AUTUMN STOPOVER ON THE ISTHMUS OF TEHUANTEPEC BY WOODLAND NEARCTIC-NEOTROPIC MIGRANTS

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ABSTRACT.—The Isthmus of Tehuantepec in southern México seems to cause a concentration of Nearctic-Neotropic migrant landbirds during migration. Despite its possible importance as an area for fat deposition, almost nothing is known about how this area is used by migrants. Of 11 small passerine species examined, 6 showed significant diurnal increases in body condition in relation to time of capture. All six showed gains suggesting low to moderate levels of fat deposition, concordant with the concept of the Isthmus as an important source of stopover resources. The area is not used in the same manner by all of these common species, however. The migrants at this site in autumn probably have not arrived via a long-distance, trans-Gulf migration. Comparison with data from other sources suggests that the energetic costs of molt are important at northerly stopover sites, and that modifications are needed in our concepts of Middle American migration routes. *Received 8 February 1994, accepted 1 April 1994.*

THE ISTHMUS OF TEHUANTEPEC in southern México is the northernmost severe narrowing of the North American continental landmass. As such, it seems to result in a funneling and concentration of Nearctic-Neotropic migrant landbirds. The role that this comparatively small area of land plays in the migration strategies of these migrants is essentially unknown. Given the large numbers of migrants that occur on the Isthmus each year, the potential demand in this region for food resources to replenish fat reserves is great. My study was designed to provide data on stopover mass gains among common songbird migrants in this region. The data address broad questions regarding geographic patterns of fat deposition, route selection, and the stopover ecology of some of these species. At present, the lack of knowledge about these basic life-history phenomena prevents an understanding of the selective pressures operating upon migrant populations in Middle America.

A new technique of mass-gain analysis (see Winker et al. 1992a) is applied to 11 species of woodland-associated passerine migrants in autumn. The technique examines all captured birds, and has decided advantages over more traditional methods that examine only recaptured individuals. These advantages include the ability to examine larger samples for each species and to avoid the tenuous assumptions associated with mass analysis of recaptures (Winker et al. 1992a). The method might be used effectively to increase our knowledge of

migrants in poorly known areas like the Isthmus of Tehuantepec. The evidence presented shows different levels of apparent use, however, and a comparison of the results with other studies suggests that we have a long way to go before we achieve a reasonable understanding of the Nearctic-Neotropic migration system and its evolution, particularly that part occurring in Middle America.

STUDY SITE AND METHODS

Field area and methods.—The study site was located in southern Veracruz, México, in the Sierra de los Tuxtlas, which occupies the northwestern region of the Isthmus of Tehuantepec. This area includes the northernmost Neotropical rainforest (Pennington and Sarukhan 1968). Birds were netted on a site located just south of the Estación de Biología Tropical "Los Tuxtlas" of the Instituto de Biología, Universidad Nacional Autónoma de México (18°34′30″N, 95°04′20″W). The site is located near the coast of the Gulf of México. The coastline in this area runs approximately north-northwest to south-southeast; the site was 5 km south and 3 km west of the coastline.

Thirty-six standard, nylon mist nets (12 × 2.6 m; 30- and 36-mm mesh) were placed in mature and second-growth wooded habitats, and were opened whenever weather permitted during daylight hours. Between 5 September and 15 November 1992, the nets were open for 12,608 net-h. Captured birds were weighed to the nearest 0.1 g on a spring scale (Pesola), and wing (chord) and tail lengths were measured to the nearest 0.1 mm using vernier calipers. The fat

level of captured individuals was scored following Helms and Drury (1960).

Mass-gain analysis.—It is assumed that birds feeding in a favorable environment will show an increase in mass during the day, and a decrease at night due to loss of undigestible material (through defecation or regurgitation) and nocturnal metabolism (see Baldwin and Kendeigh 1938, Mueller and Berger 1966, Kendeigh et al. 1969). Birds not feeding, and/or birds in an unfavorable environment, should show a decrease in mass during the day due to metabolism. The method of mass-gain analysis used here examines univariate and multivariate characteristics of captured individuals in relation to time of capture, seeking evidence for significant species-level trends among the entire captured sample. Body mass is the most important of these variables.

Body mass varies due to several factors, but in migrants the amount of fat carried is the most important variable affecting mass (Connell et al. 1960, Odum 1960). Body size also influences mass, and attempting to remove some of the variation in mass caused by size improves estimates of fat content (Connell et al. 1960). Data from fat extractions in a variety of migrant songbird species (e.g. Connell et al. 1960, Odum 1960, Rogers and Odum 1964, Child 1969) suggest that accurate estimates of an individual's fat content can be made using body mass adjusted for individual size (wing length). Based on these findings, I calculate a "condition index" ([mass/size variable] × constant) for captured individuals; it is assumed that this condition value is correlated with the amount of fat carried by the individual, but no attempt is made to estimate the fat content of individuals. Use of the term "condition" is not intended to impart value judgments on individual physical status; high condition index values (implying high fat reserves) are not necessarily "better" (Winker et al. 1992a). Condition values are examined in relation to the time of capture using simple linear regression.

Some comments are in order regarding the use of morphological characters to modify body-mass values to obtain a figure closely related to actual fat content. Linear regressions examining the relationship between time of capture and body mass alone (where variation includes that due to body size) are less likely to reveal significant relationships in populations that are gaining mass during the day because there is more "noise" in the data set. Removing some of the individual variation in mass caused by body size through adjustment of body mass with a size variable is an important exercise (cf. Connell et al. 1960). Such modifications should improve the ability of linear regression to detect diurnal mass changes if they are occurring, and enable more accurate estimates of the degree of these changes. Choosing a character as an estimate of size is not simple. For studies of migrants, a character is needed that, when applied in some fashion to body mass, gives a value that is strongly correlated with individual fat content. The usefulness of wing length in conjunction with body mass for estimating the fat content of individual nocturnal passerine migrants is well established for some species (e.g. Connell et al. 1960, Rogers and Odum 1964, 1966). These authors did not examine other characters, however, and other authors have suggested that wing length is a poor indicator of body size (Rising and Sommers 1989, Freeman and Jackson 1990). Tarsometatarsus ("tarsus") and tibiotarsus lengths have been suggested as reasonable univariate estimates of size based on careful analysis of four passerine species (Rising and Sommers 1989, Freeman and Jackson 1990). However, I found tarsus length to be much less useful than wing or tail lengths in predicting the fat content of individual Tennessee Warblers (*Vermivora peregrina*; unpubl. data). The usefulness of wing length and other characters as size indicators probably varies among species.

A hidden assumption in this method of mass-gain analysis is that there is no temporal bias to size in captured birds. This was not listed as an assumption of the technique by Winker et al. (1992a); I did not think of this possibility. As I will show here, this bias is present in some cases. I do not know why the bias occurs, but the fact that it does suggests data collection should include measurement of more than one character (see Discussion), and data analysis should include examination of morphological characters in relation to time of capture. In cases where size variables are correlated with time of capture, their use in modifying body mass may impart a significant relationship upon condition and time of capture, when in fact what is being observed is a size relationship that has not been completely removed from body mass. Conversely, the effect may be to render invisible an existing mass-related relationship (see *Setophaga ruticilla* below). Much remains to be learned about using morphological characters to remove the effects of individual size variation from body-mass values. It is likely that the best characters (or combinations thereof) will vary with specific morphology.

In Winker et al. (1992a) the size character (flattened wing length) was cubed to bring the linear nature of this variable into concordance with the volumetric nature of mass. This would be appropriate if the character was a perfect indicator of body size; however, because it is not, this method is less accurate than using unmodified values. Using a cubed size variable resulted in condition-index values that were less able to predict actual fat content than unmodified (linear) characters in a sample of Tennessee Warblers (unpubl. data). Linear values are used here.

I follow Nisbet et al. (1963) and Rogers and Odum (1966) in assuming that water loss during nocturnal migration in songbirds is negligible, and that diurnal increases (when present) are not due to recuperation of lost water. Evidence supporting this assumption is presented below.

TABLE 1. Sample sizes, age structure, and mensural characteristics ($\bar{x} \pm$ SD) of the most common woodland migrant species captured.

Species	n	Percent imma- ture[a]	Mass (g)	Wing (mm)	Tail (mm)	r[b]
Catharus mustelinus	60	60.0	44.25 ± 3.63	102.71 ± 3.39	67.53 ± 3.06	0.68
Dumetella carolinensis	107	74.8	33.81 ± 2.72	88.47 ± 2.47	89.36 ± 3.67	0.65
Vireo griseus	140	51.4	10.78 ± 0.89	59.71 ± 1.76	48.25 ± 2.15	0.55
V. olivaceus	273	81.7	18.55 ± 2.24	76.99 ± 2.35	58.85 ± 2.64	0.62
Dendroica magnolia	83	37.3	7.45 ± 0.57	58.54 ± 2.09	48.70 ± 2.07	0.71
Setophaga ruticilla	50	28.0	7.33 ± 0.52	61.05 ± 1.74	55.44 ± 1.90	0.29
Helmitheros vermivorus	34	58.8	12.22 ± 0.77	67.03 ± 2.36	48.79 ± 2.09	0.56
Seiurus aurocapillus	110	42.7	17.29 ± 1.59	73.90 ± 2.50	53.48 ± 2.35	0.69
Oporornis formosus	87	55.2	12.44 ± 1.01	65.83 ± 2.45	47.72 ± 2.11	0.67
Wilsonia citrina	97	45.4	9.48 ± 0.71	63.26 ± 2.50	54.34 ± 2.24	0.66
W. pusilla	30	60.0	6.62 ± 0.45	54.43 ± 1.85	48.66 ± 1.92	0.51

[a] Percent of total sample composed of first-year, or "HY" birds.
[b] Correlations between wing and tail lengths in captured individuals.

For species showing significant relationships between condition index and time of capture, estimates can be made for the mass change of an average individual during a 24-h period. These estimates are made by first calculating the gross daily gains of an individual of average body mass and size; a linear model is used for that particular sample and the average day length for the netting period (here I use 0620-1745 CST, based on field notes of bird activity). Estimates of nocturnal loss are then subtracted from this value. Nocturnal loss estimates (two are used) include: (1) 4.5% of body mass, which was found by Baldwin and Kendeigh (1938:428–429) to be about the average daily variation in body mass among free-living, breeding birds (primarily small passerines, probably not depositing fat); and (2) 4.5% of body mass plus fat lost during nocturnal metabolism. Estimates of fat used in nocturnal metabolism follow the results of Mueller and Berger (1966) for an average Swainson's Thrush (*Catharus ustulatus*) during an 8-h night. This value was scaled for body size to the other species considered here using the field metabolic rates (FMR) for passerines given by Nagy (1987), using average fat-free mass values for species' size. Resting cost for an 8-h night was scaled to the average night length during the netting period, and the mass of fat used in nocturnal metabolism was calculated using an energy content of 39.8 kJ/g of fat (Nisbet et al. 1963).

Values of fat-free mass for all but one of the species showing significant diurnal trends were taken from Odum (*in* Dunning 1993). For Wilson's Warbler (*Wilsonia pusilla*), a fat-free mass of 5.72 g was estimated using the linear model

$$Y = 0.1878 + 0.8357X, \qquad (1)$$

where Y is fat-free mass in grams and X is the mean autumn mass in grams of captured individuals. This model was based on the high correlation ($r^2 = 0.997$) found between fat-free mass and mean autumn mass

among 10 Nearctic-Neotropic migrant species by Winker et al. (1992a).

RESULTS

Eleven migrant species with 30 or more captured individuals are examined; mean body-mass and size characteristics of these birds are given to allow comparison with other studies (Table 1). All birds were in basic plumage, and actively growing feathers were rare. Thus, energetic needs were limited to migration and maintenance costs.

Differences among the 11 species in apparent mass gain are evident from an examination of the characteristics of captured individuals in relation to their time of capture (Table 2). Three species showed no apparent diurnal trends: Wood Thrush (*Catharus mustelinus*), Ovenbird (*Seiurus aurocapillus*), and Hooded Warbler (*Wilsonia citrina*). White-eyed Vireos (*Vireo griseus*) showed no mass-related trends. At the species level, it seems unlikely that average birds of these four species were depositing fat at this site.

Worm-eating Warblers (*Helmitheros vermivorus*) showed a significant diurnal increase in fat level, and may have been depositing fat (Table 2). However, perhaps due to small sample size, verification of fat deposition and estimates of its extent cannot be made because no other relationship was evident.

Five species showed a significant relationship between body mass and time of capture, and six exhibited a relationship between one or both of the condition indices and capture time (Table

TABLE 2. Relationships between characteristics of captured individuals and time of capture. Results from linear regressions.[a]

| Species | Mass | Wing | Tail | Fat | Condition index[b] | |
					1	2
Catharus mustelinus	ns	ns	ns	ns	ns	ns
Dumetella carolinensis[c]	+	ns	ns	+	+	+
Vireo griseus	ns	−	−	ns	ns	ns
V. olivaceus[c]	+	ns	ns	ns[d]	+	+
Dendroica magnolia[c]	+	ns	ns	+	+	+
Setophaga ruticilla[c]	+	+	ns	+	ns	+
Helmitheros vermivorus	ns	ns	ns	+	ns	ns
Seiurus aurocapillus	ns	ns	ns	ns	ns	ns
Oporornis formosus[c]	+	ns	ns	ns	+	ns
Wilsonia citrina	ns	ns	ns	ns	ns	ns
W. pusilla[c]	ns	ns	ns	+	+	ns

[a] Plus ("+") indicates positive association; negative ("−") indicates negative association ($P < 0.05$); ns indicates $P > 0.05$.
[b] Condition index 1 calculated as 100 mass/wing; index 2 as 100 mass/tail.
[c] Species appears to be gaining mass during daylight hours.
[d] Suggestive but nonsignificant positive trend ($P = 0.08$).

2). These species appear to be gaining mass at the site during the day, and estimates of gross and net daily gains can be made. Given the frequency of significant diurnal increases in fat levels (Table 2), it is unlikely that mass (or condition) gains are the result of compensation for water lost during migration.

As in previous studies using this method of analysis (e.g. Winker et al. 1992a, b), no negative diurnal trends (significantly negative linear regressions) were evident. Negative trends might occur at stopover sites in hostile environments (e.g. deserts; see Biebach 1988).

White-eyed Vireos and American Redstarts showed significant correlations between a morphological character and time of capture (Table 2). The reasons for these relationships are unknown. A decrease in wing and tail lengths during the day suggests that larger White-eyed Vireos tended to be captured earlier in the day. American Redstarts showed a positive relationship between wing length (but not tail length) and time of capture (Table 2). A diurnal increase in mass and fat level in this species (Table 2) suggests that a condition index should also show an increase. The condition index using tail length as a size modifier shows the expected relationship, but the index using wing length does not (Table 2). The lack of relationship between the wing-based condition index and capture time is probably a result of the positive correlation between wing length and time of capture.

Findings for three species show that the choice

of morphological character used to calculate a condition index can affect the outcome of a regression examining the relationship between condition and time of capture (see American Redstart, Kentucky Warbler [*Oporornis formosus*], and Wilson's Warbler; Table 2). If wing and tail lengths were equivalent predictors of overall body size, they would be perfectly correlated ($r = 1.0$). The relationships between wing and tail lengths show that this is not so (Table 1). Two of the three species showing significant relationships using only one of the two condition indices have the lowest correlations between wing and tail lengths (Table 1). Among captured American Redstarts this relationship is particularly low ($r = 0.29$; Table 1).

Estimates of the daily gains apparent in six species were calculated using linear models (Table 2). A choice must be made among different linear models to execute these calculations (see Table 2). To help make this choice, gross daily gains were first calculated for each significant model (Table 3). Estimates based on mass increases alone are presented for reference only (Table 3; also see Methods). For three species, there is a choice of which condition index to use for making gain estimates: the Gray Catbird (*Dumetella carolinensis*), Red-eyed Vireo (*Vireo olivaceus*) and Magnolia Warbler (*Dendroica magnolia*; Tables 2 and 3). Gross daily gains estimated for the Gray Catbird and Red-eyed Vireo using both models differed by 0.036 and 0.145 g, respectively. These values represent 1.1 and 9.8%, respectively, of means of the two esti-

TABLE 3. Summary of gross daily mass-gain (g) estimates calculated using significant linear models summarized in Table 2.

| Species | Mass | Condition index[a] | |
		1	2
Dumetella carolinensis	3.46	3.22	3.25
Vireo olivaceus	1.28	1.40	1.55
Dendroica magnolia[b]	0.92	1.06	0.79
Setophaga ruticilla	0.73	—	0.77
Oporornis formosus	1.06	1.21	—
Wilsonia pusilla	—	0.54	—

[a] Condition index 1 calculated as 100 mass/wing; index 2 as 100 mass/tail.

[b] Because of magnitude of differences among estimates for this species, another condition index (100 mass/[wing + tail]) is used to calculate a gross daily gain estimate of 0.91 g (see Table 4).

Fig. 1. Condition (100 mass/wing chord) plotted against time of capture for first captures of Gray Catbirds (*Dumetella carolinensis; n* = 107). Linear model given in Table 4.

mates for these species. The Magnolia Warbler showed a wider divergence between estimates made from the two condition indices: 0.27 g or 29.2% of the mean of the two estimates. This rather large difference prompted the use of another condition index that employs both characters to remove size variability from body-mass values: 100 mass/(wing + tail). This compromise produced a gross-gain estimate close to that calculated using the linear model based on mass alone (see Tables 3, 4, and 5). Estimates of gross daily gains are based entirely on field data (e.g. Fig. 1, Tables 3 and 4). Because a gram of mass gain is not equivalent for each species considered (due to differences in body size, metabolic rates, etc.), it is necessary to consider estimates of net daily gain and their energetic consequences.

Estimates of net daily gains are made using various formulae, estimates, and values from the literature. To calculate these estimates, I chose to use the condition index based on wing length where possible (except for Magnolia Warblers), because the usefulness of this character has been demonstrated in fat-extraction studies on many species (see Connell et al. 1960, Rogers and Odum 1964, 1966). Table 4 presents the linear models used to calculate net daily gains; Table 5 completes the calculations. In birds depositing fat, 24-h (diel) gains will be positive; nocturnal losses will not exceed diurnal gains. Estimates of the mass of major nonfat and metabolized-fat nocturnal losses are subtracted from gross daily-gain figures to produce diel-gain estimates. There are valid reasons for considering two estimates of nocturnal loss (see Baldwin and Kendeigh 1938). The fact
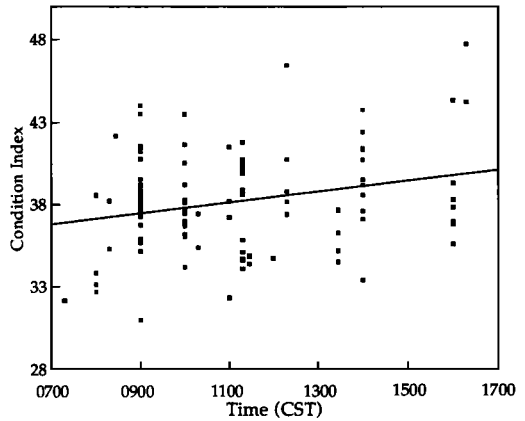
that several variables affect daily changes in body mass (see King 1972) makes it important to recognize that figures for diel changes are only estimates. These estimates, therefore, are given as a range.

Estimates of net daily gains for each species range from a low of approximately 1.7% of mean body mass (Red-eyed Vireo, Wilson's Warbler) to highs of 5.7% (Magnolia Warbler; Table 5) and 8.2% (Traill's Flycatcher [*Empidonax* "*traillii*"]; Winker 1995). Only Wilson's Warbler includes a negative value in the range of net-gain estimates (Table 5). Average individuals of several species may be gaining enough fat at the site to fly for several hours, but, excluding Traill's Flycatcher (see Winker 1995), none of the increases suggest that average individuals are gaining enough to fly for a full night (energetic calculations follow Tucker 1974; Table 5).

Of the species considered, only the Red-eyed Vireo does not winter in the region. All Red-eyed Vireos are transients on the Isthmus of Tehuantepec, en route in autumn to wintering grounds in South America (AOU 1983). The Isthmus is within the wintering ranges of the other 10 species. The study site was small enough that few individuals could overwinter, so the vast majority of birds were transients, and would, therefore, continue on for unknown distances. The farthest that these birds would be traveling in autumn would be to northern Nicaragua (White-eyed Vireo), Panamá (Wood Thrush, Gray Catbird, Magnolia Warbler, Worm-eating Warbler, Hooded Warbler, Wilson's War-

TABLE 4. Summary of linear models for diurnal change in condition (three condition indices used) for species in Table 2 for which gains can be estimated.[a]

| Species | Regression | | | | | |
	b	m	F	P	r	Gain/day[b]
Dumetella carolinensis[c]	34.67	0.0031836	6.73	0.011	0.25	3.636
Vireo olivaceus[c]	22.17	0.0015954	5.16	0.024	0.14	1.822
Dendroica magnolia[d]	6.07	0.0007426	14.18	<0.001	0.40	1.935
Setophaga ruticilla[e]	11.75	0.0012118	4.48	0.040	0.30	1.384
Oporornis formosus[c]	17.10	0.0016104	7.50	0.008	0.29	1.839
Wilsonia pusilla[c]	11.17	0.0008660	4.34	0.047	0.37	0.989

[a] Equations are $Y = b + mX$, where Y is condition (100 × g/mm), b is Y-intercept, m is slope (condition gained per h/100), and X is time (h/100). F-statistic and corresponding P-value indicate how well regression model fits data. r is correlation coefficient, and serves as measure of strength of relationship between time (X) and condition (Y).

[b] Gain in condition for one average day (11.42 h) during netting period.

[c] Linear model based on condition index of 100 mass/wing.

[d] Linear model based on condition index of 100 mass/(wing + tail).

[e] Linear model based on condition index of 100 mass/tail.

bler), northwestern Ecuador to northwestern Brazil (American Redstart), or northern Colómbia and Venezuela (Ovenbird, Kentucky Warbler; AOU 1983). Although these maximum distances provide an estimate of how far these birds might continue to migrate, minimum distances are unknown for all species except the Red-eyed Vireo. The distance yet to be traveled in migration probably plays a role in individual fat-deposition strategies, but no relationships are apparent between percent mass gain and the maximum-possible continued migration distance at the species level, whether considering all 11 species examined or only the subset of 6 species gaining mass. Similarly, the difference between mean autumn mass at this site and fat-free mass (as percent of fat-free mass) is not correlated with the diurnal gains apparent at this site (not shown). Thus, given present

knowledge, the among-species differences observed cannot be explained.

I did not perform a systematic examination of foods used by migrants at this site to sustain the mass gains observed, but both fruits and insects were consumed (unpubl. data). Fruits of *Rivina humilis* (Phytolaccaceae) and *Siparuna andina* (Monimiaceae) were particularly important to Red-eyed Vireos. The availability of these fruits seemed to peak and fade with the abundance of migrants in general, and with Red-eyed Vireos (the most abundant migrant) in particular.

Discussion

Individuals of several species appear to use this area for the deposition of low to moderate amounts of fat. There is clearly a difference

TABLE 5. Estimating net daily increase in mass by applying linear models in Table 4 to average individuals in captured samples. Units are grams, except where noted.

| Species | Gross Δg/day[a] | Nocturnal loss[b] | 4.5% of mass[c] | Net gain/day[d] | | Increase as percent of mass | Flight cost (g/h)[e] | Hours of flight[f] |
				1	2			
Dumetella carolinensis	3.22	0.94	1.52	1.70	0.75	2.23–5.01	0.296	2.54–5.72
Vireo olivaceus	1.40	0.53	0.83	0.57	0.04	0.23–3.06	0.139	0.30–4.09
Dendroica magnolia	0.91	0.30	0.34	0.57	0.27	3.67–7.71	0.067	4.08–8.56
Setophaga ruticilla	0.77	0.29	0.33	0.44	0.15	2.06–5.97	0.063	2.39–6.94
Oporornis formosus	1.21	0.44	0.56	0.65	0.22	1.73–5.23	0.109	1.98–5.98
Wilsonia pusilla	0.54	0.26	0.30	0.24	−0.02	−0.31–3.63	0.056	0–4.31

[a] Mass gain (g) during one day for average individual, using average size for wing and/or tail from Table 1.

[b] Grams of fat used in nocturnal metabolism, calculated for average fat-free individual (values from Odum *in* Dunning 1993).

[c] 4.5% of mean body mass (g) of individuals captured at study site.

[d] Net mass gain (g) in 24-h period after subtraction of nocturnal losses, estimated as: (1) 4.5% of body mass alone; and (2) 4.5% of body mass and fat lost to nocturnal metabolism.

[e] Cost of flight in grams of fat per hour, calculated after Tucker (1974:306) using average mass of captured individuals.

[f] Hours of flight possible if net gain is all fat.

among the most commonly occurring migrants in the degree to which they use the site for fat deposition, however. In this respect, my results are similar to those obtained at a northerly stopover site in Minnesota (Winker et al. 1992a). At present, there are no robust hypotheses to explain why differences among species occur in the patterns observed, but these differences are probably related to physiological demand and resource availability, both of which vary geographically and temporally. Abundance (as reflected by capture rates, at least) does not correspond to use of the stopover site for food resources (at the species level) among the woodland migrants examined so far.

How representative are data from a single year? Similar analyses for a three-year study in Minnesota show that if a species has significant daily gains in one, two, or three years, a pooling of data from all years also reveals significant gains (Winker et al. in prep.). Thus, single-year trends showing gains imply that gains occur among years. Conversely, a lack of significant trends in a single year does not mean that gains do not occur. The latter situation may be due to the problems inherent in small samples, or slopes that are close to zero, coupled with the "noise" present in a comparison of individual condition and time of capture.

Four species examined at this site show trends suggesting no mass increase. At the species level, it seems that Wood Thrushes, White-eyed Vireos, Ovenbirds, and Hooded Warblers are not depositing fat at this site. However, it is not safe to assume that the transient populations of these species are not gaining mass during the day. I have many observations of unbanded individuals of these species feeding on the study site, and all four are common in the area during the winter, suggesting that resources are available to satisfy the maintenance costs of some birds. (I estimate that these four species winter in this area at densities of about 1–3 individuals/ha; the study site was approximately 2.3 ha.) More data are needed to determine whether sample size alone is responsible for a lack of significant trends in these species, and whether gains are absent or simply low. A larger sample might also clarify both the occurrence and extent of apparent fat deposition in the Worm-eating Warbler.

The degree of resource uncertainty is probably higher as one travels north into the Temperate Zone in spring than as one travels south in autumn. Autumn fattening for "insurance," unless a bird is approaching an ecological barrier, should be less frequent. Thus, low to moderate mass gains at stopover sites in autumn might be expected of birds not approaching an ecological barrier. The low to moderate mass gains I recorded are consistent with this idea; these individuals were not approaching any nearby ecological barrier, where greater gains (and higher condition levels) would be expected. Conversely, in birds approaching their wintering destinations (by land, at least), low gains (or perhaps even losses) should be expected, because wintering migrants generally carry low levels of fat (e.g. Rappole and Warner 1980:381). Possibly, the samples of species not showing gains are composed of a higher percentage of individuals near their winter destinations, but evaluating this idea is impossible at present. However, the gains at this site are considerable in many cases (e.g. Gray Catbird, Magnolia Warbler, American Redstart, Kentucky Warbler, and Traill's Flycatcher), suggesting that resources in the area are being used to fuel substantial levels of continued migration. In this respect, the Isthmus of Tehuantepec provides important resources to some autumn passage migrants.

Autumn birds in the Minnesota study (Winker et al. 1992a) included a large proportion of molting birds. Unlike spring diel mass gains, autumn estimates of net gain for some species were fully negative (despite significantly positive diurnal trends in condition; Winker et al. 1992a). None of the species showing positive diurnal trends on the Isthmus of Tehuantepec exhibited estimates of net diel gains that were completely negative. Net autumn gains as a percentage of body mass ranged from −6.1 to 9.5% in the Minnesota study; the range for the current study was −0.3% to 10.1% (Table 5; Winker 1995). The values for the current study are more consistently positive. Although the energetic demands of molt undoubtedly affected autumn mass gains at the Minnesota site, the effects differed among species, and it was not clear how the demands of molt acted together with other factors to affect diel mass change (Winker et al. 1992a, b). Molt is not an energetic consideration in autumn migrants on the Isthmus of Tehuantepec. This is probably a factor contributing to the differences observed between these two studies, reaffirming the importance of the energetic demands of molt at northerly stopover sites.

Although a different condition index (10,000 mass/wing length[3]) was used by Winker et al. (1992a), large-scale differences occur between the two sites in species such as the Gray Catbird, Red-eyed Vireo, and Magnolia Warbler. These differences are not likely to be artifacts due to the different condition indices used. Gray Catbirds appeared to be losing mass at the Minnesota site in autumn, while Red-eyed Vireos showed no significant diurnal condition trends. Both species gained mass on the Isthmus of Tehuantepec (Table 5). Magnolia Warblers were losing or maintaining mass at the Minnesota site, while on the Isthmus substantial gains were evident (Tables 3 and 5). American Redstarts showed small to moderate gains at both sites (Table 5; Winker et al. 1992a). Given these between-site differences within species, the among-species variation in mass gains exhibited at both sites does not appear to be an artifact of the analytical method.

Comparison with Panamá.—Rogers and Odum (1966) presented data on the body mass of autumn migrants in northwestern Panamá (near Almirante), allowing a between-site comparison of four species in the Neotropics. Differences in mean body mass between the two samples are: Wood Thrush, 1.63 g; Gray Catbird, 2.49 g; Red-eyed Vireo, 1.80 g; and Ovenbird, 1.55 g. Averages were significantly higher for the four species on the Isthmus of Tehuantepec ($0.025 < P < 0.05$ for the Wood Thrush; $P < 0.001$ for the other three species; t-test). Mass values may not be directly comparable between the two sites for two reasons: (1) Rogers and Odum (1966) held their birds before weighing to reduce gut contents (differences, therefore, are not all fat); and (2) individuals of the three species wintering in the respective areas may represent different populations (apparent differences may be partly due to dissimilarities in size). Nevertheless, the comparison is valuable.

The possibility that gut contents contribute to the differences observed is real. However, even if guts were full at weighing on the Isthmus (generally not the case; pers. obs.), subtraction of a full gut (ca. 4.5% of body mass; Baldwin and Kendeigh 1938) renders only the difference observed in the Wood Thrush questionable (4.5% of mean body mass is 1.99 g). Differences in the other three species are rather large. Rogers and Odum (1966) found that Gray Catbirds and Ovenbirds in Panamá showed an average mass that was actually lower than the

fat-free mass of each species: individuals of these two species were generally fat-depleted. Although possible size differences cannot be addressed, individuals of these two species were fatter on the Isthmus of Tehuantepec. Only 18.7% of Gray Catbirds and 12.7% of Ovenbirds had fat classes of zero, and none showed breast-muscle reduction as described by Rogers and Odum (1966:418). Population-related size differences are less likely to exist between Red-eyed Vireos at the two sites because this species is transient at both. Although individuals captured in Panamá carried an average of 2.5 g of fat, they carried perhaps as much as a gram more on the Isthmus of Tehuantepec. Individuals of this species were quite fat; none showed a fat class of zero, and 65.9% had fat levels of 2.5 or higher.

In sum, Gray Catbirds, Ovenbirds, and Red-eyed Vireos are more fat-depleted in northwestern Panamá in autumn than on the Isthmus of Tehuantepec. This observation is not consistent with the idea that trans-Gulf migrants make up the sample from the Isthmus of Tehuantepec (or there would be some evidence of fat depletion). It also raises questions about the extent of overwater crossings in the western Caribbean.

Middle American migration routes.—Although many of the Nearctic-Neotropic nocturnal migrants occurring in the study area belong to species in which individuals make autumn trans-Gulf crossings (Cooke 1904, Rappole et al. 1979), several lines of evidence make it unlikely that many of the birds examined here arrived via a long (>1,000 km) trans-Gulf flight. First, such a crossing is not possible for small songbirds to complete in one night under most weather conditions (see Nisbet et al. 1963, Gauthreaux 1971, Able 1972, Buskirk 1980). Diurnal arrivals, therefore, are expected on the southern Gulf coast. Buskirk (1968) observed trans-Gulf migrants arriving on the coast of Yucatán during daylight hours on 36 of 45 days of observation (2 September–23 October). Fifty or more diurnally-arriving migrants were observed on 24 of these 36 days (Buskirk 1968:table 1). Arrival times varied considerably, with peak times shifting throughout the day according to weather conditions over the Gulf. In comparison, diurnal flights of nocturnal migrants are rare on the Isthmus of Tehuantepec (pers. obs.; R. J. Oehlenschlager and W. J. Schaldach, Jr. pers. comm.). Second, although migrants can

appear in high numbers with the arrival of a cold front from the north, autumn "waves" of migrants are not of remarkable intensity, and the bulk of passage seems to occur in the day-to-day turnover of birds (rather than on a few striking "peak" days each season). Finally, the incidence of emaciated birds is very low.

In many hundreds of hours of careful diurnal observation in this area, I have not seen nocturnal migrants dropping out of the sky into the local habitats, as occurred regularly in autumn migration in Minnesota during the hour around sunrise (unpubl. data). Buskirk (1968) estimated the distances between his Yucatán site and shore departure points along the northern Gulf coast to be about 1,050 km. The trans-Gulf distance between Galveston, Texas, and Los Tuxtlas is about 1,150 km, and between Los Tuxtlas and Mobile, Alabama, about 1,500 km. It is not likely that differences in distance explain these differences in observations of diurnally-arriving nocturnal migrants.

Observations of large, diurnal autumn landfalls of trans-Gulf migrants (e.g. Paynter 1953, Buskirk 1968, 1980), or of emaciated trans-oceanic migrants (e.g. Wetmore 1939, Voous 1957), have not been described for the Isthmus of Tehuantepec (or anywhere else in México besides the Yucatán Peninsula). If such a combination of events was common in the southern Gulf, it is likely to have been observed (e.g. Thiollay 1977), particularly in Los Tuxtlas: the orographic effect of the mountains causes the area to be visible (due to cloud formation) at ground level from 150 km on most days during autumn. This distance would be greater from higher altitudes, and might serve as a signal to birds at sea that land is near, attracting them from long distances.

This evidence suggests that the Isthmus of Tehuantepec is not a major area of landfall for autumn trans-Gulf migrants. The Yucatán Peninsula is such an area (Paynter 1953, Buskirk 1968, 1980). Landfalls on the Yucatán Peninsula are an unlikely source of common autumn migrants on the Isthmus of Tehuantepec, however. Yet, the autumn scarcity in southern Texas of many of the species considered here (see Rappole et al. 1979) argues against a completely land-based autumn migration for the individuals I captured.

On the Isthmus, the relative infrequency of diurnal flights of nocturnal migrants, the early morning arrival times of those flights observed

(W. J. Schaldach, Jr. pers. comm.), and the scarcity of emaciated individuals suggest that the vast majority of nocturnal migrants occurring in this area arrive via shorter, largely nocturnal flights. This leads to the hypothesis that trans-Gulf passage is often shorter. Birds departing from southern Louisiana and eastern Texas, for example, might fly in a southwesterly direction (see Williams 1951, Lowery and Newman 1966, Able 1972), making landfall in Tamaulipas or northern Veracruz, and then progressing south-southeast along and near the coast in largely nocturnal journeys. This hypothesis would be consistent with the observations reported here and the abundance patterns observed between southern Veracruz and southern Texas (Rappole et al. 1979). Based on the evidence considered, I recommend that Cooke's (1915:8) trans-Gulf route 4 be modified by pushing it eastward, and that his shorter, western, trans-Gulf route 5 (Cooke 1915:8, 15) be increased in breadth and importance. These modifications are shown in the autumn route proposed for the Red-eyed Vireo by Winker (1995).

A relatively short trans-Gulf crossing with landfall occurring in Tamaulipas or northern Veracruz would lower the incidence of emaciated and exhausted birds on the Isthmus of Tehuantepec, and would probably have a moderating effect on the significance of weather-stimulated migration "waves" in southern Veracruz. Unfortunately, no observations are available for Tamaulipas and northern Veracruz. The distances between these locations and southern Louisiana or eastern Texas are such that diurnal arrival times would be expected under the predominant autumn weather conditions (see Able 1972). Buskirk (1980) judged that birds arriving on the Yucatán were primarily coming from Florida, leaving the Mexican zone of landfall for birds departing from southern Louisiana as yet undetermined.

Rogers and Odum (1966:420) postulated that some birds at Almirante, Panamá had made a nonstop flight from North America. The levels of fat depletion that they found in some Gray Catbirds and Ovenbirds make a long, trans-Caribbean flight a probability. These species also winter on Isla San Andrés (east of Nicaragua; Paulson et al. 1969), a further implication of trans-Caribbean flights. However, individuals of these two species may also have come to Panamá from the Greater Antilles (see Cooke 1904, Voous 1957, Bond 1971), a route representing

the eastern part of a route proposed for the Ovenbird by Cooke (1904). Finally, as Rogers (1965) and Rogers and Odum (1966:420) noted, some of the individuals found in Panamá in autumn migration probably stopped off further to the northwest in Middle America.

Conclusions.—We know relatively little about migratory routes and the geographic patterns of fat deposition in Nearctic-Neotropic landbird migrants. The fact that the Red-eyed Vireo has a long distance yet to travel in autumn migration might explain why it is fattening on the Isthmus of Tehuantepec, while its congener (*Vireo griseus*) is not. As shown above, however, these simple comparisons do not hold up among the species considered, and a better understanding of routes, sources, and destinations might help explain patterns of resource use and fattening on the Isthmus of Tehuantepec and elsewhere in Middle America. Eventually, a grasp of the complexities at specific and subspecific levels will be needed if we are to understand the evolution of the Nearctic-Neotropic migration system and work intelligently toward reasonable conservation goals.

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