

# Preformative molt in Neotropical Cardinalidae

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## Abstract

Neotropical Cardinalidae consists of 40 species in 10 genera that have diversified across the Americas. We provide quantitative information on the preformative molt of 21 Cardinalidae species of seven genera, plus one Thraupidae species placed within Cardinalidae until recently. From 155 preformative molt cards, we calculated molt extent estimates, computed frequencies of molt patterns, and summarized observed frequencies of wing-feather replacement in wing diagrams. We found 17 species with partial preformative molts, four species with eccentric preformative molts (outer but not inner primaries replaced), and one species with a complete preformative molt. Preformative molt extent and patterns were similar within Cardinalidae genera, including genera with Nearctic representatives, such as the complete preformative molt of Northern Cardinal *Cardinalis cardinalis* or the eccentric molt of *Passerina* buntings. Our results cover an important gap in the knowledge of the natural history of Cardinalidae, generate important criteria to determine the age of Neotropical Cardinalidae, and provide essential information to test hypotheses on the ecology and evolution of molt in this passerine family.

**Keywords** Age determination · Bayesian bootstrapping · Molt extent · Molt patterns

## Introduction

The preformative molt occurs within the first year of life (or molt cycle) of birds and is unique to this cycle (Howell et al. 2003). It has been found to vary substantially among avian species, from absent (no feathers replaced) to complete (all feathers replaced), but is partial or incomplete in most species. There is much interest in what phylogenetic and environmental factors influence the extent of the preformative molt both

within and among bird families. For example, the preformative molt extent in passerines has been reported to correlate to breeding latitude (Kiat and Izhaki 2016), migration distance (Kiat et al. 2019a), delayed plumage maturation (Kaspar Delhey pers. comm.), habitat (Willoughby 1991), and even climate change (Kiat et al. 2019b).

Cardinalidae is a family of small to mid-sized passerine birds, which comprises 52 species in 11 genera (Klicka et al. 2007; Billerman et al. 2020). These species are distributed throughout the Americas, with 40 species residing strictly in the Neotropical region, three species breeding in both the Neotropical and the Nearctic regions, and nine species migrating between these regions to breed (Billerman et al. 2020). Most species in the family Cardinalidae are sexually dichromatic, *Caryothraustes* being the only exception. Many long-distance migrants show striking seasonal plumage changes through prealternate molts (e.g., species within *Piranga* and *Passerina*), and males in species of all genera except *Cardinalis* exhibit delayed plumage maturation (i.e., do not acquire a definitive-like appearance following the preformative molt).

Extensive basic natural history information of most Cardinalidae species has been documented (Billerman et al. 2020), especially of those species that migrate to Nearctic regions to breed (e.g., Pyle 1997a and references therein).

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However, molt strategies in Neotropical Cardinalidae are poorly understood, with more than half of the species lacking any information (Billerman et al. 2020). Thus, the objective of this study is to provide preformative molt information of Neotropical species in the family Cardinalidae (see Table 1 for species and scientific names). Having quantitative information on the preformative molt extent of Neotropical Cardinalidae will not only increase our knowledge on the biology of this family and enhance our ability to age Cardinalidae, it will also allow us to test ecological and evolutionary hypotheses (e.g., Rohwer et al. 2005; de la Hera et al. 2013).

## Methods

We obtained information on preformative molt in 22 species, 21 species of Neotropical Cardinalidae (seven genera), and one species of Thraupidae, Yellow-shouldered Grosbeak *Parkerthraustes humeralis*, placed within Cardinalidae until recently (Table 1).

We completed 142 molt cards from specimens of Neotropical Cardinalidae deposited in five museum collections in North America and Europe (see Acknowledgments) and added 13 molt cards from a large published dataset (Guallar and Jovani 2020). Molt cards present quantitative data on molt of individual wing, tail, and body feathers, as well as date and locality of collection or capture and museum where specimens are deposited (Suppl. Mat. Table S1).

## Molt data

We summarized molt information for every species following Guallar et al. (2018). For estimates of molt extent among wing feathers and rectrices, we scored non-active molt data on one wing and the tail, specifying which wing feathers and rectrices were replaced. We used established aging criteria to identify first-year birds having undergone the preformative molt, as based on feather coloration, shape, and wear (Jenni and Winkler 1994; Pyle 1997a; Suppl. Mat. Fig. S1). We aged Vermilion Cardinals *Cardinalis phoeniceus* based on juvenile specimens that were halfway or more through the complete molt sequence, as in Northern Cardinal *Cardinalis cardinalis* (Pyle 1997a). Based on date of collection and feather wear, we carefully considered whether or not any feathers may have been replaced during a first prealternate molt. Replaced formative feathers were scored 1 and retained feathers 0. The nine visible primaries, six secondaries, three tertials, three alula feathers, nine primary coverts, carpal covert, 10 greater coverts, eight median coverts on the upper wing, and the 12 rectrices were scored individually. Replaced lesser coverts were scored as an approximate percentage of the feathers forming the tract, and then expressed as a decimal (from 0 to

1). Wing-feather molt extent was computed as the sum of feather scores for the left wing, and ranged from 1 to 50 (the latter corresponding to complete molt). Tail-feather molt extent was computed as the sum of rectrix scores for the left half of the tail, and ranged from 1 to 6.

Wing-feather molt patterns are classes of observed phenotypes grouped under certain criteria of similarity (Guallar and Jovani 2020). We computed observed frequencies for each of the preformative wing-feather molt patterns present. Individuals within and among species can show more than one pattern. Briefly, there are nine wing-feather molt patterns described thus far (see details in Table 1 and Fig. 1 in Guallar and Jovani 2020): (1) complete (full replacement); (2) abridged I (retention of a variable number of secondaries); (3) abridged II (retention of a variable number of primary coverts); (4) eccentric (retention of a variable number of inner primaries, outer secondaries, and primary coverts); (5) general (replacement of coverts and tertials from leading to trailing edge); (6) proximal (replacement of coverts and tertials, prioritizing feathers closer to the body); (7) inverted (replacement of inner secondaries and secondary coverts from trailing to leading edge); (8) limited (replacement of lesser and median coverts); and (9) reduced (replacement of one to a few tertials and/or secondary coverts).

Observed frequencies of preformative wing-feather replacement for each species were computed as the arithmetic mean score of every individual wing-feather (mean percentage for the block of lesser coverts) following Guallar et al. (2018).

## Statistical analyses

We estimated sample mean and 95% density intervals of both wing-feather and tail-molt extents for every study species with  $n > 1$ . We applied Bayesian bootstrapping using default settings (4000 iterations), as implemented in the R 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 which do not reasonably fit a known distribution. Bayesian statistics add the advantage of allowing direct probabilistic statements. However, statistics cannot account for low sample size and limited geographic sampling (see Table 1). Therefore, inference from these analyses inherits the limitations of the sampled information, and variations for many species are far from being represented.

Because species' evolutionary histories are closer within than among genera, congeneric species are expected to be more similar than non-congeneric ones. To compare molt extent among species within the genera we sampled, we used ANOVA and post hoc analyses. ANOVA were not phylogenetically corrected due to the small number of comparisons (genera in our dataset contain information for up to four

**Table 1** Estimates of wing-feather and tail-feather preformative molt extent (only left wing and rectrices), and observed frequencies of molt patterns (five columns on the right) for 22 study species. Extent estimates correspond to Bayesian bootstrapped means and 95% density intervals within parentheses. It is worth noting that species with low sample size may miss rare and occasional molt patterns; therefore, estimates must be taken with caution. Bold geographic origin indicates all subspecies and countries of occurrence were sampled

Species	English name	Geographic origin	n	Wing extent	Tail extent	Complete	Abridged II	Eccentric	General	Proximal
<i>Pheucticus chrysopleus</i>	Yellow Grosbeak	GU, MX	16	20.5 (19.3–21.7)	0.1 (0–0.3)				13	3
* <i>Pheucticus tibialis</i>	Black-thighed Grosbeak	CR	1	20	1				1	1
<i>Pheucticus chrysogaster</i>	Golden Grosbeak	PE	1	17	0				1	
<i>Pheucticus aureoventris</i>	Black-backed Grosbeak	A, V	4	18.7 (15.8–21.6)	0.2 (0–0.6)				4	
* <i>Granatellus venustus</i>	Red-breasted Chat	<b>MX</b>	12	21.1 (20.7–21.4)	0.2 (0–0.4)				12	
* <i>Granatellus franciscoe</i>	Tres Marias Chat	MX	5	20.8 (20.5–21.0)	0.4 (0–1.0)				5	
<i>Granatellus sallaei</i>	Gray-breasted Chat	MX	5	21.2 (20.3–22.1)	0				5	
<i>Granatellus pelzelni</i>	Rose-breasted Chat	BG, BR, V	8	19.9 (18.2–21.3)	0				7	1
* <i>Passerina rosiata</i>	Rose-bellied Bunting	<b>MX</b>	18	24.5 (22.9–26.3)	5.9 (5.7–6)		3		14	1
<i>Passerina leclancherii</i>	Orange-breasted Bunting	<b>MX</b>	23	32.4 (31.6–33.4)	5.2 (4.5–5.7)		23			
<i>Cyanoloxia cyanoides</i>	Blue-black Grosbeak	South MX, CR, PN	5	21.6 (19.1–24.)	0				5	
* <i>Cyanoloxia rothschildii</i>	Amazonian Grosbeak	PE	1	22	0				1	
<i>Cyanoloxia brissonii</i>	Ultramarine Grosbeak	BR, CO	7	31.3 (25.3–36.7)	†2.9 (1.0–4.7)		2		1	1
* <i>Cyanoloxia glaucocaeerulea</i>	Glaucous-blue Grosbeak	North A, PR	8	29.1 (23.7–34.1)	6 (6–6)			5	2	1
<i>Piranga roseogularis</i>	Rose-throated Tanager	MX	5	20.6 (20.2–21.0)	0				5	
<i>Piranga leucoptera</i>	White-winged Tanager	MX, PN	5	21.8 (21.7–22.9)	0				4	1
* <i>Cardinalis phoeniceus</i>	Vermilion Cardinal	V	1	50	6	1				
<i>Caryothraustes poliogaster</i>	black-faced Grosbeak	GU, south MX	7	20.7 (20.3–21.2)	0				7	
<i>Caryothraustes canadensis</i>	Yellow-green Grosbeak	BG, BR	11	18.3 (16.0–20.4)	0.4 (0–0.9)				9	2
* <i>Caryothraustes celaeno</i>	Crimson-collared Grosbeak	<b>East MX</b>	9	12.2 (11.6–12.9)	0				9	
* <i>Caryothraustes erythromelas</i>	Red-and-black Grosbeak	BG	1	26	0				1	
* <i>Parkerthraustes humeralis</i>	Yellow-shouldered Grosbeak	CO	2	21.0 (19.2–22.9)	0				1	1

A Argentina, BG British Guiana, BR Brazil, CO Colombia, CR Costa Rica, GU Guatemala, MX Mexico, PE Peru, PN Panama, PR Paraguay, V Venezuela

\*Monotypic species

† Ultramarine Grosbeak tail extent ranged 0–6

species). All analyses were carried out within the R environment (R Core Team 2019).

## Results

Of our 22 study species, mean preformative wing-feather molt extent ranged from 12.2 in the Crimson-collared Grosbeak *Caryothraustes celaeno* to 50 in the Vermilion Cardinal (Table 1). Species within genera tended to have similar wing-feather molt extents. Thus, for the six genera comprising more than one species in our dataset, we only found significant differences within *Passerina* and *Caryothraustes* (Table 2). Within *Passerina*, Orange-breasted Bunting *Passerina leclancherii* replaces eight more remiges on average than Rose-bellied Bunting *Passerina rositae*. Within *Caryothraustes*, Crimson-collared Grosbeak has significantly smaller molt extent than the other three species in our dataset (Tukey test,  $P < 0.001$ ). Despite two of the four *Cyanoloxia* species regularly replacing remiges, we did not find significant differences within this genus (Tukey test,  $P > 0.05$ ) as a consequence of the wide overlap among the four species in our dataset (Fig. 1, Table 1).

Median molt extent in our dataset was 23.4. We used this value as a reference point to rank and compare relative molt extents among species and genera (Fig. 1). Thus, fifteen species in the genera *Pheucticus*, *Granatellus*, *Piranga*, *Caryothraustes*, and *Parkerthraustes* had mean wing-feather molt extents below the median, whereas six species in the genera *Cyanoloxia*, *Passerina*, and *Cardinalis* had mean molt extents above this value. Genera *Passerina*, *Cyanoloxia*, and *Caryothraustes* had species that scored both below and above this value (Table 1).

Individuals in 17 species did not replace rectrices during the preformative molt, whereas individuals from five species replaced them all (Table 1, Suppl. Mat. Table S1). Ten species had at least some individuals with incomplete rectrix replacement, often limited to the central pair.

**Table 2** ANOVA results showing comparisons of wing-feather molt extent among species within genera. All three *Cardinalis* species (not included in this analysis) undergo a complete preformative molt (Pyle 1997a). Note that species with  $n = 1$  cannot be included in the comparisons

Genus	Statistic	<i>P</i>	Species sampled
<i>Pheucticus</i>	$F_{1,18} = 1.14$	0.538	2
<i>Granatellus</i>	$F_{3,26} = 1.16$	0.344	4
<i>Passerina</i>	$F_{1,39} = 65.57$	< 0.001	2
<i>Cyanoloxia</i>	$F_{2,17} = 2.29$	0.203	3
<i>Piranga</i>	$F_{1,8} = 2.88$	0.128	2
<i>Caryothraustes</i>	$F_{2,24} = 19.85$	< 0.001	3

We found five patterns associated with the preformative molt (Table 1). The complete pattern was found in Vermilion Cardinal. The abridged II pattern was found in Ultramarine Grosbeak *Cyanoloxia brissonii*. The eccentric pattern was only found in four species of two genera (*Passerina* and *Cyanoloxia*). The general and proximal patterns were present in all species except Orange-breasted Bunting and Vermilion Cardinal. We did not find the abridged I, inverted, limited, or reduced molt patterns in any species.

Although variation among species in molt pattern was relatively high, variation within species tended to be low. Thus, for 17 species with  $n > 1$ , nine species (53%) presented only one molt pattern, five showed two patterns, two showed three patterns, and only one species, the Ultramarine Grosbeak, showed four patterns (Table 1). Because of the low sample sizes, the absolute frequencies at which molt patterns are present in our dataset are uncertain; however, relative frequencies are likely representative of the expected variation. Thus, most individuals showed the general molt pattern (69%), followed by the eccentric molt pattern (23%), and the proximal molt pattern (7%), with only two Ultramarine Grosbeaks showing the abridged II molt pattern (1%).

All species in our sample replaced lesser, median, and inner greater coverts. The frequency of replacement of the remiges was similar within genera. Thus, *Cardinalis* species replaced all remiges, and *Passerina* and *Cyanoloxia* replaced many but not all remiges (22% Rose-bellied Bunting actually retained all remiges, and Blue-black *Cyanoloxia cyanoides* and Amazonian *Cyanoloxia rothschildii* Grosbeaks never replaced primaries or secondaries). On the other hand, *Pheucticus* and some *Caryothraustes* showed a high frequency of tertial, but no other remex replacement. The remaining genera retained all remiges (Fig. 2, Suppl. Mat. Fig. S1). Thus, *Passerina* and *Cyanoloxia* are likely to show molt limits within remiges. The other five Neotropical genera in the family Cardinalidae (except *Cardinalis*, which undergoes a complete preformative molt) would typically show molt limits within alula feathers, greater coverts, and/or tertials, or between these groups and adjacent tracts.

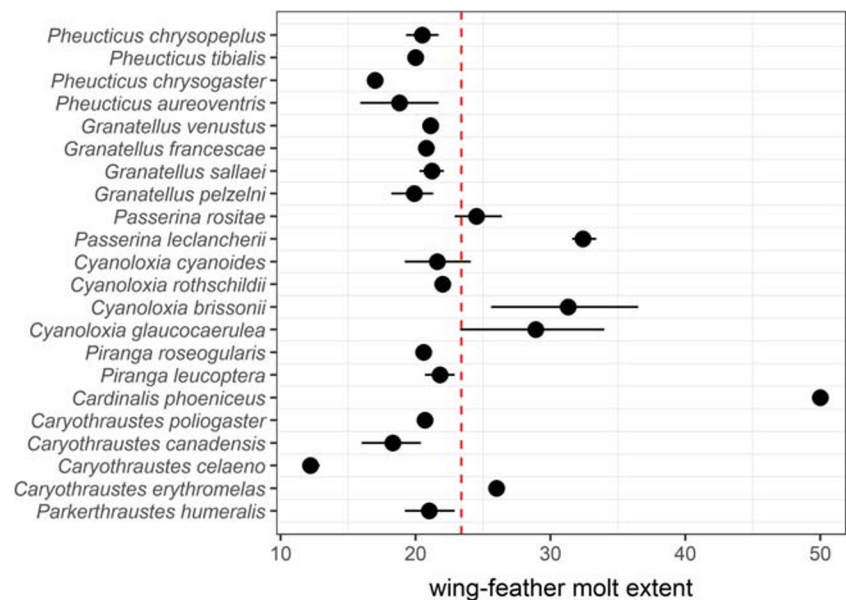
## Discussion

We have described extent, patterns, and frequency of replacement of wing-feather molt in 21 Neotropical Cardinalidae species and one close relative, Yellow-shouldered Grosbeak, currently placed within Thraupidae. Along with descriptions from six other Nearctic migrant species published elsewhere (Pyle 1997a; Guallar et al. 2009, 2016, 2018), two-thirds of the preformative molt of Neotropical species in this family are now documented.

Although uncertainty of estimates may be high for species with small sample sizes (McCarthy 2007), and infrequent or



**Fig. 1** Estimated mean (points) and 95% bootstrapped intervals (lines) of wing-feather preformative molt extent for 22 study species. Dashed red line depicts the median molt extent in our dataset. Intervals only shown for species with  $n > 1$



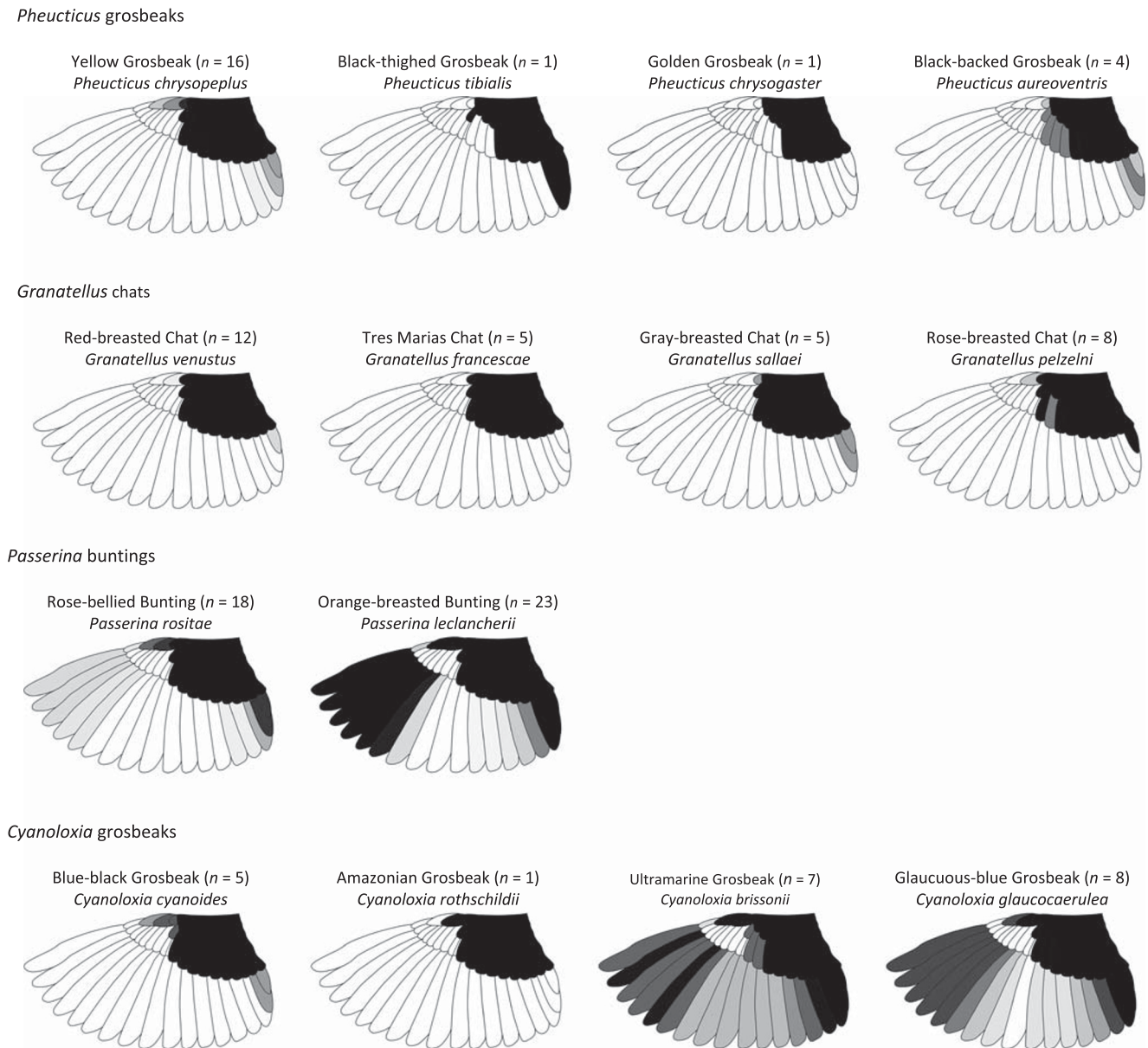
occasional wing-feather molt patterns may remain undetected for some of them, our results are consistent with the scarce information published on the preformative molt of Neotropical Cardinalidae species (Johnson and Wolfe 2018). Moreover, they support the expected similarities within passerine genera (Jenni and Winkler 1994; Pyle 1997a). For example, Neotropical species within the genera *Pheucticus* and *Granatellus* have similar estimates of molt extent and patterns (Table 1), and estimates of the extent of wing-feather molt in Neotropical species also overlap those published for north-temperate species within *Cardinalis*, *Passerina*, *Pheucticus*, and *Piranga* (Pyle 1997b). These similarities suggest phylogenetic inertia likely associated with shared ancestry and comparable natural histories and/or environments.

However, we also detected some differences within genera. The general pattern (a molt pattern that does not include primaries) is dominant in Rose-bellied Bunting, instead of the eccentric pattern (which includes outer primaries and inner secondaries), which is pervasive in the remaining *Passerina* species (Rohwer 1986; Thompson 1991; Young 1991; Pyle 1997a). This is intriguing because this species forages and nests in the same lowland areas as Orange-breasted Buntings that largely undergo an eccentric molt (Thompson and Leu 1995; Guallar and Jovani 2020). This contrast might represent an evolutionary transition toward a smaller investment in preformative molt (unpubl. data). Reasons behind this shift are obscure, but we propose four non-exclusive explanations: (1) hardening of the remex structure (e.g., via pigmentation; Burt 1979; Bonser 1995); (2) differential resource allocation during juvenile plumage growth, so that juvenile remiges become more resistant than the feathers that will be replaced during the preformative molt (de la Hera et al. 2010); (3) increased tolerance to flight-efficiency loss

(e.g., modifying behavior; Vega-Rivera et al. 1998); and (4) increased ability to reduce abrasion through behavioral adaptations (e.g., reducing insolation or contact with abrasive vegetation; Willoughby 1991).

*Passerina* species are not the only example of within-genus differences. Within *Cyanoloxia*, Ultramarine and Glaucous-blue *Cyanoloxia glaucocaerulea* Grosbeaks have a more extensive preformative molt, and the former presents more molt patterns than its congeners (Table 1), resembling more the patterns of Blue Bunting *Cyanocompsa parellina*, formerly considered congeneric. Thus, ultramarine and Glaucous-blue Grosbeaks may also have undergone an evolutionary transition toward a greater investment in preformative molt. Preformative molt extent also varies within *Caryothraustes*, from 12 in Crimson-collared Grosbeak to 26 in Red-and-black Grosbeak *Caryothraustes erythromelas*. Similarly, noticeable variations in preformative molt extents have been observed in other Neotropical passerine genera with similar natural histories (e.g., *Empidonax*, *Vireo*, *Turdus*, *Habia*, and *Spinus*; Pyle 1997a, b; Guallar et al. 2016, 2018). Further research is needed to identify environmental correlates and somatic effects to explain within-genera differences, along with possible evolutionary explanations.

This work documents preformative molt for 21 Cardinalidae species and one closely related Thraupidae species. However, this documentation is handicapped by two deficiencies that overall plague the knowledge on the preformative molt of Neotropical birds (Rueda-Hernández et al. 2018). First, it presents low sample sizes for 17 of the study species. The smaller the sample size is, the narrower the molt variation one may capture within species. While some species are known to present a wide variation both in preformative wing-feather molt pattern and extent (e.g.,



**Fig. 2** Frequency of preformative wing-feather replacement in 22 study species. Gray shades on wing diagrams depict observed replacement frequencies (white = 0, black = 100; see legend on bottom row).

Blue-black Bunting; Guallar and Jovani 2020), others are known to be quite homogeneous (e.g., many species in the family Parulidae; Guallar and Jovani 2020). This pattern can also be detected within our study species (check dispersion around the mean in Fig. 1). Thus, Red-breasted Chat *Granatellus venustus* presents a very small variation despite its moderate sample size, whereas Ultramarine and Glaucous-blue Grosbeaks present a large variation despite their low sample sizes (Fig. 1, Table 1). Since molt is one of the main natural history traits of passerines, molt changes can have profound effects on many other traits. Thus, most of the pattern and variation that we observe are a consequence of both

Specimens showing molt limits can be checked in Suppl. Mat. Fig. S1. It is worth noting that species with low sample size may miss rare and occasional molt patterns; therefore, estimates must be taken with caution

phylogenetic constraints and drastic evolutionary transitions (e.g., habitat shifts; unpubl. data).

The second deficiency in our study arises from the incomplete geographic origin of the information we could compile. This information represents neither the distribution range at country scale for 18 species nor the subspecific diversity for 11 species (Table 1). Geographic origin is considered to have an important influence on preformative molt extent variation (e.g., Kiat and Izhaki 2016). Therefore, inadequate geographic sampling may have precluded detection of differences in molt extent among subspecies with diversified ecological requirements. For example, if degree of ecological specialization is an important constraint upon preformative molt variation

*Piranga* tanagers

Rose-throated Tanager ( $n = 5$ )  
*Piranga roseogularis*

White-winged Tanager ( $n = 5$ )  
*Piranga leucoptera*



Cardinals

Vermilion Cardinal ( $n = 1$ )  
*Cardinalis phoeniceus*



*Caryothraustes* grosbeaks

Black-faced Grosbeak ( $n = 7$ )  
*Caryothraustes polioaster*

Yellow-green Grosbeak ( $n = 11$ )  
*Caryothraustes canadensis*

Crimson-collared Grosbeak ( $n = 9$ )  
*Caryothraustes celaeno*

Red-and-black Grosbeak ( $n = 1$ )  
*Caryothraustes erythromelas*



*Parkerthraustes* grosbeak (Thraupidae)

Yellow-shouldered Grosbeak ( $n = 2$ )  
*Parkerthraustes humeralis*

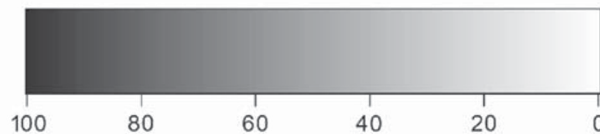
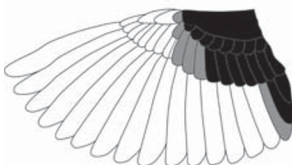


Fig. 2 (continued)

within species, we hypothesize that specialists will present smaller preformative molt variation than generalists.

The shortcomings we mentioned recommend caution before applying the results of this study. However, two lines of evidence makes us confident about the validity of our findings: (1) we found consistent results with the preformative molt information published for the Amazonian and Yellow-green *Caryothraustes canadensis* Grosbeaks (Johnson and Wolfe 2018); and (2) our data were consistent within genera (Table 2), both in this study and when compared with other well-studied congeneric species (i.e., *Pheucticus*, *Passerina*, *Piranga*, *Cardinalis*; Pyle 1997a; Table 2). We speculate that the interaction among the factors known to have influenced the evolution of passerine preformative molt and the strength

of the potential constraints (e.g., food resources) may vary sufficiently among closely related species to explain certain divergences that we have found (e.g., between the two *Passerina* buntings). For example, delayed plumage maturation is fairly common within Cardinalidae, and is known to be one of the most influential factors in the evolution of passerine preformative molt (Kaspar Delhey pers.comm.). Detectable differences between the plumage of juveniles and adults can be easily achieved simply by decreasing molt extent, thus acting as a signal of lower status, and reducing aggressive interactions with older conspecifics (Senar 2006; Guallar and Figuerola 2016). Further research on plumage, habitat, solar exposure, and migratory behavior within the family Cardinalidae may also help explain some of this variation.



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**Author contributions** All authors contributed to the study conception, data collection, and study design. Analyses were performed by S.G. The first draft of the manuscript was written by S.G., and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

## Compliance with ethical standards

**Conflict of interest** R. R-H. received a grant from Dirección General de Asuntos de Personal Académico-UNAM.

**Informed consent** Authors agreed with the content, gave explicit consent to submit the manuscript to Ornithology Research, and obtained consent from the reserves and museums where the data was gathered.

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