Preformative molt extent of *Cardellina* warblers increases with breeding latitude and migration distance

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ABSTRACT—The New World warbler genus *Cardellina* consists of 3 long-distance migrants breeding in boreal and montane forests (Canada [*C. canadensis*], Wilson's [*C. pusilla*], and Red-faced [*C. rubrifrons*] warblers) and 2 sedentary species living in montane forests of northern Central America (Red [*C. rubra*] and Pink-headed [*C. versicolor*] warblers). We quantified wing-feather molt extent and frequency of wing-feather replacement of the preformative molt for all 5 species, then used these data to test whether the preformative molt extent is influenced by breeding latitude and migration distance. Our dataset consisted of molt cards from a published dataset and 2 online photographic libraries. Due to the small number of sampled species, we applied a 3-way approach: (1) comparison of molt extent among species using a post hoc pair-wise *t*-test; (2) comparison of molt extent between migratory and sedentary species using phylogenetic ANOVA; (3) PGLS regression of molt extent on breeding latitude and on migration distance. Contrary to our prediction, sedentary species had significantly lower molt extents, and a linear, although not significant, increase with breeding latitude and migration distance. We propose that loss of migratory behavior allowed Red and Pink-headed warblers to allocate resources to the synthesis of more energy-costly pigments. *Received 26 April 2022. Accepted 8 December 2022.*

Key words: carotenoid pigmentation, citizen science, Macaulay library, Naturalista, Neotropical warblers.

La extensión de la muda preformativa en el género *Cardellina* aumenta con la latitud de cría y la distancia de migración

RESUMEN (Spanish)—El género *Cardellina* de chipes del Nuevo Mundo consta de 5 especies migratorias de larga distancia que se reproducen en bosques montanos y boreales (*C. canadensis*, C. pusilla y *C. rubrifrons*) y 2 especies sedentarias que viven en los bosques de montaña del norte de América Central (*C. rubra* y *C. versicolor*). Cuantificamos la extensión y la frecuencia de reemplazo de las plumas del ala en la muda preformativa de estas 5 especies, luego usamos estos datos para probar si la extensión de la muda preformativa disminuye a medida que aumenta la latitud de cría y la distancia de migración. Nuestro conjunto de datos constaba de fichas de muda de 1 base de datos pública y de 2 colecciones fotográficas. Debido al pequeño número de especies que componen el género *Cardellina*, aplicamos un enfoque de 3 vías: i) comparación de la extensión de la muda entre especies usando una t de Student post-hoc comparando pares de especies; ii) comparación de la extensión de la muda entre especies migratorias y sedentarias utilizando una ANOVA filogenética; iii) Regresión PGLS de la extensión de la muda sobre la latitud de cría y sobre la distancia de migración. Contrariamente a nuestra predicción, las especies sedentarias mostraron extensiones de muda significativamente menores (las 3 especies migratorias reemplazaron de 4–6 plumas más) y un aumento lineal, aunque no significativo, con la latitud de cría y la distancia de migración. Proponemos que la pérdida del comportamiento migratorio permitió a *C. rubra* y *C. versicolor* ahorrar recursos y destinarlos a la síntesis pigmentos más costosos energéticamente.

Palabras clave: biblioteca Macaulay, ciencia ciudadana, Naturalista, parúlidos neotropicales, pigmentación por carotenoides.

Despite being one of the most important stages in a bird's annual cycle, our knowledge on many aspects of molt remains deficient (Bridge 2011, Guallar 2021). Although this knowledge has been especially limited outside the Holarctic region, the Neotropics have seen a growing interest in the study of molt in the last 3 decades (Wolfe and Pyle 2012, Rueda-Hernández et al. 2018), including adaptation of terminology (Johnson et al. 2011, Wolfe et al. 2014, Howell and Pyle 2015, Pyle 2022a) and documentation of molt extent, timing, and duration (Thompson and Leu 1995, Marini

and Durães 2001, Gómez et al. 2012, Johnson et al. 2012, Johnson and Wolfe 2017).

Many of these efforts have used data retrieved from long-term bird-banding studies, and have produced practical guidelines to age and sex determination (e.g., Pyle et al. 2004, 2015; Guallar et al. 2009, Johnson and Wolfe 2017). Furthermore, researchers have resorted to scientific specimen collections to obtain molt information for wider distributional, environmental, and time ranges, as well as for studying species for which field studies have yielded insufficient information (Guallar et al. 2016, 2018, 2021a), altogether allowing a deeper understanding of molt strategies and their evolution within and among passerine species (Delhey et al. 2020, Guallar et al. 2021b). However, modern scientific sources of avian information have expanded beyond museum collections, increasingly incorporating digital re-

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Table 1. Bootstrapped estimates (mean and 95% confidence intervals) of preformative wing-feather molt extent for the 5 *Cardellina* species. Migration distance retrieved from Dufour et al. (2020). Breeding latitude calculated from the centroid of the species' range (weighed mean of the centroids when species has discontinuous range).

Species (*n*)	Mean extent [CI]	Migration distance (km)	Breeding latitude (°)
Canada Warbler (15)	21.5 [21.1 – 21.9]	4,356	49.77
Wilson's Warbler (61)	21.0 [20.6 – 21.3]	3,687	56.96
Red-faced Warbler (12)	20.3 [19.8 – 20.7]	1,058	29.63
Red Warbler (13)	15.7 [15.0 – 16.3]	176	20.13
Pink-headed Warbler (6)	16.0 [15.2 – 16.9]	57	15.42

sources, many of them based on citizen science (Pyle 2022b). Among these are online photographic archives of biodiversity such as Macaulay Library (macaulaylibrary.org), which has a worldwide scope, and Naturalista (naturalista.mx), which is focused on Mexico. This article applies information retrieved from these 2 websites to fill a small gap in our knowledge of molt of Neotropical passerines, specifically focusing on the preformative molt of *Cardellina* warblers.

The genus *Cardellina* consists of 5 species that breed in North and Central American forests (Chesser et al. 2021). Two breed in boreal and montane forests in the United States and Canada: Canada Warbler (*C. canadensis*) and Wilson's Warbler (*C. pusilla*), which are long-distance migrants formerly placed in the genus *Wilsonia* (Ammon and Gilbert 2020, Reitsma et al. 2020). Red-faced Warbler (*C. rubrifrons*) is a medium-distance migrant with populations breeding in montane forests of the southwestern United States and northern Mexico and wintering southward along the Sierra Madre Occidental down to Guatemala and Honduras. The last 2 *Cardellina* species were formerly placed in the genus *Ergaticus*: Red Warbler (*C. rubra*) and Pink-headed Warbler (*C. versicolor*), which are sedentary endemics to the highlands of Mexico and Guatemala, overlapping in central Chiapas (Dreelin 2020, Martin and Barber 2020, Partida-Lara et al. 2020).

The preformative molt of the 3 migratory *Cardellina* species includes all body feathers and lesser and median coverts, and a variable number of greater coverts, alula feathers, and tertials (Pyle 1997a, 1997b; Guallar et al. 2009). However, this information is entirely lacking for the 2 sedentary species. The first objective of this study is to quantify wing-feather molt extent and frequency of

wing-feather replacement of the preformative molt for all 5 *Cardellina* species. This knowledge would not only enhance our ability to age individuals in monitoring projects, it could be directly used to test hypotheses on the evolutionary drivers of molt extent across and within passerine genera (Guallar et al. 2021b, Pérez-Granados et al. 2021). For example, birds synchronize their circannual cycles, including molt, with changes in photoperiod (Gwinner 1986, Dawson 2007). Passerines use day-length reduction as a cue to initiate the preformative molt, resulting in late-hatched birds having less time to molt and undergoing smaller molt extents (Bojarinova et al. 1999, Elrod et al. 2011). Time constraints could even be stronger in migratory species, especially in those that engage in long-distance migrations and breed at high latitudes (Kiat and Izhaki 2016). Thus, the second objective of this study is to test within the genus *Cardellina* the hypothesis that preformative molt extent is influenced by time constraints. According to this hypothesis, preformative molt extent before migration is expected to decrease as breeding latitude and migration distance increase

Methods

Information on preformative molt of *Cardellina* species was retrieved from Macaulay Library and Naturalista and a published dataset (Guallar and Jovani 2019). Our final dataset consisted of 107 molt cards: 40 new molt cards for Red-faced, Canada, Red, and Pink-headed warblers obtained from the online libraries, and 67 molt cards for Wilson's and Red-faced warblers from the published source (Table 1, Supplemental Table S1). We selected images from the photographic libraries that provided a complete view of the bird's alar

tracts, avoiding low resolution or blurred images, regardless of the year they were taken. Since Canada, Wilson's, and Red-faced warblers do not molt wing feathers during the boreal winter period neither during their first annual cycle nor during subsequent annual cycles (Pyle 1997a, Guallar et al. 2009), we were able to use all available images (and published molt cards) regardless of month. Given that Parulidae undergo a partial preformative molt during their first annual cycle (Pyle 1997a, Guallar et al. 2009, Wolfe et al. 2010), we looked for birds with retained juvenile feathers in the wing and tail, which were considered in formative plumage. Molt limits and juvenile feathers were detected using contrasts in color, shape, and wear among formative and juvenile wing and tail feathers (Pyle 1997a). To enable recognition of juvenile feathers, we previously examined birds in juvenile plumage from both field captures and images.

Our data on molt extent among wing feathers were taken only from birds in non-active molt on each of the 9 visible primaries, 6 secondaries, 3 tertials, 3 alula feathers, 9 primary coverts, carpal covert, 10 greater coverts, and 8 median coverts on the upper wing, to determine whether each was replaced during the preformative molt, and scored 1 if replaced and 0 if retained. Replaced lesser coverts were scored as an approximate fraction of this tract, from none (0) to all (1). Wing-feather molt extent was computed as the sum of feather scores for the wing.

Migration distance was obtained from Dufour et al. (2020). Breeding latitude was obtained from each species' geographic range from BirdLife International and Handbook of the Birds of the World (2021). We computed centroid coordinates for the breeding and wintering ranges using QGIS (QGIS Development Team 2022). For species with discontinuous ranges, we calculated average centroids weighing for the area of each polygon (Table 1).

Statistical analyses

All analyses were carried out within the R environment (R Core Team 2022). To estimate sample mean and 95% confidence intervals for the wing-feather molt extent, we applied Bayesian bootstrapping using default settings (4,000 itera-tions), as implemented in the library *bayesboot* (Bååth 2016). Bootstrapping is a resampling technique not limited by the assumptions of parametric approaches, and therefore is adequate for small datasets and/or variables that do not reasonably fit a known distribution.

Cardellina is formed by only 5 extant species, a low sample size from which to draw robust statistical inference using phylogenetic regression, which takes each species as a case. Therefore, we applied a 3-way approach to test the hypothesis according to which preformative molt extent is influenced by time constraints. First, we compared molt extent among species using a post hoc pairwise *t*-test corrected by the Holm method (Holm 1979). Our last 2 approaches took into account that species traits are phylogenetically conserved, so that trait correlation among species tends to be higher as the phylogenetical distance among species is reduced, thus violating the non-independence assumed by most statistical analyses. Thus, we compared mean molt extent between migratory and nonmigratory species using the function *aov.phylo* as implemented in package *geiger* (Harmon et al. 2008). Finally, we applied phylogenetic generalized least squares (PGLS) regression to the mean molt extent on breeding latitude and on migration distance using function *phylolm* implemented in the *phylolm* package (Ho and Ané 2014). For both models, we obtained 2 values of R^2 using function *R2.lik* from the package *rr2* (Ives and Li 2018). This function compares the likelihood of the model of interest with a given null model. Here, we compared each PGLS with 2 null models: (1) a simple linear regression with neither the independent variable nor the phylogeny effect, and (2) a phylogenetic linear regression without the independent variable. Thus, the first R^2 value quantifies the effects of the independent variable and phylogeny (equivalent to R^2 conditional), whereas the second R^2 value estimates the contribution of the independent variable without accounting for the effect of the phylogeny. To build our phylogeny for the *Cardellina* species, we downloaded 1,000 trees from BirdTree.org (Ericson backbone; Jetz et al. 2012), derived a consensus tree with least-squares branch lengths using package *phytools* (Revell 2012), and forced tips to be contemporaneous (Pagel 1992). Then, we rooted the phylogenetic

tree using Red-breasted Chat (*Granatellus venus-tus*) as outgroup.

Results

Preformative molt extent and frequency of feather replacement

We reviewed ~5,000 images published in Naturalist and Macaulay Library: all 2,158 photographs from the Red and Pink-headed warblers, about 30% of the 4,037 photographs from the Red-faced Warbler, and about 10% of the 21,691 published photographs from the Canada Warbler. From these images, we filled in 40 wing-feather molt cards that were added to the 67 molt cards gathered from a published dataset. Retained juvenile coverts in first-cycle Red and Pink-headed warblers are dull orangish, strongly contrasting with the fresh red formative feathers (Fig. 1). Retained juvenile feathers in first-cycle of the other 3 *Cardellina* species are dull grayish, contrasting with the bluish or greenish formative coverts (Pyle 1997a; Fig. 1).

Replacement of tertials was only found in 10 individuals belonging to all species except Pink-headed Warbler. The lesser alula feather was replaced in 74 individuals, although it was always retained in Red and Pink-headed warblers. Only 4 Canada and 7 Wilson's warblers replaced the central alula feather, whereas the greater alula was always retained. Greater coverts were fully replaced by 87 birds, although Red and Pink-headed warblers always retained some outer ones. Median and lesser coverts and all body feathers were replaced in 100% of birds. Primaries, secondaries, and primary coverts were always retained.

Effect of time constraints on preformative molt extent

Canada, Wilson's, and Red-faced warblers (group of northern species) replaced 4–6 more feathers during their preformative molt than the group of southern species, Red and Pink-headed warblers (pairwise *t*-test: $P < 0.001$ for all species-pair comparisons between these 2 groups, whereas all comparisons within these groups were nonsignificant; Table 1). The same differences were also detected when grouping species by migratory behavior (Table 1): resident species had significantly lower molt extents (phylogenetic ANOVA:

$F_1 = 115.24$, $P = 0.005$). Indeed, molt extent showed a linear increase with breeding latitude and migration distance although the trend was not significant due to the large confidence intervals for the PGLS (molt extent on breeding latitude: $t = 1.98$, $P = 0.14$, $R^2adj = 0.42$; molt extent on migration distance: $t = 2.09$, $P = 0.13$, $R^2adj = 0.46$; Fig. 2). However, ordinary least square regression showed significant increases suggesting that the lack of significance of PGLS was caused by small sample size (molt extent on breeding latitude: $t = 3.27$, $P = 0.047$, $R^2adj = 0.71$; molt extent on migration distance: $t = 16.35$, $P = 0.053$, $R^2adj = 0.68$; Fig. 2). Bivariate models accounted for nearly 60% of the variation in molt extent (conditional $R^2_{breedlat} = 0.60$ and conditional $R^2_{migrdist} = 0.58$), but most of this was due to shared phylogenetic history, since the explanatory variables only explained 1.2–1.3% variation of each model.

Discussion

We have further shown the utility of online-image libraries based on citizen science as valuable resources to cover gaps of knowledge on passerine molt (see also Pyle 2022b). Advantages of using these resources include fast and cheap data collection within and across many years, especially of species that rarely get mist-netted or with little information from winter grounds; further, photographs can be easily checked for later examination and multiple researchers. However, image libraries also have limitations. The vast majority of photographs show birds in odd angles that only allow for partial molt examination (if at all), the quality of a high fraction of the images is deficient, and molt data retrieved from images cannot be cross-checked against biometric data or other in-hand information such as skull condition or extent of pin feathers indicating body molt. Photographs showing lateral and dorsal views of birds in all plumages throughout the whole annual cycle are highly valuable to molt studies, and as digital collections grow in size, we anticipate their value to increase for studies of molt.

Specifically, we have used the genus *Cardellina* as a study case for this novel approach. We first described the preformative molt extent and

frequency of wing-feather replacement of all 5 species in the genus, and then tested whether breeding latitude and migratory distance may have shaped the evolution of their preformative molt extent.

Preformative molt extent and frequency of feather replacement

Following the most common pattern among New World warblers, the 3 northern *Cardellina* species generally replace all wing coverts but few or no tertials as previously reported (Pyle 1997a, 1997b; Guallar et al. 2009). Most of the variation was found within the carpal alular area, affecting the number of replaced alula feathers, carpal covert, and outer greater coverts, which are a mere 3% of the wing-feather mass (Guallar and Jovani 2020). Although small, these differences are consistent among the sedentary Red and Pink-headed warblers and the migratory *Cardellina* species.

Effect of time constraints on preformative molt extent

Contrary to our prediction, we found that preformative molt extent increased with breeding latitude and migration distance, thus matching the effect that was found for the preformative molt extent in the Cardinalidae family (Guallar et al. 2021b) and for the completeness of the preformative molt across the order Passeriformes (Delhey et al. 2020). The increase of preformative molt extent with migration distance in *Cardellina* species could be an adaptation to increased solar abrasion during migration, especially if they would stop over to refuel in open areas with high sun exposure (Bergman 1982, Newton 2007). Lack of selective pressure of migration on Red and Pink-headed warblers would have reduced investment in preformative molt extent, therefore allowing them to reallocate these freed physiological resources to a more expensive plumage coloration (Terrill et al. 2020).

Contrastingly, the preformative molt extent in the genus *Oenanthe* prior to southbound migration was found to decrease with breeding latitude and migration distance (Pérez-Granados et al. 2021). This contradiction could be explained by a decrease in solar irradiance with latitude or even by the slower metabolism of tropical bird species

(Wiersma et al. 2007): at equal time constraints, species with slower metabolism would replace fewer wing feathers; however, as at least some *Oenanthe* species appear to suspend preformative molt for migration (Cramp 1988), more study is needed on the effect of migration distance and molt after accounting for molt suspension (cf. Pyle 2022a). The little variation explained by our 2 proxies of time constraint suggest that factors other than time are likely influencing preformative molt extent in *Cardellina*. One factor that could explain constancy of molt extent within the 3 northern species is the unusual preformative molt undergone by most northern-breeding wood-warbler species, which may begin in the nest, complete shortly after fledging, and affect all secondary coverts synchronously (Pyle et al. 2015). However, we do not know whether the southern *Cardellina* species have a later and more prolonged preformative molt strategy.

Otherwise, our results highlight the large influence of shared evolutionary history shaping the preformative molt extent in the genus *Cardellina*. Concretely, differences in preformative molt extent between the sedentary Red and Pink-headed warblers and their migratory congenerics associate with the recent branching of the former 2 species (Winger et al. 2012). *Cardellina* species have similar sizes and diet, and occupy a similar habitat (save Canada Warbler, which winters in South America; the other 4 species can be found in the same forests during winter and even forage in the same mixed flocks; pers. obs.), suggesting that the evolutionary shift toward a reduction in molt extent in Red and Pink-faced warblers does not seem to correlate to an ecological adaptation (Guallar et al. 2016, 2021b).

Following, we propose an additional explanation linking plumage coloration and the loss of selective pressure of migration in the genus *Cardellina*. Lack of migratory selective pressure on Red and Pink-faced warblers would reduce investment on preformative molt, allowing them to reallocate physiological resources that later could have driven evolutionary shifts in plumage coloration (Terrill et al. 2020). Birds obtain yellow and some red pigments from carotenoids in the diet. These pigments act as honest signals of individual quality because they indicate diet quality, which correlates with territory quality or ability to compete for food resources with
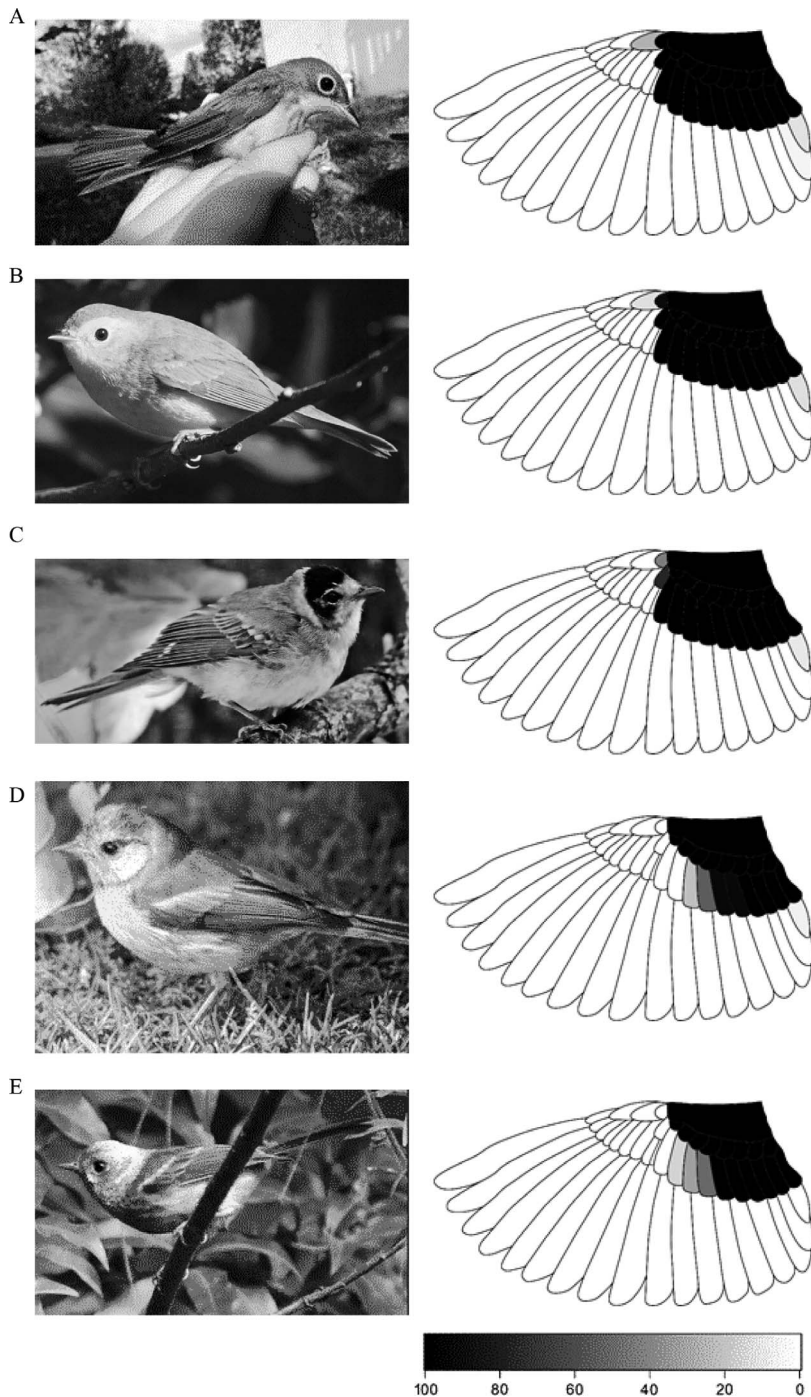
Figure 1. Preformative molt in *Cardellina* species. Left, formative plumage. (A) Canada Warbler: formative body feathers, carpal, lesser, median, and greater coverts, as well as the lesser alula (14 Aug 2018 Maison de la Mer, La Haute-Côte-Nord). (B) Wilson's Warbler: formative body feathers, carpal, lesser, median, and greater coverts, and lesser alula (19 Sep 2009 Cromwell Valley, Hampton). (C) Red-faced Warbler: formative body feathers, lesser, median, and 7 innermost greater coverts (14 Jul 2021 Santa Catalina Mts). (D) Red Warbler: formative body feathers, lesser, median, and 7 innermost greater coverts
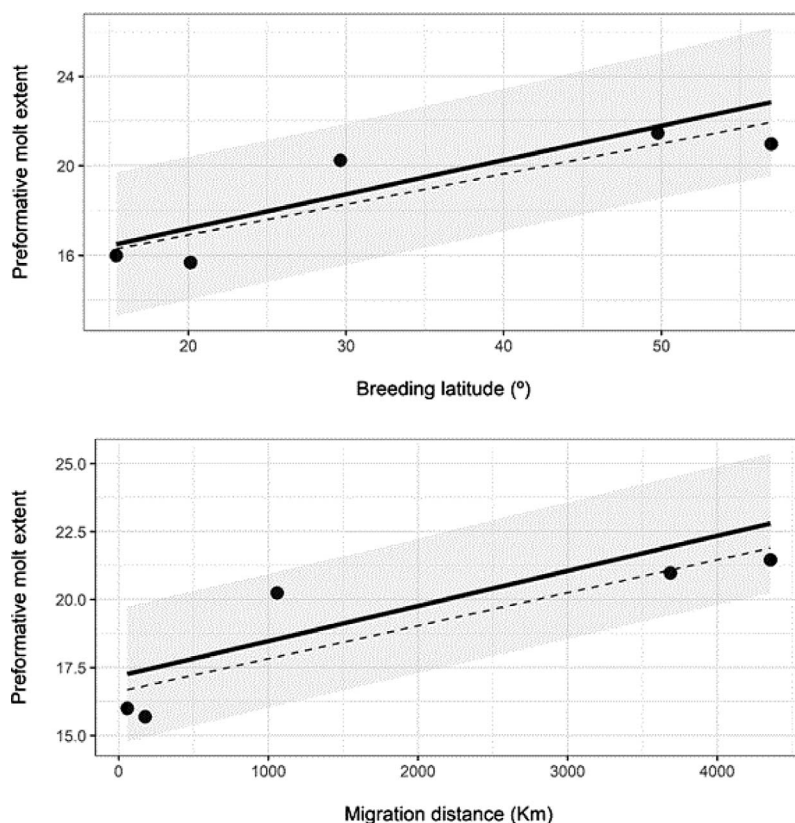
Figure 2. Phylogenetic regression models of molt extent on breeding latitude ($y = 0.115x \pm 0.058$) and on migration distance ($y = 0.001x \pm 0.0006$). Shaded areas show 95% confidence intervals. Dashed lines depict simple liner regression lines: $y = 0.136x \pm 0.041$ (breeding latitude), $y = 0.001x \pm 0.0004$ (migration distance).

conspecifics (Hill 1991), and because they are also necessary for other important physiological processes, including immune response (Chew and Park 2004). However, not all passerines deposit carotenoids in their molting feathers directly from their diets—some species transform them metabolically, thus adding an extra physiological cost to the synthesis of carotenoid-based plumage coloration (Weaver et al. 2018). One example is the transformation of some β-carotenes to red pigments through ketolation found in most bird species with red plumages (Goodwin 1986, Stradi

et al. 1998). If the yellow plumage of Wilson's and Canada warblers were based on untransformed carotenoids like in other Parulidae species (McGraw et al. 2003, Parker et al. 2003), and the red plumages of Red and Pink-headed warblers were based on transformed carotenoids, the cost of synthesizing the same feathers would be higher for the latter 2 species. Red and Pink-headed warblers could have allocated physiological resources that migratory *Cardellina* species invest in preformative molt to synthesize their costly red plumage.

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(21 Jan 2018 Cd. Universitaria, Mexico City). (E) Pink-headed Warbler: formative body feathers, lesser, median, and 7 innermost greater coverts (4 Dec 2019 San Cristóbal de las Casas, Chiapas). Right, frequency of preformative wing-feather replacement. Gray shades on wing diagrams depict observed replacement frequencies (white = 0, black = 100). Photos used by license agreement from Naturalista and the Macaulay Library at the Cornell Lab of Ornithology: © Elliott GG (A, ML365067001), Frode Jacobsen (B, 184922772), Ad Konings (C, 143784946), Jesús Alonso López Villanueva (D, 13162382), and Lev Frid (E, ML192320211).

Initial studies on the evolution of passerine molt focused on the influence of ecological factors (Svensson and Hedenström 1999, Figuerola and Jovani 2001, Guallar et al. 2016). Recently, the role of life-history factors on the preformative molt extent has gained increasing attention, including sexual dichromatism, delayed plumage maturation, and male plumage coloration (Delhey et al. 2020, Terrill et al. 2020, Kiat and Sapir 2022). In this work, we have proposed a link between plumage coloration and the evolution of the preformative molt extent through the energetic cost of plumage coloration mediated by a change in migratory behavior, presenting a third broad category that should be considered when evaluating evolutionary drivers of molt extent.

Acknowledgments

Literature cited

Ammon EM, Gilbert WM. 2020. Wilson's Warbler (*Cardellina pusilla*), version 1.0. In: Rodewald PG, editor. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.wlswar.01

Bååth R. 2016. Package 'bayesboot'. An implementation of Rubin's (1981) Bayesian bootstrap. Version 0.2.1 [cited 24 Feb 2022]. https://github.com/ rasmusab/bayesboot

Bergman G. 1982. Why are the wings of *Larus f. fuscus* so dark? Ornis Fennica. 59:77–83.

BirdLife International and Handbook of the Birds of the World. 2021. Bird species distribution maps of the world. Version 2021.1 [cited 21 Mar 2022]. http://datazone.birdlife.org/species/requestdis

Bojarinova JG, Lehikoinen E, Eeva T. 1999. Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. Journal of Avian Biology. 30:437–446.

Bridge ES. 2011. Mind the gaps: What's missing in our understanding of feather molt. Condor. 113:1–4.

Chesser RT, Billerman SM, Burns KJ, Cicero C, Dunn JL, et al. 2021. Check-list of North American birds (online) [cited 5 Feb 2022]. American Ornithological Society. http://checklist.aou.org/taxa

Chew BP, Park JS. 2004. Carotenoid action on the immune response. Journal of Nutrition. 134:S257–S261.

Cramp S, editor. 1988. The birds of the Western Palearctic. Vol. 5. Oxford (UK): Oxford University Press.

Dawson A. 2007. Seasonality in a temperate zone bird can be entrained by near equatorial photoperiods. Proceedings of the Royal Society of London B. 274:721–725.

Delhey K, Guallar S, Rueda-Hernández R, Valcu M, Wang D, Kempenaers B. 2020. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. Journal of Animal Ecology. 89:2896–2908.

Dreelin A. 2020. Red Warbler (*Cardellina rubra*), version 1.0. In: Schulenberg TS, editor. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.redwar1.01

Dufour P, Descamps S, Chantepie S, Renaud J, Guéguen M, et al. 2020. Reconstructing the geographic and climatic origins of long-distance bird migrations. Journal of Biogeography. 47:155–166.

Elrod ML, Seavy NE, Cormier RL, Gardali T. 2011. Incidence of eccentric molt in first-year Wrentits increases with fledge date. Journal of Field Ornithology. 82:325–332.

Figuerola J, Jovani R. 2001. Ecological correlates in the evolution of moult strategies. Evolutionary Ecology. 15:183–192.

Gómez C, Botero-Delgadillo E, Bayly NJ, Moreno MI, Páez CA. 2012. Documentando estrategias de muda naves neotropicales: Ejemplos de la Sierra Nevada de Santa Marta, Colombia [Documenting molt strategies in Neotropical birds: examples from the Sierra Nevada de Santa Marta, Colombia]. Ornitología Neotropical. 23:S129–S138. Spanish.

Goodwin T. 1986. Metabolism, nutrition, and function of carotenoids. Annual Review of Nutrition. 6:273–297.

Guallar S. 2021. Structure, regulation, and evolution of passerine molt [dissertation]. Barcelona (Spain): University of Barcelona.

Guallar S, Jovani R. 2019. Data from: Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny [cited 24 Feb 2022]. https://doi.org/10.6084/m9.figshare.9896516

Guallar S, Jovani R. 2020. Data from: Moult nestedness and its imperfections: Insights to unravel the nature of passerine wing-feather moult rules [cited 24 Feb 2022]. https://figshare.com/articles/dataset/Moult_nestedness_and_its_imperfections_insights_to_unravel_the_nature_of_passerine_wing-feather_moult_rules/12782153/3

Guallar S, Rueda-Hernández R, Pyle P. 2021a. Preformative molt in Neotropical Cardinalidae. Ornithology Research. 28:250–257.

Guallar S, Rueda-Hernández R, Pyle P. 2021b. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. Ornithology. 138:ukaa070.

Guallar SX, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P. 2016. Molt strategies of ten Neotropical forest passerine species. Wilson Journal of Ornithology. 128:543–555.

Guallar SX, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P. 2018. Preformative wing molt in 23 Neotropical resident passerine species. Ornitología Neotropical. 29:S3–S10.

Guallar S, Santana E, Contreras S, Verdugo H, Gallés A. 2009. Paseriformes del Occidente de México: Morfometría, datación y sexado [Passerines from

Western Mexico: Morphometry, aging and sexing]. Barcelona: Museu de Ciències Naturals de Barcelona. Spanish.

Gwinner E. 1986. Circannual rhythms. Berlin: Springer.

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: Investigating evolutionary radiations. Bioinformatics. 24:129–131.

Hill GE. 1991. Plumage coloration is a sexually selected indicator of male quality. Nature. 350:337–339.

Ho LS, Ané C. 2014. A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. Systematic Biology. 63:397–408.

Holm S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics. 6:65–70.

Howell SNG, Pyle P. 2015. Use of 'definitive' and other terms in molt nomenclature: A response to Wolfe et al. (2014). Auk. 132:365–369.

Ives AR, Li D. 2018. rr2: An R package to calculate R^2s for regression models. Journal of Open Source Software. 3:1028.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. Nature. 491:444–448.

Johnson EI, Stouffer PC, Bierregard RO. 2012. The phenology of molting, breeding and their overlap in central Amazonian birds. Journal of Avian Biology. 43:141–154.

Johnson EI, Wolfe JD, Ryder TB, Pyle P. 2011. Modifications to a molt-based ageing system proposed by Wolfe et al. 2010. Journal of Field Ornithology. 82:422–424.

Johnson EI, Wolfe JD. 2017. Molt in Neotropical birds: Life history and aging criteria. Boca Raton (FL): CRC Press.

Kiat Y, Izhaki I. 2016. Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. Journal of Avian Biology. 47:47–56.

Kiat Y, Sapir N. 2022. Evolutionary trade-off between male colouration and feather moult extent also indirectly determines female moult. Journal of Evolutionary Biology. 35:278–287.

Marini MÂ, Durães R. 2001. Annual patterns of molt and reproductive activity of passerines in SC Brazil. Condor. 103:767–775.

Martin TE, Barber PM. 2020. Red-faced Warbler (*Cardellina rubrifrons*), version 1.0. In: Poole AF, Gill FB, editors. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.refwar.01

McGraw KJ, Beebee MD, Hill GE, Parker RS. 2003. Lutein-based plumage coloration in songbirds is a consequence of selective pigment incorporation into feathers. Comparative Biochemistry and Physiology B. 135:689–696.

Newton I. 2007. The migration ecology of birds. London (UK): Academic Press.

Pagel M. 1992. A method for the analysis of comparative data. Journal of Theoretical Biology. 156:431–442.

Parker T, Stansberry B, Becker C, Gipson P. 2003. Do melanin- or carotenoid-pigmented plumage ornaments signal condition and predict pairing success in the Kentucky Warbler? Condor. 105:663–671.

Partida-Lara R, Enríquez PL, Vázquez-Pérez JR. 2020. Pink-headed Warbler (*Cardellina versicolor*), version 1.0. In: Schulenberg TS, editor. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.pihwar1.01

Pérez-Granados C, Calleja JC, Seoane J, Fernández-Tizón M, Vigalondo B, et al. 2021. Time available for moulting shapes inter- and intra-specific variability in post-juvenile moult extent in wheatears (genus *Oenanthe*). Journal of Ornithology. 162:255–264.

Pyle P. 1997a. Identification guide to North American birds. Part I: Columbidae to Ploceidae. Bolinas (CA): Slate Creek Press.

Pyle P. 1997b. Molt limits in North American passerines. North American Bird Bander. 22:49–89.

Pyle P. 2022a. Defining moults in migratory birds: A sequence-based approach. Journal of Avian Biology. 2022:e02958.

Pyle P. 2022b. Examination of digital images from Macaulay Library to determine avian molt strategies: A case study on hummingbirds. Wilson Journal of Ornithology. 134:52–65.

Pyle P, Engilis A Jr, Kelt DA. 2015. Manual para estimar edad y sexo de aves terrestres del Parque Nacional Bosque Fray Jorge y Chile Central, con notas sobre rangos de distribución y estación reproductiva [Manual for ageing and sexing landbirds of Bosque Fray Jorge National Park and north-central Chile, with notes on occurrence and breeding seasonality]. Special Publication of the Occasional Papers of the Museum of Natural Science. Baton Rouge (LA): Louisiana State University. Spanish.

Pyle P, McAndrews A, Veléz P, Wilkerson RL, Siegel RB, DeSante DF. 2004. Molt patterns and age and sex determination of selected southeastern Cuban landbirds. Journal of Field Ornithology. 75:136–145.

QGIS Development Team. 2022. QGIS Geographic Information System. QGIS Association. http://www.qgis.org

R Core Team. 2022. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Reitsma LR, Hallworth MT, McMahon M, Conway CJ. 2020. Canada Warbler (*Cardellina canadensis*), version 2.0. In: Rodewald PG, Keeney PK, editors. Birds of the world. Ithaca (NY): Cornell Lab of Ornithology. https://doi.org/10.2173/bow.canwar.02

Revell L. 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Rueda-Hernández R, Guallar S, Ruiz-Sánchez A, Pyle P. 2018. The molt issue: Where do we go from now? Ornitología Neotropical. 29:1–2.

Stradi R, Hudon J, Celentano G, Pini E. 1998. Carotenoids in bird plumage: The complement of yellow and red pigments in true woodpeckers (Picinae). Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology. 120:223–230.

Svensson E, Hedenström A. 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers. Biological Journal of the Linnean Society. 67:263–276.

Terrill RS, Seeholzer GF, Wolfe JD. 2020. Evolution of breeding plumages in birds: A multiple-step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae). Ecology and Evolution. 10:9223–9239.

Thompson CW, Leu M. 1995. Molts and plumages of Orange-breasted Buntings (*Passerina leclancherii*): Implications for theories of delayed plumage maturation. Auk. 112:1–19.

Weaver RJ, Santos ESA, Tucker AM, Wilson AE, Hill GE. 2018. Carotenoid metabolism strengthens the link between feather coloration and individual quality. Nature Communications. 9:73.

Wiersma P, Muñoz-Garcia A, Walker A, Williams JB. 2007. Tropical birds have a slow pace of life. Proceedings of the National Academy of Sciences. 104:9340–9345.

Winger BM, Lovette IJ, Winkler DW. 2012. Ancestry and evolution of seasonal migration in the Parulidae. Proceedings of the Royal Society Biological Sciences B. 279:610–618.

Wolfe JD, Johnson EI, Terrill RS. 2014. Searching for consensus in molt terminology 11 years after Howell et al.'s "first basic problem." Auk: Ornithological Advances. 131:371–377.

Wolfe JD, Pyle P. 2012. Progress in our understanding of molt patterns in Central American and Caribbean landbirds. Ornitología Neotropical. 23:S169–S176.

Wolfe JD, Ryder TB, Pyle P. 2010. Using molt cycles to categorize the age of tropical birds: An integrative new system. Journal of Field Ornithology. 81:186–194.