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Prealternate molt intensity and timing in six Nearctic-Neotropical migratory warblers

Intensidad y momento de la muda prealterna en seis reinitas migratorias neárticas-neotropicales

Shae A. Turner [1], *Christopher M. Tonra* [2], *Bryant C. Dossman* [3], *Mateen R. Shaikh* [4], *Ivy A. Ciaburri* [2], *Christina R. Robinson* [5], *Peter P. Marra* [6] and *Matthew W. Reudink* [1]

ABSTRACT. Molt is vital for maintaining year-round feather function yet is one of the least understood events in the annual cycle of migratory birds. In Nearctic-Neotropical migratory songbirds, prealternate molt has received far less study than prebasic molt because it typically occurs during the least studied period of the annual cycle: the stationary nonbreeding period. Improving our basic understanding of prealternate molt is fundamental for identifying how it interacts with other life history stages across the annual cycle. Here, we provide a detailed quantification of the timing and intensity of prealternate molt for six species of parulid warblers on their stationary nonbreeding grounds in Jamaica. We demonstrate that head and body feather molt is common for Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*), and for most species increases in frequency and intensity later in the nonbreeding period. Black-and-white Warbler and American Redstart demonstrated age-specific differences in molt intensity, with greater molt intensity exhibited by first-cycle than definitive-cycle birds. In addition, we provide support for the occurrence of a prealternate molt in Ovenbirds (*Seiurus aurocapilla*). These findings advance our understanding of prealternate molt in the study species and can serve as a foundation for investigating the mechanisms that regulate prealternate molt and potential carry-over effects from the nonbreeding grounds.

RESUMEN. La muda es vital para mantener la función de las plumas durante todo el año, pero es uno de los eventos menos comprendidos en el ciclo anual de las aves migratorias. En los pájaros cantores neárticos-neotropicales, la muda prealterna ha sido estudiada mucho menos que la muda prebásica porque suele ocurrir durante el período menos estudiado del ciclo anual: el período estacionario no reproductivo. Mejorar nuestra básica comprensión de la muda prealterna es fundamental para identificar cómo interactúa con otras etapas de la historia de vida a través del ciclo anual. Aquí, brindamos una cuantificación detallada del momento e intensidad de la muda prealterna para seis especies de parúlidos en sus zonas estacionarias no reproductivas en Jamaica. Demostramos que la muda de plumas de la cabeza y el cuerpo es común para la Reinita charquera norteña (*Parkesia noveboracensis*), Reinita trepadora (*Mniotilta varia*), Candelita norteña (*Setophaga ruticilla*), Parula norteña (*Setophaga americana*) y Reinita galana (*Setophaga discolor*), y para la mayoría de las especies aumenta en frecuencia e intensidad más tarde en el período no reproductivo. La Reinita trepadora y la Candelita norteña demostraron diferencias específicas por edad en la intensidad de la muda, con una mayor intensidad de muda exhibida por aves del primer ciclo que por aquellas del ciclo definitivo. Además, proporcionamos evidencia sobre la ocurrencia de una muda prealterna en las Reinitas horneras (*Seiurus aurocapilla*). Estos hallazgos amplían nuestra comprensión sobre la muda prealterna en las especies estudiadas y pueden servir como base para investigar los mecanismos que regulan la muda prealterna y los posibles efectos de arrastre desde las zonas no reproductivas.

Key Words: *Jamaica; Mniotilta varia; nonbreeding period; Parkesia noveboracensis; Seiurus aurocapilla; Setophaga americana; Setophaga discolor; Setophaga ruticilla; wintering*

INTRODUCTION

An understanding of how life history stages interact across the full annual cycle is needed to effectively conserve declining migratory bird populations (Marra et al. 2015a, Rosenberg et al. 2019). This task is particularly challenging for migratory species whose life history stages are separated temporally and spatially across the annual cycle. Molt, the periodic replacement of feathers, is one stage for which substantial knowledge gaps remain (Bridge 2011, Pyle et al. 2018, Pyle 2022a, Kiat 2023). Understanding aspects of molt strategy, such as the timing and intensity of molt, is imperative given its year-round importance to feather function and its potential to influence subsequent life history stages through seasonal interactions.

Molt is vital to maintaining a myriad of feather functions from flight and movement (Hedenström 2002, Jenni and Winkler 2020a), to thermoregulation (Wolf and Walsberg 2000), visual communication (Hill and McGraw 2006, Santos et al. 2011, Jenni and Winkler 2020a, Terrill et al. 2020), protection from parasites

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[1]Department of Biological Sciences, Thompson Rivers University, Kamloops, BC, Canada, [2]School of Environment and Natural Resources, The Ohio State University, Columbus, OH, USA, [3]The Earth Commons Institute and Department of Biology, Georgetown University, Washington, D. C., USA, [4]Department of Mathematics and Statistics, Thompson Rivers University, Kamloops, BC, Canada, [5]Independent Researcher, Portland, Jamaica, [6]The Earth Commons Institute, Department of Biology, and McCourt School of Public Policy, Georgetown University, Washington, D.C., USA

(e.g., Gunderson et al. 2008), and solar radiation, among others (for a full review of feather function, see Terrill and Shultz 2023). Because molt has a high energetic cost (Lindström et al. 1993), molt in migratory birds is typically scheduled not to overlap with breeding and migration (Barta et al. 2008, Wingfield 2008), two other energetically costly events, though molt strategies vary (Rohwer et al. 2005, for examples see Evans Ogden and Stutchbury 1996, Mulvihill et al. 2009). Some evidence suggests that the timing of molt can carry over to influence birds' migratory timing (e.g., Carlisle et al. 2005, Stutchbury et al. 2011, Kiat and Izhaki 2016), and that conditions experienced prior to molt can influence its timing (e.g., molt initiation date; Danner et al. 2015), and the production of phenotypic plumage traits that may impact individual fitness (e.g., Saino et al. 2004, Sparrow et al. 2017).

Each year, adults of all species of passerines molt most or all contour and flight feathers during the prebasic molt (Humphrey and Parkes 1959), typically occurring after the breeding season in north-temperate resident and Nearctic-Neotropical migratory birds (Pyle 2022b). Some species replace contour feathers a second time in the annual cycle during a prealternate molt, typically occurring prior to the breeding season (Humphrey and Parkes 1959, Pyle 2022b). Prealternate molt is thought to have evolved to maintain feather function in long-distance migratory birds, following which some species have evolved seasonal dichromatism, with males showing more brightly colored alternate feathers than females (Kiat et al. 2019, Terrill et al. 2020, Cuervo et al. 2022). Most Nearctic-Neotropical migratory songbirds are thought to complete prealternate molt on the stationary nonbreeding grounds (hereafter "nonbreeding grounds") prior to prebreeding (northward) migration (Pyle 2022b), though the number of species that employ a prealternate molt-migration may be underestimated (Leu and Thompson 2002, Tonra and Reudink 2018, Wright et al. 2018).

Given that the study of migratory birds has long been biased toward the breeding period and breeding grounds (Marra et al. 2015a, Kiat 2023), it is unsurprising that the study of molt has focused heavily on the prebasic molt, leaving a significant knowledge gap in our understanding of the prealternate molt. Although detailed information is available for the timing and extent of prebasic molt for almost all Nearctic-Neotropical migratory songbirds, such information on prealternate molt ranges from limited to absent (Pyle 2022b). Not only are many descriptions of the timing and extent of prealternate molt lacking detail when compared with the prebasic molt, but for some species the extent (e.g., Black-and-white Warbler *Mniotilta varia*) or occurrence of prealternate molt (e.g., Ovenbird *Seiurus aurocapilla*) remain uncertain. Descriptions of prealternate molt intensity are even more scarce (but see Lefebvre et al. 1992 for molt data September through May, which we interpret to include the prealternate molt). Further, most study of the prealternate molt has focused on wing feather replacement (e.g., Pyle 1997), thus emphasizing species that include wing feathers in their prealternate molt. This bias is likely because prealternate molt limits on passerines can be easily detected on the wings of museum specimens (e.g., Pyle and Carnes 2022) and on birds captured on the breeding grounds (e.g., Crary and Rodewald 2012, Jones et al. 2014, Cimprich 2018, Carnes et al. 2021), prior to the prebasic molt. Once prealternate molt is completed, molt limits between the tiny contour feathers of small birds are challenging to detect in the field, becoming near impossible to detect when replaced alternate feathers are the same color as retained basic feathers. This challenge has likely contributed to a biased focus on prealternate contour feather molt in particular regions of the body that contribute to seasonal dichromatism (e.g., Boone 2006, Boone et al. 2010), leading to a reduced understanding of prealternate molt on other regions of the body. Studying birds in active prealternate molt, whether wild birds captured on the molting grounds (e.g., Lefebvre et al. 1992, Guallar et al. 2009, Mettke-Hofmann et al. 2010, Renfrew et al. 2011, Danner et al. 2015, Wright et al. 2018) or museum specimens (e.g., Rohwer et al. 1983, Jackson et al. 1992, Voelker and Rohwer 1998, Voelker and McFarland 2002, Sieburth and Pyle 2018), allows for greater capacity to accurately quantify the extent or intensity of prealternate contour feather molt but these studies are relatively rare.

Of the 46 Nearctic-Neotropical migratory warbler species (Family: Parulidae), 33 (72%) are thought to have a prealternate molt episode in at least some individuals, and the occurrence of prealternate molt remains uncertain in an additional 5 species (Pyle 2022b). For 8 (24%) of the 33 species thought to have a prealternate molt episode, there is some level of uncertainty in the extent of feathers molted (Pyle 2022b). Aside from Guallar et al. (2009) and recent updates to species molt accounts in *Identification Guide to North American Birds, Part I* (Pyle 2022b), prealternate molt has largely been overlooked in the study of wild Nearctic-Neotropical migratory warblers over the past two decades. A systematic search of scientific papers in The Web of Science yielded only four peer-reviewed papers since the year 2000 that included a field study of prealternate molt in any Nearctic-Neotropical migratory parulid species (conducted June 2024, using the search terms "prealternate moult" or "prealternate molt" alongside each species' common name). Only one of these studies aimed to quantify prealternate molt in all feather groups during active molt: in the Lucy's Warbler (*Leiothlypis luciae*) and Virginia's Warbler (*Leiothlypis virginiae*; Voelker and McFarland 2002). Studies of the Magnolia Warbler (*Setophaga magnolia*; Boone et al. 2010) and Yellow Warbler (*Setophaga petechia*; Quinlan and Green 2011, Crary and Rodewald 2012) aimed to understand links between feathers molted during the prealternate molt and another life history stage, using data collected away from the molting grounds. We know of one additional published study on the Yellow Warbler (Jones et al. 2014) that was not captured by this search.

Collecting detailed information on the timing and intensity of prealternate molt in all areas of the bird's body is the necessary first step to facilitate future study of the mechanisms that regulate prealternate molt, such as body condition, and how prealternate molt interacts with other life history stages. As such, it will be critical to gather fundamental information of how prealternate molt varies across species, age and sex classes, and eventually across the nonbreeding period for individual species. Here, we provide a detailed quantification of the timing and intensity of prealternate molt for six species of parulid warbler on their nonbreeding grounds in Jamaica: Ovenbird, Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler, American Redstart (*Setophaga ruticilla*), Northern Parula

(*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*). This study represents the first quantification of prealternate molt intensity in the Northern Parula and Prairie Warbler and builds upon the work of Lefebvre et al. (1992) and Guallar et al. (2009) for the other species studied. We examine how molt intensity varies across the molting period and test whether molt intensity varies across species, age, and sex classes.

METHODS

Study species

Our study focused on six primarily insectivorous, long-distance, Nearctic-Neotropical migratory species that are commonly captured in Jamaica during their nonbreeding period: Ovenbird, Northern Waterthrush, Black-and-white Warbler, American Redstart, Northern Parula, and Prairie Warbler. Although several of these species have been the subject of extensive research on the nonbreeding grounds (e.g., Lefebvre et al. 1992, Dugger et al. 2004, Studds and Marra 2005, 2007, 2011, Reudink et al. 2009, Smith et al. 2010, 2011, Wilson et al. 2013, Tonra et al. 2014, Marra et al. 2015b, Sherry et al. 2016, Kent and Sherry 2020, Cooper et al. 2021, Powell et al. 2021, Kent et al. 2022, Dossman et al. 2023a, 2024), relatively little is known about their prealternate molt, which has been suggested to occur during this portion of the annual cycle (Guallar et al. 2009, Kricher 2020, Moldenhauer and Regelski 2020, Nolan et al. 2020, Porneluzi et al. 2020, Sherry et al. 2020, Whitaker and Eaton 2020, Pyle 2022b). Guallar et al. (2009) report that Ovenbirds molt continuously from October to April on their nonbreeding grounds in Western Mexico, but whether this molt is part of protracted preformative/prebasic molt or part of a prealternate molt requires confirmation (Porneluzi et al. 2020, Pyle 2022b). At least some individuals of the other five species complete a limited to partial prealternate molt, defined as the replacement of some contour feathers and typically no wing feathers (Pyle 2022b).

Study site

We conducted this study on the southwest coast of Jamaica within the Font Hill Nature Preserve (18.0391°N, 77.9411°W, < 100 m above sea level), St. Elizabeth Parish, from 13 January through 18 April 2023. Precipitation at this site is strongly seasonal, with a wet season typically from August to November (average monthly precipitation > 100 mm) and dry season from December through May (average monthly precipitation < 25 mm; Powell et al. 2021).

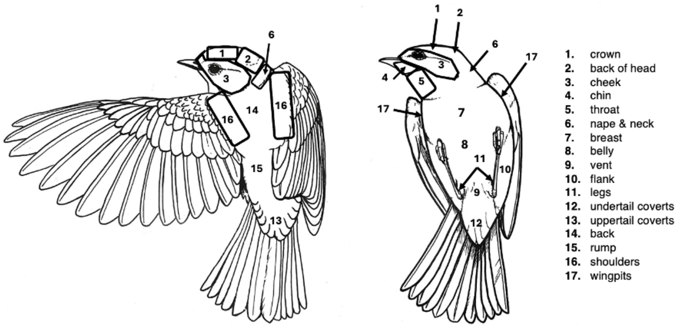
We captured warblers in two second-growth dry scrub forest plots and three mangrove plots, ranging in size from 5 to 7 ha each. See Cooper et al. (2021) for a description of vegetation structure and composition in these two habitat types. Scrub plots remained dry without standing water throughout the study period, typical of dry season conditions for this habitat (Marra et al. 2015b, Cooper et al. 2021). Mangrove plots typically hold 0.3 to 2 m of standing brackish water throughout the dry season (Cooper et al. 2021). Because of relatively low levels of precipitation preceding and during the study period, water levels in the mangrove plots remained low, with some areas occasionally becoming completely dry. Similar conditions have occurred at the study site in previous dry years (e.g., Cooper et al. 2015, Brunner et al. 2022, Dossman et al. 2023b).

Field methods

We captured warblers by mist-netting on 47 days between 13 January through 18 April 2023, using a combination of passive netting and target netting with an audio lure. We banded each individual with a uniquely numbered United States Geological Survey aluminum band. We determined sex for species with sex-based differences in plumage characteristics (Pyle 2022b): American Redstart, Black-and-white Warbler, Northern Parula, and Prairie Warbler. We were unable to determine sex using morphometric measurements for Ovenbird or Northern Waterthrush (Pyle 2022b). We determined age class based on molt and plumage characteristics (Pyle 2022b), following the WRP age classification system (Wolfe et al. 2010) most recently modified by Pyle et al. (2022). Thereby, we assigned molting individuals to one of two age classes, First Prealternate Molt (FPA, hereafter "first-cycle") or Definitive Prealternate Molt (DPA, hereafter "definitive-cycle").

We systematically searched for active contour feather molt (pinfeathers) by blowing on the feathers (Mettke-Hoffman et al. 2010, Wright et al. 2018) in each of 17 patches across the head and body (Fig. 1; Wright et al. 2018). For each patch, we scored the percentage of feathers in active molt on a scale of zero to four, where 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% of active molt per patch. We adapted this method from Greenwood et al. (1983) and Wright et al. (2018), electing to reduce false precision by dividing the percentage of feathers in active molt into quarters rather than to the nearest 10%. To minimize observer error, molt scores for each bird were collected by one of two skilled observers (SAT and IAC). At the beginning of the field season, we repeated molt scoring on the same birds to standardize our measurements and reduce variability associated with the observer. We periodically repeated this process for feather patches with active molt throughout the season.

Fig. 1. Diagram of 17 contour feathers patches in which we scored prealternate molt intensity. Illustration by Stephen Joly.



We considered all instances of contour feather molt to be part of a prealternate molt episode, rather than part of a protracted or suspended (Jenni and Winkler 2020b, Pyle 2022b) preformative/prebasic molt (Howell et al. 2003), or adventitious feather replacement. Five of the six study species were not molting during the first four weeks of capture, so we are confident that we observed seasonal prealternate molt. We captured a Northern Waterthrush in molt on the first day that we captured the species (25 January), so prealternate molt for some individuals of the species may have commenced earlier in January than we could document. We refer to the first observed occurrence of molt for each species as the "observed onset" of molt for that species.

We could not easily distinguish retained contour feathers from those replaced on the nonbreeding grounds prior to capture, except in first-cycle male American Redstarts when recently replaced feathers were black. For males of other focal species with distinct basic and alternate plumages, the considerable variation in plumage appearance made it difficult to determine how much contour feather molt had been completed before capture; only feathers in active molt could be identified. For example, both first- and definitive-cycle male Black-and-white Warblers displayed wide variation in the number and position of black feathers on the cheeks and throat. For this reason, we used molt intensity, rather than extent, as our molt metric.

We also examined the wings and rectrices for active molt, symmetrical or not, and recorded the number and position of coverts, flight feathers, or rectrices in pin. The study species are not known to molt wing or tail feathers as part of their prealternate molt strategies (though some American Redstarts may molt one to three greater coverts; Pyle 2022b), so the few individuals we observed molting these feathers likely did so adventitiously, as previously documented in American Redstarts at the study site (Tonra et al. 2014). We excluded this information from the statistical analyses.

Quantifying molt intensity and prevalence

To describe the intensity of active molt per individual, we calculated a combined contour molt index (CCMI) modified from Wright et al.'s (2018) variation of the Greenwood et al. (1983) method. Each bird received a CCMI score on an ordinal scale from zero to four, the sum of all patch scores divided by the total number of patches (17). Our modification resulted in a CCMI score that divided the percentage of active molt across the entire head and body into quarters rather than tenths as in Wright et al. (2018); for example, a bird with a CCMI score of 1 was actively molting between 1 and 25% of all contour feathers.

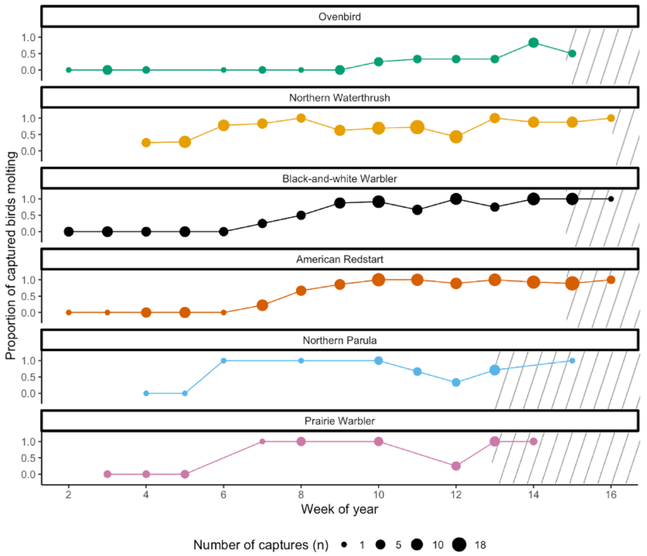
Because we anticipated differences in molt intensity between the head and body in most species, to facilitate comparison we also grouped the feather patches by head (6 patches) and body (11 patches; Fig. 1) and calculated a CCMI score for each patch group. To compare molt intensity among molting individuals across species, we calculated the mean CCMI score for each species including only birds that were actively molting at capture and had a CCMI score recorded. We then calculated mean molt intensity for each patch, per species, only including individuals actively molting that patch at capture (Wright et al. 2018).

For each species, we also aimed to determine the population-level peak in molt prevalence, as in the period where the greatest proportion of weekly captures was molting. When presenting the results we use the term population-level peak to describe the clear peak only observed in the Northern Waterthrush and Ovenbird (Fig. 2).

Statistical analyses

To compare the prevalence of prealternate molt across the six species, we used a Pearson's chi-squared test of the proportion of individuals from each species that were molting versus not molting, excluding captures from before the observed onset of molt in each species. We used ANOVA to compare mean CCMI across species. We used paired t-tests to determine if CCMI differed between the head and body patch groups within individuals of each species. For all statistical analyses, we evaluated the significance of parameter estimates at a $\alpha = 0.05$. The results did not change qualitatively when we excluded recaptures, so we report test statistics from tests that included recapture data. We performed all statistical analyses in R 4.4.0 (R Core Team 2024).

Fig. 2. The proportion of captured birds of six species molting by week of year from 13 January through 18 April 2023, at Font Hill Nature Preserve, Jamaica. The size of the circles represents the number (*n*) of captured birds per week. The hatched area shows where the molting period overlaps with the early end of migration departure windows from Jamaica for each species, based on eBird data (Fink et al. 2023) and unpublished tracking data from the study site (unpublished data, BCD and PPM).



We examined the influence of Julian date, age, sex, and their interactions on CCMI for each species using a linear mixed-effect (function *lmer,* R package *lme4*; Bates et al. 2015) or linear model (function *lm*) and a stepwise backward variable removal procedure where we started with the initial full model and iteratively removed non-significant explanatory variables ($p > 0.05$) to arrive at a single best fit model. We ran a separate model for each species because exploratory analysis revealed a strong species effect on molt intensity. Exploratory analyses identified a quadratic relationship between molt intensity and Julian date in American Redstart and Prairie Warbler, so for these species only we included Julian date^2 as an explanatory variable in the initial model to account for both the linear and quadratic components of the relationship, following Wright et al. (2018). We included sex in the initial models, but it was not a significant predictor of molt intensity for any species; consequently, we excluded it from all final models.

Table 1. Summary for each study species of the unique individuals captured by age and sex, the percentage of unique individuals scored for molt more than once, the total number of molt scores, the percentage of birds scored for molt that were in active molt, the mean ± SD Combined Contour Molt Index (CCMI), and the range of CCMI values for molting birds. *n* is the same for percentage in active molt (%) and mean ± SD CCMI unless specified. *n* is the same for mean ± SD CCMI and CCMI range.

Species	Total number of unique individuals; number of first-cycle individuals	Sex ratio (M:F)	Percentage (%) of unique individuals scored for molt more than once (i.e., recaptures)	Total number of molt scores (initial and recaptures combined)	Percentage (%) of scored birds in active molt	Mean ± SD CCMI	CCMI range
Ovenbird	33; 9	NA	12 (*n* = 4)	37[†]	26 (*n* = 10)	0.29 ± 0.23 (*n* = 9[†])	0.06–0.59
Northern Waterthrush	95[‡]; 39	NA	16 (*n* = 15)	110	67 (*n* = 75)	0.26 ± 0.26	0.06–1.41
Black-and-white Warbler	73; 23	29:44	22 (*n* = 16)	99[§]	62 (*n* = 62)	0.74 ± 0.73 (*n* = 61[§])	0.06–3.35
American Redstart	100; 26	58:42	15 (*n* = 15)	112[‖]	79 (*n* = 89)	0.50 ± 0.47 (*n* = 81[‖])	0.06–1.88
Northern Parula	21; 8	13:8	0	21	67 (*n* = 14)	0.34 ± 0.23	0.06–0.77
Prairie Warbler	27; 19	15:12	4 (*n* = 1)	28	64 (*n* = 18)	0.26 ± 0.21	0.06–0.59

[†] One additional Ovenbird was molting at first capture, but we did not collect the patch scores needed to calculate CCMI.

[‡] Four individuals were scored for molt but not aged.

[§] One additional Black-and-white Warbler was molting at second capture, but we did not collect the patch scores needed to calculate CCMI.

[‖] We recorded the presence of active contour molt for an additional 8 American Redstart captures (6 first capture, 1 second capture, 1 third capture) but did not collect the patch scores needed to calculate CCMI.

We ran a linear mixed-effect model with the individual as a random effect to account for recaptures for Ovenbird, Northern Waterthrush, and Black-and-white Warbler. For the remaining species, we ran a linear model with no random effect because we either had no recaptures (Northern Parula), or the recaptures after the observed onset of molt did not contain all age-sex combinations (American Redstart and Prairie Warbler), making model fitting unreliable. For American Redstart and Prairie Warbler, we ran the model three ways to handle individuals with repeated measurements. First, we included only the first capture record. Second, we included only the second capture record. Finally, we included all capture records without accounting for the effect of individual, for the sake of comparison. The estimates for explanatory variables varied among approaches between 0 and 42.3%, but the results did not differ qualitatively ($p > 0.05$), so here we report the models including only the first capture records (see Appendix 1 for the results of all approaches). We excluded capture data prior to the observed onset of molt for all species. We present results below only for the species in which molt intensity was predicted by at least one explanatory variable: Northern Waterthrush, Black-and-white Warbler, American Redstart, and Prairie Warbler.

RESULTS

In total we recorded the presence or absence of contour feather molt 418 times for six focal species combined. Those records came from 349 unique individuals, 54 (15%) of which we recaptured at least once, with 15 individuals recaptured two, three, or four times. The average time between successive captures was 24.8 ± 19.7 days (mean ± SD). In total we determined that 64% of birds were actively molting at capture ($n = 268$ of 418).

We assigned CCMI scores for 408 captures (first and recaptures combined); we were unable to assign CCMI scores for 10 captures because of high capture volumes and time constraints. For 51 individuals, we successfully scored molt two to five times throughout the season. In Table 1, we summarize for each species the percentage of birds scored for molt more than once (i.e., recaptures), the total number of molt scores, and the percentage of birds molting at capture.

Each species showed active prealternate molt, involving some scattered head and body feathers or the simultaneous molt of many feathers from multiple tracts. The observed onset of molt in the study species ranged from late January to early March, though for most species, molt commenced in early to mid-February (Figure 2, split by age-class in Appendix 2). The prevalence of molt generally increased in all species from the observed onset through the end of the study period. After the observed onset of molt, the proportion of molting individuals varied markedly across species (Pearson's chi-squared test: $X^2_{(5)} = 22.3$, $p < 0.001$, $n_{total} = 342$; see Appendix 5 for each species' sample sizes).

We observed both intra- and inter-specific variation in individual molt intensity. However, although mean molt intensity varied across species (ANOVA: $F_{(5)} = 8.18$, $p < 0.001$), all species had a mean CCMI score < 1 (Table 1), meaning that on average, birds from all species were not actively molting more than 25% of their contour feathers at once. Only a few Black-and-white Warblers ($n = 4$) had CCMI scores ≥ 2, as in simultaneously molting more than 25% of contour feathers.

Species accounts

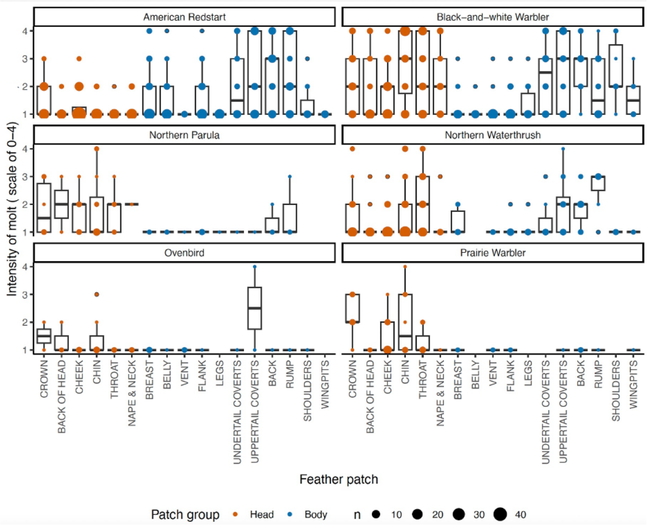
Ovenbird

We captured molting Ovenbirds three to six weeks later than the observed onset of molt in other species of this study, between 9 March and 9 April (Fig. 2). The prevalence of molt within the population peaked from 3 April to 6 April (83% of captures that week were in molt). We observed active molt in all feather patches except for the legs and axillaries (i.e., feathers of the wingpits), and most frequently on the chin and cheeks (Appendix 3). We did not detect a difference in molt intensity between the head and the body when comparing CCMI scores for the two patch groups (paired t-test: $t_{(8)} = 1.91$, $p = 0.09$; Appendix 4). Although in other species we found clear statistically significant trends in increasing molt intensity over time, Ovenbirds showed a similar general relationship albeit not statistically significant (Julian date: $df = 15.00$, $t = 1.68$, $p = 0.11$).

Northern Waterthrush

We captured the first molting Northern Waterthrush earlier than all other species in this study, on 25 January (Fig. 2). The prevalence of molt peaked twice during the study period, from 19 to 25 February

Fig. 3. The intensity of molt, on a scale of zero to four, per 17 feather patches for six species captured from 13 January through 18 April 2023, at Font Hill Nature Preserve, Jamaica. The size of the circles represents the number (*n*) of molting birds sampled that had the corresponding molt intensity score for each patch.



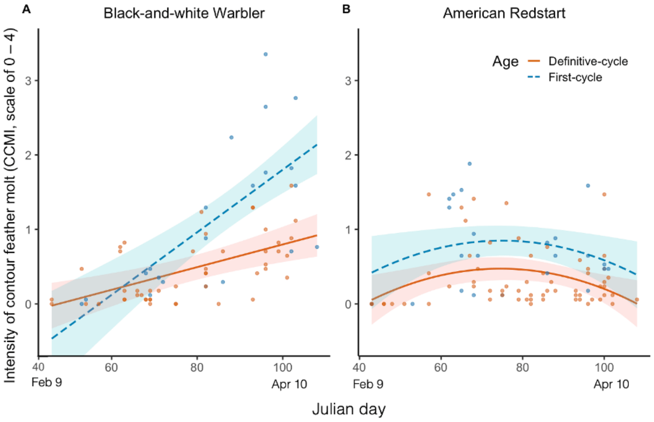
and 26 March to 1 April, with all captures molting during those weeks. After 1 April, molt prevalence remained high (≥ 88% of weekly captures in molt) through 18 April. The Northern Waterthrush showed active molt in all feather patches except for the belly (Appendix 3). Active molt was most frequent on the chin, throat, and cheek. Per feather patch, mean molt intensity was greatest on the rump, the only feather patch with more than 50% of feathers in active molt (Fig. 3). Molt intensity also differed by patch group; mean CCMI was greater on the head than the body (paired t-test: $t_{(74)} = 5.58$, $p < 0.001$; Appendix 4). When we examined changes in molt intensity over time from the observed onset of molt in the study population (25 January), we found that CCMI increased linearly through the end of the study period (Julian date: $df = 104.36$, $t = 3.73$, $p < 0.001$).

Black-and-white Warbler

Black-and-white Warblers showed active molt between 15 February and 18 April (Fig. 2). Molt was most prevalent within the population from March 19 onward when most (≥ 75%) or all captures each week were molting. We observed active molt in all 17 feather patches, and most frequently on the chin, cheek, and throat (Appendix 3). Mean molt intensity per patch was greatest on the back and chin (Fig. 3), and when compared between the head and body patch groups, mean CCMI was greater on the head (paired t-test: $t_{(60)} = 6.70$, $p < 0.001$; Appendix 4).

When we examined changes in molt intensity over time from the observed onset of molt (15 February), we found an Age*Julian Date interaction ($df = 62.87$, $t = 3.27$, $p = 0.002$) indicating that CCMI increased more strongly over time in first-cycle than definitive-cycle birds (Fig. 4). When we examined the age classes separately, both first-cycle (Julian date: $df = 7.79$, $t = 6.06$, $p < 0.001$) and definitive-cycle (Julian date: $df = 43.15$, $t = 5.21$, $p < 0.001$) birds saw an increase in CCMI over time.

Fig. 4. Effects of Julian date and age on contour feather molt intensity, measured as a Combined Contour Molt Index (CCMI) on a scale of zero to four. The relationship between CCMI and Julian date is linear in Black-and-white Warblers, *Mniotilta varia* (A) and quadratic in American Redstarts, *Setophaga ruticilla* (B). Models include data from the first date we observed molt: 15 February for Black-and-white Warblers and 12 February for American Redstarts, through the end of the study period, 18 April 2023. The lines represent the predicted relationships between CCMI and Julian date for each age class (definitive-cycle in solid, first-cycle in dashed). The data points shown are the predicted values. The shaded areas represent the 95% confidence intervals of the prediction.



American Redstart

We captured molting American Redstarts between 12 February and 18 April (Fig. 2). Molt was most prevalent within the population from 26 February onward when most (≥ 86%) or all captures each week were molting. American Redstarts showed active molt in all 17 feather patches, and most frequently on the cheek, breast, and crown (Appendix 3). The back, rump, uppertail coverts, and undertail coverts had the greatest mean molt intensities of all patches (Fig. 3). However, CCMI did not differ between the head and body patch groups (paired t-test: $t_{(80)} = -0.70$, $p = 0.49$; Appendix 4). Molt intensity followed a parabola, with peak CCMI in the middle of the observed molt period based on the quadratic term for time (Julian date: $df = 82$, $t = 2.67$, $p = 0.009$; Julian date^2: $df = 82$, $t = -2.71$, $p = 0.008$; Fig. 4). When we examined the relationship between molt intensity and age from the observed onset of molt in the study population, CCMI was greater for first-cycle than definitive-cycle individuals (Age: $df = 82$, $t = 3.55$, $p = 0.0007$; Fig. 4).

Northern Parula

We captured Northern Parulas in molt between 6 February and 11 April (Fig. 2). Weekly capture sample sizes were small ($n = 1$, 3, or 7), making it difficult to determine the population-level peak of molt prevalence. Northern Parulas showed active molt in all feather patches except for the shoulders and axillaries (Appendix 3). We observed active molt most frequently on the chin, crown, and cheeks. Per feather patch, mean molt intensity was greatest on the crown, chin, and throat (Fig. 3). Northern Parulas molted head feathers more intensely than body feathers, based on a comparison of mean CCMI for the head and body patch groups (paired t-test: $t_{(13)} = 3.24$, $p = 0.006$; Appendix 4).

Prairie Warbler

Prairie Warblers showed prealternate molt between 12 February and 3 April (Fig. 2). All birds captured between 12 February and 3 April were molting, aside from three individuals (first-cycle male, first-cycle female, and definitive-cycle female) captured on 23 March, though sample sizes for weekly captures were small ($n \leq 6$). We observed active molt in all feather patches except for the belly, legs, and shoulders (Appendix 3). Active molt was most frequent on the cheeks, crown, and chin. Prairie Warblers molted the uppertail coverts most intensely of all 17 patches (Fig. 3), but molt intensity was greater on the head than the body when comparing CCMI for the two patch groups (paired t-test: $t_{(17)} = 4.31$, $p < 0.001$; Appendix 4). Molt intensity followed a parabola, with peak CCMI in the middle of the observed molt period based on the quadratic term for time (Julian date: $df = 17$, $t = 2.96$, $p = 0.009$; Julian date^2: $df = 17$, $t = -3.23$, $p = 0.005$).

DISCUSSION

Here, we provide detailed information on the timing and intensity of prealternate molt in six parulid warbler species, information that remains extremely limited for most parulid warblers, despite the critical importance of feather quality for these birds. We demonstrate that both head and body feather molt is common in the Northern Waterthrush, Black-and-white Warbler, American Redstart, Northern Parula, and Prairie Warbler, and for most species increases in frequency and intensity later in the nonbreeding period, though timing varied markedly across species. Although our sample size for Ovenbirds is modest, because we documented molt from March to April following two months without molt, we provide support for the occurrence of a prealternate molt in some individuals, though likely not all, rather than a suspended and protracted preformative/prebasic molt or a continuous molt from October through April (as in Guallar et al. 2009). We also demonstrate age-specific differences in the intensity of molt in the American Redstart and Black-and-white Warbler.

The evolutionary drivers behind prealternate molt in birds remain unclear, but the feather wear hypothesis proposed by Pyle and Kayhart (2010), and supported by Wolfe and Pyle (2011), Terrill et al. (2020), and Cuervo et al. (2022), may explain the age-specific differences in molt intensity that we observed. The feather wear hypothesis proposes that prealternate molt evolved primarily to renew feathers for maintaining feather function, rather than for breeding plumage, but was then co-opted during the evolution of seasonal dichromatism (Terrill et al. 2020). We observed higher molt intensity in first-cycle than definitive-cycle Black-and-white Warblers and American Redstarts, a trend that was also documented in Prothonotary Warblers (*Protonotaria citrea*) during part of the nonbreeding period (mid-December through early February) in Panama (Ames 2021). Consistent with the feather wear hypothesis, first-cycle birds may benefit more than definitive-cycle birds from an intense prealternate molt if they are replacing relatively poor-quality contour feathers (i.e., either retained juvenile or formative feathers). In the American Redstart, prealternate molt can contribute to the slow acquisition of black (definitive) feathers in first-cycle males (Rohwer et al. 1983). Contrasting with Tonra et al. (2014), first-cycle males in this study did not exclusively replace gray contour feathers with black feathers; some new feathers were black, some were gray, and some birds molted new feathers in both colors simultaneously. The production of gray alternate feathers in first-cycle males is an example of a prealternate molt that does not exclusively contribute to plumage maturation or seasonal dichromatism, suggesting that the replacement of these feathers may be primarily driven by feather maintenance. Further supporting the feather wear hypothesis, the patches most frequently molted across all species tended to be areas of the body that are exposed to the sun when birds are perching (Terrill et al. 2020): the head, in particular the cheek, chin, and crown, followed by the breast.

Notably, we did not observe sex-based differences in molt intensity for any species. Our study included four sexually dichromatic and two sexually monochromatic species. It has been suggested that the prealternate molt differs and is potentially more extensive in male than female American Redstarts and Prairie Warblers (Rohwer et al. 1983, Nolan et al. 2020, Sherry et al. 2020, Pyle 2022b), two sexually dichromatic species. Given the dearth of information on prealternate molt, particularly of the contour feathers, bias toward the study of male plumage and molt (e.g., Rohwer et al. 1983), and focus on regions of the body that contribute to seasonal and sexual dichromatism (e.g., Boone 2006, Boone et al. 2010), we suggest that further detailed study is needed to clarify our collective knowledge of age- and sex-based differences in prealternate molt. For species, age, or sex classes that replace basic contour feathers in the same color as alternate feathers, as we have documented in all age and sex classes of American Redstarts, it is possible that previous studies of molt and plumage may have missed the replacement of same-color alternate feathers or mischaracterized late-winter contour feather molt as adventitious rather than obligate. We suggest that by collecting detailed molt data at the feather patch level across the entire head and body during the molt period on the nonbreeding grounds, along with more rigorous mark-recapture efforts through the molt period, further studies can clarify our knowledge of prealternate molt and its potential variation across species, age and sex classes, nonbreeding populations, and years.

Molt intensity often follows a parabolic curve from start to finish, peaking during the middle of molt (e.g., Wright et al. 2018, Hutton et al. 2021, Guallar 2024). We observed this relationship in the American Redstart and Prairie Warbler but only captured a linear increase in molt intensity over time in the other species, indicating that the molt period for the Ovenbird, Northern Waterthrush, Black-and-white Warbler, and Northern Parula may have extended beyond 18 April. Indeed, Lefebvre et al. (1992) observed molt in nonbreeding Northern Waterthrushes through the end of April. Individuals from all six of our study species showed active molt into early or mid-April, coinciding with timing windows for pre-breeding migration departures from Jamaica (Fink et al. 2023; BCD and PPM, *unpublished data*; Fig. 2). This result suggests that for many birds, molt likely overlaps with migratory fattening, and that some birds may continue molting until departure, or while migrating (i.e., prealternate molt-migration; Tonra and Reudink 2018, Wright et al. 2018). Mid-April aligns with early departures for Ovenbird, Northern Waterthrush, Black-and-white Warbler, and American Redstart (Studds and Marra 2007, 2011, Tonra et al. 2013, Cooper et al. 2015), but late departures for Northern Parula and Prairie Warbler based on ebird relative abundance data (Fink et al. 2023). As far as we know, most Nearctic-Neotropical migratory parulids have prealternate molt schedules that occur before pre-breeding migration (Billerman et al. 2022, Pyle 2022b), likely to avoid energetic conflicts (Froehlich et al. 2005). Because migration constrains their prealternate molt spatially and temporally, and the resources needed to facilitate energetically demanding events vary seasonally in Jamaica (Parrish and Sherry 1994, Strong and Sherry 2000, Johnson and Sherry 2001, Studds and Marra 2007, 2011), the study species may be faced with trade-offs between migratory fattening and maximizing alternate feather quality by molting closer to departure (Froehlich et al. 2005). Future studies should explore this potential trade-off and evaluate its consequences by determining if the timing of individual molt is associated with the timing of migratory fattening and pre-breeding migration departure. Collecting such data for the same individuals over multiple years could be used to elucidate whether individuals adjust their molt and migration strategies according to interannual variation in seasonal resource availability during the nonbreeding period.

With an improved understanding of prealternate molt in six species of Nearctic-Neotropical migratory warblers, we can now use data on the timing and intensity of molt to begin to evaluate how prealternate molt interacts across the annual cycle with other crucial life history stages, including pre-breeding migration. Understanding the individual timing of migration in relation to molt, together with the underlying influence of habitat quality and individual body condition on molt and migration, are the next steps in disentangling the role of prealternate molt in potential nonbreeding period carry-over effects in the study species. To that end, it will be crucial for researchers in the Global North to establish equitable collaborations with local Neotropical researchers (Soares et al. 2023, Albert et al. 2025) to aid in furthering prealternate molt research on the nonbreeding grounds of many migratory birds. This knowledge is critical for determining which life history stages limit bird populations in the annual cycle (Marra et al. 2015a).

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Data Availability:

The data and code that support the findings of this study are available on Dryad: https://doi.org/10.5061/dryad.qbzkh18x0.

LITERATURE CITED

Albert, S., A. Ash, R. S. Quintero Félix, and J. C. Fernández-Ordóñez. 2025. El monitoreo de aves migratorias neártico-neotropicales en su temporada no reproductiva: éxitos, desafíos, y nuevas iniciativas del programa MoSI. Ornitología Neotropical 35:107-111. https://doi.org/10.58843/ornneo.v35i2.657

Ames, E. M. 2021. Linking events across the annual cycle, in a Neotropical migratory songbird of conservation concern, the Prothonotary Warbler (*Protonotaria citrea*). Dissertation. The Ohio State University, Columbus, Ohio, USA.

Barta, Z., J. M. McNamara, A. I. Houston, T. P. Weber, A. Hedenström, and O. Feró. 2008. Optimal moult strategies in migratory birds. Philosophical Transactions of the Royal Society B 363:211-229. https://doi.org/10.1098/rstb.2007.2136

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1-48. https://doi.org/10.18637/jss.v067.i01

Billerman, S. M., B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg, editors. 2022. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow

Boone, A. T. 2006. Seasonal interactions between migration and winter in a migratory songbird, the Magnolia Warbler (*Dendroica magnolia*). Thesis. The Ohio State University, Columbus, Ohio, USA.

Boone, A. T., P. G. Rodewald, and L. W. DeGroote. 2010. Neotropical winter habitat of the Magnolia Warbler: effects on molt, energetic condition, migration timing, and hematozoan infection during spring migration. Condor 112(1):115-122. https://doi.org/10.1525/cond.2010.090098

Bridge, E. S. 2011. Mind the gaps: what's missing in our understanding of feather molt. Condor 113(1):1-4. https://doi.org/10.1525/cond.2011.100228

Brunner, A. R., P. P. Marra, and C. M. Tonra. 2022. Vulnerable Neotropical migratory songbird demonstrates flexibility in space use in response to rainfall change. Ornithology 139(2):ukac005. https://doi.org/10.1093/ornithology/ukac005

Carlisle, J. D., G. S. Kaltenecker, and D. L. Swanson. 2005. Molt strategies and age differences in migration timing among autumn landbird migrants in southwestern Idaho. Auk 122(4):1070-1085. https://doi.org/10.1093/auk/122.4.1070

Carnes, B. H., C. M. Godwin, K. R. Foster, and P. Pyle. 2021. Clarification of molt strategies in three *Empidonax* flycatchers. Wilson Journal of Ornithology 133(1):34-42. https://doi.org/10.1676/20-00109

Cimprich, D. A. 2018. Molt limits reveal extent of molt and age in Black-capped Vireos. North American Bird Bander 43 (4):86-95.

Cooper, N. W., T. W. Sherry, and P. P. Marra. 2015. Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird. Ecology 96 (7):1933-1942. https://doi.org/10.1890/14-1365.1

Cooper, N. W., M. A. Thomas, and P. P. Marra. 2021. Vertical sexual habitat segregation in a wintering migratory songbird. Ornithology 138(1):ukaa080. https://doi.org/10.1093/ornithology/ukaa080

Crary, A. L., and P. G. Rodewald. 2012. Plumage coloration and ornamentation as predictors of nest survival and number of young fledged in Yellow Warblers. Journal of Field Ornithology 83(2):130-140. https://doi.org/10.1111/j.1557-9263.2012.00363.x

Cuervo, J. J., J. Morales, J. J. Soler, and J. Moreno. 2022. Sexual selection, feather wear, and time constraints on the pre-basic molt explain the acquisition of the pre-alternate molt in European passerines. Ecology and Evolution 12(9):e9260. https://doi.org/10.1002/ece3.9260

Danner, R. M., R. S. Greenberg, J. E. Danner, and J. R. Walters. 2015. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. Functional Ecology 29(2):259-267. https://doi.org/10.1111/1365-2435.12322

Dossman, B. C., A. D. Rodewald, and P. P. Marra. 2024. Hidden space use behaviors of a nonbreeding migratory bird: the role of environment and social context. Movement Ecology 12(1):82. https://doi.org/10.1186/s40462-024-00523-4

Dossman, B. C., A. D. Rodewald, C. E. Studds, and P. P. Marra. 2023a. Migratory birds with delayed spring departure migrate faster but pay the costs. Ecology 104(2):e3938. https://doi.org/10.1002/ecy.3938

Dossman, B. C., C. E. Studds, S. L. LaDeau, T. S. Sillett, and P. P. Marra. 2023b. The role of tropical rainfall in driving range dynamics for a long-distance migratory bird. Proceedings of the National Academy of Sciences 120(52):e2301055120. https://doi.org/10.1073/pnas.2301055120

Dugger, K. M., J. Faaborg, W. J. Arendt, and K. Hobson. 2004. Understanding survival and abundance of overwintering warblers: Does rainfall matter? Condor 106(4):744-760. https://doi.org/10.1093/condor/106.4.744

Evans Ogden, L., and B. J. M. Stutchbury. 1996. Constraints on double brooding in a Neotropical migrant, the Hooded Warbler. Condor 98(4):736-744. https://doi.org/10.2307/1369855

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, C. Crowley, K. Dunham, et al. 2023. eBird Status and trends, data version: 2022; Released: 2023. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/ebirdst.2022

Froehlich, D. R., S. Rohwer, and B. J. Stutchbury. 2005. Spring molt constraints versus winter territoriality: Is conspicuous winter coloration maladaptive? Pages 321-335 in R. S. Greenberg, and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Greenwood, H., P. J. Weatherhead, and R. D. Titman. 1983. A new age- and sex-specific molt scheme for the Red-Winged Blackbird. Condor 85(1):104-105. https://doi.org/10.2307/1367901

Guallar, S. 2024. From partial to complete: wing- and tail-feather moult sequence and intensity depend on species, life-cycle stage, and moult completeness in passerines. Avian Research 15:100163. https://doi.org/10.1016/j.avrs.2024.100163

Guallar, S., E. Santana, S. Martínez-Conteras, H. Verdugo, and A. Gallés. 2009. Paseriformes del Occidente de México: morfometría, datación y sexado. Museu de Ciències Naturals de Barcelona, Institut de Cultura, Ajuntament de Barcelona, Spain. http://doi.org/10.13140/2.1.2516.3208

Gunderson, A. R., A. M. Frame, J. P. Swaddle, and M. H. Forsyth. 2008. Resistance of melanized feathers to bacterial degradation: is it really so black and white? Journal of Avian Biology 39 (5):539-545. https://doi.org/10.1111/j.0908-8857.2008.04413.x

Hedenström, A. 2002. Aerodynamics, evolution and ecology of avian flight. Trends in Ecology & Evolution 17(9):415-422. https://doi.org/10.1016/S0169-5347(02)02568-5

Hill, G. E., and K. J. McGraw, editors. 2006. Bird coloration: function and evolution. Harvard University Press, Cambridge, Massachusetts, USA.

Howell, S. N. G., C. Corben, P. Pyle, and D. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105(4):635-653. https://doi.org/10.1093/condor/105.4.635

Humphrey, P. S., and K. C. Parkes. 1959. An approach to the study of molts and plumages. Auk 76(1):1-31. https://doi.org/10.2307/4081839

Hutton, P., J. McKenna, and K. J. McGraw. 2021. Urban links to molt schedule, body condition and carotenoid-based coloration in the House Finch *Haemorhous mexicanus*. Journal of Avian Biology 52(5):jav.02761. https://doi.org/10.1111/jav.02761

Jackson, W. M., C. S. Wood, and S. Rohwer. 1992. Age-specific plumage characters and annual molt schedules of Hermit Warblers and Townsend's Warblers. Condor 94(2):490-501. https://doi.org/10.2307/1369221

Jenni, L., and R. Winkler. 2020a. Moult and ageing of European passerines, Second edition. Helm, London, England.

Jenni, L., and R. Winkler. 2020b. The biology of moult in birds. Helm, London, England.

Johnson, M. D., and T. W. Sherry. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. Journal of Animal Ecology 70(4):546-560. https://doi.org/10.1046/j.1365-2656.2001.00522.x

Jones, T. B., A. Drake, and D. J. Green. 2014. Individual quality explains association between plumage colouration, arrival dates and mate acquisition in Yellow Warblers (*Setophaga petechia*). BMC Ecology 14(1):13. https://doi.org/10.1186/1472-6785-14-13

Kent, C. M., K. M. Huh, S. C. Hunter, K. Judson, L. L. Powell, and T. W. Sherry. 2022. High resource overlap and small dietary differences are widespread in food-limited warbler (Parulidae) communities. Ibis 164(1):44-59. https://doi.org/10.1111/ibi.13006

Kent, C. M., and T. W. Sherry. 2020. Behavioral niche partitioning reexamined: Do behavioral differences predict dietary differences in warblers? Ecology 101(8):e03077. https://doi.org/10.1002/ecy.3077

Kiat, Y. 2023. Moult terminology: Let's make it simpler! Ibis 165 (2):697-703. https://doi.org/10.1111/ibi.13164

Kiat, Y., and I. Izhaki. 2016. Moult strategies affect age differences in autumn migration timing in east Mediterranean migratory passerines. PLoS ONE 11(1):e0147471. https://doi.org/10.1371/journal.pone.0147471

Kiat, Y., I. Izhaki, and N. Sapir. 2019. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. Biological Reviews 94(2):700-720. https://doi.org/10.1111/brv.12474

Kricher, J. C. 2020. Black-and-white warbler (*Mniotilta varia*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.bawwar.01

Lefebvre, G., B. Poulin, and R. McNeil. 1992. Abundance, feeding behavior, and body condition of Nearctic warblers wintering in Venezuelan mangroves. Wilson Bulletin 104(3):400-412.

Leu, M., and C. W. Thompson. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for neotropical migrants. Biological Conservation 106 (1):45-56. https://doi.org/10.1016/S0006-3207(01)00228-2

Lindström, Å., G. H. Visser, and S. Daan. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. Physiological Zoology 66(4):490-510. https://doi.org/10.1086/physzool.66.4.30163805

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015a. A call for full annual cycle research in animal ecology. Biology Letters 11(8):20150552. https://doi.org/10.1098/rsbl.2015.0552

Marra, P. P., C. E. Studds, S. Wilson, T. S. Sillett, T. W. Sherry, and R. T. Holmes. 2015b. Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. Proceedings of the Royal Society B: Biological Sciences 282 (1811):20150624. https://doi.org/10.1098/rspb.2015.0624

Mettke-Hofmann, C., P. H. Sinclair, P. B. Hamel, and R. Greenberg. 2010. Implications of prebasic and a previously undescribed prealternate molt for aging Rusty Blackbirds. Condor 112(4):854-861. https://doi.org/10.1525/cond.2010.100150

Moldenhauer, R. R., and D. J. Regelski. 2020. Northern parula (*Setophaga americana*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.norpar.01

Mulvihill, R. S., S. C. Latta, and F. L. Newell. 2009. Temporal constraints on the incidence of double brooding in the Louisiana Waterthrush. Condor 111(2):341-348. https://doi.org/10.1525/cond.2009.080037

Nolan Jr, V., E. D. Ketterson, and C. A. Buerkle. 2020. Prairie warbler (*Setophaga discolor*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.prawar.01

Parrish, J. D., and T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: importance of resource seasonality. Auk 111(1):38-49. https://doi.org/10.2307/4088503

Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2020. Ovenbird (*Seiurus aurocapilla*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.ovenbi1.01

Powell, L. L., E. M. Ames, J. R. Wright, J. Matthiopoulos, and P. P. Marra. 2021. Interspecific competition between resident and wintering birds: experimental evidence and consequences of coexistence. Ecology 102(2):e03208. https://doi.org/10.1002/ecy.3208

Pyle, P. 1997. Molt limits in North American passerines. North American Bird Bander 22(2):49-81.

Pyle, P. 2022a. Defining moults in migratory birds: a sequence-based approach. Journal of Avian Biology 2022(5):e02958. https://doi.org/10.1111/jav.02958

Pyle, P. 2022b. Identification guide to North American birds: Part I. Second edition. Slate Creek Press, Forest Knolls, California, USA.

Pyle, P., and B. H. Carnes. 2022. Molt strategies by age and subspecies in the Willow Flycatcher. Western Birds 53(3):216-231. https://doi.org/10.21199/WB53.3.4

Pyle, P., M. Gahbauer, E. I. Johnson, T. B. Ryder, and J. D. Wolfe. 2022. Application of a global age-coding system ("WRP"), based on molts and plumages, for use in demographic and other studies of birds. Ornithology 139(1):ukab063. https://doi.org/10.1093/ornithology/ukab063

Pyle, P., and R. Kayhart. 2010. Replacement of primaries during the prealternate molt of a Yellow Warbler. North American Bird Bander 35(4):178-181.

Pyle, P., J. F. Saracco, and D. F. DeSante. 2018. Evidence of widespread movements from breeding to molting grounds by North American landbirds. Auk 135(3):506-520. https://doi.org/10.1642/AUK-17-201.1

Quinlan, S. P., and D. J. Green. 2011. Variation in deuterium (δD) signatures of Yellow Warbler *Dendroica petechia* feathers grown on breeding and wintering grounds. Journal of Ornithology 152 (1):93-101. https://doi.org/10.1007/s10336-010-0553-5

R Core Team. 2024. R: A language and environment for statistical computing. https://doi.org/10.32614/R.manuals

Renfrew, R. B., S. J. K. Frey, and J. Klavins. 2011. Phenology and sequence of the complete prealternate molt of Bobolinks in South America. Journal of Field Ornithology 82(1):101-113. https://doi.org/10.1111/j.1557-9263.2010.00312.x

Reudink, M. W., C. E. Studds, P. P. Marra, T. K. Kyser, and L. M. Ratcliffe. 2009. Plumage brightness predicts non-breeding season territory quality in a long-distance migratory songbird, the American Redstart *Setophaga ruticilla*. Journal of Avian Biology 40(1):34-41. https://doi.org/10.1111/j.1600-048X.2008.04377.x

Rohwer, S., L. K. Butler, and D. Froehlich. 2005. Ecology and demography of east-west differences in molt scheduling of

Neotropical migrant passerines. Pages 87-105 in R. S. Greenberg, and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Rohwer, S., W. P. Klein, Jr., and S. Heard. 1983. Delayed plumage maturation and the presumed prealternate molt in American Redstarts. Wilson Bulletin 95(2):199-208.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, M. Parr, and P. P. Marra. 2019. Decline of the North American avifauna. Science 366(6461):120-124. https://doi.org/10.1126/science.aaw1313

Saino, N., T. Szép, R. Ambrosini, M. Romano, and A. P. Møller. 2004. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. Proceedings of the Royal Society B: Biological Sciences 271(1540):681-686. https://doi.org/10.1098/rspb.2003.2656

Santos, E. S. A., D. Scheck, and S. Nakagawa. 2011. Dominance and plumage traits: meta-analysis and metaregression analysis. Animal Behaviour 82(1):3-19. https://doi.org/10.1016/j.anbehav.2011.03.022

Sherry, T. W., R. T. Holmes, P. Pyle, and M. A. Patten. 2020. American Redstart (*Setophaga ruticilla*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.amered.01

Sherry, T. W., M. D. Johnson, K. A. Williams, J. D. Kaban, C. K. McAvoy, A. M. Hallauer, S. Rainey, and S. Xu. 2016. Dietary opportunism, resource partitioning, and consumption of coffee berry borers by five species of migratory Wood Warblers (Parulidae) wintering in Jamaican shade coffee plantations. Journal of Field Ornithology 87(3):273-292. https://doi.org/10.1111/jofo.12160

Sieburth, D., and P. Pyle. 2018. Evidence for a prealternate molt-migration in the Rufous Hummingbird and its implications for the evolution of molts in Apodiformes. Auk 135(3):495-505. https://doi.org/10.1642/AUK-17-231.1

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2010. Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird. Ecology 91(10):2874-2882. https://doi.org/10.1890/09-2212.1

Smith, J. A. M., L. R. Reitsma, and P. P. Marra. 2011. Multiple space-use strategies and their divergent consequences in a nonbreeding migratory bird (*Parkesia noveboracensis*). Auk 128 (1):53-60. https://doi.org/10.1525/auk.2011.10241

Soares, L., K. L. Cockle, E. Ruelas Inzunza, J. T. Ibarra, C. I. Miño, S. Zuluaga, E. Bonaccorso, J. C. Ríos-Orjuela, F. A. Montaño-Centellas, J. F. Freile, et al. 2023. Neotropical ornithology: reckoning with historical assumptions, removing systemic barriers, and reimagining the future. Ornithological Applications 125(1):duac046. https://doi.org/10.1093/ornithapp/duac046

Sparrow, K. L., K. K. Donkor, N. J. Flood, P. P. Marra, A. G. Pillar, and M. W. Reudink. 2017. Conditions on the Mexican moulting grounds influence feather colour and carotenoids in Bullock's orioles (*Icterus bullockii*). Ecology and Evolution 7 (8):2643-2651. https://doi.org/10.1002/ece3.2836

Strong, A. M., and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of Ovenbirds wintering in Jamaica. Journal of Animal Ecology 69(5):883-895. https://doi.org/10.1046/j.1365-2656.2000.00447.x

Studds, C. E., and P. P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86(9):2380-2385. https://doi.org/10.1890/04-1145

Studds, C. E., and P. P. Marra. 2007. Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. Climate Research 35 (1-2):115-122. https://doi.org/10.3354/cr00718

Studds, C. E., and P. P. Marra. 2011. Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird. Proceedings of the Royal Society B: Biological Sciences 278(1723):3437-3443. https://doi.org/10.1098/rspb.2011.0332

Stutchbury, B. J. M., E. A. Gow, T. Done, M. MacPherson, J. W. Fox, and V. Afanasyev. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. Proceedings of the Royal Society B: Biological Sciences 278(1702):131-137. https://doi.org/10.1098/rspb.2010.1220

Terrill, R. S., G. F. Seeholzer, and J. D. Wolfe. 2020. Evolution of breeding plumages in birds: a multiple-step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae). Ecology and Evolution 10(17):9223-9239. https://doi.org/10.1002/ece3.6606

Terrill, R. S., and A. J. Shultz. 2023. Feather function and the evolution of birds. Biological Reviews 98(2):540-566. https://doi.org/10.1111/brv.12918

Tonra, C. M., K. L. D. Marini, P. P. Marra, R. R. Germain, R. L. Holberton, and M. W. Reudink. 2014. Color expression in experimentally regrown feathers of an overwintering migratory bird: implications for signaling and seasonal interactions. Ecology and Evolution 4(8):1222-1232. https://doi.org/10.1002/ece3.994

Tonra, C. M., P. P. Marra, and R. L. Holberton. 2013. Experimental and observational studies of seasonal interactions between overlapping life history stages in a migratory bird. Hormones and Behavior 64(5):825-832. https://doi.org/10.1016/j.yhbeh.2013.10.004

Tonra, C. M., and M. W. Reudink. 2018. Expanding the traditional definition of molt-migration. Auk 135(4):1123-1132. https://doi.org/10.1642/AUK-17-187.1

Voelker, G., and S. L. McFarland. 2002. Molt patterns and molting grounds of Lucy's and Virginia's Warblers: similar yet different. Wilson Bulletin 114(2):255-263. https://doi.org/10.1676/0043-5643(2002)114[0255:MPAMGO]2.0.CO;2

Voelker, G., and S. Rohwer. 1998. Contrasts in scheduling of molt and migration in eastern and western warbling-vireos. Auk 115 (1):142-155. https://doi.org/10.2307/4089119

Whitaker, D. M., and S. W. Eaton. 2020. Northern Waterthrush (*Parkesia noveboracensis*), version 1.0. In A. F. Poole, editor. Birds of the world. Cornell Lab of Ornithology, Ithaca, New York, USA. https://doi.org/10.2173/bow.norwat.01

Wilson, S., P. P. Marra, and T. S. Sillett. 2013. The effects of experimental irrigation on plant productivity, insect abundance and the non-breeding season performance of a migratory songbird. PLoS ONE 8(1):e55114. https://doi.org/10.1371/journal.pone.0055114

Wingfield, J. C. 2008. Organization of vertebrate annual cycles: implications for control mechanisms. Philosophical Transactions of the Royal Society B: Biological Sciences 363(1490):425-441. https://doi.org/10.1098/rstb.2007.2149

Wolf, B. O., and G. E. Walsberg. 2000. The role of the plumage in heat transfer processes of birds. American Zoologist 40:575-584. https://doi.org/10.1093/icb/40.4.575

Wolfe, J., and P. Pyle. 2011. Featured photo: first evidence for eccentric prealternate molt in the Indigo Bunting: possible implications for adaptive molt strategies. Western Birds 42:257-262.

Wolfe, J. D., T. B. Ryder, and P. Pyle. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. Journal of Field Ornithology 81(2):186-194. https://doi.org/10.1111/j.1557-9263.2010.00276.x

Wright, J. R., C. M. Tonra, and L. L. Powell. 2018. Prealternate molt-migration in Rusty Blackbirds and its implications for stopover biology. Condor 120(3):507-516. https://doi.org/10.1650/CONDOR-17-177.1

APPENDIX 1 – Supplemental Materials for Prealternate molt intensity and timing in six Nearctic-Neotropical migratory warblers

Table A1.1. Estimates for significant predictors (*p*-value < 0.05) of molt intensity as measured by the Combined Contour Molt Index, in the American Redstart and Prairie Warbler, modelled three ways using a linear model to handle individuals with repeated measurements (recaptured birds): a. excluding the second capture, b. excluding the first capture, and c. including both captures. Linear modelling followed a stepwise regression (backward elimination), starting with the full initial model including the explanatory variables: Julian date, Julian date^2, age, and sex. We included sex in the initial models, but it was not a significant predictor of molt intensity for either species; consequently, we excluded it from the final models. For the American Redstart, we considered the interaction term age*Julian date. It was not significantly related to molt intensity, so we removed it from the final model.

Species	Model	Explanatory variable	Estimate	Residual standard error (degrees of freedom)	*t*-value	*p*-value
American Redstart	a. excluding second capture	Julian date	0.063	0.024 (82)	2.667	0.009
		Julian date^2	-0.0004	0.0002 (82)	-2.710	0.008
		Age	0.377	0.106 (82)	3.545	0.0007
	b. excluding first capture	Julian date	0.061	0.023 (82)	2.683	0.009
		Julian date^2	-0.0004	0.0001 (82)	-2.817	0.006
		Age	0.307	0.103 (82)	2.976	0.004
	c. including both captures	Julian date	0.063	0.022 (90)	2.930	0.004
		Julian date^2	-0.0004	0.0001 (90)	-3.034	0.003
		Age	0.335	0.100 (90)	3.347	0.001
Prairie Warbler	a. excluding second capture	Julian date	0.086	0.029 (17)	2.955	0.009
		Julian date^2	-0.0007	0.0002 (17)	-3.229	0.005
	b. excluding first capture	Julian date	0.056	0.026 (17)	2.141	0.047
		Julian date^2	-0.0005	0.0002 (17)	-2.461	0.025
	c. including both captures	Julian date	0.060	0.027 (18)	2.285	0.035
		Julian date^2	-0.0005	0.0002 (18)	-2.585	0.019

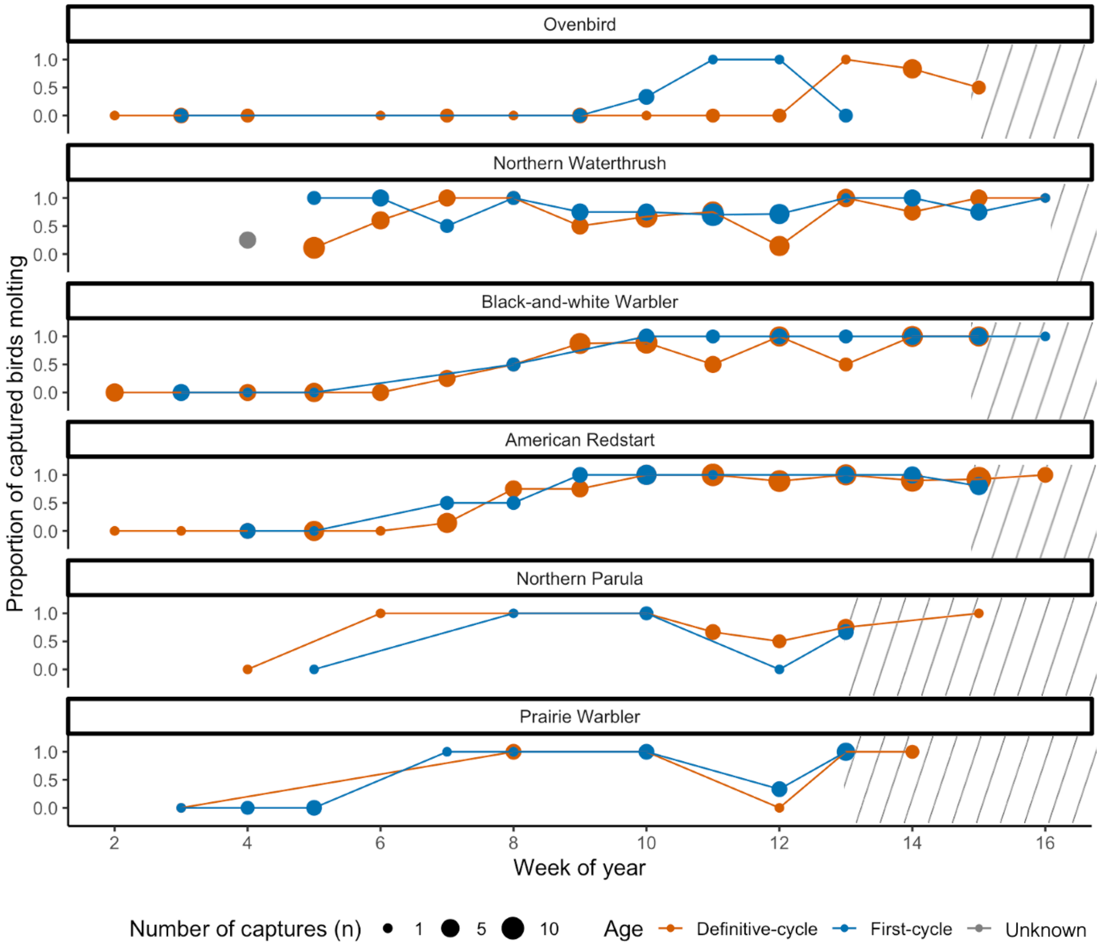

Figure A1.1. The proportion of captured birds of six species, split by age class molting by week of year from 13 January through 18 April 2023, at Font Hill Nature Preserve, Jamaica. The size of the circles represents the number (*n*) of captured birds of each age class per week. The hatched area shows where the molting period overlaps with the early end of migration departure windows from Jamaica for each species, based on eBird data (Fink et al. 2023) and unpublished tracking data from the study site (*unpublished data*, BCD and PPM).

Table A1.2 Sample sizes of the numbers of six species molting and not molting at capture, after the observed onset of molt, used as input for a Pearson's chi-squared test.

Species	# molting	# not molting
Ovenbird	10	8
Northern Waterthrush	75	36
Black-and-white Warbler	62	8
American Redstart	89	14
Northern Parula	14	5
Prairie Warbler	18	3

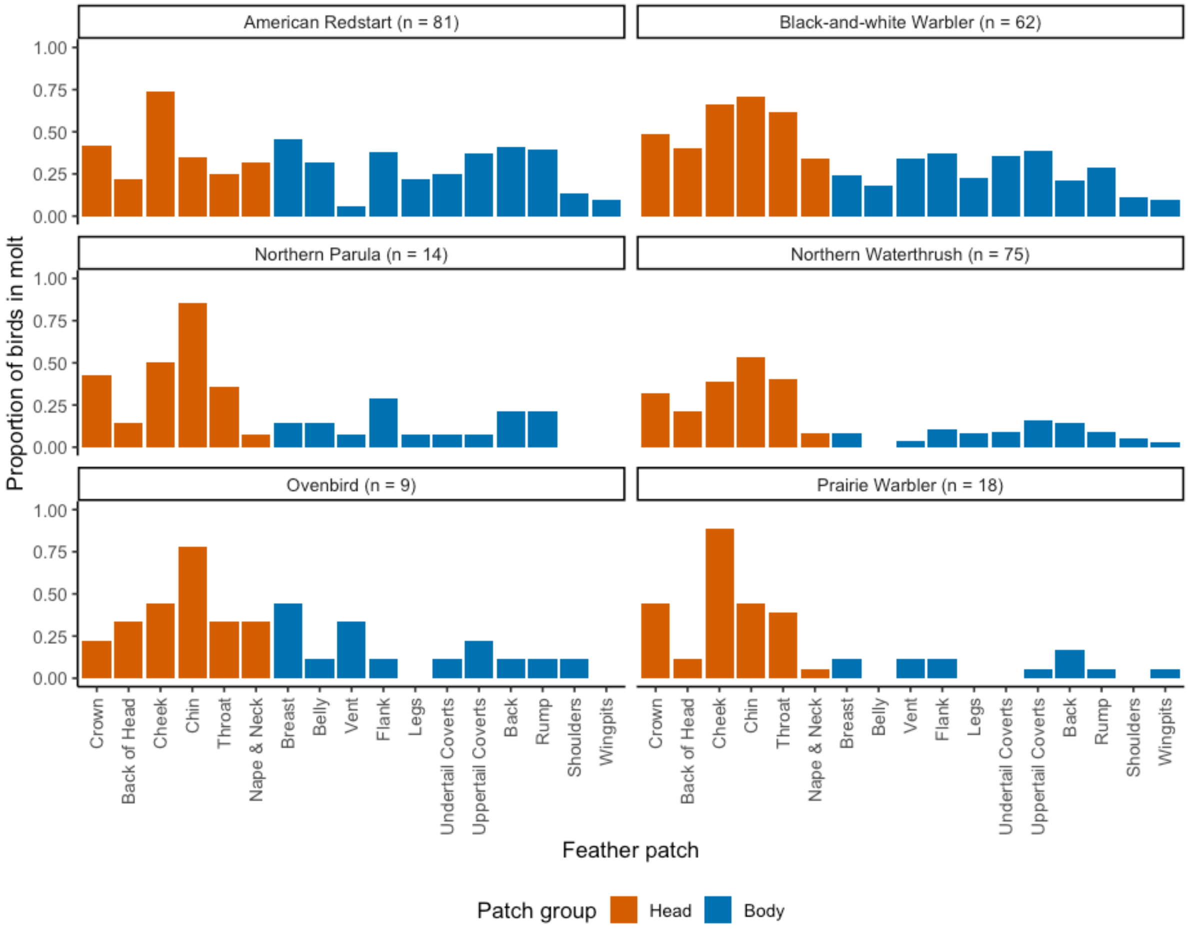

Figure A1.2. The proportions of birds from six species molting each of 17 contour feather patches captured from 13 January through 18 April 2023, at Font Hill Nature Preserve, Jamaica. To highlight that molt intensity tended to be greater in patches on the head than on the body, we show patches on the head in orange and patches on the body in blue.

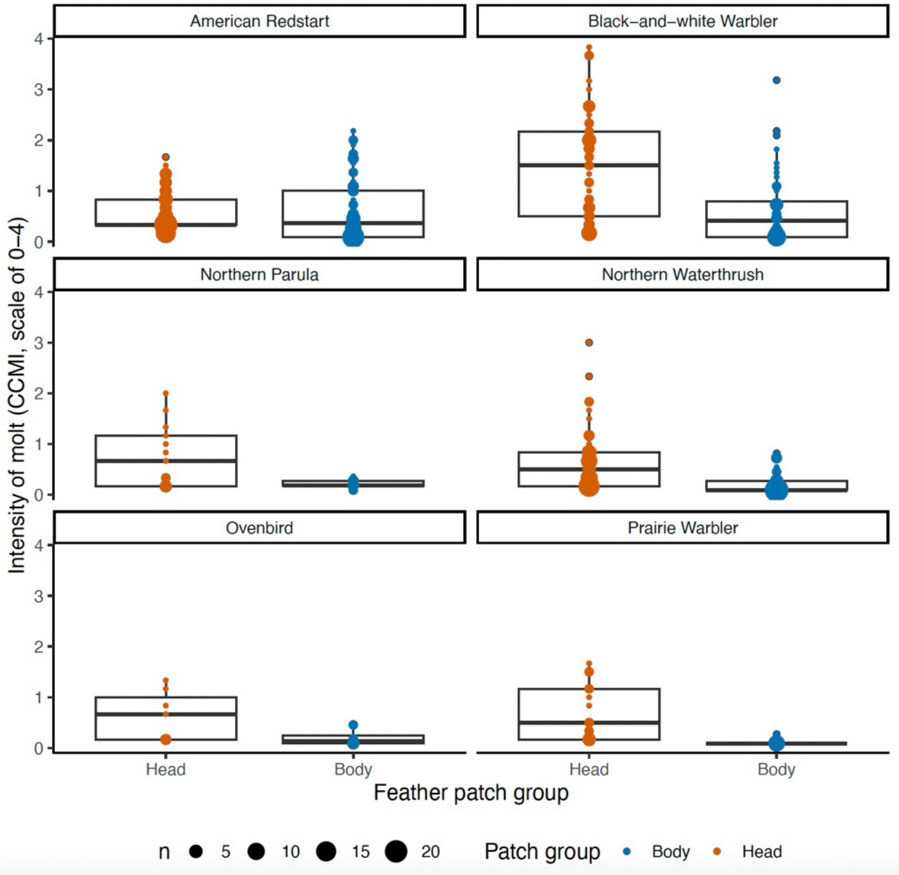

Figure A1.3. The intensity of molt, measured as a Combined Contour Molt Index on a scale of zero to four, for head feathers and body feathers in six species captured from 13 January through 18 April 2023, at Font Hill Nature Preserve, Jamaica. The size of the circles represents the number (*n*) of birds sampled that had the corresponding molt intensity score for each patch group. For each bird sampled, we scored the intensity of molt on a scale of zero to four in each of 6 feather patches on the head and 11 on the body. We then used those scores to calculate a Combined Contour Molt Index for each of the head and body, by summing the patch scores and dividing by the number of patches (6 for the head, 11 for the body).