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Sex- and age-related differences in post-breeding molt phenology are phylogenetically and ecologically widespread in passerines

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ABSTRACT

Assessment of within-population variation in the timing and duration of molt is crucial to understanding how molt overlaps and interacts with other important phases of the avian annual cycle, including breeding and migration. We investigated the effects of sex and adult age on phenology of the post-breeding prebasic molt in an assemblage of migratory songbird species captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Across all species examined, males consistently initiated molt earlier than females (14 of 15 species), and young adults hatched the previous year consistently initiated molt earlier than experienced older adults (13 of 13 species). Sex also had a weaker but significant effect on molt duration, with females completing molt more rapidly than males in 67% of the species examined. Adult age, in contrast, had no significant effect on molt duration. A review of the literature indicates that similar patterns are observed in the post-breeding molt of passerines worldwide, with females showing delayed but more rapid molt in diverse geographic, phylogenetic, and ecological contexts. The delayed onset of post-breeding molt in female passerines probably reflects either (1) their generally greater reproductive effort in egg-laying, incubation, and brooding of young, or (2) sex-specific physiological constraints imposed by the shared neuroendocrine mechanisms that regulate both avian reproduction and molt. The shorter duration of post-breeding molt in females may partially reflect their smaller body size and shorter flight feathers. Earlier onset of molt in young adults probably reflects their worn retained juvenile plumage, lower probability of successful nesting, and early termination of their initial breeding season. Regardless of the causes, strong sex- and age-based differences in the phenology of post-breeding molt are likely to produce cascading trade-offs with other aspects of the songbird annual cycle, including the timing of breeding, late-season parental care, and migration.

Keywords: age differences, molt, molt-breeding overlap, phenology, passerines, Pimm regression, post-breeding molt, prebasic molt, sex differences, songbirds

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LAY SUMMARY

- Molt, the replacement of feathers in the plumage, is an energetically demanding phase of the avian annual cycle, and its timing and duration can create trade-offs with reproduction, parental care, and migration.
- We examined how sex and adult age affected the timing and duration of the post-breeding molt in migratory songbird species captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA.
- Across all species examined, males and young adults initiate molt consistently earlier than females and older adults, and molt duration is usually shorter in females; a review of the literature indicates that the same patterns are evident worldwide, even among songbird species with widely varying ecologies and evolutionary histories.
- Our results suggest that strong sex- and age-based differences in the timing and duration of post-breeding molt are likely to have cascading implications for parental care, the timing of migration, and other important aspects of the songbird annual cycle.

"Las diferencias relacionadas al sexo y la edad en la fenología de la muda posterior a la reproducción están ampliamente distribuidas filogenética y ecológicamente en los paseriformes"

RESUMEN

La evaluación de la variación intra-poblacional del momento y la duración de la muda es crucial para comprender cómo la muda se superpone e interactúa con otras fases importantes del ciclo anual de las aves, incluida la reproducción y la migración. Investigamos los efectos del sexo y la edad adulta en la fenología de la muda prebásica posterior a la reproducción en un conjunto de especies de aves canoras migratorias capturadas durante

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sesiones de anillado en el Centro de Investigaciones de Aves Powdermill, en el suroeste de Pensilvania, EE. UU. En todas las especies examinadas, los machos iniciaron la muda consistentemente antes que las hembras (14 de 15 especies), y los adultos jóvenes nacidos el año anterior iniciaron la muda consistentemente antes que los adultos de más edad y experiencia (13 de 13 especies). El sexo también tuvo un efecto más débil pero significativo en la duración de la muda, con las hembras completando la muda más rápido que los machos en el 67% de las especies examinadas. La edad adulta, en contraste, no tuvo un efecto significativo en la duración de la muda. Una revisión de la literatura indica que se observan patrones similares en la muda posterior a la reproducción en paseriformes de todo el mundo, con hembras que muestran una muda retrasada pero más rápida en diversos contextos geográficos, filogenéticos y ecológicos. El inicio retrasado de la muda posterior a la reproducción en las hembras paseriformes probablemente refleje (1) su mayor esfuerzo reproductivo en la puesta de huevos, incubación y crianza de los polluelos, o (2) restricciones fisiológicas específicas del sexo impuestas por los mecanismos neuroendocrinos compartidos que regulan tanto la reproducción como la muda en las aves. La menor duración de la muda posterior a la reproducción en las hembras puede reflejar en parte su menor tamaño corporal y sus plumas de vuelo más cortas. El inicio más temprano de la muda en adultos jóvenes probablemente refleje su plumaje juvenil retenido desgastado, una menor probabilidad de anidación exitosa y la finalización temprana de su primera temporada reproductiva. Independientemente de las causas, las marcadas diferencias basadas en sexo y edad en la fenología de la muda posterior a la reproducción probablemente produzcan compensaciones en cascada con otros aspectos del ciclo anual de las aves canoras, incluido el momento de la reproducción, el cuidado parental de fin de temporada y la migración.

Palabras clave: aves canoras, diferencias de edad, diferencias de sexo, fenología, muda, muda prebásica, muda posterior a la reproducción, paseriformes, regresión de Pimm, superposición entre muda y reproducción

INTRODUCTION

Molt is a nutritionally and energetically demanding stage of the avian annual cycle (Murphy and King 1992, Lindström et al. 1993, Jenni and Winkler 2020). Because loss and replacement of flight feathers can also produce substantial deficits in flight performance (Swaddle and Witter 1997, Hedenström 2023), the timing of molt is crucial in reducing potential conflict with two other challenging phases of the annual cycle, breeding and migration. Molt phenology is especially important in species with a complete post-breeding molt, which creates the potential for overlap and trade-offs between molt and the end of nesting and post-fledging parental care (Svensson and Nilsson 1997, Hemborg 1999, Mumme 2018). In migratory species, the phenology of post-breeding molt can also create trade-offs with migration, including impacts on the date of migratory departure and stopover behavior (Stutchbury et al. 2011, Mitchell et al. 2012).

Within-population variation in the phenology of post-breeding molt introduces additional complications, as the potential overlap and interactions with late-season nesting, parental care, and migration will vary for different subsets of a population. Two major sources of within-population heterogeneity in molt phenology are sex and adult age (Jenni and Winkler 2020). Sex differences in the phenology of post-breeding molt are well documented; in passerines, the most frequently reported pattern is that the molt of females is delayed and of shorter duration than that of males (e.g., Ligon and White 1974, Rimmer 1988, Voelker 2000, Strinella et al. 2011), but exceptions also have been reported (Bonnevie and Oschadleus 2010, Gow and Stutchbury 2013). The earlier post-breeding molt of males frequently results in a sex-specific trade-off between molt and late-season parental care, as molting males in several species may desert late-season nestlings and fledglings, leaving females solely responsible for all remaining parental care (e.g., Nolan 1978, Morton and Morton 1990, Hemborg 1999, Mumme 2018). In migratory species, the typically earlier molt of males also has potential implications for sex differences in the timing of migration (e.g., Briedis et al. 2019).

The effects of adult age on the phenology of post-breeding molt have been less frequently investigated, but in passerines some evidence indicates that yearling adults that hatched the previous year and have just gone through their first breeding season initiate molt earlier than experienced older adults (e.g., Snow 1969, Bancroft and Woolfenden 1982, Newton and Rothery 2005, Hegelbach 2014). Early molt may occur more frequently in yearlings because they are often less likely to obtain territories or mates in their initial breeding season (e.g., Bancroft and Woolfenden 1982, Smith and Arcese 1989) or less likely to attempt late second broods (e.g., Bulluck et al. 2013, Woodworth et al. 2017). Furthermore, yearlings often have more heavily worn plumage than older adults (Hegelbach 2014, Jenni and Winkler 2020, Pyle 2022), and this may place an additional premium on earlier molt, potentially altering conflicts and trade-offs with the end of their initial nesting season, parental care, and migration.

Overall, however, the extent of sex- and age-based variation in the phenology of post-breeding molt is difficult to assess, for two reasons. First, studies of molt phenology have used widely varying methodologies and statistical approaches that are subject to their own particular types of sampling and analytical bias (Pimm 1976, Underhill and Zucchini 1988, Boersch-Supan et al. 2024, Mumme et al. 2025a), complicating interpretation of the published literature. For example, recent work has shown that the widely used maximum likelihood methods of Underhill and Zucchini (1988) (Erni et al. 2013, Scott and Underhill 2024) can produce biased and inaccurate estimates of molt phenology under molt-dependent sampling bias, which appears to be common and occurs whenever molt status affects capture probability (Boersch-Supan et al. 2024, Mumme et al. 2025a). Second, reporting bias is also likely to be a problem, as studies that find no evidence of sex- or age-based variation in the phenology of molt may be less likely to be written or published. What is needed, therefore, are investigations that examine the effects of sex and adult age on molt phenology by applying a consistent and unbiased methodology to a large multi-species sample. Here, we provide such a study; using long-term data collected at Powdermill Avian Research Center in the northeastern United States, we document sex- and age-based variation in the phenology of post-breeding molt for a large assemblage of migratory songbird species. To place our study in its global context, we also compare our findings to those that emerge from a comprehensive review of the literature on the effects of sex on post-breeding molt in passerines.

METHODS

Collection of Molt Data

Molt data analyzed for this study were collected from 1986 to 2004 in conjunction with year-round mist-netting and bird-banding operations at Powdermill Avian Research Center

(40.1637°N, 79.2674°W), the field station of Carnegie Museum of Natural History, in southwestern Pennsylvania, USA. After identifying each captured individual to species and banding it with a uniquely numbered U.S. Bird Banding Laboratory band, we determined its sex using either plumage characteristics (for sexually dimorphic species) or the presence of a brood patch or cloacal protuberance. Adults were age-classified as either SY (second-year birds hatched the previous calendar year) or ASY (after-second-year birds hatched two or more calendar years ago), based on wing molt limits (Mulvihill 1993) and other plumage criteria that have since become standard in passerine aging (Pyle 2022). Each individual was then assigned a total flight-feather molt score (0–90) based on the molt stage of the 18 remiges (9 primaries and 9 secondaries) on the right wing. We used the 0–5 molt scoring system of Ginn and Melville (1983): 0 = old feather, 1 = old feather missing or new pin feather, 2 = new feather emerging from sheath up to one-third grown, 3 = new feather between one-third and two-thirds grown, 4 = new feather more than two-thirds grown but still sheathed at base, and 5 = fully grown new feather with no trace of the sheath at its base. All assignments of sex, age, and molt score were performed by a single individual. In the present study, we focused on species that undergo a complete post-breeding prebasic molt on their breeding grounds and excluded individuals that showed evidence of partial or suspended molts.

Our analysis of sex differences was limited to species with at least 25 records of known-sex individuals in active molt (i.e., with molt scores 1–89). In addition, we selected species with at least some data from birds recaptured and re-scored during the same molt cycle, as data from recaptured individuals greatly improves estimation of molt phenology (Boersch-Supan et al. 2024, Mumme et al. 2025a). A total of 15 species representing 5 families, all passerines that are either completely (13 species) or partially migratory (2 species), met these criteria for inclusion. Total sample size available for analysis of sex differences was 2,470 molt records—1,251 from males and 1,219 from females.

Similarly, the dataset for our analysis of age differences was based on species for which there was at least some recapture data and at least 25 records of actively molting known-age adults classified as SY or ASY. Thirteen species representing 5 families, all passerines that at Powdermill are completely migratory, met these criteria for inclusion, and the final dataset comprised 1,552 molt records—749 from SY birds and 803 from ASY individuals.

Statistical Analysis

Flight-feather molt in most temperate-zone passerines is a nonlinear sigmoidal process; it progresses gradually at the beginning and end of molt, when only a few flight feathers are being replaced, but more rapidly during intermediate stages, when multiple flight feathers are being replaced simultaneously (Dawson and Newton 2004, Newton 2009, Mumme et al. 2021, Guallar and Quesada 2023). To help linearize the molt process and make it more amenable to statistical modeling, we followed Mumme et al. (2025a) by transforming total molt scores as arcsine (square root[molt score/90]), and then rescaling the resulting transformed values as a proportion between 0 and 1. Using this transformed molt index, we then estimated molt start and molt duration separately for the 4 sex and age categories—males, females, SY birds, and ASY birds—using the mixed-model extension of Pimm regression (Pimm 1976) developed by Mumme et al. (2025a). In this approach, ordinal capture date (the dependent y variable) is regressed on the transformed molt index (the independent x variable), and bird-year—the unique band number coupled with the year captured—is included as a random effect to account for the non-independence arising from multiple measures of molt obtained from the same individual during a single molt cycle. This mixed-model extension of Pimm regression, which allows molt duration and start date to be estimated directly from the slope and intercept of the resulting regression equation, is the most appropriate method for analyzing the Powdermill data; it is unaffected by molt-dependent sampling bias, which is pronounced in the Powdermill data, and produces accurate and unbiased estimates of molt phenology whenever molt data are collected across a broad range of dates (Mumme et al. 2025a).

We examined the statistical effects of sex on molt phenology by additional Pimm mixed models in which sex, and the interaction between sex and transformed molt index, were included as fixed effects. We interpreted significant main effects of sex on ordinal date as evidence of sex-based differences in the onset of molt, and significant interactions between sex and transformed molt index as evidence of sex-based differences in molt duration. We used comparable mixed models that included age, and its interaction with transformed molt index, to test the effects of adult age on molt phenology. All mixed models were built using JMP Pro 17.2 (SAS Corporation, Cary, NC USA).

To control for phylogenetic effects in across-species comparisons, we used R version 4.4.2 (R Core Team 2024) and the R packages *ape* 5.8.1 (Paradis and Schliep 2019) and *phytools* 2.4-4 (Revell 2024) to incorporate appropriate evolutionary trees and calculate phylogenetic correlation coefficients and phylogenetic matched-pairs *t*-tests. Trees were based on data drawn from birdtree.org (Jetz et al. 2012) and a multilocus phylogeny of the Parulidae (Lovette et al. 2010), and branch lengths were estimated using the modified Grafen method (Revell 2024).

Quantitative Literature Review

To provide global context for our Powdermill data, we performed a comprehensive and quantitative review of the published literature on the effects of sex on the phenology of post-breeding molt in passerines. In our review, we searched for and included studies of post-breeding molt that reported at least 1 of the following variables of interest: (1) was female molt delayed relative to that of males? (yes or no), (2) did females complete molt more rapidly than males? (yes or no), (3) the difference (in days) between the onset of female molt and the onset of male molt, and (4) the percentage difference between females and males in molt duration. In total, our literature review encompassed 60 studies of 51 species representing 23 passerine families, although sample size for any given variable of interest was smaller (range: 46–51 studies) as not all reviewed studies provided complete data. We quantitatively summarized the results by calculating either overall percentage (variables 1–2) or mean ± SD difference (variables 3–4).

Although we attempted a similar literature review on the effects of adult age on molt phenology, too few relevant studies were found for meaningful quantitative analysis; consequently, this literature is treated qualitatively in the Discussion.

RESULTS

Estimation of Molt Parameters and Model Fit

Molt parameters estimated from Pimm mixed-model regression generally provided excellent statistical and visual fit to the observed Powdermill molt data, and accurately reflected the molt trajectories of individual birds captured multiple times during the same molt cycle (Figure 1, Supplementary Material Figures S1–S28). The estimated mean dates of molt initiation showed considerable interspecific, intersexual, and age-related variation (Tables 1 and 2)—for example, ranging from 14 Jun in male *Parkesia motacilla* (Louisiana Waterthrush) to 11 Sep in female *Spinus tristis* (American Goldfinch). Estimates of molt duration also varied widely (Tables 1 and 2)—for example, from 43 days for female and SY *Setophaga petechia* (Yellow Warbler) to 91 days for SY *Pheucticus ludovicianus* (Rose-breasted Grosbeak).

Sex Differences in Molt Phenology

Although male and female dates of molt initiation were highly correlated across species (phylogenetic correlation coefficient $r = 0.98$, $P < 0.001$; Figure 2A), females initiated molt later than males in 14 of the 15 species examined, significantly so in 10 species (Table 1). Across all 15 species, the mean ± SD date of female molt initiation was 7.3 ± 4.7 days later than that of males (phylogenetic paired t-test $t = 6.32$, df = 12, $P < 0.001$).

Duration estimates for males and females were also highly correlated across species (phylogenetic $r = 0.97$, $P < 0.001$), but were shorter for females than for males in 10 of the 15 species, significantly so in 4 species (Table 1). Across all 15 species, estimated molt duration was 2.7 ± 4.6 days shorter (4.3 ± 8.3% shorter) in females than in males (phylogenetic paired t-test $t = 2.36$, df = 12, $P = 0.036$; Figure 3A).

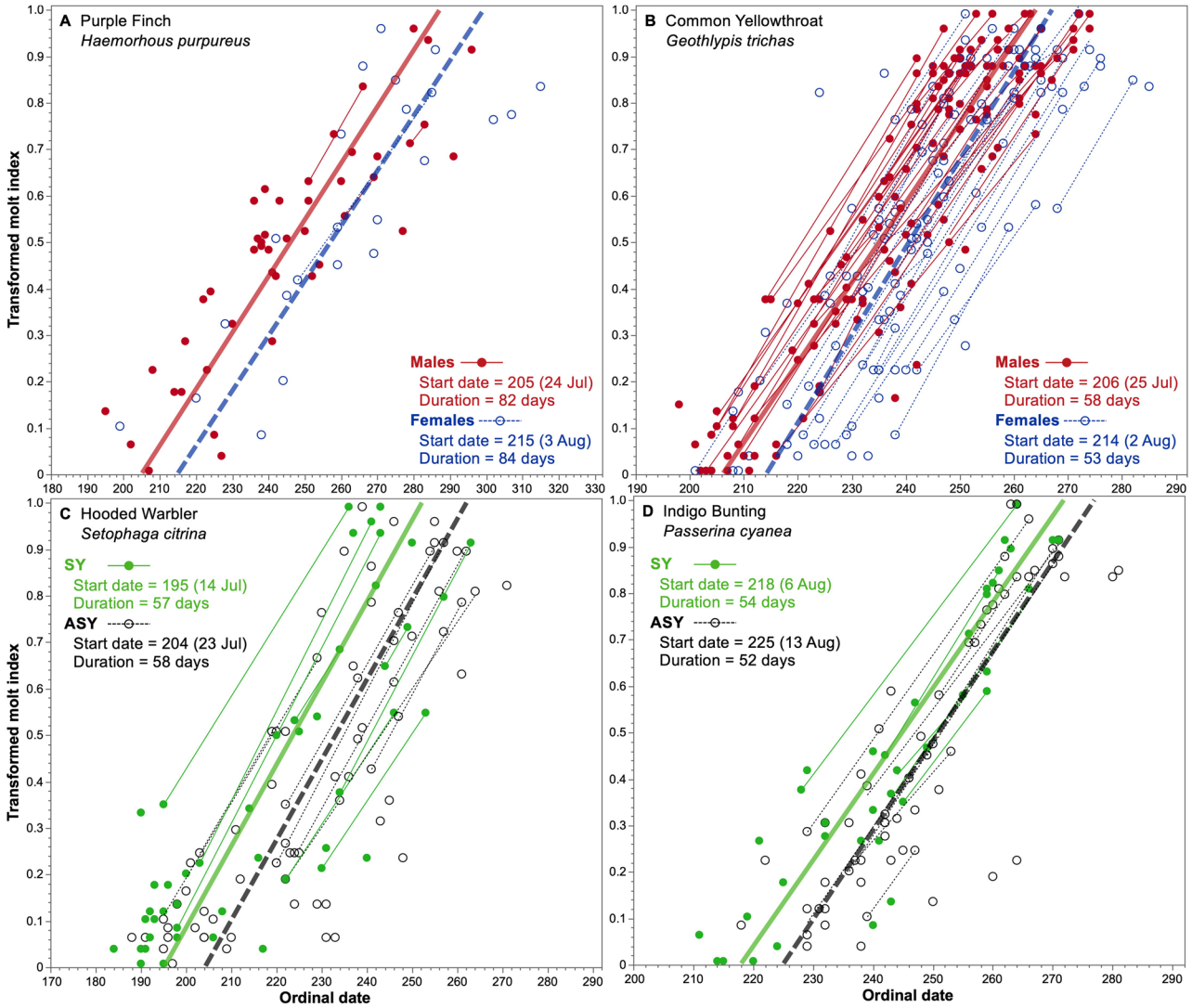

FIGURE 1. Selected examples of the effects of sex (panels **A** and **B**) and age (panels **C** and **D**) on molt phenology of 4 migratory songbird species captured during active molt at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Thin lines represent the molt trajectories of individual birds recaptured during the same molt cycle. Heavy lines represent the mean molt trajectories of males and females (panels **A** and **B**) or second-year (SY) and after-second-year (ASY) individuals (panels **C** and **D**) as estimated by mixed-model Pimm regression. Plots for all species examined are provided in the Supplementary Material Figures S1–28.

TABLE 1. Sex differences in the estimated start date and duration of flight-feather molt in 15 species of migratory passerines examined during active molt at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Parameter estimates for males and females, and statistical significance of sex differences, determined from Pimm mixed-model regressions. For each species the 4-letter codes used in Figures 2 and 3 are also shown.

Species	Molt parameter	Males (mean ± SE)	Females (mean ± SE)	F	P
Vireo griseus	Start	20 Jul ± 3 days	24 Jul ± 2 days	$F_{1,32.3} = 1.20$	0.28
White-eyed Vireo (WEVI)	Duration	62 ± 3 days	62 ± 2 days	$F_{1,30.0} = 0.00$	0.96
Catharus fuscescens	Start	10 Jul ± 1 days	12 Jul ± 1 days	$F_{1,54.9} = 5.23$	0.026*
Veery (VEER)	Duration	44 ± 2 days	48 ± 2 days	$F_{1,55.0} = 0.10$	0.75
Haemorhous purpureus	Start	24 Jul ± 3 days	3 Aug ± 8 days	$F_{1,62.0} = 8.94$	0.004*
Purple Finch (PUFI)	Duration	82 ± 6 days	84 ± 13 days	$F_{1,3.8} = 1.96$	0.24
Spinus tristis	Start	1 Sep ± 1 days	11 Sep ± 1 days	$F_{1,200.9} = 92.3$	<0.001*
American Goldfinch (AMGO)	Duration	66 ± 2 days	61 ± 3 days	$F_{1,516.0} = 2.25$	0.13
Seiurus aurocapilla	Start	7 Jul ± 1 days	4 Jul ± 2 days	$F_{1,71.5} = 0.44$	0.51
Ovenbird (OVEN)	Duration	52 ± 1 days	58 ± 2 days	$F_{1,19.7} = 1.26$	0.28
Parkesia motacilla	Start	14 Jun ± 2 days	25 Jun ± 2 days	$F_{1,34.7} = 7.58$	0.009*
Louisiana Waterthrush (LOWA)	Duration	57 ± 4 days	49 ± 2 days	$F_{1,8.0} = 7.68$	0.024*
Vermivora chrysoptera	Start	17 Jun ± 3 days	28 Jun ± 2 days	$F_{1,22.4} = 6.60$	0.017*
Golden-winged Warbler (GWWA)	Duration	58 ± 3 days	48 ± 1 days	$F_{1,8.1} = 6.26$	0.036*
Mniotilta varia	Start	24 Jun ± 2 days	4 Jul ± 2 days	$F_{1,81.5} = 20.6$	<0.001*
Black-and-white Warbler (BAWW)	Duration	55 ± 3 days	58 ± 2 days	$F_{1,37.2} = 1.21$	0.28
Geothlypis formosa	Start	7 Jul ± 3 days	12 Jul ± 2 days	$F_{1,49.7} = 0.70$	0.41
Kentucky Warbler (KEWA)	Duration	58 ± 5 days	51 ± 2 days	$F_{1,26.6} = 2.20$	0.15
Geothlypis trichas	Start	25 Jul ± 1 days	2 Aug ± 1 days	$F_{1,185.4} = 16.2$	<0.001*
Common Yellowthroat (COYE)	Duration	58 ± 1 days	53 ± 1 days	$F_{1,108.5} = 14.6$	<0.001*
Setophaga citrina	Start	13 Jul ± 2 days	22 Jul ± 1 days	$F_{1,127.1} = 8.99$	0.003*
Hooded Warbler (HOWA)	Duration	58 ± 2 days	55 ± 1 days	$F_{1,32.5} = 0.80$	0.38
Setophaga ruticilla	Start	20 Jun ± 1 days	3 Jul ± 1 days	$F_{1,511.1} = 149.7$	<0.001*
American Redstart (AMRE)	Duration	52 ± 1 days	50 ± 1 days	$F_{1,96.8} = 2.86$	0.09
Setophaga petechia	Start	22 Jun ± 2 days	24 Jun ± 2 days	$F_{1,59.5} = 0.01$	0.94
Yellow Warbler (YEWA)	Duration	46 ± 2 days	43 ± 1 days	$F_{1,8.9} = 0.67$	0.44
Pheucticus ludovicianus	Start	1 Jul ± 2 days	8 Jul ± 3 days	$F_{1,42.4} = 2.25$	0.14
Rose-breasted Grosbeak (RBGR)	Duration	85 ± 3 days	78 ± 5 days	$F_{1,121.0} = 1.67$	0.20
Passerina cyanea	Start	9 Aug ± 1 days	21 Aug ± 2 days	$F_{1,151.7} = 30.2$	<0.001*
Indigo Bunting (INBU)	Duration	53 ± 1 days	47 ± 2 days	$F_{1,86.0} = 25.9$	<0.001*

*indicate statistically significant sex differences.

Age Differences in Molt Phenology

Estimated dates of molt initiation were highly correlated for SY and ASY individuals across species (phylogenetic $r = 0.99$, $P < 0.001$; Figure 2B), and ASY birds initiated molt later in all 13 species examined, significantly so in 9 species (Table 2). On average, ASY birds initiated molt 5.7 ± 3.3 days later than SY individuals (phylogenetic paired t-test $t = 3.55$, df = 10, $P = 0.005$). The generally later onset of molt in ASY birds is also evident from 20 individual *Setophaga ruticilla* (American Redstart), 10 males and 10 females, initially captured and scored as SY before being recaptured as ASY in a subsequent year. We estimate that these 20 individuals initiated molt 8.8 ± 15.2 days later as ASY birds than as SY birds (Figure 4).

Estimates of molt duration for SY and ASY birds were highly correlated across species (phylogenetic $r = 0.96$, $P < 0.001$), but overall, the 2 age classes did not differ in molt duration (phylogenetic paired t-test $t = 0.99$, df = 10, $P = 0.35$; Figure 3B); significant age-related differences in molt duration were detected in only one species, *Vireo griseus* (White-eyed Vireo; Table 2). On average, across all 13 species, molt duration was 0.4 ± 5.1 days shorter (0.1 ± 9.0% shorter) in ASY birds than in SY birds.

Quantitative Literature Review

Our review of the published literature on passerine molt (Supplementary Material Table S1) reveals strong sex differences in the timing and duration of post-breeding molt that are strikingly similar, both qualitatively and quantitatively, to the sex differences in molt phenology we observed in the Powdermill data; females initiate molt later but complete molt sooner in the great majority of published studies (Table 3).

DISCUSSION

Three main conclusions can be drawn from our study. First, the initiation of post-breeding prebasic molt is strongly and significantly influenced by both sex and adult age in a large sample of migratory passerine species from eastern North America; males initiate molt consistently earlier than females, and young SY (second year) adults—birds embarking on their first complete molt—initiate molt consistently earlier than older ASY (after second year) adults (Figure 2). Second, sex has a weaker but nonetheless significant effect on molt duration, with females usually completing molt more rapidly than earlier-molting males. Adult age, in contrast, has no consistent or significant effect on molt duration (Figure 3). Third, a comprehensive review of the literature on passerines that undergo a complete post-breeding molt shows that strikingly similar patterns of sex differences in molt phenology occur globally, with females showing delayed but more rapid molt in a substantial majority of cases (Table 3, Supplementary Material Table S1).

TABLE 2. Age differences in the estimated start date and duration of flight-feather molt in 13 species of migratory passerines examined during active molt at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Parameter estimates for second-year (SY) and after-second-year (ASY) individuals, and statistical significance of age differences, determined from Pimm mixed-model regressions.

Species	Molt parameter	SY (mean ± SE)	ASY (mean ± SE)	F	P
Vireo griseus	Start	17 Jul ± 2 days	31 Jul ± 3 days	$F_{1,36.5} = 7.48$	0.010*
White-eyed Vireo (WEVI)	Duration	65 ± 1 days	53 ± 3 days	$F_{1,18.9} = 21.0$	<0.001*
Dumatella carolinensis	Start	29 Jul ± 2 days	1 Aug ± 2 days	$F_{1,94.6} = 12.1$	<0.001*
Gray Catbird (GRCA)	Duration	49 ± 3 days	55 ± 3 days	$F_{1,86.3} = 0.85$	0.36
Catharus fuscescens	Start	10 Jul ± 2 days	14 Jul ± 2 days	$F_{1,46.8} = 7.26$	0.010*
Veery (VEER)	Duration	44 ± 4 days	47 ± 2 days	$F_{1,58.0} = 0.04$	0.84
Seiurus aurocapilla	Start	2 Jul ± 2 days	8 Jul ± 2 days	$F_{1,68.5} = 2.67$	0.11
Ovenbird (OVEN)	Duration	55 ± 3 days	52 ± 2 days	$F_{1,24.4} = 0.01$	0.91
Vermivora chrysoptera	Start	19 Jun ± 5 days	23 Jun ± 2 days	$F_{1,16.0} = 0.96$	0.40
Golden-winged Warbler (GWWA)	Duration	57 ± 5 days	54 ± 3 days	$F_{1,7.9} = 0.36$	0.56
Mniotilta varia	Start	29 Jun ± 2 days	30 Jun ± 2 days	$F_{1,72.6} = 0.34$	0.56
Black-and-white Warbler (BAWW)	Duration	56 ± 1 days	56 ± 2 days	$F_{1,34.0} = 0.01$	0.93
Geothlypis formosa	Start	9 Jul ± 2 days	14 Jul ± 5 days	$F_{1,27.9} = 3.74$	0.06
Kentucky Warbler (KEWA)	Duration	52 ± 2 days	60 ± 7 days	$F_{1,14.8} = 0.58$	0.46
Geothlypis trichas	Start	25 Jul ± 1 days	30 Jul ± 1 days	$F_{1,166.5} = 9.83$	0.002*
Common Yellowthroat (COYE)	Duration	56 ± 1 days	55 ± 1 days	$F_{1,101.6} = 0.27$	0.60
Setophaga citrina	Start	14 Jul ± 2 days	23 Jul ± 2 days	$F_{1,96.3} = 14.8$	<0.001*
Hooded Warbler (HOWA)	Duration	57 ± 2 days	58 ± 1 days	$F_{1,23.8} = 0.48$	0.50
Setophaga ruticilla	Start	22 Jun ± 1 days	1 Jul ± 1 days	$F_{1,407.4} = 70.6$	<0.001*
American Redstart (AMRE)	Duration	50 ± 1 days	50 ± 1 days	$F_{1,62.8} = 0.08$	0.77
Setophaga petechia	Start	21 Jun ± 1 days	24 Jun ± 2 days	$F_{1,45.8} = 5.88$	0.019*
Yellow Warbler (YEWA)	Duration	43 ± 1 days	45 ± 3 days	$F_{1,11.2} = 0.40$	0.54
Pheucticus ludovicianus	Start	27 Jun ± 2 days	3 Jul ± 2 days	$F_{1,61.0} = 5.05$	0.028*
Rose-breasted Grosbeak (RBGR)	Duration	91 ± 5 days	86 ± 6 days	$F_{1,61.0} = 0.47$	0.50
Passerina cyanea	Start	6 Aug ± 2 days	13 Aug ± 1 days	$F_{1,79.0} = 9.44$	0.003*
Indigo Bunting (INBU)	Duration	54 ± 2 days	52 ± 1 days	$F_{1,20.1} = 0.93$	0.35

*indicate statistically significant age differences.

The widespread sex and age differences in passerine molt phenology that we have documented are likely to have cascading implications for other life-history traits, such as the timing of breeding, late-season parental care, and migration phenology. For example, the earlier molt of SY individuals nesting for the first time may reflect failure to obtain a territory or mate or a shorter duration of their initial nesting season, with reduced probabilities of late renesting and double brooding (Smith and Arcese 1989, Geupel and DeSante 1990, Evans Ogden and Stutchbury 1996, Mulvihill et al. 2009, Woodworth et al. 2017). In migratory passerines, the earlier molt of SY birds could also lead to an early migratory departure (e.g., Stutchbury et al. 2011), a difference in migration phenology that would be difficult to detect because plumage-based distinctions between SY and ASY adults are typically erased once molt is completed (Pyle 2022). The earlier onset of molt in males is linked to male desertion of late-season nestlings and fledglings in at least some passerines (Hemborg 1999, Mumme 2018, Harrod and Mumme 2021), and circumstantial evidence suggests that molt-associated male desertion is probably widespread but often overlooked (Nolan 1978, Ezaki 1988, Morton and Morton 1990). Finally, under some circumstances the short-duration molt of females could potentially compromise feather quality, which can have negative consequences for future thermoregulatory ability, flight performance, and survival (Dawson et al. 2000, de la Hera et al. 2010, Vágási et al. 2012).

Sex Differences in Molt Phenology

Our finding that the sexes differ consistently in both the onset and duration of the post-breeding molt (Table 1, Figures 1A and 2A) is primarily based on data for 15 migratory passerine species from a single location, Powdermill Avian Research Center, in southwestern Pennsylvania, USA. However, our review of the passerine literature (Table 3) shows that similar sex differences in the onset and duration of post-breeding molt are found in diverse phylogenetic, geographical, and ecological contexts (Supplementary Material Table 1), and are not restricted to northern temperate migratory species like those in the Powdermill dataset (Tables 1 and 2). For example, the list of species where the post-breeding molt of females begins later than that of males includes cooperatively breeding jays (Ligon and White 1974, Bancroft and Woolfenden 1982), tropical frugivores (Kamtaeja et al. 2015, Nwaogu et al. 2019), a South African nectarivore that initiates post-breeding molt during the lengthening days of the austral spring (*Anthobaphes violacea* [Orange-breasted Sunbird]; Bonnevie and Oschadleus 2010, Cheke and Mann 2020), and a promiscuous, non-territorial, temperate-zone sparrow where males play no role in parental care (*Ammodramus caudacutus* [Saltmarsh Sparrow]; Borowske et al. 2017). Clearly, the passerine-typical pattern of delayed post-breeding molt in females requires a general explanation—one that does not rely on the particular ecologies, life histories, and social systems of individual species.

We propose two hypotheses for why the post-breeding molt of female passerines is usually delayed. First, as previously suggested by others (Rimmer 1988, Hemborg 1999, Serra et al. 2010), the generally greater parental effort by females over the course of the nesting season may account for their delayed molt, as parental investment in egg-laying, incubation of eggs, and brooding of young is strongly female-biased in passerines

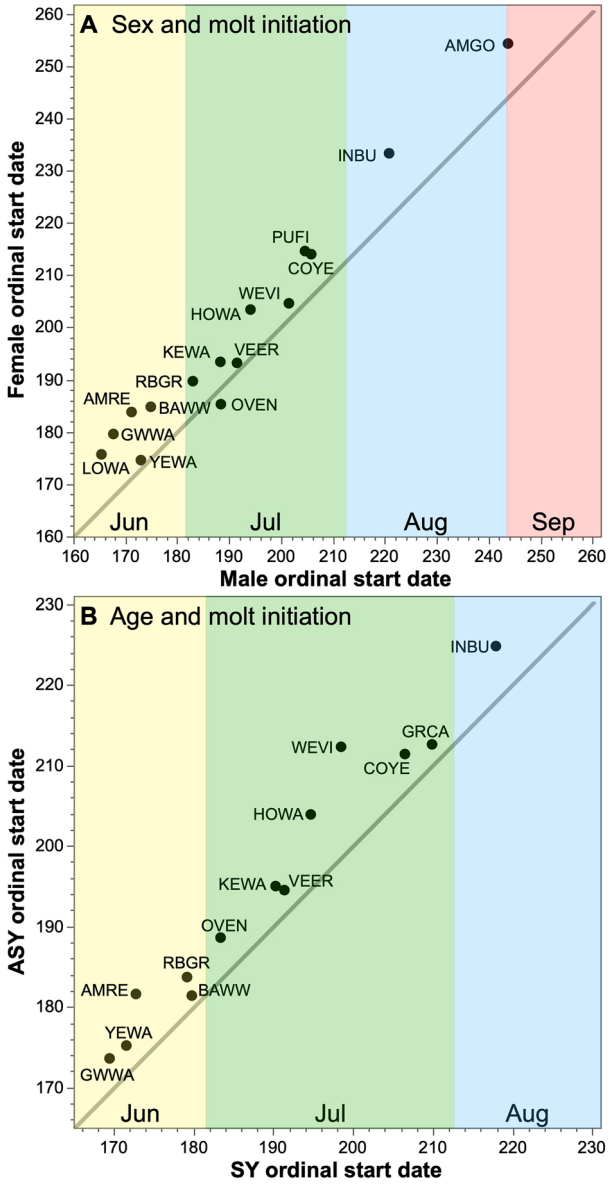

FIGURE 2. Despite considerable interspecific variation in the timing of flight-feather molt initiation, females consistently begin molt later than males (**A**), and ASY (after-second-year) adults consistently initiate molt later than SY (second-year) adults (**B**). Data derived from migratory passerines captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA. In both panels the diagonal line indicates the expected values under the null hypothesis of no difference between the sexes (**A**) and ages (**B**); points above the line indicate species where females initiate molt later than males (**A**) or species where ASY birds initiate molt later than SY individuals (**B**). Each species is identified by the 4-letter codes shown in Tables 1 and 2.

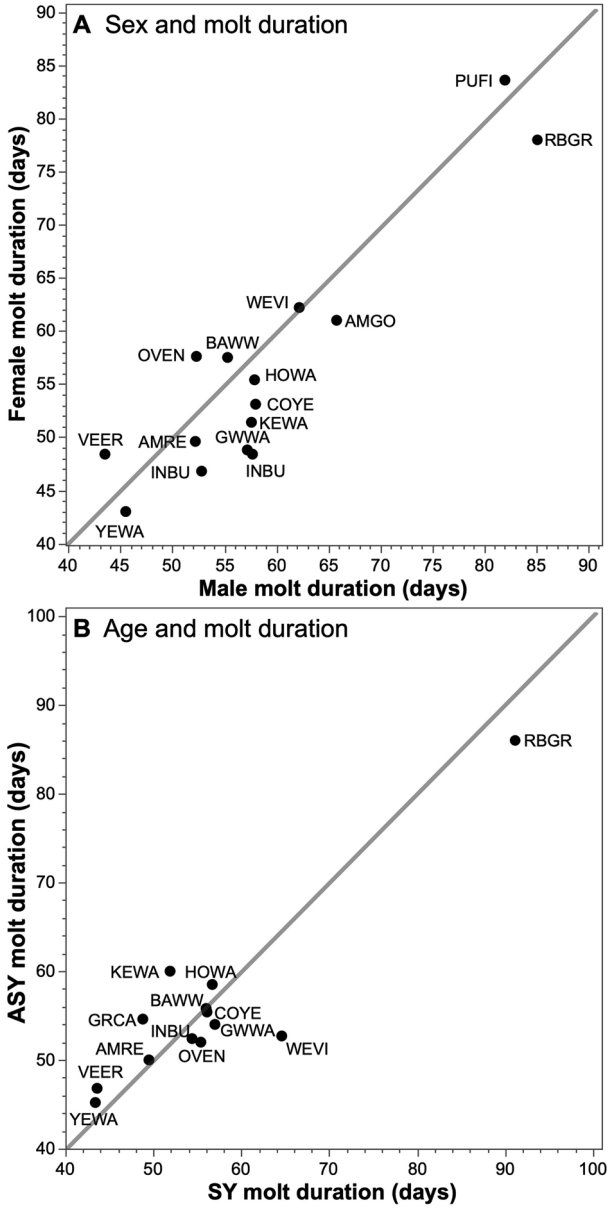

FIGURE 3. Although molt duration varies considerably among species, sex (**A**) has modest but statistically significant effects on molt duration, and adult age (**B**) has no effect. Data derived from migratory passerines captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA. In both panels, the diagonal line indicates the expected values under the null hypothesis of no difference between the sexes (**A**) and ages (**B**); points below the line indicate species where females molt more rapidly than males (**A**) or species where ASY (after-second-year) birds molt more rapidly than SY (second-year) individuals (**B**). Each species is identified by the 4-letter codes shown in Tables 1 and 2.

and may mandate additional physiological recovery time before transitioning from breeding to the prebasic molt.

Second, it is also possible that the delayed onset of post-breeding molt in female passerines is a constraint or incidental byproduct of fundamental differences between the sexes in reproductive endocrinology (Ketterson and Nolan 1999); many of the hormones that regulate breeding and parental care are also involved with post-breeding molt. For example, the peptide hormone prolactin plays multiple roles in parental care (Smiley 2019), but decreasing prolactin levels also have been implicated as a key factor in the timing of molt initiation (Dawson 2006, 2008). If the different reproductive roles played by females and males during nesting result in different expression patterns of either prolactin or prolactin receptor proteins late in the breeding season, as some evidence suggests (Ketterson et al. 1990, Farrar et al. 2022, Li et al. 2022), delayed post-breeding molt in females could be an incidental byproduct of sex differences in late-season prolactin or receptor profiles.

Possible support for this endocrinological constraint hypothesis comes from *Cygnus olor* (Mute Swan), a non-passerine

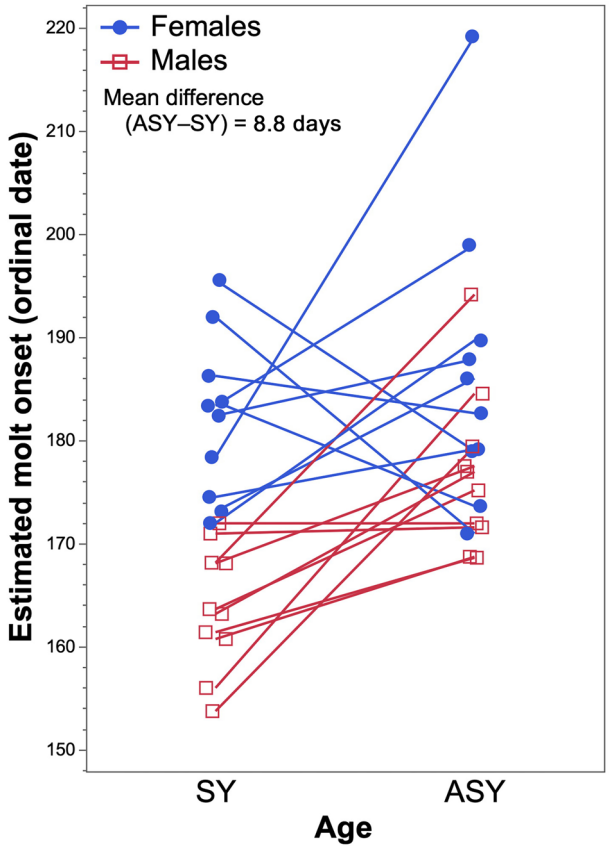

FIGURE 4. Twenty individual *Setophaga ruticilla* (American Redstart) on average initiated molt earlier as young SY (second year) adults than as older ASY (after second year) adults. Molt initiation dates were estimated by using the calculated mean duration of molt for this species (Table 1) and the transformed molt score index for each individual when captured. For reference, ordinal date 182 corresponds to 1 July. In a general linear mixed model in which each individual's unique band number was included as a random effect, sex ($F_{1,18} = 30.0$, $P < 0.001$) and age ($F_{1,18} = 7.0$, $P = 0.017$) both had significant effects on the estimated date of molt onset, but the sex × age interaction was not significant ($F_{1,18} = 1.6$, $P = 0.22$). Points are jittered against the *x*-axis to reduce overplotting.

timing of post-breeding molt, and how those mechanisms interact with nesting and post-nesting parental care, is an area where additional research is clearly needed (Dawson 2008).

We also found a weaker but significant relationship between sex and molt duration, with females completing post-breeding molt more rapidly than males in about two-thirds of the cases in both the Powdermill dataset and in our review of the literature (Table 3). In species breeding in the temperate zone, shorter duration of female molt is sometimes interpreted as a mechanism to compensate for its delayed start, thereby allowing females to complete molt either before the onset of deteriorating ecological conditions (e.g., reduced food availability; Orell and Ojanen 1980, Serra et al. 2010) or without undue delay to the onset of migration (Ryder and Rimmer 2003). Consistent with this interpretation, experimental evidence indicates that shortening of photoperiod often accelerates the pace of molt (Dawson 2004, Serra et al. 2010, Vágási et al. 2012). However, it is worth noting that a shorter duration of female molt has also been observed in some non-migratory species that initiate molt well before the summer solstice (e.g., *Gymnorhinus cyanocephalus* [Pinyon Jay] and *Apalis thoracica* [Bar-throated Apalis]; Ligon and White 1974, Bonnevie and Oschadleus 2010), when days are lengthening and there is no obvious ecological constraint that would put a premium on accelerated female molt. It is therefore worth considering other factors that might also explain why the post-breeding molt of female passerines is often of shorter duration than that of males.

One additional factor that may contribute to the generally shorter duration of female molt is simply sexual size dimorphism in wing and tail length. With rare exceptions (e.g., Neotropical manakins where short wings and agility are advantageous in male lek displays; Shogren et al. 2022), male passerines typically have wings and tails that average ~5% longer, even in socially monogamous species (Hughes and Hughes 1986, Murphy 2007, Cueto et al. 2015). At Powdermill, wing length is significantly longer in males than females in 70 of 71 passerine species examined (Mulvihill et al. 2004), and the longer flight feathers of males may increase the time required to complete molt (Rohwer et al. 2009, Serra et al. 2010, Bonnevie and Craig 2014). A second factor that may prolong male molt is testosterone, which can slow the pace of molt in at least some circumstances (Schleussner et al. 1985, Kurvers et al. 2008). The relative roles of testosterone and sexual size dimorphism in prolonging male molt merit additional research effort.

TABLE 3. Comparable sex differences in the timing and duration of post-breeding molt are evident in data obtained from both Powdermill Avian Research Center (this study) and from a comprehensive review of the published literature (Supplementary Material Table S1). For each molt statistic, the number of studies, species, and avian families represented are also shown. Estimates from Powdermill (this study) are based on the number of species, while those from the literature are based on the number of separate studies.

Molt statistic	Data source	Estimate	*n* studies	*n* species	*n* families
Percent of passerine species/studies where female post-breeding molt is delayed relative to males	This study	93%	1	15	5
	Literature review	86%	51	45	20
Mean ± SD delay in female post-breeding molt relative to male molt	This study	7.3 ± 4.7 days	1	15	5
	Literature review	7.6 ± 8.5 days	46	39	19
Percent of passerine species/studies where females complete post-breeding molt more rapidly than males	This study	67%	1	15	5
	Literature review	69%	48	41	19
Mean ± SD percentage by which females complete post-breeding molt more rapidly than males	This study	4.3 ± 8.3%	1	15	5
	Literature review	6.1 ± 11.2%	47	40	18

Age Differences in Molt Phenology

Age differences in the timing of molt initiation were consistently strong among the migratory passerines in the Powdermill dataset; in all 13 species we examined, younger (SY) adults initiated post-breeding molt earlier than older (ASY) birds, on average 5–6 days earlier (Table 2). Two factors may contribute to the early start of SY adults. First, SY individuals are probably less likely to obtain territories or mates, less likely to breed successfully, and less likely to attempt double brooding or late renesting following nest failure (Bancroft and Woolfenden 1982, Smith and Arcese 1989, Bulluck et al. 2013, Woodworth et al. 2017). Early cessation of breeding and parental care is associated with earlier molt in numerous passerines (Stutchbury et al. 2011, Hegelbach 2014, Mumme 2018), and this is likely the major reason for the earlier onset of molt in SY birds. Second, by mid-summer young SY birds are usually in heavily degraded plumage; their retained juvenile flight feathers are typically worn for several weeks longer than the flight feathers of older adults, and the relatively poor condition of their plumage may put a premium on earlier molt (Hegelbach 2014, Jenni and Winkler 2020, Pyle 2022). These two factors are not necessarily mutually exclusive; for example, heavily worn plumage may be a contributing factor as to why SY young adults are often less likely to attempt late renesting or second broods.

Unlike in females, where a late molt start is associated with a shorter molt duration (Table 1), we found no compelling evidence in the Powdermill dataset that ASY birds have an accelerated pace of post-breeding molt relative to SY birds (Table 2); despite the later start of ASY birds and some interspecific variation (Figure 3B), ASY and SY birds were overall nearly identical in mean molt duration. This finding suggests that the generally shorter duration of post-breeding molt in females, discussed in the previous section, is more likely to be a result of sex differences in flight-feather length or reproductive endocrinology, and not directly attributable to the later molt initiation of females.

The published literature on how adult age affects molt phenology is much less extensive than the literature on sex differences, but earlier post-breeding molt by SY birds has been reported in several North American corvids (Pitelka 1945, 1958, Mewaldt 1958, Ligon and White 1974, Bancroft and Woolfenden 1982) and in a smattering of other passerines, including *Cinclus cinclus* (White-throated Dipper; Hegelbach 2014), *Turdus merula* (Eurasian Blackbird; Snow 1969), and *Chloris chloris* (European Greenfinch; Newton and Rothery 2005). Very few previous studies have estimated molt duration for SY and ASY passerines, but strong or consistent differences are absent, with two studies reporting slightly longer durations for SY birds (Samson 1976, Newton and Rothery 2005), one the reverse (Ligon and White 1974), and one reporting no difference (Rimmer 1988).

Conclusions and Future Directions

In this article, we have documented sex- and age-related differences in the phenology of post-breeding molt that are part of a complex interacting web of intrinsic and ecological factors that regulate one of the key events in the passerine annual cycle (Dawson 2008). An additional challenge in understanding post-breeding molt in particular is its frequent partial overlap with the end of breeding, including late-season nesting and post-fledging parental care (Orell and Ojanen 1980, Morton and Morton 1990, Hemborg 1999, Mumme 2018). Because the neuroendocrine mechanisms that appear to regulate the phenology of post-breeding molt are also critical in regulating nesting and parental care (Dawson 2006, 2008), it is likely that molt phenology is subject to neuroendocrine constraints that limit its phenotypic flexibility and potential for adaptive evolution (Ketterson and Nolan 1999). A significant challenge for future work will be to disentangle this complex web of interaction and clarify the degree to which the shared neuroendocrine mechanisms regulating breeding and post-breeding molt constrain molt phenology.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

The data reported here were collected as part of long-term bird-banding operations and related field research at Powdermill Avian Research Center, and authorized under a series of banding permits from the U. S. Bird Banding Laboratory and the Pennsylvania Game Commission.

Conflict of interest statement

The authors declare that they have no conflict of interest.

Author contributions

R.S.M. and D.N. collected, curated, maintained, and provisionally analyzed the Powdermill molt data. All three authors conceived and initiated the project. R.L.M fully analyzed the data and prepared an initial draft of the manuscript, and all three authors contributed to editing and revising the manuscript.

Data availability

The data underlying this manuscript are archived and publicly available at Mumme et al. (2025b).

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