Comparison of autumn and spring migration strategies of Neotropical migratory landbirds in northeast Belize

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ABSTRACT. Migration represents one of the most vulnerable stages of a migrant's life cycle, but the strategies and stopover sites used by Neotropical migrants in Central America are not well known. We carried out constant-effort mist netting and conducted censuses along transects during one autumn (2007) and one spring (2008) migration in northeast Belize. We recorded more landbird migrant species in autumn (63) than in spring (54), and spring abundance was >25% lower for 88% of transient species. These differences in presence and abundance indicate that routes and stopover strategies vary between seasons and species. In autumn, fuel loads, calculated as any increase in mass above lean body mass (LBM), were generally small (mean = 5.9% LBM and 10.1% LBM for wintering and transient species, respectively) and fuel deposition rates and minimum stopover durations suggest that some individuals replenished energy reserves in our study area. Variation in autumn fuel loads meant that some individuals had reserves sufficient for flights >1000 km. Fuel loads were larger in spring for 16 of 17 species, and the mean spring fuel load for transient species (32.5% LBM) was sufficient for a flight from northeast Belize to North America without refueling. The similarity in spring passage times between northeast Belize and the Gulf Coast of the United States also suggests that energy reserves were not replenished in northeast Belize prior to crossing the Gulf of Mexico. We hypothesize that sufficient energy reserves are accumulated during spring stopovers in northern South America or elsewhere in Mesoamerica to allow migrants to fly directly to North America without refueling.

RESUMEN. **Una comparación de las estrategias migratorias de las aves migratorias Neotropicales en primavera y otoño en el nororiente de Belice**

La migración representa una de las etapas más vulnerables del ciclo anual de las aves migratorias Neotropicales, pero las estrategias y sitios de parada que utilizan en Centroamérica no son bien conocidos. En este estudio utilizamos capturas de esfuerzo constante y observaciones en transectos, durante una migración de otoño (2007) y una de primavera (2008), en el nororiente de Belice. Registramos más riqueza de especies migratorias en otoño (63) que en primavera (54) y la abundancia en la primavera fue >25% menor en 88% de las especies transitorias. Estas diferencias en presencia y abundancia indican que tanto las rutas como las estrategias de parada son diferentes entre periodos y especies. En otoño la carga energética, calculada como un aumento sobre la masa corporal sin grasa (LBM), fue pequeña (promedio = 5.9% LBM y 10.1% LBM en especies invernantes y especies transitorias respectivamente) y las tasas de deposición de combustible y duración mínima de las paradas sugieren que algunos individuos utilizaron nuestra área de estudio para aumentar sus reservas energéticas. La variación en las cargas energéticas durante el otoño mostró que algunos individuos tenían reservas suficientes para realizar vuelos de >1000 km. Sin embargo, en 16 de 17 especies estudiadas aquí, las cargas energéticas fueron mayores durante la primavera y el promedio de carga energética en las especies transitorias en primavera (32.5% LBM) fue suficiente para completar un vuelo directo desde el nororiente de Belice hasta Norteamérica sin necesidad de hacer paradas de reabastecimiento. La similitud entre los tiempos de paso en primavera por el nororiente de Belice y por la costa del Golfo en Norteamérica, también sugiere que las reservas energéticas no fueron obtenidas en el nororiente de Belice antes de cruzar el Golfo de México. Nuestra hipótesis es que las aves acumulan suficientes reservas energéticas para volar directamente hasta Norteamérica, durante paradas en el norte de Sudamérica o en otras áreas de Centro América.

Key words: Central America, flight ranges, fuel loads, stopover behavior

Migration occupies up to one third of the annual cycle of migratory birds (Mehlman et al. 2005) and is considered one of the most vulnerable stages of a migrant's life cycle (Newton 2006, Holmes 2007). Despite considerable concern for populations of many Neotropical migrants (Terborgh 1989, Rappole 1995), the migratory stage of their life cycles has received relatively little attention. In particular, the location of stopover sites used by migrants in their annual journeys between North America and nonbreeding areas in Central and South America and the Caribbean are poorly known (Johnson and Winker 2008).

Many migratory species that breed in eastern North America encounter ecological barriers

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during migration that provide few or no opportunities to feed and must be crossed using energy reserves. Many species cross the Gulf of Mexico (over 1400 km) during autumn and spring migration (Moore et al. 1990), and make flights of varying lengths across the Caribbean Sea to reach South America. The sites and habitats used to recover after the Gulf crossing and to replenish energy reserves for the next phase of migration in autumn are not well defined, nor are the sites used during spring migration on the return journey (Johnson and Winker 2008). Although the Yucatan Peninsula is recognized as a major flyway for Neotropical migrants (e.g., Curson et al. 1994), few investigators have examined how migrants use this region (Johnson and Winker 2008). In southern Belize, Johnson and Winker (2008) recorded many species of Neotropical migrants in autumn and found evidence of refueling. Nevertheless, many species arrived in southern Belize with medium to large fuel reserves that were presumably either left over after crossing the Gulf of Mexico or were accumulated farther north on the Yucatan Peninsula. Spring migration in the Yucatan and Latin American region remains largely unstudied (but see Wilson et al. 2008) despite the potential effect of changes in stopover habitat quality on migratory success, arrival times at the breeding grounds, and subsequent reproductive success (Norris et al. 2004, Moore et al. 2005, Newton 2006).

To increase our understanding of the migratory strategies of Neotropical migratory landbirds in Central America and to facilitate the process of identifying and prioritizing stopover sites for protection in this region (Heglund and Skagen 2005), we studied Neotropical migrants during migration in northeast Belize. Located near the Caribbean coast and supporting extensive natural habitats, we expected our study area to provide suitable stopover conditions for a variety of species during autumn and spring migration. Because spring migration in northeast Belize occurs at the height of the dry season, we hypothesized that this region, representing the interface between the drier forests of the Yucatan ecoregion and the moister forests of the Selva Maya ecoregion, may be an important stopover site for migrants preparing to cross the Gulf of Mexico. We also hypothesized that the region would support migrants replenishing their energy reserves after trans-

Gulf flights in autumn. Our objectives were to determine: (1) the species composition and abundance of Neotropical migrants in northeast Belize and how they differed between autumn and spring, (2) the extent of migrant energy reserves and how this varies among species and between migrations, (3) if there is evidence for replenishment of energy reserves in northeast Belize, and (4) the possible strategies of migrants after leaving our study area.

METHODS

Our study was conducted in northeast Belize in the southeastern portion of the Yucatan peninsula (Fig. 1). All work was carried out in the Corozal district in an area containing a matrix of largely unmodified natural habitats (see Fig. 1). We had three study sites (Fig. 1; habitat descriptions follow Meerman and Sabido 2001): (1) La Isla, where most of our study was conducted, was located on the northeast shore of Shipstern Lagoon, ~2.5 km south of Sarteneja village (18°20′06″N, 88°07′29″W) and centered on a property known as La Isla. Habitats included red mangrove forest (*Rhizophora mangle*) associated with Shipstern Lagoon, black mangrove (*Avicennia germinans*), tropical semi-deciduous broadleaf forest (hereafter semi-deciduous forest), Milpa agriculture, and salt marsh. (2) Shipstern Nature Reserve is a private nature reserve located west of the village of Sarteneja (18°18′04″N, 88°12′44″W) that supported both tropical evergreen broadleaf forest (hereafter evergreen forest) and semi-deciduous forest. (3) Balam included Balam Na private nature reserve and the Balam Jungle Estate and was located within the largest contiguous forest block in northeast Belize (18°06′15″N, 88°16′09″W), consisting primarily of evergreen forest.

All study sites were impacted to some degree by Hurricane Dean that passed north of our study area on 21 August 2007. Personal observations suggest an approximate gradient of damage from north to south and, although the hurricane did not flatten the forest, it caused localized severe canopy damage. The altered forest structure might have affected migrant use of the study sites.

Transects and casual observations. We established 18 500-m transects along existing forest trails, following the straightest line
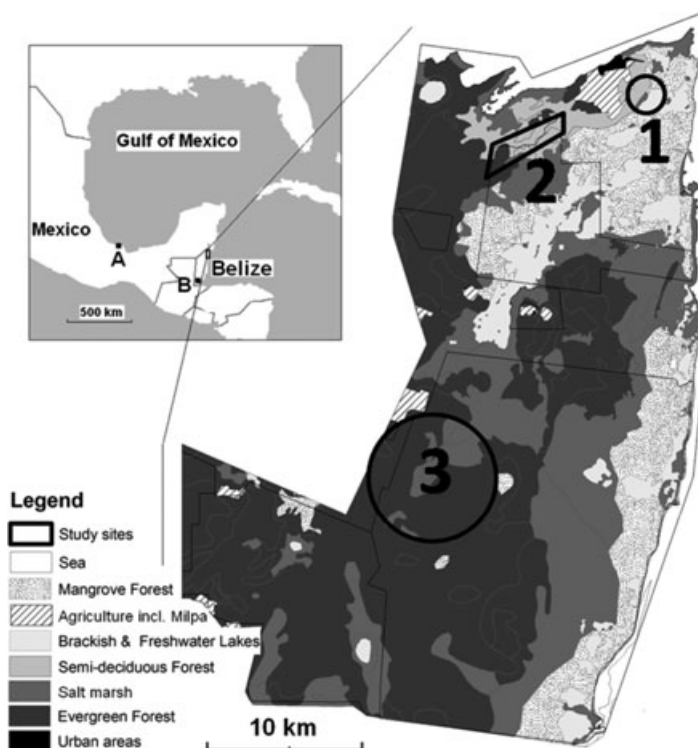
Fig. 1. Location of the study region in Central America (inset) and of study sites in northeast Belize (numbered 1–3 such that: 1. La Isla; 2. Shipstern Nature Reserve; 3. Balam). Habitat types delineated in the map follow Meerman and Sabido (2001). The location of other studies mentioned in the text are indicated by letters in the insert: A = Veracruz, Mexico (Winker 1995), and B = southern Belize (Johnson and Winker 2008).

possible, at La Isla (3 transects), Shipstern Nature Reserve (4), and Balam (11). Transects at La Isla were located in semi-deciduous forest intermixed with Milpa (2) and in salt marsh (1). All transects at Shipstern and Balam were in evergreen forest. Transects were censused between 1 August and 10 November 2007 (autumn) and between 15 March and 15 May 2008 (spring). At La Isla, at least one transect was censused on 62% of days in autumn and 80% of days in spring. Transects were sampled on 30 August, 7 October, and 1 November 2007 at Balam, and on 13 April, 26 April, and 5 May 2008 at Shipstern Nature Reserve. On each occasion, we conducted censuses along four to 11 transects.

All transects were censused in the first 3 h after sunrise by the first author (mean start times: autumn 07:45 CST, spring 06:15 CST). Transects were walked at a steady pace such that mean census duration at La Isla was 21.4 ± 5.9 (SD) min ($N = 62$) in autumn and 19.9 ± 5.1 min ($N = 60$) in spring. All birds either seen or heard along transects were recorded and assigned to one of five distance bands based on observer estimates of their perpendicular distance from the transect line (1 = 0–5 m, 2 = 5–10 m, 3 = 10–25 m, 4 = 25–50 m, and 5 = 50–100 m). Observations of migratory species made while moving between transects, when mist-netting, and within the study area were also recorded as casual observations.

Mist-netting and data collection.   All mist-netting took place at La Isla, with mist nets operated daily for 3.5 hr after first light from 2 September to 10 November 2007 and from 17 March to 14 May 2008 when weather conditions allowed. During the spring, mist nets were also operated for 3 hrs prior to sunset on 15 days. Mist nets were checked at regular intervals ($\leq$40 min) and all birds captured were taken to a banding station for processing. Provided there was sufficient time to process each bird fully

and safely, all captured birds were fitted with a uniquely numbered metal band and we noted their age and sex (Pyle 1997), fat score (visible fat deposits scored on a nine-point scale following Kaiser 1993), wing chord (± 1 mm), and body mass (±0.1 g, using an electronic balance).

Mist nets were operated in three habitats (red mangrove forest, semi-deciduous forest, and, during spring migration only, black mangrove) to maximize the community of migrants sampled. Nets were placed nonrandomly at sites expected to maximize capture rates such as where distinct borders were formed by Shipstern lagoon or with salt marsh habitat. Within forests, nets were orientated east to west and several locations were selected because of their low canopies. Mist nets were 12 m or 18 m long, 2.5 m high, with a mesh size of 32 mm or 36 mm. During autumn, mean daily mist-net effort ($N = 60$ days) was 54.3 ± 18.1 (SD) mist-net hours (1 mist-net hour = one 12-m net open for 1 hr or one 18-m net for 40 min), with a total of 1816 hrs in semi-deciduous forest and 1444 hrs in red mangrove forest. During spring, mean daily mist-net effort ($N = 59$ days) was 79.3 ± 24.1 mist-nets hours, with a total of 2724 h in semi-deciduous forest, 1356 h in red mangrove forest, and 600 h in black mangrove. We used a sound lure consisting of songs played from speakers placed next to one net for three species, including Red-eyed Vireos (*Vireo olivaceus*; 26 days in autumn and 14 days in spring), Yellow Warblers (*Dendroica petechia*; 20 days in spring), and Prothonotary Warblers (*Protonotaria citrea*; 17 days in autumn). These species were selected subjectively to increase the number of captures of common transient species (N. J. Bayly and C. Gómez, pers. observ.) that are responsive to playback.

Species composition, abundance, and phenology. The presence or absence of migratory landbird species during migration in northeast Belize was assessed using transect records, mist-net captures, and casual observations. We classified species as either wintering (present in Belize throughout the nonbreeding season) or as transients (species that winter south of Belize, e.g., South America) based on information provided by Jones (2003) and Gómez and Bayly (2010).

To assess species abundance, we estimated mean daily density (unadjusted) during migration from transect observations and we present mist-net capture totals corrected for effort. To estimate mean daily unadjusted densities, we selected observations from periods of equal length during each migration period (autumn: 16 September – 31 October, spring: 31 March – 15 May) to facilitate comparisons. To ensure that comparability was not affected by variation in transect coverage, we selected observations from one transect at La Isla that was censused on 30 days during autumn and 38 days during spring. This transect passed through semi-deciduous forest (78% of transect length) intermixed with regenerating Milpa (18% of transect length). Densities were then calculated by species and by period using the formula:

daily unadjusted density (individuals per km^2) $= \Sigma$ individuals in day i/Σ transect area for day i,

where the sum of individuals only included individuals recorded within 25 m of transects and where transect area is expressed in km^2. Unadjusted densities will underestimate true densities because detectability is not 100% within 25 m of transects and the density of shy or nonvocal, but commonly occurring, species will be underestimated more than easily detected species. Interspecies comparisons must therefore be made cautiously.

To facilitate inter-seasonal comparisons of mist-net captures, we calculated total captures by species and corrected for mist-net effort by season. Because black mangrove was only sampled in the spring, captures in this habitat were excluded from the analysis. We corrected capture totals for mist-net effort such that corrected totals represent the number of birds captured per 4000 mist-net hours. We selected 4000 so that corrected capture totals closely reflected actual totals (mist net effort: autumn = 3260 mist-net hours, spring = 4080 mist-net hours). Interpretation of corrected capture totals must take into account the use of sound lures for three species.

The probability of detection on transects or of capture in mist nets can vary among species. The unadjusted densities and capture totals presented here must therefore be considered on a species by species basis, taking into account a variety of ecological traits and also considering that mist nets sampled mangrove habitats in addition to semi-deciduous forest.

To examine the timing of migration, we created autumn and spring phenologies using

two datasets: (1) daily totals of transient species recorded on one transect at La Isla (note that transect effort was equal across days). We considered only transient species to remove the confounding effect of individuals that wintered in the survey area. (2) Daily totals of new captures of all migratory species, corrected for mist-net effort. By including all species, but excluding recaptured individuals, the passage of individuals from species with wintering populations is better represented, but the influence of wintering individuals on daily totals is not completely removed.

Variation in energy reserves. To examine variation in energy reserves, we selected 17 species with 30 or more individuals captured during our study. We used two measures of energy reserves, body mass and fuel load, to make comparisons within and between species. Body mass has been shown to be closely related to increases in deposits of fat, the main fuel for migration (Piersma 1990, Redfern et al. 2004). Body mass of songbirds typically exhibits a regular diurnal increase (Thomas 2000, Lilliendahl 2002) and this should be accounted for when comparing condition between species, sites, and seasons. We looked for evidence of diurnal increases in body mass using General Linear Models (GLMs) containing the terms hour of capture and wing length, analyzing autumn and spring separately for each species. Because body mass may also vary with age, we ran GLMs including the terms age and wing length for each species, again analyzing autumn and spring separately.

Fuel load was calculated as any increase in body mass above lean body mass (LBM) and is expressed as a percentage of LBM (Ellergen and Fransson 1992). LBM is expected to represent the mass of a bird with no energy reserves and was estimated from the regression equation, $LBM = a + b*$wing length, where estimates for a and b were produced for each species by regressing the body mass of all individuals with a fat score of zero against wing length. Because fuel load is presented as a percentage of the LBM of each species, interspecies comparisons of the magnitude of fuel loads can be made. Estimates of LBM typically overestimate the body mass of a bird with no fuel reserves because they do not take into account gut content and nonvisible fat deposits. We therefore present fat free mass (FFM) based on lipid extraction from specimens

(Dunning 1993), where they exist, to highlight overestimates.

Within species ($N = 17$), we compared body mass of individuals captured during autumn and spring using two-sample *t*-tests. Between species, we compared fuel loads of wintering and transient species during both autumn and spring migration using Mann-Whitney tests (because fuel load was not normally distributed). Because transient species may or may not stopover in the study region, differences in fuel load between wintering and transient species can highlight different migration strategies.

To place the body masses of migrants recorded in northeast Belize in a regional context, we compared mean body mass of birds captured during our study with those recorded previously at approximately the same latitude in Veracruz, Mexico (Winker 1995), and with those recorded in southern Belize (Johnson and Winker 2008; see Fig. 1 for locations). To test for possible differences relative to our study area in northeast Belize, we ran one-sample *Z*-tests using the means and standard deviations presented by Winker (1995) and Johnson and Winker (2008).

Evidence for increases in energy reserves. To determine if energy reserves were increasing and to what extent, we calculated fuel deposition rates and minimum stopover durations based on individuals captured on more than one occasion. We quantified fuel deposition rate (FDR) as the percentage of a bird's LBM (see above) accumulated per day for individuals recaptured at least one day after initial capture. We only present FDRs for transient species because recaptures of nontransient species may include individuals that remained in the study area during the nonbreeding season and were therefore not on stopover. Minimum stopover duration was calculated as the number of days between the first and last capture of an individual, including the first and last days, for all recaptured individuals of transient species. More accurate methods of estimating stopover duration are available, but require higher capture and recapture rates than those in our study (Morris et al. 2005).

Flight ranges. To determine the distance individual birds could travel after leaving our study site without stopping to accumulate more energy reserves, we calculated flight ranges using version 1.15 of the Program Flight (Pennycuick

and Battley 2003) for three species (see further). To calculate ranges, we determined wingspans and wing areas using measurements taken in the field (following Pennycuick 1999) and assumed a flight altitude of 1000 m (varying flight altitude has little effect on estimates). The default setting of 0.17 was used for the flight-muscle fraction. Fat mass was calculated by subtracting the LBM of a bird of mean wing length from the "empty mass" (body mass of bird with empty crop) and taking 85% of that figure. Thus, 85% of any increase above LBM is expected to be fat, with protein combined with water making up the rest (Piersma 1990). Actual fat content may be higher because Baggott (1986) found that fat accounted for 100% of the mass increase above mean LBM for Grasshopper Warblers (*Locustella naevia*). Default settings were used for all other inputs. Values for wingspan and wing area were 0.234 m and 0.0108 m^2, respectively, for Red-eyed Vireos ($N = 5$), 0.202 m and 0.0084 m^2, respectively, for Prothonotary Warblers ($N = 4$), and 0.180 m and 0.0070 m^2, respectively, for Magnolia Warblers (*Dendroica magnolia*; $N = 5$).

To illustrate flight ranges, we determined the "empty mass" required to fly 1000 km, 2000 km, and 3000 km, respectively, for each of the three species considered. All flight-range estimates assume that birds are able to maintain their body mass during daytime stops and that energy reserves are only consumed during nocturnal flights. Flight ranges were calculated for still air so would increase if there were tailwinds.

Statistical analysis. Regression analyses, *t*-tests, *Z*-tests, and Mann-Whitney tests were conducted using Minitab release 13.3. Summary data for body mass, fat scores, and fuel loads are presented as means ±1 SD.

RESULTS

Species composition and abundance and migration phenology. We recorded 110 species of Neotropical migratory birds in northeast Belize (see Table S1), with 84 species recorded during autumn migration and 67 species during spring migration. Migratory landbirds were represented by 63 species in autumn and 54 species in spring, with 24 and 19 species, respectively, classified as transient species. Some species were notably absent during spring migration, e.g., *Empidonax* flycatchers

(Table 1). All migratory landbirds recorded at least twice at La Isla are listed in Table 1. We found no difference in species composition between La Isla and the evergreen forests at Shipstern and Balam.

Changes in seasonal abundance are expected to be reflected to the same degree for both transect observations and captures, and we found agreement in the direction of change for 74% of the species in Table 1. The general direction of this change was toward either reduced abundance or complete absence in the spring (9 species). Of 18 transient species captured in autumn, 16 showed a decrease >25% in captures between autumn and spring. Unadjusted densities and mist-net captures indicated greater abundance during spring for only two species (Magnolia Warblers and Yellow Warblers; Table 1).

Neotropical migrants began passing through northeast Belize in August, but the first significant arrivals occurred in mid-September. From mid-September to early November, passage was relatively constant, aside from a notable peak on 11 October. The spring passage period was more clearly defined and shorter, with 75% of new captures concentrated in a two-week period centered on 29 April (Fig. 2).

Variation in energy reserves. Of 17 migrant species examined, body mass was significantly related to hour of capture for just one (Hooded Warbler) and only in autumn (Table 2), and we found no significant relationships between age and body mass (Table 2). For the following analyses of body mass, age classes were therefore combined and we made no correction for hour of capture.

Mean body mass was greater in spring than autumn for all but one species (Yellow Warbler), and the difference was significant for nine of 15 species (Table 3). For most species, body mass varied less in autumn. Mean fuel loads in autumn were generally small (Table 3), representing 5.9% LBM for wintering species and 10.1% LBM for transient species (Mann-Whitney test, $W = 77.0$, $P = 0.12$). During spring, mean fuel load was lower for wintering ($x^- = 11.7\%$ LBM) than for transient species ($x^- = 32.5\%$ LBM, $W = 57.0$, $P = 0.006$). Because FFMs reported by Dunning (1993) averaged 6% lower than our estimates of LBM, fuel loads might be up to 6% greater than those reported in Table 3.

Table 1. Species presence and relative abundance in northeast Belize during spring and autumn migration based on transect observations (unadjusted density, individuals/km^2) and mist-net captures (number of individuals/4000 mist-net hours).

Species[a]	Scientific Name	Unadjusted density[b]		Mist-net captures[c]	
		Autumn	Spring	Autumn	Spring
Yellow-billed Cuckoo (T)	*Coccyzus americanus*	3			1
Eastern Wood-Pewee (T)	*Contopus virens*	64	4	25	
Acadian Flycatcher (T)	*Empidonax virescens*	7		20	
Alder Flycatcher (T)	*E. alnorum*	3		43	
Willow Flycatcher (T)	*Empidonax traillii*			86	
Traill's Flycatcher (T)	*E. traillii/alnorum*	5		53	
Least Flycatcher	*Empidonax minimus*	25	9	7	
Great Crested Flycatcher (T)	*Myiarchus crinitus*	1		4	1
White-eyed Vireo	*Vireo griseus*	29	12	69	7
Yellow-throated Vireo	*Vireo flavifrons*	8		13	2
Philadelphia Vireo (T)	*Vireo philadelphicus*			6	
Red-eyed Vireo (T)	*Vireo olivaceus*	9	11	113	75
Yellow-green Vireo	*Vireo flavoviridis*			9	6
Veery (T)	*C. fuscescens*			7	8
Gray-cheeked Thrush (T)	*Catharus minimus*			6	3
Swainson's Thrush (T)	*Catharus ustulatus*	11		61	5
Wood Thrush	*H. mustelina*			9	6
Gray Catbird	*Dumetella carolinensis*	9	2	118	18
Blue-winged Warbler	*Vermivora pinus*	1		4	1
Golden-winged Warbler (T)	*Vermivora chrysoptera*			4	
Tennessee Warbler (T)	*Oreothlypis peregrina*	15	45	31	19
Northern Parula	*Parula americana*	17	2	2	2
Yellow Warbler	*Dendroica petechia*	9	191	43	95
Chestnut-sided Warbler	*Dendroica pensylvanica*	5	6	15	5
Magnolia Warbler	*Dendroica magnolia*	73	222	101	123
Yellow-rumped Warbler	*Dendroica coronata*		1		4
Black-throated Green Warbler	*Dendroica virens*	13	5	15	2
Blackburnian Warbler (T)	*Dendroica fusca*	1		1	
Yellow-throated Warbler	*Dendroica dominica*			1	
Prairie Warbler	*Dendroica discolor*		1	1	
Bay-breasted Warbler (T)	*Dendroica castanea*	1	8	2	8
Black-and-white Warbler	*Mniotilta varia*	12	9	75	13
American Redstart	*Setophaga ruticilla*	35	31	86	15
Prothonotary Warbler (T)	*Protonotaria citrea*	7	4	80	19
Worm-eating Warbler	*Helmitheros vermivorus*		1	25	1
Swainson's Warbler	*Limnothlypis swainsonii*			7	
Ovenbird	*Seiurus auricapillus*	23	6	56	4
Northern Waterthrush	*Parkesia noveboracensis*	51		129	20
Kentucky Warbler	*Oporornis formosus*	1		9	1
Common Yellowthroat	*Geothlypis trichas*	12	13	27	16
Hooded Warbler	*Wilsonia citrina*	71	8	74	11
Canada Warbler (T)	*Wilsonia canadensis*	1		4	
Yellow-breasted Chat	*Icteria virens*	9		13	1
Summer Tanager	*Piranga rubra*	8		26	1
Scarlet Tanager (T)	*Piranga olivacea*	1	6	11	3
Rose-breasted Grosbeak (T)	*Pheucticus ludovicianus*	7	2	5	2
Indigo Bunting	*Passerina cyanea*	20	14	29	12
Dickcissel (T)	*Spiza americana*		4		

[a]Species with <2 observations or captures combined were excluded from the table (9 species). T denotes species considered transient in Belize.
[b]Unadjusted densities were estimated from observations made during transects at La Isla in semi-deciduous forest interspersed with regenerating Milpas.
[c]Mist-net captures in semi-deciduous forest and red mangrove were corrected for mist-net effort and rounded to whole numbers.
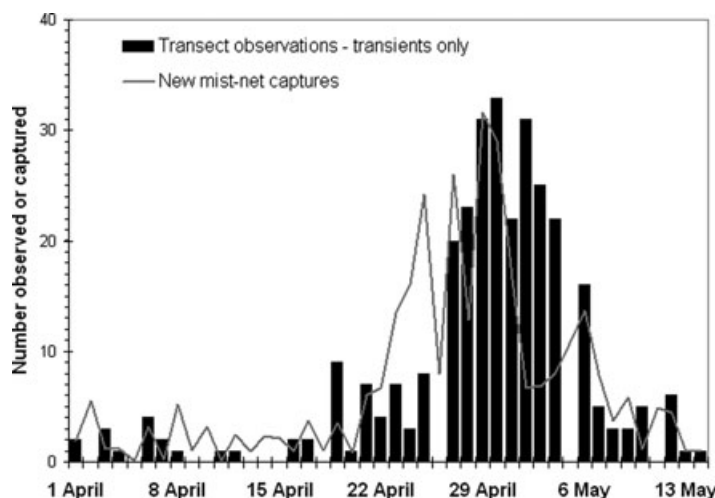
Fig. 2. Phenology of spring migration in northeast Belize based on: (1) the total number of individuals of transient species observed daily on a 500 m transect in semi-deciduous forest interspersed with Milpas, (2) daily capture totals for all species from the "forest" mist nets, having excluded recaptures and corrected for mist net effort. Days when the transect was not walked are indicated with*. The forest mist nets were operated on all days.

At the regional level, body masses recorded in northeast Belize in autumn in our study did not differ dramatically from those previously reported at Veracruz or southern Belize. Nevertheless, for species studied at both locations, we found significant differences for three of seven species (Veracruz study) and for seven of 10 species (southern Belize study), respectively (Table 4).

Evidence for increases in energy reserves.   Recapture rates were low for all transient species recorded (mean recapture rate = 3.8% of first captures) so it was not possible to analyze fuel deposition rates and minimum stopover durations for each species. We therefore present FDRs and stopover durations for individual birds for six transient species. FDRs in these individuals were generally positive and, in some cases, rates were rapid, e.g., up to 8% LBM/day, and minimum stopover durations were typically <4 days (Fig. 3).

Flight ranges.   For the three selected species, estimated flight ranges in autumn were shorter than those in spring. For Red-eyed Vireos and Prothonotary Warblers, estimated flight ranges from northeast Belize in autumn suggest that a two-or-more-stage strategy would be required to reach nonbreeding grounds over 1000 km to the south (Fig. 4). In spring, most

Red-eyed Vireos and Prothonotary Warblers captured in northeast Belize were capable of flying to or near their breeding grounds, whereas most Magnolia Warblers would have required additional reserves just to cross the Gulf of Mexico to the United States.

DISCUSSION

The Yucatan peninsula has long been considered a major flyway for Neotropical migrants during autumn migration (Buskirk 1968, Curson et al. 1994). The high species richness and abundance of migrants recorded in our study confirms that northeast Belize, located mid-way down the Yucatan peninsula, is part of this major autumn flyway. The role of the Yucatan peninsula during spring migration is less well known (Johnson and Winker 2008). Migrant species richness in northeast Belize was high in the spring (54 landbird species). However, transient species had large fuel reserves and were generally uncommon, indicating there was neither a hypothetical need nor physical evidence for transient species refueling in our study area. Because use of stopover sites can vary between years with weather conditions and population changes (e.g., Dunn 2000), our results should only be considered representative

Table 2. Relationship between hourly gain in body mass (g) and hour of capture and age for 17 species of Neotropical migrants during autumn and spring migration in northeast Belize. The coefficient of hourly gain (g/h), F-statistics, and P-values result from General Linear Models including the term wing length.

Species	Autumn migration						Spring migration					
	N	Hourly gain	F (hour)	P (hour)	F (age)	P (age)	N	Hourly gain	F (hour)	P (hour)	F (age)	P (age)
Alder Flycatcher	35	0.16	1.5	0.22	3.2	0.082	0	–	–	–	–	–
Willow Flycatcher	69	−0.49	0.6	0.45	–	–	0	–	–	–	–	–
Traill's Flycatcher	43	0.00	0.0	0.99	0.0	0.88	0	–	–	–	–	–
Red–eyed Vireo	92	0.07	0.3	0.59	0.0	0.99	82	0.13	0.5	0.48	1.8	0.18
White–eyed Vireo	56	0.13	2.5	0.12	0.2	0.67	9	0.12	1.3	0.30	–	–
Swainson's Thrush	50	0.38	1.7	0.20	4.0	0.051	5	−0.03	0.0	0.99	3.1	0.33
Gray Catbird	96	0.18	0.9	0.46	1.9	0.2	20	0.47	0.3	0.61	0.0	0.82
Tennessee Warbler	25	0.00	0.0	0.91	–	–	21	−0.27	4.5	0.05	2.2	0.16
Yellow Warbler	36	0.00	0.0	0.99	0.0	0.90	137	0.00	0.0	0.94	1.8	0.18
Magnolia Warbler	81	0.05	1.2	0.28	0.0	0.97	135	0.01	0.0	0.87	0.5	0.48
Black–and–white Warbler	51	0.04	0.2	0.70	1.1	0.30	15	0.01	0.0	0.97	1.7	0.22
American Redstart	70	0.10	2.8	0.10	1.1	0.30	21	−0.01	0.0	0.93	0.7	0.41
Prothonotary Warbler	65	0.18	1.7	0.20	0.8	0.37	28	0.04	0.3	0.62	1.8	0.19
Ovenbird	46	0.26	2.7	0.11	0.1	0.75	4	0.04	0.0	0.90	–	–
Northern Waterthrush	105	0.22	3.4	0.067	0.2	0.67	45	0.07	0.9	0.36	0.6	0.43
Common Yellowthroat	22	−0.18	2.0	0.17	0.1	0.83	20	0.06	0.5	0.51	0.3	0.60
Hooded Warbler	54	0.18	4.7	0.035	1.9	0.17	14	0.07	0.1	0.83	0.6	0.46
Indigo Bunting	24	0.07	0.8	0.38	1.4	0.25	25	0.12	0.7	0.40	3.3	0.08

of the one autumn and one spring migration when data were collected.

Species composition and abundance, and migration phenology. Species presence and abundance varied between spring and autumn migration for most transient species and some wintering species (e.g., Ovenbird, Seiurus auricapillus), with a general pattern of lower abundance, or even complete absence, in spring. For example, Alder (*Empidonax alnorum*) and Willow (*E. traillii*) flycatchers were abundant during autumn, but absent during spring, suggesting the use of an alternate spring migration route. The use of alternate routes between migrations is poorly documented, but the temporal distribution of records for a number of species in Belize suggest that such routes exist (Jones 2002), as do the distributional records of Veerys

(*Catharus fuscescens*) at a continental scale (Remsen 2001). Tracking data have also revealed different migration routes between seasons for Wood Thrushes (*Hylocichla mustelina*; Stutchbury et al. 2009), and further work with geolocators may reveal the prevalence of alternate routes by other Neotropical migrants. Instead of taking an alternative route, spring migration strategies may take birds over the Yucatan peninsula, but not involve a stopover in northeast Belize. This could explain the lower spring abundance of species such as Swainson's Thrush (*Catharus ustulatus*) and Eastern Wood-Pewee.

Comparing our results to those of other studies in the region, differences in species composition are evident. At Sian Ka'an Biosphere Reserve, Mexico, 200 km north of our study site, Acadian (*Empidonax virescens*), Alder, and

Table 3. A comparison of measures of energy reserves in selected Neotropical migratory birds during spring and autumn migration, with significance testing for differences in body mass between autumn and spring. LBM and FFM are provided to put body mass in context. Sample sizes are in parentheses.

Common name[a]	Autumn		Spring			LBM[e] (grams)	FFM[e] (grams)
	Mean body mass (grams)[b]	Mean fuel load %LBM[c]	Mean body mass (grams)[b]	Mean fuel load %LBM[c]	P-value for difference in body mass[d]		
Alder Flycatcher (T)	12.1 ± 0.9 (36)	4.7 ± 5.8	(0)	–	–	11.7	–
Willow Flycatcher (T)	11.4 ± 1.0 (69)	3.8 ± 7.0	(0)	–	–	11.0	–
Traill's Flycatcher (T)	12.0 ± 1.1 (43)	6.7 ± 7.6	(0)	–	–	11.2	–
Red-eyed Vireo (T)	16.3 ± 1.9 (91)	13.9 ± 11.9	19.7 ± 2.2 (80)	34.7 ± 14.6	<0.001	14.3	14.6
White-eyed Vireo	10.6 ± 0.7 (56)	4.8 ± 5.1	11.0 ± 0.8 (9)	7.6 ± 7.7	0.17	10.2	–
Swainson's Thrush (T)	28.2 ± 3.1 (51)	16.9 ± 11.6	37.8 ± 3.4 (5)	55.7 ± 14.2	0.004	24.3	24.2
Gray Catbird	33.6 ± 2.7 (94)	5.7 ± 6.7	39.9 ± 4.3 (20)	23.4 ± 12.6	<0.001	32.2	31.8
Tennessee Warbler (T)	8.7 ± 1.1 (25)	10.9 ± 12.2	9.8 ± 0.8 (21)	23.2 ± 10.2	<0.001	8.0	7.9
Yellow Warbler	9.2 ± 0.8 (35)	7.7 ± 7.1	9.2 ± 1.0 (136)	9.4 ± 9.3	0.69	8.4	–
Magnolia Warbler	7.7 ± 0.7 (79)	6.2 ± 7.5	8.2 ± 0.9 (135)	12.6 ± 11.4	<0.001	7.3	6.9
Black-and-white Warbler	9.6 ± 0.7 (60)	8.2 ± 7.6	9.7 ± 1.3 (15)	10.8 ± 14.0	0.65	8.9	–
American Redstart	7.3 ± 0.6 (69)	6.2 ± 6.5	7.4 ± 1.0 (21)	8.2 ± 12.3	0.75	6.9	6.5
Prothonotary Warbler (T)	13.3 ± 1.5 (65)	16.2 ± 12.9	14.8 ± 1.6 (28)	29.1 ± 13.9	<0.001	11.4	11.0
Ovenbird	17.7 ± 1.7 (46)	5.4 ± 7.7	19.9 ± 0.9 (4)	14.2 ± 5.5	0.013	16.9	15.5
Northern Waterthrush	16.3 ± 1.4 (103)	3.6 ± 6.5	17.1 ± 1.9 (45)	7.9 ± 8.8	0.009	16.1	13.7
Common Yellowthroat	9.4 ± 0.7 (21)	5.1 ± 6.3	9.9 ± 1.2 (20)	10.6 ± 11.1	0.22	9.1	8.4
Hooded Warbler	9.9 ± 0.9 (59)	6.3 ± 6.2	10.6 ± 1.6 (14)	12.2 ± 16.3	0.14	9.4	8.2
Indigo Bunting (T)	13.9 ± 0.9 (23)	7.4 ± 6.2	15.5 ± 2.0 (25)	19.8 ± 14.4	0.001	12.9	12.3

[a] Species that only occurred as transients in the study area are denoted by T.

[b] Only first captures were included in calculations to minimize the inclusion of over-wintering birds and sample sizes are presented in brackets. Body mass is given in grams ± SD.

[c] Fuel load is the difference in mass between observed mass and LBM, expressed as a percentage of the LBM.

[d] Difference in body mass is the P-value resulting from a t-test comparing autumn and spring body masses; mean spring mass was greater than mean autumn mass in all cases.

[e] LBM estimates were based on fat-zero individuals captured during the study, whereas FFM estimates were obtained from Dunning (1993).

Table 4. Comparison of mean body masses of Neotropical migratory landbirds captured in autumn in northeast Belize (this study), Veracruz, Mexico (Winker 1995), and southern Belize (Johnson and Winker 2008).[a]

Species	Northeast Belize	Veracruz, Mexico	Southern Belize
Red-eyed Vireo	16.28 ± 1.91 (91)	18.55 ± 2.24 (273)**	16.88 ± 1.50 (88)**
White-eyed Vireo	10.60 ± 0.68 (56)	10.78 ± 0.89 (140)	–
Swainson's Thrush	28.20 ± 3.09 (51)	–	29.36 ± 3.13 (305)*
Gray Catbird	33.64 ± 2.66 (94)	33.81 ± 2.72 (107)	34.35 ± 2.88 (268)*
Magnolia Warbler	7.69 ± 0.66 (79)	7.45 ± 0.57 (83)**	7.17 ± 0.47 (78)**
American Redstart	7.29 ± 0.58 (69)	7.33 ± 0.52 (50)	6.93 ± 0.50 (34)**
Ovenbird	17.70 ± 1.65 (46)	17.29 ± 1.59 (110)	17.44 ± 1.25 (44)
Northern Waterthrush	16.29 ± 1.39 (103)	–	15.53 ± 1.41 (85)**
Common Yellowthroat	9.40 ± 0.67 (21)	–	9.31 ± 0.69 (47)
Hooded Warbler	9.89 ± 0.87 (59)	9.48 ± 0.71 (97)**	9.41 ± 0.62 (50)**
Indigo Bunting	13.87 ± 0.92 (23)	–	13.50 ± 1.06 (88)

[a]Mean body mass in grams ±SD is followed by sample size in parentheses. Where body mass at either Veracruz or southern Belize was significantly different than that in our study (northeast Belize), significance is indicated by *$P < 0.05$ or **$P < 0.001$.

Willow flycatchers were not recorded during the same autumn migration season as our study in Belize (A. Raymundo, pers. comm.), but the relative abundance of other species was similar. In southern Belize, 230 km to the south, species composition was also similar, although Swainson's Thrushes and Veerys appeared more abundant (Johnson and Winker 2008). These differences suggest that the location of stopover sites on the Yucatan peninsula is species dependent.

We found that migration was relatively protracted in the autumn, whereas most individuals passed through our study site in just a matter of weeks during the spring. The timing of migration through northeast Belize depends on the strategies species use, e.g., if transient species were making a spring stopover in the study area prior to crossing the Gulf of Mexico, the peak in passage in Belize should precede that on the Gulf coast of North America. Contrary to this expectation, peak migration at our study site occurred during the last week of April and first week of May, following the same pattern recorded on the Gulf coast of the United States (Moore et al. 1990, Yong and Moore 1997). This pattern suggests that many species paused briefly in our study area, perhaps only making a daytime stop, before crossing the Gulf of Mexico using energy reserves accumulated elsewhere.

Variation in energy reserves between species and migration seasons. Energy reserves of migrants in northeast Belize, as measured by body mass and fuel loads, varied among species and between seasons. In autumn, fuel loads were similar across species and no difference was found between wintering and transient species. Given that the ultimate destination of transient species is different than that of wintering species, larger loads might be expected in transient species, but this was not
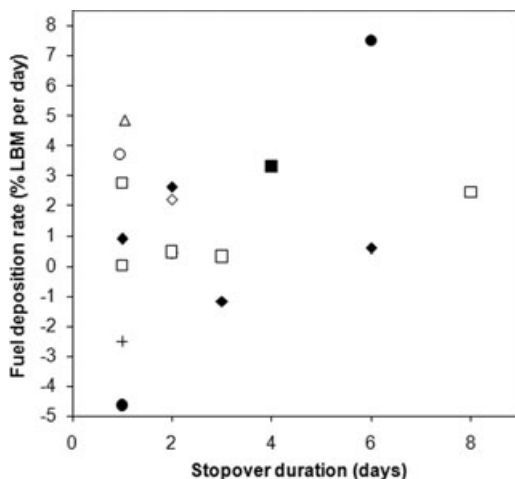

Fig. 3. Fuel deposition rate relative to minimum stopover duration of individual Neotropical migrants captured on more than one occasion in northeast Belize. All recaptured individuals of species classified as transients in Belize are included. Autumn migration: □ = Willow Flycatcher, ○ = Traill's Flycatcher, △ = Red-eyed Vireo, ◇ = Prothonotary Warbler, and + = Tennessee Warbler. Spring migration: ◆ = Prothonotary Warbler, ● = Indigo Bunting, and ■ = Painted Bunting.
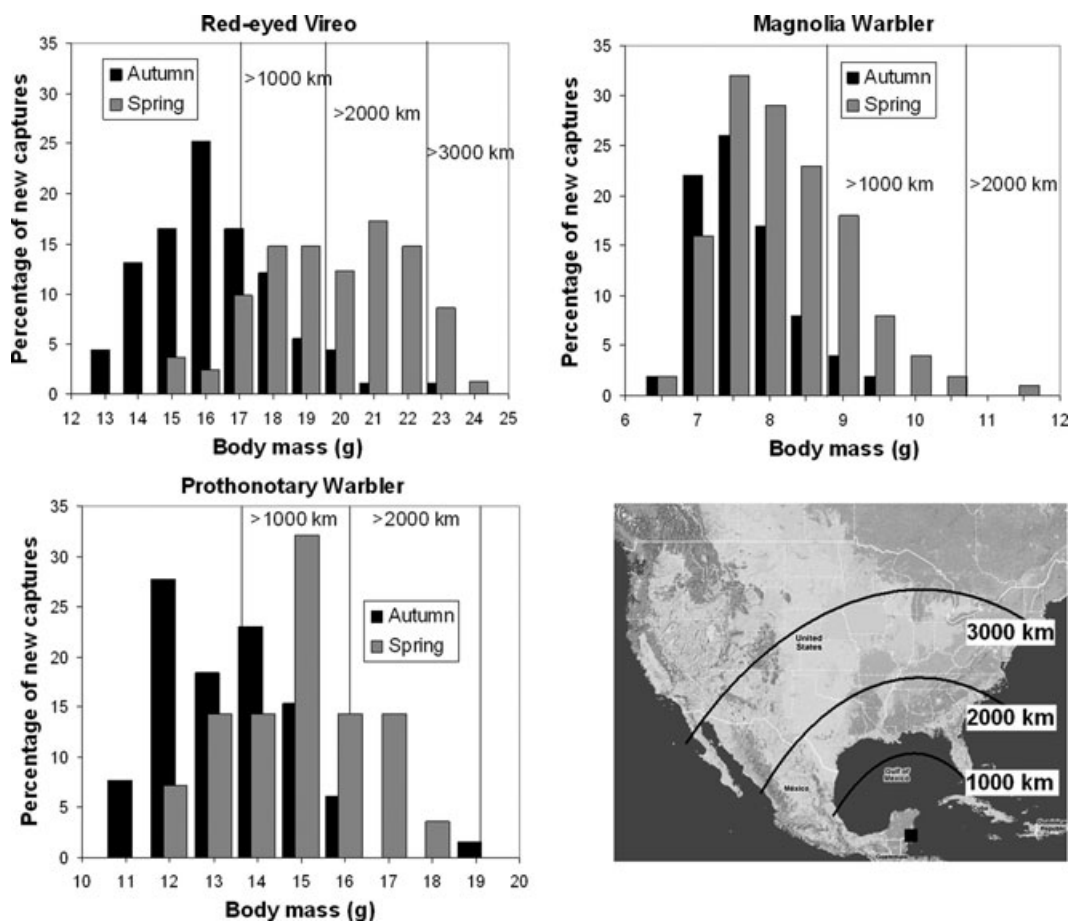
Fig. 4. Body mass distribution during autumn and spring migration relative to estimated flight ranges for Red-eyed Vireos, Magnolia Warblers, and Prothonotary Warblers. The distance that can be flown for a given body mass is indicated in bands by vertical lines and accompanying distances in kilometers. The map of North America with distance bands from the study site in northeast Belize (black square) can be used to relate migratory goals (e.g., breeding grounds) to flight ranges for a given body mass. The breeding range of Red-eyed Vireos covers most of eastern North America, Magnolia Warblers breed in the boreal region primarily above the 3000-km band, and Prothonotary Warblers breed in the southeastern United States below the 3000-km band.

the case. The mean autumn fuel load of 10% LBM in transient species suggests an average onward flight of approximately 500 km, indicating that species whose destination is South America would require further stopovers to complete their journey. Certain transient species, however, carried larger reserves, e.g., Red-eyed Vireos, Swainson's Thrushes, and Prothonotary Warblers, indicating that fuel loads accumulated prior to crossing the Gulf of Mexico vary among species, as do onward strategies to wintering regions. Within species, fuel loads also varied (see

standard deviations in Table 3); some individuals had exhausted their fuel reserves by the time they arrived at our study site, whereas others were capable of an unbroken flight to South America (1650 km; see Fig. 4).

The small or moderate fuel reserves of most individuals captured during autumn migration in our study presumably either remained after crossing the Gulf of Mexico or were accumulated further north on the Yucatan. There was therefore no immediate need for birds to make a stopover in northeast Belize, possibly explaining

why recapture rates were low and minimum stopover durations short. However, a small percentage of individuals of all species arrived with no visible fat deposits and would have been expected to refuel to some extent in our study area. The few recaptured individuals in our study generally had positive FDRs, but, given the duration of stopovers, the level of refueling was likely minimal. Our study region may therefore act like a "convenience store" (following the terminology of Mehlman et al. 2005) for many species in autumn, i.e., a place they can rest for a day and potentially add to their reserves, but not where they accumulate sufficient reserves for long flights. Further studies generating more within-day and between-day recaptures would be useful for better understanding the true nature of autumn fueling behavior by migrants in the Yucatan region.

Of the 10 species considered both in our study and by Johnson and Winker (2008) in southern Belize, mean body mass was higher at our study site in northeast Belize for seven species and significantly so for four. A pattern of decreasing body mass as one moves south across the Yucatan could reflect a strategy where reserves are not replenished at more northerly locations on the Yucatan and therefore decrease as birds move south. Red-eyed Vireos, Swainson's Thrushes, and Gray Catbirds showed the opposite pattern of increasing body mass, perhaps reflecting a strategy of refueling at sites in the Yucatan. At the same latitude as our study site, autumn body masses of seven species were broadly similar in Veracruz (Winker 1995). There were significant differences, however, and these might be due to birds following an overland route to Veracruz or to inter-annual variation among other possibilities. Given that wintering areas differ between species, it is not surprising that autumn migration strategies in Central America differ as well.

Mean body masses and fuel loads were greater in spring than autumn for all but one species (Yellow Warbler), and body mass was significantly higher in 60% of the species analyzed. The mean difference in fuel load between autumn and spring across all wintering species was 5.8% LBM, with transient species averaging 19.4% LBM (equating to an additional 900 km of potential flight range). This difference is not unexpected given that birds in autumn had recently completed the 1400 km flight across the Gulf of Mexico, whereas they were preparing for the reverse journey in the spring. However, contrary to our expectation, this marked difference in fuel load suggests that transient species arrived in northeast Belize in spring with sufficient fuel to continue directly to North America and were therefore unlikely to be fuelling in the region for the Gulf crossing. This conclusion is further supported by the low abundance of transient species in spring. Transient species that were abundant in autumn (e.g., Swainson's Thrush) were observed and captured in lower numbers in spring, and individuals that were captured were carrying large fuel loads. The phenology of spring migration, as discussed above, also supports the notion that transient species were not stopping over in northeast Belize.

There was, however, variation in fuel loads of transient species and, for some species such as Prothonotary Warblers, a few captured individuals needed to fuel extensively to cross the Gulf of Mexico. For these individuals, there is evidence that fueling occurred in the study area and, with observed rates around 3–4% of LBM per day, a stopover of about 10 days may have been necessary.

For some wintering species, a marked increase in observations and captures during late April was evidence of a large transient population in our study area during spring. Indeed, Magnolia and Yellow warblers were largely responsible for the increase in new mist-net captures after 20 April. These findings suggest that, unlike most transient species, certain species that winter in Central America may stopover in northeast Belize in spring, prior to crossing the Gulf of Mexico.

The range of spring strategies is illustrated by three species (Fig. 4). Red-eyed Vireos winter in South America and arrived in our study area with sufficient fuel to cross the Gulf of Mexico and, presumably, to fly to their breeding areas throughout eastern North America (up to 3000 km to the north). Prothonotary Warblers share a similar strategy, with a sizeable percentage of the population captured in northeast Belize having the potential to fly direct to breeding grounds in southeastern North America – the shorter distance to their breeding grounds presumably explains the lower fuel loads compared to Red-eyed Vireo. Around 40% of captured Prothonotary Warblers, however, needed to increase their fuel reserves before attempting the Gulf crossing. In contrast, Magnolia Warblers

arrived in our study area with insufficient reserves to make an unbroken flight across the Gulf of Mexico to the United States, and limited evidence from recaptured individuals suggests that additional reserves were accumulated in our study area (e.g., mean FDR = 3.9% LBM, $N = 4$). Magnolia Warblers are primarily a boreal-breeding species and flight ranges even for individuals with the largest fuel loads in Belize suggest that another stopover would be necessary in southern North America before reaching the breeding grounds.

Transient species in spring generally carried large energy reserves in our study, raising the question of where these reserves were accumulated. For species that winter in South America, we hypothesize two strategies: (1) these species accumulate sufficient fuel in northern South America or southern Central America to complete the journey to North America without the need to refuel, and (2) a two-or-more-stage strategy involving stopovers in South America and at one or more sites in Mesoamerica. Regardless of which hypothesis is correct, our results suggest that stopover sites may be more localized during spring migration and high resource levels may be essential for accumulating the large fuel loads we recorded. Identifying the regions and sites used during spring migration is crucial if we are to determine the degree to which the modification and degradation of such sites is contributing to population declines.

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Supporting Information

The following supporting information is available for this article online:

Table S1. List of all Neotropical migrants recorded in NE Belize during the study with their relative abundance during autumn migration (1 August–15 November), winter (16 November–14 March), and spring migration (15 March–15 May).

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