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DAILY MASS CHANGES IN LANDBIRDS DURING MIGRATION STOPOVER ON THE SOUTH SHORE OF LAKE ONTARIO

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Abstract.—Assigning conservation priorities to areas used by birds during migration requires information on the relative quality of areas and habitats. The rate at which migratory birds replenish energy reserves during stopover may be used as an indicator of stopover-site quality. We estimated the rate of mass gain of 34 landbird species during stopover at a near-shore terrestrial site on the south shore of Lake Ontario in New York during 12 migration seasons from 1999 to 2004. The average rate of mass gain was estimated by relating a measure of condition to time of capture (hour after sunrise) with linear regression. Data from 25,385 captures were analyzed. Significantly positive rates of mass change were detected for 20 of 30 species during spring migration and 19 of 21 species during autumn migration. No significantly negative trends were detected in either season. Daily rates of mass gain across all species averaged 9.84% of average lean body weight during spring migration and 9.77% during autumn migration. Our regression estimates were significantly greater than estimates from traditional analyses that examine mass changes in recaptured birds. Analyses of mass changes in recaptured birds revealed a mean daily change of –0.68% of average lean mass in spring and 0.13% in autumn. Because of sampling biases inherent in recapture analyses, the regression approach is likely more accurate when the assumptions of the method are met. Similar studies in various habitats, landscapes, and regions are required to prioritize conservation efforts targeting migratory stages of the annual cycle. *Received 13 February 2005, accepted 7 February 2006.*

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Daily Mass Changes in Landbirds during Migration Stopover on the South Shore of Lake Ontario

Resumen.—Assigning conservation priorities to areas used by birds during migration requires information on the relative quality of areas and habitats. The rate at which migratory birds replenish energy reserves during stopover may be used as an indicator of stopover-site quality. We estimated the rate of mass gain of 34 landbird species during stopover at a near-shore terrestrial site on the south shore of Lake Ontario in New York during 12 migration seasons from 1999 to 2004. The average rate of mass gain was estimated by relating a measure of condition to time of capture (hour after sunrise) with linear regression. Data from 25,385 captures were analyzed. Significantly positive rates of mass change were detected for 20 of 30 species during spring migration and 19 of 21 species during autumn migration. No significantly negative trends were detected in either season. Daily rates of mass

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gain across all species averaged 9.84% of average lean body weight during spring migration and 9.77% during autumn migration. Our regression estimates were significantly greater than estimates from traditional analyses that examine mass changes in recaptured birds. Analyses of mass changes in recaptured birds revealed a mean daily change of –0.68% of average lean mass in spring and 0.13% in autumn. Because of sampling biases inherent in recapture analyses, the regression approach is likely more accurate when the assumptions of the method are met. Similar studies in various habitats, landscapes, and regions are required to prioritize conservation efforts targeting migratory stages of the annual cycle.

Migratory birds face numerous challenges during biannual journeys between breeding and wintering areas. Challenges include the need to locate resources in novel environments (Barlein 1983, Hutto 1985, Moore et al. 1995), to avoid predation by a changing suite of predators (Lindstrom 1989, Moore 1994), to correct for orientation and navigational errors (Ralph 1978), and to survive weather conditions that are adverse for migratory flight (Whitmore et al. 1977, Richardson 1978). Although migrants may only spend 8–12 weeks in transit annually, a recent study concluded that ~85% of annual adult mortality in one population of Black-throated Blue Warblers occurred during the migratory phases of the annual cycle (Sillett and Holmes 2002). The relative importance of mortality during migration for other populations and species remains unknown, but to avoid mortality during transit, all migrants must locate suitable stopover sites in which to rest, avoid predation, and refuel for the next step of migration. As such, protecting suitable stopover habitats is a conservation priority (Donovan et al. 2002). Yet incorporating specific stopover sites into conservation plans has been limited by an inability to prioritize areas or habitats used by migrants, and few comparisons between stopover sites have been conducted (Dunn 2002).

Developing conservation priorities for stopover sites requires information regarding the locations and landcover characteristics of areas where birds concentrate, as well as information on the quality of those sites for migrants. Large bodies of water may function as temporary barriers to migration, and concentrations of migrants have been documented at near-shore sites (Moore and Kerlinger 1987, Gauthreaux and Belser 1998). The rate of mass gain during stopover at these near-shore sites is expected to be positively related to habitat quality (Parnell 1969) and has been used as an indicator of stopover-site quality (Dunn 2002). To quantify the quality of a stopover site on the south shore of Lake Ontario that is known to host large concentrations of migrants, we assessed the rate of mass change during spring and autumn migration in 34 landbird species.

Previous studies have used mass changes in recaptured birds to quantify site quality (Cherry 1982, Moore and Kerlinger 1987). However, the use of recapture data may be biased and has been criticized (Winker et al. 1992). Sample sizes for recapture analyses are generally small, because only a limited number of transients are encountered more than once. Furthermore, recaptured individuals may not represent the bulk of the migrant population, because birds in poorer condition are more likely to be recaptured (Winker et al. 1992, present study). And the effects of capturing and handling birds may influence the rate of mass change (Schwilch and Jenni 2001; but see Hansson and Pettersson 1989).

An alternative approach for assessing changes in condition during stopover is to relate a measure of condition to time of capture during the day for all individuals encountered of a given species (Winker et al. 1992, Dunn 2000). The slope of the resulting regression line represents the average hourly change in condition for birds at the site. Our objectives were to (1) use the regression technique to quantify mass changes in migratory birds stopping along the south shore of Lake Ontario, (2) compare our results with those from other sites that employed this technique (Dunn 2002), and (3) compare regression estimates of mass change with those calculated by traditional recapture estimates.

Methods

Birds were captured at Braddock Bay Bird Observatory (43°19′N, 77°43′W) during spring (~24 April to ~6 June) and autumn (~20 August to ~31 October) migrations from 1999 to 2004. The study site was located on the south shore of Lake Ontario near Rochester, New York (Fig. 1), and was characterized by a mix of abandoned field and early-successional landcover types dominated by viburnum (*Viburnum* sp.), dogwood (*Cornus* sp.), honeysuckle (*Lonicera* sp.), ash (*Fraxinus* sp.) and alder (*Alnus* sp.). The Braddock Bay site was surrounded by a landscape (5-km radius) characterized by water cover (59%) and agricultural land-use (27%), with lesser amounts of forest (9%), developed areas (4%), and wetlands (1%). Given radar analyses indicating that most migratory landbirds flew directly over Lake Ontario (D. Bonter unpubl. data), near-shore habitats on the south shore of the lake were the final possible stopover location before crossing in the spring, and the first available landfall after crossing during autumn migration.

Birds were captured in 30-mm-mesh mist nets that were operated daily during the migration periods, weather permitting. Nets were opened by sunrise and operated for a minimum of 6 h per day. Birds were removed from nets at 30-min intervals. Captured birds were transported to a central processing location, where we recorded time of capture, net location, species, age, sex, unflattened wing length, mass (to nearest 0.1 g on a digital electronic balance), and subcutaneous fat load (0 = no visible fat, 1 = trace of fat visible in furcular region, 2 = furcular region filling but concave, 3 = furcular region filled with fat, 4 = furcular region convex and fat visible on abdomen, 5 = furcular region convex and abdomen mounded, following Helms and Drury [1960]). All individuals were marked with a federal leg band and released. Recaptured birds were reprocessed without reference to data collected at previous encounters (Braddock Bay Bird Observatory 1999).

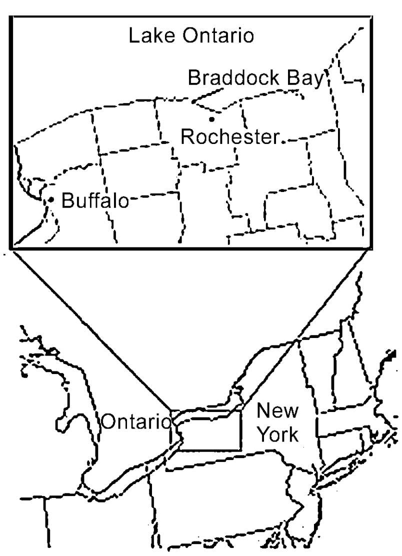

Fig. 1. Location of Braddock Bay study site.

Regression Analyses

Analyses were limited to the peak migration period for each species to quantify rates of mass gain for the bulk of the population, to eliminate atypical individuals, and to reduce the influence of seasonal variability in rates of mass change on regression estimates. To identify the peak migration period, daily capture rates for each species were plotted (all years combined), and a peak 14-day migration window was identified. Regression equations were calculated for all species, with $n > 100$ birds captured during the species' peak migration window. Data from only the first 8 h of operation daily were included in analyses, because sampling past hour 8 was sporadic. Although many individuals were recaptured more than one day after initial capture at our sites, regression analyses were limited to data from the first capture only.

The condition of each bird was calculated as an adjusted measure of mass based on body size (Winker 1995), using the formula

$$\text{Condition} = \frac{\text{mass (g)}}{\text{wing length (mm)}} \times 100$$

Such estimates of condition would be biased if capture rates for different-sized birds varied during the day. However, we detected no significant relationship between morphological measurements (wing length) and capture time (hour after sunrise) in any of the species analyzed (wing length regressed on hour, hour^2, and hour^3; $P > 0.05$ after Bonferroni correction for multiple tests).

Simple linear regressions of condition on capture time were calculated by species as

$$C = b_0 + b_1 H$$

where C is the estimate of condition and H is the hour (after sunrise) of capture. The intercept, b_0, is an estimate of the average condition of birds at daybreak before foraging. The slope of the regression line, b_1, is the estimate of hourly change in condition.

Estimates of net daily change in condition were calculated for each species by multiplying the slope of the regression line by an estimate of foraging time based on day length (12 h in autumn, 15 h in spring). Estimated losses in condition resulting from nocturnal metabolism were then subtracted (4.5% of mean condition; Winker et al. 1992). Note that actual nocturnal losses likely varied in relation to body size (Dunn 2001) and environmental conditions, and the fixed 4.5% value is intended only to provide an approximation of losses.

Regression results from the present study were compared with those from a previous study using the same methods with data from 15 banding stations in southern Canada (Dunn 2002). Rates of change in condition were converted to average hourly mass change as a percentage of lean mass to allow for comparisons among species and studies (Dunn 2002). All birds with fat load ≤ 1 (see above) were included in calculations of mean lean mass. The mean wing chord for each species-by-season combination was used in the transformation (see Appendix for mean lean mass and wing chord values by season).

Traditional Recapture Analyses

To compare regression estimates of mass gain with a more traditional measure, we estimated daily mass changes in recaptured birds by examining differences in recorded mass and capture time from the first and last encounter of each individual. Because birds generally gained mass as the day progressed, mass at first and last encounter was adjusted to a standard capture time using the estimated hourly changes from the above regression analyses. Adjusted mass difference (M_A) was calculated as

$$M_A = (M_2 - M_1) + (H_1 - H_2) \times b_1$$

where M_2 is mass at last encounter, M_1 is mass at first encounter, H_1 is capture time at first encounter, H_2 is capture time at last encounter, and b_1 is the slope of the regression equation for that species. If the slope of the regression equation was nonsignificant ($P > 0.05$), we set $b_1 = 0$. Daily changes were then calculated by dividing the adjusted mass difference by the number of days between captures:

$$\frac{M_A}{D_2 - D_1}$$

where D_2 is the Julian date of the last encounter and D_1 is the Julian date of the first encounter.

Mass changes from recapture data were calculated for all species with ≥10 recaptured individuals per season.

Only a few individuals of a small number of species (mostly Gray Catbird, Yellow Warbler, Common Yellowthroat, Swamp Sparrow, and Song Sparrow) nested or wintered locally at the study site, so data were collected almost exclusively from transient individuals. Any individual captured in multiple migration seasons or captured on more than one occasion >14 days apart was assumed to be a locally breeding or wintering bird and was eliminated from analyses.

Results

During autumn migration from 1999 to 2004, we captured 12,860 individuals during the peak migration windows for each species and recorded 1,532 recaptures of species included in the analyses. During spring migration in the five years, we captured 12,525 individuals and recorded 637 recaptures of analyzed species (see Appendix for scientific names, common names, species codes, mean lean mass values, and mean wing chord measurements for each species used in the analyses).

Regression Analyses

Twenty of 30 species showed significant ($P < 0.05$) changes in condition throughout the day during spring migration (Table 1). Of these 20 species, estimates of mean hourly mass change ranged from 0.41% (Magnolia Warbler) to 1.42% (Golden-crowned Kinglet). Average estimated hourly mass change across all species was 0.62% of mean lean body mass.

Table 1. Regression estimates of daily changes in condition during spring migration.

Species	*n*	*F*	*P*	Mean hourly mass change [a]	Previous studies [b]
Yellow-bellied Flycatcher	203	5.00	0.027	0.53% ± 0.23%	–
"Traill's" Flycatcher [c]	569	3.15	0.076	0.28% ± 0.15%	–
Least Flycatcher	332	10.19	0.002	0.58% ± 0.18%	0.17%
Red-eyed Vireo	220	9.96	0.002	1.18% ± 0.37%	–
Brown Creeper	117	8.12	0.005	0.88% ± 0.31%	–
Golden-crowned Kinglet	189	29.34	<0.001	1.42% ± 0.27%	–
Ruby-crowned Kinglet	1,536	61.81	<0.001	0.77% ± 0.10%	0.32%
Swainson's Thrush	234	0.09	0.762	–0.11% ± 0.38%	–0.06%
Hermit Thrush	169	1.47	0.228	0.35% ± 0.29%	–
Gray Catbird	698	34.22	<0.001	0.79% ± 0.14%	–
Nashville Warbler	245	0.14	0.710	0.09% ± 0.24%	–
Yellow Warbler	587	23.55	<0.001	0.59% ± 0.12%	–
Chestnut-sided Warbler	257	6.92	0.009	0.64% ± 0.24%	–
Magnolia Warbler	1,264	13.02	<0.001	0.41% ± 0.11%	0.17%
Black-throated Blue Warbler	291	5.46	0.020	0.52% ± 0.22%	–
Yellow-rumped Warbler	993	26.06	<0.001	0.54% ± 0.11%	0.28%
Palm Warbler	440	65.37	<0.001	0.99% ± 0.12%	–
Blackpoll Warbler	114	1.50	0.223	0.76% ± 0.62%	1.95%
Black-and-white Warbler	138	22.33	<0.001	1.13% ± 0.24%	–
American Redstart	954	32.18	<0.001	0.51% ± 0.09%	0.67%
Northern Waterthrush	100	2.77	0.099	0.63% ± 0.37%	0.58%
Mourning Warbler	190	12.28	0.001	1.09% ± 0.31%	–
Common Yellowthroat	569	21.19	<0.001	0.78% ± 0.17%	–
Wilson's Warbler	544	22.03	<0.001	0.78% ± 0.16%	0.68%
Canada Warbler	332	3.31	0.070	0.33% ± 0.18%	–
Lincoln's Sparrow	147	0.76	0.385	0.31% ± 0.36%	0.38%
White-throated Sparrow	675	18.89	<0.001	0.63% ± 0.14%	0.68%
White-crowned Sparrow	102	4.21	0.043	0.94% ± 0.46%	0.47%
Dark-eyed Junco	153	0.92	0.339	0.26% ± 0.27%	0.41%
American Goldfinch	163	0.00	0.970	–0.01% ± 0.28%	–
Average:				0.62%	0.52%

[a] Hourly mass change (SE) expressed as percentage of lean body mass h^{-1}.
[b] Mean hourly mass change from 15 sites in southern Canada, reported in Dunn (2002).
[c] Includes Willow Flycatcher and Alder Flycatcher.

A higher proportion of species (19 of 21) showed significant changes in condition during autumn migration (Table 2). Mean hourly mass change ranged from 0.22% (Hermit Thrush) to 1.58% (Common Yellowthroat). The average estimated rate of gain across all species during autumn migration was 0.80% of mean lean mass per hour.

Average rates of hourly mass change across species during spring migration were comparable to those reported by Dunn (2002) for 15 sites in southern Canada (paired *t*-tests, $t = 0.20$, df = 12, $P = 0.848$; Table 1). However, average rates of hourly mass change across species during autumn were greater in the present study than the average across the Canadian sites ($t = 4.74$, df = 9, $P = 0.001$; Table 2).

Traditional Recapture Analyses

We quantified mass changes with traditional recapture analyses for 16 species during spring and 16 species during autumn migration. Estimated daily mass changes were low in all species, averaging –0.08% in spring and 0.02% in autumn (Table 3).

Comparing estimates of mass changes from recapture analyses with regression estimates

TABLE 2. Regression estimates of daily changes in condition during autumn migration.

Species	*n*	*F*	*P*	Mean hourly mass change[a]	Previous studies[b]
Red-eyed Vireo	201	14.63	<0.001	1.14% ± 0.30%	–
Brown Creeper	315	19.03	<0.001	0.71% ± 0.16%	–
Winter Wren	321	13.69	<0.001	0.62% ± 0.17%	–
Golden-crowned Kinglet	1,454	98.68	<0.001	0.87% ± 0.09%	–
Ruby-crowned Kinglet	1,541	100.67	<0.001	0.82% ± 0.08%	0.72%
Gray-cheeked–Bicknell's Thrush	661	13.76	<0.001	0.62% ± 0.17%	–
Swainson's Thrush	428	3.97	0.047	0.41% ± 0.21%	0.10%
Hermit Thrush	1,200	6.54	0.011	0.22% ± 0.09%	–
Gray Catbird	195	3.62	0.059	0.53% ± 0.28%	–
Magnolia Warbler	545	25.02	<0.001	0.89% ± 0.17%	0.57%
Black-throated Blue Warbler	187	7.58	0.007	0.79% ± 0.29%	–
Yellow-rumped Warbler	274	11.22	0.001	0.80% ± 0.24%	0.40%
Blackpoll Warbler	353	25.30	<0.001	0.91% ± 0.18%	0.44%
American Redstart	181	22.39	<0.001	1.25% ± 0.27%	0.56%
Common Yellowthroat	233	20.49	<0.001	1.58% ± 0.35%	–
Wilson's Warbler	132	5.81	0.017	0.98% ± 0.40%	0.79%
Song Sparrow	151	5.21	0.024	0.68% ± 0.30%	–
Swamp Sparrow	116	8.88	0.004	0.91% ± 0.31%	–
White-throated Sparrow	3,850	184.92	<0.001	0.73% ± 0.06%	0.46%
White-crowned Sparrow	140	2.43	0.121	0.54% ± 0.35%	0.55%
Dark-eyed Junco	382	25.63	<0.001	0.73% ± 0.14%	0.52%
Average:				0.80%	0.51%

[a] Hourly mass change (SE) expressed as percentage of lean body mass h^{-1}.
[b] Mean hourly mass change from 15 sites in southern Canada, reported in Dunn (2002).

revealed large differences (Table 3). Regression estimates were greater than recapture estimates in both spring (paired *t*-test, $t = 8.53$, df = 15, $P < 0.001$) and autumn ($t = 5.40$, df = 15, $P < 0.001$). Recorded maximum daily mass changes in recaptured birds were comparable to the regression estimates, which indicates that rates of mass gain detected in the regression analyses were physiologically possible at our study site (paired *t*-tests; spring: $t = 0.84$, df = 15, $P = 0.413$; autumn: $t = 1.22$, df = 15, $P = 0.240$).

To investigate potential biases in recapture data, we compared the average mass of individuals that were never recaptured with the average mass at initial encounter of recaptured birds. On average, individuals that were never recaptured had greater mass values than those that were recaptured in 14 of 16 species examined during autumn migration, and this pattern was significant for nine species (paired *t*-tests, $P < 0.05$; Fig. 2). The initial mean mass of individuals that were recaptured was never significantly greater than the mean mass of birds that were encountered only once. A similar pattern was detected during spring migration, with once-encountered Magnolia Warblers having significantly greater mass values than recaptured birds (Fig. 2).

We further found that estimates calculated by one method could not be used as an index to predict changes calculated by the other method (linear regression of recapture estimate vs. regression estimate; spring migration: $F = 3.04$, df = 1 and 14, $P = 0.103$; autumn migration: $F = 0.89$, df = 1 and 14, $P = 0.362$).

DISCUSSION

Rates of mass gain may vary among species, within and between seasons, or in relation to the number of individuals using a site (Moore and Yong 1991). On average, however, individuals improved their condition ~9.8% per day during stopover at our site. These results indicate that many migrants acquired adequate resources to fuel the next migratory step. Hence, this near-shore stopover site not only hosted large numbers of migrants during stopover periods, but also provided the resources many birds required

Table 3. Comparison of regression and recapture methods for estimating mass change during stopover.

Species	Recaptured (n)	Recapture estimate: Daily mass gain (g): Mean[a]	Minimum	Maximum	Mean daily change[b]: Recapture estimate (%)	Regression estimate (%)
Spring migration						
Least Flycatcher	11	0.09	–0.33	1.03	0.95	8.70
Golden-crowned Kinglet	11	–0.12	–0.72	0.10	–2.16	21.30
Ruby-crowned Kinglet	184	–0.02	–0.65	1.78	–0.34	11.55
Hermit Thrush	16	–0.19	–1.70	0.77	–0.67	5.25
Gray Catbird	36	0.02	–2.28	1.77	0.07	11.85
Yellow Warbler	17	–0.10	–0.60	0.17	–1.02	8.85
Chestnut-sided Warbler	11	0.13	–0.43	0.93	1.37	9.60
Magnolia Warbler	60	–0.03	–1.64	1.09	–0.42	6.15
Black-throated Blue Warbler	15	–0.22	–1.00	0.39	–2.37	7.80
American Redstart	66	0.01	–0.58	0.80	0.13	7.65
Mourning Warbler	16	–0.35	–0.94	0.22	–2.92	16.35
Common Yellowthroat	68	–0.06	–1.06	0.46	–0.60	11.70
Wilson's Warbler	74	–0.05	–1.18	0.77	–0.64	11.70
Canada Warbler	27	–0.03	–0.90	1.30	–0.32	4.95
Lincoln's Sparrow	15	–0.16	–1.70	1.00	–0.94	4.65
White-throated Sparrow	10	–0.23	–0.65	0.60	–0.95	9.45
Average:		–0.08			–0.68	9.84
Autumn migration						
Red-eyed Vireo	40	0.23	–1.40	1.20	1.32	13.68
Brown Creeper	16	–0.14	–0.48	0.28	–1.70	8.52
Winter Wren	43	0.02	–0.51	0.40	0.23	7.44
Golden-crowned Kinglet	85	0.01	–0.63	0.72	0.17	10.44
Ruby-crowned Kinglet	173	–0.02	–2.95	1.35	–0.38	9.84
Gray-cheeked–Bicknell's Thrush	133	0.09	–1.80	2.57	0.28	7.44
Swainson's Thrush	43	0.01	–1.80	2.27	0.04	4.92
Hermit Thrush	219	0.00	–2.08	2.42	–0.01	2.64
Gray Catbird	26	0.17	–0.90	1.80	0.44	6.36
Magnolia Warbler	98	0.03	–0.56	0.52	0.43	10.68
Black-throated Blue Wabler	37	0.03	–0.45	0.40	0.35	9.48
Blackpoll Warbler	48	0.04	–0.93	0.84	0.36	10.92
American Redstart	25	0.05	–0.21	0.52	0.66	15.00
Common Yellowthroat	26	–0.02	–0.48	0.58	–0.16	18.96
Wilson's Warbler	27	0.05	–0.31	0.23	0.77	11.76
White-throated Sparrow	493	–0.16	–4.86	3.05	–0.66	8.16
Average:		0.02			0.13	9.77

[a]Average of the adjusted mass change per stopover length for each recaptured bird.
[b]As percentage of mean lean mass.

to continue their journeys. Migratory bird populations may benefit from greater conservation attention being focused on similar near-shore terrestrial sites. Many similar areas are likely important stopover locations and are often under significant development pressure (Reid and Holland 1997).

Our regression results indicated that more species significantly improved in condition at our study site during autumn migration than during spring migration, a result likely related to differences in food availability between seasons. Resources are limited during spring migration at our study site, because the cold waters of Lake

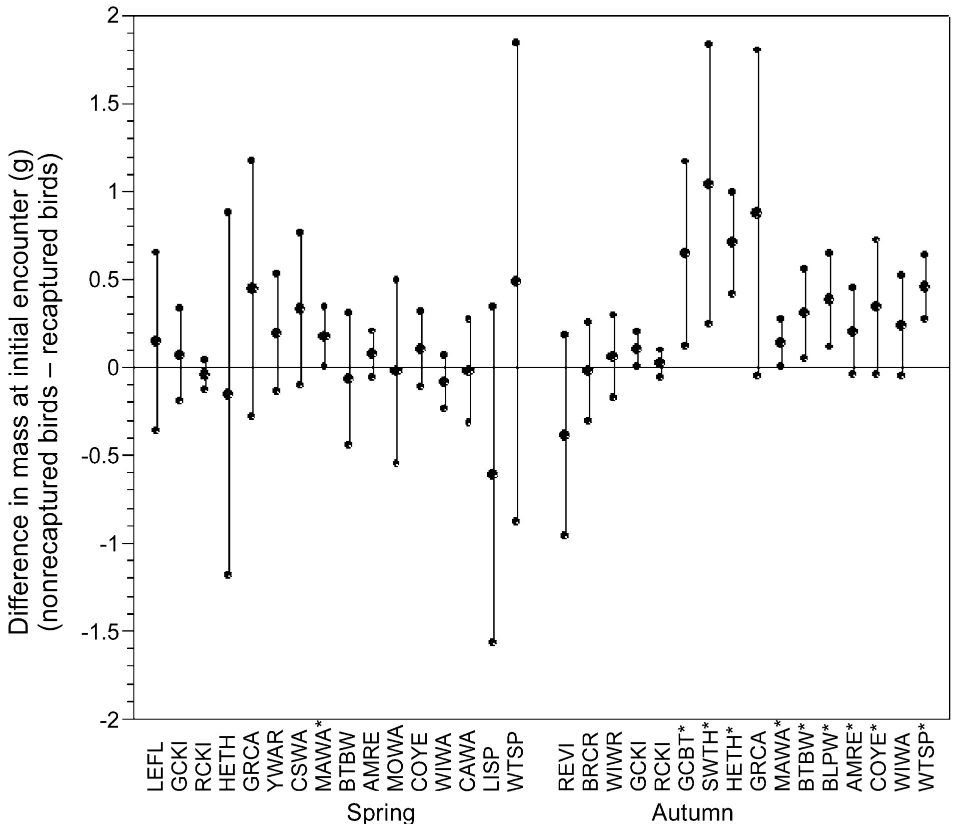

Fig. 2. Comparison of initial condition between recaptured birds and birds encountered only once. See Appendix for species codes. Error bars represent 95% confidence intervals, * $P < 0.05$.

Ontario negatively influence local temperatures. The relatively cold spring temperatures at near-shore sites delay leaf development and suppress insect activity. In addition, most fruit and seed resources from the previous growing season have been depleted by spring migration. Autumn, by contrast, is a time of relatively abundant food resources in near-shore areas. Warm lake waters positively influence local temperatures, insects are active, and fruit and seed resources are at their peak. As such, nearly all species sampled during autumn migration showed significantly positive rates of mass gain. These seasonal differences in mass change suggest that migrants may follow different mass-gain strategies at different stages of the annual cycle. Furthermore, seasonal differences show that single-season studies are unlikely to yield a comprehensive picture of how migrants use stopover sites during migration.

The regression and recapture methods of estimating change in condition produced divergent results with regard to the quality of our stopover site. Changes in mass calculated from recapture data suggested that our sites were poor-quality stopover locations. Most recaptured individuals barely maintained their mass during stopover, and most failed to build the energy reserves required for the next step in migration. By contrast, data from regression analyses suggested that individuals of many species were building significant reserves during stopover along the south shore of Lake Ontario.

Evidence from this and other studies (Winker et al. 1992, Woodrey and Moore 1997) suggests that using data from recaptured individuals does not reveal stopover patterns for the population as a whole. Handling at first capture may have an adverse effect on subsequent body mass development, a possible explanation for the significantly lower rates of mass gain in recaptured birds (Schwilch and Jenni 2001). Although regression estimates of daily mass gain for some species may seem high, comparing these estimates to the maximum actual changes recorded in recaptured birds indicates that daily rates of gain exceeding 10% of lean mass are possible. In contrast with the recapture method, the regression method allows researchers to use data from all individuals captured, and estimates are likely more representative of the population than estimates generated from a biased subsample of that population.

In comparing regression results with recapture results, we assumed that mass continued to increase throughout daylight hours at the same rate as during hours 0 to 8 after sunrise. This assumption may be violated if foraging activity is not constant throughout a day. However, even when we assumed no further mass gains after hour 8 (the most conservative approach), the regression method returned greater estimates of mass change during stopover than the recapture method.

The regression method also assumes that all individuals arrive at the site at night and begin foraging by sunrise. This assumption was likely valid at our sites, because radar data indicated that nearly all birds terminated migratory flights before sunrise (D. Bonter unpubl. data). This assumption would be violated at stopover sites near larger geographic barriers where nocturnal migratory flights over the barrier necessarily extend into the next day (i.e., flights across the Gulf of Mexico; Yong and Moore 1997). In such instances, birds captured later in the day may have just completed a migratory flight or may have been actively foraging for an undetermined amount of time. Diurnal migrants also violate the assumption of homogeneous arrival times, and the method should not be used for those species.

When the assumptions of the regression method are supported, this method likely provides better estimates of rates of mass gain for the population as a whole than estimates from recapture data. Similar studies are required in various habitat types, regions, and at varying distances from geographic barriers to identify patterns of mass change during stopover and to help inform conservation efforts.

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APPENDIX. Scientific names, common names, species codes, mean lean mass, and mean wing chord for species used in analyses. Dash indicates inadequate sample size for species–season combination.

			Spring		Autumn	
Scientific name	Common name	Species code	Mean lean mass (g)	Mean wing chord (mm)	Mean lean mass (g)	Mean wing chord (mm)
Empidonax flaviventris	Yellow-bellied Flycatcher	YBFL	11.49	65.65	–	–
E. alnorum & E. traillii	"Traill's Flycatcher"	TRFL	13.03	69.56	–	–
E. minimus	Least Flycatcher	LEFL	9.79	60.00	–	–
Vireo olivaceus	Red-eyed Vireo	REVI	16.35	78.25	17.11	77.44
Certhia americana	Brown Creeper	BRCR	7.59	62.70	7.94	63.83
Troglodytes troglodytes	Winter Wren	WIWR	–	–	8.27	46.26
Regulus satrapa	Golden-crowned Kinglet	GCKI	5.66	55.70	5.85	56.66
R. calendula	Ruby-crowned Kinglet	RCKI	6.12	56.61	6.07	56.94
Catharus minimus–C. Bicknelli	Gray-cheeked Thrush–Bicknell's Thrush	GCBT	–	–	32.51	100.08
C. ustulatus	Swainson's Thrush	SWTH	30.47	95.79	29.86	95.83
C. guttatus	Hermit Thrush	HETH	28.03	88.98	28.99	89.60
Dumetella carolinensis	Gray Catbird	GRCA	34.31	87.51	37.25	87.36
Vermivora ruficapilla	Nashville Warbler	NAWA	8.08	57.88	–	–
Dendroica petechia	Yellow Warbler	YWAR	9.41	60.03	–	–
D. pensylvanica	Chestnut-sided Warbler	CSWA	9.30	60.30	–	–
D. magnolia	Magnolia Warbler	MAWA	8.05	57.21	7.98	57.97
D. caerulescens	Black-throated Blue Warbler	BTBW	9.19	61.44	9.14	62.34
D. coronata	Yellow-rumped Warbler	MYWA	11.89	70.40	11.33	70.10
D. palmarum	Palm Warbler	WPWA	9.67	62.84	–	–
D. striata	Blackpoll Warbler	BLPW	12.14	70.54	11.58	72.48
Mniotilta varia	Black-and-white Warbler	BAWW	9.73	67.58	–	–
Setophaga ruticilla	American Redstart	AMRE	7.95	60.25	7.62	59.70
Seiurus noveboracensis	Northern Waterthrush	NOWA	16.09	72.54	–	–
Oporornis philadelphia	Mourning Warbler	MOWA	12.03	59.02	–	–
Geothlypis trichas	Common Yellowthroat	COYE	9.72	52.98	9.79	53.52
Wilsonia pusilla	Wilson's Warbler	WIWA	7.39	52.97	7.01	53.39
W. canadensis	Canada Warbler	CAWA	9.82	62.13	–	–
Melospiza melodia	Song Sparrow	SOSP	–	–	20.11	64.46

Appendix. Continued.

Scientific name	Common name	Species code	Spring		Autumn	
			Mean lean mass (g)	Mean wing chord (mm)	Mean lean mass (g)	Mean wing chord (mm)
Melospiza lincolnii	Lincoln's Sparrow	LISP	16.51	60.21	–	–
M. georgiana	Swamp Sparrow	SWSP	–	–	16.33	58.55
Zonotrichia albicollis	White-throated Sparrow	WTSP	24.25	70.12	24.38	70.73
Z. leucophrys	White-crowned Sparrow	EWCS	27.63	75.85	25.73	76.58
Junco hyemalis	Dark-eyed Junco	SCJU	18.29	73.03	17.56	73.84
Carduelis tristis	American Goldfinch	AMGO	12.39	69.84	–	–