

AUTUMN STOPOVER NEAR THE GULF OF HONDURAS BY NEARCTIC-NEOTROPIC MIGRANTS

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ABSTRACT.—The southeastern Yucatan Peninsula hosts high numbers of transient Nearctic-Neotropical migrants during autumn migration, but the importance of this region during migratory stopover has not been addressed. We studied autumn stopover body mass gains among passerine migrants in tropical lowland forest 20 km inland from the Gulf of Honduras. Most individuals captured had some subcutaneous fat. Ten of 15 taxa with sufficient sample sizes had significant positive diel (24 hr) gains in a body condition index. Estimates of net mass gains in these 10 taxa suggested they all were depositing fat; average individuals in four of these taxa were depositing sufficient fuel to undertake an entire night of migration after only 1 day of fattening: *Empidonax* spp., Red-eyed Vireo (*Vireo olivaceus*), Gray Catbird (*Dumetella carolinensis*), and Northern Waterthrush (*Seiurus noveboracensis*). Two (Wood Thrush [*Hylocichla mustelina*] and Common Yellowthroat [*Geothlypis trichas*]) of the four species apparently not gaining mass at the study site migrate late in the season and occurred only after Hurricane Iris severely altered the habitat. Four other species (Gray Catbird, Magnolia Warbler [*Dendroica magnolia*], American Redstart [*Setophaga ruticilla*], and Indigo Bunting [*Passerina cyanea*]) had significant gains in mass after the hurricane. These data demonstrate the importance of the region as an autumn stopover site for some species and suggest that stopover areas farther north are also important to migrants passing through the southeastern part of the Yucatan Peninsula. Received 19 January 2006. Accepted 25 September 2007.

The geography of North America causes Nearctic-Neotropical migrants that breed across thousands of square kilometers of boreal and temperate forest to funnel through a small fraction of the land area in the forests of Central America during the nonbreeding season. This concentration of migrants likely makes forests in Central America vital as both wintering and stopover habitat. Many migrant species have winter ranges that extend far beyond the Gulf of Honduras (AOU 1998), and forests adjacent to the Gulf of Honduras are probably important stopover habitat. Published accounts of high volumes of transient Nearctic-Neotropical migrants in Panama (Galindo et al. 1963, Galindo and Mendez 1965) suggest there should be similar numbers of migrants farther north. Monroe (1968) documented a large spring migration northward across the Gulf of Honduras and speculated that a large autumn migration also occurs. However, there has been no information published about how transient migrants use stopover sites in this region.

Few studies have addressed energetic needs

of migrants in Central America (Rogers and Odum 1966; Child 1969; Winker 1995a, b), and there are no published studies of migrant stopover ecology near the Gulf of Honduras. We chose a site near the Gulf of Honduras in lowland tropical forest to examine the autumn migration of Nearctic-Neotropical migrants. We provide the first extensive data on autumn stopover by woodland migrants in this region and address the following questions: (1) what levels of fat are carried in the region; (2) do migrants refuel at this site and, if so, to what extent; and (3) do species that have farther to migrate fuel more?

METHODS

Study Area.—Our study site was a 25-year-old, second-growth, lowland forest adjacent to a citrus orchard in the floodplain of the Rio Grande (16° 16' N, 88° 52' W) near Big Falls Village, Toledo District, Belize (Fig. 1). The site was in a matrix of human-altered habitats (primary forest remnants, citrus orchard, fields, and habitats in stages of regrowth) that had a canopy height of ~20 m with some gaps filled with dense woody vegetation and vine tangles 3 m in height.

Trapping.—We established a 1.26-ha study site in August 2001 and placed 30 12-m mist nets in two parallel rows of 15 nets spaced 30 m apart. Each net was spaced 30 m apart from its neighbor within each row, and we alter-

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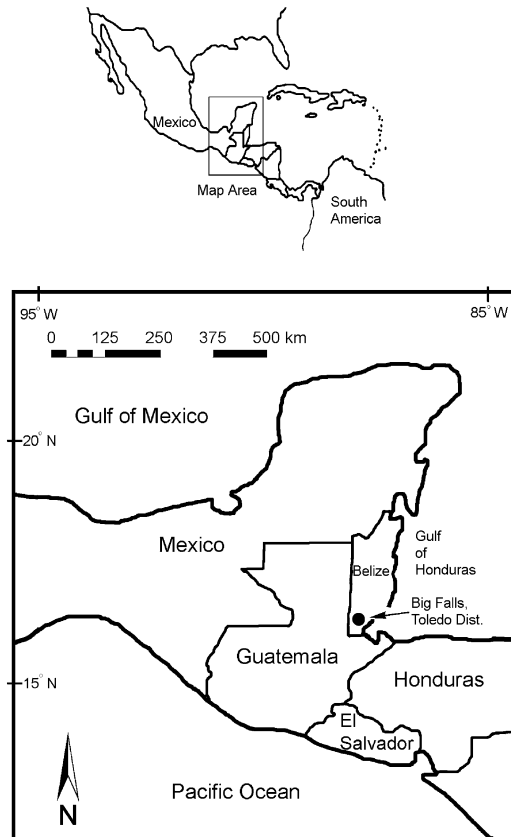


FIG. 1. Big Falls, Toledo District study site in Belize in northern Central America on the Yucatan Peninsula.

nated mesh sizes between 30 and 36 mm. Nets were opened beginning on 11 August and were open all day when conditions permitted. We accrued 8,805 net hrs until 7 October, when we removed nets from the study site in anticipation of Hurricane Iris, which struck on 8 October. The effect of Hurricane Iris on the site changed the habitat from a nearly closed, 20-m high canopy to a 5-m high tangle of uprooted and broken trees, broken branches, and vines. We re-opened 15 nets placed on the original site on 19 October. Five nets were placed in their original net lanes and others were placed as close as possible to their original positions. Placement of nets was constrained by the drastically altered forest structure (e.g., fallen trees and dense tangles of vines). We only netted during mornings and evenings during this period due to lack of

shade on the site. We accrued 1,114 more net hrs and concluded the effort on 15 November.

Each bird captured was identified to species, age class, and whether it was male or female when possible. Time and net of capture, body mass, and chord of closed wing (hence 'wing chord,' as traditionally used, see Stiles and Altshuler 2004) were recorded for all birds captured; tail, tarsometatarsus, and bill lengths were recorded for most individuals. Subcutaneous fat deposits were scored following Helms and Drury (1960). All *Empidonax* were treated as a single taxon for this study, and included five Nearctic-Neotropical migrant species verified by museum specimens (*traillii*, *alnorum*, *flaviventris*, *virescens*, and *minimus*).

Daily Mass Gains.—The extent of mass gain was estimated at the species level following Winker et al. (1992) and Winker (1995a). This method calculates a condition index for each individual and examines the relationship between condition index and time of capture using simple linear regression.

Rising and Somers (1989) and Freeman and Jackson (1990) suggested that no single linear external measurement of a bird is a good correlate of body size, although these studies suggested that tarsometatarsus ("tarsus") or tibiotarsus was the best univariate indicator of body size. However, Connell et al. (1960) and Rogers and Odum (1964, 1966) showed that wing length was a good predictor of fat-free mass in some passerines during migration, although they did not examine other variables. Winker (1995a) found a condition index based on wing chord or tail to be a better predictor of fat content than one based on tarsus in a sample of fat-extracted Tennessee Warblers (*Vermivora peregrina*). We used wing chord to standardize body mass by calculating a condition index for all species except Kentucky Warbler (*Oporornis formosus*).

A condition index for each individual was calculated by dividing its mass by its wing chord (Winker 1995a). The condition index was examined for each species with respect to time of day (equivalent to time of capture of each individual; hereafter referred to simply as 'time') using simple linear regression. Regressions of fat scores, mass, and condition indices using other morphological characters (tail, tarsometatarsus, and bill lengths) with

respect to time were used to corroborate wing chord condition index trends. A condition index constructed using the first principal component of wing chord, tail length, tarsometatarsus, and bill lengths combined was also explored as an option, but the estimates were not an improvement over the use of a single morphological character. Multiple regression was also tried (Dunn 2000), but the estimates were similar and did not justify the added complexity of the analyses.

Estimates of net 24-hr mass changes were made for species having regression slopes of condition index with respect to time significantly different from zero ($\alpha = 0.05$). The slope of the condition index regression was converted to estimated daily gross mass gains for the average individual in a species by multiplying by 12.42 hrs (average length of daily bird activity from field notes) and multiplying by the sample's mean wing chord. Net mass gains were calculated by subtracting estimates of nightly metabolic demands from the estimated gross daily gains. Our estimate of nocturnal loss was a mass-specific existence metabolism estimate (Kendeigh 1970:60) using both fat-free mass data when available (Dunning 1993) and average "lean mass" (Dunn 2002) from birds captured at the site.

We used a value of 30.2 kJ energy per g fuel (Pennycuick 2003) for our flight capacity estimates, which assumes the fuel used during migration is 95% fat. Our taxon-averaged flight capacity estimates would have to be revised downward from our present energetic estimates if it is found that migrants in this region are depositing protein to the extent as trans-Saharan Eurasian Blackcaps (*Sylvia atricapilla*) (Karasov and Pinshow 1998). Fuel composed of 30% protein would reduce our flight capacity estimates by about 50% (Pennycuick 2003: equation 12).

We assumed mass gain was not the result of rehydration after migration (Nisbet et al. 1963). Catabolism of lipids produces water that helps to maintain water balance, and Rogers and Odum (1966) showed that, even in emaciated post-flight birds in Panama, water content was not different from that of fat birds. Bauchinger and Biebach (2000) also showed that water content did not differ among pre-migratory, immediately post-migratory, or post-migratory birds that had 7

days to recover with free access to food and water.

Morphological data for each taxon were checked for normality. Mass and morphological variables used to estimate net mass gains in each species were normally distributed except for wing chord in American Redstart (*Setophaga ruticilla*). Transformations of wing chord for American Redstart failed to normalize these data. Tail length was not recorded in this species. Residuals were checked for normality using quantile-quantile plots following regression analyses and examined visually to ascertain whether there were any patterns that indicated unequal variance. Residuals were normal and no patterns indicating heteroscedasticity were found in any of these taxa.

Hurricane Iris struck on 8 October 2001 and the drastic habitat change that resulted may have had an effect on fat deposition by migrants. No taxon had sufficiently large sample sizes ($n \geq 30$) pre- and post-hurricane to conduct separate analyses before and after the storm. Consequently, each migrant taxon was based on a sample from either entirely before or entirely after the hurricane; samples were not pooled between pre- and post-hurricane efforts.

Flight Capacity Estimates.—Maximum hours of flight possible for the average individual gain in each taxon at the site were calculated using net gain estimates from this study, published values for the energetic content of fuel (30.2 kJ per g; Pennycuick 2003), and size-specific rate of energy use during migration (Tucker 1974). These values were used to estimate the duration an average individual of each species could fly in a night. The methodology of Pennycuick (1989) was not applicable because we did not record wing span measurements.

Mass Comparisons.—Condition index analyses provide a species-level estimate of daily gains in mass, but do not consider the amount of fat already carried by individuals of a species. Average mass from each species was compared to its fat-free mass to examine the fat load the average individual of each species was carrying (Dunning 1993), and to average "lean mass" (mean mass of individuals from our site with fat scores of zero; Dunn 2002) using two-sample *t*-tests. The paucity of in-

dividuals of some species that had fat scores of zero at our site made the latter comparison tenuous (e.g., no Red-eyed Vireos [*Vireo olivaceus*] or Veeries [*Catharus fuscescens*] had fat scores of zero).

RESULTS

We captured 30 or more individuals of 14 species and the genus *Empidonax*, and present summary statistics of morphological characters to allow comparisons with other studies (Table 1). We encountered no emaciated individuals. We rarely observed actively growing feathers and assumed that energetic demands for the vast majority of these birds were limited to migration and maintenance costs.

Comparisons of Mass with Fat-free and Lean Mass.—All taxa but Wood Thrush (*Hylotichla mustelina*) were significantly heavier than the species' average fat-free mass (Table 2), and most individuals were carrying visible subcutaneous fat (82% of the individuals of the 15 taxa had fat scores >0). Many Veeries and Swainson's Thrushes (*Catharus ustulatus*) had heavy fat loads (Table 1; all Veeries had fat scores >0). Few taxa were significantly heavier than lean mass, but all taxa except Wood Thrush were significantly heavier than fat-free mass (Table 2). We observed frequent defecation by birds during handling that suggested they were feeding at this site. The peak of migration, especially of *Catharus* thrushes, corresponded with ripening of large amounts of fruits on our site, particularly the understory tree, *Dendropanax arboreus* (Araliaceae).

Estimates of Daily Mass Gain.—Eleven taxa had significant slopes of mass with respect to time (Table 3). Nine taxa had regressions of wing chord condition index with respect to time with significant *F*-values (slopes different from zero); all slopes were positive (Table 3). Kentucky Warblers and Veeries did not show significant gains in wing chord condition index, even though regressions of mass on time had significant positive slopes, and fat score regressions with respect to time also showed significant positive slopes for Kentucky Warblers (Table 3). Both species had marginal *P*-values for gain in wing chord condition index with respect to time (Kentucky Warbler, *P* = 0.064; Veery, *P* = 0.068).

Four taxa had significantly positive slopes

TABLE 1. Mean \pm SD morphological characters (*n*) of autumn migrants mist-netted at Big Falls, Belize, 11 August–15 November 2001.

Species	Mass	Wing chord	Tail length	Tarsus ^a length	Fat score
<i>Empidonax</i> spp.	11.73 \pm 1.39 (88)	65.88 \pm 3.14 (88)	54.19 \pm 2.93 (86)	15.52 \pm 0.98 (88)	0.7 (79)
Red-eyed Vireo, <i>Vireo olivaceus</i>	16.88 \pm 1.50 (39)	74.92 \pm 2.35 (39)	50.44 \pm 2.97 (39)	17.67 \pm 1.32 (39)	1.3 (39)
Veery, <i>Catharus fuscescens</i>	32.15 \pm 4.29 (67)	92.70 \pm 3.05 (67)	66.51 \pm 3.75 (67)	28.85 \pm 1.46 (67)	1.7 (67)
Swainson's Thrush, <i>C. ustulatus</i>	29.36 \pm 3.13 (305)	93.22 \pm 2.90 (305)	64.05 \pm 3.25 (305)	26.99 \pm 1.39 (305)	1.7 (305)
Wood Thrush ^b , <i>Hylotichla mustelina</i>	42.93 \pm 3.17 (45)	101.36 \pm 3.69 (45)	68.00 \pm 2.54 (19)	30.01 \pm 0.99 (19)	0.7 (42)
Gray Catbird ^b , <i>Dumetella carolinensis</i>	34.35 \pm 2.88 (268)	85.53 \pm 2.44 (269)	88.02 \pm 4.29 (117)	Not measured	1.4 (265)
Magnolia Warbler ^b , <i>Dendroica magnolia</i>	7.17 \pm 0.47 (78)	56.46 \pm 2.26 (77)	47.70 \pm 2.19 (76)	17.24 \pm 0.93 (5)	0.6 (79)
American Redstart ^b , <i>Setophaga ruticilla</i>	6.93 \pm 0.50 (34)	57.71 \pm 1.84 (31)	53.71 \pm 2.13 (28)	16.76 \pm 0.59 (27)	0.4 (34)
Worm-eating Warbler, <i>Helminthos vermivorus</i>	12.27 \pm 0.80 (31)	64.85 \pm 1.86 (31)	46.76 \pm 2.22 (31)	17.83 \pm 0.50 (31)	0.7 (29)
Ovenbird, <i>Seturus auricapillus</i>	17.44 \pm 1.25 (44)	70.28 \pm 2.69 (43)	50.88 \pm 2.50 (42)	21.54 \pm 0.93 (43)	0.7 (44)
Northern Waterthrush, <i>S. noveboracensis</i>	15.53 \pm 1.41 (85)	71.22 \pm 2.15 (84)	49.28 \pm 2.55 (84)	21.08 \pm 0.53 (84)	1.0 (86)
Kentucky Warbler, <i>Oporornis formosus</i>	12.77 \pm 1.11 (60)	63.59 \pm 2.55 (59)	45.88 \pm 2.62 (59)	21.56 \pm 0.73 (59)	1.0 (56)
Common Yellowthroat ^b , <i>Geothlypis trichas</i>	9.31 \pm 0.69 (47)	51.99 \pm 2.42 (48)	48.50 \pm 2.62 (31)	19.61 \pm 0.62 (29)	0.9 (47)
Hooded Warbler, <i>Wilsonia citrina</i>	9.41 \pm 0.62 (50)	61.55 \pm 2.22 (51)	54.64 \pm 1.80 (50)	19.12 \pm 0.62 (49)	0.4 (49)
Indigo Bunting ^b , <i>Passerina cyanea</i>	13.50 \pm 1.06 (88)	62.40 \pm 2.50 (87)	49.33 \pm 2.33 (65)	16.85 \pm 0.54 (83)	0.9 (84)

^a Tarsometatarsus.

^b Entire sample from after 8 October 2001 (the date when Hurricane Iris struck).

TABLE 2. Body mass of woodland migrants mist-netted in Big Falls, Belize, 11 August–15 November 2001.

	Lean mass ^a	Mean mass	Fat-free mass ^b	Lean mass <i>r</i> ^c	Fat-free mass <i>r</i> ^c
Red-eyed Vireo ^d		16.88	14.59		10.14***
Veery ^d		32.15	26.66		8.92***
Swainson's Thrush	26.5	29.36	24.18	3.34*	23.50***
Wood Thrush	42.0	42.93	42.21	1.12	1.23
Gray Catbird	32.4	34.35	31.80	4.17*	8.17***
Magnolia Warbler	7.0	7.17	6.92	1.87	2.63**
American Redstart	6.75	6.93	6.49	1.11	5.03***
Worm-eating Warbler	12.0	12.27	10.79	1.12	7.17***
Ovenbird	16.7	17.44	15.52	1.94	7.54***
Northern Waterthrush	15.3	15.53	13.68	0.698	9.02***
Kentucky Warbler	12.0	12.77	11.36	2.87*	9.25***
Common Yellowthroat	9.15	9.31	8.36	0.836	5.38***
Hooded Warbler	9.5	9.41	8.2	-0.692	9.37***
Indigo Bunting	13.1	13.50	12.34	1.23	8.76***

^a Mean mass of individuals with fat score of zero.

^b Dunning (1993).

^c * $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$.

^d No Veeries or Red-eyed Vireos had a fat score of zero.

of fat scores with respect to time (Table 3), and all of these species also had significant slopes of mass with respect to time. Kentucky Warblers had significant slopes of mass and fat score with respect to time, and it appeared this species was fattening at the site even though the wing chord condition index regression with respect to time was not significant (Table 3). Tail length condition index in

this species had a slope significantly different from zero (Table 3), which was used to obtain an estimate of net daily mass gain. Veeries did not show any other evidence of mass gain besides a significant positive slope in mass with respect to time, and they were excluded from further analyses.

Regressions of wing chord with respect to time for Swainson's Thrushes and Red-eyed

TABLE 3. Relationships between morphological characters and time of capture of individual woodland migrants in Big Falls, Belize mist-netted between 11 August and 15 November 2001. Values are *F*-statistics from linear regressions of the character against time and test the null hypothesis that slope of the linear model was not significantly different from zero. Asterisks indicate $P < 0.05$ for the *F*-test.

Species	Mensural characters				Condition indices ^a	
	Wing chord	Tail length	Mass	Fat	Wing chord	Tail length
<i>Empidonax</i>	0.2	3.1	8.8*	7.7*	9.8*	4.8*
Red-eyed Vireo	5.3*	2.3	8.3*	0.5	4.1*	3.0
Veery	1.9	1.2	4.8*	3.0	3.5	2.8
Swainson's Thrush	8.5*	4.0*	7.9*	13.1*	4.2*	3.2
Wood Thrush	0.2	0.2	0.1	2.8	0.2	
Gray Catbird	2.2	0.2	24.2*	0.6	18.8*	5.0*
Magnolia Warbler	0.4	0.4	6.5*	3.4	7.0*	8.7*
American Redstart	2.2 ^b		6.7*	6.6*	6.6*	
Worm-eating Warbler	1.1	1.1	8.6*	1.2	6.5*	4.0
Ovenbird	0.0	0.0	2.1	2.0	2.9	1.6
Northern Waterthrush	0.1	1.8	8.2*	2.8	8.8*	3.1
Kentucky Warbler	3.9	0.5	7.4*	4.4*	3.6	5.2*
Common Yellowthroat	0.2	0.0	0.8	0.4	0.5	1.8
Hooded Warbler	0.0	0.2	1.8	0.2	2.3	1.4
Indigo Bunting	0.0	0.9	4.3*	0.1	5.0*	0.9

^a Mass divided by morphological character.

^b Variable not normally distributed.

TABLE 4. Linear models for diurnal change in condition index for woodland migrants^a at Big Falls, Toledo District, Belize, 11 August–15 November 2001.

Species	<i>n</i>	<i>b</i>	<i>m</i>	SE <i>m</i>	<i>F</i>	<i>P</i>	<i>r</i> ²	Condition gain/day ^b
<i>Empidonax</i>	88	0.14936	0.00260	0.00083	9.8	0.0025	0.11	0.03228
Red-eyed Vireo	39	0.19128	0.00276	0.00136	4.1	0.0504	0.10	0.03427
Veery	66	0.31382	0.00287	0.00154	3.4	0.0675	0.05	^c
Swainson's Thrush	306	0.29956	0.00133	0.00065	4.2	0.0418	0.01	0.01651
Wood Thrush	45	0.43273	-0.0012	0.00251	0.2	0.6334	0.01	^c
Gray Catbird	269	0.36757	0.00406	0.00094	18.8	<0.0001	0.07	0.05041
Magnolia Warbler	77	0.11762	0.00106	0.00040	7.0	0.0100	0.09	0.01316
American Redstart	31	0.11017	0.00086	0.00034	6.6	0.0157	0.18	0.01071
Worm-eating Warbler	31	0.17130	0.00160	0.00063	6.5	0.0165	0.19	0.01987
Ovenbird	43	0.23247	0.00146	0.00086	2.9	0.0955	0.07	^c
Northern Waterthrush	84	0.19323	0.00250	0.00085	8.8	0.0041	0.10	0.03104
Kentucky Warbler ^d	59	0.25142	0.00243	0.00106	5.2	0.0259	0.09	0.03017
Common Yellowthroat	48	0.17598	0.00360	0.00052	0.5	0.4916	0.01	^c
Hooded Warbler	51	0.14421	0.00085	0.00056	2.3	0.1372	0.05	^c
Indigo Bunting	87	0.20401	0.00138	0.00062	5.0	0.0274	0.06	0.01714

^a Equations are $Y = b + mX$, where Y is condition (g/mm), m is slope (condition change/hr), b is the Y intercept, and X is time (hr). F -statistic and corresponding P -value indicate whether the slope differed from zero; r^2 is the coefficient of determination and is a measure of the strength of the relationship between time (X) and condition (Y).

^b Units are g/mm for the average day length of 12.42 hrs.

^c Slope not significantly different from zero and gains were not estimable.

^d Tail condition index used to estimate mass gain.

Vireos revealed a significant positive slope (Table 3), suggesting that larger individuals of these two species were more likely to be captured later in the day. We divided the sample of Swainson's Thrushes in half by wing chord to examine the possibility that wing chord might impart, rather than remove, a size bias when calculating individual condition index values. We tested whether the longer-winged half of our sample had greater condition indices than the shorter-winged half using a one-tailed t -test. There was no difference in condition indices between the two groups ($t = 0.62$, $df = 303$, $P = 0.27$), suggesting the significant relationship of wing chord with time of day in these species was not causing the significant relationship between our wing chord-based condition index and time of day.

Linear models (Table 4) for the 10 taxa that had significant slopes of condition index with respect to time (Table 3) were used to estimate average gross and net daily mass gains (Table 5). Net estimates of mass gain were variable among those species showing gains. For example, average gains for Swainson's Thrush were less than 4% of lean body mass, but in four taxa (*Empidonax*, Gray Catbird [*Dumetella carolinensis*], Red-eyed Vireo, and Northern Waterthrush [*Seiurus noveboracen-*

sis]) our estimates showed net diel mass gains of more than 10% of mean body mass (Table 5).

Flight Capacity Estimates.—Estimates of flight times possible with taxon-average gains varied from <3 to >10 hrs. Average individuals of four taxa (*Empidonax*, Gray Catbird, Red-eyed Vireo, and Northern Waterthrush) were estimated to be capable of flying for between 8 and 11 hrs if all mass gained was fat (i.e., an entire night after just 1 day of fattening; Table 5).

DISCUSSION

Our data suggest that 10 of the 15 taxa studied used this site to acquire resources and gain mass, and that no taxa had significantly negative daily mass gain estimates. The extent of mass gain varied among taxa at the site. All taxa with significant mass gains gained sufficient mass to more than offset estimated nocturnal losses.

The substantial net gain estimates in some taxa (*Empidonax*, Red-eyed Vireo, Gray Catbird, and Northern Waterthrush) suggest that habitat at this site was sufficiently favorable to allow for nearly a full night of migration after only 1 day of feeding; 90% of the taxa had a net gain of at least 5% of lean mass per

TABLE 5. Estimates of daily net increases in mass using wing chord condition index (Kentucky Warbler uses tail condition index) for woodland migrants captured in Big Falls, Toledo District, Belize, 11 August–15 November 2001. Units are g, except where noted.

Species	Gross gain per day ^a	Existence metabolism ^b	Existence metabolism as percentage of lean mass	Net gain per day ^c	Increase as percentage of lean mass	Flight cost (g/hr) ^d	Hours of flight ^e
<i>Empidonax</i>	2.13	0.53		1.60	11.43	0.15	10.82
Red-eyed Vireo	2.57	0.44	2.82	2.13	13.64	0.21	10.10
Swainson's Thrush	1.54	0.61	2.30	0.93	3.51	0.36	2.57
Gray Catbird	4.31	0.69	2.13	3.62	11.18	0.42	8.61
Magnolia Warbler	0.74	0.27	3.86	0.47	6.76	0.09	5.17
American Redstart	0.62	0.26	3.85	0.36	5.31	0.09	4.05
Worm-eating Warbler	1.29	0.37	3.08	0.92	7.65	0.15	5.95
Northern Waterthrush	2.21	0.43	2.81	1.78	11.64	0.19	9.17
Kentucky Warbler	1.38	0.37	3.08	1.01	8.42	0.16	6.29
Indigo Bunting	1.07	0.39	2.98	0.68	5.18	0.17	4.01

^a Mass gain during 1 day for average individual using average size for wing chord (Kentucky Warbler uses tail length).

^b Mass loss due to existence metabolism (Kendeigh 1970).

^c Net 24-hr mass gain after subtraction of nightly mass loss of existence metabolism from gross gain/day.

^d Cost of flight in g of fat/hr calculated following Tucker (1974:306) using average mass of captured individuals.

^e Hours of flight possible calculated from Tucker (1974) using an energy value of 30.2 kJ per g (Pennyquick 2003).

day (Table 5). Our estimates are conservative for individuals that stopped for only 1 day and did not spend a night at our site because, as nocturnal migrants, they would lose little to nocturnal resting metabolism, and the amount available for migration would be closer to the gross mass gain estimates.

Only 40% of species with significant mass gain estimates also had significant fat score trends. Fat scores are subjective ordinal estimates of the fat content in birds, not absolute measures, and they estimate only visible subcutaneous deposits on the venter of a bird, even though fat is also deposited in other areas (King and Farner 1965). The association between lipid index (g lipid per g lean dry mass) from fat extractions and fat scores for wintering Dark-eyed Juncos (*Junco hyemalis*) taken by one experienced observer on the same birds was high ($r^2 = 0.974$; Rogers 1991). Rogers (1991) showed that an experienced observer could detect small changes in fat stores by scoring visible fat, but he cautioned that inter-observer differences in fat scores could affect analyses of fat score data. Fat scores were taken by two observers during our study, and one had not previously used the technique. It is likely the lack of significance in fat score regressions when so many species showed significant mass and condition index gains was, at least in part, due to inter-observer variation and the confounding factor

of observer inexperience. Thus, we emphasize these are estimates, but assume that gains in condition index reflect gains in mass.

If the significance of the relationship of wing chord with respect to time could impart a bias to wing chord condition index values, as Winker (1995a) suggested might occur, one would expect a significant difference between the mean condition indices of the larger (longer-winged) individuals and the smaller (shorter-winged) individuals. Our analysis of Swainson's Thrushes, showing the longer-winged half of our sample did not have different condition indices than the shorter-winged half, demonstrated concern about a possible failure of this methodology is unwarranted.

The year-to-year variability at this site cannot be addressed with these data, especially since the site was severely altered by Hurricane Iris. Species with significant daily gains in 1 year in Minnesota during a 3-year study often showed significant gains in more than 1 year (Winker 1995a). However, Dunn (2000) has shown significant differences in mass gains among years at a single site in a single species. Habitat damage caused by Hurricane Iris may have changed the suitability of the site for some migrants, although it is notable that four of the six species in our sample still had significant mass gains at this site after Hurricane Iris.

Species such as Veery and Swainson's Thrush, whose winter ranges are entirely or largely in South America, might have been expected to be fattening as much as Red-eyed Vireos, which also winter entirely in South America. A migration strategy that would account for low levels of fattening is that higher resource certainty in the tropics compared to temperate habitats might not require depositing large amounts of fat; individuals may even be less likely to fatten if they are already close to their winter destinations (Winker 1995a). However, this hypothesis does not seem to apply to Veeries and Swainson's Thrushes, which were generally carrying large amounts of fat at our site (Table 1). This may explain why Veeries apparently were not fattening at the site (Table 3) and Swainson's Thrushes had the lowest estimate of all fattening species (Table 5), even though they were among the species with the farthest minimum distance yet to travel. The significant differences in several species between lean or fat-free mass and mean mass at our site (and the generally heavy fat loads for several species; Table 1) demonstrate that stopover sites farther north are important areas for fattening for some species. Where the species that arrive fat obtain this fat, and why some species arrive fatter than others, remain important ecological and evolutionary questions.

The high level of fattening by some species and the high level of fat already carried by others is similar to the amount of fattening observed in migrants preparing to make western trans-Atlantic flights from New England (e.g., Nisbet et al. 1963) and trans-gulf flights from the central coast of the Gulf of Mexico (Woodrey and Moore 1997). This is in contrast to the generally low levels of fattening observed in other, mid-continental studies (Winker et al. 1992, Dunn 2002), and is different from the low levels of fattening observed by Winker (1995a) on the Isthmus of Tehuantepec. The high levels of fat observed at our site may be in preparation for a long-distance migratory flight, rather than shorter flights south through Central America. The emaciated migrants observed by Rogers and Odum (1966) in Panama would seem to suggest they arrived from a great distance, also supporting the possibility of longer flights over Central America, rather than shorter

flights through it. Mass gain data from farther south in Central America would be useful in elucidating this situation.

Our study suggests that lowland forests in the southeastern Yucatan Peninsula are important to many species of transient migrants as an area to build fuel stores. Some species showed average trends of depositing sufficient fat in 1 day for an entire night of migration. However, some species arrived at this site carrying substantial fat loads apparently from farther north. This study combined with other studies of fattening and stopover ecology of Nearctic-Neotropical migrants is helpful for developing hypotheses about geographic variation and interspecific differences in fuel deposition strategies in the Nearctic-Neotropical migration system. Much work remains to be done in many of these same areas during spring migration, and there are few or no published data collected during any season from South America, Central America between Belize and Panama, or the southeastern United States. It does appear that more than one strategy for fattening in northern Central America has evolved among passerine migrants.

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