they forage on foliage-dwelling arthropods, fruit, and/or nectar. The Yellow Warbler and the Prothonotary Warbler glean foliage-dwelling arthropods in both the canopy and the understory; the Black-and-white Warbler gleans arthropods from the trunks and limbs of trees and, to a lesser extent, large shrubs; and the Northern Waterthrush and the Ovenbird forage by gleaning ground-dwelling arthropods from the soil, litter, or water. The Ruby-throated Hummingbird is a nectarivore that is active primarily in the understory, where it searches for nectar in flowering shrubs and forbs, whereas the Indigo Bunting is a granivore, relying heavily on grasses and seed-bearing forbs.

Large ecological and spatial scale

Broad vegetation types.—We surveyed fall migrants in five broadly defined coastal and interior vegetation types in the eastern region of the Reserve: coastal dune scrub, abandoned coconut plantation, mangrove, forest, and pasture. Each of these vegetation types is widely represented throughout the Yucatan Peninsula, particularly in coastal regions, and all are comparable both structurally and floristically to those found in other tropical regions of the Gulf and Caribbean basins (Moreno-Casasola and Espejel 1986, Britton and Morton 1989, Lynch 1989, Lopez Ornat and Lynch

1990, Universidad Autónoma de Yucatán 1999). See Appendices B and C for photographs and detailed descriptions of these vegetation types.

Coastal dune scrub is a dominant vegetation type along the Yucatan coast. In the Reserve this vegetation type is restricted to the barrier beach and is characterized by dense woody shrubs, succulents, herbaceous plants, and local abundances of several native palm species. Coastal scrub is relatively short and reaches a mean height of 2.6 m in the Reserve. Dominant species include *Pseudophoenix sargentii*, *Thrinax radiata*, *Pithecellobium keyense*, *Bravaisia tubiflora*, and *Caesalpinia vesicaria*.

Abandoned coconut (*Cocos nucifera*) plantations occupy large areas of the barrier beach. Remnant palms are still present in these areas and represent a unique feature of the landscape. The understory of the abandoned plantations is dominated by short, coastal scrub vegetation with a well-developed herbaceous layer and scattered patches of shrubs (mean vegetation height = 0.8 m). Because of the dominance of coconut palms and our interest in understanding how birds use anthropogenically altered vegetation, we treated abandoned coconut plantations as a distinct vegetation type.

Mangroves, characterized by halophytic, wetland species, including *Rhizophora mangle*, *Avicennia germinans*, *Conocarpus erectus*, *Batis maritima*, and *Salicornia bigelovii*, are located along the northern and southern margins of the coastal lagoon and along the Reserve's eastern limit; we restricted our study to the former. The mangroves surveyed in our study were short (mean height = 2.2 m) and were inundated or had saturated soil through most of the fall migration.

Forested areas surveyed in our study are located 8–9 km inland from the coast in the southeastern region of the Reserve and are classified as medium-stature semi-evergreen forest (selva mediana subperennifolia) with small, dispersed patches of low-stature, seasonally inundated deciduous forest (selva baja caducifolia inundable). Medium-stature semi-evergreen forest ranges in height from 15 to 25 m, has a well-developed overhead canopy and moderately vegetated understory, and ~25% of the species drop their leaves during the dry season (November through April; Universidad Autónoma de Yucatán 1999). Dominant tree species include *Manilkara zapota*, *Sideroxylong foetidissium*, *Metopium brownii*, *Ceiba aesculifolia*, and *Bursera simaruba* (Carabias Lillo et al. 1999, Universidad Autónoma de Yucatán 1999). Seasonally inundated deciduous forest is associated with depressions in the limestone substrate that flood during the wet season (May through October). Vegetation in these areas is shorter (mean height = 10 m) and has a more poorly developed understory and lower plant species richness than the surrounding semi-evergreen forest. Common plant species include *Haematoxylon campechianum*, *Acoelorrhaphe wrightii*, *Bucida espinosa*, and *Erythroxylum confusum* (Universidad Autónoma de Yucatán 1999).

Most livestock grazing near the village of El Cuyo (see Appendix A) is conducted on a small scale; pastures, or fields, varied in size up to 50 ha in the areas that we surveyed. Pastures contain remnant trees, forest patches, and living fences, and they have greater architectural heterogeneity and plant species diversity than areas mechanically cleared for large-scale livestock grazing (100+ ha). Pastures are dominated by *Panicum* spp. and other introduced forage grasses, and remnant trees are those found in semi-evergreen or inundated deciduous forests. Grazing activity in the surveyed areas was light during our study, and grasses reached a mean height of 1.2 m. Surveyed pastures were located between 4 and 8 km inland from the coast in the eastern region of the Reserve.

Bird surveys.—We used point counts to survey fall migrants at the large ecological and spatial scale. We established 12 point count locations in each of the five broad coastal and interior vegetation types, with a minimum of 200 m between points. The 12 points were distributed among two to five sites to provide true replicates of each vegetation type, and all sites were located within a 252-km^2 (28 × 9 km) area. We divided the 60 points into two groups of 30 (six points per vegetation type), and we surveyed the two groups of points on an alternating basis approximately every two weeks during fall 2002 and 2003. Although we surveyed points multiple times during a single year, successive counts at any particular point were separated by approximately one month. Estimated mean stopover lengths for migratory land birds at other sites are much shorter than this time interval, generally less than five days (Kuenzi et al. 1991, Morris et al. 1996, Woodrey and Moore 1997, Yong and Moore 1997), so we considered successive counts to be independent replicates (Hutto 1985b).

Two observers surveyed birds using 10-min, fixed-radius point counts, and each observer visited the five vegetation types with equal frequency so that vegetation type and observer were not confounded. Observers waited at a point 5 min prior to beginning the count, during which time they recorded environmental data. When necessary, observers spent up to 5 min after the termination of the point count to look for birds and/or record vocalizations to confirm species identifications. All point counts were conducted within 3.5 h after sunrise, when activity dropped noticeably. A total of 499 point counts were conducted during 2002 and 2003.

We used audiovisual surveys to sample migrants across the five broad coastal and interior vegetation types instead of mist nets because of the variable height of the vegetation. Many birds in forest and other tall vegetation (e.g., forest patches in pastures) are active above the effective sampling height of mist nets, which results in underestimates of the abundances of canopy-dwelling species in those vegetation types (Rappole 1995, Rappole et al. 1998).

Small ecological and spatial scale

Fine-scale coastal vegetation types.—We used mist nets to survey birds in coastal vegetation on the barrier beach. Architecture and plant species composition of coastal dune scrub and mangrove on the barrier beach is the result of complex interactions among abiotic factors, including wind, salt spray, soil salinity, proximity to the ground water table, and topography. Variations in abiotic conditions along the barrier beach create bands of relatively distinct vegetation types apparent as one moves from the ocean inland toward the lagoon. We used a cluster analysis to classify nets into fine-scale vegetation assemblages within coastal scrub and mangrove on the barrier beach regardless of the site on which they occurred based on measurements of vegetation architecture and plant species composition at each net location averaged over the three years of the study (see Appendix D).

Our cluster analysis classified nets into six coastal vegetation types: back dune, palm- and shrub-dominated thickets on fixed sand dunes, humid dune slacks, and primary and secondary mangrove assemblages (see Appendix B). These six vegetation types correspond to plant assemblages described by Moreno-Casasola and Espejel (1986) for this region, except that our analysis divided mangroves into two groups. Appendix B provides photographs and a detailed description of each coastal vegetation type, and Appendices E–G provide mean values of architectural variables and common plant species abundances in each vegetation class.

The back dune (BD) is the sheltered zone of vegetation located behind the sparsely vegetated fore dune and is characterized by a well-developed herbaceous layer and scattered, dense patches of short, thick-leaved shrubs able to tolerate salt spray and strong winds. Trees are scarce, and the vegetation has a low height and foliage profile diversity. Common species include *Coccoloba uvifera*, *Pithecellobium keyense*, *Ambrosia hispida*, *Alternanthera ramosissima*, and *Gossypium hirsutum*.

Palm- and shrub-dominated thickets are found on stabilized sand dunes. Thickets generally consist of three vegetative layers and are taller, have a better-developed canopy, and are more structurally and floristically diverse than back dune vegetation. The two thicket types at our site share many plant species in common and are distinguished primarily by differences in plant species abundances and architectural features. Palm-dominated thickets (PT) are taller and have more trees, a better-developed canopy and, as their name implies, a much higher abundance of the three native palm species, *Pseudophoenix sargentii*, *Thrinax radiata*, and *Coccothrinax readii*, than shrub-dominated thickets (ST).

Humid (or wet) dune slacks (HS) are located in low-elevation areas between stabilized dunes and support a combination of coastal scrub and wetland plant species. The lowest and wettest regions of the slacks have very little shrub or tree cover but dense ground cover, which is dominated by halophytic species able to tolerate periodic inundation during the wet season (May to October). At the higher-elevation margins of the slacks, shrub and tree densities are higher, vegetation is taller, foliage profile diversity is greater, and thicket-associated species are more common. *Conocarpus erectus*, a mangrove species, also is frequently present in slacks.

Secondary mangroves (SM) lie beyond the direct, prolonged influence of the lagoon and are dominated by the tree species *Conocarpus erectus*, which tolerates only periodic inundation. Next to palm-dominated thickets, secondary mangroves are the tallest plant assemblages on the barrier beach. They have a well-developed canopy layer; relatively open shrub layer; moderate ground cover dominated by halophytic subshrubs, forbs, and graminoids; and low plant species diversity.

Primary mangroves (PM) sampled in our study are located along the edge of the coastal lagoon and are dominated by *Rhizophora mangle* and *Avicennia germinans*, which are more tolerant of high salinity and prolonged inundation than *C. erectus*. Primary mangroves at our sites typically occur as small, dispersed hummocks and are best described as mangrove scrub. They have a relatively short stature with reduced tree and shrub density, low canopy cover, and a low foliage profile diversity. Primary mangroves have the lowest species diversity of the six coastal vegetation types. The higher elevation and relatively drier portions of the mangrove hummocks are associated with halophytic forbs and graminoids in the understory.

Bird surveys.—We used mist nets to survey migrant birds in coastal dune scrub and mangrove on the barrier beach in 2001–2003. In early fall 2001 we surveyed migrants at five sites along the barrier beach. By mid-fall 2001 we reduced the number of sites to three, including one of the original five sites and two new sites. We surveyed these three sites on a rotational basis throughout the remainder of the study (see Appendix A for map of sites). The farthest sites were separated by 28 km. Eight to nine mist nets (12 m long × 2.5 m high, 30 mm mesh), located at least 30 m apart, were placed along a transect from the ocean to the lagoon in each site to maximize the variation in coastal vegetation sampled. As noted, we measured vegetation architecture and plant species composition at each net location and used a cluster analysis to classify nets into coastal vegetation types. Each of our three survey sites contained four or five of the six vegetation types subsequently defined by our cluster analysis, and with two exceptions, each vegetation type was present at two or three of the sites to provide true replicates. Most of our analyses are restricted to our three primary sites, although our assessment of the relationship between migrant distributions and vegetation attributes for several bird species include data from the additional four sites sampled in early fall 2001.

We surveyed birds four to six days each week in 2001 and three days per week in 2002–2003 with several

exceptions when strong winds, precipitation, or flooding prevented us from operating nets. We opened mist nets approximately 15 min prior to sunrise and operated them for up to 6.25 h (3.43 ± 0.02 h [mean ± SE]). We checked nets at least every 30 min and closed them late in the morning to avoid heat stress and mortality to birds. We concentrated our capture efforts in the morning during the period of peak activity. Each bird was banded with an aluminum leg band (U.S. Geological Survey) to allow the identification of recaptured individuals.

We observed migrants' behavior during each day of netting to ensure that birds were actually using our survey sites (e.g., foraging, resting for extended periods, preening, engaging in aggressive interactions) and not simply passing through the area. On several occasions we observed behavior that suggested that migrants had just arrived on the peninsula or were adjusting their location following arrival the previous evening (observations suggest that birds arrive at our site late in the evening as well as in the morning): birds passed through the site in extensive numbers as large mixed-species flocks; birds flew in a uniform direction (toward the east, parallel to the coast) generally high above the vegetation and without stopping in the area; frequent contact calls were heard; some individuals exhibited disoriented behavior; and birds were not observed foraging or resting. On a few days migrants' behavior suggested that they were engaging in an exploratory phase: birds moved in a uniform direction (toward the east or west but parallel to the coast) in small mixed-species flocks, and birds periodically interrupted flight to engage in very brief foraging or resting bouts before resuming flight and leaving the area. Migrants captured on days when observations suggested that they had just arrived, were adjusting their position, or were exploring were omitted from analysis to ensure that we were assessing the habitat use patterns of birds that had already settled in a vegetation type.

Vegetation measurements

At the conclusion of fall migration, we measured architectural variables at point count and mist net locations using a modified circular plot technique (5-m radius; James and Shugart 1970). Some point counts in coastal scrub and mangrove vegetation were located in close proximity to mist net locations (<75 m), and for those points we used vegetation measurements collected at the closest mist net location.

Point count vegetation measurements.—We measured the diameter at breast height (dbh, 1.4 m above the ground surface) of all trees ≥2 m tall with a dbh ≥ 5 cm within the circular plot. We calculated the basal area of each tree assuming the trunk was circular ($A = \pi r^2$), and we summed basal area over all trees in the plot to yield total basal area for the point. At the four cardinal directions along the circumference of the plot, we measured vegetation height. Mean vegetation height

was calculated by averaging over the four measurements taken along the plot circumference, and we determined maximum vegetation height by measuring the tallest point of vegetation in the plot.

We measured total linear cover (all species combined) of understory vegetation, including herbaceous, shrub, and tree (sapling) species ≤2 m tall, along two 5-m transects placed parallel to one another within the plot (transects were separated by 3 m). We used a sighting tube to record the presence/absence of live vegetation on the ground at 20 random points within the circular plot, and ground cover was quantified as the percentage of points with living vegetation. We measured canopy cover at 10 random points in the plot using a spherical crown densiometer (convex, model A; Forestry Suppliers, Jackson, Mississippi, USA), and we averaged the measurements to yield an estimate of percent overhead canopy cover at each survey location.

Mist-net vegetation measurements.—Total basal area, mean and maximum vegetation height, and percent canopy and ground cover were measured and calculated at mist net locations in the same way as described in *Point count vegetation measurements*.

We measured additional architectural and floristic attributes of the vegetation at mist net locations. We measured the vertical distribution of foliage at the four cardinal directions along the plot circumference by placing a graduated pole marked at 20-cm increments vertically in the vegetation and recording the number of times foliage hit the pole within each 20-cm increment (Bibby et al. 1992). During subsequent analyses we pooled hits over 20-cm increments to generate estimates of foliage density in the following three vegetation layers: ground (0.0–0.4 m), shrub (>0.4–2.0 m), and canopy (>2.0 m). We used the Shannon-Weaver diversity index (H') to calculate the vertical foliage profile diversity based on the proportion of hits in the three vegetation layers (Bibby et al. 1992).

We calculated the basal area of each tree species by summing across all individuals of the species in the circular plot. We used two 5-m line transects, one on either side of the net but beyond the cleared net lane, to quantify the linear cover of understory vegetation (0–2 m tall), including herbaceous, shrub, and tree (sapling) species. For each net we calculated the total cover of each species along the two transects. We calculated diversity of the understory vegetation using the Shannon-Weaver diversity index.

Habitat use at temperate stopover sites

We summarized species' habitat use during migration at stopover sites in the United States and Canada and compared it to habitat use at our site to evaluate similarity in species' habitat use between our tropical coastal stopover site in the northern Yucatan Peninsula and stopover sites at temperate latitudes. Due to geographic variation in plant communities among our study site and the temperate stopover sites studied by

others, we summarized and compared species use of three broad habitat types: forest, scrub/shrub, and field/grassland; multiple vegetation types were grouped into each of the three broad classes. Our summary of temperate habitat use is based primarily on *Birds of North America* species' accounts (Poole and Gill 1992–2003), field guides, natural history accounts, and peer-reviewed articles that fit the following criteria: (1) species-level analyses were performed; (2) information on the relative abundance, density, or frequency of occurrence of species in each habitat type was provided; (3) two or more of the following habitat types were included in the study: forest, scrub/shrub, and field/grassland; and (4) studies were conducted in the eastern or central United States and Canada (see Appendix L for list of citations used to generate our summary). All vegetation types regularly used by a species in at least 50% of the studies or species accounts were identified as appropriate habitat for the species. We also identified the use of wetland habitat in each category (e.g., wet forests or wet scrub). The summary of habitat use at our site was based on habitat associations at the large ecological and spatial scale.

Statistical analysis

Migrant associations with vegetation types at the large and small spatial scales.—We quantified vegetation associations for 16 common migrant species at the large and small spatial scales in our study using general linear models (GLMs; SPSS version 11.0.1; SPSS 2002; see Appendix H for list of species).

At the large scale (five broad coastal and interior vegetation types) we calculated species' abundances during each point count by summing all individuals heard or seen within 50 m of the point center, excluding flyovers. At the small scale (six fine-scale coastal vegetation types) we calculated the total number of individuals of each of the 16 species captured in each net over the entire season and divided it by the corresponding number of mist net hours to yield species abundance per net-hour (one 12-m net operated one hour = 1 net-hour). We restricted this analysis to net locations surveyed at the three primary sites, and we only included first captures and transient individuals (i.e., birds that do not spend the winter at our site). For species known to have winter populations in Yucatan (Howell and Webb 1995), we identified winter residents based on recapture data and truncations of species' annual migration curves (i.e., chronologies) following the criteria outlined by Deppe and Rotenberry (2005) and removed those individuals from our analyses. We applied square root or log transforms to our point count and mist net data to improve their fit to the assumptions of normality and homogeneity of variance. We present untransformed data in our graphs, and all results are reported as mean abundance/100 point counts ± SE and mean abundance/100 net hours ± SE.

We used GLMs to evaluate differences in mean species abundance among years and vegetation types at each spatial scale. Preliminary analyses at both scales demonstrated no vegetation × year interaction for any of the bird species, so we eliminated the interaction term from our final model to allow us to shift the additional df to the error term. To control our Type I error rate, we evaluated the significance of species' vegetation associations at each spatial scale using a sequential Bonferroni test for k comparisons based on the Dunn-Sidák method, where $k = 16$ (species) and the "table-wide" error was controlled at $\alpha = 0.05$ (Rice 1989, Sokal and Rohlf 1995). We used post hoc pairwise multiple comparisons (Tamhane's tests) to clarify our interpretation of species–habitat associations (SPSS 2002).

Architectural and floristic gradients at the large and small spatial scales.—We used principal components analysis (PCA; Tabachnick and Fidell 1996) and detrended correspondence analysis (DCA; Hill and Gauch 1980, Gauch 1982) to identify latent variables in our architectural and floristic data sets, respectively, and to reduce the number of vegetation variables used in our analyses of species–habitat associations.

For the architectural data collected at point count survey locations, we performed a PCA using the following six variables: mean and maximum vegetation height; total basal area; and percent canopy, understory, and ground cover. We performed a separate PCA on the 10 architectural variables measured at our mist net survey locations, including mean and maximum vegetation height; total basal area; percent canopy and ground cover; foliage density in the canopy, shrub, and ground layers; foliage profile diversity; and understory species diversity. To facilitate our interpretation of the components at the two scales, we used a varimax rotation and evaluated the loading matrix (SPSS version 11.0.1; SPSS 2002). Point counts and mist nets were assigned scores on each principal component (PC) in their respective analyses. Principal components derived from our analysis at the large spatial scale are labeled PC-LS and those at the small scale are labeled PC-SS to avoid confusion.

To fully describe the floristic turnover among net locations at our site, we included information on basal area of tree species and linear cover of understory species in a single DCA. Because basal area and cover were measured in different units, each plant species was standardized by dividing its basal area or cover at a particular net location by its total basal area or cover across all nets to ensure that each variable was weighted equally in the analysis. We used the same suite of plant species included in our cluster analysis (species occurring at ≥5% of net locations). We used PC-ORD version 4.0 (McCune and Mefford 1999) to perform the DCA. Both nets and plant species were assigned scores on each detrended correspondence analysis axis (DC), which we graphed to assist in the interpretation of the gradients. We performed Pearson's correlations between PC and

DC scores for nets at the small spatial scale to enhance our interpretation of the vegetation gradients and quantify relationships between vegetation architecture and floristics.

Relative importance of vegetation architecture and plant species composition in explaining migrant species' distributions at the small scale.—To evaluate our hypothesis that vegetation architecture is a better predictor of bird species' distributions than plant species composition, we used Akaike's information criterion (AIC; Burnham and Anderson 2002) to identify the set of vegetation variables, or gradients, that best explained migrant distributions within coastal dune scrub and mangrove vegetation on the barrier beach. We compared three multiple logistic regression models, architectural, floristic, and global, for explaining species' distributions or occurrences along the barrier beach (Hosmer and Lemeshow 1989, Tabachnick and Fidell 1996). Each model contained a different set of vegetation gradients; the architectural model contained only the retained PCs as explanatory variables, the floristic model contained only the DCs, and the global model included all PCs and DCs. All three models included year effects (dummy coded) as an explanatory variable. We determined species' presence or absence at net locations for each year of the study. For several species that arrive in early fall, we included nets from all seven sites surveyed during our three-year study, including our three primary sites and the four additional sites monitored in early fall 2001. For all other species we restricted our analysis to nets operated at the three primary sites.

We calculated AIC values for each model based on the maximum log likelihood estimate. Due to our small sample size we calculated second-order information criterion (AIC_c) following the formula in Burnham and Anderson (2002). We evaluated goodness of fit and overdispersion using the Hosmer-Lemeshow chi-square statistic associated with the global model (Burnham and Anderson 2002). None of the species demonstrated signs of overdispersion, so we report AIC_c values for all species. We performed logistic regressions using SPSS version 11.0.1 (SPSS 2002).

We ranked the architectural, floristic, and global models according to their AIC values and then calculated AIC differences ($\Delta_i = AIC_i - AIC_{min}$) and Akaike model weights (w_i) for each of the three candidate models. The AIC difference is an estimate of the expected Kullback-Leibler (K-L) information or distance between the best model (i.e., the one with the lowest AIC value) and any other candidate model in the set, and it provides an index of empirical support in favor of a model being the best approximating model (Burnham and Anderson 2002). By definition the best model has a Δ_i of zero. Models with $\Delta_i < 2$ also have strong empirical support; models with Δ_i between 4 and 7 have much less support; and models with $\Delta_i > 10$ have almost no support. In cases in which multiple models have $\Delta_i < 2$, there is substantial uncertainty as to which model is the actual best model. The AIC model weights indicate the likelihood of a model being the best approximating model relative to other models in the candidate set based on the data. All weights sum to one across the set of models, and larger weights provide greater support for the model (Burnham and Anderson 2002).

Associations between migrant distributions and architectural gradients at the large and small scales.—We used AIC to identify which architectural gradient or combination of gradients best explained migrant distributions at the large and small scales. This analysis was restricted to migrant species for which the architectural model had strong empirical support ($\Delta_i \leq 2.0$) in our comparison of vegetation architecture and floristics at the small scale. We considered all possible combinations of architectural gradients at each scale, and we used Δ_i values and model weights to identify the architectural gradient(s) that best explained migrant species' distributions at those scales. We evaluated variable weights to assess the relative importance of each architectural gradient (PC) in explaining the occurrence of migrants at each scale. We calculated variable weights by summing model weights over all models in the candidate set that contained the gradient (Burnham and Anderson 2002). Variable weights range from 0.0 to 1.0, and higher values indicate a stronger association between the explanatory and response variables. We also evaluated standardized logistic regression coefficients (Exp(B)) to describe the nature (positive/negative) of the association between species' distributions (presence/absence) and each architectural gradient. In many species there was substantial uncertainty regarding the best model. For those species we averaged parameter estimates over all models including the parameter of interest using the "natural" average approach outlined by Burnham and Anderson (2002).

Although Burnham and Anderson (2002) caution against comparing all possible combinations of variables, we feel that this "all possible combinations" approach is justified in this particular analysis for two reasons. First, the purpose of this analysis was primarily exploratory. Second, by comparing models with all possible combinations of vegetation gradients we achieved a balance in the number of models containing each gradient and avoided biasing variable weights in favor of those gradients appearing in a greater number of models (Burnham and Anderson 2002).

RESULTS

Migrant associations with broad coastal and interior vegetation types at the large ecological and spatial scale

The Common Yellowthroat was the only species that demonstrated a significant difference in abundance across years ($P = 0.03$) prior to applying a sequential Bonferroni adjustment, and the Hooded Warbler showed a similar but nonsignificant pattern ($P = 0.07$).

Both species were more abundant in 2003 than 2002. (See Appendix H for a list of bird species scientific names and codes.)

Species demonstrated a range of habitat associations at the large ecological and spatial scale in our study (Fig. 1). Fourteen out of the 16 species that we evaluated in our study demonstrated significant associations with one or more of the broad coastal and interior vegetation types, and patterns remained significant in 11 species after applying a sequential Bonferroni test.

The Northern Waterthrush was the most common migrant species at our site and was most abundant in mangrove and forest, where it was primarily associated with patches of inundated forest (Fig. 1). Although the Northern Waterthrush was the most common species encountered in mangrove, two other species, the Yellow Warbler and the Prothonotary Warbler, reached their highest abundance in this vegetation type. Both Yellow and Prothonotary Warblers were considered "mangrove species"; however, they occasionally used coastal scrub, and the Prothonotary Warbler was also observed in living fences and forest patches in pastures (Fig. 1).

The Ruby-throated Hummingbird, the Palm Warbler, and the Tennessee Warbler were considered "scrub/ shrub species" (Fig. 1). The Ruby-throated Hummingbird was encountered most often in coastal dune scrub, while the Palm Warbler was most abundant in abandoned coconut plantations. The Tennessee Warbler was equally abundant in coastal scrub, abandoned plantations, and pastures, where it was observed foraging on isolated outbreaks of large larvae in the grassy area of the fields.

The Indigo Bunting was the only species classified as a field specialist, even though other species, such as the Common Yellowthroat, were also abundant in the grassy portions of the pasture (Fig. 1). The Common Yellowthroat was broadly distributed across vegetation types at this large spatial and ecological scale and could be classified as a "scrub/field species"; we observed the species frequently in pastures, coastal scrub, mangroves, and to a lesser extent abandoned coconut plantations, but rarely in forest.

Many species associated with forest during other periods of the annual cycle were most abundant in forest in the Reserve during fall migration, including the Ovenbird, the American Redstart, the Hooded Warbler, the Magnolia Warbler, the Northern Parula, and the Black-and-white Warbler (Fig. 1). The White-eyed Vireo, a shrub-breeding species that frequently occupies forest during winter, also reached its greatest abundance in forest at our site. Most species associated with forest in the Reserve also were observed using remnant forest patches and living fences in pasture, particularly the White-eyed Vireo, the Ovenbird, and the Magnolia Warbler. The White-eyed Vireo and the Magnolia Warbler were active in the trees of forest patches and living fences, whereas the Ovenbird was observed on the ground. The American Redstart demonstrated a slightly broader distribution and was occasionally encountered in mangrove, pasture, and coastal dune scrub in addition to forest. Although the Northern Parula was observed most often in forest, it also regularly occupied mangrove, pasture, and, to a lesser extent, coastal scrub; however, parulas avoided abandoned coconut plantations.

Only one species was a true habitat generalist at this scale. The Gray Catbird was evenly distributed across the entire range of broadly defined coastal and interior vegetation types surveyed by point counts in our study (Fig. 1).

Migrant associations with fine-scale coastal vegetation types at the small ecological and spatial scale

Five species, the Ruby-throated Hummingbird, the Gray Catbird, the Northern Parula, the Prothonotary Warbler, and the Tennessee Warbler, demonstrated significant differences in capture rates among years ($P < 0.05$). The Ovenbird, the Yellow Warbler, the Black-and-white Warbler, and the Common Yellowthroat demonstrated marginally significant year effects ($P = 0.06$–0.08). Abundances of the Ovenbird, the Northern Parula, the Tennessee Warbler, and the Black-and-white Warbler were greatest in 2001, while the remaining four species were most abundant in 2002. No species reached its highest abundance in 2003. Once we applied a sequential Bonferroni adjustment none of the annual differences remained significant.

Thirteen species demonstrated significant differences in their use of the six fine-scale vegetation types within coastal dune scrub and mangrove prior to applying a Bonferroni adjustment, after which nine remained significant. Twelve species reached their highest mean abundance in one of the moist vegetation types on the barrier beach; three species were most abundant in primary mangrove (the Northern Waterthrush, the Yellow Warbler, and the Prothonotary Warbler), four in secondary mangrove (the Ruby-throated Hummingbird, the Northern Parula, the American Redstart, and the Magnolia Warbler), and five in humid slacks (the White-eyed Vireo, the Tennessee Warbler, the Black-and-white Warbler, the Ovenbird, and the Indigo Bunting; Fig. 2). These species, with the exception of the Northern Waterthrush, frequently used two or three of the moist vegetation types, although they varied greatly in their particular distribution patterns on the barrier beach and the extent to which they used dry coastal scrub vegetation; consequently, they failed to form any clear groupings based on their vegetation associations (Fig. 2). The Northern Waterthrush demonstrated the most restrictive distribution of all species on the barrier beach and was considered a primary mangrove specialist. The Northern Parula, the Yellow Warbler, the White-eyed Vireo, the Tennessee Warbler, and the Ovenbird were primarily restricted to moist vegetation types. Although the Prothonotary Warbler, the American Redstart, the Magnolia Warbler, the
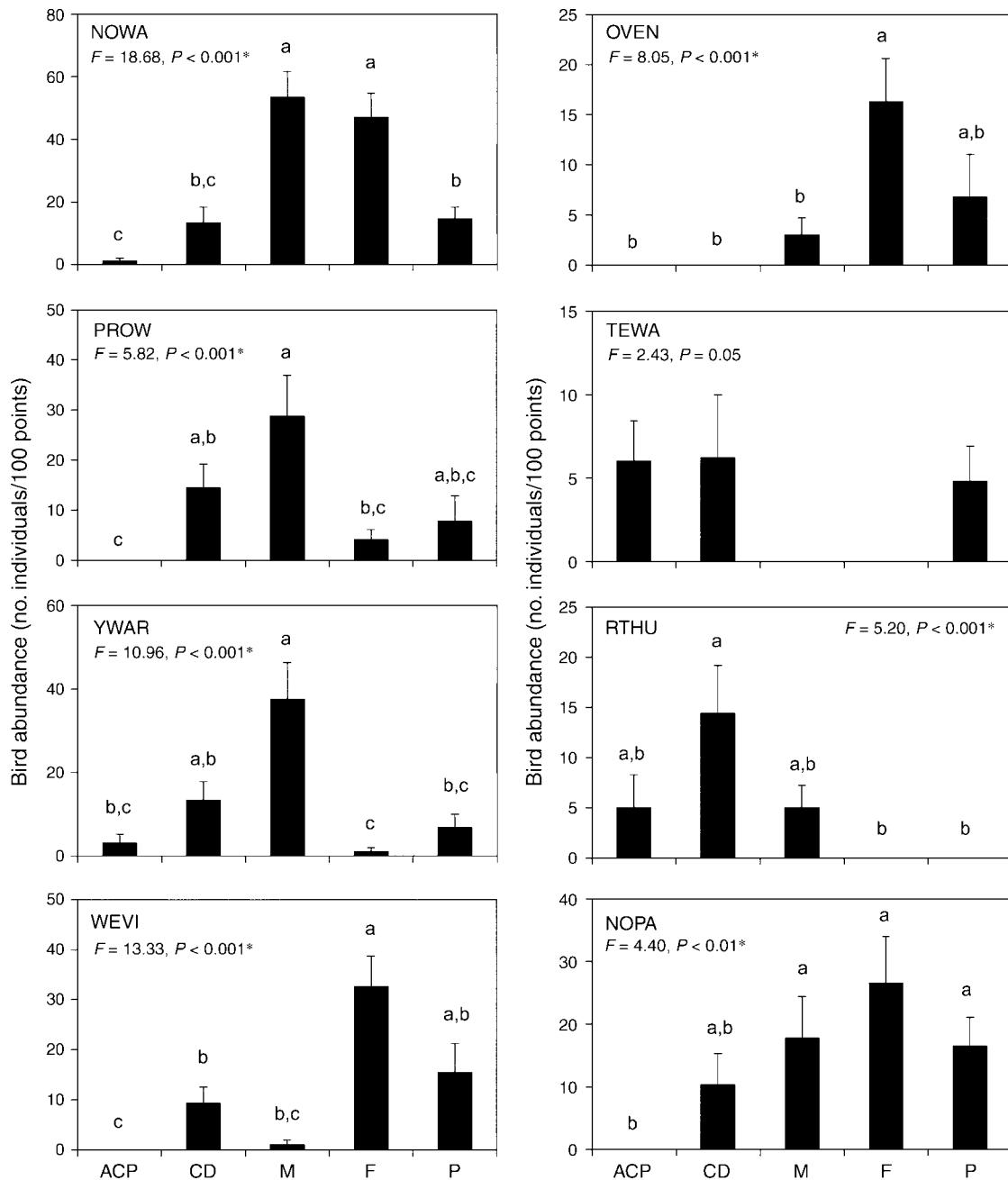
FIG. 1. Distribution of 16 common migratory bird species across five broad coastal and interior vegetation types based on point count data collected in the Ria Lagartos Biosphere Reserve (located along the northern coast of the Yucatan Peninsula in northeastern Yucatan, Mexico) during fall migration 2002–2003. General linear models were performed on transformed data, but untransformed data are presented in graphs for ease of interpretation. For all species, df = 4, 493. An asterisk following the P value indicates significant difference after application of a sequential Bonferroni test (table-wide $\alpha = 0.05$, $k = 16$). Vegetation types with the same lowercase letter above the bars are not significantly different from one another. Vegetation type abbreviations are: ACP, abandoned coconut plantation; CD, coastal dune scrub; M, mangrove; F, forest; P, pasture. See *Methods: Large ecological and spatial scale: Broad vegetation types* for description of vegetation types. Note that the scale of the *y*-axis is not the same for all species. See Appendix H for a definition of bird species codes.

Black-and-white Warbler, the Ruby-throated Hummingbird, and the Indigo Bunting were closely associated with mangroves and slacks, these species tended to be more evenly distributed along the barrier beach and also used some of the drier coastal scrub plant assemblages.

The three species that demonstrated a significant preference for mangrove at the large scale, the Northern
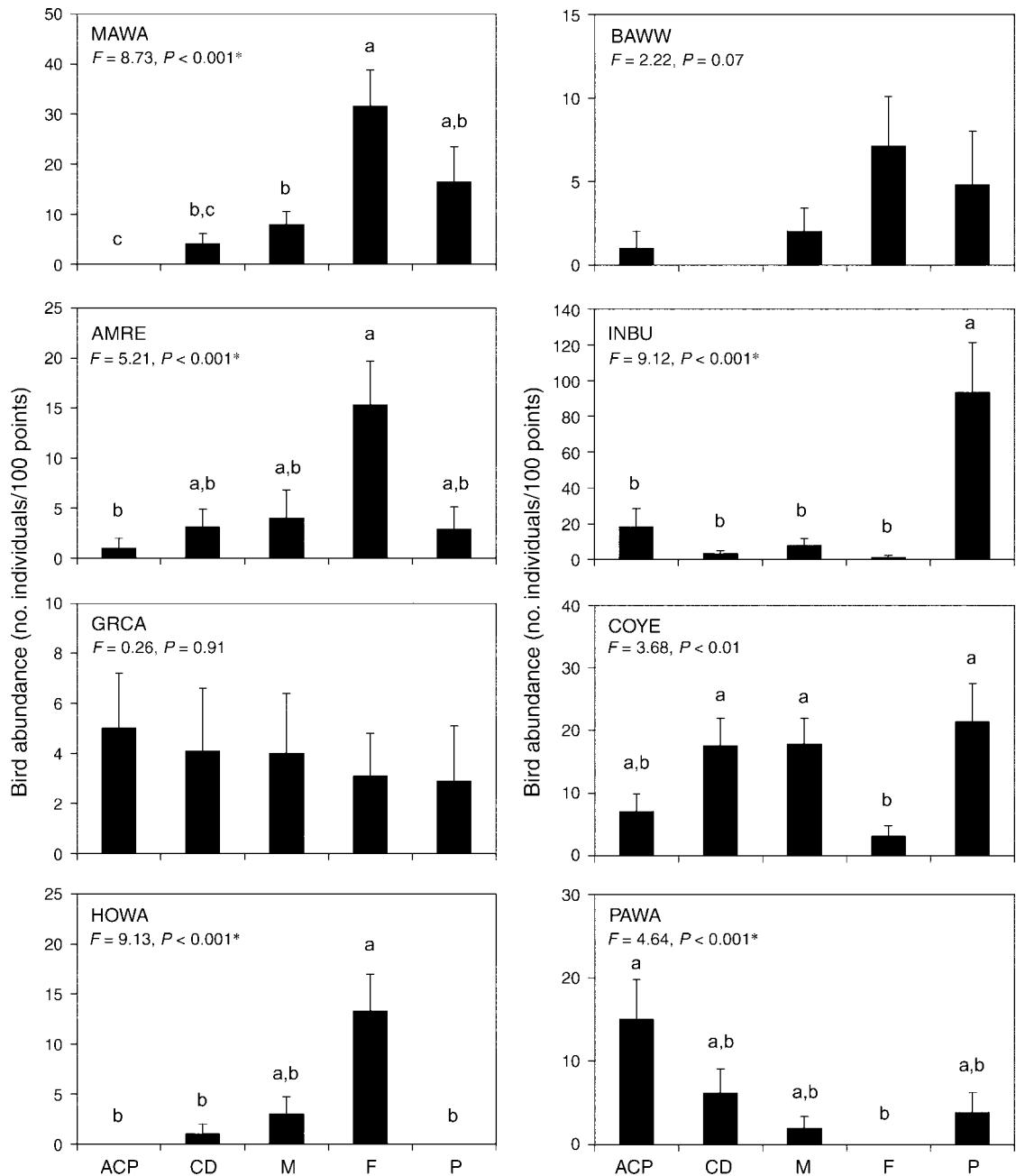
FIG. 1. Continued.

Waterthrush, the Prothonotary Warbler, and the Yellow Warbler, all demonstrated a preference for primary mangrove over secondary mangrove within this broad vegetation type on the barrier beach. Additionally, species that used forest and pasture most frequently at the large scale used humid slacks and/or mangrove, particularly secondary mangroves, at the smaller scale.

Several species were considered habitat generalists at the small ecological and spatial scale, including the Palm Warbler, the Common Yellowthroat, and the Hooded Warbler, which were evenly distributed across all six coastal vegetation types on the barrier beach (Fig. 2). The Gray Catbird also was widely distributed across the coastal vegetation types but demonstrated a significant aversion to primary mangrove. With the exception of the Gray Catbird, these species all demonstrated differences in their distribution across vegetation types at the large scale.

Architectural and floristic gradients at the small scale

Our PCA of the 10 architectural variables measured at mist net locations extracted three components (PCs)

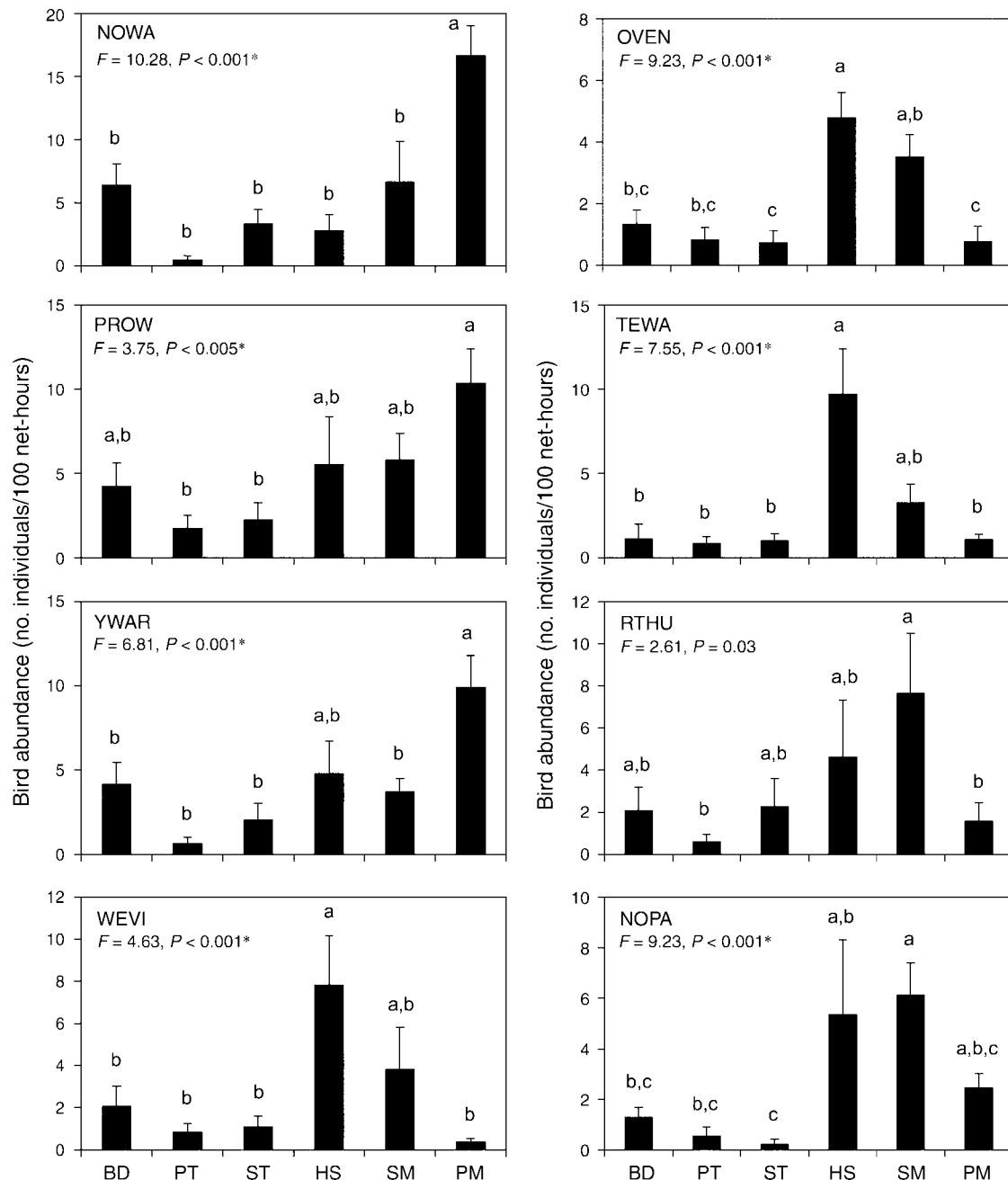JILL L. DEPPE AND JOHN T. ROTENBERRY

FIG. 2. Distribution of 16 common migratory bird species across six fine-scale coastal vegetation classes based on mist net data collected in the Ria Lagartos Biosphere Reserve during fall migration 2001–2003. Mist nets were classified into six vegetation types using a cluster analysis of architectural attributes and plant species abundances measured at each net location (see Appendix D). General linear models were performed on transformed data, but untransformed data are presented in graphs for ease of interpretation. For all species, df = 5, 72. An asterisk following the P value indicates significant difference after application of a sequential Bonferroni test (table-wide $\alpha = 0.05$, $k = 16$). Vegetation types with the same lowercase letter above the bars are not significantly different from one another. Vegetation type abbreviations are: BD, back dune; PT, palm-dominated thicket; ST, shrub-dominated thicket; HS, humid dune slack; SM, secondary mangrove, and PM, primary mangrove. Note that the scale along the y-axis is not the same for all species. See Appendix H for bird species codes.

with eigenvalues > 1.0 that accounted for 72.8% of all variance in the data matrix. The first PC (PC1-SS, eigenvalue = 3.99) represented a canopy gradient and was positively associated with overhead canopy cover, vegetation height, tree density, foliage density in the canopy layer, and foliage profile diversity (Table 1). Back dune vegetation had the lowest (negative) PC1-SS scores, and palm-dominated thickets had the highest
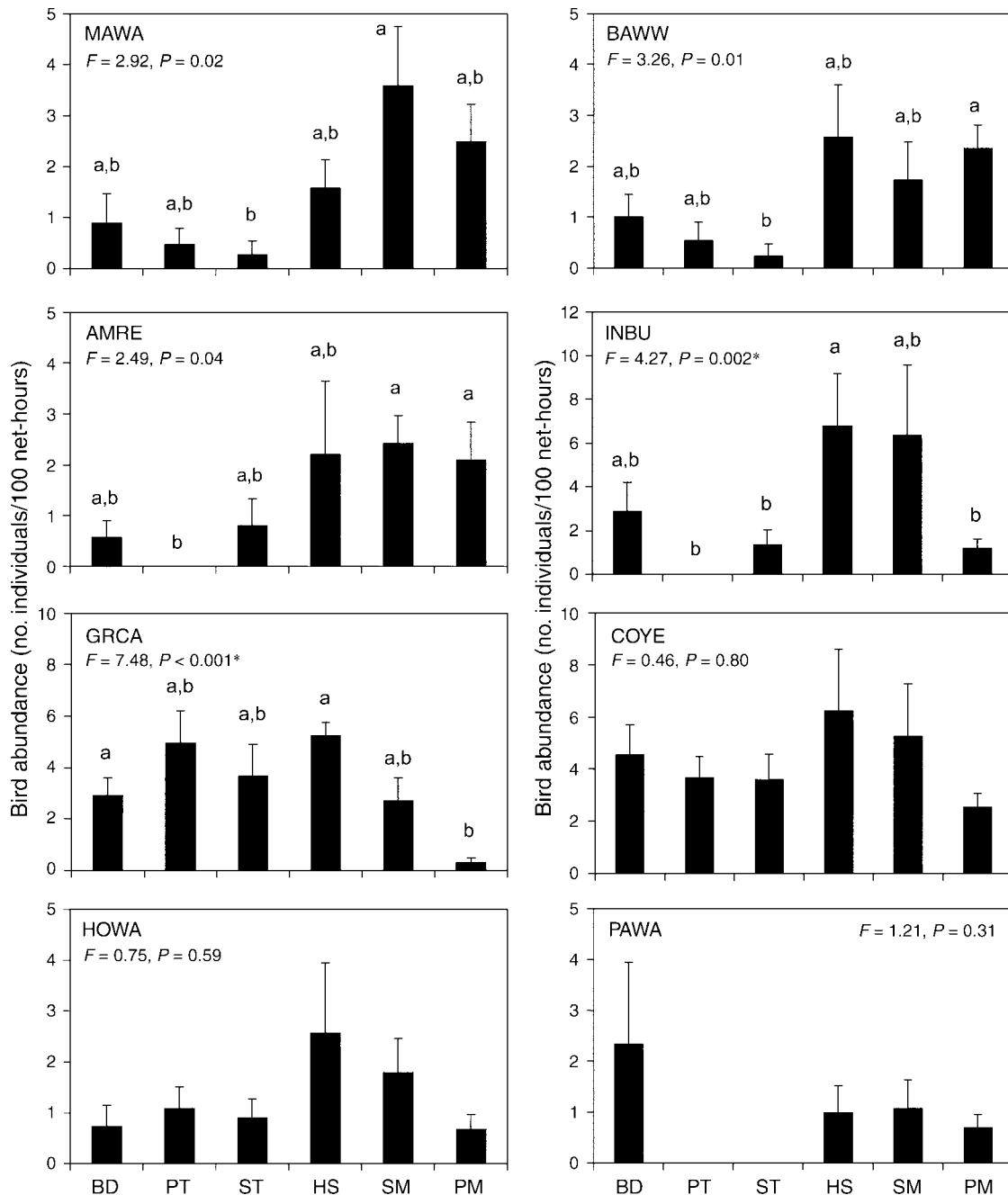
Fig. 2. Continued.

PC1-SS scores (see Appendix I). The second PC (PC2-SS, eigenvalue = 1.94) represented a gradient describing vegetation in the understory; larger values along PC2-SS were associated with greater foliage density in the shrub layer, greater understory diversity, and, to a lesser extent, more ground cover (Table 1). Primary mangrove had the lowest PC2-SS scores, whereas palm-dominated thicket was associated with the highest PC2-SS scores (Appendix I). Finally, PC3-SS (eigenvalue = 1.36) was positively associated with increasing ground cover and

foliage density in the ground layer (Table 1), ranging from primary mangrove at the negative end to humid dune slacks at the positive end.

Our DCA identified two biologically meaningful gradients in plant species composition (Fig. 3). The first axis (DC1: eigenvalue = 0.94, length = 8.3) represented a scrub–mangrove gradient associated with increasing soil moisture and salinity: coastal dune scrub/thicket vegetation had low DC1 values, humid dune slacks had intermediate values, and mangroves had high DC1

TABLE 1. Factor loadings for a principal components analysis of 10 architectural variables, measured at 52 mist net locations on the barrier beach.

Architectural variable	Gradient		
	Canopy (PC1-SS)	Understory (PC2-SS)	Ground (PC3-SS)
Mean height (m)	0.91		
Maximum height (m)	0.75		
Foliage density in canopy layer	0.90		
Canopy cover (%)	0.84		
Foliage profile diversity (H')	0.78		
Total basal area (cm^2)	0.64		
Foliage density in shrub layer		0.84	
Understory species diversity (H')		0.83	
Ground cover (%)		0.51	0.62
Foliage density in ground layer			0.90
Eigenvalue	3.99	1.94	1.36

Notes: Only loadings $>|0.5|$ are shown. The first three principal components (PC) accounted for 72.5% of the total variance in the data matrix. See *Methods: Vegetation measurements: Point count vegetation measurements* and *Methods: Statistical analysis: Architectural and floristic gradients at the large and small spatial scales* for a description of vegetation measurements and analysis. Key to abbreviations: H', Shannon-Weaver diversity index; SS, small scale. The study was conducted in the eastern region of the Ría Lagartos Biosphere Reserve located along the northern coast of the Yucatan Peninsula in northeastern Yucatan, Mexico.

values (Fig. 3; see Appendix I). The high eigenvalue indicates that nets were reliably distinguished from one another based on basal area and cover of plant species (eigenvalues may have a maximum value of 1.0; Jongman et al. 1995). The length of >8.0 indicates that the composition of species turned over approximately twice, such that nets at opposite ends of the axis share few, if any, species in common with one another or with nets at intermediate values (DC scores are scaled such that a length of 4.0 is a benchmark, and nets 4.0 units or more apart share essentially no species; Hill and Gauch 1980, Wilson and Mohler 1983). The second axis (DC2: eigenvalue = 0.50, length = 5.1) defined a within-scrub gradient associated with increasing wind and salt spray, which distinguished among different types of coastal dune scrub (Fig. 3). Back dune vegetation located closest to the ocean was at the positive end of the axis, whereas thickets characteristic of stabilized sand dunes were located at the negative end of the axis; humid dune slacks had intermediate scores along DC2 (Appendix I). Few, if any, species were shared between nets at opposite ends of DC2.

Principal components and detrended components demonstrated significant relationships with one another, indicating, not surprisingly, that plant species composition and architecture were not independent (Table 2). The PC1-SS (canopy gradient) was negatively associated with DC2 (within-scrub gradient); coastal thickets at the

negative end of DC2 have a better-developed overhead canopy, more trees, taller vegetation, and a higher foliage profile diversity than back dunes at the positive end of DC2. The PC2-SS (understory gradient) was negatively associated with both DC1 (scrub/mangrove gradient) and DC2 (within-scrub gradient). Coastal dune scrub has greater shrub cover and understory diversity than mangroves, and along the within-dune gradient, thickets have a better-developed understory than back dune vegetation.

Relative importance of vegetation architecture and plant species composition in explaining bird distributions at the small scale

The architecture model was the best approximating model for explaining variation in the distributions of the Ruby-throated Hummingbird, the Prothonotary Warbler, the Tennessee Warbler, the Palm Warbler, the American Redstart, and the Indigo Bunting on the barrier beach (Table 3). However, for the Ruby-throated Hummingbird, the Palm Warbler, and the American Redstart, there was also substantial support for the global model ($\Delta_i < 2.0$) and some uncertainty in selecting the best approximating model. The weight of evidence in favor of the architectural model being the best model for explaining the distribution of the Palm Warbler was twice as large as that in favor of the global model ($w_a = 0.65$ vs. $w_g = 0.31$), whereas for the American Redstart and the Ruby-throated Hummingbird the weight of evidence in favor of the architectural model was 1.3 times greater than that in favor of the global model, indicating greater model uncertainty in these species.

The floristic model was the best approximating model for explaining the occurrences of the Yellow Warbler, the Magnolia Warbler, the Common Yellowthroat, the Northern Waterthrush, the Black-and-white Warbler, and the Hooded Warbler on the barrier beach (Table 3). The architectural model was also strongly supported for these last four species, and consequently, it could not be ruled out as a plausible best model. Based on model weights, the evidence in support of the floristic model was 2.4, 2.2, 1.8, and 1.4 times greater than that for the architectural model for the Common Yellowthroat, the Northern Waterthrush, the Black-and-white Warbler, and the Hooded Warbler, respectively.

The distributions of the Gray Catbird and the Northern Parula were best explained by the global model, which was strongly supported over both the architectural and floristic models (Table 3). The global model was also ranked as the best approximating model for explaining the occurrence of the Ovenbird on the barrier beach, although there was substantial evidence in support of the architectural model as well. The weight of evidence in favor of the global model was only slightly greater than that in favor of the architectural model. For the White-eyed Vireo all three models had Δ_i values <2.0 and model weights ≤0.49, indicating considerable

FIG. 3. Detrended component analysis axis (DC) scores for plant species and mist nets on the barrier beach. Eigenvalues for DC1 and DC2 are 0.94 and 0.50, respectively. Gradient lengths of DC1 and DC2 are 8.3 and 5.1, respectively. See Appendices F and G for plant species names; only representative plant species are shown in graph. Plant species that occurred in the canopy layer are underlined and in boldface type. Nets are separated into their corresponding vegetation types identified by the cluster analysis, and lines have been drawn around nets in each vegetation type to facilitate interpretation.

uncertainty in the selection of the best model for this species.

Architectural gradients at the large scale

Our PCA of architectural variables measured at point count locations extracted two components (PCs) with eigenvalues >1.0 that accounted for 80.0% of the total variance in the data matrix. The first PC (PC1-LS, eigenvalue = 3.49) represented a canopy gradient; tall vegetation dominated by trees and a well-developed overhead canopy had high scores on PC1-LS, and shorter vegetation with few trees and a poorly developed overhead canopy had low PC1-LS scores (Table 4). Forest had the highest PC1-LS scores, and abandoned coconut plantation and mangrove had the lowest PC1-LS scores. The second PC (PC2-LS, eigenvalue = 1.31) represented a gradient describing understory and ground vegetation; high values along PC2-LS were associated with vegetation types characterized by a well-developed, dense understory (vegetation <2 m tall), high ground cover, and low canopy cover (Table 4). Abandoned coconut plantation and coastal scrub had the highest PC2-LS scores, whereas forest had the lowest PC2-LS scores.

Comparison of bird species' associations with vegetation architecture at the large and small scales

Bird species' associations with architectural variables were often different between the large and small scales (Table 5). At both scales the first principal component described an architectural gradient of increasing vegetation height, tree density, and overhead canopy cover. The distributions of several forest species (the American Redstart, the Hooded Warbler, the Ovenbird, and the White-eyed Vireo) demonstrated positive associations with the canopy gradient (PC1-LS and PC1-SS) at both

TABLE 2. Pearson's correlations between principal components (PC) and detrended correspondence analysis axes (DC) for mist net locations on the barrier beach.

	Detrended component	
Principal component	Scrub-mangrove gradient (DC1)	Within-scrub gradient (DC2)
Canopy gradient (PC1-SS)	−0.07	−0.50**
Understory gradient (PC2-SS)	−0.82**	−0.29**
Ground gradient (PC3-SS)	−0.15	0.21

** $P < 0.01$.

TABLE 3. Akaike's information criterion (AIC_c) for three multiple logistic regression models explaining the influence of vegetation architecture and/or plant species composition on the occurrence of migratory bird species on the barrier beach.

Species	Global			Architectural			Floristic		
	AIC_c	Δ_i	w_i	AIC_c	Δ_i	w_i	AIC_c	Δ_i	w_i
Architectural									
Prothonotary Warbler	131.64	4.41	0.10	127.23	0.00	0.86	133.18	5.95	0.04
Tennessee Warbler	121.48	4.20	0.09	117.28	0.00	0.70	119.72	2.44	0.21
Indigo Bunting	113.26	2.39	0.23	110.87	0.00	0.76	122.15	11.28	0.00
Architectural/global									
Palm Warbler	88.61	1.51	0.31	87.10	0.00	0.65	92.50	5.40	0.04
American Redstart	104.74	0.62	0.42	104.12	0.00	0.57	115.21	11.09	0.00
Ruby-throated Hummingbird	102.87	0.45	0.44	102.42	0.00	0.55	115.42	13.00	0.00
Floristic									
Yellow Warbler	122.78	5.96	0.05	122.44	5.62	0.05	116.82	0.00	0.90
Magnolia Warbler	118.39	6.34	0.03	115.39	3.34	0.15	112.05	0.00	0.81
Floristic/architectural									
Common Yellowthroat	105.68	2.65	0.16	104.80	1.77	0.25	103.03	0.00	0.60
Northern Waterthrush	118.39	3.61	0.10	116.35	1.57	0.28	114.78	0.00	0.62
Black-and-white Warbler	109.41	4.84	0.05	105.38	0.81	0.38	104.57	0.00	0.57
Hooded Warbler	126.64	5.20	0.04	122.10	0.66	0.40	121.44	0.00	0.56
Global									
Gray Catbird	89.00	0.00	0.87	93.20	4.20	0.11	96.60	7.60	0.02
Northern Parula	127.46	0.00	0.64	130.10	2.64	0.17	129.86	2.40	0.19
Global/architectural									
Ovenbird	129.07	0.00	0.55	129.47	0.40	0.45	141.54	12.47	0.00
Global/architectural/floristic									
White-eyed Vireo	114.06	0.00	0.49	115.68	1.62	0.22	115.05	1.00	0.30

Notes: The global model contains the three architectural gradients (small-scale principal components, PC-SS) and two floristic gradients (detrended components, DC). For simplicity, species are organized into groups based on the best approximating model or best model subsets (models with $\Delta_i < 2.0$); for the latter group, species are listed in descending order based on Δ_i values for the second-best model. See Appendix H for species' scientific names. AIC_c is the second-order Akaike information criterion; Δ_i refers to the difference in AIC_c between the candidate model and the best approximating model (i.e., the model with the lowest AIC_c value); w_i is the Akaike weight of the model, or probability that the candidate model is the Kullback-Leibler (K-L) best model; model weights sum to 1.0 across models in the set, although slight deviations from 1.0 may result from rounding errors.

scales, suggesting that when deciding where to settle at the broad and fine vegetation scales in our study, taller vegetation with more trees and greater overhead canopy cover was preferred. However, most migrant species did not show the same relationship with the canopy gradient at the two spatial scales. The Northern Waterthrush and the Black-and-white Warbler, species that often occur in forested habitat, demonstrated a positive association with the canopy gradient at the large scale, but at the small scale the former species was negatively associated with the canopy gradient and latter species showed no association with the gradient. The distributions of shrub- and grassland-associated bird species (the Prothonotary Warbler, the Tennessee Warbler, the Indigo Bunting, the Palm Warbler, the Ruby-throated Hummingbird, and the Common Yellowthroat) exhibited a negative relationship with vegetation height, tree density, and overhead canopy cover at the large scale but a positive relationship or no association at the small scale.

At the large spatial scale our PCA identified a single component (PC2-LS) describing a gradient of increasing understory cover (primarily shrubs and saplings) and ground cover, whereas at the small scale our PCA identified two separate components, one (PC2-SS)

describing a gradient of increasing understory cover and, to a lesser extent, ground cover, and another (PC3-SS) representing a gradient of increasing ground cover. The identification of two separate gradients at the level of fine-scale vegetation types suggests that at this small spatial scale understory and ground cover vary some-

TABLE 4. Factor loadings for a principal components analysis of six architectural variables measured at point count locations in five broad coastal and interior vegetation types.

Architectural variable	Canopy gradient (PC1-LS)	Understory/ ground gradient (PC2-LS)
Mean height (m)	0.90	
Maximum height (m)	0.88	
Total basal area (cm^2)	0.92	
Canopy cover (%)	0.68	−0.50
Understory cover (%)		0.88
Ground cover (%)		0.86
Eigenvalue	3.49	1.31

Notes: Only loadings $>|0.5|$ are shown. The first two principal components (PC) accounted for 80.0% of the total variance in the data matrix. See *Methods: Vegetation measurements: Point count vegetation measurements* and *Methods: Statistical analysis: Architectural and floristic gradients at the large and small spatial scales* for description of vegetation measurements and analysis; LS stands for "large scale."

TABLE 5. Associations between migratory bird species and architectural variables at the large and small spatial scales based on Akaike's information criterion (AIC) variable weights and average standardized logistic regression coefficients.

	Broad scale		Fine scale		
Species	Canopy (PC1-LS)	Understory/ground (PC2-LS)	Canopy (PC1-SS)	Understory (PC2-SS)	Ground (PC3-SS)
Prothonotary Warbler	−	− − −	+	− − −	− − −
Tennessee Warbler	− − −	+ +	+ + +	−	+
Indigo Bunting	− −	+ + +		− −	+ + +
Palm Warbler	− −	+ + +		− − −	+
American Redstart	+ + +	− − −	+ +	− − −	+
Ruby-throated Hummingbird	− −	+ +	+ + +	− −	+ + +
Common Yellowthroat	− − −	−	+	+	−
Northern Waterthrush	+ +	− − −	− −	− − −	−
Black-and-white Warbler	+	− −		− − −	
Hooded Warbler	+ + +	− − −	+ + +	+	
Ovenbird	+ + +	− − −	+ + +	−	+ + +
White-eyed Vireo	+ + +	− − −	+ + +		+

Notes: Our comparison of the importance of architectural variables in explaining bird distributions at the two spatial scales was restricted to migrant species for which the architectural model had strong empirical support ($\Delta_i \leq 2.0$) in our comparison of vegetation architecture and floristics at the small spatial scale. Variable weights, ranging from 0.0 to 1.0, provide an index of the relative importance of each architectural gradient; higher values indicate a stronger association between the explanatory and response variables. Strong relationships between architectural gradients and migrant species' distributions, indicated by AIC variable weights 0.75–1.00, are denoted by + + + or − − −; moderately strong relationships associated with AIC variable weights 0.50–0.74 are denoted by + + or − −; weak relationships indicated by AIC variable weights 0.25–0.49 are denoted by + or −; the sign indicates direction of the relationship. Blank cells indicate that the architectural gradient was not contained in the set of best models and had a low variable weight (≤0.30), suggesting a negligible relationship with bird species distribution. See Appendices J and K for model selection results at the small (SS) and large scales (LS), respectively, and for exact variable weights and average parameter estimates.

what independently of one another, whereas at the large scale these architectural features are more strongly correlated. The Prothonotary Warbler and the Northern Waterthrush demonstrated the same association with understory and ground cover at the large and small spatial scales; both species' distributions were negatively related with understory and ground cover. At the other extreme, two species, the Hooded Warbler and the White-eyed Vireo, failed to demonstrate consistent associations with either understory or ground cover between the two spatial scales.

Eight species demonstrated similar associations with one of the architectural attributes (understory or ground cover) at the two scales but different associations with the other. Five species demonstrated similar relationships with ground cover at both spatial scales but different associations with understory cover, whereas three other bird species exhibited the same association with understory cover but different associations with ground cover. At the large scale the Tennessee Warbler, the Indigo Bunting, the Palm Warbler, and the Ruby-throated Hummingbird demonstrated positive associations with understory and ground cover (PC2-LS). They maintained a positive association with ground cover (PC3-SS) but not understory cover (PC2-SS) at the small scale, although for the Palm Warbler the positive relationship with ground cover was weaker at the small scale than at the large scale. The distribution of the Common Yellowthroat was negatively associated with

ground cover at both spatial scales but exhibited different relationships with understory cover between the two scales, negative at the large scale and positive at the small scale. The Black-and-white Warbler, the American Redstart, and the Ovenbird were negatively associated with understory cover at the large and small spatial scales but demonstrated inconsistent associations with ground cover between the two scales.

Overall, migrant species demonstrated stronger associations with vegetation architecture at the large scale than at the small scale. At the large scale, 9 of the 12 species we considered demonstrated moderate to strong associations with both of the architectural gradients, and the remaining three species demonstrated moderate or strong associations with one of the gradients and a weak association with the other. On the other hand, at the small scale a larger proportion of the associations between species distributions and individual architectural gradients were weak or negligible (18 out of 36 at the small scale vs. 3 out of 24 at the large scale).

Comparison of habitat use at a tropical site vs. temperate sites

Habitat use at temperate stopover sites and our tropical stopover site along the northern Yucatan coast was generally similar, and most changes involved ones of degree rather than shifts to novel habitat types. Species typically inhabiting forest or woodlands at temperate sites regularly used forest and remnant forest

TABLE 6. Summary of species' habitat use at temperate stopover sites in the United States and Canada based on published accounts and habitat use at our tropical stopover site along the northern coast of the Yucatan Peninsula.

Species common name	Habitat associations	
	Temperate (United States and Canada)	Tropical (Yucatan)
Ruby-throated Hummingbird	forest, scrub	scrub†
White-eyed Vireo	scrub	forest, field‡
Gray Catbird	scrub	forest, scrub,† field‡
Tennessee Warbler	forest, scrub	scrub, field
Northern Parula	forest,† scrub	forest,† scrub,† field‡
Yellow Warbler	scrub†	scrub†
Magnolia Warbler	forest, scrub	forest, field‡
Palm Warbler	scrub, field	scrub,† field
Black-and-white Warbler	forest,† scrub	forest, scrub,† field‡
American Redstart	forest,† scrub	forest, scrub,† field‡
Prothonotary Warbler	forest, scrub	scrub,† field‡
Common Yellowthroat	scrub,† field	scrub,† field
Northern Waterthrush	forest,† scrub†	forest,† scrub†
Ovenbird	forest	forest, field‡
Hooded Warbler	forest	forest, scrub†
Indigo Bunting	scrub, field	field

Notes: Temperate stopover sites included coastal and interior study locations. Forest includes temperate and tropical deciduous, coniferous, mixed deciduous–coniferous, broadleaf evergreen, semi-deciduous, semi-evergreen, cloud forest, rain forest, swamp, cypress, floodplain, bottomland hardwood, mangrove forest, and wet and dry forest. Scrub/shrub includes dry or wet scrub, brush, thicket, shrub, early-successional forest or second growth, abandoned or overgrown field or pasture (implied to have a shrubby structure), fence or hedgerows, and dune vegetation. Mangroves sampled at our tropical site in northern Yucatan are classified as wet scrub. Field/grassland includes exotic and native grasslands, savanna, pasture (actively grazed or recently abandoned), and weedy areas. See Appendix L for the list of references used to generate our summary of temperate stopover habitat use. Species are listed in phylogenetic order.

† Species uses wetland vegetation in this habitat type.

‡ Species uses forest fragments and living fences in pastures.

patches and living fences in pastures at our site (Table 6). In cases in which species differed in their use of broad vegetation classes between our site and temperate stopover sites, habitat use in northern Yucatan was similar to that observed on the wintering grounds, suggesting that the differences in habitat use that we observed may reflect general latitudinal changes in habitat use or, in other words, shifts from temperate, breeding-type habitat to tropical, winter-type habitat.

The Yellow Warbler, the Palm Warbler, the Black-and-white Warbler, the American Redstart, the Common Yellowthroat, the Northern Waterthrush, the Northern Parula, and the Ovenbird exhibited similar habitat associations during migration through our site along the northern Yucatan coast and stopover sites at temperate latitudes, although the Black-and-white Warbler, the Northern Parula, the Ovenbird, and the American Redstart used forest fragments in fields in addition to large forest tracts in the Reserve.

Six species at our site demonstrated differences in habitat breadth between our tropical stopover site in Yucatan and temperate sites; four species appeared to reduce their habitat breadth at our site whereas two others increased the range of habitats used (Table 6). The Ruby-throated Hummingbird and the Indigo Bunting had a narrower habitat breadth at our site and used only scrub and field, respectively. The Magnolia Warbler used scrub/shrub habitat less in northern Yucatan, where it was found most frequently in forest and forest patches in fields, than at temperate stopover sites. The Prothonotary Warbler substantially reduced its use of forest habitat at our site and used primarily scrubby habitat (mangrove and coastal scrub) and, to a lesser extent, remnant forest patches and living fences embedded in pastures. On the other hand, the Gray Catbird and the Hooded Warbler increased their habitat breadth and frequently used forest, scrub, and field habitat (primarily forest fragments and living fences) in the Reserve. Both species are known to use a greater range of vegetation types on their tropical wintering grounds than their temperate breeding grounds.

Two species demonstrated shifts in habitat use between temperate stopover sites and our tropical stopover site. The Tennessee Warbler demonstrated a partial shift from forest and scrub/shrub at temperate latitudes to scrub/shrub and field/grassland in northern Yucatan. The White-eyed Vireo demonstrated an almost complete shift from scrub/shrub habitat at temperate stopover sites to forest at our site, including forest fragments in pastures. The White-eyed Vireo is more widely distributed across vegetation types in the tropics than in temperate areas (Ramos and Warner 1980, Rappole and Warner 1980, Lynch 1989, Greenberg 1992, Wunderle and Waide 1993). In the Yucatan Peninsula the species is restricted primarily to forest

and forest patches in pastures and agricultural areas in the winter (Lynch 1992, Greenberg et al. 1993).

DISCUSSION

Scale-dependent habitat use

Nearctic–Neotropical migratory land birds stopping along the northern coast of the Yucatan Peninsula during fall migration demonstrate hierarchical, scale-dependent patterns in habitat use. Bird species were nonrandomly distributed across broad- and fine-scale vegetation types, and patterns of habitat use varied between the two spatial and ecological scales. Regardless of their associations with broadly defined coastal and interior vegetation types, almost all species refined their distributions at the smaller scale within coastal scrub and mangrove. The different associations observed between many bird species and architectural variables at the two scales provide additional evidence in support of the scale-dependent nature of species' habitat associations and also suggest potential cues used by birds when deciding where to settle at each scale. Our observations of scale-dependent habitat use by en route migratory birds are similar to observations made on birds during nonmigratory periods (Saab 1999, Sodhi et al. 1999, Luck 2002) as well as a wide variety of other migratory and nonmigratory animals (e.g., darkling beetle, *Eleodes hispilabris*, McIntyre 1997; mountain caribou, *Rangifer tarandus caribou*, Apps et al. 2001; red-backed voles, *Clethrionomys gapperi*, Keinath and Hayward 2003; mule deer, *Odocoileus hemionus*, D'Eon and Serrouya 2005; eastern massasauga rattlesnake, *Sistrurus catenatus catenatus*, Moore and Gillingham 2006). The ubiquitous nature of scale-dependent habitat use across periods of the annual cycle and diverse taxonomic groups emphasizes the importance of multiscale approaches for studying animals' habitat requirements (Johnson 1980, Hutto 1985a, George and Zack 2001). In addition, our results demonstrate that even relatively subtle differences in the scale at which habitat relationships are assessed and the range of vegetation types or amount of variation in vegetation attributes considered are important factors influencing how we perceive animal–habitat associations (e.g., Colwell and Futuyma 1971, Porter and Church 1987, Wiens et al. 1987, Orians and Wittenberger 1991).

When we compared migrants' habitat use between the two ecological and spatial scales examined in our study, several interesting patterns emerged. First, all species that failed to demonstrate an association at one scale exhibited a significant association at the other. Second, species that used forest and pasture most frequently at the large scale used humid slacks and/or mangroves, particularly secondary associations, at the small scale, suggesting that on the barrier beach, which lacks forest, these coastal vegetation types provide appropriate habitat for birds that do not settle farther inland. Third, the three species that showed a significant preference for mangrove vegetation at the large scale all demonstrated

a preference for primary mangrove associations over secondary ones within this broad vegetation type, indicating that they refine their distributions at smaller spatial and ecological scales and that not all mangroves provide equally suitable habitat for these species. Fourth, several migrant species that we considered scrub species at the large scale failed to show clear habitat associations when we narrowed the scale of our study to the barrier beach. This last pattern likely is the result of surveying different ranges of vegetation types at the two spatial scales, where scrub species are distributed across only a subset of vegetation types at the large scale that encompasses scrub, field, and forest habitat, but are broadly distributed among vegetation assemblages at the small scale that is restricted to scrub vegetation, i.e., coastal dune scrub and mangrove (scrub). Wiens and Rotenberry (1981) observed similar scale-dependent patterns when they compared habitat associations of breeding shrubsteppe bird species at two spatial scales encompassing different ranges of vegetation types in the Great Basin. There, shrubsteppe species demonstrated significant habitat associations at the large, continental scale that contained a broad spectrum of tallgrass prairie and shrubsteppe vegetation, but failed to exhibit strong habitat affinities at the smaller, regional scale in which only shrubsteppe vegetation was represented (Wiens and Rotenberry 1981: Fig. 3). Colwell and Futuyma (1971) considered this sampling issue conceptually and illustrated how sampling different ranges of habitats, which they referred to as resource states, influences estimates of habitat, or niche, breadth (Colwell and Futuyma 1971: Fig. 1, Site I vs. Site II). Although they demonstrated this sampling effect using an example of a continuously varying environmental gradient, the same theory applies to discrete environmental variation, such as the vegetation types we surveyed in northern Yucatan.

An alternative explanation is that our use of different survey methods, point counts and mist nets, is responsible for the differences in habitat use that we observed between the two spatial scales. To evaluate this possibility we quantified net captures in coastal scrub and mangrove by summing over the four coastal scrub assemblages and the two mangrove associations surveyed on the barrier beach. With few exceptions, the differences in migrant abundances between these two broad vegetation types based on net captures were similar to those based on point count surveys. In some species the difference in abundance between coastal scrub and mangrove was significant using capture or count data but not the other; however, the direction of the difference was the same based on both data sets. Thus, it is not likely that the different habitat associations observed at the two spatial scales in our study are attributable to the use of different sampling methods.

Similar to other animals, en route migratory land birds demonstrate different associations with vegetation architecture at the two spatial and ecological scales,

suggesting that birds use different architectural features when deciding where to settle among and within broad vegetation types. While in some cases bird species showed the same association with a particular architectural gradient at both scales, in many instances species exhibited different associations with a gradient or attribute at the two spatial scales; species either showed a relationship (positive or negative) with an architectural variable at one scale but not the other or they demonstrated a positive association with the variable at one scale and a negative association at the other. In the former case, species generally exhibited a preference for the architectural variable at the large scale but not the small scale. Overall, fewer strong or moderately strong relationships were detected at the small scale than the large scale, a pattern that probably reflects the reduced amount of variation in vegetation architecture at the small scale in our study (see Appendices C and E). In order to detect associations between environmental factors and animals' habitat use, sufficient variation in the habitat attribute needs to be present (Orians and Wittenberger 1991). In the absence of such variation, or if individuals cannot perceive existing variation, species may fail to show a pattern of association and appear to use habitat randomly (Wootton et al. 1986). Similar to our findings, Apps et al. (2001) observed fewer associations between mountain caribou and habitat variables at finer spatial scales than larger scales in their study, which they proposed was due to a more even distribution of habitat attributes at the smaller scales they examined.

Alternatively, the different relationships between bird species and architectural variables at the two scales in our study may reflect a compromise between conflicting demands. For example, the Ruby-throated Hummingbird preferred areas with shorter vegetation, reduced overhead canopy cover, lower tree density, and greater understory (shrub) cover at the large scale, but at the small scale the species selected areas with taller vegetation, greater canopy cover, higher tree density, and reduced understory cover. This pattern could represent a trade-off between feeding requirements satisfied by scrub/shrub habitats characterized by flowering shrubs and forbs at the large scale and the need for shelter against predation offered by areas of higher canopy cover and greater tree density at the smaller scale within scrub habitat. Similar trade-offs between competing demands manifested as scale-dependent associations with habitat attributes have been observed in other animals. Compton et al. (2002) observed differences in wood turtles' (*Clemmys insculpta*) selection of forest at the two spatial scales examined in their study, which they proposed reflected a compromise between foraging requirements satisfied by partially forested areas within watersheds at the large scale and thermoregulatory needs met by nonforested, open-canopy sites within activity areas at the small scale. In addition, elk demonstrated different preferences for

roads at the different spatial scales studied by Anderson and his colleagues (2005); elk avoided high road densities when establishing their home ranges presumably to reduce mortality, but within home ranges they concentrated their activity near roads because of the high abundance of food resources along open roadsides. The complexity of associations that we and others have observed between animals and vegetation architecture or physiognomy at different ecological and spatial scales highlights the importance of scale-dependent and species-level approaches for understanding the proximate factors and processes underlying habitat associations.

Relative importance of vegetation architecture and plant species composition

Our comparison of the relative importance of architectural and floristic attributes in explaining the distributions of migratory land bird species on the barrier beach demonstrated that both aspects of vegetation played a role in refining species' distributions at the small scale within broad vegetation types, in contrast to our hypothesis that architecture plays a dominant role. Vegetation architecture or plant species composition alone explained the occurrences of five species at our site, whereas these two aspects of the vegetation played redundant and/or complementary roles in explaining the distributions of the remaining 11 bird species. For five migrant species the architectural and floristic models were both strongly supported, suggesting that vegetation architecture and plant species composition provide redundant information regarding habitat suitability for those species in northern Yucatan. This may arise because particular plant species have unique structures (Holmes and Robinson 1981, Robinson and Holmes 1982, 1984, Parrish 1995). The significant correlations that we observed between the PCs and DCs in our study illustrate the relationship between architecture and plant species composition (Table 2). On the other hand, the global model had substantial empirical support for seven migratory species, revealing strong associations between their occurrences on the barrier beach and a combination of architectural and floristic gradients, implying that these two aspects of the vegetation provide some bird species with complementary information about the distribution of appropriate resources or conditions for them at our site. Architectural and floristic features may provide information regarding different habitat requirements, for example, overhead canopy cover may provide cues to the distribution of shelter, while gradients in plant species composition could indicate the location of suitable food resources. For one of these 11 species, the White-eyed Vireo, all three models were strongly supported, suggesting that architecture and floristics provide redundant and complementary information. A comprehensive understanding of the independent, redundant, and complementary roles that vegetation

architecture and plant species composition play in shaping patterns of species' distribution and abundance will provide valuable data required for habitat restoration by ensuring that the appropriate habitat requirements for migrants are satisfied (Barrow et al. 2000, Nabhan 2001, 2004).

The role of plant species composition in shaping birds' en route habitat associations has been underestimated in discussions of stopover ecology. Vegetation structure is often proposed as a variable impacting birds' decisions to use stopover habitat because of its influence on birds' foraging efficiency and the availability of resting sites and shelter (Moore et al. 1993, Moore and Aborn 2000, Petit 2000). The importance of plant species composition is generally omitted from such discussions except where it is mentioned in terms of its relationship with vegetation structure. Two factors likely contribute to the underestimation of the importance of plant species composition in shaping the distribution and abundance patterns of migrants at stopover sites: (1) many studies have addressed habitat use at the scale of relatively broad vegetation types in which vegetation architecture may be of overriding importance and (2) the general lack of studies evaluating associations between plant species composition and migratory bird distributions at stopover sites. In studies in which researchers have considered plant species composition in their assessment of bird–habitat associations during migration, they have usually found significant patterns, although these relationships are evident primarily in fruit-eating species and often at small spatial scales within broad vegetation types (Martin 1985, Barrow et al. 2000, Suthers et al. 2000). However, associations between plant species composition and bird distributions are likely to extend beyond the direct relationship between frugivores and nectarivores and edible, fruit- or nectar-bearing plant species, respectively (Rotenberry 1985, Barrow et al. 2000). Some insectivorous bird species, such as the Yellow Warbler and the Northern Waterthrush, are strongly associated with plant species characteristic of mangroves at our site along the northern Yucatan coast, possibly because of the type and/or abundance of arthropods that these plant species support or their particular structural features, which may facilitate migrants' exploitation of food resources (Holmes and Schultz 1988). We suggest that greater attention should be devoted to quantifying migrants' associations with vegetation architecture and plant species composition at multiple ecological and spatial scales during migration to foster a comprehensive understanding of the proximate cues influencing habitat use.

Similar to individual architectural attributes, the relative importance of vegetation architecture and plant species composition is likely scale-dependent. Upon arrival at a stopover site migrants may adopt a "niche gestalt" approach to selecting among broad vegetation types or habitats (James 1971, Moore and Aborn 2000), especially in light of the high variation in plant species assemblages that birds encounter along the migratory route. Chernetsov (2006) proposed that "habitat (pre)-selection" by en route migratory passerines takes place before and during landfall, and habitat configuration or gross structural features are implied to serve as cues to appropriate habitat at this ecological scale as most land birds are required to make such decisions under low-light conditions and in unfamiliar areas. Observations of migrants at our site suggest that they arrive in the evening or in the morning, although morning flights may reflect local movements of birds to adjust their location following their arrival the previous evening rather than migratory movements. Once migrants have settled in a particular habitat or general vegetation type (e.g., scrub, forest, etc.) they may redistribute themselves within that habitat in relation to fine-scale vegetative attributes, as did migrant birds settling in coastal vegetation on the barrier beach in the Ría Lagartos Biosphere Reserve. During an exploratory or sampling phase birds may locate specific areas where they can most efficiently satisfy their physiological and ecological requirements (Moore et al. 1990, Aborn and Moore 1997, Chernetsov 2006). At this finer, within-habitat scale both plant species composition and small-scale variation in vegetation architecture, including microhabitat features (J. L. Deppe, *unpublished data*), may provide migrants with information regarding the distribution of suitable foraging opportunities, shelter, and rest/perch sites. Studies of avian habitat use during the breeding season have demonstrated that vegetation configuration, or architecture, is more important at the level of broad vegetation types, whereas plant species composition takes on a dominant role in explaining species' habitat associations at finer scales within broad vegetation classes (e.g., Rotenberry 1985, Bersier and Meyer 1994, Estades 1997, Lee and Rotenberry 2005). Thus, the types of proximate cues and mechanisms used by birds in selecting habitat at these different ecological and spatial scales may be similar throughout the annual cycle.

Other animals also may use architecture and plant species composition in a scale-dependent fashion when selecting habitat, although the scale at which each type of vegetative attribute dominates may vary among taxonomic groups. The close association between migratory nectarivorous lesser long-nosed bats, *Leptonycteris curasoae*, and Cactaceae and Agavaceae plant species along their spring and fall migratory routes through western Mexico suggests that plant species composition is likely to play a more dominant role in shaping this species' distribution at larger, e.g., regional and macrohabitat, scales than the migratory bird species examined in our study (Fleming et al. 1993, Nabhan 2001, Fleming 2004). For migratory monarch butterflies that intersperse reproduction with migration along spring migration routes (Brower and Malcolm 1991), floristics also may be particularly important in determining where individuals settle at large spatial scales

because of the species' highly specialized reproductive requirements for milkweed (*Asclepias*) species (Brower et al. 2006). Patterns in the relative importance of plant species composition and architecture among different spatial scales are expected to vary among taxonomic groups and likely are a function of species' feeding and reproductive requirements, life-history strategies, the period of the annual cycle considered, and the scale at which the animal moves and, thus, perceives variation in environmental factors.

Geographic patterns in stopover habitat use

The habitat use patterns observed at our site in northern Yucatan were similar to patterns of habitat use observed at temperate stopover sites for most of the bird species we analyzed, indicating that affinities for general habitat types, such as forest, scrub/shrub, and/or field/grassland, are maintained along some migratory routes despite latitudinal differences in abiotic and biotic variables. The general consistencies in habitat use that we observed between temperate latitudes and our tropical site at the level of broad habitat types may reflect ecomorphological constraints that predispose migrants to settling in those vegetation types that they can exploit most efficiently (Robinson and Holmes 1982, 1984, Winkler and Leisler 1985, Bairlein 1992, Boonman et al. 1998) and, presumably, where they can achieve the highest foraging and refueling rates and probability of survival. Consistent habitat use patterns over such a large geographic region suggest that migrants may select among broad vegetation types based on overall architectural configuration or gross structural features characteristic of preferred vegetation life forms. Some migrant species appeared to increase or decrease their habitat breadth between the geographic regions included in our comparison, but these changes were typically ones of degree of use rather than complete shifts to novel habitat types. In general, en route migratory bird species stopping at our tropical site, particularly those species demonstrating changes in habitat use or breadth, exhibited habitat associations similar to those documented on their tropical wintering grounds. Petit (2000) has provided evidence that habitat use is similar between temperate stopover sites and temperate breeding grounds.

The White-eyed Vireo was the only species that demonstrated a shift from scrub/shrub at temperate stopover sites (Moore et al. 1990, McCann et al. 1993, Hopp et al. 1995) to forest along the northern Yucatan coast (as seen in this study). The White-eyed Vireo generally occupies scrub and early secondary vegetation on its temperate breeding grounds and expands its habitat breadth to include scrub, secondary vegetation, mangrove, and forest throughout its tropical winter range (Ramos and Warner 1980, Rappole and Warner 1980, Lynch 1989, 1992, Greenberg 1992, Wunderle and Waide 1993), suggesting that the difference we observed between our site in northern Yucatan and temperate

stopover sites may reflect a more general geographic shift in habitat use from temperate, breeding-type habitat to tropical, winter-type habitat. In the northern Yucatan Peninsula this habitat shift appears to be directly associated with the distribution of the fruit-bearing tree species *Bursera simaruba*, whose exploitation by the White-eyed Vireo may have ultimately facilitated its coexistence with the Mangrove Vireo (*Vireo pallens*), a tropical resident congener and scrub specialist, by reducing habitat overlap (Greenberg et al. 1993, 1995). At other tropical stopover sites where the Mangrove Vireo is absent, the White-eyed Vireo may be expected to use scrub habitat more frequently than observed here. In general, our knowledge of winter habitat associations is likely to contribute greater insight toward understanding habitat use during stopover at tropical latitudes for the species considered in our study, whereas breeding habitat associations should be more relevant to understanding habitat use at temperate stopover sites due to greater similarities in specific vegetation types, plant species, food resources, resident competitors, predators, and climate.

Other groups of migratory birds or long-distance migratory animals may be expected to show considerable variation in habitat use along their migratory routes. Nearctic–Neotropical migratory land bird species migrating through western North America may be expected to demonstrate greater geographic variation in habitat use during migration than those migrating through eastern regions (those examined in the current study), because the former encounter more extreme variation in vegetation types and environmental conditions along their migratory routes, ranging from high-elevation coniferous forests to arid desert scrub. Some migratory insects, such as monarch butterflies and green darner dragonflies (*Anax junius*), are known to reproduce during migration, such that some locations along migratory routes might be used for refueling and others for reproduction (Brower and Malcolm 1991, Brower et al. 2006, Holland et al. 2006, Wikelski et al. 2006, Matthews 2007). To the extent that reproduction imposes different constraints on habitat use than refueling, which is likely to be the case with monarch butterflies that have generalized adult nectar-feeding requirements but specialized reproductive requirements (Brower et al. 2006), habitat associations are expected to vary during migration. Examination of geographic consistency in habitat use along migratory routes of eastern and western migratory birds as well as other migratory animals, such as bats, dragonflies, and butterflies, will further our understanding of the mechanisms driving geographic patterns in migration ecology and contribute valuable information toward the conservation and management of migratory animals that depend on habitat en route.

While our general comparison of habitat use between our tropical stopover site and temperate sites offers insight into geographic patterns in habitat use along

portions of the migratory route used by eastern land birds, rigorous, quantitative assessments of patterns in habitat use and breadth among stopover sites or among breeding, winter, and migratory periods will need to take into account variation in the range of habitat or vegetation types among study sites and differences in the spatial scale considered at each site. In addition, comparisons among temperate and tropical coastal stopover sites as well as between coastal and interior stopover sites will be particularly valuable for determining geographic variation in habitat use patterns and the processes and factors shaping those patterns.

Conclusions

Animals' habitat use impacts individual fitness and population regulation; consequently, animal conservation and management strategies often take a habitat-based approach (Van Horne 1983, Barrows et al. 2005). Given the available information on en route ecology of migratory animals, the quantity and quality of stopover habitat have the potential to influence survival and/or reproductive success through their impact on physical condition, rate of mass and energy gain, migration speed, and, in the case of monarch butterflies and green darner dragonflies, the availability of reproductive sites (Russell et al. 1994, Yong et al. 1998, Moore et al. 2005a, Brower et al. 2006, Matthews 2007), emphasizing the importance of understanding habitat use during this period of the annual cycle. For migratory animals effective conservation strategies need to consider habitat requirements throughout the annual cycle and the geographic range of the species at multiple spatial scales (Moore and Simons 1992, Brower and Pyle 2004, Fleming 2004, Nabhan 2004, Moore et al. 2005b, Brower et al. 2006); this includes protection of habitat for breeding, wintering, and stopover along entire migratory routes or corridors. Activities that reduce the quantity or quality of stopover habitat or impede animal movement among areas required to satisfy animals' reproductive and survival requirements threaten the integrity of the migration process, resulting in what Brower and Malcolm (1991) term an "endangered phenomenon."

Our study provides empirical support for scale-dependent habitat use patterns among and within broad vegetation types for migratory land birds, describes their scale-dependent associations with vegetation architecture, and quantifies the relative importance of vegetation architecture and plant species composition and their independent, redundant, and complementary roles in refining bird species' habitat associations within broad coastal vegetation types during migration at a tropical stopover site. Multiscale studies of stopover habitat selection and ecology along migratory routes of other terrestrial taxonomic groups that exhibit long-distance migratory behavior, such as bats, dragonflies, butterflies, and moths, will be invaluable. Studies that explicitly compare across animal classes, among taxa within

classes (e.g., shorebirds vs. passerines), as well as among different migration systems within a single migratory group (e.g., eastern vs. western Nearctic–Neotropical land birds) will enable an evaluation of the robustness of the patterns described here and contribute insight into the factors and mechanisms driving stopover habitat selection and use by migratory animals (Dingle 1996, Kelly and Hutto 2005, Holland et al. 2006, Dingle and Drake 2007, Matthews 2007).

Literature Cited

Aborn, D. A., and F. R. Moore. 1997. Pattern of movement by Summer Tanagers (*Piranga rubra*) during migratory stopover: a telemetry study. Behaviour 134:1077–1100.

Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. Journal of Wildlife Management 69:298–310.

Apps, C. D., B. N. McLellan, and T. A. Kinley. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. Journal of Wildlife Management 65:65–77.

Bairlein, F. 1992. Morphology–habitat relationships in migrating songbirds. Pages 356–369 in J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Barrow, W. C., Jr., C. Chao-Chieh, R. B. Hamilton, K. Ouchley, and T. J. Spengler. 2000. Disruption and restoration of en route habitat, a case study: the Chenier Plain. Studies in Avian Biology 20:71–87.

Barrows, C. W., M. B. Swartz, W. L. Hodges, M. F. Allen, J. T. Rotenberry, B. Li, T. Scott, and X. Chen. 2005. A framework for monitoring multiple-species conservation plans. Journal of Wildlife Management 69:1333–1345.

Bersier, L. F., and D. R. Meyer. 1994. Bird assemblages in mosaic forests: the relative importance of vegetation structure and floristic composition along the successional gradient. Acta Oecologica 15:561–576.

Bertolino, S. 2006. Microhabitat use by garden dormice during nocturnal activity. Journal of Zoology 272:176–182.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird census techniques. Academic Press, London, UK.

Boonman, A. M., M. Boonman, F. Bretschneider, and W. A. van de Grind. 1998. Prey detection in trawling insectivorous bats: duckweed affects hunting behavior in Daubenton's bat, *Myotis daubentonii*. Behavioral Ecology and Sociobiology 44: 99–107.

Britton, J. C., and B. Morton. 1989. Shore ecology of the Gulf of Mexico. University of Texas Press, Austin, Texas, USA.

Brower, L. P., L. S. Fink, and P. Walford. 2006. Fueling the fall migration of the monarch butterfly. Integrative and Comparative Biology 46:1123–1142.

Brower, L. P., and S. B. Malcolm. 1991. Animal migrations: endangered phenomena. American Zoologist 31:265–276.

Brower, L. P., and R. M. Pyle. 2004. The interchange of migratory monarchs between Mexico and the western United States, and the importance of floral corridors to the fall and spring migrations. Pages 144–166 *in* G. P. Nabhan, editor. Conserving migratory pollinators and nectar corridors in western North America. University of Arizona Press, Tuscon, Arizona, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Buskirk, W. H. 1980. Influence of meteorological patterns and trans-gulf migration on the calendars of latitudinal migrants. Pages 485–491 *in* A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Carabias Lillo, J., E. Provencio, Elvira de la Maza J., and J. R. Rubio Ortiz. 1999. Programa de Manejo Reserva de la Biósfera Ría Lagartos. Instituto Nacional de Ecología, Cuidad de México, México, Distrito Federal, México.

Chernetsov, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. Journal of Ornithology 147:185–191.

Colwell, R. K., and D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567–576.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83:833–843.

D'Eon, R. G., and R. Serrouya. 2005. Mule deer seasonal movements and multiscale resource selection using global positioning system radiotelemetry. Journal of Mammalogy 86:736–744.

Deppe, J. L., and J. T. Rotenberry. 2005. Temporal patterns in fall migrant communities in Yucatan, Mexico. Condor 107: 228–243.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, New York, New York, USA.

Dingle, H., and A. Drake. 2007. What is migration? BioScience 57:113–121.

Estades, C. F. 1997. Bird–habitat relationships in a vegetational gradient in the Andes of central Chile. Condor 99:719–727.

Fleming, T. H. 2004. Nectar corridors: migration and the annual cycle of lesser long-nosed bats. Pages 23–42 *in* G. P. Nabhan, editor. Conserving migratory pollinators and nectar corridors in western North America. University of Arizona Press, Tuscon, Arizona, USA.

Fleming, T. H., R. A. Nunez, and L. da Silveira Lobo Sternberg. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia 94:72–75.

Gauch, H. G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge, UK.

George, T. L., and S. Zack. 2001. Spatial and temporal considerations in restoring habitat for wildlife. Restoration Ecology 9:272–279.

Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. Pages 273–286 *in* J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Greenberg, R., M. S. Foster, and L. Marquez-Valdelamar. 1995. The role of the White-eyed Vireo in the dispersal of *Bursera* fruit on the Yucatan Peninsula. Journal of Tropical Ecology 11:619–639.

Greenberg, R., D. K. Niven, S. Hopp, and C. Boone. 1993. Frugivory and coexistence in a resident and a migratory vireo on the Yucatan Peninsula. Condor 95:990–999.

Hagan, J. M., III, and D. W. Johnston. 1992. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Hilden, O. 1965. Habitat selection in birds: a review. Annales Zoologici Fennici 2:53–75.

Hill, M. O., and H. G. Gauch. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42:47–58.

Holland, R. A., M. Wikelski, and D. S. Wilcove. 2006. How and why do insects migrate? Science 313:794–796.

Holmes, R. T., and S. K. Robinson. 1981. Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35.

Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Canadian Journal of Zoology 66:720–728.

Hopp, S. L., A. Kirby, and C. A. Boone. 1995. White-eyed Vireo (*Vireo griseus*). Number 168 *in* A. Poole and F. Gill, editors. The Birds of North America. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.

Hosmer, D. W., Jr., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Howell, S. N. G. 1989. Additional information on the birds of the Campeche Bank, Mexico. Journal of Field Ornithology 60:504–509.

Howell, S. N. G., and S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford University Press, New York, New York, USA.

Hutto, R. L. 1985a. Habitat selection by nonbreeding, migratory land birds. Pages 455–476 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

Hutto, R. L. 1985b. Seasonal changes in the habitat distribution of transient insectivorous birds in southeastern Arizona: Competition mediated? Auk 102:120–132.

James, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin 83:215–236.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge, UK.

Keinath, D. A., and G. D. Hayward. 2003. Red-backed vole (*Clethrionomys gapperi*) response to disturbance in subalpine forests: use of regenerating patches. Journal of Mammalogy 84:956–966.

Kelly, J. F., and R. L. Hutto. 2005. An east–west comparison of migration in North American wood warblers. Condor 107: 197–211.

Kuenzi, A. J., F. R. Moore, and T. R. Simons. 1991. Stopover of Neotropical landbird migrants on East Ship Island following trans-gulf migration. Condor 93:869–883.

Law, B., and M. Chidel. 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. Journal of Applied Ecology 39:605–617.

Lee, P., and J. T. Rotenberry. 2005. Relationships between bird species and tree species assemblages in forested habitats of eastern North America. Journal of Biogeography 32:1139–1150.

Lopez Ornat, A., and J. F. Lynch. 1990. Landbird communities of the coastal dune scrub in the Yucatan Peninsula: species composition, ecology and zoogeographic affinities. Vida Silvestre Neotropical 2:21–31.

Luck, G. W. 2002. The habitat requirements of the rufous treecreeper (Climacteris rufa). 1. Preferential habitat use demonstrated at multiple spatial scales. Biological Conservation 105:383–394.

Lynch, J. F. 1989. Distribution of overwintering nearctic migrants in the Yucatan Peninsula. I: General patterns of occurrence. Condor 91:515–544.

Lynch, J. F. 1992. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula. II: Use of native and human-modified vegetation. Pages 178–196 in J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Martin, T. E. 1985. Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density. Journal of Tropical Ecology 1:157–170.

Matthews, J. H. 2007. Research in motion: patterns of large-scale migration in dragonflies and birds. Dissertation. University of Texas at Austin, Austin, Texas, USA.

McCann, J. M., S. E. Mabey, L. J. Niles, C. Bartlett, and P. Kerlinger. 1993. A regional study of coastal migratory stopover habitat for Neotropical migrant songbirds: land management implications. Transactions of the 58th North American Wildlife and Natural Resources Conference 58:398–407.

McCune, B., and M. J. Mefford. 1999. Multivariate analysis of ecological data. Version 4.0. MjM Software, Gleneden Beach, Oregon, USA.

McIntyre, N. E. 1997. Scale-dependent habitat selection by the darkling beetle Eleodes hispilabris (Coleoptera: Tenebrionidae). American Midland Naturalist 138:230–235.

Mills, E. D., and D. T. Rogers. 1990. Nearctic passerine fall migration in central Belize. Wilson Bulletin 102:146–150.

Moore, F. R., and D. A. Aborn. 2000. Mechanisms of en route habitat selection: How do migrants make habitat decisions during stopover? Studies in Avian Biology 20:34–42.

Moore, F. R., S. A. Gauthreaux, Jr., P. Kerlinger, and T. R. Simons. 1993. Stopover habitat: management implications and guidelines. Pages 58–69 in D. Finch and P. Stangel, editors. Status and management of neotropical migratory birds. General Technical Report RM-229. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.

Moore, F. R., P. Kerlinger, and T. R. Simons. 1990. Stopover on a Gulf coast barrier island by spring Trans-Gulf migrants. Wilson Bulletin 102:487–500.

Moore, F. R., and T. R. Simons. 1992. Habitat suitability and stopover ecology of neotropical landbird migrants. Pages 345–355 in J. M. Hagan III and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Moore, F. R., R. J. Smith, and R. Sandberg. 2005a. Stopover ecology of intercontinental migrants: solutions to problems and consequences for reproductive performance. Pages 251–261 in R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. Johns Hopkins University Press, Baltimore, Maryland, USA.

Moore, F. R., M. S. Woodrey, J. J. Buler, S. Woltmann, and T. R. Simons. 2005b. Understanding the stopover of migratory birds: a scale dependent approach. Pages 684–689 in C. J. Ralph and T. D. Rich, editors. Bird conservation implementation and integration in the Americas. Proceedings of the Third International Partners in Flight Conference. USDA Forest Service General Technical Report PSW-191. Pacific Southwest Research Station, Albany, California, USA.

Moore, J. A., and J. C. Gillingham. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the eastern massasauga (Sistrurus catenatus catenatus). Copeia 4:742–751.

Moreno-Casasola, P., and I. Espejel. 1986. Classification and ordination of coastal sand dune vegetation along the Gulf and Caribbean Sea of Mexico. Vegetatio 66:147–182.

Morris, S. R., D. W. Holmes, and M. E. Richmond. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. Condor 98:395–409.

Nabhan, G. P. 2001. Nectar trails of migratory pollinators: restoring corridors on private lands. Conservation in Practice 2:20–26.

Nabhan, G. P. 2004. Stresses on pollinators during migration: Is nectar availability at stopovers the weak link in plant–pollinator conservation? Pages 3–22 in G. P. Nabhan, editor. Conserving migratory pollinators and nectar corridors in western North America. University of Arizona Press, Tuscon, Arizona, USA.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137:S29–S49.

Parmenter, R. R., C. A. Parmenter, and C. D. Cheney. 1989. Factors influencing microhabitat partitioning among coexisting species of arid-land darkling beetles (Tenebrionidae): behavioral responses to vegetation architecture. Southwestern Naturalist 34:319–329.

Parrish, J. D. 1995. Effects of needle architecture on warbler habitat selection in a coastal spruce forest. Ecology 76:1813–1820.

Paynter, R. A., Jr 1953. Autumnal migrants on the Campeche Bank. Auk 70:338–349.

Petit, D. R. 2000. Habitat use by landbirds along nearctic–neotropical migration routes: implications for conservation of stopover habitats. Studies in Avian Biology 20:15–33.

Poole, A., and F. Gill, editors. 1992–2003. The birds of North America. Numbers 1–716. The Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; The American Ornithologists' Union, Washington, D.C., USA; The Birds of North America, Philadelphia, Pennsylvania, USA.

Porter, W. F., and K. E. Church. 1987. Effects of environmental pattern on habitat preference analysis. Journal of Wildlife Management 51:681–685.

Pounds, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland Anolis community. Ecological Monographs 58:299–320.

Ramos, M. A., and D. W. Warner. 1980. Analysis of North American subspecies of migrant birds wintering in Los Tuxtlas, southern Veracruz, Mexico. Pages 173–180 in A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Rappole, J. H. 1995. The ecology of migrant birds: a neotropical perspective. Smithsonian Institution Press, Washington, D.C., USA.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353–393 in A. Keast and E. S. Morton, editors. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, D.C., USA.

Rappole, J. H., K. Winker, and G. V. N. Powell. 1998. Migratory bird habitat use in southern Mexico: mist nets versus point counts. Journal of Field Ornithology 69:635–643.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology 63:1918–1931.

Robinson, S. K., and R. T. Holmes. 1984. Effects of plant species and foliage structure on the foraging behavior of forest birds. Auk 101:672–684.

Rodewald, P. G., and M. C. Brittingham. 2004. Stopover habitats of landbirds during fall: use of edge-dominated and early-successional forests. Auk 121:1040–1055.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: Physiognomy or floristics? Oecologia 67:213–217.

Row, J. R., and G. Blouin-Demers. 2006. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. Ecoscience 13:443–450.

Ruelas Inzunza, E., S. W. Hoffman, and L. J. Goodrich. 2005. Stopover ecology of Neotropical migrants in Central Veracruz. Pages 657–672 in C. J. Ralph and T. D. Rich, editors. Bird conservation implementation and integration in the Americas. Proceedings of the Third International Partners in Flight Conference. USDA Forest Service General Technical Report PSW-191. Pacific Southwest Research Station, Albany, California, USA.

Russell, R. W., F. L. Carpenter, M. A. Hixon, and D. C. Paton. 1994. The impact of variation in stopover habitat quality on migrant Rufous Hummingbirds. Conservation Biology 8:483–490.

Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications 9:135–151.

Sapir, N., Z. Abramsky, E. Shochat, and I. Izhaki. 2004. Scale-dependent habitat selection in migratory frugivorous passerines. Naturwissenschaften 91:544–547.

Sodhi, N. S., C. A. Paszkowski, and S. Keehn. 1999. Scale-dependent habitat selection by American Redstarts in aspen-dominated forest fragments. Wilson Bulletin 111:70–75.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. Third edition. W. H. Freeman, New York, New York, USA.

SPSS. 2002. SPSS 11.0 for Macintosh brief guide. Version 11.0. SPSS, Chicago, Illinois, USA.

Suthers, H. B., J. M. Bickal, and P. G. Rodenwald. 2000. Use of successional habitat and fruit resources by songbirds during autumn migration in central New Jersey. Wilson Bulletin 112:249–260.

Tabachnick, B. G., and L. S. Fidell. 1996. Using multivariate statistics. Third edition. Harper Collins, New York, New York, USA.

Terborgh, J. 1989. . Where have all the birds gone? Princeton University Press, Princeton, New Jersey, USA.

Universidad Autónoma de Yucatán. 1999. Atlas de procesos territoriales de Yucatán. Universidad Autónoma de Yucatán, Merida, Yucatán, Mexico.

Vanhooydonck, B., R. Van Damme, and P. Aerts. 2000. Ecomorphological correlates of habitat partitioning in Corsican Lacertid lizards. Functional Ecology 14:358–368.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893–901.

Wiens, J. A., and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs 51:21–41.

Wiens, J. A., J. T. Rotenberry, and B. Van Horne. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132–147.

Wikelski, M., D. Moskowitz, J. S. Adelman, J. Cochran, D. S. Wilcove, and M. L. May. 2006. Simple rules guide dragonfly migration. Biology Letters 2:1–5.

Wilson, M. V., and C. L. Mohler. 1983. Measuring compositional change along gradients. Vegetatio 54:129–141.

Winker, K. 1995. Habitat selection in woodland nearctic–neotropical migrants on the Isthmus of Tehuantepec I. Autumn migration. Wilson Bulletin 107:26–39.

Winkler, H., and B. Leisler. 1985. . Pages 415–434 in M. L. Cody, editor. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

Woodrey, M. S., and F. R. Moore. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. Auk 114:695–707.

Wootton, J. T., E. K. Bollinger, and C. J. Hibbard. 1986. Mating systems in homogeneous habitats: the effects of female uncertainty, knowledge costs, and random settlement. American Naturalist 128:499–512.

Wunderle, J. M., and R. B. Waide. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. Condor 95:904–933.

Yong, W., D. M. Finch, F. R. Moore, and J. F. Kelly. 1998. Stopover ecology and habitat use of migratory Wilson's warblers. Auk 115:829–842.

Yong, W., and F. R. Moore. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. Auk 114:263–278.

APPENDIX A

A map of the Ria Lagartos Biosphere Reserve in northeastern Yucatan, Mexico (*Ecological Archives* M078-018-A1).

APPENDIX B

Descriptions and photographs of broad- and fine-scale vegetation types surveyed in the Ria Lagartos Biosphere Reserve (*Ecological Archives* M078-018-A2).

APPENDIX C

Mean values of six architectural variables in five broad coastal and interior vegetation types (*Ecological Archives* M078-018-A3).

APPENDIX D

A description of the cluster analysis used to classify mist nets into fine-scale coastal vegetation classes (*Ecological Archives* M078-018-A4).

APPENDIX E

The mean values of 10 architectural variables in six fine-scale coastal vegetation types on the barrier beach (*Ecological Archives* M078-018-A5).

APPENDIX F

The mean cover of common understory plant species in six fine-scale coastal vegetation types on the barrier beach (*Ecological Archives* M078-018-A6).

APPENDIX G

The mean basal area of tree species in six fine-scale coastal vegetation types on the barrier beach (*Ecological Archives* M078-018-A7).

APPENDIX H

A list of 16 migratory land bird species with their scientific names and four-letter species codes (*Ecological Archives* M078-018-A8).

APPENDIX I

The mean detrended component (DC) and principal component (PC) scores for mist nets in the six coastal vegetation types (*Ecological Archives* M078-018-A9).

APPENDIX J

The associations between bird species' distributions and individual architectural and floristic gradients at the small spatial scale (*Ecological Archives* M078-018-A10).

APPENDIX K

The associations between bird species' distributions and individual architectural gradients at the large spatial scale (*Ecological Archives* M078-018-A11).

APPENDIX L

A list of references used to generate a summary of species' habitat use at temperate stopover sites in the United States and Canada (*Ecological Archives* M078-018-A12).