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SEASONAL CHANGES TO ARTHROPOD ABUNDANCE IN SUCCESSIONAL FORESTS OF THE YUCATAN PENINSULA, WITH IMPLICATIONS FOR OVERWINTERING FOREST BIRDS

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Resumen. – Los cambios estacionales en la abundancia de artrópodos en los bosques sucesionales de la Península de Yucatán, México, y sus implicaciones para las aves de bosque transinvernales. – En el Neotrópico, es típico que la abundancia de artrópodos disminuye durante la época de sequía con tendencia a limitar la cantidad de alimento disponible a las aves de bosque migratorias. Es posible también que la deforestación en beneficio de la agricultura contribuya a la escasez del alimento mediante la eliminación de las selvas maduras y su sustitución por etapas serales más recientes. Sin embargo, pocos estudios se han dedicado a examinar los efectos de esta conversión de hábitat sobre la disponibilidad de alimento a las aves migratorias en el Neotrópico. En el presente estudio examinamos artrópodos de follaje con redes aéreas y garrochas para determinar si los niveles de abundancia cambian en las diferentes etapas de vegetación sucesional, contrastando la época lluviosa y la época de sequía en la Península de Yucatán. También examinamos los hábitos de forrajear de dos especies de aves insectivoras, el Chipe Flameante (*Setophaga ruticilla*) y el Chipe de Magnolia (*Dendroica magnolia*), con objeto de evaluar si nuestros métodos reflejaron fielmente la disponibilidad del alimento a estas aves. De hecho, la selva madura tuvo la mayor abundancia total de artrópodos en las colecciones efectuadas con redes aéreas, y los niveles aumentaron en todos los hábitats conforme al cambio de épocas: de lluvias a la sequía. Por otra parte, en las colecciones basadas en el uso de la garrocha los niveles de los artrópodos fueron más altos en la selva madura que en la selva media madura, pero niveles no variaron en ningún hábitat por época. En ambos casos, constatamos que las arañas constituyeron el orden de mayor abundancia. Las dos especies de aves migratorias buscaban alimento principalmente en el follaje. La altura de su forrajeo correspondía a la que encontramos en nuestras colecciones en la vegetación sucesional de tipo menos maduro. Por otra parte, constatamos que a veces la altura del forrajeo superaba la de las etapas más maduras. Durante la época de lluvias, las aves atacaban a su presa con mayor frecuencia en la selva madura, lo que coincidió con los niveles de artrópodos más altos en nuestras colecciones efectuadas con redes aéreas. En la época de sequía no encontramos correspondencia nítida entre los ataques a la presa y los niveles de alimento potencial. Al contrario de nuestra expectativa, estos resultados sugieren que las aves de bosque transinvernales en la Península de Yucatán no sufren una disminución de alimento durante la época no reproductiva. Sin embargo, la pérdida de selva madura en la región tal vez tenga efectos negativos a la disponibilidad de alimento para las aves migratorias.

Abstract. – Arthropod levels typically decline during the Neotropical dry season, potentially limiting food availability for overwintering migratory forest birds. Land clearing for agriculture may further exacerbate food shortages, as mature late successional forest is replaced with younger stages of second growth habitat. The effects of this habitat conversion on food availability for overwintering migratory forest birds, however, have been little studied. We used sweepnet and branch clipping methods to examine whether foliage arthropod levels varied across a successional forest gradient during the wet and dry seasons in the Yucatan Peninsula. We also documented the foraging behavior of two migratory insectivores, American Redstart (*Setophaga ruticilla*), and Magnolia Warbler (*Dendroica magnolia*), to determine if our collection methods accurately reflected food availability for these birds. For sweepnet collections, late successional forest had the highest overall abundance of arthropods, and densities increased in all habitats from the wet to dry season. For branch clipping collections, late successional forest had more arthropods than mid successional forest, but arthropod levels did not vary by season in any habitat. Spiders were the most abundant order sampled by both methods. Both migrant species foraged predominantly on foliage in all habitats. Their foraging height overlapped with our sampling heights in early successional forest, but sometimes exceeded sampling heights in older seral stages. Highest foraging attack rates in the wet season were observed in late successional forest, coinciding with highest sweepnet arthropod levels. In the dry season no clear pattern between foraging attack rates and potential prey levels was found. In contrast to expectations, these results suggest that overwintering migratory insectivorous birds in the Yucatan Peninsula may not face food declines during the non-breeding season. However, food availability may be adversely affected by the ongoing loss of late successional forest in the region. *Accepted 30 October 2007.*

Key words: Arthropods, *Dendroica magnolia*, dry season, Neotropics, *Setophaga ruticilla*, successional forests, Yucatan Peninsula.

INTRODUCTION

Migratory songbirds wintering in the northern Neotropics experience drastic seasonal changes in abiotic and biotic conditions. Arriving at the end of the rainy season, these birds overwinter during the height of the dry season when arthropod food resources generally decline across a range of habitats (Waide *et al.* 1980, Lefebvre *et al.* 1994, Strong & Sherry 2000, Sherry *et al.* 2005). Widespread territoriality of migrant species and local population changes linked to fluctuating arthropod levels suggest that food availability may limit these birds during the non-breeding season (Terrill 1990, Sherry & Holmes 1996, Johnson 2000a, Johnson & Sherry 2001, Sherry *et al.* 2005). Since food resources may be important determinants of overwinter body condition and survival (Parrish & Sherry 1994, Strong & Sherry 2000, Johnson *et al.* 2006), documenting their distribution and use by migratory birds in the tropics can reveal critical information on habitat suitability during the non-breeding season. However, determining the role of food resources in shaping migrant habitat use depends on first measuring prey availability from the birds' perspective (Wolda 1990, Poulin & Lefebvre 1997). For example, the absolute abundance of potential arthropod prey may not accurately reflect its availability to foraging birds. Instead, factors such as prey size, life stage, palatability, nutritive value, coloration, activity patterns, and motility can all influence the probability that prey is detected, captured and ultimately eaten (Poulin & Lefebvre 1997).

Physiognomy and floristics of vegetation influence arthropod distribution and their detectability and accessibility for birds, leading to variation in food availability by habitat (Holmes & Schultz 1988). The high primary productivity associated with early seral stages of forest supports increased numbers of herbivorous insects, which in turn may attract greater densities of insectivorous birds compared to more mature forest (Petit *et al.* 1995). Nonetheless, mature forest appears to retain moisture during the dry season better than younger sites, thereby acting as a refuge for insects (Janzen 1973) and birds (Sherry & Holmes 1995). Contiguous habitat comprised of different successional stages can thus vary substantially in microclimate and in seasonal productivity of arthropods, potentially causing suitable habitat for birds to be intensely limited (Parrish & Sherry 1994). Food availability may also vary within the non-breeding season, leading some migrants to track resources across habitats (Lefebvre & Poulin 1996), join mixed flocks to increase foraging efficiency (Hespenheide 1980) or switch their diets (Morse 1989, Johnson 2000b). For example, Morton (1980) documented movement of migrants from xeric to mesic habitats as the dry season progressed in Panama, accompanied by a switch from insect to fruit foraging in some species.

People have been clearing land for agriculture in Central America for thousands of years (Lynch 1989). The traditional method of slash and burn farming practiced in the Yucatan Peninsula was conducted on a relatively small scale until recently (Whitacre *et al.* 1993) and created a landscape mosaic of cultivated plots, pasture and regenerating forest at various stages of succession. Thus, migrant and resident birds in the region likely evolved adaptations to the successional landscape mosaic (Waide 1980). In recent decades, however, increasing human populations have shifted land clearing to a larger scale, as monoculture plantations, cattle ranches and urban settlements begin to dominate the once forested landscape (Terborgh 1992). Consequently, a heterogeneous landscape comprised of various habitat types and ages has been lost, replaced largely by fragmented, edge-dominated early successional vegetation (Petit *et al.* 1992). If mature forest is associated with higher levels of arthropod prey, loss of this habitat type may have serious consequences for the overwinter survival of migratory insectivores.

In this paper we compare arthropod distribution patterns across a successional forest gradient to determine how food resource availability differs by habitat for migratory insectivores during the non-breeding season. Following Wolda's (1990) definition of prey availability as the "abundance of potential prey items within the microhabitat used by a bird searching for food" we also examine the foraging behavior of two migratory birds, American Redstarts (*Setophaga ruticilla*) and Magnolia Warblers (*Dendroica magnolia*) to test that our arthropod sampling methods accurately represent food availability for migratory insectivores in these habitats. Observing bird foraging behavior can reveal information such as the type of arthropod prey (e.g., foliage vs. aerial prey), microhabitat use (e.g., understory vs. canopy) and relative prey density (e.g., feeding rate should be proportional to food density, Hutto 1990).

Both American Redstarts and Magnolia Warblers appear to forage exclusively on arthropods when in the tropics (Martin & Karr 1990, Poulin *et al.* 1994), incorporating a variety of maneuvers (e.g., gleaning, hawking, hovering) into their foraging behavior (Ehrlich *et al.* 1988). Although the study species occur in a range of habitats in the Yucatan Peninsula, the relative value of these different environments, in terms of food availability, remains unquantified. In particular, we ask the following questions in the current study: (1) Do arthropod levels differ spatially (by successional stage) and/or temporally (from the wet to the dry season) in the Yucatan Peninsula? (2) Are arthropod levels reliable estimates of food availability for migratory insectivores in this region?

METHODS

Study area. This study was conducted from October 1995 through March 1996 within the Calakmul Model Forest (17°49'11"–18°50'32"N, 89°09'08"– 89°52'34"W) near the village of Nuevo Becal, in the state of Campeche, Mexico. The landscape of the region is typically flat and of low elevation, with few permanent bodies of surface water (García 1988, Sales-Gutierrez 1996). The climate is hot and sub-humid with an average annual temperature of 24.4°C and ~1000 mm of precipitation per year (INEGI 2007). A marked dry season extends from December to May, when typically < 50 mm of rain falls monthly (García 1988, INEGI 2007) and approximately 60% of leaf litter accumulates (Lawrence & Foster 2002). In the 1995–96 non-breeding season, higher than average rainfall was recorded in October and December (~150–300 mm) but lower than average rainfall occurred in November (~ 6 mm), January, February and March (~0–13 mm) (INEGI 2007).

The natural mature vegetation found in the Model Forest region is semi-deciduous, medium-height dry forest (Flores & Carvajal 1994) and the dominant tree species in successional forests include *Bursera simaruba*, *Croton arboreus*, *Licaria campechiana*, *Psidium sartorianum*, and *Thevetia gaumerii* (Smith *et al.* 2001).

To document food resources of migratory birds in successional forests we classified habitat as early successional (5–7 years since agricultural abandonment, mean canopy height 7 m), mid successional (17–20 years, mean canopy height 8 m), and late successional (> 50 years, mean canopy height 15 m, Smith *et al.* 2001). We included three stands of each type of forest for a total of nine stands. The pattern of land use in the study area resulted in early and mid successional forest stands which ranged in size from 10 to 20 ha, while late successional forest stands ranged in size from 50 to 100 ha.

Arthropod abundance. Arthropods were collected at the end of the rainy season (October–December 1995, 'wet season') and the middle of the dry season (January–March 1996, 'dry season'). In each stand, collections were made at three to four random points located within a grid (grids ranged in size from 2.5 to 3 ha). Different random points were selected for each sampling event. Stands were sampled twice in the wet season and five to six times in the dry season, and samples were subsequently pooled within each season. Since many migratory insectivores use a suite of foraging maneuvers and locations when searching for and capturing prey, we sampled arthropods with two methods: sweepnetting for relatively mobile and branch clipping for relatively sessile arthropods, at three vegetation heights: low (1.5–2 m), mid (3.5–4 m), and high (5–6 m) between 06:30–11:00 h (CST). Sampling was conducted on dry vegetation only.

The first plant (bush or tree) to the south of a random point was sampled by sweepnet, with 20 180° horizontal sweeps constituting one sweepnet sample at each height interval. Arthropods captured by sweepnet were immediately immersed in 70% ethanol. Branches were clipped from the first three or four plants found to the north of a point at each height interval and collected on a tarpaulin set out on the ground below. Branches were immediately placed, along with any arthropods expelled onto the tarpaulin, into large garbage bags containing acetone to kill invertebrates (Cooper & Whitmore 1990). Arthropods were later removed from vegetation, and leaves (including petioles) were stripped from stems and dried in a drying oven for 12–24 h. Dry weights of leaves were then obtained for each branch clipping sample. All arthropods collected by each method were counted and identified to order (except for larvae which were grouped together into a single category) and sorted into size classes (i.e., 0– 5mm, 5.1–10 mm, 10.1– 5 mm, > 15 mm). The majority of arthropods (70–80%) were less than 5 mm in length, regardless of collection method or habitat.

TABLE 1. Number of observations of foraging American Redstarts and Magnolia Warblers during the study period.

	Wet season			Dry season		
	Successional stage			Successional stage		
Species	Early	Mid	Late	Early	Mid	Late
American Redstart	4	12	3	2	5	3
Magnolia Warbler	4	11	12	7	10	4

Foraging behavior. Observations of the foraging behavior of American Redstarts and Magnolia Warblers were made in each stand throughout the study and were assigned to either the wet or dry season sampling periods. Between 06:00–11:00 h (CST), we systematically surveyed each stand until an individual of either species was encountered. We then followed the bird for as long as possible, recording the following into a microcassette recorder: location within grid, height from ground and top of canopy, and temporal sequence and duration of activities (e.g., reach glean, hop, fly, preen etc.; see Remsen & Robinson 1990). Once a bird was out of sight for more than 5 min, we began searching for other individuals. Each observation lasted at least 1 min, and usually 1 to 3 min. To minimize the risk of duplicating observations of a particular bird during one visit, we always moved in the opposite direction to where a bird was last seen when searching for new individuals.

Foraging data were later transcribed with a stopwatch to measure time of each event. To test the accuracy of our food availability estimates, we calculated the following variables for each observational sequence: 1) Foraging maneuver is defined as the bird's activity from the time a food item is sighted to the moment at which a capture attempt is made (activities included reach, sally-hover, and flush-pursue; see Remsen & Robinson 1990 for definitions); 2) Attack rate is defined as the number of prey attacks divided by the time spent actively searching (We considered any foraging maneuver to represent an attack); 3) Relative foraging height is the average height at which a bird foraged, divided by the average canopy height of vegetation available in a particular habitat.

Few American Redstarts or Magnolia Warblers were banded in the study area, making it difficult to assess whether foraging observations were in fact independent (i.e., of different individuals), or pseudoreplicates within a site visit, or from one visit to the next. In addition, the number of total observations was small (Table 1). For these reasons, statistical analyses were not conducted on foraging data.

Statistical analyses. Statistical comparisons of arthropod abundances were carried out using both univariate and multivariate statistical tests at the $P < 0.05$ significance level.

A three-factor analysis of variance (ANOVA) was conducted using the JMP statistical package, version 3.1 (SAS Institute 1995), with stand age, season and sampling height as the factors. All data were tested for normality and homogeneity of variance and log transformations were applied to non-normal distributions. Sequential Bonferroni tests were run on results to control for type I errors. The Tukey-Kramer post hoc multiple comparison test was used on significant results involving more than two treatments to determine where differences occurred (Sokal & Rohlf 1995). Since no difference in arthro-

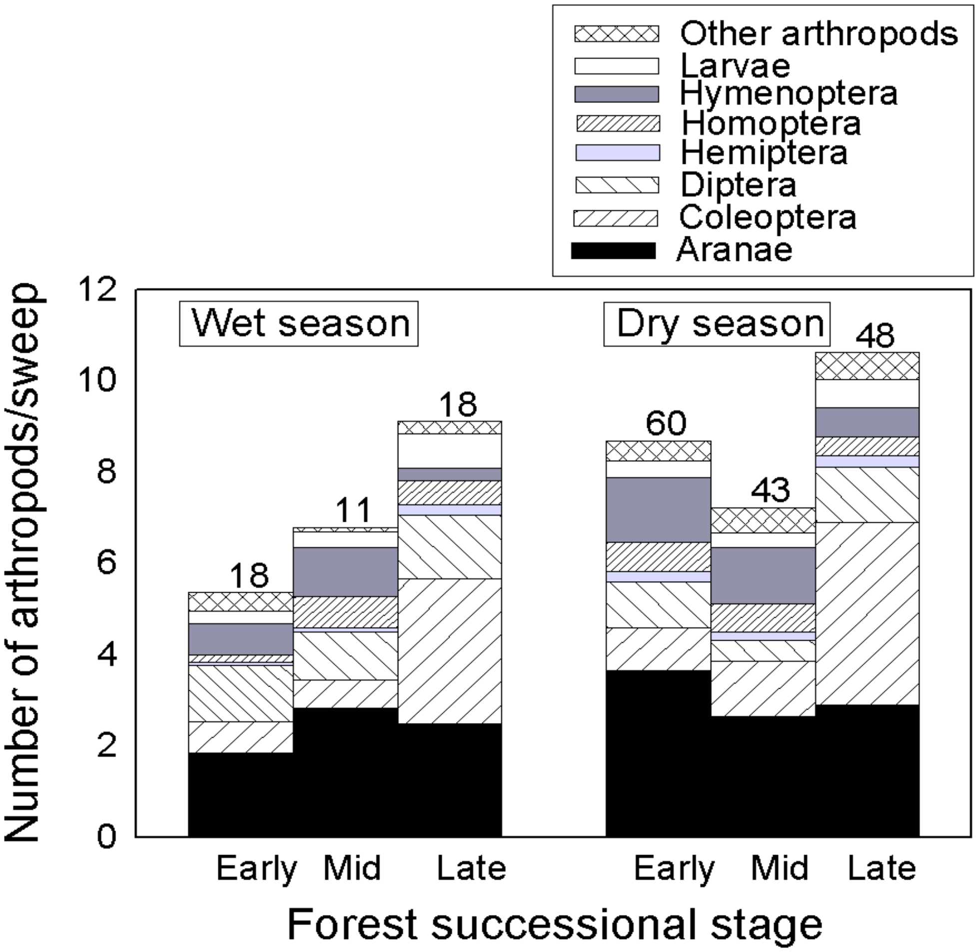

FIG. 1. Composition and abundance of arthropods collected by sweepnets during the wet and dry seasons in three stages of successional forest. Values above bars indicate the number of collections made (including all vegetation heights and random sampling points) in each habitat within each season.

pod abundance was found among sampling heights (see Results) for either sweepnet or branch clipping methods, we pooled data from different vegetation heights for subsequent analyses.

We used the PRIMER statistical software, version 5 (Clarke & Gorley 2001), to test for differences among habitats and between seasons in arthropod abundances using a two-way crossed Analysis of Similarities (ANOSIM), a non-parametric test analogous to a multivariate two-factor ANOVA. A Bray-Curtis similarity index was first calculated on sweepnet and branch clipping data and the resulting similarity matrices were used to perform ANOSIM with 999 permutations. Similarity percentage analyses (SIMPER) were applied to significant results to determine which arthropod orders contributed most to spatial and/or temporal differences.

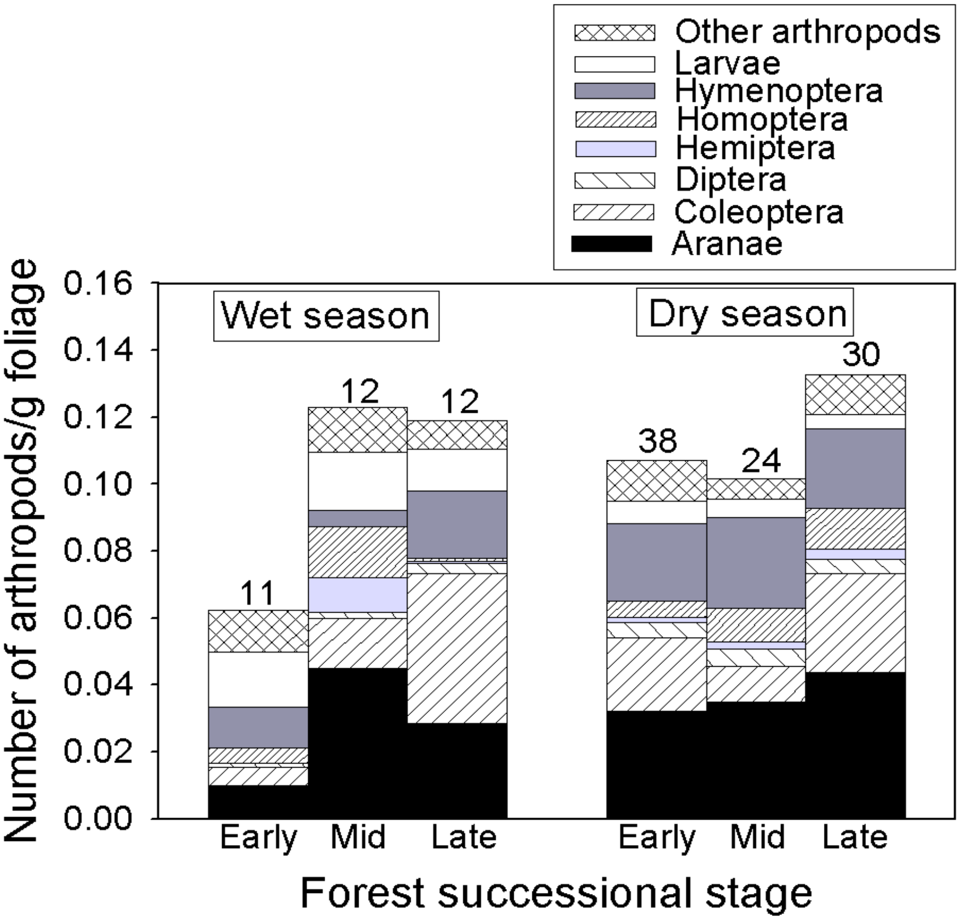

FIG. 2. Composition and abundance of arthropods collected by branch clipping during the wet and dry seasons in three stages of successional forest. Values above bars indicate number of collections made in each habitat within each season.

For all tests, mean values are expressed ± SE, except for average dissimilarity values in SIMPER, which are expressed ± SD.

RESULTS

Arthropod abundance

Sweepnet samples. Higher numbers of arthropods were recorded in late successional forest compared to both early and mid successional forests over the entire study period (ANOVA $F_{2,27} = 7.85$, $P = 0.001$; ANOSIM $R = 0.13$, $P = 0.001$). More arthropods were collected in the dry season than in the wet season (ANOVA $F_{1,27} = 20.86$, $P < 0.0001$; ANOSIM $R = 0.28$, $P = 0.001$) overall, but no interaction was found between sampling period and habitat (ANOVA $F_{2,27} = 0.92$, $P > 0.1$) (Fig. 1). Overall abundance of sweepnet arthropods did not vary by height of vegetation (ANOVA $F_{2,27} = 0.08$, $P > 0.9$) and no interactions among height, stand age and sam-

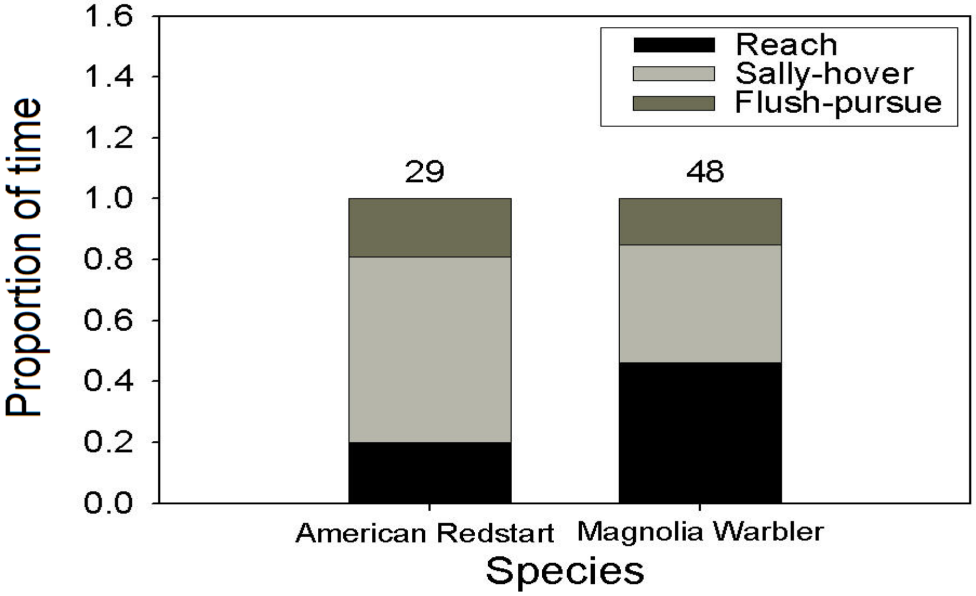

FIG. 3. Proportion of total prey attacks comprised of each foraging maneuver for American Redstarts and Magnolia Warblers. Values above bars indicate number of observations made of foraging birds over the entire study period.

pling period were significant (ANOVA stand x height: $F_{4, 27} = 0.84$, $P > 0.5$; ANOVA season x height: $F_{2, 27} = 0.70$, $P = 0.5$; ANOVA stand x season x height: $F_{4, 27} = 0.20$, $P > 0.9$ $F_{2, 27} = 0.08$, $P > 0.9$).

Spiders (order Araneae) represented the largest group in sweepnet samples overall (2.89 ± 0.15 individuals/sweep sample), and increased in density in all habitats during the dry season (ANOVA $F_{1, 27} = 6.22$, $P = 0.02$; SIMPER average dissimilarity = 16.58 ± 1.27). Spiders dominated collections in early and mid successional forest, but were replaced by Coleoptera as the most numerous order in late successional forest (ANOVA $F_{2, 27} = 48.59$, $P < 0.0001$; SIMPER average dissimilarity = 18.80 ± 1.20). Hymenoptera increased in all habitats from the wet to dry season (ANOVA $F_{1, 27} = 140.98$, $P < 0.0001$; SIMPER average dissimilarity = 8.82 ± 0.87), while Coleoptera declined overall (SIMPER average dissimilarity = 15.51 ± 0.99) (Fig. 1).

Branch clipping samples. Overall arthropod abundance was higher in late successional forest than in mid successional forest (ANOSIM $R = 0.08$, $P = 0.002$), driven largely by the higher numbers of Coleoptera and Hymenoptera present (Coleoptera SIMPER average dissimilarity = 14.11 ± 0.98; Hymenoptera SIMPER average dissimilarity = 11.77 ± 0.77). No significant difference in arthropod numbers was found between the same habitats in different seasons (ANOVA $F_{2, 27} = 1.88$, $P > 0.1$) (Fig. 2). Arthropod densities were similar at the three vegetation heights collected for branch clipping samples (ANOVA $F_{2, 27} = 2.77$, $P = 0.08$). No significant interactions occurred among the three factors tested (ANOVA stand x height: $F_{4, 27} = 0.89$, $P > 0.4$; ANOVA season x height:

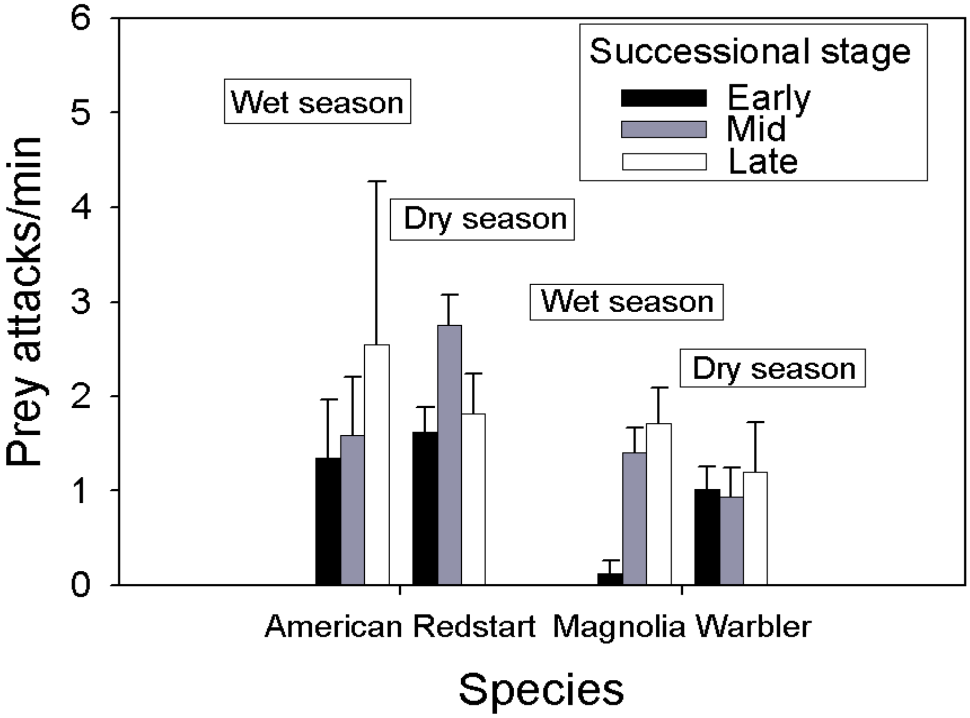

FIG. 4. Foraging attack rates of American Redstarts and Magnolia Warblers in the wet and dry seasons in three stages of successional forest ± SE. See Table 1 for number of foraging observations.

$F_{2,27} = 0.02$, $P > 0.9$; ANOVA stand x season x height: $F_{4,27} = 0.62$, $P > 0.6$).

As in sweepnet samples, spiders represented the most abundant group of arthropods collected overall (0.03 ± 0.003/g foliage), although Coleoptera, Hymenoptera and larvae of various taxa figured prominently in all habitats and during both sampling periods (Fig. 2). Coleoptera had highest densities overall in late successional forest (ANOVA $F_{2,27} = 8.21$, $P = 0.002$) and lowest densities at the highest sampling height, regardless of habitat or season (ANOVA $F_{2,27} = 10.01$, $P = 0.0006$). Coleoptera, Aranae and Hymenoptera increased across all habitats during the dry season (Coleoptera SIMPER average dissimilarity = 15.51 ± 0.99; Aranae SIMPER average dissimilarity = 16.58 ± 1.27; Hymenoptera SIMPER average dissimilarity = 8.82 ± 0.87) (Fig. 2).

Foraging behavior of focal species

Both warbler species mainly foraged for prey on vegetation. The foraging behavior of American Redstarts was dominated by hovering in the air to catch prey on vegetation (sally-hover; 61% of all observed maneuvers) while attacking a prey item on bark or leaves by reaching for it from either a stationary or hopping position (reach; 20%) and pursuing aerial prey flushed from a substrate (flush-pursue; 19%) were less prominent (Fig. 3). The most common foraging maneuver exhibited by Magnolia Warblers, in comparison, was the "reach" (46% of all observed maneuvers) with sally-hovers and flush-pursues comprising

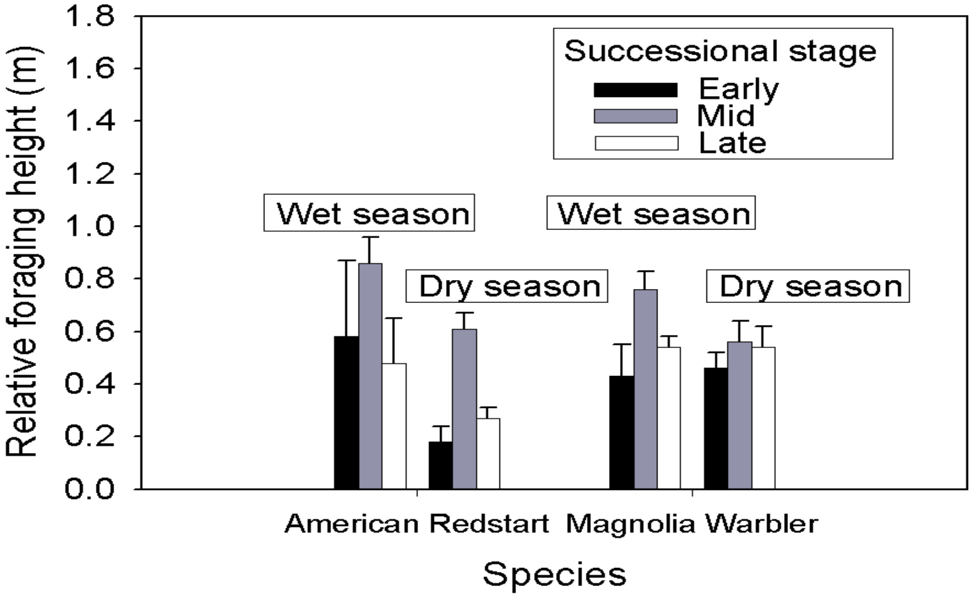

FIG. 5. Relative foraging height (average foraging height divided by the average canopy height of vegetation) of American Redstarts and Magnolia Warblers in the wet and dry seasons in three stages of successional forest ± SE. See Table 1 for number of foraging observations.

39% and 15% of all maneuvers respectively (Fig. 3).

In the wet season both species displayed the highest attack rates in late successional forest and the lowest in early successional forest. In the dry season attack rates were similar across habitats for Magnolia Warblers, but higher in mid compared with either early or late successional forest for American Redstarts (Fig. 4).

Both warbler species foraged in the understory (below 4 m) in early successional forest, coinciding with our low to mid arthropod sampling heights. In the older seral stages, however, both species also foraged in the canopy (e.g., 6–9 m above ground), which exceeded our highest sampling height (6 m) (Fig. 5). American Redstarts and Magnolia Warblers foraged proportionally higher in mid-successional forest than in early or late successional stages (Fig. 5).

DISCUSSION

Distribution of arthropods. The distinct dry season that characterizes much of the Neotropics is commonly believed to cause declines in food resources (such as arthropods and fruits) available to birds (Waide 1981, Johnson 2000a, Strong & Sherry 2000, Sherry *et al.* 2005). In contrast to other studies (e.g.,Waide *et al.* 1980, Lefebvre *et al.* 1994, Strong & Sherry 2000) however, we found that mobile foliage arthropods (collected with sweepnets) increased in density in all habitats from the wet to dry season. In particular, arthropods in the orders Aranae and Hymenoptera were more numerous in sweepnet samples collected in the dry season (although Coleoptera declined during the same period). In contrast, branch clipping collections showed no change in overall arthropod densities by season, although Aranae, Coleoptera and Hymenoptera were more abundant in all habitats during the wet season.

If the dry season is sufficiently mild, and loss of soil moisture is minimal, the increased sun and warm temperatures associated with this season can increase plant productivity, leading to greater arthropod numbers (Janzen 1973, Buskirk & Buskirk 1976). Alternatively, some environments may be better protected than others from the severe effects of the dry season. Aerial and foliage arthropods have been found to increase over the dry season in humid forest in Panama (Karr & Brawn 1990, Poulin & Lefebvre 1996) and mangroves in Venezuela (Lefebvre *et al.* 1994), suggesting that the increased moisture content of these habitats buffers them from seasonal fluctuations in rainfall and arthropod resources (Lefebvre & Poulin 1996). Many types of dry forest vegetation also have their flowering peaks during the dry season (Stiles & Wolf 1970) which may account for increases in insects such as Hymenoptera over the study period.

Since this study took place over one year only, it is difficult to determine if the observed patterns of arthropod abundance are due to an unusually mild dry season, an unusually stormy wet season, or to inherent characteristics of these successional habitats, which protect them from dry season effects. Although the dry season in the Yucatan Peninsula is pronounced, it may be considerably less severe in the southern portion of the region (Lynch 1992). Furthermore, hurricanes and cold fronts, known as "northerns", can bring heavy rains to southeastern Campeche as late as December, increasing precipitation during the late wet and early dry seasons (Rumney 1968). In fact, two hurricanes, Opal and Roxanne, hit the peninsula in early October 1995, and precipitation was higher than normal in both October and December (INEGI 2007). However, less precipitation than average fell from January to March 1996 (INEGI 2007). Thus, heavy rainfall late in the wet season may have buffered arthropod communities from a subsequent drought period in the study area. Alternatively, the hurricanes may have led to short-term declines in arthropod abundances during the late wet season, followed by an increase in numbers once the stormy season subsided. The Yucatan Peninsula experiences significant annual variation in hurricane activity, yet over the century-scale hurricane frequency is high (Boose *et al.* 2003). Consequently the 1995–96 weather likely was not an anomaly and the observed increase in arthropod abundances may be a common seasonal occurrence.

Our results indicate that arthropod abundances are higher in late successional forest than in earlier stages during the non-breeding season. The larger trees and greater canopy cover associated with late successional forest in the study area (Smith *et al.* 2001) may confer increased resilience to desiccation, perhaps accounting for higher levels of mobile arthropods overall and Coleoptera and Hymenoptera specifically here than in earlier stages throughout the non-breeding season. Additionally, the greater tree species richness of late successional forest sites (Smith *et al.* 2001) could lead to a greater diversity and abundance of arthropods in this successional stage (Holmes & Schultz 1988). Whether this spatial pattern affects food availability for migratory insectivorous forest birds in the region is unclear. In a concurrent study of the distribution of the entire bird community within these successional forest sites we found highly similar bird assemblages and no change in bird abundance by habitat type, including for American Redstarts and Magnolia Warblers (Smith *et al.* 2001). Nevertheless, similar densities of migratory birds across different habitat types may not necessarily indicate equal habitat suitability. Migratory birds may respond to spatial variation in food abundance instead through intraspecific dominance interactions, which restrict less dominant (e.g., juvenile or female) individuals to lower quality habitat, such as earlier successional stages of forest (Sherry & Holmes 1996, Marra & Holmes 2001).

Foraging behavior of focal species. Documenting prey availability from a bird's perspective remains a challenge for ornithologists (Wolda 1990, Poulin & Lefebvre 1997). In the case of insectivores, measuring arthropod abundance and distribution alone is not sufficient to determine whether birds will actually detect, accept, pursue, capture and eat potential prey items (Wolda 1990). Instead, arthropod sampling should be supplemented by information on the type and distribution of foraging maneuvers used by birds within microhabitats, and the kind of prey taken (Wolda 1990).

In this study, American Redstarts and Magnolia Warblers were used as representatives of the migratory insectivore guild typically found in forests of the northern Neotropics. Observations of their foraging behavior revealed that most foraging attacks were directed toward prey on vegetation, which tend to be well sampled by branch clipping (Johnson 2000b). In fact, branch clipping has been demonstrated to be an appropriate prey sampling method for overwintering migratory warblers in Jamaica (Johnson 2000b). While this method may be biased against more active arthropods (e.g., Odonata, Diptera), our sweepnet samples presumably should have balanced out any under-representation of these taxa, and thus accounted for prey potentially taken with aerial attacks by migratory insectivores. Interestingly, the two sampling methods yielded different results in our study. While branch clipping collections showed no difference in density by season, sweepnet collections had higher densities in the dry season, primarily driven by greater numbers of Aranae and Hymenoptera during this period.

If migratory insectivores are tracking food resources, their attack rates should be expected to reflect relative prey densities by habitat (Johnson 2000b). In the current study we found that attack rates in different habitats varied by time of year and by species. During the wet season, both American Redstarts and Magnolia Warblers had highest attack rates in late successional forest, coinciding with highest overall arthropod densities and highest levels of Coleoptera occurring in this habitat. However, in the dry season no clear correlation between attack rate and habitat was apparent. The greater numbers of arthropods in all habitats during this season may have lead to similar attack rates for Magnolia Warblers across the successional gradient. In contrast, the highest attack rates of American Redstarts in mid successional forest was not reflected in our arthropod collections, suggesting that our sampling methods may not be entirely representative of the prey availability perceived by the study species. One potential reason for the decoupling between foraging behavior and measured arthropod densities is the fact that foraging height often exceeded our sampling height in mid and late successional forest. Both warbler species foraged proportionally higher in mid successional forest, perhaps because this seral stage has more vertical structure than either early or late successional habitat (Smith *et al.* 2001).

Without detailed knowledge of the distribution, territoriality and site tenacity of American Redstarts and Magnolia Warblers in the Yucatan Peninsula it is difficult to assess whether these birds track arthropod resources across habitats during the non-breeding season, although evidence from Jamaica strongly suggests that they (and other migratory insectivores) do (Johnson & Sherry 2001). Lack of direct dietary information on these species also confounds the determination of food availability and its effects on their distribution and behavior (Poulin & Lefebvre 1997). Furthermore, our focus on numerical abundance of arthropods, rather than on their energetic value to migratory birds (e.g., a single caterpillar may be of greater nutritive value than many small spiders) may conceal spatial or temporal differences in resource availability. Nevertheless, while Poulin *et al.* (1992) suggest it is essentially impossible to assess food availability for birds, at least at the community level, they add that measures of arthropod abundance can provide an indication of the relative spatio-temporal resources to which birds are exposed. In this study we found that arthropod resources were most numerous in the oldest forest stage and that, contrary to other neotropical studies, overall arthropod abundance remained the same (for sessile) or increased (for mobile) arthropods from the wet to dry season. These findings suggest that migratory insectivores in the southern Yucatan Peninsula may not experience drastic food declines during the overwintering period. However, loss of mature successional forest due to increased land clearing in the region may negatively affect food availability in the future for these birds.

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