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A CROSS-CANADA COMPARISON OF MASS CHANGE IN BIRDS DURING MIGRATION STOPOVER

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ABSTRACT.—I estimated hourly mass change at stopover sites for 14 species of migrant passerines from 15 sites across southern Canada by analyzing size-corrected mass of birds at first capture as a function of time of day of handling. Mean mass gains were 0.40% of lean body mass/h during spring and 0.53% during fall. Mass gain estimates varied significantly with season, site, and species, and were negatively related to condition of birds in the early morning. However, standard errors were large, such that few individual estimates were significantly different. Several sites with consistently low rates of mass gain had characteristics that probably reduced local food supply. Swainson's Thrushes (*Catharus ustulatus*) also had consistently low rates of mass gain. I estimated the time required to accumulate sufficient mass to fuel a 10-h migratory flight, and found that the majority of estimated mass gains were sufficient for birds to refuel during <1 week of stopover in southern Canada. At mean rates of mass gain from this study, migrants in southern Canada could potentially refuel completely during 2–3 days in both seasons, but true periods are likely somewhat longer. Analysis of mass change along migration routes (instead of across them, as in this study) is needed to detect whether there are differences among species in timing and location of maximum fuel deposition, as has been found in Europe. *Received 2 November 2001, accepted 30 June 2002.*

Between migratory flights, birds must replenish energy stores in order to successfully complete their journeys, and the rate at which birds change mass during stopover should be an index of site quality. This measure reflects food abundance as well as incorporating effects of weather conditions, levels of competition and predator harassment, and other external factors that could affect mass change. However, endogenous factors also affect fattening rates, and must be taken into account when interpreting mass change with respect to site quality. For example, birds with optimal fat stores should maintain mass rather than gain more, and optimal fuel loads may vary according to proximity to the final destination or to large geographic barriers such as the Gulf of Mexico. Finally, there may be differences in migratory strategy among species, such as speed of migration or length of migratory flights, that also could affect mass change patterns.

Study of mass change at many sites across a large geographic area may help to tease these factors apart. The only example of such a study to date on nocturnally migrating passerines involved six species captured at 34 sites distributed from northern Europe to North Africa (Schaub and Jenni 2000). Results showed marked differences among species in overall migration strategy, with variation in the time period and location at which maximum fuel loads were accumulated. Such differences have important implications for conservation planning and protection of stopover sites. Similar variation is likely in North American passerine migrants, yet there are only a few studies that have compared mass change among sites, and these were very limited in geographic scope (Dunn 2000, 2001).

Here I compare mass change of 14 species of nocturnally migrating passerines at 15 sites across southern Canada, with the aim of detecting and explaining variation in mass gain among locations. Sample sites were distributed across the main migration routes (Brewer et al. 2000) rather than along a path between breeding and wintering areas. Because all sites were close to the breeding grounds of the target species and distant from major geographic barriers, I expected variation in physiological condition and migratory motivation to be small. Any marked and consistent variation in mass change, therefore, likely would be related to the quality of sites and their surrounding landscapes. The second aim of the study was to estimate the amount of time it would take for actively migrating birds to refuel in southern Canada following depletion of fat reserves. While many assumptions were involved in the model, it provided context for interpretation of the mass change estimates.

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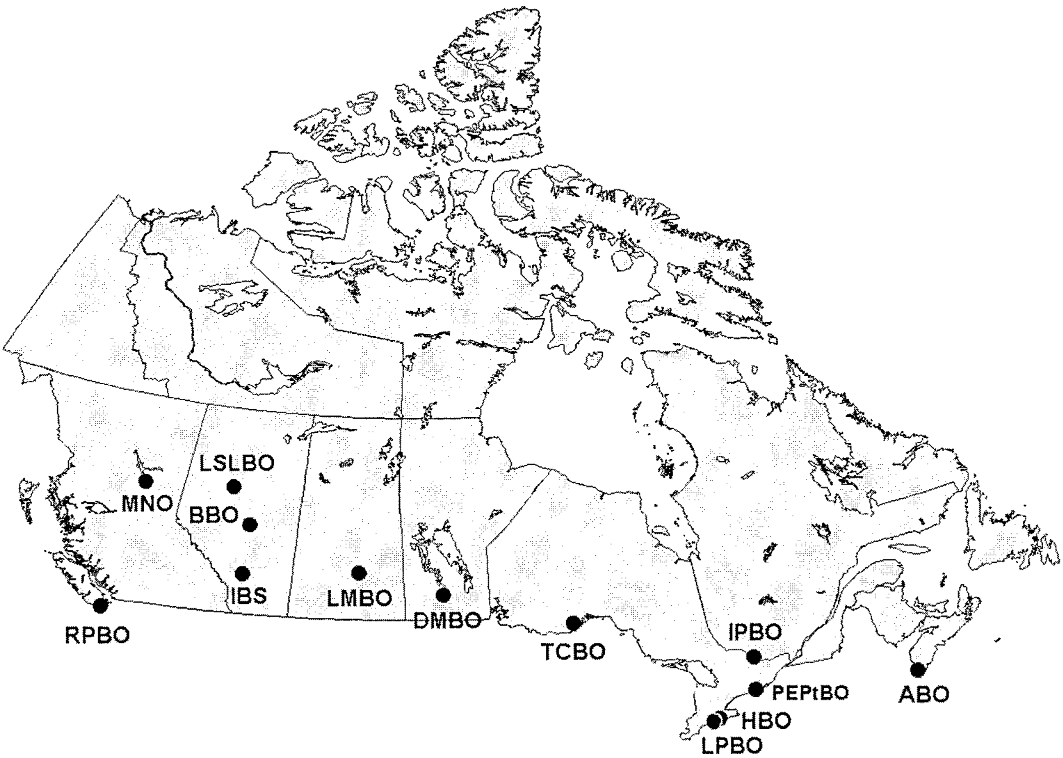

FIG. 1. The Canadian Migration Monitoring Network stations contributing data on mass change during migration stopover to this study were distributed across all of southern Canada. Station names are shown in Table 1.

METHODS

I assessed mass change by regression of mass at first capture on time of day (Morris et al. 1996, Jones et al. 2002). Assumptions of this method are discussed in Winker et al. (1992), Winker (1995), and Dunn (2000, 2001).

Data set.—Data from 15 sites were contributed by 13 member stations in the Canadian Migration Monitoring Network (CMMN), including the three stations operated by Long Point Bird Observatory (LPBO; Fig. 1). I chose 14 target species for analysis (see results) because they were broadly distributed across Canada and large numbers were captured at many CMMN stations. All were small nocturnal migrants, ranging in mean mass from 6.6–31.5 g (median = 12.0 g).

All birds included in analyses were caught in mist nets or in Heligoland traps (Hussell and Woodford 1961). Birds caught in baited ground traps were excluded due to the likelihood of unusual mass gain due to eating baits. Nets were opened at or before dawn and were run for ≥6 h on a daily basis during one or both migration seasons, weather permitting. Birds were transported and held individually in cloth bags or holding boxes until banding, at which time wing chord was measured (unflattened, to the nearest mm) and birds were weighed (usually to the nearest 0.1 g on a triple beam balance or electronic scale). Fat in furcular deposits was scored using a variety of scoring systems, but in all cases it was possible to identify birds that had no fat or only a trace amount of fat, and these were the only fat data used in this paper. Time of day was recorded as shown in Table 1, usually to the nearest 10 min. For this analysis, I expressed times as decimal values and converted them to h after local sunrise to account for progressive change in timing of sunrise during each season. For each site, I applied the sunrise data for 1999 to all years, since variance in the time of sunrise among years was trivial.

Most data came from the late 1990s, but LPBO data covered the 1980s as well. Unless there are long term trends in conditions affecting mass change at a particular site, comparisons among sites should not be affected by variation in the time periods analyzed. Dunn (2000) demonstrated annual variation in rate of mass change and recommended that estimates be based on several years of data to best reflect typical conditions, but those results gave no evidence of long term trends.

To standardize hours of coverage among sites, I limited analysis for each species to data from the first 7 h after sunrise. A few sites operated for only 6 h, but birds captured at the end of the day often were weighed after nets were closed, and the 7-h cutoff al-

TABLE 1. Mass change data of migrating passerines were obtained from 15 stopover sites.

Station	Seasons[a]	Years in sample	Time recorded[b]
Atlantic Bird Observatory (Bon Portage), NS (ABO)	F	1996–98	CS
Beaverhill Bird Observatory, AB (BBO)	B	1997–98	CE
Delta Marsh Bird Observatory, AB (DMBO)	S	1992–99	W (1992–94), CS
Delta Marsh Bird Observatory, AB (DMBO)	F	1995–99	CS
Innis Point Bird Observatory, ON (IPBO)	F	1997–99	W
Inglewood Bird Sanctuary, AB (IBS)	B	1995–99	CS
Haldimand Bird Observatory (Selkirk), ON (HBO)	S	1996–99	CE
Last Mountain Bird Observatory, SK (LMBO)	B	1989–99	W
Lesser Slave Lake Bird Observatory, AB (LSLBO)	B	1994–99	C
Long Point Bird Observatory, ON (LPBO): 3 sites	B	1980–96	CM+W
Mackenzie Nature Observatory, BC (MNO)	F	1996–99	CS
Prince Edward Point Bird Observatory, ON (PEPtBO)	S	1995–99	W
Rocky Point Bird Observatory, BC (RPBO)	F	1999	CS
Thunder Cape Bird Observatory, ON (TCBO)	B	1991–98	CM+W

[a] Season for which data were contributed. S = spring, F = fall, B = both.

[b] C = time of capture. CS = start of net check, CM = approximate middle of net check, CE = end of net check, W = time of weighting. Where both capture and time of weighing were recorded (CM+W), time of capture was used in analyses.

lowed these individuals to be included. For each site, I deleted records of individuals with mass or wing length falling below the 1st percentile or above the 99th percentile of all measurements taken at that site, to exclude possible errors in measurement or recording. I also restricted the data for each species from a given site to the species specific migration period at that site. This was determined by plotting number of birds weighed against date and, for species that summer or winter at or near that site, eliminating data beyond the range of dates during which there was a marked build-up to, and drop-off from, a strong seasonal peak in numbers banded. This limitation, and the fact that I included only first captures in the analyses, minimized the inclusion of locally breeding or overwintering individuals. I did not analyze data for a species unless the final data set for the site and season included ≥100 individuals.

Statistical analyses.—I adjusted mass for body size by calculating a condition index (CI = mass × 100/wing length, in which multiplication by 100 reduces rounding error). Some previous analyses used a different index (e.g., mass × 10,000/wing length^3; Winker et al. 1992, Dunn 2001). However, Winker (1995) found that the newer formula was more effective at correcting mass for structural body size. The regression model was $CI = b_0 + b_1H$, where H is the time of day of capture or weighing, expressed as h after sunrise. The coefficient b_1 is the estimate of hourly change in condition index and can be converted to hourly change in mass using the formula: mass change = b_1(wing length)/100. Wing length used in the conversion was the mean for each species, specific to site and season. The result gave an estimate of hourly mass change for a bird of mean wing length at mean date of capture for the site and season.

The sites contributing to this study recorded time of day of handling in different ways (Table 1). I analyzed data for 39 species from three high volume sites where times were recorded for both capture and weighing, and found that when the latter was used in analysis instead of time of capture, mass change estimates were slightly reduced (due to mass loss prior to weighing; Dunn 1999). However, the mean reduction was only 2% (EHD unpubl. data), so any effect of variation in weighing time among contributing sites should be small.

I compared mass change over the first 7 h after sunrise to mass change over the same period exclusive of the first hour, to determine whether there was an initial rapid gain due to birds filling their guts after a night of fasting. The mean 7-h mass change was only slightly higher than the 6-h change (0.015% of lean mass/h, paired $t_{123} = 1.09$, $P = 0.18$), but there was no consistent pattern among cases in whether the mass change estimate increased or decreased when birds captured during the first hour were omitted. Results presented here are for the full 7-h period, to take advantage of the larger sample size. Two sites, LPBO and Thunder Cape Bird Observatory regularly operated for ≥12 h. For these sites, I estimated mass change over the first 12 h after sunrise, as well as over the first 7 h, to investigate variation in rate of mass change over the course of the day.

I converted all estimates of hourly mass change to percent of lean body mass to allow direct comparison among species of different body size. I defined lean body mass for each species (calculated separately for each site and season to account for any differences in populations being sampled) as the mean mass for birds classified as having no visible fat in the furculum. In a few cases, the mean mass for birds with no fat and a trace of fat combined was lower than the mean for birds with no fat alone (apparently due to individual variation in fat scoring), in which case the lower value was taken as the lean mass. Readers should note that this definition of lean differs from the conventional definition, usually meaning fat free.

For an index of mean physiological condition of birds at a site during early morning, I calculated mean mass during the first 3 h after sunrise, subtracted lean mass (mass of birds with no visible fat) and expressed the difference as a percent of lean mass to remove effects of different body size among species; small samples at some sites precluded use of data from the first hour or two alone. I examined variation in morning condition according to site, season, and species using general linear models (GLM). I also used GLM to examine the effect of these factors and of morning condition on hourly mass gain, using Tukey's studentized range test to evaluate the significance of effects.

Estimates of hourly mass change can be interpreted more easily if compared with some threshold value, which was defined here as the energetic break even point over 24 h during which no migration takes place. For each species, I estimated overnight energy use as existence energy costs (Kendeigh 1970) between sunset and sunrise at the mean passage date for the site and season. I then converted energy use to mass loss, on the assumption that all energy came from burning fat (see Dunn 2001 for additional details and justification of assumptions). This threshold value must be surpassed with energy gain during daytime feeding if energy is to be accumulated for fueling of continued migration. While based on many assumptions, this value can be used as a general reference point for interpreting results of mass change analyses.

For each site, season, and species, I estimated the number of days of refueling that would be required for a lean bird (one without visible fat) to gain enough mass to sustain a 10-h migratory flight without falling below its lean mass. I conducted two analyses: one assuming that rate of change over the first 7 h of the day would be continued over all daylight hours (specific to season, site, and species), and the other assuming no further gain or loss during daylight hours subsequent to 7 h of feeding. For these estimations I assumed that mass loss on nights without migration was the threshold value described above, and that hourly mass loss during migration was $0.0533 \times \text{mass}^{0.40}$ (Hussell and Lambert 1980). The latter formula was based on mass loss experienced by nine small passerine species during actual nocturnal migration (exclusive of Blackpoll Warbler, *Dendroica striata*, for which mass loss was exceptionally low), and amounted to about 0.9% of body mass/h.

Mass change estimates are presented as the estimate ± SE, expressed as percent of lean body mass/h. Results were considered significant if $P < 0.05$. Other mean values are shown as the estimate ± SD.

RESULTS

Hourly mass change estimates for each site and season are listed in Table 2. Mean rates were 0.40% of lean body mass/h during spring ($n = 76$) and 0.53% during fall ($n = 106$). Comparison of values for species-sites for which results were available from both seasons showed that fall values were significantly higher (paired $t_{52} = 2.18$, $P = 0.034$), and were less likely to fall below threshold values (19% of cases during fall versus 38% during spring).

Standard errors of mass change estimates were high, so there were few significant differences among estimates (Table 2), despite their spanning a broad range of values (−0.66 to 1.95% of lean mass/h). Nonetheless, there were some exceptions. During spring there were three sites at which fewer than half of the species met or surpassed threshold values (Beaverhill and Last Mountain bird observatories, and site 1 at LPBO; Table 3). During fall, only Atlantic Bird Observatory had a low proportion of species surpassing their thresholds. Delta Marsh Bird Observatory had a particularly high mean mass change during spring, as did Rocky Point Bird Observatory during fall (Table 3).

Table 4 shows a similar summary of data for species. During spring, there were two species that failed to attain or surpass threshold mass change at half or more of the sites for which they were analyzed: Swainson's Thrush (*Catharus ustulatus*), and White-crowned Sparrow (*Zonotrichia leucophrys*). During fall, only the Swainson's Thrush fell below this level.

The mean value of early morning mass (first 3 h after sunrise) relative to lean mass was low (1.20 ± 2.87% above lean body mass, $n = 182$). However, this index of early morning condition varied significantly with species, site, and season (Table 5). For species-sites for which there were data for both seasons, early morning mass was higher during spring than during fall (1.21% versus −0.05% above lean mass, respectively; paired $t_{52} = 3.74$, $P < 0.001$). Among species, Swainson's Thrushes were the heaviest during early morning (5% above lean mass during spring and 2.8% above during fall). Among sites, early morning mass was highest at Delta Marsh and Haldimand bird observatories during spring (5.4% and 8.7% above lean mass, respectively), and at Atlantic Bird Observatory during fall (6.3% above lean mass). Rate of mass gain was negatively related to the difference between early morning and lean mass

TABLE 2. Estimated rates of mass change[a] during migration stopover covered a wide range of values, but had large standard errors. Most estimates showed mass gain sufficient to support a 10-h migratory flight within 1 week (median = 4 days during spring and 3 days during fall). See Table 1 for site names.

	Spring					Fall			
Species and site	*n*	Difference[b]	Mass change (mean ± SE)	Days to refuel[c]	Difference between seasons	*n*	Difference	Mass change (mean ± SE)	Days to refuel[c]
Least Flycatcher, *Empidonax minimus*									
BBO	117	a	−0.43 ± 0.33	—		198	b	0.43 ± 0.21	4
DMBO	226	a	0.61 ± 0.28	2		380	ab	0.67 ± 0.17	2
LMBO	292	a	0.12 ± 0.31	—	*	683	a	1.39 ± 0.25	1
LPBO-1	1,415	a	0.07 ± 0.09	—	*	1,612	b	0.66 ± 0.09	2
LPBO-2	424	a	0.21 ± 0.20	—		571	b	0.52 ± 0.15	3
LPBO-3	653	a	0.40 ± 0.15	4		618	b	0.45 ± 0.16	4
LSLBO	330	a	0.22 ± 0.21	8		210	b	0.06 ± 0.23	—
MNO						324	b	0.40 ± 0.15	3
TCBO						143	b	0.21 ± 0.28	—
Ruby-crowned Kinglet, *Regulus calendula*									
DMBO						236	b	0.75 ± 0.18	3
HBO	411	a	0.89 ± 0.24	2					
IPBO						102	bc	0.44 ± 0.32	20
LMBO						251	abc	0.72 ± 0.23	4
LPBO-1	1,490	b	−0.23 ± 0.11	—		2,188	c	0.09 ± 0.09	—
LPBO-2	1,774	b	−0.25 ± 0.11	—					
LPBO-3	2,980	a	0.48 ± 0.08	5		5,135	b	0.72 ± 0.06	4
MNO						898	b	0.56 ± 0.10	4
PEPtBO	1,013	a	0.85 ± 0.17	2					
RPBO						181	a	1.73 ± 0.29	2
TCBO	106	ab	0.16 ± 0.45	—		374	ab	0.78 ± 0.19	4
Swainson's Thrush, *Catharus ustulatus*									
DMBO	122	a	0.69 ± 0.56	1		262	a	0.11 ± 0.34	—
HBO	169	a	0.06 ± 0.33	—					
IBS						102	a	−0.19 ± 0.46	—
LMBO	139	a	−0.20 ± 0.61	—		182	a	0.43 ± 0.40	2
LPBO-1	305	a	−0.60 ± 0.35	—		1,319	a	−0.10 ± 0.11	—
LPBO-2	216	a	−0.03 ± 0.36	—		1,036	a	−0.04 ± 0.12	—
LPBO-3	504	a	0.20 ± 0.22	5		1,707	a	0.10 ± 0.09	—
MNO						250	a	0.38 ± 0.22	2
PEPtBO	149	a	−0.57 ± 0.48	—					
TCBO						926	a	0.14 ± 0.12	—
Tennessee Warbler, *Vermivora peregrina*									
BBO						149	ab	0.23 ± 0.33	20
DMBO						1,345	b	0.09 ± 0.11	—
LMBO						440	a	1.21 ± 0.28	1
LPBO-1						235	ab	0.41 ± 0.29	6
LPBO-2						545	ab	0.67 ± 0.23	3
LPBO-3	307	b	−0.21 ± 0.38	—		358	a	0.93 ± 0.22	2
TCBO	515	a	1.17 ± 0.18	1	*	841	ab	0.45 ± 0.15	4
Magnolia Warbler, *Dendroica magnolia*									
HBO	229	a	0.81 ± 0.32	2					
LMBO						223	a	0.78 ± 0.29	2
LPBO-1	600	b	−0.66 ± 0.20	—	*	723	a	0.93 ± 0.15	2
LPBO-2	509	ab	0.22 ± 0.24	—		1,649	a	0.58 ± 0.10	4
LPBO-3	2,890	a	0.02 ± 0.09	—	*	1,732	a	0.65 ± 0.10	3
LSLBO						101	a	0.16 ± 0.37	—
MNO						200	a	0.44 ± 0.20	4
PEPtBO	485	a	0.23 ± 0.23	25					
TCBO	330	a	0.39 ± 0.19	4		659	a	0.45 ± 0.14	5

TABLE 2. Continued.

Species and site	Spring				Difference between seasons	Fall			
	n	Difference[b]	Mass change (mean ± SE)	Days to refuel[c]		*n*	Difference	Mass change (mean ± SE)	Days to refuel[c]
Yellow-rumped Warbler, *D. coronata*									
ABO						512	abc	0.26 ± 0.22	—
BBO						429	abc	0.36 ± 0.16	6
DMBO	279	a	1.03 ± 0.35	1		580	ab	0.57 ± 0.14	3
HBO	258	ab	0.25 ± 0.28	11					
IBS						1,084	ab	0.68 ± 0.13	2
IPBO	446	a	0.43 ± 0.24	3					
LMBO	260	ab	0.05 ± 0.36	—		4,025	c	0.26 ± 0.06	—
LPBO-1	900	b	−0.43 ± 0.15	—	*	3,135	c	0.16 ± 0.07	—
LPBO-2	595	ab	−0.04 ± 0.20	—		207	abc	0.67 ± 0.24	3
LPBO-3	614	a	0.63 ± 0.19	2		5,155	a	0.66 ± 0.06	3
LSLBO	172	ab	0.24 ± 0.27	7		673	bc	0.32 ± 0.11	7
MNO						328	bc	0.14 ± 0.16	—
PEPtBO	813	a	0.35 ± 0.16	4					
TCBO	323	a	0.31 ± 0.21	5		675	abc	0.37 ± 0.14	12
Blackpoll Warbler, *D. striata*									
ABO						218	a	−0.06 ± 0.46	—
LMBO						623	a	0.39 ± 0.17	5
LPBO-1						1,333	a	0.73 ± 0.11	2
LPBO-2						708	a	0.60 ± 0.16	3
LPBO-3	104		1.95 ± 0.51	1		388	a	0.75 ± 0.20	2
TCBO						348	a	0.25 ± 0.21	—
American Redstart, *Setophaga ruticilla*									
ABO						149	b	−0.14 ± 0.39	—
DMBO	153	a	1.64 ± 0.42	1		408	ab	0.93 ± 0.17	2
LMBO						456	ab	0.56 ± 0.18	3
LPBO-1	213	c	−0.04 ± 0.31	—		498	ab	0.47 ± 0.16	6
LPBO-2	154	ab	1.36 ± 0.30	1	*	637	b	0.37 ± 0.15	11
LPBO-3	515	bc	0.43 ± 0.18	4		831	ab	0.72 ± 0.13	3
LSLBO	423	c	0.28 ± 0.18	6		831	ab	0.52 ± 0.12	3
MNO						1,150	ab	0.69 ± 0.09	2
PEPtBO	206	a	0.63 ± 0.29	2					
TCBO	460	c	0.36 ± 0.15	5	*	1,553	a	0.90 ± 0.10	2
Northern Waterthrush, *Seiurus noveborecensis*									
ABO						131	a	0.57 ± 0.27	2
DMBO						365	a	0.79 ± 0.21	1
IBS						180	a	0.79 ± 0.29	1
LMBO						215	a	0.19 ± 0.34	36
LPBO-1						262	a	0.95 ± 0.29	1
LPBO-2	140	a	0.42 ± 0.38	3		822	a	0.20 ± 0.16	—
LPBO-3	132	a	0.74 ± 0.45	1		313	a	0.60 ± 0.26	2
MNO						887	a	0.31 ± 0.10	4
TCBO						376	a	0.40 ± 0.22	3
Wilson's Warbler, *Wilsonia pusilla*									
DMBO	171	a	1.78 ± 0.50	1					
IBS						516	a	0.84 ± 0.18	2
LMBO						482	a	0.37 ± 0.27	7
LPBO-1	136	b	−0.21 ± 0.44	—		233	a	0.94 ± 0.28	2
LPBO-2	190	ab	0.68 ± 0.37	2		240	a	0.84 ± 0.27	2
LPBO-3	617	ab	0.47 ± 0.21	4		388	a	0.99 ± 0.23	2
LSLBO						120	a	0.96 ± 0.37	2
MNO						309	a	0.86 ± 0.15	2
RPBO						236	a	0.55 ± 0.16	3

TABLE 2. Continued.

Species and site	Spring				Difference between seasons	Fall			
	n	Difference[b]	Mass change (mean ± SE)	Days to refuel[c]		*n*	Difference	Mass change (mean ± SE)	Days to refuel[c]
Lincoln's Sparrow, *Melospiza lincolnii*									
IBS						154	a	1.13 ± 0.39	1
LMBO						232	a	0.50 ± 0.31	3
LPBO-1	651	a	0.16 ± 0.18	—					
LPBO-2	407	a	0.83 ± 0.27	1					
LPBO-3	551	a	0.38 ± 0.20	3					
MNO						117	a	0.31 ± 0.45	4
PEPtBO	105	a	0.13 ± 0.43	—					
RPBO						138	a	0.98 ± 0.36	1
TCBO						188	a	1.06 ± 0.25	1
White-throated Sparrow, *Zonotrichia albicollis*									
ABO						114	ab	0.07 ± 0.46	—
DMBO	270	a	1.72 ± 0.25	1		399	a	1.04 ± 0.19	1
HBO	559	b	0.49 ± 0.18	2					
IBS						210	ab	0.38 ± 0.32	3
IPBO	110	ab	0.87 ± 0.38	1					
LMBO	223	bc	0.36 ± 0.31	2		412	ab	0.43 ± 0.21	3
LPBO-1	4,333	c	−0.05 ± 0.06	—		1,056	b	0.17 ± 0.11	—
LPBO-2	3,040	b	0.56 ± 0.07	1					
LPBO-3	3,767	b	0.57 ± 0.06	1		2,123	a	0.71 ± 0.09	1
LSLBO	262	abc	0.67 ± 0.30	1		162	ab	0.52 ± 0.24	2
PEPtBO	719	ab	0.91 ± 0.18	1					
TCBO	204	ab	0.65 ± 0.29	1		236	ab	0.34 ± 0.21	3
White-crowned Sparrow, *Z. leucophys*									
LPBO-1	1,072	b	0.02 ± 0.15	—		467	a	0.20 ± 0.19	—
LPBO-2	1,051	b	0.00 ± 0.15	—					
LPBO-3	119	a	1.38 ± 0.46	1		204	a	0.64 ± 0.30	2
MNO						108	a	0.39 ± 0.29	2
TCBO						237	a	0.95 ± 0.22	1
Dark-eyed Junco, *Junco hyemalis*									
DMBO						274	ab	0.70 ± 0.18	2
HBO	253	ab	0.39 ± 0.27	3					
IPBO	192	a	0.77 ± 0.24	1		119	ab	0.52 ± 0.36	3
LMBO						1,082	ab	0.53 ± 0.12	3
LPBO-1	2,154	b	−0.15 ± 0.09	—		1,766	b	0.27 ± 0.09	—
LPBO-2	1,016	a	0.44 ± 0.12	3					
LPBO-3	784	a	0.43 ± 0.15	3		930	a	0.84 ± 0.12	2
MNO						435	b	0.16 ± 0.15	—
PEPtBO	314	a	0.84 ± 0.25	1					
TCBO	482	ab	0.14 ± 0.16	—		2,421	a	0.61 ± 0.07	2

[a] Mass change ± SE, expressed as % of lean body mass/h.

[b] Within species and season, sites not sharing a letter in common were significantly different (Tukey's studentized range tests). Asterisks in the center column indicate significant differences in seasonal values.

[c] Calculation based on the assumption that hourly rate of mass gain was maintained over all daylight hours. A dash indicates that mass was being lost, or gained at a rate insufficient to support a full night of migration within 40 days.

(Table 5), such that a species with early morning mass 5% above lean mass would be expected to have an hourly rate of mass gain about 15% below that of a species starting the day at lean mass.

Estimates of the number of days required to build up enough fuel to sustain 10 h of migration without falling below lean mass (based on the assumption that estimated hourly mass change continued over all daylight h) showed that most birds could completely refuel in ≤1 week (59% of species during

TABLE 3. Sites varied in mean mass change values and in the percent of species achieving net gains over 24-h. Although sites differed in the suite of species analyzed, three sites (BBO, LMBO, and LPBO-1) had consistently low values during spring, and one (ABO) during fall. See Table 1 for site names.

	Spring				Fall			
Site	Mean mass change[a]	Mean threshold[b]	Percentage over threshold[c]	Number of species	Mean mass change	Mean threshold	Percentage over threshold	Number of species
ABO					0.14	0.27	20	5
BBO	−0.43	0.14	0	1	0.34	0.21	100	3
DMBO	1.25	0.14	100	6	0.63	0.22	78	9
HBO	0.48	0.19	83	6				
IBS					0.61	0.20	83	6
IPBO	0.69	0.17	100	3	0.48	0.33	100	2
LMBO	0.08	0.13	25	4	0.60	0.23	100	13
LPBO-1	−0.19	0.18	9	11	0.45	0.27	54	13
LPBO-2	0.37	0.18	67	12	0.49	0.26	89	9
LPBO-3	0.56	0.18	86	14	0.67	0.27	92	13
LSLBO	0.35	0.13	100	4	0.42	0.19	67	6
MNO					0.42	0.18	82	11
PEPtBO	0.42	0.18	75	8				
RPBO					1.09	0.30	100	3
TCBO	0.45	0.17	71	9	0.53	0.24	77	13

[a] Mean of species values, expressed as % of lean body mass/h.
[b] Mean across species of hourly mass gain that must be met or surpassed for mass equilibrium over 24 h with no migration (see Methods).
[c] Percentage of species with data from this site that met or surpassed their thresholds for 24-h mass balance.

spring and 73% during fall; Table 2). Median time to refuel was 4 days during spring and 3 days during fall. At the mean rates of mass change (0.40% of lean body mass/h during spring and 0.53% during fall), estimated refueling time for 12 and 20 g birds was 2–3 days, regardless of season (Fig. 2A). Larger birds required shorter refueling periods because maintenance costs decrease in proportion to increased mass. Refueling time was very sensitive to changes in mass gain up to about 1.75 times the gain needed to maintain

TABLE 4. Compared to other migrating passerines, the Swainson's Thrush stood out as having consistently low rates of mass change at most sites, during both seasons.

	Spring				Fall			
Species	Mean mass change[a]	Mean threshold[b]	Percent over threshold[c]	Number of sites	Mean mass change	Mean threshold	Percent over threshold	Number of sites
American Redstart, *Setophaga ruticilla*	0.67	0.18	86	7	0.56	0.24	89	9
Blackpoll Warbler, *Dendroica striata*	1.95	0.17	100	1	0.44	0.25	67	6
Least Flycatcher, *Empidonax minimus*	0.17	0.16	57	7	0.53	0.21	78	9
Lincoln's Sparrow, *Melospiza lincolnii*	0.38	0.16	75	4	0.80	0.21	100	5
Magnolia Warbler, *D. magnolia*	0.17	0.20	67	6	0.57	0.25	86	7
Yellow-rumped Warbler, *D. coronata*	0.28	0.18	70	10	0.40	0.27	73	11
Northern Waterthrush, *Seiurus noveborencis*	0.58	0.16	100	2	0.53	0.18	100	9
Ruby-crowned Kinglet, *Regulus calendula*	0.32	0.25	50	6	0.72	0.38	88	8
Dark-eyed Junco, *Junco hyemalis*	0.41	0.18	71	7	0.52	0.26	71	7
Swainson's Thrush, *Catharus ustulatus*	−0.06	0.12	29	7	0.10	0.17	25	8
Tennessee Warbler, *Vermivora peregrina*	0.48	0.18	50	2	0.57	0.23	86	7
White-crowned Sparrow, *Zonotrichia leucophys*	0.47	0.13	33	3	0.55	0.21	75	4
Wilson's Warbler, *Wilsonia pusilla*	0.68	0.21	75	4	0.79	0.26	100	8
White-throated Sparrow, *Z. albicollis*	0.68	0.13	90	10	0.46	0.21	75	8

[a] Mean of site values, expressed as % of lean body mass/h.
[b] Mean across sites of hourly mass gain that must be met or surpassed for mass equilibrium over 24 h with no migration (see Methods).
[c] Percentage of sites at which species met or surpassed its threshold for 24-h mass balance.

TABLE 5. Morning condition (the difference between mean mass during the first 3 h of the day and lean mass, expressed as % of lean mass) varied with season, site and species (general linear models). Rate of mass gain also varied with these factors, and decreased with improved morning condition.

Source of variation	df	SS	*F*	*P*
Morning condition				
Season	1	88.49	30.42	<0.001
Species	13	207.67	5.49	<0.001
Site	14	747.01	18.34	<0.001
Rate of mass gain				
Season	1	0.74	6.20	0.01
Species	13	5.39	3.50	<0.001
Site	14	8.23	4.95	<0.001
Morning condition	1	1.17	14.05	<0.001

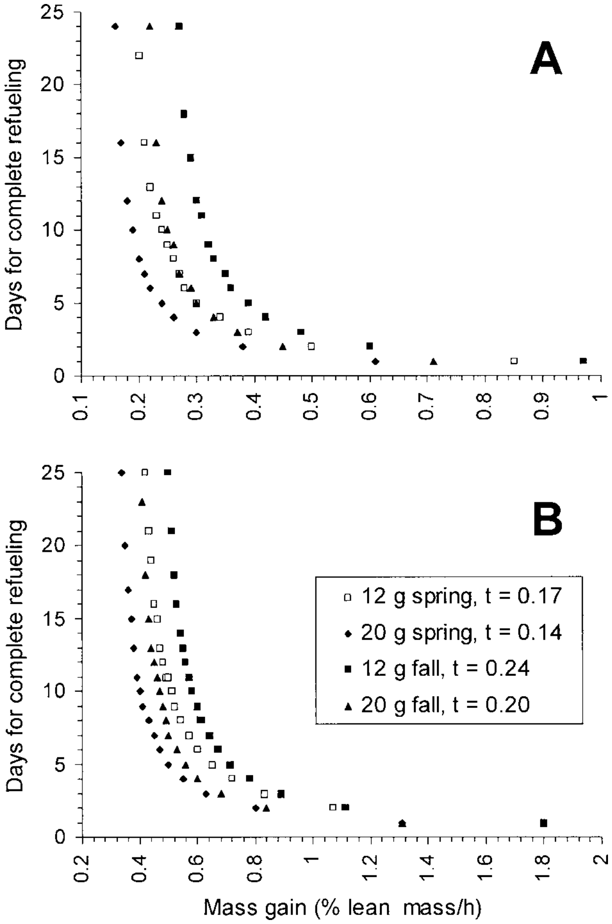

FIG. 2. Results of a model estimating days required for lean birds of two sizes to gain sufficient mass in southern Canada to undertake a 10-h migratory flight without falling below their lean mass (see Methods). (A) Birds were assumed to gain mass during every daylight hour (15 h during spring and 13 h during fall). (B) Birds gained mass for 7 h and maintained stable mass over the remaining daylight hours. Birds in Fig. 2A could fly for 10 h after 2–3 days of refueling in both seasons, whereas refueling time in Fig. 2B rose to as much as 3 weeks (note difference in x-axis scales).

24-h mass balance, after which increased rate of gain made relatively little difference.

When mass change was assumed to cease after 7 h (with mass maintained, but not increased over remaining daylight hours), refueling curves shifted to the right (Fig. 2B). Birds gaining for only 7 h would have to double their hourly mass gain in order to refuel as fast as birds that gained mass throughout the day.

At sites where data often were collected for ≥12 h (Thunder Cape Bird Observatory and LPBO), hourly mass change estimates based on 12 h were significantly higher than those based on 7 h during spring (0.46% of lean mass/h versus 0.31%, respectively; paired $t_{45} = 4.02$, $P < 0.001$), but were not significantly different during fall (0.57% of lean mass/h versus 0.53%, respectively; paired $t_{48} = 1.49$, $P = 0.14$). Results were similar for each season at each site.

DISCUSSION

Although estimates of hourly mass change varied widely, confidence intervals were so broad that there were few significant differences among them. Wide confidence intervals are inevitable in analyses of this kind because there will nearly always be large variation in individual mass at any given time of day. This variation results from factors such as length of stopover prior to first capture, fat stores remaining at the end of the migratory flight preceding stopover, weather conditions, and fluctuations in daily food supply. Consistent results should nonetheless reflect biologically meaningful differences among estimates (Dunn 2001, Jones et al. 2002).

Two sites had consistently low mass change estimates for spring (Table 3): Last Mountain Bird Observatory and the LPBO site at the extreme end of Long Point in Lake Erie (LPBO-1). Beaverhill Bird Observatory also had a low spring value, but data were available for only one species. Last Mountain Bird Observatory is surrounded by extensive agricultural grassland, and appears to attract birds during spring primarily under unusual weather conditions, rather than serving as a regular stopover site (A. R. Smith pers. comm.). Plant phenology at LPBO-1 is strongly delayed because of the cold spring temperature of surrounding Lake Erie (Dunn 2000, 2001). The only site with consistently low mass gains during fall, Atlantic Bird Observatory, also is affected by cool surrounding water, in this case the Atlantic Ocean, and may experience more fog and high winds than other sites. Birds at this location were heavier early in the morning than birds at other sites during fall, but the predicted reduction in mass gain as a result of higher early morning mass was not enough to explain the low gains at the site.

Among species, the Swainson's Thrush was the only one to have consistently low mass gains during both seasons (Table 4). Dunn (2001) hypothesized that low mass gain for all thrushes at LPBO was a result of poor habitat for ground foragers. At sites other than LPBO, early morning mass of Swainson's Thrushes was up to 9% above lean mass, but again, rate of gain was too low to be explained by this alone.

High relative mass of birds during the early morning probably is an indicator of stopover length. At sites from which birds move on quickly, estimates of mass gain should indicate the true potential for rapid accumulation of mass at the site. Somewhat paradoxically, if birds stay on for more than a day or two at a site that has good food resources, mass gain estimates may be reduced. Heavy birds need not gain as much mass as light ones and, more importantly, may reduce the rate or cease feeding earlier in the day, violating the assumption of the analysis method that there is no bias in time of day that birds of different mass will be captured. This is a topic that needs further investigation.

Mass gain was significantly lower during spring than during fall. Migrants in southern Canada are closer to their final destination during spring and may not need to accumulate as much fuel for continued flight as during fall. However, birds moving northward often carry extra reserves (Sandberg and Moore 1996), and the many instances of spring mass loss in this study suggested that feeding conditions at the study sites often were poor. Temperatures in southern Canada during spring migration can range from near freezing to >20°C, affecting plant phenology and insect activity accordingly, whereas fall weather is much more predictable and benign.

A comparison of mass change at Delta Marsh Bird Observatory during cold versus warm spring seasons might be a good test of the importance of weather effects. This site stood out as having particularly high mass gains during spring (Table 3), but most of the data came from a series of years with warm, early springs (H. den Haan pers. comm.). In recent years there have been several very late springs, and a comparison of mass change during early versus late seasons would be of interest.

The model of refueling time (Fig. 2) demonstrated some interesting facets of stopover energetics. The shape of the relationship between refueling time and mass gain was little affected by changing assumptions about hours of daily feeding or costs of overnight metabolism and migration, which served mainly to shift the location of the curves in the graphical space. The model showed that the number of hours of gain during the day had an important influence on refueling period (Fig. 2). In both seasons, day length varied considerably among sites, and a single species could experience as much as 3.5 h difference in daylight, depending upon latitude of the site and mean passage date. It is therefore important to consider the amount of daylight that actually is used for feeding.

Limited information in the literature indicated that birds foraged at a high rate during the first 7 h of the day, followed by rest for several hours prior to renewed feeding in late afternoon (Graber and Graber 1983). This pattern corresponds with the experience of banders, who see similar fluctuation in capture rates of migrants. One would expect individual variation in feeding intensity and duration to be great, depending upon factors such as the bird’s fuel stores, its motivation to undertake another migratory flight quickly, its need for rest, and conditions of weather and predator abundance, and it is possible that more actively foraging birds have a higher chance of being captured. If that is the case, the data presented here showing that rate of mass gain remains high throughout the day may be biased upwards. The figures shown for refueling times in Table 2 and Fig. 2A should therefore be considered potential periods, while actual periods are likely to be longer. However, they are unlikely to be as long as shown in Fig. 2B, as there is no reason to expect that all birds would cease gaining mass entirely after 7 h of feeding.

The refueling periods described here are not the same as stopover periods. Depending upon factors such as local foraging conditions, weather, body condition, and motivation, birds may undertake a migratory flight of a few hours without waiting long enough to accumulate sufficient fuel to support a full night of sustained migration (Biebach et al. 1986, Moore et al. 1995). Other birds will arrive with some fuel reserves remaining, so will not have to stay in the area for the full refueling period. Stopover also could be longer than the predicted refueling period, as when weather conditions preclude continued migration.

This study was the first in North America to compare mass gain of passerines during migratory stopover across a large geographic area. It examined data retrospectively, however, and the search for patterns was hampered by the fact that data for the same species were not available from all sites and both seasons. Even with similar limitations, however, a similar study of variation in body condition and rates of mass gain along a north-south transect should be able to detect whether there are gradual or sudden changes along the migration route. For example, fall migrants thought to have migrated overland to a study site in southern Mexico had low mean mass, and mass gains were similar to those from this study (Winker 1995). In contrast, birds captured during fall along the central U.S. Gulf coast, and expected to make trans-Gulf flights, were heavier and were maintaining rather than gaining mass (Woodrey and Moore 1997). However, it is unknown whether birds intending trans-Gulf flights gain mass gradually along the migration route, or rely on good conditions for refueling close to the geographic barrier. I sought data from locations in eastern North America to undertake an analysis of mass gain along a migration route, but found there were essentially no data available from the southeastern United States. The alternative is to design a focused study similar to that described by Schaub and Jenni (2000). Results from studies on geographic patterns in mass gain are needed if conservation planners are to make informed decisions on the type and distribution of stopover habitat that should be protected along migration routes.

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