SPRING STOPOVER AND REFUELING AMONG MIGRANT PASSERINES IN THE SIERRA DE LOS TUXTLAS, VERACRUZ, MEXICO

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ABSTRACT.—The narrowing of the North American continent at the Isthmus of Tehuantepec creates an important geographic bottleneck for songbirds on their northward spring migrations. The Sierra de Los Tuxtlas, in the northwestern portion of the Isthmus, provide an ideal location from which to address questions of resource use and fuel acquisition during migration. We operated mist nets during morning and evening to capture passerines during spring migration in 2003 and 2004. Seven of 13 taxa had significant diurnal increases in body condition (an index of size-adjusted mass): Swainson's Thrush (*Catharus ustulatus*), Wood Thrush (*Hylocichla mustelina*), Magnolia Warbler (*Dendroica magnolia*), Kentucky Warbler (*Oporornis formosus*), Hooded Warbler (*Wilsonia citrina*), Worm-eating Warbler (*Helmitheros vermivorum*), and Ovenbird (*Seiurus aurocapilla*). All of these species, except Ovenbird, also had a significant increase in fat score. Indigo Buntings (*Passerina cyanea*) had a significant increase in fat score but not in condition index. A comparison with autumn migration at this site showed overall similarities in percentage of species gaining mass and in the amount gained, but there were seasonal differences within species. There was no relationship between increase in body condition and a mainland versus trans-gulf migratory strategy. *Received 13 November 2007. Accepted 19 March 2011.*

Migration places intense physical demands on birds. One of the main adaptations enabling birds to make long-distance seasonal migrations is fat deposition (Blem 1990, Rogers 1991). Food resources at stopover locations are likely critical and, because the geography of Middle America causes a relatively rapid latitudinal decline in available space for landbirds migrating south in autumn, competition for food resources may be high. Land availability for these birds during spring migration increases rapidly north of the Isthmus of Tehuantepec. Several studies have addressed refueling and stopover ecology during autumn on this isthmus and farther south in Middle America (Galindo et al. 1963; Galindo and Mendez 1965; Rogers and Odum 1966; Child 1969; Winker 1995a, b; Johnson and Winker 2008), but there are few reports of work conducted in spring (e.g., Galindo et al. 1963, Wilson et al. 2008).

Our field site in the Sierra de Los Tuxtlas in the northwestern portion of the Isthmus of Tehuantepec, Mexico, provides an ideal location from which to study refueling strategies and stopover ecology among migrant songbirds. The ecology of migrating birds in this region is only beginning to be understood (Rappole and Warner 1980; Rappole 1995; Winker 1995a, b). This site was used

previously to investigate refueling by autumn migrants (Winker 1995a), which permits direct comparisons of seasonal refueling strategies. Our objectives were to gather data on fat levels and mass gains among the common, nocturnally migrating passerines passing through Los Tuxtlas during spring migration to understand seasonal and geographic patterns of fuel deposition and route selection in this region. Specifically, we collected data during two migratory seasons to address four questions. (1) What quantity of fat do spring migrants carry through this region? (2) Do they show a net gain in fuel during stopover? (3) Are there differences in how this site is used for refueling between spring and autumn? (4) What can be inferred about route selection in this region?

METHODS

Study Area.—We conducted fieldwork in the Sierra de Los Tuxtlas (Fig. 1) in southern Veracruz, Mexico, 90 km southeast of Veracruz city. This range of mountains is in the northwestern portion of the Isthmus of Tehuantepec and is isolated from the Sierra Madre Oriental by extensive lowlands. The Los Tuxtlas region encompasses ~4,200 km² and is dominated by Volcan San Martin and Volcan Santa Marta, each reaching >1,500 m in elevation. The Gulf of Mexico is a short distance from the mountains to the north and east. Habitat in the region was formerly dominated by the farthest north neotropical evergreen rain forest but, due to deforestation,

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FIG. 1.   Mexico and Central America indicating location of field site in the Sierra de Los Tuxtlas, Mexico.

it is now a mosaic with a high percentage of pasture, fence rows, and isolated trees (Dirzo and Garcia 1992). Andrle (1964) estimated that 50% of the region was forested in 1962; by 1986 15% of forests remained (Winker et al. 1990, Dirzo and Garcia 1992), and in 1994 only 7–10% of the region was forested (Winker 1997). The remaining forest is primarily in the highlands and is scarce below 500 m above sea level (Rappole et al. 1994).

Our field site is on the southern edge of the 700-ha Estacion de Biologia Los Tuxtlas (18° 34′ 30″ N, 95° 04′ 20″ W) operated by the Instituto de Biologia at the Universidad Nacional Autonoma de Mexico. The field station protects one of the few remaining large tracts of lowland evergreen forest in the region. The climate is hot and wet with a mean annual temperature of 25° C (Soto and Gama 1997). Annual precipitation is 4.5–4.9 m with a short drier season from March to May (Soto and Gama 1997). Our netting site was on the edge of the Estacion in primary and second-growth forests ∼150 m above sea level. The exact netting site was used previously by Winker (1995a), and we placed nets as precisely

as possible in the same net lanes. Canopy heights in the primary forest ranged from 30 to 35 m (Ibarra-Manriquez et al. 1997). Second growth areas had variable canopy heights from 3 to 20 m.

Data Collection.—Thirty-six standard nylon mist nets (12 × 2.6 m, 30 and 36 mm mesh) were placed 30 m apart in primary and second-growth forest and operated (weather permitting) during daylight hours. The outer rows of nets encompassed an area of ∼1.8 ha. Effort was concentrated in the morning and evening. Nets were open for 8,395 net hrs between 21 February and 27 April 2003 and for 2,312 net hrs from 5 to 29 April 2004. We placed captured birds in light cloth bags and brought them to a central processing area. Birds were banded, wing chord and tail lengths were measured to the nearest 0.1 mm using vernier calipers, and birds were weighed to the nearest 0.1 g using Pesola spring scales. Fat scores were assigned following Helms and Drury (1960).

Data Analyses.—T-tests were used to examine gross differences in overall condition (mass/wing chord × 100) between years. We pooled data from both field seasons because only Hooded

TABLE 1. Sample sizes and quantified variables with means (SD) for 13 taxa captured during spring 2003 and 2004 in the Sierra de Los Tuxtlas, Mexico. (Hooded Warblers are for 2003 only).

Species	*n*	Mean time of capture	Mass, g	Wing chord, mm	Tail, mm	Fat score
Empidonax spp.	35	1111	11.8 (4.91)	66.5 (7.75)	55.5 (5.07)	0.8 (0.9)
Gray-cheeked Thrush (*Catharus minimus*)	58	1157	27.1 (3.14)	98.8 (3.78)	69.1 (4.52)	1.4 (0.9)
Swainson's Thrush (*C. ustulatus*)	323	1147	30.8 (3.40)	95.5 (5.68)	66.2 (3.52)	2.1 (1.2)
Wood Thrush (*Hylocichla mustelina*)	120	1118	47.6 (5.99)	100.0 (14.73)	67.7 (3.39)	2.1 (1.5)
Gray Catbird (*Dumetella carolinensis*)	38	0929	35.1 (2.62)	86.9 (2.65)	89.8 (3.83)	1.3 (1.1)
Magnolia Warbler (*Dendroica magnolia*)	39	1212	7.9 (0.83)	57.5 (2.07)	47.2 (2.11)	0.9 (1.0)
Kentucky Warbler (*Oporornis formosus*)	136	1151	13.4 (1.67)	65.0 (2.60)	46.8 (2.41)	1.7 (1.4)
Hooded Warbler (*Wilsonia citrina*)	171	1132	11.0 (2.93)	61.9 (3.98)	53.8 (4.23)	1.8 (1.3)
Worm-eating Warbler (*Helmitheros vermivorum*)	78	1124	13.7 (1.82)	66.7 (2.91)	47.7 (2.36)	2.5 (1.6)
Yellow-breasted Chat (*Icteria virens*)	43	1042	26.4 (2.81)	73.6 (2.53)	71.4 (3.76)	2.4 (1.3)
Ovenbird (*Seiurus aurocapilla*)	68	1125	18.5 (1.81)	72.7 (2.62)	51.6 (1.83)	1.3 (1.1)
Painted Bunting (*Passerina ciris*)	31	1013	15.8 (1.89)	69.4 (2.67)	53.8 (2.46)	1.4 (1.3)
Indigo Bunting (*P. cyanea*)	159	1111	15.2 (4.57)	65.7 (4.94)	50.0 (3.39)	1.4 (1.2)

Warbler (*Wilsonia citrina*) had a significant difference between years ($t = 1.99$, $P = 0.013$). We selected 2003 for analyses for the Hooded Warbler to avoid confounding analyses with apparent between-year differences; 2003 had the larger sample (2003:171 vs. 2004:36). Twelve migrant species and the genus *Empidonax* had sufficient numbers of captures for analyses ($n \geq 30$; Table 1). We pooled data for Least Flycatcher (*E. minimus*) and 'Traill's' flycatchers (*E. alnorum* and *E. traillii*) to increase sample size sufficiently for *Empidonax* flycatchers to be included in analyses (this may have included a few *Empidonax virescens*, although we had no specimens). The *Empidonax* group is hereafter referred to as one of the study 'species.' One of our goals was to contrast migrants at this site in spring with the same site in autumn; thus, we followed Winker (1995a) in analytical assumptions and in including all first captures, which for some species may include a small number of locally wintering birds. We reduced the likelihood of including these in three ways. (1) Early-season captures of overwintering species were banded and excluded. (2) The site is small, most of these species are territorial in winter and, if step one missed a few birds, they were numerically swamped by passage migrants. (3) We focused netting during 2004 on the period of greatest migrant movement through this area.

Our method of quantitatively estimating mass gains among stopover migrants assumes that birds foraging in a suitable environment will have a diurnal mass increase from food intake and fuel deposition with subsequent loss at night due to fasting, nocturnal metabolism, and excretion of undigestible material. Non-foraging individuals, or those in an unsuitable environment, will show a diel or 24-hr mass decrease. We created a 'condition index' for each first-time capture by dividing mass by wing chord and multiplying this value by a constant (100). Wing chord has been shown to be an appropriate proxy for size (Winker et al. 1992a, Winker 1995a). We then regressed condition index on time of day of capture (first captures only) to examine whether there was diurnal increase in condition, averaged across all sampling days. This technique follows Winker et al. (1992a) and Winker (1995a) and examines species-level trends. Body mass is the most important variable, and inclusion of a size-related variable in the condition index somewhat corrects for size differences among individuals. (Linear regressions of wing chord on time of day showed no significant relationships for any species examined.) Mass has been shown in fat-free mass studies to correlate with fat carried (Rogers 1965, Rogers and Odum 1966). The underlying assumption is that condition index is correlated with amount of fuel carried.

We used fat scores, gauged from visible furcular and abdominal fat, to corroborate evidence for trends observed in condition indices (Winker 1995a, Dunn 2002). Fat scores are somewhat qualitative and subject to variation between observers, and are not suitable for

quantitative estimates of gains. Standard linear regressions may not be appropriate due to the categorical nature of fat scores; but they have been used in other studies (e.g., Dunn 2001, 2002; Johnson and Winker 2008) and have heuristic and comparative value. We conducted both linear and ordinal regressions to examine whether using an ordinal regression would yield different results. We regressed fat scores on time of capture using both methods.

We compared (at the species level) estimated daily gains with an estimated distance of migration yet to be accomplished to examine whether migration distance affected fattening strategy. We used linear regression to compare the slopes of the lines from the condition index versus time of day regressed against the distance to the middle of each species' breeding range. Distances were estimated using range maps in the Birds of North America series (Payne 1992, Briskie 1994, Evans Ogden and Stutchbury 1994, Hall 1994, Van Horn and Donovan 1994, Cimprich and Moore 1995, Roth et al. 1996, Hanners and Patton 1998, McDonald 1998, Lowther et al. 1999, Evans Mack and Wang 2000, Sedgwick 2000, Eckerle and Thompson 2001, Lowther et al. 2001). Migration strategies differ among our study species with some categorized as exclusively trans-gulf migrants, others following the coast northward, and a few using both routes; these same references were used to categorize each species.

We estimated diurnal mass gains for each species by taking the slope of the regression line for trends in condition index versus time of day (if significantly different from zero), multiplying it by the average number of hours of bird activity (12.5 hrs from field notes), multiplying this value by the average wing chord of the individuals in the sample, and dividing by 100. Recaptures were excluded (Winker 1992b). Total 24-hr mass gains were estimated by subtracting nocturnal loss (estimated as 4.5% of average body mass from Mueller and Berger 1966) from the estimated average diurnal increase. We used a value of 30.2 kJ energy/g fuel (Pennycuick 2003: Table 1) for our flight capacity estimates, which assumes a fat to protein ratio of 0.95 for deposited fuel (Johnson and Winker 2008).

We examined whether species carrying a higher proportion of fat at first capture acquire less fuel than those with relatively low reserves by regressing the estimate of percent of mass gained in a 24-hr period against percent of a species' average mass greater than fat-free mass (after Dunning 1993) for the species that showed significant diel gains. We arcsine transformed the data and used linear regression due to the apparently linear nature of the data.

Percentages of species recaptured after a night or more at the site were regressed against slopes of the condition index regression to examine whether a relationship was present between time on the site and refueling. The number of hours and distance that the average captured individual was capable of flying were estimated using the average species-level diel gains, rates of energy use during migration (Tucker 1974), and published values for the energetic content of fat and flight speed: 30.2 kJ/g (Pennycuick 2003) and 40.7 km/hr (Nisbet et al. 1963). The latter estimate is based on Swainson's Thrush (*Catharus ustulatus*) and might vary among our study species (Alerstam et al. 2007). We also calculated the proportion of the population capable of making the flight from the Sierra de Los Tuxtlas northward across the Gulf of Mexico in a single flight, using Galveston, Texas as the destination.

RESULTS

Swainson's Thrushes, Wood Thrushes (*Hylocichla mustelina*), Hooded Warbers, Magnolia Warblers (*Dendroica magnolia*), Kentucky Warblers (*Oporornis formosus*), and Ovenbirds (*Seiurus aurocapilla*) had significant positive slopes in condition index (Table 2, Fig. 2). No species had significant negative slopes. Diurnal condition slopes did not differ significantly from zero in six taxa: *Empidonax,* Gray-cheeked Thrushes (*Catharus minimus*), Gray Catbirds (*Dumetella carolinensis*), Worm-eating Warblers (*Helmitheros vermivorum*), Yellow-breasted Chats (*Icteria virens*), Painted Buntings (*Passerina ciris*), and Indigo Buntings (*P. cyanea*).

Both linear and ordinal regressions of fat scores on time of day indicated the same species had significant gains. These results corroborated the observed increases in condition index. Only the Ovenbird had significant diurnal condition gains but did not have corresponding diurnal increases in fat score. The Indigo Bunting did not have positive condition gains but had a significant increase in fat score (Table 2). A considerable percentage of Indigo Buntings (34%), Magnolia Warblers (34%), and *Empidonax* flycatchers (36%) had some body molt. This additional

TABLE 2.   Regression of condition index (1) and fat score (2) on time of capture and migration strategy for 13 taxa captured during spring migration in the Sierra de Los Tuxtlas, Mexico. All significant regressions were positive; regression slopes are in Table 3.

Species	Condition index			Fat score			Migration strategy
	r^2	F	P	r^2	F	P	
Empidonax spp.	0.071	2.36	ns	0.076	2.53	ns	mainland
Gray-cheeked Thrush	0.005	0.28	ns	0.003	0.16	ns	trans-gulf
Swainson's Thrush	0.038	12.10	<0.001	0.069	24.37	<0.001	mainland and gulf
Wood Thrush	0.088	11.06	<0.001	0.067	8.16	0.005	mainland and gulf
Gray Catbird	0.003	0.09	ns	0.011	0.40	ns	mainland and gulf
Magnolia Warbler	0.130	5.39	0.026	0.163	7.03	0.012	trans-gulf
Kentucky Warbler	0.048	6.59	0.011	0.065	8.98	0.003	mainland
Hooded Warbler	0.063	11.33	<0.001	0.160	31.94	<0.001	trans-gulf
Worm-eating Warbler	0.058	4.62	0.035	0.066	5.27	0.025	trans-gulf
Yellow-breasted Chat	0.007	0.31	ns	0.011	0.44	ns	mainland and gulf
Ovenbird	0.057	4.01	0.049	0.037	2.48	ns	trans-gulf
Painted Bunting	0.002	0.05	ns	0.014	0.42	ns	mainland and gulf
Indigo Bunting	0.009	1.34	ns	0.063	10.31	0.002	trans-gulf

energetic demand may limit the amount of fat individuals can carry and their ability to refuel. Of these three species, Magnolia Warblers had a significant positive increase in both body condition and fat score throughout the day, and Indigo Buntings had significant positive diurnal gains in fat score.

Diurnal mass gains were estimated for the seven species with non-zero trends in condition index. Subtracting estimated nocturnal losses gave an estimate of average mass gain over a 24-hr period. Mass gain estimates varied from 2.8 to 7.7% of a species' average body mass (Table 3). No species had a net loss in condition. Estimated gains were lowest for Swainson's Thrush (2.8% of mean body mass) and highest for Wood Thrush (7.7%; Table 3).

Nine of the 10 species in our study for which fat-free mass data were available (mean, sample size, min-max, and SD) were significantly heavier than fat-free mass (Table 4). Only Magnolia Warblers were not significantly different. However, the lack of visible fat does not preclude the presence of internal or blood-borne fat (extracted by Odum, *in* Dunning 1993), and fat scoring is subject to variation (Krementz and Pendleton 1990; Table 5). However, use of fat-free estimates based on fat scores provides a second useful method for estimating the amount of fat available for migration.

There was no relationship between refueling level and migration distance from Los Tuxtlas to the center of the breeding range ($F = 0.271$, $P =$ 0.62). There was a significant negative correlation between average amount of fuel carried and extent of refueling observed for the seven species with significant diel gains (arcsine transformed data; $F = 10.31$, $P = 0.024$; Fig. 3). A significant relationship was found ($r^2 = 0.399$, $F = 7.289$, $P = 0.021$) when percent of recaptures (after 24 hrs; Table 6) was regressed against the slopes of the condition index regressions for all study species (Table 3). This indicates that species with a higher proportion of individuals spending more than 1 day on the site refuel more than those with higher rates of daily departure (Table 6).

Flight capacities were estimated for those species for which fat-free mass data were available. The average individual of these species was capable of between 2 and 7 hrs of flight after a single day's foraging (Table 7), based on net daily gains for those species showing significant refueling (Table 3). Total flight distances, assuming still air and exhaustion of all fuel reserves, would allow a range of 323 to 674 km, depending on species (Table 7). These distances are clearly insufficient for a trans-gulf flight in still air of 1,150 km departing from Los Tuxtlas to Galveston, Texas. These distances are substantially reduced, from 66 to 425 km, when using flight capacity estimates based on the average mass of individuals with zero fat score, as are the number of individuals capable of completing a trans-gulf flight to Galveston (Table 8). The average mass of Gray-cheeked Thrushes with zero fat score, perhaps due to geographic variation in body size,
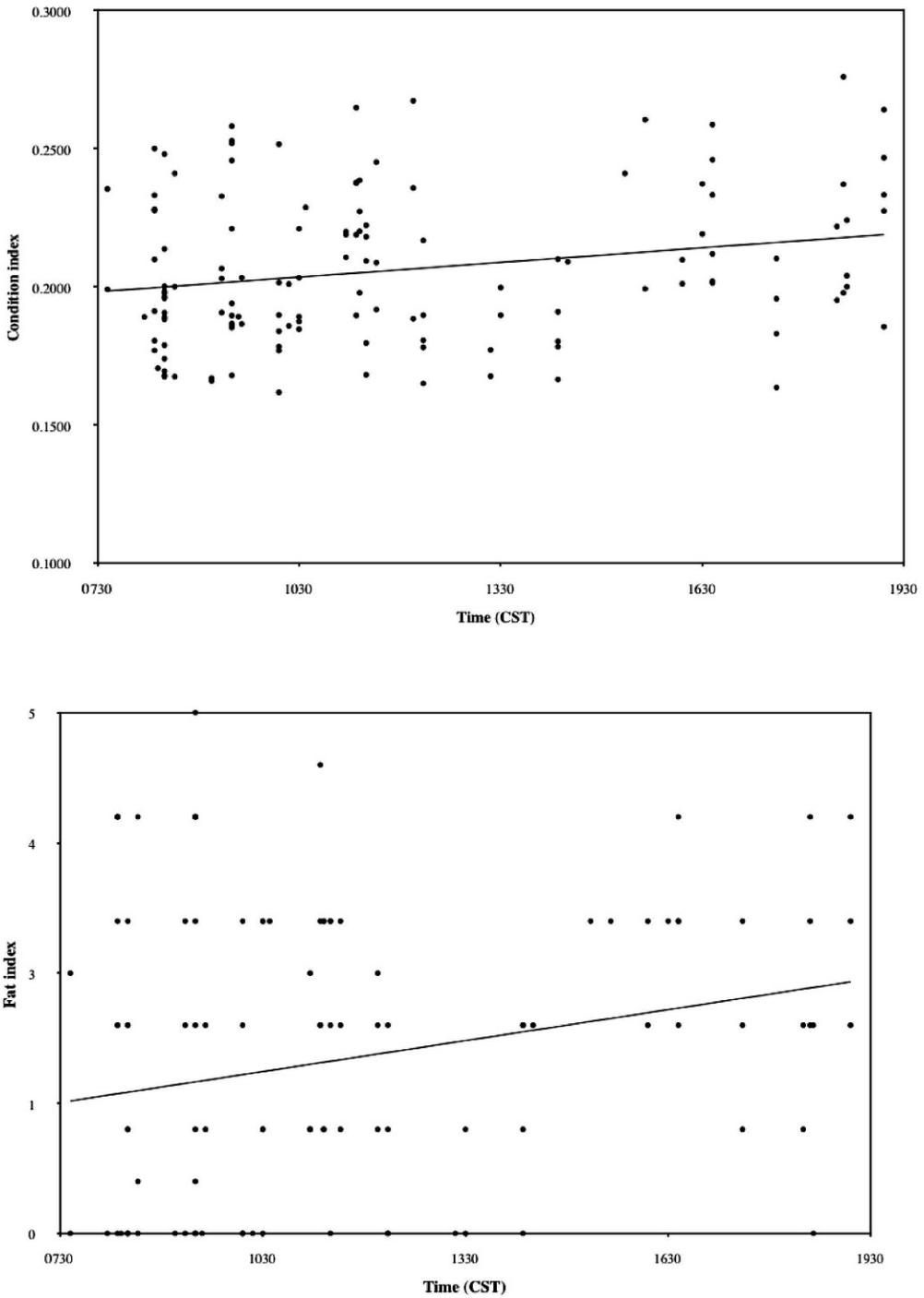
FIG. 2.   Condition and fat indices regressed against time for Kentucky Warblers captured during spring migrations, 2003 and 2004, in the Sierra de Los Tuxtlas, Mexico (condition: $n = 133$, $r^2 = 0.05$, $P = 0.004$; fat index: $n = 133$, $r^2 = 0.065$, $P = 0.003$) showing the best linear model.

TABLE 3. Change in mass, indicating slope (m), diurnal gain (g) based on a 12.5-hr day, nocturnal loss (g) based on 4.5% of species' mean mass, estimated 24 hr net gain (g), and percentage of the species' average mass in the Sierra de Los Tuxtlas, Mexico in spring.

Species	m	Diurnal gain	Nocturnal loss	Net gain/day	% of mass
Swainson's Thrush	0.00188	2.243	1.386	0.858	2.79
Wood Thrush	0.00465	5.813	2.141	3.671	7.72
Magnolia Warbler	0.00146	1.046	0.411	0.634	6.94
Kentucky Warbler	0.00171	1.393	0.601	0.791	5.92
Hooded Warbler	0.00118	0.913	0.488	0.424	3.91
Worm-eating Warbler	0.00150	1.253	0.615	0.638	4.67
Ovenbird	0.00156	1.418	0.831	0.587	3.18

sex ratios, or unknown factors, was 0.7 g less than the fat-free mass. The average mass of individuals with fat scores of zero for all other species was greater than the fat-free mass.

We examined the proportion of the sample population capable of completing a trans-gulf flight in still air by calculating the amount of fuel necessary for each species using both techniques for estimating fuel content and comparing it to the estimated amount of fuel carried by each individual (Table 8). Percentages of the populations of study species capable of the flight varied from 0 to 15.4% using a base of fat-free mass, and from 0 to 9% using a base of zero-fat score individuals. Hooded Warblers had the most dramatic difference between the two techniques (13.5 vs. 0%), whereas some species varied little or none.

We used ANOVA comparing the standard errors of the regressions to ascertain whether single-route migrants fattened differently than dual-route migrants; this test failed to show significant differences between groups ($F = 0.144$, $P = 0.932$).

DISCUSSION

The majority of migrant passerines in our study carried substantial quantities of fat. Nine of the 10 study species that were comparable with Odum (in Dunning 1993) had an average body mass significantly greater than fat-free mass. The amount of fuel estimated varied from 7 to 23% of live mass. Eight of the 13 study taxa had significant diel gains in either body condition or fat score. However, neither diel gains nor total fat carried (Tables 5, 7) were sufficient for the average individual of any species to cross the Gulf of Mexico from Los Tuxtlas in still air (Fig. 4). A lack of power due to small sample sizes cannot fully explain why some but not all taxa had significant gains. Species such as Yellow-breasted Chat and Gray-cheeked Thrush did not have any indication of change in diurnal condition or fat score trends despite substantial sample sizes (Tables 1, 2).

Body molt was noted in three taxa; two had significant diel gains either in condition index or fat score. Molt places additional energetic de-

TABLE 4. Comparison of fat-free mass (from Odum *in* Dunning 1993) to mean mass of study species captured in spring in the Sierra de Los Tuxtlas, Mexico using two-sample *t*-tests.

Species	Fat free mass (g)	Tuxtlas mass (g)	Difference (g)	% of live mass	t	P
Gray-cheeked Thrush	25.30	27.13	1.93	7	3.78	<0.001
Swainson's Thrush	24.18	30.79	6.61	21	28.89	<0.001
Wood Thrush	42.21	47.54	5.33	11	8.37	<0.001
Gray Catbird	31.80	35.09	3.29	9	6.94	<0.001
Magnolia Warbler	6.92	7.89	0.97	12	0.75	ns
Kentucky Warbler	11.36	13.38	2.02	15	13.61	<0.001
Hooded Warbler	8.20	10.60	2.40	23	22.63	<0.001
Worm-eating Warbler	10.79	13.62	2.83	21	12.08	<0.001
Ovenbird	15.52	18.55	3.03	16	10.87	<0.001
Indigo Bunting	12.34	14.70	2.36	16	14.58	<0.001

TABLE 5.   Flight capacity estimates based on birds captured in the Sierra de Los Tuxtlas, Mexico presenting mean mass of zero fat score birds, sample sizes and standard deviations, estimated fat, and maximum hours and distances possible assuming all mass greater than the average when fat score is zero is fuel that could be used for migration.

Species	Tuxtlas zero fat score (*n*, SD)		Estimated fat (g)	Maximum hrs of flight	Maximum flight distance (km)
Empidonax spp.	10.81	(12, 1.09)	1.02	6.85	279
Gray-cheeked Thrush	24.50	(5, 2.81)	2.63	7.86	320
Swainson's Thrush	26.84	(16, 2.13)	3.95	10.44	425
Wood Thrush	42.29	(13, 4.81)	5.25	9.09	370
Gray Catbird	34.39	(7, 2.70)	0.70	1.63	66
Magnolia Warbler	7.64	(7, 0.85)	0.34	3.38	138
Kentucky Warbler	11.99	(37, 0.85)	1.39	8.27	337
Hooded Warbler	9.52	(28, 0.68)	1.08	8.07	328
Worm-eating Warbler	11.86	(8, 1.00)	1.76	10.30	419
Yellow-breasted Chat	23.00	(1, n/a)	3.38	10.39	423
Ovenbird	17.59	(21, 2.09)	0.96	4.16	169
Painted Bunting	15.44	(4, 0.71)	0.37	1.87	76
Indigo Bunting	13.66	(33, 1.24)	1.51	7.95	324

mands on migrating birds, but it did not appear to prevent net fuel gains at this site; examination of the percentage of individuals molting in a species versus the estimated diel mass gain showed no relationship (not shown).

Spring vs. Autumn.—Sandberg (1996) and Sandberg and Moore (1996) hypothesized that

resource uncertainty and the impending breeding season would cause spring migrants to fatten more dramatically during migration through more northern latitudes than in autumn. Winker (1995a) proposed this same pattern might be found at the Los Tuxtlas stopover site. However, the percentage of species with significant refuel-
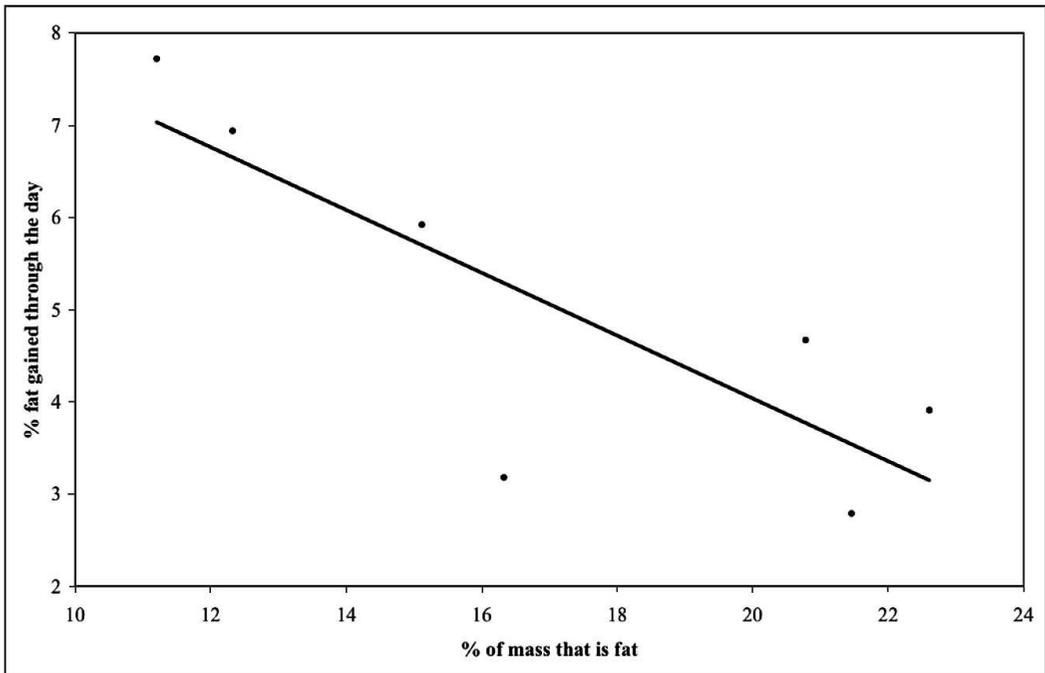

FIG. 3.   Regression of percent of mass carried above fat-free mass (estimated from Odum *in* Dunning 1993) vs. estimated percent of mass (based on g of fuel from Table 1) gained during the day in the Sierra de Los Tuxtlas, Mexico for the seven migrant species showing significant positive increases in body condition ($r^2 = 0.675$, $P = 0.023$).

TABLE 6. Total captures, numbers and percent of individuals recaptured >1 night after initial capture, and numbers and percent of individuals recaptured >2 nights after initial capture in the Sierra de Los Tuxtlas, Mexico.

Species	Total captures	Recaptures (n)	Percent recaptured	Recaptured after 48 hrs (n)	Percent recaptured after 48 hrs
Empidonax spp.	35	2	5.7	2	5.7
Gray-cheeked Thrush	58	3	5.2	1	1.7
Swainson's Thrush	323	20	6.2	9	2.8
Wood Thrush	120	26	21.7	15	12.5
Gray Catbird	38	1	2.6	1	2.6
Magnolia Warbler	39	4	10.3	4	10.3
Kentucky Warbler	136	25	18.4	22	16.2
Hooded Warbler	171	42	24.6	30	17.5
Worm-eating Warbler	78	17	21.8	12	15.4
Yellow-breasted Chat	43	3	7.0	2	4.7
Ovenbird	68	19	27.9	14	20.6
Painted Bunting	31	2	6.5	1	3.2
Indigo Bunting	159	5	3.1	4	2.5

ing was not different between seasons at this site: six of 11 species (55%) in Winker (1995a) and seven of 13 species (54%) in this study. Diel gains, estimated using identical assumptions (Winker 1995a), were remarkably similar among species gaining mass at this site, averaging 5.1% in autumn (Winker 1995a) versus 5.0% in spring. Species that had significant gains differed between seasons but, in spring, no species had a net loss in condition as occurred on the site during autumn (Winker 1995a).

Winker (1995a) detected no significant diel condition increases in Wood Thrushes, Hooded Warblers, and Ovenbirds at this site in autumn, but each had significant increases at this same site during spring. All three of these species winter in large numbers in Los Tuxtlas and surrounding regions. It is likely that many individuals captured in autumn were arriving on or near their wintering areas and had no need to refuel. In spring, these species are embarking on migration and/or arriving from areas to the south, and the need for refueling may be greater. However, Gray Catbirds also winter at Los Tuxtlas, and Winker (1995a) detected significant autumn diel gains in this species where none was apparent in spring. The reasons for seasonal differences remain unclear.

Route Selection.—Migrants at this site were carrying insufficient fuel for long-distance flight. Trans-gulf migrants should be expected to demonstrate higher levels of refueling or to remain

TABLE 7. Flight capacity estimates for average individuals of the study species indicating cost of flight (g of fuel/hr), maximum hours possible based on a single day in the Sierra de Los Tuxtlas, Mexico, and estimates for maximum hours and distances possible.

Species	Flight cost (g/hr)[a]	Hours of flight daily gains[b]	Maximum hrs of flight[c]	Maximum flight distance (km)[d]
Gray-cheeked Thrush	0.33	NA	5.78	235
Swainson's Thrush	0.38	2.26	17.47	711
Wood Thrush	0.58	6.33	9.22	375
Gray Catbird	0.43	NA	7.66	312
Magnolia Warbler	0.10	6.34	9.68	394
Worm-eating Warbler	0.17	3.75	16.56	674
Kentucky Warbler	0.17	4.65	12.04	490
Hooded Warbler	0.13	3.26	17.90	729
Ovenbird	0.23	2.55	13.12	534
Indigo Bunting	0.18	NA	12.83	522

[a] Based on calculations from Tucker (1974).
[b] Capacity estimates based on 30.2 kJ/g of fuel (Pennycuick 2003).
[c] Calculated by subtracting average mass from average fat-free mass (from Odum *in* Dunning 1993) and assuming difference is fuel.
[d] Assuming average speed of 40.7 km/hr for an average Swainson's Thrush (Nisbet et al. 1963).

longer at the site to accomplish a long overwater flight. If a direct overwater route is followed from Los Tuxtlas by any of our study species, two possible destinations are Galveston, Texas and Mobile, Alabama, which are each 1,150 km from the Sierra de Los Tuxtlas. Our calculations, based on Tucker (1974) and Nisbet et al. (1963), indicate that individuals of the study species varied in the distances they are capable of flying from the site. For no taxa did the average individual carry sufficient fuel reserves for a single trans-gulf flight (Tables 7, 8; Fig. 4). No greater proportion of the populations of trans-gulf migrants was capable of making such a flight than taxa with coastal or dual migration strategies (Table 8). This provides strong inference that birds were generally not crossing the Gulf of Mexico directly from the Isthmus of Tehuantepec on the night following their capture, and that this stopover site is used more for short-distance movements than as a staging site for long movements (Warnock 2010). These estimates assume calm wind conditions across the Gulf of Mexico. The proportion of individuals capable of the flight might increase substantially with a tail wind.

TABLE 8. Number of sampled individuals and estimated proportion of the population with sufficient fuel to fly 1,150 km in still air from the Sierra de Los Tuxtlas, Mexico to Galveston, Texas using fat-free mass (1), (from Odum *in* Dunning 1993), and (2) from zero fat score individuals as a base.

Species	# of individuals		% of population	
	1	2	1	2
Empidonax spp.	NA	0	NA	0.0
Gray-cheeked Thrush	2	2	3.5	3.5
Swainson's Thrush	35	18	11.0	5.7
Wood Thrush	3	3	2.6	2.6
Gray Catbird	0	0	0.0	0.0
Magnolia Warbler	2	1	5.1	2.6
Kentucky Warbler	12	7	9.0	5.3
Hooded Warbler[a]	23	0	13.5	0.0
Worm-eating Warbler	12	7	15.4	9.0
Yellow-breasted Chat	NA	0	NA	0.0
Ovenbird	2	0	2.9	0.0
Painted Bunting	NA	0	NA	0.0
Indigo Bunting	13	1	8.3	0.6

[a] The dramatic difference between the two methods may be a result of the substantial difference between the average fat-free masses of the two techniques in a relatively small species (1.32 g).
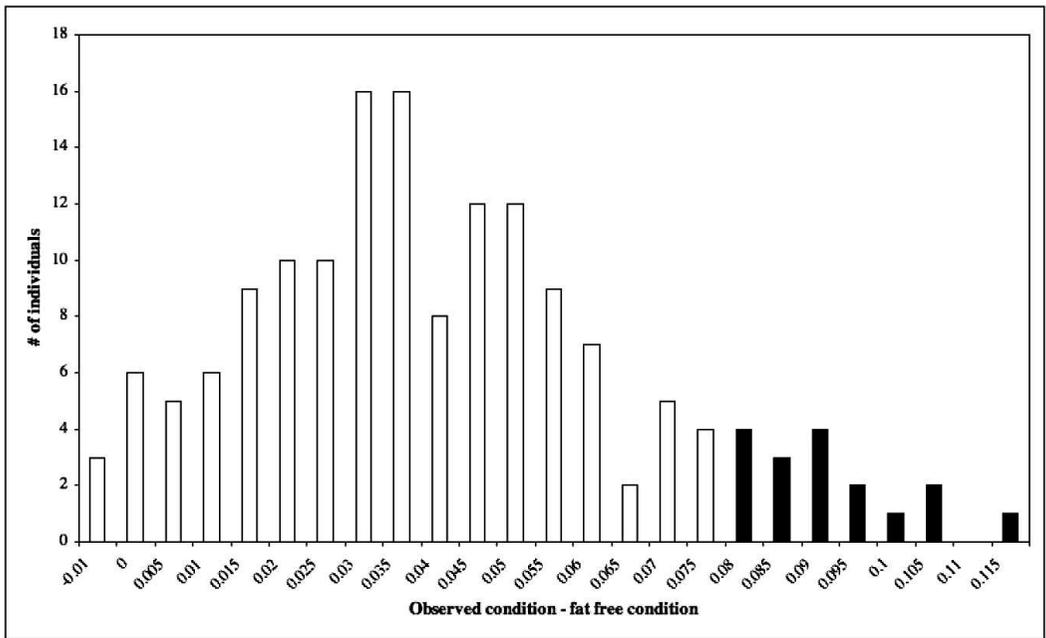

FIG. 4.   Relationship of estimated fat (Observed condition index – fat free condition) for Indigo Buntings captured in spring in the Sierra de Los Tuxtlas. Those with sufficient fat to complete a flight of 1,150 km (the distance from Los Tuxtlas to Galveston, Texas) are shown in black.

Winker (1995a) suggested the majority of captures at this site during autumn were not birds arriving from a trans-gulf flight, but were likely birds moving south along the coast to arrive in Los Tuxtlas. Birds from this same site in spring were likely reversing Winker's (1995a) proposed route and following the coast northward before perhaps making shorter overwater crossings of the northern Gulf or avoiding overwater flights altogether. Eleven of our 13 study taxa occurred in substantial numbers in Rappole et al.'s (1979) study of a stopover site in southern Texas in spring. This suggests some individuals of species thought to be exclusively trans-gulf migrants are moving northward along the Gulf Coast, perhaps crossing few areas or only short distances over open water. Another possibility is that trans-gulf migrants are moving eastward along the southern coast of the Gulf of Mexico and making the crossing by way of the Yucatan Peninsula. Both possibilities allow for arrival of migrants at observation points in the southeastern United States either by land or water (Stevenson 1957, Gauthreaux 1971, Rappole et al. 1979, Wang and Moore 1997). Sampling migrant abundance along the Gulf Coast from the Isthmus northward would provide valuable information about departure and arrival points for trans-gulf migrants.

Fueling Strategies.—Migration routes and distances to breeding areas failed to explain variation in mass gains among species either within or between seasons. Species-level comparisons for our distance estimates to breeding areas are complicated by two factors that we cannot address: the origins and destinations of captured individuals are unknown, and both will likely affect fattening strategies. However, most variation in our data may have a proximate explanation in the relationship found by Dunn (2001): that individuals arriving at a site with lower mass gain more than those arriving with more substantial reserves. Dunn (2001) proposed that individuals arriving at a stopover site with sufficient resources only need a place to rest and maintain reserves, and they may not have substantial net gains even in ideal habitat. The significant negative relationship we found (Fig. 3) between a species-level estimate of fat levels and the amount of fuel a species gained (on average) in a day at this site suggests this relationship may scale up to the species level and help explain single-site patterns among species. A second and perhaps not unlinked relationship that we found is that species that tend to spend more time on the site were also likely to show higher diel gains than those remaining only a few hours (Tables 3, 6). We found a significant positive correlation between the percent of recaptures occurring after 24 hrs (Table 6) and the slopes of the condition index gains. These two findings may provide better insight into interspecific patterns of refueling in Los Tuxtlas than routes, distances traveled, or even seasonality through a complete migration cycle.

Current hypotheses regarding migration through Middle America need refinement. Species thought to be exclusively trans-gulf migrants were, on average, carrying insufficient resources to accomplish a Gulf crossing from Los Tuxtlas and may often not make such crossings. Refueling rates at this site are not higher in spring, and considerable variation occurs among species and between seasons. The total amount of fat carried and time spent at the site appear to be the best predictors of diel refueling gains.

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