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## TEMPORAL PATTERNS IN FALL MIGRANT COMMUNITIES IN YUCATAN, MEXICO

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**Abstract.** We quantified temporal turnover in the composition of fall migrant landbird communities along the northern coast of the Yucatan Peninsula using Detrended Correspondence Analysis. The presence of winter residents of many migrant species at the site prevented turnover from being complete. However, early and late season transient communities shared few, if any, species in common. Point-count surveys showed greater compositional change than net surveys that included winter residents. The rate of species turnover was generally slow until the middle of the season, when it reached a maximum, and decreased again toward the end of the season as species composition began to converge on that characteristic of the winter community. Within-season patterns of species turnover were similar between net- and point-count surveys and were consistent across years. Species that winter farther south arrived at the site significantly earlier than those wintering at more northern latitudes; however, there was no association with breeding latitude. Additionally, insectivores arrived significantly earlier than omnivores and granivores. The amount of turnover among foliage-gleaning insectivores was less than that for all species in the community, which is inconsistent with the hypothesis that competition during migration has played a role in shaping temporal patterns in species co-occurrence and turnover. For species that co-occur in time during migration, spatial segregation at various scales, as well as differences in foraging behavior and diet, may act to reduce competition at stopover sites.

**Key words:** biogeography, community turnover, Detrended Correspondence Analysis, fall migration, foraging ecology, landbirds, Yucatan Peninsula.

### Patrones Temporales en Comunidades Migratorias de Otoño en Yucatán, México

**Resumen.** Cuantificamos el recambio temporal en la composición de comunidades de aves terrestres migratorias de otoño a lo largo de la costa norte de la península de Yucatán usando análisis de correspondencia con efecto de arco corregido. La presencia de residentes invernales de muchas especies migratorias en el sitio evitó el recambio completo de especies. Sin embargo, las comunidades transitorias a principios y fines de la estación compartieron pocas o ninguna especie. Los muestreos de conteos por punto mostraron cambios en la composición mayores que los muestreos de redes de niebla que incluyeron residentes invernales. La tasa de recambio de especies fue generalmente lenta hasta mediados de la estación, cuando alcanzó un máximo, y disminuyó de nuevo hacia finales de la estación a medida que la composición de especies comenzó a parecerse a la de la comunidad invernal. Los patrones de recambio de especies de cada estación fueron similares entre los muestreos de redes de niebla y los conteos por punto, y fueron consistentes entre años. Las especies que invernaron más al sur llegaron al sitio significativamente más temprano que aquellas que invernaron en latitudes más septentrionales; sin embargo, no hubo una asociación con la latitud en la que criaron las especies. Además, los insectívoros llegaron significativamente más temprano que los omnívoros y los granívoros. La cantidad de recambio entre insectívoros que toman sus presas en el follaje fue menor que el recambio de todas las especies de la comunidad consideradas juntas, lo cual no es consistente con la hipótesis de que la competencia durante la migración ha jugado un papel en modelar los patrones temporales en la presencia conjunta y el recambio de especies. Para las especies cuya presencia coincide en el tiempo durante la migración, la segregación espacial a varias escalas, como también las diferencias en el comportamiento de forrajeo y en la dieta, pueden operar para reducir la competencia en los sitios de escala.

### INTRODUCTION

Avian migration is a complex phenomenon characterized by variation in time and space. While

researchers have recently devoted much effort toward identifying spatial patterns of species' distributions and the mechanisms responsible for them, temporal patterns have generally received less attention. Temporal dynamics of migrants have been quantified primarily on a species by species basis in terms of mean and median ar-

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rival dates (Winker et al. 1992, Yong and Finch 1997), duration of migration or range of passage dates (Keast 1980, Richardson et al. 2003), age- and sex-dependent differences in timing of migration (Woodrey and Chandler 1997, Yong et al. 1998, Morris et al. 2003), and annual variation in timing of migration (Weydemeyer 1973, Pinkowski and Bajorek 1976) and bird abundance (Winker et al. 1992). Community-level analyses of temporal patterns are limited in the literature (Rotenberry and Chandler 1999, Wilson and Twedt 2003), yet such analyses may provide information regarding possible mechanisms responsible for the timing of species' migrations, as well as indicate suites of species that co-occur in time and, consequently, have the potential to interact.

Patterns in the timing and sequence of migration of Nearctic-Neotropical species have generally been examined at stopover sites in Canada and the United States, and studies of spring migrants predominate in the literature. Here, we provide a quantitative description of the degree and nature of temporal turnover in a fall migrant community at a southern stopover site located along the northern coast of the Yucatan Peninsula. Migrants arrive at the site after crossing the Gulf of Mexico. In the fall, transGulf flights are associated with postfrontal systems that provide northerly tailwinds for southbound migrants (Gauthreaux and Able 1970, Able 1972). Such weather conditions occur infrequently during the fall (Able 1972, Buskirk 1980); thus, species may be expected to arrive along the northern Yucatan coast in waves, producing pulsed rather than continuous community change. Weather patterns over the Gulf and the rest of the migratory route, as well as conditions on the breeding grounds, create annual fluctuations in species' abundances and timing of migration that may result in annual variation in compositional turnover in migrant communities. Furthermore, unlike sites farther north, our study area maintains winter populations of many Nearctic-Neotropical migrant species, in addition to transient populations that use the site only briefly during migration.

Several factors may be responsible for the timing of species' migration and the subsequent sequence of turnover observed at stopover sites during the fall, including biogeography, diet, and interspecific competition. The timing of species' fall migration has been associated with both

winter and breeding location. Species wintering farther south (Neotropics) migrated through Minnesota earlier than those wintering farther north (temperate zone; Weisbrod et al. 1993), and migrants from southern breeding ranges passed through Pennsylvania earlier than those from northern ranges (Rotenberry and Chandler 1999). Alternatively, species breeding farther north may be expected to initiate migration earlier than species breeding farther south because of the indirect effects of climate at northern latitudes and potentially greater migration distances between breeding and wintering grounds. The sequence of migrant turnover may also reflect differences in species' diets. Birds that are primarily insectivorous on temperate-breeding grounds may migrate earlier than species that are omnivorous, granivorous, or frugivorous because these species can use food resources that are available longer into the fall (Buskirk 1980). Finally, temporal patterns of species turnover and co-occurrence may be an evolutionary consequence of interspecific competition. High densities of energy-depleted migrants constrained by time limitations have a strong potential to compete at stopover sites. Using predator enclosures, Moore and Yong (1991) experimentally demonstrated that spring migrants arriving in Louisiana depleted the abundance of natural food resources, and there was an inverse relationship between the rate of mass gain and the abundance of migrants present at the site. If interspecific competition has structured, at least in part, patterns in the timing of species' migrations, then we may expect a more distinct temporal separation of ecologically similar species throughout the season, resulting in greater turnover than when all species in the community are included (Rotenberry and Chandler 1999).

We describe temporal changes in the migrant landbird community along the northern coast of the Yucatan Peninsula during fall migration. We employed Detrended Correspondence Analysis (DCA) to address the following six questions. (1) How much compositional turnover occurs throughout the fall in migrant communities with and without winter residents? (2) What is the pattern of species turnover throughout the season; is it continuous or does it occur in pulses? (3) Does the within-season pattern of compositional turnover vary annually? (4) What is the sequence of species turnover? (5) How is the sequence of turnover related to the location of

species' breeding and wintering grounds and diet? (6) Is competition a potential factor influencing temporal patterns in species turnover?

## METHODS

### STUDY AREA

We studied the fall migrant community in the Ría Lagartos Biosphere Reserve located along the northern coast of the Yucatan Peninsula in the northeastern portion of the state of Yucatan, Mexico (21°31'N, 87°40'W). Bird communities were surveyed at two spatial and temporal scales using two methodologies. We used mist nets to survey migrants weekly in coastal vegetation, and we used point counts to survey migrants bi-weekly in coastal and interior vegetation. All mist-net and point-count locations were located within a 250-km<sup>2</sup> area. We studied migrants during fall migration in 2001 (12 August to 6 November), 2002 (4 August to 16 November), and 2003 (6 August to 27 November).

### MIST-NET SURVEYS

We operated mist nets at three sites, each containing at least two of three coastal vegetation types, including mid-successional coastal dunes (characterized by *Metopium brownei*, *Pithecellobium keyense*, and *Malvaviscus arboreus*), late-successional coastal dunes (characterized by *Pseudophoenix sargentii*, *Thrinax radiata*, and *Jacquinia aurantiaca*), and mangroves (dominated by *Rhizophora mangle*, *Avicennia germinans*, and *Conocarpus erectus*). Each vegetation type was present at two or more of the sites to provide true replicates. We operated eight to nine nets at each of the three sites, which were surveyed on a rotational basis. In 2001, we surveyed birds on four to six days each week, with the exception of two weeks toward the end of the season when nets were operated only on two days due to inclement weather (strong winds or precipitation). In 2002 and 2003, we surveyed birds three days per week, with five exceptions when one, two, four or six surveys were conducted. In 2002, no surveys were conducted for two weeks following Hurricane Isidore (22 September through 7 October) when inclement weather and flooding in the area prevented us from operating nets or gaining access to sites. We opened mist nets approximately 15 min prior to sunrise and ran them for up to 6.25 hr (mean  $\pm$  SE = 3.43  $\pm$  0.02 hr). We checked nets approximately 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. Although we frequently observed birds foraging in the afternoon (16:00–19:00), attempts to operate nets at this time yielded low capture rates. Furthermore, migrants did not appear to arrive at Ría Lagartos during this period, unlike spring stopover sites along the northern coast of the Gulf of Mexico where fallouts occasionally occur in the afternoon due to weather conditions over the Gulf (D. Aborn, pers. comm.). Migrants appeared to arrive at our site in the morning, between 08:00–12:00, and in the evening, roughly between 17:00–22:00, based on observations of birds.

Patterns in species turnover throughout migration may include a spatial component (Wilson and Twedt 2003); however, our focus here is to examine temporal patterns in turnover. Thus, we summed the number of birds of each species captured over all survey days and vegetation types during a week and divided by the total number of mist-net hours for that week (hereafter referred to as a net survey). To reduce the complexities that spatial heterogeneity introduces to analysis of temporal patterns of species turnover, we surveyed all three vegetation types during each weekly survey, with a single exception when only two vegetation types were visited. Therefore, the range of spatial heterogeneity was constant across surveys throughout the season and across years, and our weekly net surveys represent a series of surveys of the migrant community through time. Only initial captures were included in our analyses, and where reported, numbers represent bird abundance per 100 mist-net hours.

To quantify turnover in the transient community, we excluded all winter residents from the analysis. Individual birds recaptured four or more days after initial capture were classified as winter residents, as well as 19 individuals captured one or two years after initial capture. We plotted the number of birds per 100 mist-net hours against the median day of the year for each weekly survey period during all three years. For each species known to have a winter population in the study area (Howell and Webb 1995; B. MacKinnon, pers. comm.), we identified the peak abundance each year and the migration curve was truncated when bird abundance decreased below 25% of the peak and re-

remained below 50% for the duration of migration. This second criterion was necessary as some species had two peaks in some years, one usually smaller than the other. We classified birds captured prior to the truncation date as transients and those captured afterwards as winter residents. For the remainder of this paper, we use "entire community" to refer to winter residents and transients, whereas "transient community" refers to the community without winter residents.

#### POINT-COUNT SURVEYS

We established 60 point-count locations in five coastal and interior vegetation types, including mangroves, coastal dunes (mid- and late-successional stages combined), abandoned coconut plantations (early-successional coastal dunes dominated by *Cocos nucifera*, *Coccoloba uvifera*, *Tournefortia gnaphalodes*, and *Opuntia stricta*), medium-stature deciduous forests (characterized by *Bursera simaruba*, *Ceiba aesculifolia*, and *Haematoxylon campechianum*), and fields (primarily grazed areas dominated by *Panicum* sp. that contained forest remnants). Twelve point counts were established in each of the five vegetation types with at least 200 m between point locations, and each vegetation type was represented at two to five sites to provide true replicates. We divided the 60 points into two groups of 30 points (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. Occasionally, inaccessibility to points, primarily due to flooding, prevented us from conducting all 30 points during a survey, and those points were completed during the subsequent survey when possible. Two observers surveyed birds using 10-min, fixed-radius point counts, and each observer visited all of the vegetation types with equal frequency so that vegetation type and observer were not confounded.

We used point counts rather than transects because they permitted a greater number of replicates in our study site. Areas of forest and mangroves sufficiently large to accommodate an adequate number of transects were not available or accessible at our site. Because migrant birds vocalize infrequently during fall migration, primarily with call notes, we performed 10-min counts rather than 5-min counts to increase our number of detections.

We calculated the abundance of each bird species by summing individual birds, including flyovers, recorded on all point counts conducted during each biweekly survey. Due to differences in the number of point counts across surveys, we divided the abundance of each bird species by the number of point counts during the survey and multiplied by 30 to yield the average number of birds recorded on 30 point counts. Each biweekly survey based on count data is referred to as a "point-count survey" and represents the entire community (both winter residents and transients). All analyses of point count data were applied to the entire community.

#### BREEDING AND WINTERING LOCATION

We classified the general breeding and wintering latitude of each species according to the criteria outlined in Hagan et al. (1991) and Rotenberry and Chandler (1999), with minor changes to the winter classification. We assigned species a breeding-range rank score of 1–3, where species' breeding ranges were defined as: (1) mostly north of 45°N, (2) straddling 45°N, or (3) mostly south of 45°N. Each species also received a corresponding rank score of 1–5 based on its wintering distributions. Species' wintering distributions were classified as primarily in: (1) the southern United States and northern Mexico, (2) central Mexico and the Caribbean, (3) southern Mexico, the Caribbean, and Central America, (4) southern Central America and northern South America, and (5) South America. To determine the breeding and wintering location of species not included in the above papers, we cross-referenced the distributions published in the *Birds of North America* species accounts (Poole and Gill 1992–2003) and several field guides (Curson et al. 1994, Howell and Webb 1995, Dunn and Garrett 1997).

#### DIET AND FORAGING GUILDS

We used published data to classify species as insectivorous, granivorous, frugivorous, nectarivorous, piscivorous, or omnivorous based on their primary diet on the breeding grounds (Table 1; Ehrlich et al. 1988, Poole and Gill 1992–2003).

To examine the possibility that competition has influenced the timing of migration among species and, subsequently, species turnover patterns, we analyzed turnover within a subset of ecologically similar species that overlapped in

their primary diet, foraging maneuver, and microhabitat throughout the year and compared it to turnover in the entire community (Table 1; Parnell 1969, Ehrlich et al. 1988, Poole and Gill 1992–2003, Barrow et al. 2000). Live-foliage gleaning insectivores that forage primarily in the canopy of trees and saplings were the only group found in sufficiently large enough abundance ( $n = 8$ ) to permit analysis.

#### STATISTICAL ANALYSES

We analyzed temporal changes in the composition of migrant communities using Detrended Correspondence Analysis (DCA; Hill and Gauch 1980, Gauch 1982, Pielou 1984). The conceptual model underlying DCA is that species are distributed along one or more environmental gradients in a unimodal fashion. Here, we treat time as the environmental gradient of interest (Rotenberry and Chandler 1999, Wilson and Twedt 2003). In DCA, surveys with similar species composition and abundance lie close to one another in ordination space, species lie close to the species with which they frequently co-occur, and species lie close to surveys on which they are most common. Both surveys and species are assigned scores on each DCA axis that reflect their relative position along the gradient. Each DCA axis is associated with an eigenvalue ( $\lambda$ ) and length. The eigenvalue indicates how well the axis distinguishes among surveys based on their overall species composition and abundance and can have a maximum value of 1 (Jongman et al. 1995). The DCA axis length represents the amount of turnover in species composition between the most dissimilar surveys. Scores are scaled such that a length of 4 is a benchmark (Hill and Gauch 1980, Wilson and Mohler 1983); samples 4 units or more apart likely share few, if any, species in common. Although DCA has been criticized as being “inelegant” (Wartenberg et al. 1987), analyses of simulated data show that it is robust in modeling patterns of community change during migration (Rotenberry and Chandler 1999). We performed separate DCAs using mist-net survey data for the entire and transient communities and point-count survey data to quantify species turnover throughout the fall migration. All subsequent analyses, except where indicated otherwise, were performed using mist-net and point-count data for the entire community.

To evaluate the pattern of species turnover through time, we plotted DCA scores for mist-net and point-count surveys against the median day of the year of each survey period. If individual species' migration curves or distributions along a temporal gradient are regularly spaced, reflecting the continuous arrival and departure of species through time, then a plot of survey scores against date produces a linear pattern (Rotenberry and Chandler 1999). Alternatively, if migration curves are aggregated in time so that species arrive in waves, then a plot of survey scores against date produces a stair-step pattern, in which periods of rapid turnover are interspersed with periods of relative stasis. Of course, purely continuous or pulsed patterns in turnover represent two extremes, and real patterns likely fall somewhere in between.

To assess annual differences in the pattern of species turnover during fall migration for net and point-count surveys, we performed ANCOVAs to test for between-year differences in mean DCA scores with day of the year as the covariate. Prior to performing correlations and ANCOVAs, we transformed DCA scores for mist-net and point-count surveys using a Box-Cox transformation so that data met the assumptions of normality and homogeneity of variance. Untransformed DCA scores are plotted in figures for ease of interpretation. To evaluate the similarity in the sequence of species turnover, we performed a Pearson correlation between species' DCA scores based on mist-net and point-count surveys. The analysis was restricted to species that were included in both analyses.

We used Spearman rank correlations to examine relationships between species' breeding and wintering latitude (rank scores) and the sequence of species turnover in the fall, represented by species' DCA scores. We hypothesized that insectivores should migrate earlier than omnivores, granivores, and frugivores, so we combined these latter foraging groups and used a one-way ANOVA to test for differences in species' scores on DCA 1 and mean passage date. For mist-net surveys the mean passage date of each species was calculated using the date of all first captures across the three years of study, while for point-count surveys, mean passage date was calculated using the date of all birds recorded on counts, including flyovers, during 2002 and 2003. In our analyses of breeding and

wintering range and diet, we used DCA scores based on net and point-count data.

For an evaluation of possible competition effects we performed a separate DCA of the live-foilage gleaning insectivore guild using net data. We compared the eigenvalues and lengths of DCA axes to those produced when all species were included in the analysis. If competition has had an effect on the timing of species' migrations and compositional turnover, we predicted that the eigenvalues and lengths of DCA axes associated with the foliage-gleaning insectivore guild would be greater than those associated with the entire community.

We used PC-ORD version 4.0 (McCune and Mefford 1999) to perform DCA analyses, and all other statistical analyses were performed using JMP version 5.1.1 (SAS institute 2004) and SPSS version 11.0.1 (SPSS 2002).

## RESULTS

### SPECIES TURNOVER

*Mist nets.* We completed 42 weekly mist-net surveys during fall 2001–2003. Sixty-nine species and 3159 individuals were captured during the surveys, but only common species occurring on at least 15% of weekly surveys, after the exclusion of winter residents, were included in our analyses (Table 1). We omitted uncommon species from analyses for both biological and statistical reasons. First, rare species may be vagrants to the site and typically do not form part of the migrant community. Second, uncommon species do not generate clear migration curves or frequency distributions and may produce spurious results depending on their position along the gradient.

Our results show that only the first DCA axis or Detrended Component (DC 1) contained relevant information (entire community, DC 1  $\lambda = 0.60$ , all other  $\lambda \leq 0.17$ ; transient community, DC 1  $\lambda = 0.71$ , all other  $\lambda \leq 0.25$ ). The high eigenvalues indicate that our data provided a relatively good fit to the DCA model. The lengths associated with DC 1 were 3.3 and 4.5 for the entire and transient communities, respectively. Total species turnover was lower when winter residents were included in the community, and the ability to distinguish among surveys based on species composition was slightly reduced, as evident by the shorter axis length and smaller eigenvalue, respectively. The presence of winter populations of early and midseason migrant spe-

cies at the site prevented complete turnover throughout the fall (length  $< 4.0$ ). Nevertheless, early and late fall communities were dissimilar in species composition. Transient communities showed virtually complete turnover in species composition (DC 1 length  $> 4.0$ ), and early and late communities shared very few, if any, species in common.

*Point counts.* We conducted a total of 17 bi-weekly point-count surveys in 2002–2003, recording 43 species and 1989 individuals. Thirty common species present on at least 15% of the surveys were included in analyses (Table 1). The eigenvalue associated with the first axis was 0.72 and those associated with all other axes were  $\leq 0.14$ . There was complete turnover in species composition between the most dissimilar point count surveys (DC 1 length = 4.6). Both the length and eigenvalue of DC 1 were greater for communities surveyed by point counts than mist nets (entire community), representing greater compositional turnover and a tighter fit of the data to the DCA model, respectively.

### WITHIN-SEASON PATTERNS OF SPECIES TURNOVER

*Mist nets.* To evaluate the temporal pattern of migration (continuous vs. pulsed species turnover) we plotted survey scores on DC 1 against the median day of the year for each survey period. A plot of weekly mist-net surveys for the entire community by survey date produced a weakly structured stair-step pattern, characterized by alternating periods of slow and rapid turnover ( $r = -0.92$ ,  $P < 0.001$ ; Fig. 1A). The initial period of slow turnover lasted from day 220 to around 250 (slope =  $-0.01$  DCA units day $^{-1}$ ) followed by a period of more rapid turnover through day 300 (slope =  $-0.06$ ). The season terminated in a second period of slow turnover, during which survey scores fluctuated between 0.0 and 1.3 (slope =  $-0.01$ ).

The transient community demonstrated a very similar pattern ( $r = 0.96$ ,  $P < 0.001$ ), except that after winter residents were excluded the period of stasis at the end of the season in the entire community was absent, and the period of rapid turnover continued at a constant rate until the end of the season (slope = 0.05). The period of slow turnover at the beginning of the season was characterized by a slope of 0.01. (Note that the difference in the sign of the slopes between the entire and transient communities does not reflect

TABLE 1. Migrant species captured in mist nets or recorded during point counts in the Ría Lagartos Biosphere Reserve during fall migration 2001–2003, arranged by mean passage date based on net data.

Species	Species code	Number of net surveys of the entire community (transients)	Number of point-count surveys	Mean first-arrival date <sup>a</sup>	Mean passage date <sup>a</sup> (point counts <sup>b</sup> )	Breeding range <sup>c</sup>	Wintering range <sup>d</sup>	Diet <sup>e</sup>	Foliage-gleaning insectivores <sup>f</sup>
Prothonotary Warbler ( <i>Protonotaria citrea</i> )	PROW	25 (25)	8	223	244 (246)	3	3	I	X
Kentucky Warbler ( <i>Oporornis formosus</i> )	KEWA	11 (11)	—	225	246 (—)	3	3	I	—
Hooded Warbler ( <i>Wilsonia citrina</i> )	HOWA	25 (20)	9	225	249 (290)	3	3	I	—
Bank Swallow ( <i>Riparia riparia</i> )	BANS	—	3	249	251 (258)	2	5	I	—
Barn Swallow ( <i>Hirundo rustica</i> )	BARS	8 (8)	12	242	252 (255)	2	4	I	—
Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	EAKI	—	6	254	256 (266)	2	5	I	—
Prairie Warbler ( <i>Dendroica discolor</i> )	PRAW	9 (9)	—	240	258 (—)	3	2	I	X
Ovenbird ( <i>Seiurus aurocapillus</i> )	OVEN	35 (24)	11	223	259 (270)	2	3	I	—
Cliff Swallow ( <i>Petrochelidon pyrrhonota</i> )	CLSW	—	4	254	259 (263)	2	5	I	—
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	REVI	27 (27)	4	234	261 (263)	2	5	I	—
Belted Kingfisher ( <i>Ceryle alcyon</i> )	BEKI	—	6	261	261 (291)	2	2	P	—
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	NOWA	39 (25)	16	227	262 (281)	2	3	I	—
Blue-winged Warbler ( <i>Vermivora pinus</i> )	BWWA	8 (8)	—	254	264 (—)	2	3	I	—
Yellow Warbler ( <i>Dendroica petechia</i> )	YWAR	39 (23)	14	225	265 (273)	2	3	I	X
Black and White Warbler ( <i>Mniotilta varia</i> )	BAWW	30 (25)	4	228	268 (279)	2	3	I	—
Purple Martin ( <i>Progne subis</i> )	PUMA	—	5	268	268 (246)	2	5	I	—
Yellow-billed Cuckoo ( <i>Coccyzus americanus</i> )	YBCU	8 (8)	4	265	269 (275)	3	5	I	—
Eastern Wood-Pewee ( <i>Contopus virens</i> )	EAWP	11 (11)	—	251	270 (—)	2	5	I	—

TABLE 1. Continued.

Species	Species code	Number of net surveys of the entire community (transients)	Number of point-count surveys	Mean first-arrival date <sup>a</sup>	Mean passage date <sup>a</sup> (point counts <sup>b</sup> )	Breeding range <sup>c</sup>	Wintering ranged	Diet <sup>e</sup>	Foliage-gleaning insectivores <sup>f</sup>
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )	CSWA	14 (14)	4	259	271 (285)	2	3	I	X
American Redstart ( <i>Setophaga ruticilla</i> )	AMRE	26 (21)	10	230	272 (284)	2	3	I	-
Magnolia Warbler ( <i>Dendroica magnolia</i> )	MAWA	20 (12)	10	262	278 (298)	2	3	I	X
Yellow-breasted Chat ( <i>Icteria virens</i> )	YBCH	10 (9)	4	264	281 (296)	2	2	O	-
Northern Parula ( <i>Parula americana</i> )	NOPA	31 (28)	11	229	284 (292)	2	2	I	X
Least Flycatcher ( <i>Empidonax minimus</i> )	LEFL	14 (14)	6	252	284 (295)	1	3	I	-
Tennessee Warbler ( <i>Vermivora peregrina</i> )	TEWA	16 (16)	8	269	288 (291)	1	3	I	-
Philadelphia Vireo ( <i>Vireo philadelphicus</i> )	PHVI	7 (7)	-	283	289 (-)	1	3	I	X
White-eyed Vireo ( <i>Vireo griseus</i> )	WEVI	18 (13)	9	268	292 (301)	3	2	I	-
Common Yellowthroat ( <i>Geothlypis trichas</i> )	COYE	24 (20)	9	269	294 (307)	2	2	I	-
Black-throated Green Warbler ( <i>Dendroica virens</i> )	BTNW	8 (8)	4	284	294 (305)	2	3	I	X
Yellow-throated Warbler ( <i>Dendroica dominica</i> )	YTWA	-	11	291	295 (292)	3	2	I	-
Painted Bunting ( <i>Passerina ciris</i> )	PABU	19 (16)	3	269	296 (312)	3	2	G	-
Indigo Bunting ( <i>Passerina cyanea</i> )	INBU	15 (13)	7	286	301 (303)	3	3	O	-
Gray Catbird ( <i>Dumetella carolinensis</i> )	GRCA	15 (15)	5	288	302 (311)	3	2	O	-
Palm Warbler ( <i>Dendroica palmarum</i> )	PAWA	15 (15)	7	283	302 (301)	1	2	I	-
Ruby-throated Hummingbird ( <i>Archilochus colubris</i> )	RTHU	17 (17)	8	277	307 (304)	2	3	N	-

a true difference between the communities, as the directionality of axes in DCA is arbitrary.)

**Point counts.** A plot of point count survey scores on DC 1 against day of the year produced a relatively weak stair-step pattern similar in overall structure to that produced by mist-net surveys including winter residents, except for an additional period of rapid turnover at the beginning of the season ( $r = 0.91$ ,  $P < 0.001$ ; Fig. 1B). From day 221 to day 230 there was a very rapid but brief increase in the DCA score associated with surveys (slope = 0.19 DCA units day<sup>-1</sup>). The first period of relatively slow turnover lasted from around day 230 to 260 (slope = 0.01) and was followed by the second period of rapid turnover through day 300 (slope = 0.12). Finally, the season terminated in a second period of slow turnover (slope = -0.01).

#### ANNUAL VARIATION IN SPECIES COMPOSITION

Mean survey scores on DC 1 did not vary across years, regardless of the presence of winter residents (mist nets: entire community,  $F_{2,38} = 2.2$ ,  $P = 0.12$ ; transient community,  $F_{2,38} = 2.4$ ,  $P = 0.10$ ) or survey method used (point counts,  $F_{1,14} = 0.1$ ,  $P = 0.72$ ).

#### SEQUENCE OF SPECIES TURNOVER

The association between individual species and the overall pattern of species turnover in the community is illustrated by a plot of species scores along the first DCA axis for mist-net (Fig. 2A) and point-count surveys (Fig. 2B). Species arriving at the site earlier in the season have higher scores on DC 1 based on mist-net data for the entire community and lower scores on DC 1 based on point-count data. As with survey scores the directionality of the DCA axes is arbitrary.

**Mist nets.** The period of slow turnover in the entire community at the beginning of the season (through day 250) was characterized by early migrant species, including Barn Swallows (*Hirundo rustica*) through Northern Waterthrushes (*Seiurus novaboracensis*), with DC 1 scores ranging from 4.26–2.42 (Fig. 2A). During this period, species turnover was slow as species arrived gradually throughout August and early September. The next period consisted of more rapid turnover (day 250–300) and coincided with a decline in abundance of early-season migrants and the arrival of mid-season migrant species, ranging from Blue-winged Warblers (*Vermivora pinus*) through Yellow-billed Cuckoos (*Coccyzus americanus*; DC 1 scores from 2.06–0.85). The period of slow turnover at the end of the season was dominated by late-arriving species, including Black-throated Green Warblers (*Dendroica virens*) through Indigo Buntings (*Passerina cyanea*; DC 1 scores 0.49 to -0.67). By this time, the rate of turnover had decreased and species composition began to converge on that of the winter community. The sequence of turnover in transient communities was similar, and species' DC 1 scores were significantly correlated between communities with and without winter residents ( $r = -0.97$ ,  $P < 0.001$ ), suggesting that the large number of transients moving through the site were driving the pattern in the sequence of species turnover in the entire community.

**Point counts.** The brief period of rapid turnover from the beginning of the season through day 230 was associated primarily with Purple Martins (*Progne subis*; DC 1 score -0.47), the earliest species arriving at the site (Fig. 2B). Prothonotary Warblers (*Protonotaria citrea*), Cliff Swallows (*Petrochelidon pyrrhonota*),

←

<sup>a</sup> Based on mist-net data.

<sup>b</sup> Mean passage dates based on mist-net data are more precise than those based on point-count data for species active in the understory due to greater temporal resolution of survey efforts. Mean passage dates based on point-count data are likely more precise for species that are active above the area effectively surveyed by nets (e.g., swallows).

<sup>c</sup> Breeding range. 1 = mostly north of 45°, 2 = straddles 45°, 3 = mostly south of 45°.

<sup>d</sup> Wintering range. 1 = southern United States and northern Mexico, 2 = central Mexico and Caribbean, 3 = Southern Mexico, Caribbean, and Central America, 4 = southern Central America and northern South America, 5 = South America.

<sup>e</sup> Primary diet type, G = granivorous, I = insectivorous, N = nectarivorous, O = omnivorous (insects, fruit, seeds, nectar, or a combination of these), P = Picivorous.

<sup>f</sup> Primarily active in trees and saplings.

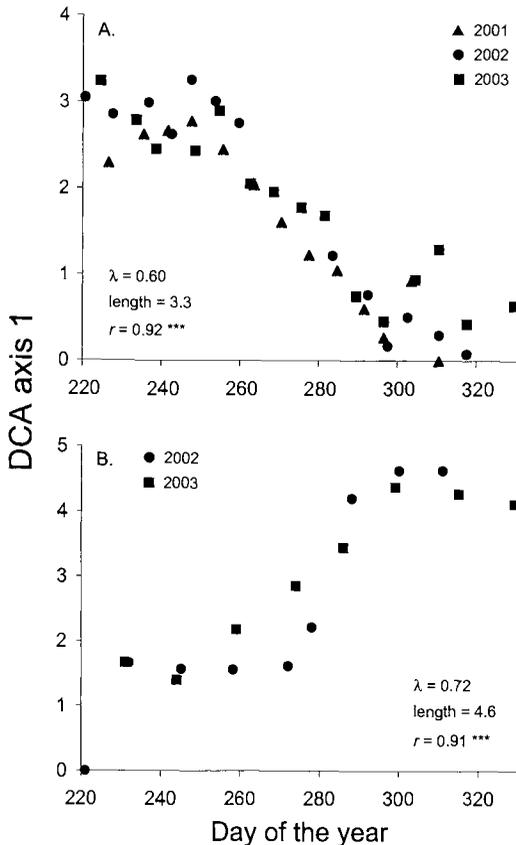


FIGURE 1. Untransformed scores on Detrended Correspondence Analysis Axis (DCA axis) 1 plotted against day of the year for fall migrants (entire community) passing through the Ría Lagartos Biosphere Reserve between 2001–2003. A) Based on mist-net captures. B) Based on point-count surveys. The date for each weekly net survey is the median day of the survey period.  $\lambda$  denotes the eigenvalue (maximum value = 1.0), length is an index of the amount of turnover (4 = complete turnover), and  $r$  is the Pearson correlation coefficient for the correlation between DCA scores for all three years and day of the year. (\*\*\*) denotes  $P < 0.001$ . Day of the year 220 = 8 August, 320 = 16 November.

Bank Swallows (*Riparia riparia*), Barn Swallows, and Red-eyed Vireos (*Vireo olivaceus*; DC I scores 0.94–1.81) dominated the first period of slow turnover from day 230 through 260, while the second period of rapid turnover, lasting through day 300, consisted of mid-season species ranging from Eastern Kingbirds (*Tyrannus tyrannus*) to Yellow-breasted Chats (*Icteria virens*; DC I scores 2.33–4.20). The period of slow turnover at the end of the season was characterized by late-arriving species, including

Palm Warblers (*Dendroica palmarum*) through Gray Catbirds (*Dumetella carolinensis*; DC I scores 4.63–5.43).

For the 24 species included in analyses of both point-count and mist-net data for the entire community, the correlation between their DC I scores for the two methods was significant ( $r = -0.84$ ,  $P < 0.001$ ), suggesting that detecting the sequence of species turnover throughout the fall is robust with respect to the survey method employed.

#### BIOGEOGRAPHIC ASSOCIATIONS

DC I based on mist-net data was significantly correlated with the location of species' wintering grounds ( $r_s = 0.42$ ,  $P = 0.02$ ; Table 1). Species wintering at southern latitudes, including Barn Swallows, Eastern Wood-Pewees (*Contopus virens*), Red-eyed Vireos, and Yellow-billed Cuckoos, passed through the site earlier than species wintering at more northern latitudes, such as Gray Catbirds, Palm Warblers, and White-eyed Vireos (*Vireo griseus*). There was no relationship between the sequence of turnover and breeding latitude ( $r_s = 0.16$ ,  $P = 0.42$ ). Point-count data demonstrated similar patterns (winter,  $r_s = -0.68$ ,  $P < 0.001$ ; breeding,  $r_s = 0.10$ ,  $P = 0.62$ ).

#### DIET

We classified 24 species captured in mist nets and point counts as insectivores, three as omnivores, and one as a granivore; no species were classified frugivores (Table 1). The Ruby-throated Hummingbird (*Archilochus colubris*) was the only species classified as nectarivorous in both mist-net and point-count surveys, and the Belted Kingfisher (*Ceryle alcyon*) was the only species classified as piscivorous on count surveys. Due to small sample sizes within these categories, we excluded both of these species from analyses. Based on mist-net data, insectivores passed through the site earlier than omnivores and granivores combined, based on species' DC I scores ( $F_{1,26} = 6.0$ ,  $P = 0.02$ ) and species' mean passage dates ( $F_{1,26} = 7.6$ ,  $P = 0.01$ ). Point-count surveys showed a similar pattern (DC I scores:  $F_{1,26} = 4.2$ ,  $P = 0.05$ ; mean passage dates:  $F_{1,26} = 7.5$ ,  $P = 0.01$ ).

#### COMPETITION EFFECTS

Based on mist-net survey data, including winter residents, the foliage-gleaning insectivore com-

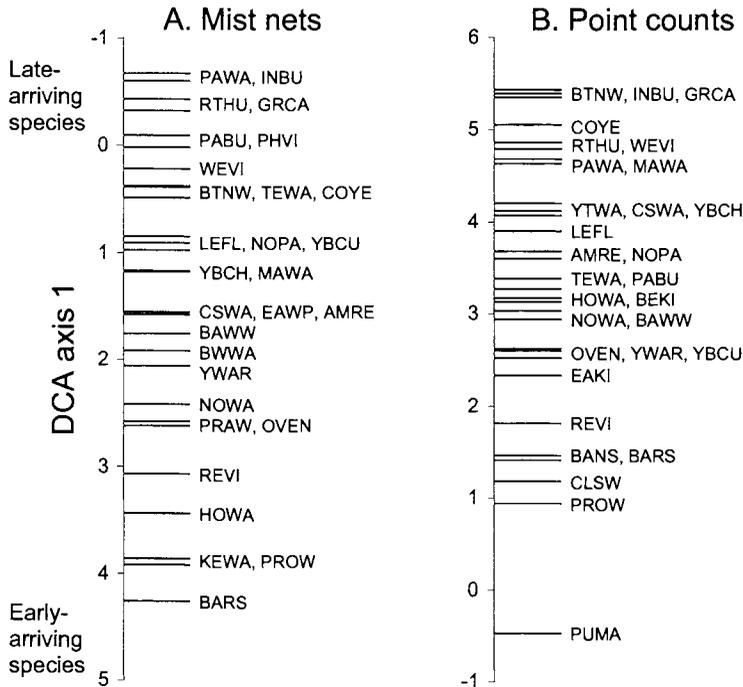


FIGURE 2. Species scores on Detrended Correspondence Analysis Axis (DCA axis) 1 for the entire migrant community in the Ría Lagartos Biosphere Reserve during fall 2001–2003. A) Based on mist-net captures. B) Based on point-count surveys. Species at the bottom of each graph arrived earliest at the site. See Table 1 for species codes.

munity demonstrated less compositional turnover throughout the season (DC 1 length = 2.4) than the entire community (all 29 species, DC 1 length = 3.3), indicating that the migration curves of this subset of species demonstrated greater temporal overlap. The ability to distinguish among surveys based on species composition was only slightly reduced (DC 1  $\lambda$  = 0.55, all other  $\lambda$  < 0.20) relative to the community as a whole (DC 1  $\lambda$  = 0.60, all other  $\lambda$  ≤ 0.17).

## DISCUSSION

On the northern coast of the Yucatan Peninsula, the amount of turnover in the entire fall migrant community indicated that species composition was dissimilar in early and late migration. However, when our analysis was restricted to the transient community, turnover was virtually complete, and early and late transient communities shared very few, if any, species in common. When winter residents were included in our analysis, many species arriving during the first half of the season, such as Northern Waterthrushes, Ovenbirds (*Seiurus aurocapillus*), Yel-

low Warblers (*Dendroica petechia*), Magnolia Warblers (*Dendroica magnolia*), and Northern Parulas (*Parula americana*) overlapped with later-arriving species. Consequently, turnover was incomplete. However, the number of winter residents was much lower than the number of transients, and this group likely exerts little competitive pressure for food resources. The temporal separation of transient populations of early and late species, reflected in the large amount of compositional turnover, may effectively reduce competition for food resources among energy-depleted migrants, although the separation itself may be the result of processes other than competition.

The amount of turnover observed in the Yucatan was similar to that found in Pennsylvania during fall (length = 3.4) and spring (length = 3.6; Rotenberry and Chandler 1999), but less than that observed in spring communities passing through the Mississippi Alluvial Valley (length = 5.95; Wilson and Twedt 2003). Differences in the amount of species turnover at these sites and what we observed in the current

study may be attributed to several factors. First, the presence of populations of winter or breeding residents at a stopover site during the fall or spring, respectively, increases the duration of a species' presence at a site, which may result in greater temporal overlap among species, leading to reduced turnover. The reduced turnover associated with the entire community at our site relative to the transient community illustrates this phenomenon. Second, a broader range of taxonomic groups (e.g., more families) present at a site or included in analyses may increase turnover. Increasing diversity of families likely leads to a greater diversity of breeding and wintering latitudes and diets in a sample, which may then result in greater variation in the timing of species' arrival at a stopover site, a more distinct separation of species' occurrences throughout the season, and, consequently, greater species turnover. Rotenberry and Chandler's (1999) analysis of spring migrants was restricted to 29 species in a single family, whereas Wilson and Twedt (2003) included 55 species from 17 families, which may have contributed to the differences in species turnover reported in these studies. Third, birds tend to migrate more quickly in spring than in fall (Morris et al. 1994), resulting in reduced temporal overlap among species, thereby leading to greater turnover (Morris et al. 1994). This, along with a different number of families, may explain the differences in turnover observed between the current study (fall, nine families) and that conducted by Wilson and Twedt (2003; spring, 17 families), both of which included a similar range of avian families. Other factors, particularly geography, may also play a role, as the location of a study site is confounded with the presence of winter or breeding populations, the number of species, and the range of families found there.

Community-level analyses of temporal patterns in migrant communities passing through stopover sites may allow us to identify periods when competition for food is likely to be the greatest, as well as identify suites of species that co-occur in time and have the potential to interact. When we considered the total number of migrant individuals summed across all 29 common species captured in the Yucatan, we identified two to three periods of peak abundance (Fig. 3). This contrasts with other sites (Wisconsin, Winker et al. 1992; New Mexico, Finch and Yong 2000; South Dakota, Swanson et al. 2003)

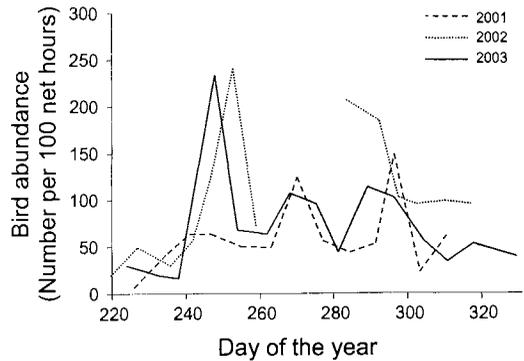


FIGURE 3. Total migrant abundance (number per 100 mist-net hours) plotted against day of the year for all 29 common species captured in the Ría Lagartos Biosphere Reserve during fall 2001–2003. Nets were not operated between days 261–282 in 2002 after Hurricane Isidore. Day of the year 220 = 8 August, and day 320 = 16 November.

that appeared to have a single period of peak migration and greater temporal overlap among migrants. Multiple peaks, representing a reduction in the amount of temporal overlap among individuals, may reduce competition pressures at a site. Differences in the amount of temporal overlap among species at various stopover sites may result in variation in the degree of competition experienced by migrants along the migratory route.

The amount of species turnover based on point-count data was greater than that observed in the entire community based on mist-net data, and the ability to distinguish among surveys based on species composition was enhanced. The greater amount of turnover observed in communities surveyed by point counts may be due to several factors, including the spatial and temporal scale over which point-count surveys were conducted and detectability biases associated with point counts (Rappole et al. 1998, Wang and Finch 2002). Point-count surveys included three additional and distinctly different vegetation types. Thus, migrants were surveyed over a greater range of vegetation types than mist nets. Additional spatial variation may contribute to greater species turnover if the following conditions occur: additional vegetation types are associated with unique species, these unique species arrive earlier or later than the suite of species included in mist-net surveys, and the species occur on the site for a brief time. Out of 35 common species recorded by one or both sur-

vey types, 24 (69%) were recorded by both methods, whereas six species were recorded only on point counts and five species were captured only in mist nets. The species most likely to enhance the amount of turnover based on point count surveys include Purple Martins, Bank Swallows, and Cliff Swallows as they arrived at Ría Lagartos earlier than most species recorded in mist-net surveys and are completely transitory at the site. However, their appearance in only point-count surveys was not associated with additional vegetation types surveyed by point counts, as they were also common in vegetation types associated with mist net sites. Rather, a bias towards a relatively low effective sampling height (up to 2.6 m) associated with mist-net surveys likely explains these differences. Explicitly including spatial variation into our analysis of point-count and mist-net data will allow us to evaluate the role of spatial variation in species turnover throughout the season (JLD, unpubl. data).

In light of the similarities in the pattern and sequence of species turnover between net and point-count surveys, the difference in the amount of species turnover is most likely the result of a detectability bias associated with point counts. Relative to mist nets, point counts are biased against detecting rare species during migration (Wang and Finch 2002). When individuals of a species first appear at a stopover site, or after the majority of individuals of that species have already passed through the site, the species is rare, being represented by a small number of individuals. Consequently, it is less likely to be detected by audio-visual counts. This detection bias, along with the decreased temporal resolution of point-count surveys, may have effectively narrowed the apparent time a species was at the site, thereby reducing the amount of temporal overlap among species. Eliminating winter residents from the community surveyed by mist nets also reduced the apparent time a species was at the site and increased turnover to an amount similar to that associated with point counts.

Based on net and point-count data, turnover in species composition along the northern coast of the Yucatan Peninsula during fall migration showed a weak stair-step structure; species arrived at the site throughout the fall but at varying rates. Turnover was generally slow until the middle of the season, when it reached a maxi-

mum, and decreased again toward the end of the season as species composition began to converge on that characteristic of the winter community. During the fall, Able (1972) observed trans-Gulf flights in Louisiana only under conditions of northerly winds accompanying post-frontal systems that extended into the Gulf. Buskirk (1980) observed a similar association along the northern Yucatan coast, in which the three days of greatest migrant density coincided with three periods of strong northerly winds across the Gulf, although he also noted that a relatively small number of migrants arrived at his site almost daily (89% of observation days). In Ría Lagartos, we observed an almost daily, but low influx of migrants that was interrupted infrequently by mass arrivals of individuals. However, the lack of a strong stair-step pattern in turnover, characterized by discrete pulses of turnover interspersed with periods of relative stasis, suggests that the arrival of species at Ría Lagartos was not associated with such weather systems. Species arrived at our site throughout the season, although at varying rates, and often appeared for the first time on days of low bird abundance rather than coinciding with mass arrival events. The similar pattern of turnover and sequence of species arrival across years lends further support that the arrival of species was not contingent upon these infrequent weather systems. The small number of birds arriving daily along the northern coast of the Yucatan Peninsula may originate from the Florida panhandle, as northerly winds favorable for southbound flight are a more regular occurrence there than along the Gulf Coast west of the Mississippi (Buskirk 1980).

In addition to similarities in the pattern of species turnover between the two methods, there was a significant correlation between species' scores on DC 1 based on mist-net and point-count data, indicating that detection of the sequence of turnover among species throughout fall migration is robust to the alternative sampling techniques. Furthermore, there was close correspondence in the most common species detected by point counts and mist nets; for the 15 most frequently detected species there was an 80% overlap in species composition.

The pattern and sequence of species turnover was consistent across all years of the study, despite annual variation in many aspects of the migrant community, such as species abundances,

first and mean passage dates, and duration of migration. Rotenberry and Chandler (1999) observed similar annual consistency in community turnover patterns in Pennsylvania, and Yong and Moore (1997) noted that the sequence of passage of thrush species was constant across years during spring migration in Louisiana.

Many factors may interact to shape the sequence of species turnover at a stopover site. The sequence of turnover was associated with the location of species' wintering grounds but not breeding grounds. Species that wintered at more southern latitudes (e.g., South America) passed through our site significantly earlier in the fall than species wintering at more northern latitudes, as also observed by Weisbrod et al. (1993). These species likely initiate migration earlier because they have a greater distance to cover before reaching their wintering grounds. Rotenberry and Chandler (1999), on the other hand, found no relationship between the sequence of migration and wintering location. Associations between the sequence of fall migration and the location of species' breeding and wintering grounds appear to have a geographic component that may be better understood once temporal patterns are described across a larger range of sites.

The sequence of migrant turnover in northern Yucatan was also related to species' primary diet on the breeding grounds. Insectivores passed through the site earlier than omnivores and granivores, probably due to decreases in the abundance and reliability of arthropod resources throughout the fall in temperate regions as temperatures decrease (Kendeigh 1979, Wolda 1988, Parrish 2000). The association between diet and sequence of migration is supported by data on mean passage dates in the fall and spring. Insectivores, primarily wood warblers, were the earliest fall arrivals observed by Buskirk (1980) in the Yucatan, followed by non-insectivorous species such as thrushes, fringillids, and Gray Catbirds.

Our results are not consistent with the hypothesis that competition has played a role in structuring the phenology of the bird community passing through the Yucatan Peninsula during fall migration. There was less compositional turnover among foliage-gleaning insectivores than among all 29 species in the community surveyed via nets, suggesting that species that are most ecologically similar, and likely to compete

for resources, show more temporal overlap than ecologically dissimilar species. Many species have been reported to shift to an omnivorous diet at some stopover sites to exploit abundant fruit resources (Parrish 2000), which may relax food-based competition among typically insectivorous species during migration and reduce selective pressures favoring their temporal displacement. However, the importance of such dietary changes in alleviating competitive pressures may be reduced in Ría Lagartos as the abundance of small fruits available to migrants is low throughout much of the fall, and only a few migrant species have been observed eating fruit at our site or captured with stained bills (JLD, pers. obs.).

Turnover is not complete among migrant species passing through the northern Yucatan due to the presence of migrants that remain as winter residents. However, peak abundances of transient individuals of early and late-arriving species are temporally separated. Migrant communities are the result of complex interactions among large-scale, extrinsic (off-site) processes and local, intrinsic (on-site) processes. Temporal patterns in the sequence of arrival and the co-occurrence of species at particular stopover sites are affected by factors away from the site, such as synoptic weather patterns, the location and condition of species' breeding and wintering grounds, species' diets during the nonmigratory period, and processes and conditions at previous stopover sites. On the other hand, spatial patterns in species' distributions and community turnover at a stopover site are determined largely by local-scale factors, including the distribution of vegetation, food abundance, predation, and competition; the relative importance of such factors in shaping spatial patterns may be mediated by the energetic condition, age, sex, or dominance status of the individual bird. Most often, spatial examinations of species and communities during migration have ignored temporal variation, yet it has been shown that spatial patterns of both species (Bairlein 1983) and communities (Wilson and Twedt 2003) may change over time during the migratory season. Thus, neither spatial nor temporal analyses alone are sufficient in identifying community patterns during migration or understanding the mechanisms responsible for such patterns, and future studies should consider both time and space.

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