

AGE-RELATED DIFFERENTIAL TIMING OF SPRING MIGRATION WITHIN SEXES IN PASSERINES

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ABSTRACT.—We examined differential timing of spring migration by age class for passerines banded at Long Point Bird Observatory from 1984 to 1998. Mean capture dates of after-second-year (ASY) males were earlier than second-year (SY) males for 19 of 20 species, 16 significantly so. Mean capture dates of ASY females were earlier than SY females for 11 of 12 species, 8 significantly so. There was no significant difference in the timing of migration between age classes for males of species with highly distinctive SY plumages and males of other species with more subtle plumage differences between age classes. For 12 species with adequate samples of both sexes, the mean difference in capture dates between age classes was significantly greater for males (3.5 days) than for females (2.1 days). These results suggest that differential migration by age class is widespread among passerines and that factors leading to the delayed arrival of young males also may affect females, though to a lesser extent. *Received 15 May 2001, accepted 31 January 2002.*

In many species of birds, males precede females on spring migration (Francis and Cooke 1986, 1990; Lozano et al. 1996; Swanson et al. 1999). Exceptions include species with polyandrous mating systems where females tend to be the dominant sex and precede males on spring migration (Oring and Lank 1982, Reynolds et al. 1986). Several possible factors have been suggested to explain these patterns. Sexual selection on the breeding grounds could lead to the sex that experiences the greatest amount of intrasexual competition for territories and/or mates arriving earlier. Related to this, the larger sex may be better able to tolerate harsh conditions early in the season (Ketterson and Nolan 1976, 1979). Intersexual competition for limited food resources on the wintering grounds could lead to the dominant sex excluding the subordinate sex from either (1) northerly wintering grounds, which would allow the dominant individuals to winter clos-

er to the breeding grounds, thus facilitating their earlier arrival (Ketterson 1979, Ketterson and Nolan 1979), or (2) habitats with better food supplies, which would decrease the subordinate sex's physical condition and delay their departure (Marra and Holberton 1998, Marra et al. 1998). Francis and Cooke (1990) suggested that these hypotheses are not mutually exclusive because selection for early arrival on the breeding grounds also could affect wintering ground choice and size dimorphism.

Less is known about the differential timing between age classes within each sex during spring migration. Differences in shape and color pattern between the feathers of younger (second-year or SY) North American passerines that retain their juvenile primaries, rectrices, and selected wing coverts, and those of older (after-second-year or ASY) birds only recently have been described for a wide range of species (Pyle et al. 1987, Pyle et al. 1997). Thus, many previous analyses of differential migration by age class have been restricted to species that have striking differences in plumage color between SY and ASY individuals (Rohwer and Niles 1979, Flood 1984, Francis and Cooke 1986, Hill 1989, Francis and Cooke 1990, Morton and Derrickson 1990). In these cases, ASY males migrate earlier than SY males.

However, in all but about 35 North American passerines, ASY and SY males have similar plumage coloration (Rohwer and Butcher 1988), hence the differential migration patterns of species with different ASY and SY

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plumages may not be typical of other species. Rohwer et al. (1980) suggested that some SY males have female-like plumage to reduce aggression from ASY males and subsequently gain breeding opportunities. They predicted that SY males with female-like plumage should arrive at the breeding grounds after ASY males whereas SY males with ASY-like plumage should arrive at the same time as ASY males.

Nevertheless, a tendency for SY males to arrive after ASY males has been shown for a number of other passerine species which do not show striking plumage differences between age classes, many of which are summarized by Hill (1989). Both Rohwer et al. (1980) and Hill (1989) have suggested that species without a distinct SY plumage show a greater overlap in ASY and SY spring arrival dates than species with distinct plumage differences between ASY and SY males. However, the methodology used to determine ASY and SY male spring arrival dates varied greatly among studies, ranging from observations of first territorial behavior on the breeding grounds (Stewart 1973, Wittenberger 1978, Eliason 1986, Hopp et al. 1999) to determining ASY and SY passage dates from museum collection dates (Johnson 1965, 1973) or from specimens collected from tower kills during migration (Nolan and Mumford 1965). In some studies age was not recorded, but differential migration between age classes was inferred based on relationships between wing chord and migration dates (Hussell 1981, Bédard and LaPointe 1984, Francis and Cooke 1986). A more consistent approach is needed to test whether the tendency of ASY males to migrate earlier than SY males is typical of passerines without distinct plumage differences between age classes and to test whether ASY and SY males of these species show less difference in their migration dates than males of other species with distinct SY male plumages.

Even less is known about age specific differences in migratory timing of females, largely because age classes generally are more difficult to distinguish. In both Purple Martins (*Progne subis*) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), ASY females arrive at the breeding grounds earlier than SY females (Crawford 1978, Morton and

Derrickson 1990). Francis and Cooke (1990) inferred that SY female Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) arrived later than ASY females based on a trend for later migrants to have shorter wing lengths, but the females in their sample were not aged.

We examined mean capture dates of 20 species of passerines captured and banded during spring migration at Long Point Bird Observatory (LPBO) from 1984 to 1998 to test whether older, ASY males migrate before younger, SY males in species with and without distinct plumage differences between male age classes and to test whether ASY females migrate before SY females.

METHODS

Capture data.—We captured birds using a combination of mist nets and Heligoland traps at three stations on Long Point, Ontario, Canada (42° 33' N, 80° 10' W), on the north shore of Lake Erie. Spring trapping was carried out daily, weather permitting, from early April to the beginning of June, 1984–1998. Further details of the banding and migration monitoring operations are described in Francis and Hussell (1998) and Dunn (2000).

We pooled data from all three banding stations over the 14-year period. We used data from all passerine species captured on spring migration that could be sexed and aged reliably (Pyle et al. 1997) and for which ≥ 50 known age birds of a particular sex, with ≥ 10 in each age class, were banded. We excluded any species-sex combinations for which aged birds constituted $< 35\%$ of the total birds captured for that sex of that species. We also excluded species that had substantial local breeding populations around the banding stations, such that many individuals captured may have been local breeders captured well after their initial arrival dates.

To test whether differences in migration dates between age classes of males were related to plumage differences, we classified species into three groups according to the plumage differences (or lack of) between ASY and SY males (Table 1). The first group included only the American Redstart (*Setophaga ruticilla*), in which SY males have a gray and yellow plumage resembling females, rather than the black and orange of ASY males. The second group consisted of species in which the SY males differ conspicuously from ASY males (e.g., by brown instead of black primaries often with substantially less bright colors elsewhere on the body), but do not resemble females. The third group consisted of the remaining species which have relatively subtle differences, in which the age classes are distinguished mainly by differences in shape, wear, or edging of the primary coverts, primaries, or rectrices.

Although mean capture dates varied among years

TABLE 1. Mean capture dates \pm SE (*n*) for after-second-year (ASY) and second-year (SY) passerines, plus birds of unknown age, captured at Long Point Bird Observatory during spring migration, 1984–1998. Dates begin April 1 (e.g., May 3 = 33). Lines indicate insufficient data for analysis. Species were classified according to the plumage differences between male age classes: D = dichromatic, where SY males have distinct subadult plumage resembling females; S = somewhat dichromatic, where SY males differ conspicuously from ASY males but do not resemble females; N = no difference, where SY males closely resemble ASY males and are distinguished from ASYs by feather wear and shape.

Species	Plumage	Males	
		ASY	SY
Tennessee Warbler (<i>Vermivora peregrina</i>)	N	44.5 \pm 0.4 (50)	47.7 \pm 0.7 (39)
Nashville Warbler (<i>Vermivora ruficapilla</i>)	N	38.5 \pm 0.6 (87)	41.3 \pm 0.4 (160)
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	N	46.0 \pm 0.6 (100)	50.1 \pm 0.4 (250)
Magnolia Warbler (<i>Dendroica magnolia</i>)	N	46.9 \pm 0.2 (970)	50.4 \pm 0.2 (1516)
Cape May Warbler (<i>Dendroica tigrina</i>)	N	42.7 \pm 0.5 (62)	44.6 \pm 0.7 (53)
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	N	41.1 \pm 0.6 (115)	45.5 \pm 0.3 (155)
Yellow-rumped Warbler (<i>Dendroica coronata</i>)	N	30.7 \pm 0.4 (297)	33.6 \pm 0.2 (1040)
Black-throated Green Warbler (<i>Dendroica virens</i>)	N	40.5 \pm 1.3 (46)	47.2 \pm 0.9 (123)
Blackburnian Warbler (<i>Dendroica fusca</i>)	N	46.5 \pm 0.8 (48)	50.0 \pm 0.8 (63)
Bay-breasted Warbler (<i>Dendroica castanea</i>)	N	45.3 \pm 0.6 (43)	49.0 \pm 0.6 (62)
Blackpoll Warbler (<i>Dendroica striata</i>)	N	52.8 \pm 1.4 (12)	54.7 \pm 0.6 (59)
Black-and-white Warbler (<i>Mniotilta varia</i>)	N	35.7 \pm 0.4 (231)	38.8 \pm 0.4 (300)
American Redstart (<i>Setophaga ruticilla</i>)	D	47.0 \pm 0.3 (305)	52.1 \pm 0.4 (314)
Canada Warbler (<i>Wilsonia canadensis</i>)	N	51.0 \pm 0.5 (91)	54.3 \pm 0.6 (128)
Scarlet Tanager (<i>Piranga olivacea</i>)	S	41.2 \pm 0.7 (36)	45.8 \pm 0.7 (59)
Eastern Towhee (<i>Pipilo erythrophthalmus</i>)	S	21.2 \pm 1.5 (44)	25.2 \pm 0.7 (203)
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	S	39.7 \pm 0.3 (261)	43.1 \pm 0.3 (337)
Indigo Bunting (<i>Passerina cyanea</i>)	S	49.6 \pm 3.0 (11)	48.5 \pm 0.7 (80)
Brown-headed Cowbird (<i>Molothrus ater</i>)	N	26.1 \pm 1.8 (81)	28.5 \pm 1.4 (129)
Baltimore Oriole (<i>Icterus galbula</i>)	S	43.4 \pm 0.5 (204)	47.4 \pm 0.4 (366)

^a Probability that the observed difference between mean ASY and SY passage dates is due to chance (Wilcoxon 2-sample test).

(e.g., due to weather conditions), capture dates were not standardized to year because the effects of weather are complex, affecting timing differently throughout the season, and also interact with both differences in trapping efforts as well as differences in population arrival (Francis and Cooke 1986). In addition, sample sizes for many species were relatively small in individual years. As few birds of most passage migrants were recaptured on subsequent days, we assumed that capture dates provide a good approximation of passage dates.

Some species included a high percentage of unknown age birds, which could lead to bias if the sample of aged birds was not representative. There are several reasons why birds may not be aged: failure to record the information, lack of knowledge or lack of experience with the aging criteria by the bander, or difficulties in deciding because the characters appear intermediate, especially for species differing in subtle characters. To test whether the sample of known age birds might be biased, we also estimated mean capture dates of unknown age birds, and tested whether differences between age classes were related to the proportion of unknown age birds.

Statistical analyses.—We based comparisons among age-sex groups on mean dates, which give greater precision than median dates, but used Wilcoxon 2-sample

tests for statistical comparisons to minimize the influence of unusually early or late arrivals on the tests. A sequential Bonferroni adjustment (Rice 1989) was made following the Wilcoxon 2-sample tests to reduce the possibility of committing a type 1 error. We used both a Spearman rank correlation and analysis of variance to test whether differences in migration dates between ASY and SY males were related to their classification based on plumage differences. We used a signed rank test to test whether the difference between age classes for males differed from that for females of the same species, for species with adequate samples of both sexes. We also used regression analysis and analysis of covariance to test whether differences between sexes or age classes differed for early-arriving and late-arriving species.

RESULTS

Adequate samples that met our criteria for inclusion were available for males of 20 species (8,456 known age individuals) and for females of 12 species (2,972 known age individuals). With the exception of the Indigo Bunting (*Passerina cyanea*), in which ASY males were captured slightly later than SY

TABLE 1. EXTENDED

Males		Females			
Unknown	P^a	ASY	SY	Unknown	P^a
47.6 \pm 0.6 (87)	0.0001	48.1 \pm 0.6 (51)	50.6 \pm 0.8 (48)	52.0 \pm 0.5 (133)	0.0395
40.7 \pm 0.3 (438)	0.0003	43.3 \pm 0.4 (75)	44.4 \pm 0.5 (114)	45.6 \pm 0.3 (338)	0.1295
46.4 \pm 0.4 (297)	0.0000	50.4 \pm 0.7 (71)	52.8 \pm 0.7 (110)	50.7 \pm (188)	0.0029
48.9 \pm 0.2 (857)	0.0000	51.4 \pm 0.3 (371)	53.9 \pm 0.2 (984)	53.0 \pm (643)	0.0000
43.1 \pm 0.8 (60)	0.1263	46.0 \pm 0.8 (39)	47.5 \pm 0.5 (78)	49.3 \pm 0.4 (131)	0.0266
44.6 \pm 0.8 (41)	0.0000	—	—	—	—
32.9 \pm 0.5 (321)	0.0000	40.3 \pm 0.6 (135)	41.8 \pm 0.4 (353)	40.6 \pm (636)	0.0336
41.5 \pm 1.0 (127)	0.0000	48.0 \pm 1.2 (37)	52.8 \pm 0.8 (78)	40.3 \pm 0.8 (117)	0.0044
48.4 \pm 0.7 (72)	0.0084	52.1 \pm 1.0 (33)	56.4 \pm 0.8 (65)	55.4 \pm 0.6 (131)	0.0026
48.9 \pm 0.5 (80)	0.0000	49.6 \pm 1.0 (21)	50.1 \pm 0.9 (30)	52.6 \pm 0.6 (85)	0.1788
54.5 \pm 0.7 (81)	0.1565	60.5 \pm 1.4 (18)	58.2 \pm 0.8 (51)	60.0 \pm 0.6 (81)	0.1709
39.8 \pm 0.7 (113)	0.0000	—	—	—	—
47.6 \pm 1.0 (19)	0.0000	—	—	—	—
52.1 \pm 0.4 (253)	0.0001	54.3 \pm 1.0 (38)	57.9 \pm 0.5 (88)	56.0 \pm 0.4 (216)	0.0002
50.0 \pm 0.7 (4)	0.0000	—	—	—	—
23.3 \pm 1.8 (27)	0.0460	30.4 \pm 1.3 (49)	32.3 \pm 2.3 (35)	32.0 \pm 0.8 (123)	0.1924
40.0 \pm 1.2 (25)	0.0000	—	—	—	—
48.5 \pm 1.6 (40)	0.8883	—	—	—	—
32.6 \pm 3.0 (22)	0.0648	—	—	—	—
48.2 \pm 1.3 (56)	0.0000	—	—	—	—

males (difference was not significant: $P = 0.89$), ASY males were captured earlier than SY males for 19 of the 20 species, 16 of them significantly so (P values <0.05 ; Table 1). With the exception of the Blackburnian Warbler (*Dendroica fusca*; $P = 0.008$) and the Eastern Towhee (*Pipilo erythrophthalmus*; $P = 0.046$), all other significant differences between ASY and SY passage dates remained significant following sequential Bonferroni adjustment ($\alpha = 0.0083$).

The difference in capture dates for male American Redstarts, with their female-like SY male plumage (5.1 days), was the second highest among all species (the Black-throated Green Warbler, *Dendroica virens*, showed the greatest difference, 6.7 days), but the mean for other species with distinctive male SY plumages (mean \pm SE: 3.0 ± 1.0 days) was slightly less than that for species with more subtle differences between SY and ASY males (3.5 ± 0.2 days). The difference between groups was not significant based on either a rank cor-

relation ($r_s = 0.28$, $P = 0.23$), or analysis of variance ($F_{2,19} = 0.81$, $P = 0.46$).

Among females, ASYs were captured earlier than SYs for 11 of the 12 species examined, 8 significantly so (P values <0.05 ; Table 1). The only exception was the Blackpoll Warbler (*Dendroica striata*) for which ASY females were captured slightly later than SY females, but the difference was not significant ($P = 0.18$). With the exceptions of the Tennessee Warbler (*Vermivora peregrina*; $P = 0.040$), the Cape May Warbler (*D. tigrina*; $P = 0.027$), and the Yellow-rumped Warbler (*D. coronata*; $P = 0.034$), differences between ASY and SY female passage dates remained significant following sequential Bonferroni adjustment ($\alpha = 0.007$).

To compare differential migration of males and females, we restricted analysis to those 12 species with adequate samples for both sexes. The mean difference between age classes was significantly larger for males than for females (males: 3.46 ± 0.36 ; females: 2.05 ± 0.50

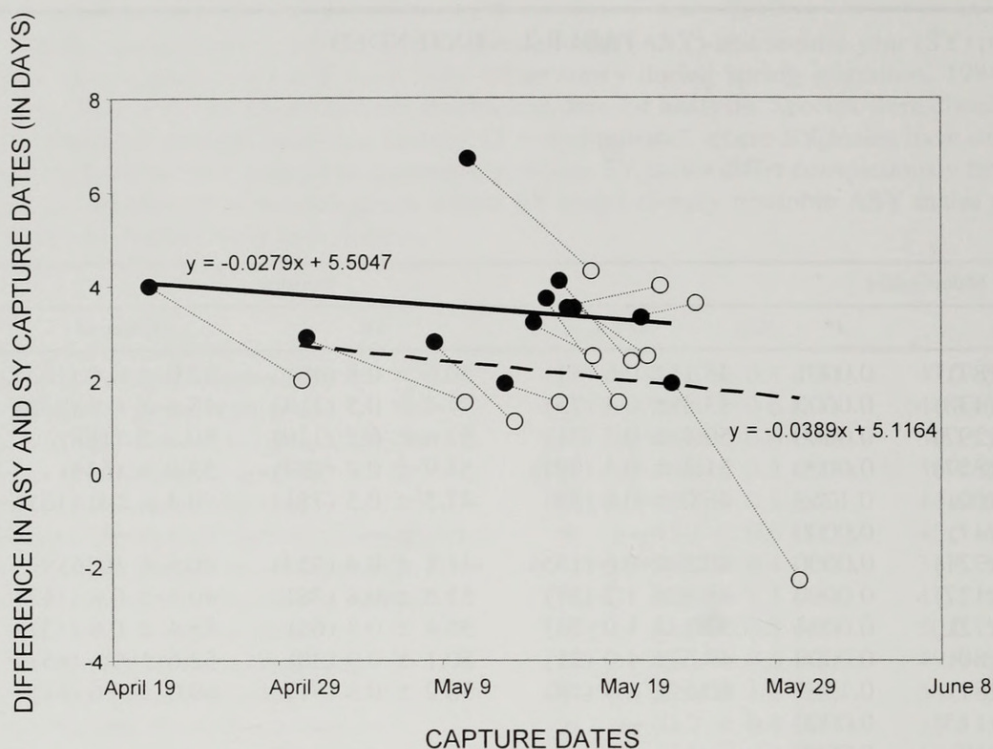


FIG. 1. The difference in capture dates between age classes in 12 passerine species was significantly greater for males (solid circles, solid line) than for females (open circles, dashed line) captured at Long Point Bird Observatory during spring migration 1984–1998, even after correcting for a tendency for differences to decline over the season. Points representing males and females of the same species are joined together by light dotted lines. See Table 1 for list of species.

days; Wilcoxon paired test, $Z = 2.74$, $P = 0.006$). Previous studies have shown that species that migrate earlier in the season have greater differences in migration dates between males and females than later migrating species (Francis and Cooke 1986), and the same pattern was apparent for the 12 species in this study (regression of difference in capture dates between ASY males and ASY females against mean capture date of ASY males; $b = -0.16$, $SE = 0.06$, $r^2 = 0.40$, $P = 0.026$). Thus, we tested whether the smaller differences between age classes of females could be related to their later arrival. Within each sex, there was a slight tendency for a reduced difference in capture dates between age classes later in the season, but it was not significantly different from zero in either case (males: $b = -0.03$, $SE = 0.04$, $r^2 = 0.04$, $P = 0.54$; females: $b = -0.04$, $SE = 0.07$, $r^2 = 0.03$, $P = 0.60$). The mean difference in arrival dates between age classes of females was still about 1.2 days less than that of males even after adjusting for differences in arrival dates (Fig. 1).

Mean capture dates for birds of unknown

age were intermediate between those of known ASY and SY birds for males in 16 of 20 species and for females of 8 of 12 species (Table 1). This suggests that for most species, the unknown birds were a mixture of both age classes. In the 8 exceptions, birds of unknown age tended to be later than SY birds, but this was significant in only two cases: female Nashville ($P = 0.017$) and Cape May warblers ($P = 0.0007$). In neither sex was there a significant relationship between the proportion of unaged birds and the difference between age classes (males: $r = -0.19$, $n = 20$, $P = 0.43$; females: $r = -0.12$, $n = 12$, $P = 0.70$).

DISCUSSION

ASY male passage dates preceded SY male passage dates for most species regardless of whether the species showed distinct plumage differences between male age classes. Thus, delayed arrival time of young birds does not appear to be associated with delayed plumage maturation. Instead, differential migration by age class appears to be widespread among passerines.

Several hypotheses have been proposed to

explain the late migration of SY males relative to ASY males. SY males may be energetically constrained to arrive later, possibly due to dominance interactions on the wintering grounds. Marra et al. (1993, 1998) found that ASY male American Redstarts excluded SY males from high quality foraging habitat during winter; consequently, SY males that occupied lower quality habitats were in reduced physical condition and departed from the wintering grounds later than individuals that occupied higher quality habitats. Even if SY males are able to depart for the breeding grounds at the same time as ASY males, SYs might not be able to withstand the harsh conditions at the breeding grounds during early spring. On the other hand, SY males may not benefit from arriving too early, particularly if later-arriving ASY males are able to usurp territories from SY males (Morse 1973, Howe 1974, Sherry and Holmes 1989). If SY males have little to gain by arriving early, they may instead benefit by arriving later, thus avoiding the energetic costs of competition and aggression from older males (Hill 1989), as well as risks associated with poor weather (Whitmore et al. 1977) or low food supplies (Nolan 1978, Lank et al. 1985) early in the season. Given that many Neotropical migrants that do not show age dichromatism are subject to similar constraints on both the wintering and breeding grounds as species that do have distinct ASY and SY plumages (Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989, Wunderle 1995), differential migration by age class should not be unexpected for these species.

In females also, there was a tendency for ASYs to arrive earlier than SYs. Like males, females may be subject to intrasexual competition for breeding resources (Krebs 1971, von Haartman 1971). They also may be subject to competition for territories and food resources on the wintering grounds (Rappole and Warner 1980, Greenberg 1986, Holmes et al. 1989). Thus, the selective pressures and other factors that have been proposed to affect arrival times of males also are likely to affect females. However, the difference between ASY and SY female mean capture dates was significantly less than the difference between ASY and SY male mean capture dates, suggesting these pressures are weaker for fe-

males. This could be related to male-biased sex ratios on the breeding grounds. For example, in a two-year study of a Baltimore Oriole (*Icterus galbula*) population, Flood (1984) found that there were considerably fewer females than males during both years and that all females and adult males bred, while only a third of the SY males bred. Male-biased sex ratios also are suggested by the disproportionately higher numbers of male floaters than female floaters in songbird populations (Arvidsson and Klaesson 1984, Sherry and Holmes 1989), and possibly higher mortality rates of females than males (Sherry and Holmes 1989, Woolfenden et al. 2001). As a result, females may be more likely to find a mate, regardless of arrival dates, though not necessarily the best quality male. Thus, the pressure to migrate early may not be as strong for females as it is for males. Also, differences in quality between winter territories of SY and ASY males could be greater than those between SY and ASY females if males are more strongly aggressive or territorial during winter. This could lead to greater differences between age classes for males than females in departure dates from wintering grounds, and thus migration dates.

In this study, the large percentage of unaged birds in some species could bias our conclusions if the aged birds are not representative of the population. However, our analyses indicate that for most species, the unaged birds appeared to be a mixture of both age classes, as would be expected if the aged birds are a representative sample. Furthermore, there was no evidence of a relationship between the proportion of unaged birds and the difference between age classes in migration dates. Thus, although unaged birds could certainly bias analyses of other parameters, such as age ratios, our analyses of differences in migration timing appear to be robust to this problem.

In summary, age-related differential migration in both sexes appears to be widespread among passerines. The constraints that affect passage dates in males with striking plumage differences between age classes apparently similarly affect species with more subtle male plumage differences. There were greater differences between ASY and SY male passage dates than between ASY and SY female pas-

sage dates, which suggests that these factors also may affect females, but to a lesser extent.

ACKNOWLEDGMENTS

We thank Bird Studies Canada for making LPBO data available, and the thousands of volunteers and many staff members over the years who have helped to collect the data. Financial support for the field operations at Long Point has been provided from many sources, including the W. Garfield Foundation, the Ontario Ministry of Natural Resources, and private donations from hundreds of Bird Studies Canada supporters. This project initially was developed as one of the student projects during the Queen's Univ. field course on bird migration, August 1999. We thank all of the participants in the course, as well as J. Jones, C. Fung and F. Francis for support during the course. We also thank S. G. Sealy for comments on the manuscript.

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