

## MASS CHANGE DURING MIGRATION STOPOVER: A COMPARISON OF SPECIES GROUPS AND SITES

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**Abstract.**—Hourly mass gain during migratory stopover in spring and fall was estimated for 48 species at three sites on Long Point, Ontario. Estimates were based on regression of size-corrected mass at first capture on time of day. Mean mass gain for all species and sites in fall was 0.61% of lean body mass/h, well over the mean estimated gain required to maintain daily energy balance (0.27% of lean body mass/h). In spring, mass gain was 0.50% of lean body mass/h at two sites but only 0.17% at the extreme tip of Long Point, where cold lake temperature in spring probably affects insect abundance. While most species fared well in fall, thrushes did not, perhaps due to poor habitat for ground foraging on Long Point. Except for the eastern tip of Long Point in spring, the study sites compare favorably in mass gain to two other stations in the northern U.S. where similar analyses have been done.

### **CAMBIOS EN MASA DURANTE PARADAS EN LA MIGRACIÓN: UNA COMPARACIÓN DE GRUPOS DE ESPECIES Y LOCALIDADES**

**Sinopsis.**—Se estimaron aumentos en masa de 48 especies durante paradas en migraciones de primavera y de otoño en Long Point, Ontario. Los estimados se basaron en regresiones de masas corregidas por tamaño en la primera captura del día usando tanto modelos de regresión simple y múltiple para evaluar la importancia de incluir los efectos de la fecha. El promedio de aumento en masa todas las especies y localidades en otoño fue de 0.61% de la masa magra de cuerpo/h, muy sobre el promedio estimado de aumento de masa requerido para mantener el balance de energía diaria (0.27% de masa magra del cuerpo/h). En la primavera, el aumento en masa fue de 0.50% de la masa magra del cuerpo/h en dos localidades, pero solo 0.17% en el extremo de la punta de Long Point, donde las temperaturas frías del lago en la primavera probablemente afectan la abundancia de insectos. Mientras a la mayoría de las especies les fue bien en el otoño, lo mismo no fue así con los miembros de la familia Turdidae, tal vez debido al pobre habitat para buscar alimento en el suelo de Long Point. A excepción de la punta oriental de Long Point en primavera, las localidades de estudio comparan favorablemente en aumento de masa en otras dos estaciones en el norte de los Estados Unidos donde se han llevado a cabo estudios similares.

Between migratory flights, birds must replenish energy stores in order to complete their journeys, and whether a migrant can gain mass during a particular stopover is an indicator of site quality. Food must be readily available, and there must be sufficient protection from predators and competitors to allow food resources to be exploited efficiently. Thus, we might compare mass gain of migrants among sites as a means of comparing quality of different stopover locations.

Mass gain of Magnolia Warblers (see Table 1 for scientific names) at three stopover sites in southern Ontario has been found to vary among sites and seasons (Dunn 2000). The three sites are on Long Point, on the north shore of Lake Erie (Fig. 1). This 35-km sand spit has an east-west succession of habitats, with an open cottonwood dune habitat and little

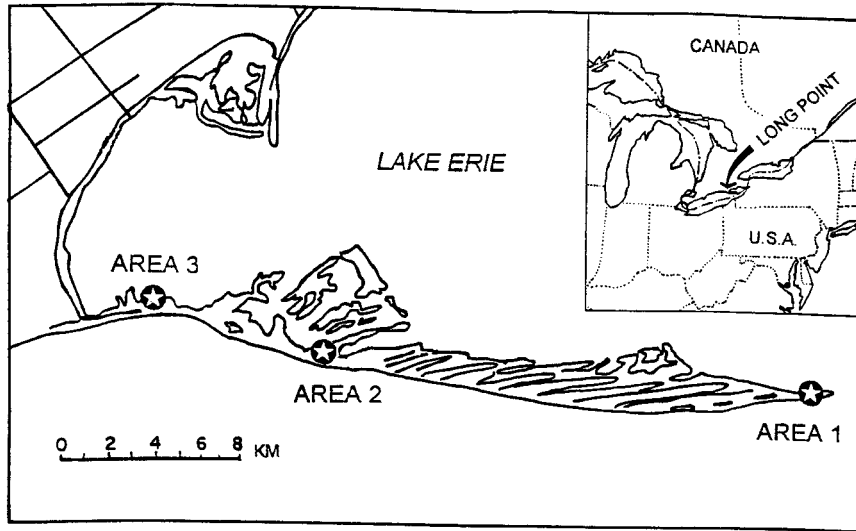


FIGURE 1. Location of Long Point (inset) and of banding sites on the point.

ground cover at Area 1, open savannah woodland with grass understory at Area 2, and a small mixed woodlot at Area 3 with shrubby understory and a modest accumulation of leaf litter. The cooling effect of Lake Erie causes delay in spring plant phenology that is particularly marked at Area 1. Magnolia Warblers lost mass at Area 1 in spring, but made net gains at the other two sites in spring and at all three sites in fall (Dunn 2000). In the study reported here, mass change at the same sites was estimated for an additional 47 species to determine how typical the results for Magnolia Warbler might be, and to learn whether high quality habitat for some species or foraging guilds might be of low quality for others.

Other authors have estimated mass change from the slope of a simple regression of size-adjusted mass at first capture on time of day (Winker et al. 1992; Morris et al. 1996). Dunn (2000) used both simple and multiple regression to analyze data for the Magnolia Warbler. The estimates of hourly mass change did not differ greatly between methods, but multiple regression allowed investigation of seasonal and annual variation in mass gain. This paper presents additional comparison of results from the two methods.

#### METHODS

Data from the Long Point Bird Observatory were analyzed for three sites (Fig. 1) for the period 1980–1996, for both spring and fall migrants. The 48 species included were all of those caught at Long Point in sufficient numbers for analysis at two or more sites in at least one season.

All birds included in analyses were caught in mist nets or Heligoland traps (Hussell and Woodford 1961), while birds caught in baited ground

traps were excluded due to the likelihood of unusual mass gain due to eating baits. Nets were normally opened at or before dawn and run for at least 6.5 h on a daily basis during both migration seasons (weather permitting). Birds were transported and held individually in cloth bags or holding boxes until banding, at which time they were weighed (to the nearest 0.1 g on a triple beam balance or electronic scale) and wing chord was measured (unflattened, to the nearest 1 mm). Fat in furcular deposits was scored as 0 for no fat, "T" for trace of fat, 1 for little fat (filling no more than 1/3 of furculum), 2 for moderate fat (furculum 1/3 to 2/3 filled) and 3 for heavy fat (furculum nearly filled to overflowing). Time of capture (removal from nets) and time of weighing were each recorded to the nearest 10 min. For this analysis, times were expressed as decimal values and were converted to hours since sunrise to account for progressive change in timing of sunrise during each season.

Analysis for each species was limited to data from the first 12 h after sunrise to exclude records of birds handled outside regular banding operations (e.g., nocturnal banding during lighthouse attractions). Individuals with mass or wing length falling below the 1st percentile or above the 99th percentile of all measurements were excluded as a means of deleting probable errors in measurement or recording. In no species did any remaining values appear to be unreasonable. Data for each species were further restricted to the species-specific migration period during which 98% of migrants normally pass through Long Point (based on data from all years and areas combined). This limitation, and the fact that only first captures were included in the analyses, ensure that locally breeding individuals of the few species that breed at Long Point were excluded to the extent possible. Finally, individuals were excluded if recorded weighing time was earlier than the capture time, or if the bird was held for more than 2 h before weighing. Analyses were run only if final sample size was greater than 120 individuals.

Data were analysed using the full regression model of Dunn (2000), with all variables entered simultaneously:

$$\hat{M} = b_0 + b_1H_c + b_2W + b_3D + b_4D^2 + b_5D^3 + b_6H_cD + b_7H_cD^2 + b_8H_cD^3 \quad (1)$$

in which  $\hat{M}$  is the regression estimate of mass,  $H_c$  = time of capture,  $W$  = wing length,  $D$  = day (Julian date),  $D^2$  = day<sup>2</sup>,  $D^3$  = day<sup>3</sup>,  $H_cD$ – $H_cD^3$  are interaction variables between time of capture and date variables, and  $b_0 \dots b_8$  are the coefficients estimated by the regression. The date terms model date-related changes in mass (higher-order terms modelling non-linear changes). Inclusion of date and wing-length terms account for some of the variation in mass that is related to differential migration of age and sex groups by date, and interaction terms allow detection of seasonal changes in mass gain (Dunn 2000).

The coefficient for time of day ( $b_1$ ) represents the average hourly change in mass for a bird of wing length 0 at the start of the migration season. Using the other coefficients estimated in the regression, hourly

TABLE 1. Estimated mass change  $\pm$  SE (and  $N$ ) of migrants at Long Point, Ontario, by season and locality, expressed as % of lean body mass/h<sup>a</sup>.

Species (Code) <sup>b</sup>	Thres- hold value <sup>c</sup>	Spring		
		Area 1	Area 2	Area 3
Northern Flicker (o) <i>Colaptes auratus</i>	0.12	0.17 $\dagger$ $\pm$ 0.09 (1102)	0.18 $\pm$ 0.19 (230)	0.26 $\pm$ .27 (191)
Eastern Wood-Pewee (i) <i>Contopus virens</i>	0.27	0.53* $\pm$ 0.21 (347)	0.55** $\pm$ 0.21 (287)	—
Yellow-bellied Flycatcher (i) <i>Empidonax flaviventris</i>	0.30	0.27 $\pm$ 0.17 (428)	—	0.30 $\pm$ 0.24 (292)
Least Flycatcher (i) <i>E. minimus</i>	0.30	0.35*** $\pm$ 0.09 (1755)	0.72*** $\pm$ 0.17 (545)	0.25 $\dagger$ $\pm$ 0.15 (767)
Red-eyed Vireo (i) <i>Vireo olivaceus</i>	0.25	0.48 $\dagger$ $\pm$ 0.26 (317)	0.45 $\dagger$ $\pm$ 0.26 (227)	0.46* $\pm$ 0.22 (585)
Brown Creeper (i) <i>Certhia americana</i>	0.34	-0.22* $\pm$ 0.09 (1940)	0.22** $\pm$ 0.08 (2166)	0.26** $\pm$ 0.09 (2622)
House Wren (i) <i>Troglodytes aedon</i>	0.30	0.14 $\pm$ 0.24 (222)	0.85*** $\pm$ 0.22 (287)	0.80*** $\pm$ 0.21 (379)
Winter Wren (i) <i>T. troglodytes</i>	0.33	0.36 $\pm$ 0.25 (200)	—	0.61*** $\pm$ 0.23 (396)
Golden-crowned Kinglet (i) <i>Regulus satrapa</i>	0.38	-0.31 $\dagger$ $\pm$ 0.18 (475)	0.45** $\pm$ 0.14 (895)	0.57** $\pm$ 0.19 (684)
Ruby-crowned Kinglet (i) <i>R. calendula</i>	0.37	0.24* $\pm$ 0.11 (1658)	0.27** $\pm$ 0.09 (2134)	0.66*** $\pm$ 0.07 (3647)
Veery (t) <i>Catharus fuscescens</i>	0.20	—	0.11 $\pm$ 0.24 (202)	0.01 $\pm$ 0.18 (471)
Swainson's Thrush (t) <i>C. ustulatus</i>	0.20	-0.59* $\pm$ 0.28 (364)	0.49 $\dagger$ $\pm$ 0.27 (279)	0.22 $\pm$ 0.17 (653)
Hermit Thrush (t) <i>C. guttatus</i>	0.20	-0.23 $\pm$ 0.14 (536)	0.12 $\pm$ 0.15 (489)	0.30*** $\pm$ 0.08 (1797)
Grey-cheeked Thrush (t) <i>C. minimus</i>	0.20	—	—	—
Wood Thrush (t) <i>Hylocichla mustelina</i>	0.17	—	0.13 $\pm$ 0.24 (177)	0.30 $\dagger$ $\pm$ 0.18 (355)
American Robin (t) <i>Turdus migratorius</i>	0.14	0.00 $\pm$ 0.22 (342)	—	0.51 $\pm$ 0.32 (179)
Gray Catbird (o) <i>Dumetella carolinensis</i>	0.19	-0.18 $\pm$ 0.16 (465)	0.27 $\dagger$ $\pm$ 0.15 (633)	0.52*** $\pm$ 0.10 (1206)
Brown Thrasher (o) <i>Toxostoma rufum</i>	0.15	0.03 $\pm$ 0.17 (357)	0.27 $\pm$ 0.22 (272)	—
Tennessee Warbler (i) <i>Vermivora peregrina</i>	0.31	—	—	-0.55 $\dagger$ $\pm$ 0.30 (405)
Nashville Warbler (i) <i>V. ruficapilla</i>	0.33	-0.07 $\pm$ 0.33 (190)	0.51 $\dagger$ $\pm$ 0.30 (242)	0.14 $\pm$ 0.17 (745)
Yellow Warbler (i) <i>Dendroica petechia</i>	0.31	0.67*** $\pm$ 0.16 (752)	0.66*** $\pm$ 0.18 (545)	1.10*** $\pm$ 0.18 (523)
Chestnut-sided Warbler (i) <i>D. pensylvanica</i>	0.31	0.16 $\pm$ 0.33 (217)	—	0.39* $\pm$ 0.18 (638)
Magnolia Warbler (i) <i>D. magnolia</i>	0.33	-0.06 $\pm$ 0.21 (727)	0.82*** $\pm$ 0.21 (644)	0.15 $\pm$ 0.09 (3596)
Cape May Warbler (i) <i>D. tigrina</i>	0.30	—	—	0.03 $\pm$ 0.30 (277)
Black-throated Blue Warbler (i) <i>D. caerulescens</i>	0.31	—	—	1.02*** $\pm$ 0.23 (408)
Yellow-rumped Warbler (i) <i>D. coronata</i>	0.29	0.22 $\pm$ 0.14 (1040)	0.71*** $\pm$ 0.17 (805)	1.22*** $\pm$ 0.18 (794)

TABLE 1. Extended.

Fall		
Area 1	Area 2	Area 3
0.37 $\dagger$ $\pm$ 0.19 (303)	—	—
0.36 $\dagger$ $\pm$ 0.21 (252)	0.42** $\pm$ 0.20 (530)	—
0.53*** $\pm$ 0.14 (585)	1.50*** $\pm$ 0.25 (189)	0.38 $\pm$ 0.24 (313)
0.53*** $\pm$ 0.07 (2086)	0.34* $\pm$ 0.14 (730)	0.24 $\pm$ 0.16 (697)
0.22 $\pm$ 0.22 (305)	0.06 $\pm$ 0.31 (270)	0.28 $\dagger$ $\pm$ 0.16 (946)
0.26*** $\pm$ 0.07 (3263)	—	0.73*** $\pm$ 0.16 (1083)
0.55** $\pm$ 0.20 (340)	—	0.30 $\pm$ 0.09 (327)
0.64*** $\pm$ 0.17 (464)	—	1.09*** $\pm$ 0.26 (387)
-0.12 $\pm$ 0.09 (2432)	—	1.22*** $\pm$ 0.16 (1608)
0.36*** $\pm$ 0.08 (2462)	—	0.85*** $\pm$ 0.06 (5935)
-0.80** $\pm$ 0.26 (161)	-0.11 $\pm$ 0.27 (250)	0.24 $\pm$ 0.23 (413)
-0.36*** $\pm$ 0.09 (1580)	0.12 $\pm$ 0.10 (1255)	0.21* $\pm$ 0.09 (1993)
-0.22* $\pm$ 0.09 (1409)	—	0.53*** $\pm$ 0.09 (1827)
-0.07 $\pm$ 0.13 (703)	0.02 $\pm$ 0.20 (403)	0.43** $\pm$ 0.15 (727)
—	—	—
—	—	—
—	—	0.51** $\pm$ 0.19 (542)
—	—	—
0.74*** $\pm$ 0.20 (318)	0.71*** $\pm$ 0.16 (821)	0.86*** $\pm$ 0.22 (423)
0.76** $\pm$ 0.23 (288)	0.91*** $\pm$ 0.22 (491)	1.09*** $\pm$ 0.19 (585)
1.19*** $\pm$ 0.18 (957)	0.87*** $\pm$ 0.16 (1549)	1.41*** $\pm$ 0.11 (2344)
0.68* $\pm$ 0.28 (194)	0.49 $\dagger$ $\pm$ 0.27 (239)	0.99*** $\pm$ 0.24 (301)
0.76*** $\pm$ 0.13 (876)	0.67*** $\pm$ 0.10 (2024)	0.81*** $\pm$ 0.10 (2012)
0.80*** $\pm$ 0.16 (537)	0.53*** $\pm$ 0.14 (1092)	0.35 $\pm$ 0.23 (387)
0.83*** $\pm$ 0.22 (246)	0.86*** $\pm$ 0.23 (369)	0.85*** $\pm$ 0.18 (560)
0.43*** $\pm$ 0.06 (3736)	0.67** $\pm$ 0.21 (281)	0.66*** $\pm$ 0.06 (5837)

TABLE 1. Continued.

Species (Code) <sup>b</sup>	Thres- hold value <sup>c</sup>	Spring		
		Area 1	Area 2	Area 3
Black-throated Green Warbler (i) <i>D. virens</i>	0.32	0.32 ± 0.32 (162)	—	0.63* ± 0.29 (287)
Blackburnian Warbler (i) <i>D. fusca</i>	0.31	—	—	0.21 ± 0.35 (254)
Palm Warbler (i) <i>D. palmarum</i>	0.31	0.57* ± 0.28 (215)	—	—
Bay-breasted Warbler (i) <i>D. castanea</i>	0.29	—	—	0.05 ± 0.35 (244)
Blackpoll Warbler (i) <i>D. striata</i>	0.29	—	—	—
Black-and-white Warbler (i) <i>Mniotilta varia</i>	0.30	—	0.36 ± 0.34 (188)	1.17*** ± 0.19 (533)
American Redstart (i) <i>Setophaga ruticilla</i>	0.33	0.00 ± 0.30 (245)	1.60*** ± 0.30 (201)	0.77*** ± 0.16 (657)
Ovenbird (i) <i>Seiurus aurocapillus</i>	0.24	-0.18 ± 0.31 (168)	0.38‡ ± 0.21 (341)	0.23 ± 0.16 (748)
Northern Waterthrush (i) <i>S. noveboracensis</i>	0.25	—	—	—
Common Yellowthroat (i) <i>Geothlypis trichas</i>	0.36	0.07 ± 0.14 (902)	0.94*** ± 0.16 (696)	0.96*** ± 0.13 (1140)
Wilson's Warbler (i) <i>Wilsonia pusilla</i>	0.34	0.30 ± 0.39 (172)	1.08*** ± 0.29 (254)	0.92*** ± 0.20 (748)
Canada Warbler (i) <i>W. canadensis</i>	0.31	—	—	0.58** ± 0.19 (576)
Chipping Sparrow (s) <i>Spizella passerina</i>	0.29	0.57*** ± 0.13 (849)	0.30* ± 0.15 (709)	—
Field Sparrow (s) <i>S. pusilla</i>	0.28	0.25‡ ± 0.15 (572)	0.11 ± 0.20 (366)	—
Song Sparrow (s) <i>Melospiza melodia</i>	0.24	0.42*** ± 0.08 (1712)	0.47** ± 0.17 (418)	0.77*** ± 0.15 (776)
Lincoln's Sparrow (s) <i>M. lincolnii</i>	0.26	0.05 ± 0.17 (787)	0.87*** ± 0.25 (477)	0.75*** ± 0.17 (692)
Swamp Sparrow (s) <i>M. georgiana</i>	0.25	0.07 ± 0.18 (457)	-0.06 ± 0.33 (223)	0.72*** ± 0.14 (997)
White-throated Sparrow (s) <i>Zonotrichia albicollis</i>	0.22	-0.03 ± 0.06 (5244)	0.27*** ± 0.06 (3776)	0.78*** ± 0.06 (4754)
White-crowned Sparrow (s) <i>Z. leucophrys</i>	0.21	0.56*** ± 0.12 (1283)	0.30* ± 0.12 (1279)	—
Dark-eyed Junco (s) <i>Junco hyemalis</i>	0.24	0.16‡ ± 0.08 (2690)	0.50*** ± 0.10 (1454)	0.50*** ± 0.12 (1005)
Rose-breasted Grosbeak (o) <i>Pheucticus ludovicianus</i>	0.17	-0.02 ± 0.23 (469)	0.00 ± 0.21 (542)	0.98*** ± 0.23 (256)
Baltimore Oriole (o) <i>Icterus galbula</i>	0.20	0.41‡ ± 0.24 (311)	0.24 ± 0.21 (408)	1.01*** ± 0.26 (205)

<sup>a</sup> Mass gain estimates from simple regression (equation 2). Symbols indicating difference of mass gain estimate from 0: ‡ = 0.05 < P < 0.10, \* = P < 0.05, \*\* = P < 0.01, \*\*\* = P < 0.001.

<sup>b</sup> Species codes (for Table 2): i = small insectivore, s = sparrow, t = thrush, o = other large species.

<sup>c</sup> Estimated hourly mass gain required for daily energy balance, expressed as % of lean body mass/h (see Methods for calculation).

TABLE 1. Extended.

Fall		
Area 1	Area 2	Area 3
0.50* $\pm$ 0.24 (213)	0.57* $\pm$ 0.29 (201)	1.48*** $\pm$ 0.33 (175)
—	0.94*** $\pm$ 0.28 (344)	0.57 $\pm$ 0.45 (173)
0.62*** $\pm$ 0.16 (616)	—	1.25** $\pm$ 0.41 (197)
0.82*** $\pm$ 0.14 (544)	0.81*** $\pm$ 0.16 (831)	0.37† $\pm$ 0.22 (421)
0.66*** $\pm$ 0.09 (1715)	0.48*** $\pm$ 0.13 (1089)	0.89*** $\pm$ 0.21 (445)
—	0.96*** $\pm$ 0.27 (293)	0.54* $\pm$ 0.25 (401)
0.55*** $\pm$ 0.14 (609)	0.74*** $\pm$ 0.15 (766)	1.02*** $\pm$ 0.17 (993)
—	0.51* $\pm$ 0.25 (235)	0.98*** $\pm$ 0.25 (251)
1.66*** $\pm$ 0.33 (273)	0.47** $\pm$ 0.14 (953)	1.01*** $\pm$ 0.25 (356)
0.87** $\pm$ 0.29 (263)	1.01** $\pm$ 0.37 (288)	0.83** $\pm$ 0.27 (630)
0.89*** $\pm$ 0.22 (281)	1.08*** $\pm$ 0.22 (308)	0.98*** $\pm$ 0.20 (458)
0.93*** $\pm$ 0.19 (332)	1.13*** $\pm$ 0.23 (319)	0.61** $\pm$ 0.20 (491)
-0.04 $\pm$ 0.37 (177)	—	—
—	—	—
0.58*** $\pm$ 0.17 (647)	—	0.66** $\pm$ 0.25 (694)
—	—	—
—	—	0.37 $\pm$ 0.27 (508)
0.36*** $\pm$ 0.09 (1321)	—	0.55*** $\pm$ 0.09 (2371)
0.35* $\pm$ 0.14 (624)	—	0.88** $\pm$ 0.28 (230)
0.15 $\pm$ 0.09 (2108)	—	0.74*** $\pm$ 0.14 (1053)
—	—	—
—	0.78* $\pm$ 0.30 (162)	-0.10 $\pm$ 0.33 (239)

mass gain was calculated for a bird of average wing length at the date of species-specific peak migration (average capture date at Long Point for spring and fall separately).

Data were also analyzed using the simple regression method of Winker et al. (1992). Those authors pre-adjusted mass for body size by calculating a "Condition Index" ( $\text{mass} \times 10,000/\text{wing length}^3$ ), and then conducted simple regressions on time of day as follows:

$$\widehat{CI} = b_0 + b_1 H_c \quad (2)$$

where  $\widehat{CI}$  is Condition Index and  $H_c$  is hour of capture. The coefficient  $b_1$  is the estimate of hourly change in Condition Index and can be converted to hourly change in mass via the formula  $\text{mass change} = b_1 (\text{wing length}^3)/10,000$ . Here I used the average wing length for the species in the conversion formula. The result gives a second estimate of hourly mass gain for a bird of average wing length, at average date of capture (since the sample is weighted by date of sampling).

All estimates of hourly mass change were converted to percent of lean body mass to allow direct comparison among species of different body size. Lean body mass for each species was defined for the purposes of this paper as the mean mass of birds with a fat class score of 0. Separate values were calculated for spring and fall (individuals from all banding sites combined), and the lowest seasonal value was chosen as the lean mass. Occasionally the average mass for birds with no-fat and trace-fat combined was lower than the mean for birds with no-fat alone (a result of individual variation in fat scoring), and in these cases, the lower value was chosen.

Estimates of hourly mass gain are more easily interpreted if they can be compared with some threshold value, which is defined here as the energetic break-even point over 24 h in which no migration takes place. This threshold must be surpassed if energy is to be accumulated for fueling continued migration. Winker et al. (1992) used a threshold of daytime gain amounting to 4.5% of body mass, which would offset overnight resting losses in the small birds they studied. However, relative energy use is lower in larger species, many of which are included in this study. I therefore calculated overnight losses based on Kendeigh's (1970) formula for existence metabolism for passerines at 30°C:  $E = 0.076W^{0.621}$ , in which  $E$  is existence metabolism in watts and  $W$  is mass in grams. Overnight existence energy cost was calculated for each species assuming a 12-h night, the average length of time between sunset and sunrise in southern Canada at the peak of fall migration (but note that nights are shorter during spring migration). The estimated energy cost was then converted to mass, assuming that all metabolic costs are supported by burning of fat with an energy value of 37.7 kJ (Rogers and Odum 1964). The resulting threshold value (shown for each species in Table 1) represents the mass a bird must gain in 12 h of daylight in order to break even energetically over a 24-h period with no migration.

Existence energy, which is about 30% higher than standard metabolic costs, represents the energy used by caged birds over the course of a day,



and includes costs of standard metabolism, specific dynamic action, and any activity taking place in the cage (Kendeigh 1970). The existence energy formula overestimates energy use during hours of sleep alone, but this is counterbalanced to some extent by an underestimation of nocturnal thermoregulatory costs in the natural environment. The threshold values calculated by this means for small passerines and for the Swainson's Thrush were close to the estimates of overnight mass loss given by Winker et al. (1992) and Mueller and Berger (1966) that were used as threshold values by those authors. It is also quite close to an experimental value for a bird resting for 12 h (after a 12 h flight and having access only to water; Klaassen et al. 2000). Regardless of the means of calculation, it must be kept in mind that this threshold is based on many assumptions and should only be used as a general reference point.

Comparisons of estimated mass gain among sites and seasons were conducted using General Linear Models (least square mean option, SAS Institute 1985). For statistical tests, acceptable significance level was based on the number of site/season comparisons within a species grouping, or on the number of species group comparisons within a site and season (see Chandler 1995 for discussion of grouping related tests for Bonferroni adjustment of probability level).

#### RESULTS

The two methods for estimating mass gain, multiple and simple regression, gave similar results overall, although there were sometimes large differences for individual cases. The mean  $\pm$  SD of 210 species-site-season values was  $0.52 \pm 0.41\%$  of lean body mass/h using multiple regression and  $0.49 \pm 0.41\%$  using simple regression. Paired *t*-tests of mass gains showed no difference between estimation methods for spring comparisons ( $P = 0.96$ ,  $N = 108$  species-site-season estimates) or for fall comparisons ( $P = 0.08$ ,  $N = 102$ ). The remainder of this paper presents results using the simple regression method.

Hourly mass change estimates for each area and season are shown in Table 1. Many of the estimates were not significantly different from zero, and those that were typically had quite large confidence intervals. Despite this, estimates were quite closely clustered around mean values for each site and season (Table 2). Mean mass gain for all species was significantly lower at Area 1 than at Areas 2 and 3 in spring, but not in fall. Only at Area 1 did mass gain differ between seasons. The same general patterns were evident for small insectivores, but were not obvious in other species groups, for which sample sizes were much smaller.

Within sites for each season, comparisons were also made between species groups. There were few significant differences (after Bonferroni adjustment of significance levels), but sample sizes were small for most groups. Nonetheless, thrushes had significantly lower mass gains than small insectivores in spring at Area 1 and in fall at Areas 1 and 2, and all three of these values for thrushes fell well below the threshold for 24 h energy balance. While other species groups also tended to fare poorly in

TABLE 2. Mean hourly mass change of migrants at Long Point, Ontario, differs among areas, but patterns vary somewhat among species groups (see Table 1 for group membership). Mass gain shown as % of lean body mass/h  $\pm$  SE (*N* of species).

Group: Threshold <sup>a</sup>	Spring			Fall		
	Area 1	Area 2	Area 3	Area 1	Area 2	Area 3
All species: 0.27	0.17 $\pm$ 0.06 (36)	0.46 $\pm$ 0.06 (33)	0.53 $\pm$ 0.06 (39)	0.50 $\pm$ 0.06 (36)	0.65 $\pm$ 0.07 (27)	0.70 $\pm$ 0.06 (39)
Differences <sup>b</sup>	a	b	b	b	b	b
Small insectivores: 0.31	0.22 $\pm$ 0.06 (20)	0.67 $\pm$ 0.08 (16)	0.52 $\pm$ 0.08 (25)	0.69 $\pm$ 0.06 (26)	0.73 $\pm$ 0.06 (23)	0.79 $\pm$ 0.06 (28)
Differences	a	b	a,b	b	b	b
Sparrows: 0.24	0.26 $\pm$ 0.09 (8)	0.36 $\pm$ 0.10 (8)	0.70 $\pm$ 0.17 (5)	0.28 $\pm$ 0.13 (5)	—	0.64 $\pm$ 0.14 (5)
Differences	a	a,b	b	a,b	—	a,b
Thrushes: 0.19	-0.27 $\pm$ 0.14 (3)	0.21 $\pm$ 0.15 (4)	0.27 $\pm$ 0.17 (5)	-0.36 $\pm$ 0.15 (4)	0.01 $\pm$ 0.17 (3)	0.64 $\pm$ 0.16 (4)
Differences	a	b	b	a	a,b	b
Other large species: 0.17	0.08 $\pm$ 0.11 (5)	0.19 $\pm$ 0.13 (5)	0.69 $\pm$ 0.19 (4)	0.37 $\pm$ 0.30 (1)	0.78 $\pm$ 0.30 (1)	0.35 $\pm$ 0.22 (2)
Differences	a	a,b	b	—	—	—

<sup>a</sup> Mean threshold value (% lean body mass/h) for species in this group. The threshold is an indicator of the break-even point for 24 h energy balance in the absence of migration.

<sup>b</sup> Means sharing a letter are not significantly different.

spring at Area 1, thrushes stood out as having particularly low mass gains in fall at the two sites farthest out on Long Point.

Mass gain at Long Point was compared to that at two sites in the northern United States where mass gain has been analyzed using methods similar to those used here (Table 3). Compared to native woodland sites in Wisconsin (Winker et al. 1992), Long Point appears to be of lower quality for migrants in spring, but only Area 1 in spring had a significantly different value (Table 3). Long Point had higher mass gains in fall than the Wisconsin site but not significantly so. A larger number of species has been analyzed for an autumn banding site on a brushy island off the coast of Maine (Morris et al. 1994, 1996). Mass gain in fall at the Maine site was lower than for Long Point, but again there were no significant differences (Table 3). Fall results were similar for the species analyzed in common by all three studies. Except at Long Point in spring, mass gain at all sites was above mean threshold values.

#### DISCUSSION

Results from this study indicate that there is little difference between estimates of hourly mass gain derived from multiple vs. simple regression methods, at least when comparing a large number of species. Unless the analyst wishes to examine variation in mass gain over the season or among years (Dunn 2000 and unpubl.), it is simpler, and evidently just as effective, to use the methods of Winker et al. (1992).

The low precision of mass gain estimates can be attributed to numerous factors. For example, there is likely to be tremendous variation in arrival mass, depending on weather conditions influencing the distance and energy cost of the previous night's flight. Heavy birds may be caught at early hours on some days and light birds at later hours on other days—even though both groups might be gaining mass on the days they are present. Moreover, feeding conditions vary from day to day (due to weather, date in season, etc.). Large samples are therefore needed to show overall trends, and it should not be a surprise that many estimates are not significant.

Mass gains at Long Point surpassed threshold values in both migration seasons, with the exception of Area 1 in spring, suggesting that Long Point for the most part is a good stopover site for migrants. With the same exception, Long Point compared favorably to sites in Maine and Wisconsin. Long Point results can also be compared to stopover mass gains that were estimated using other methods. The average daily mass gain at Long Point for all species is 6.0% of lean body mass/d in spring (excluding Area 1) and 7.3%/d in fall (assuming 12 h/day of active foraging). These values are higher than mean gains estimated from retrapping of individual migrants (which range from 4.3–5.4% of body mass for 10–20 g passerines; Lindström 1991), and are much higher than the median value of 2.4% of body mass gained per day that was reported in another review (covering 31 species of passerines; Alerstam and Lindström 1990). However, mass gain of retrapped individuals may be atypical

TABLE 3. Mass gain at Long Point compares favorably to that at other sites, except for Area 1 in spring.<sup>a</sup> Mass gain shown as % of lean body mass/h  $\pm$  SE (*N* of species).

Season: threshold	Ontario			Wisconsin <sup>a</sup>	Maine <sup>a</sup>
	Area 1	Area 2	Area 3		
Spring: 0.27 <sup>b</sup>	0.04 $\pm$ 0.14 (5)	0.56 $\pm$ 0.16 (4)	0.45 $\pm$ 0.14 (5)	0.94 $\pm$ 0.14 (5)	—
Differences	a	b	b	b	—
Fall: 0.29 <sup>c</sup>	0.66 $\pm$ 0.07 (6)	0.61 $\pm$ 0.08 (7)	0.74 $\pm$ 0.08 (8)	0.46 $\pm$ 0.08 (8)	—
Differences	a	a	a	a	—
Fall: 0.28 <sup>d</sup>	0.56 $\pm$ 0.10 (14)	0.59 $\pm$ 0.09 (17)	0.58 $\pm$ 0.09 (17)	—	0.43 $\pm$ 0.09 (17)
Differences	a	a	a	—	a
Fall: 0.30 <sup>e</sup>	0.61 $\pm$ 0.10 (4)	0.56 $\pm$ 0.09 (5)	0.75 $\pm$ 0.09 (5)	0.45 $\pm$ 0.09 (5)	0.45 $\pm$ 0.09 (5)
Differences	a	a	a	a	a

<sup>a</sup> Wisconsin values calculated from data in Winker et al. (1992) and Maine values calculated from data in Morris et al. (1996). For this table only, Long Point mass gains are expressed as % of mean (instead of lean) body mass, for comparison with results from the other two sites. Each comparison is limited to species analyzed in the Wisconsin or Maine studies and at least one of the Ontario sites. See Table 2 footnotes for additional explanatory notes.

<sup>b</sup> Species: Least Flycatcher, Gray Catbird, Chestnut-sided Warbler, Common Yellowthroat, and Ovenbird.

<sup>c</sup> Species: same as above, plus Tennessee Warbler, Magnolia Warbler, and American Redstart.

<sup>d</sup> Species: Least Flycatcher, Red-eyed Vireo, Veery, Swainson's Thrush, Tennessee Warbler, Nashville Warbler, Magnolia Warbler, Cape May Warbler, Black-throated Blue Warbler, Bay-breasted Warbler, Black-and-white Warbler, American Redstart, Ovenbird, Northern Waterthrush, Wilson's Warbler, Canada Warbler, and Baltimore Oriole.

<sup>e</sup> Species: Least Flycatcher, Tennessee Warbler, Magnolia Warbler, American Redstart, and Ovenbird.

(Winker et al. 1992; Woodrey and Moore 1997), and many individuals lose mass during the first day after initial capture. Lindström (1991) cited numerous instances of retrapped small passerines gaining 8–12% of lean body mass/d, so the estimates of 6–7%/d at Long Point are not unreasonable. This comparison also suggests that, except for Area 1 in spring, Long Point is a good stopover site.

Seasonal patterns of mass gain at Long Point are probably dependent on differences in resource levels. The supply of aerial insects at all three sites is high as a result of close proximity to marshes and ponds, but the timing of availability probably differs among sites. Hussell and Quinney (1987) showed that aerial insect abundance at Area 1 reached its peak in late June, a full month after peak abundance at mainland sites near the base of Long Point (although the peak at Area 1 was ultimately much higher). The cold water surrounding Long Point delays phenology of plants in the early stages of spring migration and doubtless affects insect supply as well. While the effect should be strongest at Area 1, insect biomass might also be lower at Areas 2 and 3 in spring than at inland sites. In fall, weather is generally more predictable and benign at Long Point than in spring, and there is plenty of foliage to provide food and shelter for insects.

Small insectivores (warblers, flycatchers, kinglets, creeper and wrens) generally fared well at Long Point except at Area 1 in spring, and the large number of species in this group drove the pattern for all 48 species combined (Table 2). There was variation among species, however; with some small insectivores falling below threshold values at some sites in fall (e.g., Red-eyed Vireo; Table 1) and some species faring well at Area 1 in spring (e.g., Eastern Wood Pewee, Palm Warbler, and Yellow Warbler).

Sparrows showed somewhat more consistency of mass gain across sites and seasons compared to small insectivores (Table 2), surpassing threshold values in all cases, but there were no significant differences in mass gain between these two species groups. Some sparrows did very well at Area 1 in spring (e.g., Chipping and Song Sparrows; Table 1). While sparrows do consume insects during migration, they eat seeds as well, and supply of seeds left over from the previous fall should be unaffected by plant and insect phenology in the current spring.

Thrushes stood out in losing mass at Areas 1 and 2 in fall, unlike any other species group. Food supply for thrushes at these two sites is likely to be low due to the soil type (unconsolidated sand) and lack of ground cover or leaf litter. At Area 3, leaf litter does cover the soil in the small woodlot where banding is carried out, although much of the surrounding area is similar in habitat to the rest of Long Point.

The differences demonstrated here among species groups and sites suggests that a greater number of similar analyses may prove valuable in defining the types of local landscapes that are most suitable as stopover sites. At a larger scale, comparison of results from different latitudes within migration routes may increase our understanding of migration strategies. For example, Magnolia Warblers gained mass at fall stopover sites in

two northern states and in Ontario (this study; Winker et al. 1992; Morris et al. 1996), but failed to do so on the coast of Alabama (Woodrey and Moore 1997). At Long Point, mean mass of Magnolia Warblers was only 6% higher than lean mass. (The average for all 48 species in this study was 5% above lean mass). In Alabama, Magnolia Warblers were considerably heavier and had high fat scores (Woodrey and Moore 1997). Once birds have accumulated the energy reserves they need to continue migration, no further mass gain is required, and at that point a good quality site is a safe spot where mass can be maintained rather than gained. For this reason, comparisons of mass gain at sites occupied during different stages of migration should take that difference into account.

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