DAILY MASS GAINS AMONG WOODLAND MIGRANTS AT AN INLAND STOPOVER SITE

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ABSTRACT.—We investigated fat deposition in transient, nocturnal, long-distance migrants at a wooded stopover site that is not near an ecological barrier (e.g. desert, large water body). The changes in body mass of recaptured birds have traditionally been used as a measure of mass gains at stopover sites. This technique ignores the majority of transients, however, possibly hindering the ability to answer species-level questions regarding stopover mass gain. We compare an analysis of recaptures with a technique that considers all captures and their condition by time of day. Eleven woodland-associated migrant species were analyzed, as well as a resident species (Black-capped Chickadee, *Parus atricapillus*) for comparison. Based on recapture data alone, our study site appears to be primarily a location of mass loss, rather than one of fat deposition. Conversely, the examination of condition by time of day suggests that individuals of several species have net daily gains greatly exceeding those of recaptured individuals. During autumn, however, several species exhibited net daily losses. Although some of these losses may be related to molt, it seems unlikely that molt is the only contributing factor. Differences among species in mass gains at our site suggest that various fat-deposition patterns (and, thus, migration strategies) may occur among migrants that are not approaching ecological barriers. *Received 10 December 1991, accepted 11 March 1992.*

FAT IS the currency of avian migration (Berthold 1975, Dawson et al. 1983), and small long-distance migrant passerines generally are unable to carry enough fat to complete their biannual migrations without replenishing fat reserves at stopover sites between breeding and wintering ranges (Nisbet et al. 1963, Berthold 1975, Bairlein 1987, Winker et al. 1992a). Resource availability at stopover sites, therefore, is an important factor in individual, population, and specific migration strategies. Although some studies (e.g. Nisbet et al. 1963, Bairlein 1988) have shown that small passerines can gain enough fat at suitable sites to enable them to traverse major ecological barriers (e.g. deserts, large water bodies), we know very little about the temporal and geographic patterns of fat deposition among long-distance migrant passerines.

In this paper we investigate whether an inland stopover site that is not near an ecological barrier is used for fat deposition by 11 common Nearctic migrant species occurring there in spring and autumn migrations. Because most transients at stopover sites are not recaptured

and provide only a single data point, mass changes among those individuals that are recaptured have been the usual means of addressing this topic. We question the rather exclusive use of this traditional approach, asking whether the recaptured minority should be considered an adequate representation of a species? Results from our site for Swainson's Thrushes (*Catharus ustulatus*) and Northern Waterthrushes (*Seiurus noveboracensis*; Winker et al. 1992a) suggested that conclusions reached from recapture analyses could be misleading. The number of individuals remaining at a stopover site for one night or more may be a poor indicator of how a site is used by transients. Also, the mass changes of recaptures may not be indicative of the entire transient population (Winker et al. 1992a). Furthermore, for migrant species with resident breeding populations there is the problem of being unable to effectively separate local breeders from transients (in autumn this is particularly difficult). Analyses of recaptures in locally breeding species probably will be biased toward resident individuals. Finally, young (inexperienced) birds and birds in molt may have a greater probability of recapture, and birds that remain at a site often are leaner at first capture than nonrecaptured individuals (e.g. Nisbet et al. 1963, Bairlein 1987, Moore and Kerlinger 1987, Winker et al. 1992a).

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Other methods of examining mass change in transient migrants generally have not been used. We have chosen the following approach. All birds in a favorable environment probably undergo diel fluctuations in mass: an increase during the day as nutrients are ingested, and a decrease at night through nocturnal metabolism (Baldwin and Kendeigh 1938). Thus, a linear regression of mass on time of day should yield a significant positive slope among birds gaining or maintaining body mass (for earlier variations, see Mueller and Berger 1966, Collins and Bradley 1971, Yablonkevich et al. 1985). Many factors affect body mass, however, and time of day is likely to have little influence upon the mass trends of a population. Therefore, the correlation coefficients of such regressions should be low, and large sample sizes would be more likely to show a significant, nonzero relationship than small ones, because variability in body mass among individuals would create such "noise" in smaller samples that the predicted diel relationship would be lost. To address the question concerning mass change in birds at our site, we examined mass changes in recaptured individuals and compared these results with average net daily gains, which are estimated from diurnal condition changes.

METHODS

Our study site was located in Washington County, Minnesota, in the St. Croix River Valley (44°55′00″N, 92°47′30″W) approximately 2 km from the river. The region consisted of a mosaic of suburban-residential, agricultural, and wooded tracts, and was not near an ecological barrier (e.g. desert, mountains, large body of water). Birds were captured in mist nets placed in five relatively discrete wooded habitat types that represented the native woodlands in the area. Netting occurred during the peaks of spring and autumn migration in 1984 through 1986. Sample effort totalled over 71,000 net-h in three spring and 65,000 net-h in three autumn seasons. Sample periods for all years spanned Julian days 118–149 (spring), and 222–268 (autumn). In nonleap years, 15 May = day 135, and 1 September = day 244. Captured birds were birds removed from the point of capture to a central location for banding (transport distance of 130–820 m). Here, birds were weighed to the nearest 0.1 g on Ohaus triple-beam balances, banded, and released. Flattened wing length and time of capture also were recorded. In 1985–1988, molt was assessed and assigned a value (1–9) based on the locations of growing feathers (0 = none). For more details regarding the study site and field methods, see Winker et al. (1992a).

The species used in these analyses are among the most common migrants at this site (Winker et al. 1992b). Five of the 11 species considered occur both as transients and resident breeders. We assume that locally breeding individuals of migrant species constitute a minority of all individuals captured (for those species analyzed here). To minimize the number of residents in these analyses, we did not consider individuals with between-season or between-year recapture records. The numbers of birds eliminated from consideration in this manner were relatively few, consistent with the small size of our net plots: Common Yellowthroat (*Geothlypis trichas*), 36; Gray Catbird (*Dumetella carolinensis*), 26; Ovenbird (*Seiurus aurocapillus*), 11; Red-eyed Vireo (*Vireo olivaceus*), 2; Ruby-throated Hummingbird (*Archilochus colubris*), 1.

The amount of fat carried by individual passerine migrants causes most of the variation in their body mass and, when standardized for body size, mass is a reasonable predictor of an individual's fat content (Odum 1960, Connell et al. 1960, Rogers and Odum 1964, 1966). We employed this relationship by calculating a "condition index" for each captured individual. Our 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," especially in autumn, when the demands of molt can conflict with the demands of migration (cf. Winker et al. 1992a). In standardizing for body size, the volumetric nature of body mass is brought into concordance with the linear nature of our morphometric estimate of size by dividing mass by the flattened wing length cubed (g/mm^3; see Davidson 1983, Summers 1988). Individual condition (g/mm^3) is then multiplied by 10,000 to avoid errors when very small numbers are rounded off in calculations (see Weisberg 1985). As applied here, this final multiplication results in more conservative estimates of diurnal mass gains (unpubl. data). The relationship between time of capture and condition is examined using simple linear regression. To estimate net daily gains from diurnal gains apparent in linear models, we first estimated gross diurnal gains for average individuals in the captured populations (average wing and body mass), then subtracted estimated nocturnal losses. Estimates of mass lost due to nocturnal metabolism follow Mueller and Berger (1966) for an average Swainson's Thrush during an 8-h night. Their figure for Swainson's Thrush was scaled for body size to the other passerines considered here using field metabolic rates (FMR) for passerines (Nagy 1987) and average fat-free body mass for size (when available). Resting cost for an 8-h night was scaled to an average day–night cycle during the periods of netting, and mass lost to metabolism was calculated using an energy content of 39.8 kJ/g of fat (Nisbet et al. 1963). Following Nisbet et al. (1963), we assume that water loss in nocturnal migration is negligible.

TABLE 1. Mass changes in individuals recaptured one night or more following first capture.

Species	Spring				Autumn			
	n	$\bar{x}$ (days)[a]	Δg/day[b]	*P*[c]	*n*	$\bar{x}$ (days)	Δg/day	*P*
Ruby-throated Hummingbird[d]	0	—	—	—	8	1.6	−0.16	0.90
Least Flycatcher	7	2.3	−0.30	0.03	13	2.6	0.03	0.04
Black-capped Chickadee[e]	14	3.6	−0.01	—	31	3.8	−0.11	—
Gray Catbird[d]	24	6.5	−0.14	0.11	69	6.9	−0.14	0.75
Red-eyed Vireo[d]	0	—	—	—	66	3.5	−0.07	0.72
Tennessee Warbler	0	—	—	—	71	6.0	−0.07	0.28
Nashville Warbler[f]	3	1.7	−0.08	—	66	3.9	−0.02	0.22
Chestnut-sided Warbler	1	1	0.60	—	33	5.0	−0.11	0.01
Magnolia Warbler	3	4	0.40	—	89	4.3	−0.02	0.38
American Redstart	5	1.2	0.13	—	56	3.3	−0.09	0.39
Ovenbird[d]	9	8.1	−0.03	0.04	67	5.6	−0.01	0.49
Common Yellowthroat[d]	30	3.3	0.03	0.10	38	9.0	−0.08	0.47

[a] Mean number of days present for all recaptured individuals.

[b] Mean change in mass per day of all recaptured birds over entire capture history. Individuals recaptured more than once can be represented more than once in these calculations.

[c] P-value of Wilcoxon rank-sum test comparing condition at first capture of recaptured individuals versus nonrecaptured individuals. For $P < 0.05$, we accept that there is a significant difference in condition at first capture between the two groups. Significant cases showed recaptured birds to be leaner except in Chestnut-sided Warbler in autumn, which showed the opposite.

[d] Migrant with resident breeding population. Individuals recaptured between years or between seasons (most likely local breeders) were eliminated from these calculations.

[e] Resident species included for comparison. Only recaptures spanning seven days or less are considered here.

[f] *Vermivora ruficapilla.*

Figures for the average fat-free mass of various species are given by Connell et al. (1960), Raveling (1963), and Rogers and Odum (1964, 1966). Fat-free mass data were unavailable for the Least Flycatcher (*Empidonax minimus*), Black-capped Chickadee (*Parus atricapillus*), and Common Yellowthroat. To estimate nocturnal losses in these species, we first examined the relationship between fat-free mass figures from the literature and the mean autumn mass at initial capture found in the same species at our site. A regression examining the relationship between these two different data sets was performed with 10 species: Ruby-throated Hummingbird, Swainson's Thrush, Gray Catbird, Red-eyed Vireo, Tennessee Warbler (*Vermivora peregrina*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Magnolia Warbler (*D. magnolia*), American Redstart (*Setophaga ruticilla*), Ovenbird, and Northern Waterthrush. Results of this comparison showed a very high correlation between the mean fat-free body mass of a species determined through fat extractions on birds from other localities and the mean autumn mass for birds of the same species captured at our site ($F = 3,167$, df = 1 and 8, $P < 0.001$, $r^2 = 0.997$). The linear model of

$$Y = 0.1878 + 0.8357X,$$

where Y is fat-free mass and X is mean autumn mass (both in grams), was used to estimate the fat-free body mass of three species at our site (estimates based on mean autumn mass at initial capture). These fat-free mass estimates were: Least Flycatcher, 8.46 g; Black-capped Chickadee, 9.77 g; and Common Yellow-throat, 8.45 g. The estimate for the Black-capped

Chickadee may be low, since it is the only nonmigrant species considered and does not deposit fat to the degree that migrant species do (thus, its mean autumn mass may include less fat than the migrant species from which the linear model was derived).

Recaptured individuals are examined from the perspective of stopover duration and mass change between captures. Stopover duration is a minimum estimate, made by subtracting date of first capture from date of last capture (after Cherry 1982). In examining nocturnal migrants, adding one day to stopover duration is probably not unreasonable, but mass change must be considered in light of the minimum estimate. We did not examine mass change in same-day recaptures or adjust the mass of recaptured individuals to a particular hour of day (see Cherry 1982). Capture and handling are stressful and can affect mass change (Rogers and Odum 1966, Nisbet and Medway 1972). Mass change in captured birds may not reflect mass changes in free-flying birds.

RESULTS AND DISCUSSION

As with most studies of migrants at stopover sites, only a minority of birds captured were ever recaptured (among species, 0–14% in spring, and 2–21% in autumn; see Tables 1 and 2). The average time spent at our site by recaptured individuals varied among species, but did not seem to be correlated with average mass change (Table 1). Four of 8 migrant species with spring recaptures showed an average mass loss among

TABLE 2. Summary of linear models for diurnal change in condition ($[mass/wing^3] \times 10,000 = Y$) in first captures (regressions for Ruby-throated Hummingbird done with mass rather than condition). Equations are $Y = b + mX$, where b is the Y-intercept, m is slope (condition gained per hundredth-hour), and X is time. Correlation coefficient (r) is measure of strength of relationship between X (time) and Y (condition). The maximum value of r is 1.0 (perfect relationship). F-statistics and corresponding P-values indicate how well regression models fit data; for $P < 0.05$, we accept the hypothesis that there is a nonzero relationship between time of day and body condition.

Species	Season	n	b	m	r	F	P	Gain/day[a]
Ruby-throated Hummingbird	Spring	78	—	—	—	1.70	0.20	—
	Autumn	357	—	—	—	1.37	0.25	—
Least Flycatcher	Spring	313	0.389	0.0000376	0.32	34.54	<0.001	0.0557
	Autumn	153	0.360	0.0000407	0.39	5.17	0.03	0.0548
Black-capped Chickadee	Spring	65	—	—	—	—	>0.50	—
	Autumn	262	0.369	0.0000217	0.19	9.94	0.002	0.0292
Gray Catbird	Spring	215	0.457	0.0000305	0.24	12.79	<0.001	0.0452
	Autumn	360	0.507	0.0000137	0.11	4.17	0.042	0.0184
Red-eyed Vireo	Spring	37	—	—	—	—	>0.50	—
	Autumn	735	—	—	—	—	>0.50	—
Tennessee Warbler	Spring	37	—	—	—	—	>0.50	—
	Autumn	740	0.321	0.0000162	0.14	16.16	0.001	0.0218
Nashville Warbler	Spring	131	—	—	—	—	>0.50	—
	Autumn	704	—	—	—	2.89	0.09	—
Chestnut-sided Warbler	Spring	30	0.354	0.0000577	0.40	5.21	0.03	0.0856
	Autumn	373	0.3668	0.0000157	0.14	7.09	0.008	0.0212
Magnolia Warbler	Spring	97	—	—	—	—	>0.50	—
	Autumn	761	0.363	0.0000150	0.11	10.15	0.002	0.0202
American Redstart	Spring	91	—	—	—	2.54	0.11	—
	Autumn	521	0.311	0.0000199	0.21	24.35	<0.001	0.0268
Ovenbird	Spring	147	0.446	0.0000214	0.16	3.65	0.058	0.0317
	Autumn	638	0.421	0.0000026	0.17	20.31	<0.001	0.00
Common Yellowthroat	Spring	216	0.549	0.0000482	0.23	12.26	<0.001	0.0715
	Autumn	184	0.581	0.0000522	0.22	4.14	0.045	0.0704

[a] Gain in condition for daylight hours of one average day during netting periods.

recaptured individuals, and 9 of 10 species with recaptures in autumn also showed an average loss (Table 1). The resident Black-capped Chickadee also showed an average loss among recaptured individuals during a seven-day period following initial capture (Table 1). Where sample sizes were sufficiently large, the condition at first capture of recaptured migrants was compared to that of nonrecapturd birds (Wilcoxon rank-sum test on $[g/mm^3] \times 10,000$, except in the Ruby-throated Hummingbird, where mass was used instead of condition). Recaptured birds showed a significantly leaner condition at first capture in the Least Flycatcher (both seasons) and the Ovenbird (spring only; Table 1).

In autumn, Chestnut-sided Warblers that were recaptured showed a *higher* condition index at first capture than nonrecaptured individuals (Table 1). This is an unusual occurrence at a stopover site, but might be predicted given that the species appears to lose mass at our site in this season (Table 3). However, none of the other four species showing net autumn losses had

a significantly greater condition at first capture among recaptures.

Although the average mass lost among recaptured birds tended to be low (-0.02 to -0.3 g/day), the largely negative values seem to indicate that our site was not used for fat deposition by the most common migrants occurring there on stopover.

Condition and time of day.—The majority of individuals encountered in a study of migration will contribute a single data point of interest in a study of this nature—body mass (or condition) at time t. Linear regression of body condition ($[mass/wing^3] \times 10,000$) on time of day revealed specific differences in diurnal mass gains. Some species showed significant positive slopes in one or both seasons, while others did not (Table 2). Positive slopes suggest that birds are gaining mass during the daylight hours, probably by feeding. No species showed significant negative slopes, which might be predicted in birds either not feeding or showing dehydration at hostile stopover sites (e.g. deserts; see Biebach

TABLE 3. Estimating net daily increase in fat reserves by applying linear models to average individuals in the transient populations. Units are grams, except as noted.

Species	Season	Wing (mm)[a]	Gross Δg/day[b]	Nocturnal loss[c]	4.5% mass[d]	Net gain/day[e] A	Net gain/day[e] B	Increase as percent of mass	Flight cost (g/h)[f]	Hours of flight[g]
Least Flycatcher	Spring	63.2	1.41	0.24	0.50	0.91	0.67	6.0 to 8.2	0.095	7.01 to 9.54
	Autumn	—	1.38	0.28	0.45	0.94	0.66	6.6 to 9.5	0.106	6.18 to 8.82
Black-capped Chickadee	Autumn	65.5	0.82	0.31	0.51	0.32	0.01	0.0 to 2.8	0.108	0.04 to 2.92
Gray Catbird	Spring	89.7	3.26	0.64	1.59	1.67	1.03	2.9 to 4.7	0.329	3.12 to 5.06
	Autumn	—	1.33	0.76	1.68	−0.35	−1.11	−3.0 to −0.9	0.347	0
Tennessee Warbler	Autumn	64.0	0.57	0.27	0.40	0.17	−0.10	−1.10 to 1.9	0.086	0.0 to 2.0
Chestnut-sided Warbler	Spring	62.3	2.07	0.23	0.45	1.62	1.39	13.8 to 16.1	0.097	14.3 to 16.6
	Autumn	—	0.51	0.27	0.42	0.09	−0.18	−1.9 to 1.0	0.090	0.0 to 1.0
Magnolia Warbler	Autumn	59.2	0.42	0.24	0.35	0.06	−0.18	−2.2 to 0.8	0.076	0.0 to 0.9
American Redstart	Autumn	61.8	0.63	0.24	0.35	0.28	0.04	0.5 to 3.5	0.076	0.5 to 3.6
Ovenbird	Spring	75.1	1.34	0.38	0.89	0.45	0.07	0.4 to 2.3	0.187	0.4 to 2.4
	Autumn	—	0.15	0.45	0.85	−0.70	−1.15	−6.1 to −3.7	0.179	0
Common Yellowthroat	Spring	55.0	1.19	0.24	0.45	0.74	0.50	5.1 to 7.5	0.095	5.3 to 7.8
	Autumn	—	1.17	0.28	0.45	0.72	0.44	4.4 to 7.2	0.096	4.6 to 7.5

[a] Mean flattened wing length (mm) for all individuals captured at site. Figures are for both seasons combined; seasonal differences were small in all cases (<1 mm).
[b] Diurnal mass gain (g/day), calculated directly from linear models in Table 2 using average wing lengths for each species at site.
[c] Fat used in nocturnal metabolism (g), calculated for an average individual of each species (fat-free mass); see text.
[d] 4.5% of mean seasonal body mass.
[e] Net mass gain in 24-h period after subtracting night losses estimated as: (A) 4.5% of body mass alone; and (B) 4.5% of body mass and nocturnal fat loss due to metabolism.
[f] Cost of flight in g/h, calculated after Tucker (1974:306) using seasonal average mass at first capture for each species.
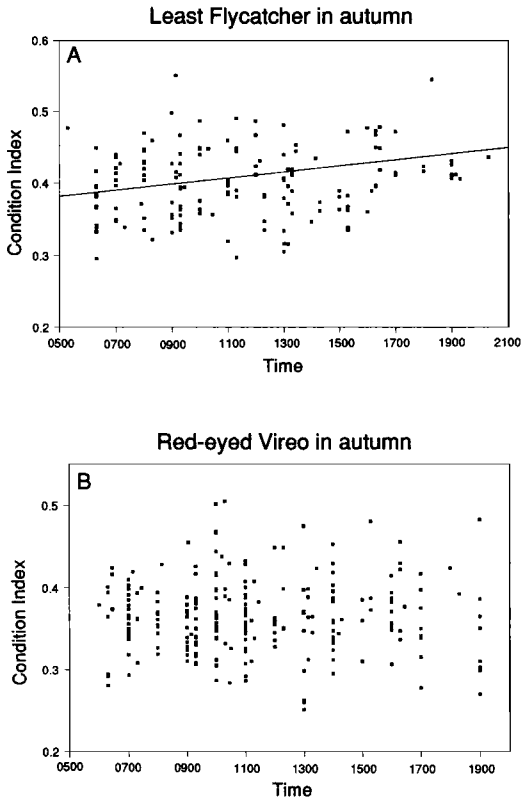[g] Hours of flight possible if net gain is positive and all fat.

Fig. 1. Condition ([mass/flattened wing length cubed] × 10,000) plotted against hour of day (Central Standard Time) in first captures of Least Flycatchers and Red-eyed Vireos. Linear regression analysis revealed a significant positive slope for Least Flycatchers, but not for Red-eyed Vireos (Table 2).

1988). Typical regressions are shown for the Least Flycatcher and Red-eyed Vireo in autumn (Fig. 1). Due to high variation in individual condition, small sample sizes are not likely to reveal significant slopes unless, perhaps, the species is exhibiting strong temporal trends. Spring regressions that do not show significant positive slopes (7 of 11; Table 2) may suffer from small sample sizes. Clearly, this is not the only factor in regressions showing a lack of significance, however, given that autumn regressions with much larger sample sizes can also lack significance. Also, 30 spring Chestnut-sided Warblers showed a strong significant positive slope, whereas five species with more than twice as many captures in spring did not show significant trends (Table 2).

Diurnal condition gains will be eroded by nocturnal losses. In birds depositing fat, diurnal gains should exceed nightly losses, resulting in a net positive daily (24 h), or diel, gain. Of the regressions showing positive diurnal gains (five spring, nine autumn), two of these relationships resulted in negative diel gains upon subtraction of nocturnal losses (Gray Catbirds and Ovenbirds in autumn; Table 3). Three other species included negative values in autumn diel gain estimates: Tennessee, Magnolia, and Chestnut-sided warblers (Table 3). Nine of the 14 positive species-season relationships showed positive diel gains, ranging from lows near 2% of mean body mass (autumn American Redstarts, spring Ovenbirds) to a high of around 15% (spring Chestnut-sided Warblers). Of the four species with significant positive slopes in both seasons, only the Least Flycatcher and Common Yellowthroat showed positive diel gains in spring and autumn. If mass gained is all fat, an average Least Flycatcher in either season may gain enough in one day's feeding at our site to fly for an entire night.

Molt.—Spring birds showing significant positive diurnal gains do not show net diel losses, encouraging an examination of autumn phenomena that might cause the diel losses observed in this season. We cannot address issues of food availability, but birds are often under very different energetic constraints in autumn. Although it is widely held that Nearctic passerine migrants undergo prebasic molt on their breeding grounds prior to migration (see Payne 1972), molting transients were common at our site (Table 4). Molt is not as energetically costly as breeding and migration, but it is believed to be costly enough to result in a general temporal segregation of these three phenomena (Payne 1972). A molting migrant may deposit less fat than if it was not molting. For example, molting recaptured Swainson's Thrushes at our site showed significantly lower mass gains than nonmolting recaptures (Winker et al. 1992a). The pattern of molt frequency among species in autumn does not seem to explain the pattern of mass loss, however (Table 4). Thus, it seems that either the species considered have different capabilities in dealing with the dual energetic demands of molt and migration (see also Berthold 1975) or other factors play a more important role (e.g. food availability).

Lack of mass gain in common species.—It is unclear what might be occurring among individuals in species and seasons not showing positive slopes (especially those with large sample sizes).

TABLE 4. Occurrence of molt at first capture in birds from autumn 1985–1986, compared with estimates of net daily mass gains. "Extensive" molt indicates birds whose molt included the alar and/or caudal tracts.

Species	n	Percent molting	Percent with molt extensive	Net daily gain estimate[a]
Ruby-throated Hummingbird[b]	256	70.7	3.9	—
Least Flycatcher	118	67.8	5.1	Positive
Black-capped Chickadee[c]	224	99.1	48.2	Positive
Gray Catbird[b]	248	95.2	60.5	Negative
Red-eyed Vireo[b]	625	53.0	11.5	—
Tennessee Warbler	687	45.3	11.6	Positive, negative
Nashville Warbler	487	43.1	10.1	—
Chestnut-sided Warbler	298	41.9	6.7	Negative, positive
Magnolia Warbler	640	28.6	3.1	Negative, positive
American Redstart	394	17.8	1.8	Positive
Ovenbird[b]	491	33.6	6.9	Negative
Common Yellowthroat[b]	110	70.9	33.6	Positive

[a] Direction of net daily gains from Table 3.
[b] Migrant species with resident breeding population.
[c] Resident species included for comparison.

On average, however, in species with large sample sizes it is virtually certain that few if any individuals are depositing fat, and it is questionable whether (again, on average) they are even maintaining (not losing) body mass. Since no significant negative slopes were found, there may be large differences among individuals in species showing no significant diurnal condition changes, with some gaining and others losing mass. A species-level approach may fail here, because it ignores differences between groups of birds (e.g. different breeding and wintering origins, age and sex structure, etc.).

Resident species for comparison.—Including the Black-capped Chickadee in these analyses provides two valuable insights. First, mass loss in recaptured birds is not unique to migrants (Table 1). This suggests that factors not related to migration may be as important to individual mass changes as "getting properly established" at a new stopover site, which has been postulated as a reason for initial mass loss in recaptured migrants (see Alerstam 1991:287). In this resident species, these factors could be the stress related to capture and handling, molt costs, or food competition from migrants. Second, the Black-capped Chickadee provides a means of evaluating our regression technique on a species that is living in a favorable environment (i.e. an area where they can remain without starving). Although the spring regression did not reveal the positive slope that we assume is present in the overall population (our sample size was not large enough), the autumn analysis

revealed diel gains of 0.0 to 2.8% of mean body mass (Table 3). Since chickadees did not appear to be depositing fat at our site (unpubl. data), we expected net daily gains of zero in this species. The positive diel gains suggested by our analysis are dependent on the mean fat-free mass of the species. Our estimate of this value for this species is likely to be low (see Methods), which has the effect of increasing net daily gain by decreasing estimated nocturnal losses.

Contrasting results from different analyses.—At the species level, the question of whether migrants gain mass at a stopover can be addressed in two ways. Both methods have inherent assumptions. The following assumptions are made when analyzing recaptures: (a) recaptured individuals are representative of noncaptured and nonrecaptured individuals; and (b) capture and handling have no effect upon individual mass change. The assumptions made when using condition-by-time-of-day technique are: (a) that captured birds are representative of all individuals occurring at a stopover site; and (b) that there is no mass-based bias to diurnal movement schedules (and resultant captures) among free-ranging individuals.

Researchers asking questions at the species level should be aware that the assumptions accompanying the analysis of recaptures at this level of investigation are frequently violated (for examples, see Nisbet et al. 1963, Bairlein 1987, Moore and Kerlinger 1987, Winker et al. 1992a). Also, handling effects have been noted in recaptured birds (Rogers and Odum 1966,

Nisbet and Medway 1972). Although the assumptions accompanying the condition-by-time-of-day method have not been tested, they seem more robust. If the assumption that there is no mass-based bias to feeding schedules is false, it would likely cause an error on the conservative side; we would expect unsatiated individuals to feed longer, perhaps biasing late afternoon and evening captures toward lighter individuals and thereby lowering the condition gain slope. The condition-by-time-of-day method gives much less consideration to the very few individuals that may remain for a long period of time at a site, molting, for example (up to 30 days in the Tennessee Warbler at our site).

Relatively few individuals remained at our site for more than one day (only 9.5% of all migrants captured; Tables 1 and 2). In most species, individuals remaining for long periods showed an average loss in mass. With recapture data alone we might conclude from such a finding that our site is largely inimical to woodland-associated migrants. Given that the assumptions accompanying the analysis of recaptures are likely to be violated, however, we reject this conclusion. The histories of recaptured birds are interesting from several perspectives (e.g. Winker et al. 1991), and analyses of recaptures should not be abandoned. Differences often exist between recaptured and nonrecaptured birds, however, and we question whether the mass changes of recaptures should be considered indicative of general migrant populations. Our analyses of broad diurnal trends among migrants at our site present a different picture of mass gain than that obtained from recapture analysis. Daily changes in mass tend to be greater in magnitude among entire transient populations than among the minority of individuals recaptured. Also, seasonal and interspecific variation appears to be greater (Tables 1, 2, and 3) when all captures are considered.

The analyses of the Black-capped Chickadee seem to provide support for use of the condition-by-time-of-day technique. If individuals of this resident species really were losing an average of 0.11 g/day as recapture analyses suggest (Table 1), we should have encountered emaciated chickadees, which we did not. The regression analysis, on the other hand, came closer to the expectation that this species should maintain body mass through the course of our autumn seasons, although, as noted, we probably underestimated the fat-free mass of this species.

A handling effect may have contributed to mass loss among recaptures at our site. Upon capture, birds were brought to a central location for banding and release. This form of displacement and the interference with feeding schedules associated with capture probably have an effect on body mass in small birds.

Species-level differences.—The negative diel gain estimates for Ovenbirds and Gray Catbirds in autumn may be the result of several factors. Both of these species breed commonly at our site, suggesting that proximity to breeding grounds might be a factor. Of the five migrant species examined with resident breeding populations, only the Common Yellowthroat showed positive diel gains. Since the Ovenbird, yellowthroat, and catbird show an incidence of molt that is not concordant with their average autumn net daily mass changes (Tables 3 and 4), molt could only be a large contributing factor in the mass losses observed if its effects are markedly different between species. This possibility should not be ignored (see Winker et al. 1992a). Mass loss might occur with more prevalence among species with resident breeding populations because of the preponderance of young birds, many of which may be only recently independent. Due to the possibility of interspecific variation in immature survival, the importance of this factor in specieswide mass changes at stopover sites might be determined through a study of intraspecific variation in mass gain and population structure along a latitudinal gradient. Finally, the mass losses described here may be due to competition for resources at a time when numbers of birds are very high (see Winker et al. 1992b). These net daily mass losses suggest that a site suitable for breeding is not suitable for premigratory fattening in at least two species. This is concordant with the observation that individuals of some species leave their breeding areas long before migration (Rappole and Ballard 1987).

Energetic considerations.—When individuals migrate at night they do not "pay" the resting cost of nocturnal metabolism. Thus, the diurnal gain (excluding nonfat components) can be used to fuel flight. In this respect, a night spent on stopover is a waste of energy that might be used in migration. However, choosing to migrate rather than remain grounded dictates a higher

metabolic cost, and individual movements should reflect this choice. Thus, it is not uncommon for recaptured migrants to be leaner at initial capture than birds that are not recaptured (birds that probably have continued to migrate). The Least Flycatcher at our site represents this typical case; birds remaining at the site for more than one night showed a lower condition index than birds that were never recaptured. However, when a stopover site is not suitable for fat replenishment, individuals attempting to accumulate fat should leave (not be recaptured), while those with greater reserves might be under less pressure to do so. Observations on Chestnut-sided Warblers at our site in autumn appeared to support this hypothesis (cf. Rappole and Warner 1976, Safriel and Lavee 1988); fat individuals were more likely to remain for a night than lean ones.

Conclusions.—Given physical constraints and distances between wintering and breeding grounds, wooded areas probably play an important role in providing transient, woodland-associated migrants with the food they need for fat deposition and continued migration. Thus, it might be assumed that a locality or habitat is important as a fattening site when a species occurs commonly there during migration. Our analyses suggest that this assumption may be invalid. The manner in which our site was used on stopover appears to vary widely among the most common migrant species occurring there. The energetic constraints of molt probably contributed to some of the specific differences observed, but food availability (although not addressed in our study) probably also played a role. In addition, the rates of movement that different species (or sexes, or populations) maintain in migration, and the different distances that they must travel, probably affect fat deposition. From our strictly local perspective, we conclude that patterns of fat deposition vary among woodland-associated, long-distance migrants both geographically and seasonally.

"Woodland-associated" migrants, therefore, constitute a heterogeneous group. Lumping them together obscures the fact that a stopover site can be used in different ways by the most common species occurring there. For some species our site is a molting ground, for others an area of fat deposition, and for still others probably just a locality that must be endured until nightfall. Even a broad array of woodlands does not appear to provide all of the common species occurring there with the resources needed for fat deposition. Wider geographic studies of this nature might illuminate the fat-deposition strategies of species like the Red-eyed Vireo and Nashville Warbler, which were common at our site, but do not appear to be depositing fat while there.

LITERATURE CITED

ALERSTAM, T. 1991. Bird migration. Cambridge Univ. Press, Cambridge.

BAIRLEIN, F. 1987. The migratory strategy of the Garden Warbler: A survey of laboratory and field data. Ringing & Migr. 8:59–72.

BAIRLEIN, F. 1988. How do migratory songbirds cross the Sahara? Trends Ecol. & Evol. 3:191–194.

BALDWIN, S. P., AND S. C. KENDEIGH. 1938. Variations in the weights of birds. Auk 55:416–467.

BERTHOLD, P. 1975. Migration: Control and metabolic physiology. Pages 77–128 *in* Avian biology, vol. 5 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

BIEBACH, H. 1988. Ecophysiology of resting Willow Warblers (*Phylloscopus trochilus*) crossing the Sahara. Pages 2162–2168 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.

CHERRY, J. D. 1982. Fat deposition and length of stopover of migrant White-crowned Sparrows. Auk 99:725–732.

COLLINS, C. T., AND R. A. BRADLEY. 1971. Analysis of body weights of spring migrants in southern California. Western Bird-Bander 46:48–51.

CONNELL, C. E., E. P. ODUM, AND H. KALE. 1960. Fat-free weights of birds. Auk 77:1–9.

DAVIDSON, N. C. 1983. Formulae for estimating the lean weight and fat reserves of live shorebirds. Ringing & Migr. 4:159–166.

DAWSON, W. R., R. L. MARSH, AND M. E. YACOE. 1983. Metabolic adjustments of small passerines for migration and cold. Am. J. Physiol. 245:R755–R767.

MOORE, F., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47–54.

MUELLER, H. C., AND D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. Bird-Banding 37:83–112.

NAGY, K. 1987. Field metabolic rate and food requirement scaling in birds and mammals. Ecol. Monogr. 57:111–128.

NISBET, I. C. T., W. H. DRURY, JR., AND J. BAIRD. 1963. Weight loss during migration. Part I: Deposition and consumption of fat in the Blackpoll Warbler *Dendroica striata*. Bird-Banding 34:107–139.

NISBET, I. C. T., AND LORD MEDWAY. 1972. Dispersion, population ecology, and migration of Eastern Great Reed-Warblers *Acrocephalus orientalis* wintering in Malaysia. Ibis 114:451–494.

ODUM, E. P. 1960. Lipid deposition in nocturnally migrant birds. Pages 563–576 *in* Proceedings XII International Ornithological Congress (G. Bergman, K. O. Doner, and L. von Haartman, Eds.). Helsinki, 1958. Tilgmannin Kirjapairo, Helsinki.

PAYNE, R. B. 1972. Mechanisms and control of molt. Pages 104–155 *in* Avian biology, vol. 2 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

RAPPOLE, J. H., AND K. BALLARD. 1987. Postbreeding movements of selected species of birds in Athens, Georgia. Wilson Bull. 99:475–480.

RAPPOLE, J. H., AND D. W. WARNER. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. Oecologia 26:193–212.

RAVELING, D. 1963. Variation among samples of Tennessee Warblers (*Vermivora peregrina*) killed in nocturnal migration at a TV tower. M.S. thesis, Univ. Minnesota, Minneapolis.

ROGERS, D. T., JR., AND E. P. ODUM. 1964. Effect of age, sex, and level of fat deposition on major body components in some wood warblers. Auk 81:505–513.

ROGERS, D. T., JR., AND E. P. ODUM. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. Wilson Bull. 78:415–433.

SAFRIEL, U. N., AND D. LAVEE. 1988. Weight changes of cross-desert migrants at an oasis—Do energetic considerations alone determine length of stopover? Oecologia 76:611–619.

SUMMERS, R. W. 1988. The use of linear measurements when comparing masses. Bird Study 36:77–79.

TUCKER, V. A. 1974. Energetics of natural avian flight. Pages 298–333 *in* Avian energetics (R. A. Paynter, Ed.). Publ. Nuttall Ornithol. Club No. 15.

WEISBERG, S. 1985. Applied linear regression. J. Wiley & Sons, New York.

WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1991. Unprecedented stopover site fidelity in a Tennessee Warbler. Wilson Bull. 103:512–514.

WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992a. The Northern Waterthrush and Swainson's Thrush as transients at a temperate inland stopover site. Pages 384–402 *in* Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan and D. W. Johnston, Eds.). Manomet Bird Observatory, Manomet, Massachusetts, and Smithsonian Institution, Washington, D.C.

WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992b. Migration of woodland birds at a fragmented inland stopover site. Wilson Bull. 104:580–597.

YABLONKEVICH, M. L., A. V. BARDIN, K. V. BOLSHAKOV, E. A. POPOV, AND A. P. SHAPOVAL. 1985. [Body weight and fat of birds passing across the middle Asia deserts in spring.] Tr. Zool. Inst. Akad. NAUK SSSR 137:11–59.