

## AGE-RELATED DIFFERENCES IN BODY MASS AND RATES OF MASS GAIN OF PASSERINES DURING AUTUMN MIGRATORY STOPOVER

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**Abstract.** Age-related differences in stopover ecology of migrant songbirds are poorly understood. We compared body mass, fat scores, and rates of mass gain of adults and immatures of 52 species of birds during autumn migration stopover at Long Point, Ontario, Canada, on the north shore of Lake Erie. Mean body mass of adults was greater than that of immatures in the majority of species with a detectable difference, but the average difference across species was only 1%. Fat scores were also higher for adults in many species, suggesting that mass differences were due to differences in condition rather than body size. Mean rate of mass gain, estimated from changes in body mass of first captures over the course of the day, did not differ significantly between adults and immatures of most species. However, the power to detect differences was low. Averaged across species ( $n = 117\,903$  birds), the estimated rate of mass gain for adults was 10% higher than that for immatures, but with 95% confidence limits ranging from 12% lower to 32% higher. The observed differences in body mass could be produced by a small difference in rate of mass gain. Small differences in body mass and rate of mass gain between immatures and adults could indicate that young passerines rapidly develop similar foraging skills to those of adults, or that young birds are not particularly disadvantaged at Long Point either because of good food supply, or because there is little need to accumulate large amounts of fat in the early stages of migration.

**Key words:** *age-related differences, body mass, Long Point, Ontario, rate of mass gain, stopover ecology.*

### Diferencias Dadas por la Edad en la Masa Corporal y la Tasa de Aumento de Masa de Aves Paserinas durante Escalas Migratorias Otoñales

**Resumen.** La ecología de las aves canoras migratorias de diferentes edades en sus sitios de descanso es poco conocida. Comparamos la masa corporal, los niveles de grasa y la tasa de aumento de masa de adultos e inmaduros de 52 especies de aves durante escalas migratorias otoñales en la costa norte del Lago Erie, Long Point, Ontario, Canadá. La masa corporal de los adultos fue superior a la de los inmaduros en la mayoría de las especies, pero en promedio esta diferencia fue sólo del 1% para todas las especies. Los niveles de grasa también fueron mayores en adultos de muchas especies, lo que sugiere que las diferencias en masa se debieron a diferencias en la condición física y no al tamaño corporal de las aves. La tasa media de aumento de masa, estimada a partir de cambios en la masa corporal de las primeras capturas en el curso del día, no difirió significativamente entre adultos e inmaduros para la mayoría de las especies, pero el poder de la prueba estadística para detectar diferencias fue bajo. Promediada para todas las especies ( $n = 117\,903$  aves), la tasa estimada de aumento de masa para los adultos fue superior en un 10% a la de los inmaduros, pero con intervalos de confianza del 95% fluctuando entre un mínimo de 12% y 32%. Las diferencias observadas en masa corporal pudieron ser producidas por una pequeña diferencia en las tasas de aumento de masa. Las pequeñas diferencias en la masa corporal y la tasa de aumento de masa entre inmaduros y adultos podrían indicar que las

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aves jóvenes desarrollan habilidades de forrajeo similares a las de los adultos rápidamente o que las aves jóvenes no están particularmente en desventaja en Long Point ya sea porque el alimento es abundante o porque no es necesario acumular grandes cantidades de grasa en las primeras etapas de la migración.

## INTRODUCTION

Despite the growing body of research in the field of migration stopover ecology, relatively little is known concerning age-related differences in body condition, rates of fat deposition, and habitat selection (Woodrey and Moore 1997, Yong et al. 1998). During fall migration, young birds captured at migratory stopover sites tend to have lower body mass than adults (Ellegren 1991, Morris et al. 1996, Woodrey and Moore 1997). Although this could be a function of different migration strategies by age class, it seems likely that these young birds are in poorer condition (Ellegren 1991). Several factors could contribute to age-related differences in body condition on migration. Young birds may have less efficient flight mechanics or poorer navigational abilities, causing them to burn more energy than adults during migration (Yong and Moore 1994, 1997). Upon arrival at a stopover site, young birds may choose less nutritious foods than adults or may be less efficient foragers, especially at unfamiliar stopover sites (Wunderle 1991, Morris et al. 1996). Furthermore, young birds may burn more energy during resting periods if their feathers provide poorer insulation, or if they are less able to choose good roosting sites. Few studies have examined the relative importance of these factors, especially differences in foraging efficiency or rates of mass gain by age class during migration. Ellegren (1991) failed to detect any differences in the rates of mass gain during migratory stopover between adult and immature birds, but that study was based on only one species.

Many studies have looked at recaptures of birds later the same day, or on subsequent days, to estimate mass gain during stopover (Mueller and Berger 1966, Moore and Kerlinger 1987, Yong and Moore 1997). However, this approach can be hampered by small sample sizes, and mass change in recaptured birds may not be representative of the rest of the migratory population (Mueller and Berger 1966, Winker et al. 1992, Dunn 2000). An alternative approach is to analyze changes in mass at first capture for different birds over the course of the day (King 1976, Winker et al. 1992, Dunn 2000). This approach assumes that birds arrive at the stopover

site at or before dawn on the date of capture, that an individual's capture time is independent of its mass at dawn, and that birds are foraging at the site during the day. If these assumptions are met, then the average change in mass of individuals over a day represents the average mass gain of individuals in the area. Dunn (2000, 2001) used this approach to compare three sites at Long Point, Ontario, Canada, and found that the rate of mass gain, averaged across species, was about double the estimated minimum required to maintain daily energy balance at two of the three sites in spring and at all three sites in autumn.

In this study we extended the approach used by Dunn (2000, 2001) to examine age-related differences in body mass, fat loads, and rates of mass gain of birds during autumn migration stopover at Long Point, Ontario. Based on documented age-class differences in foraging ability (Wunderle 1991), we predicted that young birds stopping over during fall migration through Long Point would have lower body masses, lower fat loads, and slower rates of mass gain than adult birds.

## METHODS

### DATA COLLECTION

We analyzed banding data collected during fall migration (August–November) by Long Point Bird Observatory (LPBO) from 1966–2000. The observatory operates three banding stations along a 35-km vegetated sand spit extending into Lake Erie. Area 1 is at the eastern tip of the spit (42°33'N, 80°10'W), Area 2 is about 20 km west, and Area 3 is 10 km farther west again, near the base of Long Point. Area 1 is characterized by open cottonwood dune habitat with minimal ground cover. The habitat at Area 2 is open savannah woodland with dense grassy ground cover. Area 3 is a small mixed-deciduous woodlot with a modest shrubby understory. More detailed descriptions of the habitat at each station are given by Dunn (2000, 2001). Banding at Areas 1 and 2 began in 1961, but ageing information was not consistent until 1966, when birds were regularly checked for degree of skull pneumatization, so we used data from 1966 on-

ward. Banding at Area 3 began in 1977, but the effort was not well standardized until 1984, so we restricted analyses from that site to 1984 onward.

At each site, birds were caught in a variety of traps including mist nets, Heligoland traps (large funnel traps into which birds are chased by banders), and various baited traps. We used data from mist net and Heligoland trap captures only, to avoid biased rates of mass gain due to bait. Mist nets were set daily during the migration season (weather permitting), usually starting around dawn and continuing for at least 6 hr. Heligoland traps, which were only in use at Areas 1 and 2, were usually operated several times a day during the same periods as the mist nets.

Among the data collected for each bird were body mass (to nearest 0.1 g), measured with a triple beam or electronic balance; unflattened wing chord (to nearest mm); age; sex; time of capture; time of weighing (both to nearest 10 min); and (from 1987 onward) a visual estimate of the amount of visible fat in the furculum (0 for none or trace; 1 for up to 1/3 full; 2 for 1/3 to 2/3 full; 3 for nearly filled or overflowing). Age was determined by methods considered 95% reliable by the banding office (Canadian Wildlife Service 1977, Pyle 1997). For most species, the vast majority of individuals were aged mainly by degree of skull pneumatization, although in some species other characters such as eye color, retention of juvenile feathers, or obvious plumage traits were used alone. More subtle characters such as differences in shape or condition of tail feathers or primary coverts (Pyle 1997), which require considerable experience to apply accurately, were only used in combination with other characters. If there was substantial doubt about the age, it was recorded as unknown. For our analysis, birds were classified as adults (after hatching year or AHY) or young (hatching year, HY), even if some adults may have been aged more precisely in the field. Unknown-age birds were excluded. In most species (40 of 52) these represented <10% of all captures (usually <5%), and in only four species (Black-capped Chickadee, Brown Creeper, Ruby-crowned Kinglet, and American Tree Sparrow) did they represent >25% of captures. All four of these species are late migrants, for which birds captured late in the season cannot be easily aged if the skull is fully pneumatized.

#### STATISTICAL ANALYSES

We initially selected all species of passerines with a minimum of 50 individuals in each age class for which capture and weighing times, body mass and age were recorded. Several species have local breeding populations in the vicinity of one or more of the banding stations. To ensure that our sample consisted primarily of passage migrants, which would presumably be trying to gain body mass, we excluded data for species at stations where local breeders were likely to be mixed with migrants throughout the migration period, as well as for species that congregate around the banding stations for several days or weeks prior to migrating (e.g., swallows and blackbirds). Furthermore, for species with small local breeding populations, we used histograms of numbers of birds caught per day to determine the timing of the main passage migration. We estimated the average date, across years, on which a substantial increase in numbers of captures occurred, and excluded captures prior to that date on the assumption that most of them were probably local residents (see also Hussell et al. 1992, Francis and Hussell 1998). Although some local residents may remain, they are unlikely to comprise more than a few percent of the remaining sample, especially as we only included newly captured birds (previously unbanded) in the analysis.

To minimize the effects of recording errors on the results, we excluded the heaviest and lightest 1% of individuals of each species (considering both age classes together) as well as any birds with inconsistencies in time (e.g., time weighed earlier than time caught). All times were adjusted to hours after sunrise, and only captures from 0.5 hr before sunrise to 7 hr after sunrise were included, as this was the period when most data were collected and most birds were likely to be foraging.

We tested for differences in mean capture times between age classes using *t*-tests. AHY individuals of seven species (Gray-cheeked Thrush, Nashville Warbler, Tennessee Warbler, Magnolia Warbler, Bay-breasted Warbler, Black-poll Warbler, and Palm Warbler) were captured significantly earlier than HY individuals, while the reverse occurred for four species (Least Flycatcher, Brown Creeper, Swamp Sparrow, and American Goldfinch; CMF, unpubl. data). However, in all cases, the differences in mean capture

time between the age classes were less than 30 min and were considered unlikely to affect our assessment of rates of mass gain.

We regressed body mass against recorded capture time (hours since sunrise) for each species to estimate the rate of mass gain over the day (Dunn 2000, 2001). We combined data from all three stations. Preliminary analyses showed that, for many species, mean body mass differed among stations, but differences between the age classes remained similar at all three stations. Because age ratios vary among stations (Dunn and Nol 1980, CMF, unpubl. data), it was thus necessary to include dummy variables for site as covariates ( $S_2 = 1$  if bird was at area 2 and 0 otherwise;  $S_3 = 1$  if bird was at area 3 and 0 otherwise) so that differences among stations would not be misinterpreted as differences between age classes (Sokal and Rohlf 1995). However, as differences between age classes appeared similar within each of the three stations, it was not necessary to include interactions between site and age class. In some species, age ratios also change over the season, with young birds migrating either earlier or later than adults (Hussell 1981). If either body mass or foraging conditions change over the season, then differences between age classes could be confounded with seasonal changes. Thus, it was also necessary to include date ( $D =$  days since July 1) as a covariate to control for increases or decreases in body mass over the season.

To test for differences in mean body mass between age classes, after controlling for covariates, we included a dummy variable for age ( $A = 1$  for AHY and 0 for HY) in the model. The regression model for this test was thus  $M = b_0 + b_1S_2 + b_2S_3 + b_3D + b_4A$ , where the regression coefficient  $b_4$  estimates the mean difference in body mass between the age classes, after adjusting for the other covariates.

To estimate the daily rate of mass gain, and differences between adults and immatures in rate of mass gain, we added regression terms for time of day ( $H$ ) and an interaction term between age class and time of day ( $AH$ ). The regression model was thus  $M = b_0 + b_1S_2 + b_2S_3 + b_3D + b_4A + b_5H + b_6(AH)$  where the regression coefficient  $b_5$  represents the hourly rate of mass gain for immature birds, and  $b_6$  represents the difference between adults and immatures in the hourly rate of mass gain, after controlling for other variables. We also used a similar model

with an interaction term between hour and date ( $HD$ ), to test whether rates of mass gain might change through the season, which could bias results for species with differential migration by age class.

Unlike Dunn (2000), we did not control for differences in wing length. A significant portion of the variation among individuals in body mass is explained by variation in structural size (James 1970, Summers 1988). This can be partially indexed by wing length, so including wing chord as a covariate could reduce the variance, and hence increase the precision of the analysis. However, young birds tend to have shorter wings than adults (Francis and Wood 1989), not necessarily because of differences in body size but because of shorter wing feathers. Hence, adjusting for wing chord could bias comparisons of body condition of young and adults. For example, if young birds had the same mean body mass as adults, they would appear to be in better condition if mass were adjusted for wing chord.

We highlight all results significant at  $P < 0.05$ . To reduce the risk of overlooking real differences, we did not use Bonferroni corrections, but we consider the problem of multiple comparisons in the discussion.

Because the precision of many of our estimates for individual species was low, we also estimated differences between age classes in body mass and rates of mass gain averaged across species. To do this, we first calculated differences between adult and immature birds in both mean mass and rate of mass gain as a percentage of mean "lean" body mass of immature birds of that species (calculated as the mean body mass of all immature birds with little or no visible subcutaneous fat). We then calculated weighted means, using as weights the square root of total sample size for that species, to avoid unduly affecting the results by species with small samples and poor estimates. The variance of the mean was calculated from the weighted variances of the estimates for individual species. This was appropriate because we are only drawing conclusions about the particular species we examined, and not making inferences about other species.

To test for differences in fat scores among age classes, we used a Mantel-Haenzel chi-square test, which tested whether there was a trend for one group to have consistently higher fat scores than the other. Because some classes for a few

species had small expected values, we used the option in SAS v8 PROC FREQ to calculate exact *P*-values (SAS Institute Inc. 1999). Values reported are means  $\pm$  SE. Scientific names for species mentioned in the text appear in Table 1.

## RESULTS

Fifty-two species met the criteria for inclusion in our analyses (Table 1). Adults (AHY) were heavier than immature birds (HY) in 21 species, lighter than immature birds in 2 species, and showed no detectable difference in 29 species (Table 1).

Adults appeared to gain mass faster than immature birds in 2 species, while immature birds appeared to gain mass faster than adults in 3 species. The remaining 47 species showed no detectable differences between age classes (Table 1).

An interaction term between hour and date, measuring the extent to which rate of mass gain changed through the season, was significant ( $P < 0.05$ ) in only 6 of the 52 species. For two species (White-crowned Sparrow and Cape May Warbler) the coefficient was positive, indicating increased rates of mass gain later in the season, while for the other four ("Traill's" Flycatcher, Blackpoll Warbler, Ovenbird, Red-breasted Nuthatch) it was negative. Only one of these six taxa ("Traill's" Flycatcher) showed significant differential migration between age classes, with adults arriving several days earlier than young (CMF, unpubl. data). Even in this case, inclusion of the interaction term did not substantially change the estimate of the difference in rates of mass gain between age classes. For this reason, and because the interaction term reduced precision of the estimate of differences between age classes, the results presented in Table 1 are from models without the interaction.

Across the 52 species, the mean difference between adult and immature birds in body mass, expressed as a percentage of mean immature lean body mass, was  $1.10 \pm 0.08\%$ . The mean rate of mass gain by immature birds was  $0.42 \pm 0.02\%$  of mean body mass  $\text{hr}^{-1}$ , while the difference in rate of mass gain between adult and immature birds was  $0.04 \pm 0.05\%$  of body mass  $\text{hr}^{-1}$ . Calculated as a percentage of the mass gain of immatures, the estimated rate of mass gain of adults was 10% higher than that of immatures, but with 95% confidence limits ranging from 12% lower to 32% higher.

Fourteen species exhibited significant age-related differences in fat scores. For 10 species (Yellow-bellied Flycatcher, Least Flycatcher, Hermit Thrush, Magnolia Warbler, Cape May Warbler, Bay-breasted Warbler, Ovenbird, Northern Waterthrush, Common Yellowthroat, Canada Warbler), adults tended to have higher fat scores than immature birds; for 4 species (Brown Creeper, Veery, Yellow Warbler, White-crowned Sparrow) the reverse was true.

## DISCUSSION

Our results are consistent with previous findings that, for the majority of species, adult birds were heavier than immature birds upon first capture at a migratory stopover site (Ellegren 1991, Morris et al. 1996, Woodrey and Moore 1997). This age-related difference is likely a product of body condition, not body size. This conclusion is supported by our fat load comparisons, which indicated that adults tended to carry more fat than did young birds (CMF, unpubl. data). However, fewer species showed significant differences in fat scores than in body mass. This could mean that some of the differences in body mass are due to factors other than fat, but could also be a result of smaller sample size (fat scores were only available for those birds caught from 1987 onward), or lower precision of the fat scores, which tend to be only moderately correlated with total body fat (Krementz and Pendleton 1990), especially if they are recorded by many different observers, as they were in this case.

In contrast, for most species we failed to detect significant differences between age classes in the rate of mass gain. Only five species out of 52 showed significant differences in rates of mass gain: 2 species in which adult birds appeared to gain mass faster and 3 species in which immature birds gained mass faster. This is only slightly more than the number of "significant" results that would be expected by chance (at  $P < 0.05$ ) if there were no difference between the age classes. These results do not support our initial expectation of greater rates of mass gain for adult birds.

However, estimates of the difference in mass gain by age class for individual species had very low precision. In many cases, the standard errors of the estimated difference in mass gain between adult and immature birds was larger than the overall rate of mass gain for immature

TABLE 1. Comparison of differences between adult (AHY) and immature (HY) birds in mean body mass and mean rate of mass gain during fall migration at Long Point Bird Observatory, Ontario, Canada. Positive differences indicate that AHY birds are heavier or gain mass faster than HY birds.

Species	AHY <i>n</i>	HY <i>n</i>	Body mass (g)		Rate of mass gain (g hr <sup>-1</sup> )	
			HY mean	Difference (AHY - HY)	HY mean	Difference (AHY - HY)
Eastern Wood-Pewee ( <i>Contopus virens</i> )	129	908	13.2	0.61 ± 0.09***	0.01	0.06 ± 0.05
Yellow-bellied Flycatcher ( <i>Empidonax flaviventris</i> )	204	1260	10.8	0.43 ± 0.07***	0.05	-0.01 ± 0.03
“Trall’s Flycatcher ( <i>Empidonax traillii/alhorum</i> )	466	1506	12.9	0.44 ± 0.07***	0.07	-0.03 ± 0.03
Least Flycatcher ( <i>Empidonax minimus</i> )	872	4341	10.1	0.33 ± 0.04***	0.05	0.01 ± 0.02
East Crested Flycatcher ( <i>Myiarchus crinitus</i> )	52	71	33.7	0.30 ± 0.51	-0.27	0.66 ± 0.26*
Eastern Kingbird ( <i>Tyrannus tyrannus</i> )	144	332	38.0	1.69 ± 0.30***	0.01	-0.13 ± 0.16
Red-eyed Vireo ( <i>Vireo olivaceus</i> )	211	1701	17.5	0.42 ± 0.10***	0.05	0.10 ± 0.06
Black-capped Chickadee ( <i>Poecile atricapilla</i> )	230	1131	10.5	0.00 ± 0.05	0.00	0.00 ± 0.03
Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	381	1177	10.6	0.13 ± 0.04**	0.03	0.05 ± 0.03
White-breasted Nuthatch ( <i>Sitta carolinensis</i> )	55	185	20.0	-0.29 ± 0.29	0.03	-0.24 ± 0.18
Brown Creeper ( <i>Certhia americana</i> )	317	3540	8.2	0.09 ± 0.04*	0.01	0.02 ± 0.02
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	144	5045	6.2	0.02 ± 0.04	0.02	0.02 ± 0.02
Ruby-crowned Kinglet ( <i>Regulus calendula</i> )	610	5913	6.4	0.14 ± 0.02***	0.05	0.00 ± 0.01
Veery ( <i>Catharus fuscens</i> )	294	894	31.9	-0.10 ± 0.17	-0.01	-0.04 ± 0.08
Gray-checked Thrush ( <i>Catharus minimus</i> )	557	2125	30.6	-0.02 ± 0.12	0.01	0.01 ± 0.06
Swainson’s Thrush ( <i>Catharus ustulatus</i> )	1443	5257	29.3	0.51 ± 0.07***	0.03	-0.02 ± 0.03
Hermit Thrush ( <i>Catharus guttatus</i> )	602	4251	29.5	0.75 ± 0.09***	0.06	-0.06 ± 0.04
American Robin ( <i>Turdus americanus</i> )	64	204	81.6	0.00 ± 0.81	0.00	0.00 ± 0.40
Gray Catbird ( <i>Dumetella carolinensis</i> )	79	706	39.4	0.00 ± 0.35	0.00	0.00 ± 0.20
Tennessee Warbler ( <i>Vermivora peregrina</i> )	208	1965	9.4	0.10 ± 0.06	0.03	0.04 ± 0.03
Nashville Warbler ( <i>Vermivora ruficapilla</i> )	197	1554	8.4	-0.04 ± 0.05	0.04	0.02 ± 0.03
Yellow Warbler ( <i>Dendroica petechia</i> )	297	2836	10.8	0.00 ± 0.07	0.00	0.00 ± 0.04
Chestnut-sided Warbler ( <i>Dendroica pensylvanica</i> )	96	853	9.6	0.20 ± 0.08*	0.10	0.05 ± 0.05
Magnolia Warbler ( <i>Dendroica magenolia</i> )	614	5683	8.3	0.11 ± 0.03***	0.07	-0.03 ± 0.01*
Cape May Warbler ( <i>Dendroica tigrina</i> )	228	2611	10.6	0.19 ± 0.06**	0.04	0.08 ± 0.03
Black-throated Blue Warbler ( <i>Dendroica caerulescens</i> )	209	1434	9.6	0.16 ± 0.05**	0.05	-0.04 ± 0.03
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	871	12 520	12.1	0.05 ± 0.03	0.07	0.04 ± 0.02**
Black-throated Green Warbler ( <i>Dendroica virens</i> )	59	753	8.8	0.11 ± 0.09	0.06	0.03 ± 0.05
Blackburnian Warbler ( <i>Dendroica fusca</i> )	64	848	9.6	0.06 ± 0.11	0.03	-0.02 ± 0.06
Palm Warbler ( <i>Dendroica palmarum</i> )	94	1104	10.2	-0.21 ± 0.09*	0.11	-0.16 ± 0.05**
Bay-breasted Warbler ( <i>Dendroica castanea</i> )	174	2290	11.8	0.02 ± 0.07	0.09	-0.03 ± 0.04
Blackpoll Warbler ( <i>Dendroica striata</i> )	1568	3064	12.1	0.08 ± 0.03*	0.09	0.01 ± 0.02
Black-and-white Warbler ( <i>Mniotilta varia</i> )	89	946	10.4	-0.21 ± 0.08*	0.05	0.05 ± 0.04
American Redstart ( <i>Setophaga ruticilla</i> )	263	2400	7.9	0.01 ± 0.04	0.05	0.00 ± 0.02
Ovenbird ( <i>Seturus aurocapillus</i> )	126	738	19.0	0.18 ± 0.14	0.08	-0.01 ± 0.07

TABLE 1. Continued.

Species	AHY		HY	Body mass (g)		Rate of mass gain (g hr <sup>-1</sup> )	
	<i>n</i>	<i>n</i>		HY mean	Difference (AHY - HY)	HY mean	Difference (AHY - HY)
Northern Waterthrush ( <i>Seiurus noveboracensis</i> )	400	1746	17.3	0.28 ± 0.08***	0.08	0.06 ± 0.04	
Connecticut Warbler ( <i>Oporornis agilis</i> )	58	53	14.0	-0.07 ± 0.22	0.14	-0.04 ± 0.11	
Mourning Warbler ( <i>Oporornis philadelphia</i> )	73	222	12.2	0.30 ± 0.16	0.16	0.00 ± 0.08	
Common Yellowthroat ( <i>Geothlypis trichas</i> )	182	917	10.5	0.00 ± 0.08	0.00	0.00 ± 0.04	
Wilson's Warbler ( <i>Wilsonia pusilla</i> )	161	1250	7.6	0.08 ± 0.05	0.08	-0.04 ± 0.03	
Canada Warbler ( <i>Wilsonia canadensis</i> )	221	1253	10.0	0.37 ± 0.06***	0.08	0.01 ± 0.03	
American Tree Sparrow ( <i>Spizella arborea</i> )	140	812	17.6	0.00 ± 0.10	0.00	0.00 ± 0.06	
Song Sparrow ( <i>Melospiza melodia</i> )	280	1302	20.9	0.00 ± 0.10	0.00	0.00 ± 0.05	
Lincoln's Sparrow ( <i>Melospiza lincolni</i> )	65	256	16.8	0.01 ± 0.21	0.19	0.02 ± 0.12	
Swamp Sparrow ( <i>Melospiza georgiana</i> )	69	862	16.4	0.00 ± 0.16	0.00	0.00 ± 0.09	
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	865	4081	25.4	-0.04 ± 0.08	0.11	0.00 ± 0.04	
White-crowned Sparrow ( <i>Zonotrichia leucophrys</i> )	380	690	28.1	0.41 ± 0.16**	0.14	-0.17 ± 0.08*	
Dark-eyed Junco ( <i>Junco hyemalis</i> )	1115	3243	18.9	0.19 ± 0.05***	0.09	0.00 ± 0.02	
Rose-breasted Grosbeak ( <i>Pheucticus ludovicianus</i> )	58	296	45.2	-0.57 ± 0.44	0.14	0.10 ± 0.23	
Baltimore Oriole ( <i>Icterus galbula</i> )	57	265	33.9	0.56 ± 0.38	0.28	-0.04 ± 0.23	
Purple Finch ( <i>Carpodacus purpureus</i> )	82	211	23.1	0.46 ± 0.23*	0.03	-0.01 ± 0.13	
American Goldfinch ( <i>Carduelis tristis</i> )	361	1380	12.5	0.07 ± 0.05	-0.07	0.04 ± 0.03	

\*  $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ ; 2-tailed tests.

birds (Table 1), clearly indicating little power to detect differences between age classes for individual species. Thus, to increase the precision, we calculated weighted averages across species. These indicated that the average difference in body mass between adult birds and immatures was only 1.1% of the immature body mass. This approach also suggested that adults may gain body mass about 10% faster than immatures, but with 95% confidence limits from 12% less efficient to 32% more efficient than immatures at assimilating body mass. Because even a 10% difference in mass assimilation could have quite important ramifications for the stopover ecology of immature and adult birds, this result indicates that our approach does not provide adequate precision to test for differences between age classes in rates of mass gain, even pooled across species with a resultant very large sample size (117 903 individuals).

The difference in body mass between adult and immature birds that we detected is lower than expected based on previous findings (Morris et al. 1996, Woodrey and Moore 1997, Yong et al. 1998). Morris et al. (1996) reported an average difference of  $2.1 \pm 0.8\%$  ( $n = 17$  species) while Woodrey and Moore (1997) reported an average difference of  $3.9 \pm 2.5\%$  ( $n = 6$  species). Ellegren (1991) found a  $\sim 2\%$  difference for females and a  $\sim 3\%$  difference for male Red-spotted Bluethroats (*Luscinia s. svecica*). These latter differences translated into an estimated difference in body fat of 20–25% (Ellegren 1991). In light of these previous findings, even our low detected difference of 1% could manifest itself in a difference in body fat of 10–15%. Such a difference would likely have a large effect on migratory preparedness and could prolong stopover periods or reduce flight distances for immature birds migrating south.

Given the low precision of our estimates, we cannot say there is no difference in the rate at which adult and immature birds gain mass during migratory stopover; indeed the difference could be as great as 30% in favor of adult birds. Despite the low precision, however, we maintain that this approach to estimating rates of mass gain during migratory stopover is valid, to the extent that estimated rates of mass gain are consistent with birds gaining net mass at the stopover site, even on the first day (Dunn 2000, 2001). Further, the mass-at-first-capture approach avoids a serious drawback of recapture

analyses. It eliminates the bias generated by the possibility that individuals in poor condition, including any that are impaired by handling, remain at the stopover site for longer, thereby increasing the likelihood of recapturing affected birds.

Differential timing of landing of adult and immature birds could also cloud any real age-related differences in mass gain during migration. If adult and immature birds arrived at the stopover site at different times in the morning, this could affect the amount of time available to a bird for foraging before capture. In our experience, few birds arrive at Long Point after dawn (CME, pers. obs.); some birds do move into the area during the course of a morning, but these birds appear to be moving along the point after a dawn landing and presumably forage while doing so. Furthermore, we found few statistically significant differences in adult and immature capture times (used as a surrogate for landing time) and these differences were small (<30 min).

Ultimately, there is still the possibility that there really is little difference between the age classes. If the expectation of a difference is based solely on potential differences in foraging ability, such a lack of difference could arise for several reasons. First of all, much of the literature that supports large differences between the foraging abilities of immature and adult birds is based on birds with complex foraging techniques (e.g., herons, Quinney and Smith 1980). Age-related differences might be expected to be much smaller for passerines performing simpler maneuvers, such as foliage gleaning. A second possibility is that, given the particularly good food supply at Long Point (E. H. Dunn, unpubl. data), even inexperienced birds are able to find sufficient food resources. A third possibility is that there is not a premium on high rates of mass gain early in migration; that is, birds may avoid putting on unnecessary “extra” mass early in migration. Any age-related differences in rates of mass gain may become more noticeable as the urgency with which birds need to store fat increases, such as at stopover sites nearer the Gulf of Mexico.

A final possibility is that the adult sample at Long Point is atypical. Relatively few adults of most species are captured during fall migration at Long Point (Dunn and Nol 1980; Table 1). The distance across Lake Erie is not great when

compared with the journeys to be undertaken by migrants captured in other mass gain studies (e.g., Sahara Desert, Biebach et al. 1986; Caribbean Sea, Woodrey and Moore 1997). Dunn and Nol (1980) suggested that adults finding themselves over Long Point at dawn may be more likely to continue across the lake to the mainland on the other side, whereas the less experienced immatures may be more likely to land. Adult birds unable or unwilling to make the short trip across Lake Erie may be in poorer condition and have lower than typical body mass; this poor condition may make them less able to gain mass quickly, thereby rendering them more similar to immature birds. Similar analyses at inland stopover sites with higher proportions of adults would be valuable to test whether birds caught at stopover sites such as Long Point really are atypical. Analyses of data from birds near major ecological barriers, such as the Gulf of Mexico, would also be valuable to test whether age-related differences are more apparent when birds need to accumulate much greater quantities of fat for migration.

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#### LITERATURE CITED

- BIEBACH, H., W. FRIEDRICH, AND G. HEINE. 1986. Interaction of body mass, fat, foraging and stopover period in trans-Saharan migrating passerine birds. *Oecologia* 69:370–379.
- CANADIAN WILDLIFE SERVICE. 1977. North American bird banding techniques. Vol. 2. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- DUNN, E. H. 2000. Temporal and spatial patterns in daily mass gain of Magnolia Warblers during migration stopover. *Auk* 117:12–21.
- DUNN, E. H. 2001. Mass change during migration stopover: a comparison of species groups and sites. *Journal of Field Ornithology* 72:419–432.
- DUNN, E. H., AND E. NOL. 1980. Age-related migratory behavior of warblers. *Journal of Field Ornithology* 51:254–269.
- ELLEGREN, H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scandinavica* 22:340–348.
- FRANCIS, C. M., AND D. J. T. HUSSELL. 1998. Changes in numbers of land birds counted in migration at Long Point Bird Observatory, 1961–1997. *Bird Populations* 4:37–66.
- FRANCIS, C. M., AND D. S. WOOD. 1989. Effects of age and wear on wing length of wood-warblers. *Journal of Field Ornithology* 60:495–503.
- HUSSELL, D. J. T. 1981. Migrations of the Least Flycatcher in southern Ontario. *Journal of Field Ornithology* 52:97–111.
- HUSSELL, D. J. T., M. H. MATHER, AND P. H. SINCLAIR. 1992. Trends in numbers of tropical- and temperate-wintering migrant landbirds in migration at Long Point, Ontario, 1961–1988, p. 101–114. *In* J. M. Hagan III and D. W. Johnston [EDS.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365–390.
- KING, R. 1976. Daily weight changes in migrant Yellow-rumped Warblers. *North American Bird Bander* 4:172–173.
- KREMENTZ, D. G., AND G. W. PENDLETON. 1990. Fat scoring: sources of variability. *Condor* 92:500–507.
- MOORE, F. R., AND P. KERLINGER. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74:47–54.
- MORRIS, S. R., D. W. HOLMES, AND M. E. RICHMOND. 1996. A ten-year study of the stopover patterns of migratory passerines during fall migration on Appledore Island, Maine. *Condor* 98:395–409.
- MUELLER, H. C., AND D. D. BERGER. 1966. Analyses of weight and fat variations in transient Swainson's Thrushes. *Bird-Banding* 37:83–112.
- PYLE, P. 1997. Identification guide to North American birds. Part 1. Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.
- QUINNEY, T. E., AND P. C. SMITH. 1980. Comparative foraging behaviour and efficiency of adult and juvenile Great Blue Herons. *Canadian Journal of Zoology* 58:1168–1173.
- SAS INSTITUTE INC. 1999. The SAS system for windows, release 8.0. SAS Institute, Inc., Cary, NC.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*. W. H. Freeman and Company, New York.
- SUMMERS, R. W. 1988. The use of linear measurements when comparing masses. *Bird Study* 36:77–79.
- WINKER, K., D. W. WARNER, AND A. R. WEISBROD. 1992. Daily mass gains among woodland migrants at an island stopover site. *Auk* 109:853–862.
- WOODREY, M. S., AND F. R. MOORE. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *Auk* 114:695–707.

- WUNDERLE, J. M., JR. 1991. Age-specific foraging proficiency in birds. *Current Ornithology* 8:273–324.
- YONG, W., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *Auk* 115:829–842.
- YONG, W., AND F. R. MOORE. 1994. Flight morphology, energetic condition, and the stopover biology of migrating thrushes. *Auk* 111:683–692.
- YONG, W., AND F. R. MOORE. 1997. Spring stopover of intercontinental migratory thrushes along the northern coast of the Gulf of Mexico. *Auk* 114:263–278.