

RESEARCH ARTICLE

Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats

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ABSTRACT

We explored adaptive factors affecting the preformative molt in the passerine family Cardinalidae, and concluded that the ancestor inhabited forest habitats and underwent a partial preformative molt that included wing coverts but not primaries. Later radiations within the family appeared to be characterized by transitions from forests toward more open habitats, and such transitions also correlated positively with increased preformative molt investment, plumage signaling, and flight. While previous studies had highlighted the role of time and energy constraints in the evolution of the preformative molt in passerines, we conclude that adaptation to the physical environment has had a greater influence than constraints on the evolution of this molt in Cardinalidae. Using molt data from 430 individuals from 41 of the 51 Cardinalidae species, we tested whether social and environmental factors (delayed plumage maturation and habitat openness), as well as that of physiological and time constraints (body mass, migration distance, and breeding latitude), have influenced the evolution of the preformative molt in this family. We predicted that these five factors could relate to the extent of the preformative molt in terms of energy investment, plumage signaling, and flight. We also examined whether or not the presence of an auxiliary preformative molt correlated to the extent of the preformative molt. We found a strong phylogenetic signal for the preformative molt in Cardinalidae due to shared ancestry, with habitat openness correlating significantly with increased molt extent. We also found a very strong relationship with the auxiliary preformative molt, indicating that both episodes form part of the early life molt strategy in this family. Evolutionary histories and the environments to which each taxonomic group has adapted can diverge across passerines, and we expect that future studies will further discover the nature and strength of the evolutionary drivers of preformative molt.

Keywords: auxiliary preformative molt, delayed plumage maturation, Passeriformes, time and energy constraints

LAY SUMMARY

- We reconstructed the evolution and investigated the factors that have influenced molt strategies during the early life of the songbird family Cardinalidae.
- This “preformative” molt, which has evolved to meet the needs of young songbirds at least during their first fall and winter, is highly variable; even birds of the same species frequently replace different wing feathers.
- We hypothesized that this variation allows adapting to the particular environment into which bird species evolve. We explored the factors that correlate with this variation in Cardinalidae, a family distributed throughout the Americas with a wide range of ecological requirements.
- Our results indicate that the ancestor of Cardinalidae was a forest-dwelling species that did not replace primaries (the longest flight feathers) during early life, but that transition from forest to open habitats during the evolution of Cardinalidae correlated with the replacement of primaries.
- Since increased solar radiation causes feather degradation, we speculate that species that colonized open habitats increased preformative molt extent to cope with exposure to increasing radiation.
- Our findings show an adaptive mechanism linking molt extent (especially replacement of primaries) to the physical environment in songbirds.

La evolución de la muda preformativa en Cardinalidae está correlacionada con transiciones entre hábitats forestales y abiertos

RESUMEN

Estudiamos una serie de factores adaptativos que pueden afectar la muda preformativa en la familia de paseriformes Cardinalidae, y concluimos que su antepasado fue un habitante forestal con una muda preformativa parcial que incluía coberteras alares pero no primarias. Descubrimos que las radiaciones posteriores dentro de la familia se caracterizaron

por transiciones de bosques a hábitats más abiertos, y que esas transiciones también se correlacionaron positivamente con una mayor inversión y señalización de la muda preformativa, incluida una mayor frecuencia en la sustitución de primarias. Si bien estudios previos habían destacado el papel de las limitaciones de tiempo y energía en la evolución de la muda preformativa en passeriformes, descubrimos que la adaptación al entorno físico ha tenido una mayor influencia en la evolución de las especies de Cardinalidae que las restricciones temporales o energéticas. Analizamos los datos de muda de 41 de las 51 especies de Cardinalidae para probar si los factores sociales y ambientales (maduración retrasada del plumaje y la apertura del hábitat), así como las restricciones fisiológicas y temporales (masa corporal, distancia de migración y latitud de reproducción) han influido en la evolución de la muda preformativa en esta familia. Estimamos si la evolución de cada uno de estos cinco predictores se correlacionó con la inversión de energía, la señalización del plumaje y el vuelo. También examinamos su relación con la muda preformativa auxiliar. Encontramos una fuerte señal filogenética para la muda preformativa en Cardinalidae debido a la ascendencia compartida, con la apertura del hábitat como el único factor significativo, y una relación muy fuerte con la muda preformativa auxiliar, lo que indica que ambos episodios forman parte de la estrategia de muda temprana en esta familia. Dado que las historias evolutivas y los entornos a los que se ha adaptado cada grupo taxonómico pueden diferir entre passeriformes, esperamos que en estudios futuros se encuentren diferencias en la naturaleza y la intensidad de los factores evolutivos de la muda preformativa.

Palabras clave: limitaciones energéticas y temporales, maduración retrasada del plumaje, muda preformativa auxiliar, passeriformes

INTRODUCTION

Reproduction, migration, and molt, the three major life-history events of passerines, conform to annual routines (i.e. they occur with an annual periodicity; [Houston and McNamara 1999](#)). However, the first annual cycle of passerines deviates from the routines of later cycles (of adults) because of the developmental events that take place during the early life of the individual. A characteristic trait of the early life of passerine species is the preformative molt, a molt episode unique to the first cycle ([Howell et al. 2003](#)), which appears to have evolved to replace weak juvenile feathers produced rapidly in the nest ([Callan et al. 2019](#)).

The preformative molt varies across passerine phylogeny, being restricted to body feathers in some species (e.g., Garden Warbler [*Sylvia borin*]; [Jenni and Winkler 1994](#)) while involving full feather replacement in others (e.g., up to 36 species of North American passerines; [Pyle 1997a](#)). Most passerines replace some but not all wing feathers (i.e. coverts, alula, tertials, secondaries, and primaries) and these are thus particularly useful to quantify this variation, since they can be individually recognized as replaced and retained ([Jenni and Winkler 1994](#), [Pyle 1997b](#)).

Variation in the preformative molt has raised the question as to what adaptive factors may have driven its evolution from its ancestral state. Numerous studies have tried to shed light on this question by focusing on both proximate and ultimate causes. These studies have shown a negative relation between preformative (or post-juvenile) molt extent and time constraints ([Bojarinova et al. 1999](#), [Kiat and Sapir 2017](#)), as well as with energy constraints ([Gosler 1991](#), [Norman 1999](#)). Time may become a fixed constraint for long-distance migrants, the more so as breeding latitude increases, where tighter schedules may become a major driver of molt at both individual and evolutionary scales ([Figueroa and Jovani 2001](#), [Kiat et al. 2019a](#)). Physiological

constraints may have also driven evolutionary change (e.g., duration of molt increases as species size increases; [Rohwer et al. 2009](#)). Likewise, changes in ecological factors may create selective pressures, eventually triggering evolutionary changes. For example, evolutionary adaptation to a new habitat can lead to a strong lineage diversification ([Petren et al. 2005](#)), potentially driving changes in the dynamics of the preformative molt ([Hope et al. 2016](#), [Guallar and Jovani 2020a](#)).

Cardinalidae is a diverse monophyletic family of New World passerines, consisting of 51 species divided into 11 genera and 5 major clades ([Klicka et al. 2007](#), [Billerman et al. 2020](#); [Figure 1](#)). It shows wide habitat diversity from forests to open areas; it occupies an ample latitudinal range throughout the Americas; and its preformative molt has been documented for 41 species of all genera, including both Neotropical migrants (e.g., [Rohwer 1986](#), [Butler et al. 2002](#)) and Neotropical residents ([Thompson and Leu 1995](#), [Johnson and Wolfe 2018](#), [Guallar and Jovani 2020a, 2020b](#), [Guallar et al. 2021](#)), and covering all genera. Most of these species only replace wing coverts and perhaps 1–2 alula or tertials during their preformative molt; however, one-third of them regularly replace primaries, at least the ones that form the wing tip (e.g., eccentric molts in genus *Passerina*), while species in the genus *Cardinalis* undergo complete preformative molts ([Pyle 1997a](#); [Guallar et al. 2009, 2020](#)).

The Cardinalidae is also one of the passerine families with a high known frequency of auxiliary preformative molts (sensu [Pyle 2008](#)), a distinct molt episode (formerly termed “first presupplemental molt”), which has been interpreted to precede the preformative molt ([Thompson and Leu 1994](#), [Pyle 1997b](#), [Howell et al. 2003](#)). This molt is poorly understood but is reported to include most to all body plumage and some of the wing coverts ([Rohwer 1986](#), [Willoughby 1986](#)). Within a species, only early hatched individuals may undergo this molt, which

produces an ephemeral plumage that is replaced during the performative molt. The auxiliary performative molt may have been part of an early life strategy that interacts with the performative molt; however, its relationship with the latter is poorly known.

We first aimed to reconstruct the ancestral state of the performative molt within the Cardinalidae. Once obtained, we used comparative analyses to test the influence of five natural history factors on the evolution of its performative molt: delayed plumage maturation, habitat openness, migration distance, breeding latitude, and body mass. Then, we tested whether performative molt has evolved in a correlated manner with these factors, and evaluated their relative importance on the evolution of the performative molt. Because primaries are essential for flight, we examined transition rates between replacement and retention of primaries against the phylogeny.

We specifically tested four hypotheses. The first hypothesis tackles the effect of delayed plumage maturation (Rohwer et al. 1980) on the performative molt. Delayed plumage maturation and performative molt may interact through a tradeoff between sexual signaling and survival (Senar 2006). In species with selective pressure to look attractive during the first breeding season, replacing more juvenile feathers with brighter formative feathers may be beneficial, although potentially at the expense of increased aggressive interactions with older birds (Senar et al. 1998, Hawkins et al. 2012). We thus predict that both performative molt extent and probability of replacing primaries (at least the most exposed ones) would increase as the formative plumage becomes more similar to the definitive basic plumage of older birds.

The second hypothesis states that lineages that move into new environments may evolve different molt strategies as they are exposed to different selective pressures (Sol et al. 2005, Hope et al. 2016, Iglesias-Carrasco et al. 2019). For example, more abrasive habitats might exert a selective pressure to invest more in feather renewal (Willoughby 1991), whereas more open habitats may have a similar effect by increasing temperatures and solar radiation on feathers (Pyle 1998, Kiat et al. 2019b). Therefore, we expect that both performative molt extent and probability of primary molt will increase as environments become more open.

The last two hypotheses deal with constraints. First, migratory behavior and breeding latitude may have driven passerine performative molt evolution by constraining the time to molt before migration (Figueroa and Jovani 2001, Kiat et al. 2019a). Analogously, favorable weather conditions during the breeding season grow shorter as latitude increases (Dawson 2008). Therefore, we would predict that species under strong time constraints before departing the breeding grounds would decrease performative molt extent as both breeding latitude and

migratory distance increase (de la Hera et al. 2009). Finally, the time costs of molt increase as species size increases (Rohwer et al. 2009). Accordingly, we predict that the performative molt extent would decrease as body mass (a surrogate of size) increases.

METHODS

Molt and Natural History Data

We built two separate datasets, one containing molt data and a second one containing natural history and geographic information. The molt dataset contained 430 performative molt cards, collected from captured birds and specimens, from 41 Cardinalidae species (Guallar et al. 2021). We excluded 10 species because of lack of molt information: one *Amaurospiza* seedeater, seven *Habia* tanagers, and two *Piranga* tanagers; all of them forest-dwelling species (Billerman et al. 2020). Of our 430 molt cards, 294 belonged to one recently published dataset (Guallar and Jovani 2020b), and 136 molt cards were collected from museum specimens for this study (Guallar et al. 2021). Molt cards contained molt state (one replaced, zero retained) for each of the larger 49 upper wing feathers: 8 median coverts, 10 greater coverts, one carpal covert, 9 primary coverts, 3 alula feathers, 3 tertials, 6 secondaries, and 9 visible primaries. Lesser wing coverts were collectively scored one when more than 70% of these feathers were replaced and zero otherwise (Guallar and Jovani 2020a). Thus, sum of molt scores ranged from 0 to 50. Identification of first-year birds was based on established aging criteria: feather coloration, shape, and wear (Pyle 1997b). For species that also undergo prealternate molts (e.g., among genera *Piranga*, *Pheucticus*, and *Passerina*), we carefully evaluated formative feathers replaced on breeding or nonbreeding grounds, excluding first-alternate feathers replaced in spring. Finally, we gathered presence/absence data on the auxiliary performative molt for each species (Appendix Table 3).

For our second dataset, we extracted habitat information from Billerman et al. (2020), and placed our sample species into one of four broad categories based on key terms mentioned in the habitat descriptions: forest, scrub (mesic), scrub-dry (xeric), and semi-open to open habitats. These categories reflect a gradient from closed and usually cooler habitats to open and usually warmer habitats (De Frenne et al. 2019). Next, we collected body mass information from Guallar et al. (2009) and Dunning (2007). Finally, we scored delayed plumage maturation based on plumage similarity between formative and definitive basic plumage, regardless of whether or not the species was sexually dichromatic (sexually monochromatic species may potentially show delayed plumage maturation as well; Woodcock

et al. 2005). We established four categories: none (1), slight (2), moderate (3), and extensive (4), reflecting whether these two plumages were essentially identical to completely different.

To complete our second dataset, we downloaded geographic ranges from *BirdLife International and Handbook of the Birds of the World* (2019). We computed centroid coordinates for the breeding and wintering ranges using QGIS (QGIS Development Team 2020). For species with discontinuous ranges, we calculated average centroids weighing for the area of each polygon. We calculated migration distances between centroids of the wintering and breeding ranges using the R function *GeoDistanceInMetresMatrix* (Rosenmai 2014), which computes geodesic distances as implemented in package *Imap* (Wallace 2020).

Molt Extent and Primary Replacement

We quantified the influence of five natural history factors on the evolution of preformative molt of Cardinalidae species, using the extent of wing-feather molt as the response variable. Concretely, we used three molt-extent metrics: count, relative mass, and relative exposure (de la Hera et al. 2013, Kiat et al. 2019b). Count is simply the number of wing feathers replaced (it is a nondimensional metric) computed as the sum of feather scores for one wing, and ranging from 0 (no molt) to 50 (complete molt). Mass and exposure are dimensional metrics with biological meaning, as they can be conceived as proxies of investment in plumage maintenance (e.g., to keep insulation) and of plumage signaling and exposure to wear, respectively, thus allowing more explicit interpretations. Since results for all three metrics were qualitatively similar, we only showed results for the count metric, unless stated otherwise.

Since wing-feather masses for Cardinalidae species are not available, we used as a proxy a wing-feather mass model built from 82 birds from 39 Palearctic passerine species collected from traffic collisions and prey (Guallar et al. 2021). We weighed each upper-wing feather to the nearest 0.01 mg. Because of their small mass, lesser and median coverts were weighed as full tracts. Mass of lesser coverts was subsequently divided by 50 (the approximate number of these feathers on a passerine wing; Online Supplemental Material Figure 1). Mass of each of the eight median coverts was estimated from a sample of known weights (Online Supplemental Material Table 1). We calculated the mean feather mass for every species (thus giving the same weight to all species), normalized species feather masses by dividing each of them by the heaviest one, and averaged all normalized species masses to obtain a mean mass per feather across species. We imputed values for the 4.9% missing feathers in our dataset using random forest predictions (Stekhoven and Bühlmann 2012, R Core Team 2019).

Increase feather exposure leads to both increased visibility and increased wear. As with wing-feather masses, wing-feather exposures for Cardinalidae species are not available. To obtain them, we created a wing-feather exposure model from photographs of 62 live birds of 62 Palearctic species (Guallar et al. 2021). Photographs showed individuals with folded wings in a standardized upright lateral stance, such that tertials were visible (note that tertials lay on top of the other remiges). We obtained the number of pixels of each upper-wing feather using an image processing program (GIMP 1995–2017; Online Supplemental Material Table 2 and Figure 2). We divided lesser wing coverts by 50, normalized the number of pixels of every wing feather by dividing each by that of the most exposed feather, and averaged all normalized values to obtain mean exposure per feather across species. Both relative mass and relative exposure were computed as the sum of normalized values of replaced feathers for each of the 430 molt cards.

However, insulation and signaling are not the only functions carried out by wing feathers. The Flight is an essential function that is mainly executed by the primaries. For this reason, we also used the presence/absence of primary replacement to evaluate the influence of the set of natural history factors on the evolution of preformative molt of Cardinalidae.

Ancestral State Reconstruction and Correlated Evolution

For our working phylogeny, we downloaded 10,000 trees for our set of species from BirdTree.org (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). We followed Klicka et al. (2007) to name the five main assemblages of this family (Figure 1). The masked clade, which contains all the genera with a facial mask (*Piranga*, *Cardinalis*, *Caryothraustes*, and the former genera *Periporphyrus* and *Rhodothraupis*); the blue clade, which contains the species showing male blue plumage (*Amaurospiza*, *Cyanocompsa*, *Cyanoloxia*, and *Passerina*), along with *Spiza*; and three monogeneric clades containing the genera *Habia* (including the former genus *Chlorothraupis*), *Granatellus*, and *Pheucticus*. To root our tree, we used Slate-throated Redstart (*Myioborus miniatus*) as the outgroup (Guallar and Jovani 2020a).

We aimed to reconstruct preformative molt evolution along the phylogenetic tree of Cardinalidae, specifically, whether or not the ancestral species of the family replaced primaries. We calculated state likelihoods at each node of the phylogenetic tree to determine the final maximum likelihood of the ancestral state (Schluter et al. 1997). We resolved polytomies using the *rerooting* algorithm by Yang

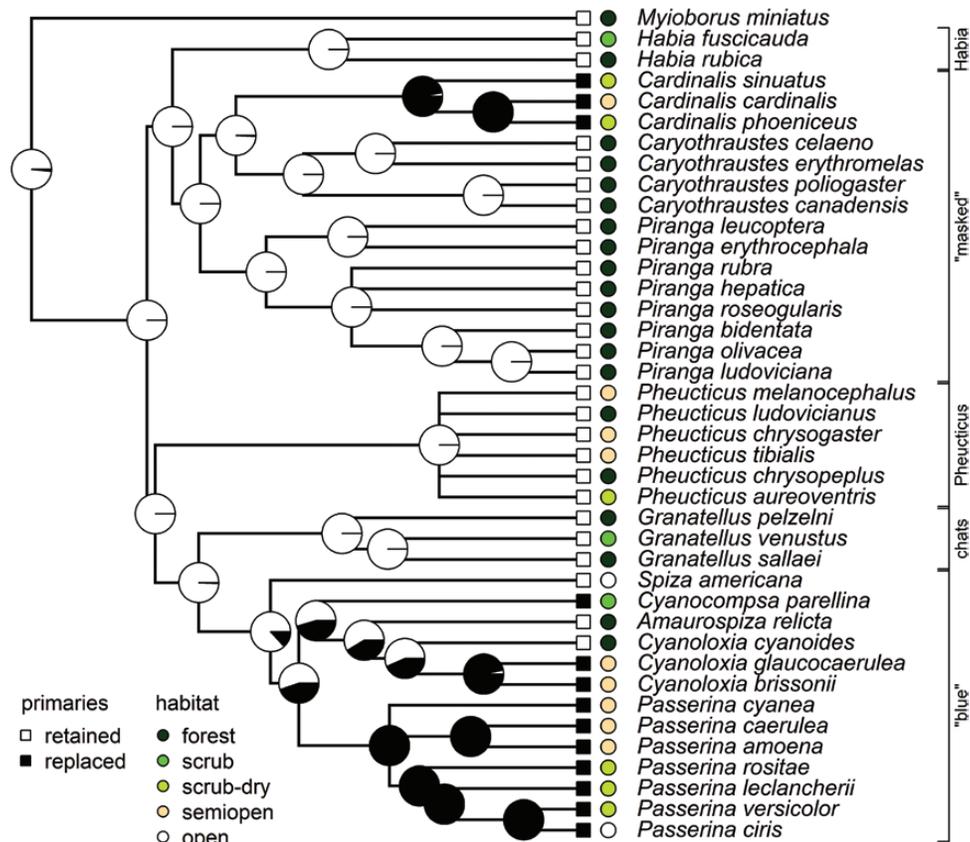


FIGURE 1. Phylogenetic reconstruction of the preformative molt of 39 Cardinalidae species. Bidtree.org does not include two of the species included in this study; Tres Marias Chat (*Granatellus francescae*) and Amazonian Grosbeak (*Cyanoloxia rothschildii*) are not split from their sister species, Red-breasted Chat (*Granatellus venustus*) and Blue-black Grosbeak (*Cyanoloxia cyanoides*), respectively. Pie charts on internal nodes depict likelihood. Tip nodes show the association between habitat types and presence-absence of primary replacement in the preformative molt for each species. Klicka et al. (2007) described five major clades: (1) a "masked" clade (*Piranga*, *Cardinalis*, and *Caryothraustes*); (2) a "blue" clade (*Amaurospiza*, *Cyanocompsa*, *Cyanoloxia*, *Passerina*, and *Spiza*); and clades containing the genera (3) *Habia*, (4) *Granatellus*, and (5) *Pheucticus*.

et al. (1995) as implemented in *phytools* (Revell 2012). We used the phylogenetic tree to show the aggregation of similarities between these two states and habitat. We then estimated transition rates from 100 trees using *fitDiscrete* function as implemented in *geiger* (Harmon et al. 2008).

We employed a second batch of comparative analyses to test whether the evolution of the preformative molt in Cardinalidae (both molt extent and presence/absence of primary molt) was correlated to the evolution of each of the five natural history factors we studied, as well as presence or absence of a documented auxiliary preformative molt. We used the continuous random walk model to test continuous variables and the MultiState method to test categorical variables as implemented in BayesTraits (Pagel 1999, Pagel et al. 2004) with default settings: MCMC analyses with 1,010,000 iterations (the first 10,000 as burn-in period), sampled every 1,000 iterations, and uniform priors (allowed for data with a strong signal). We ensured that the acceptance rate was 20–40% indicating that chains mixed

adequately. We averaged the results of 10 runs to account for randomness. We assessed the evidence for correlated evolution vs. evidence against it using Bayes factors, concretely the logarithmic scale proposed by Kass and Raftery (1995).

Relative Importance of Natural History Factors

Shared ancestry affects biological traits, such that trait values will be more similar in closely related than in distantly related species (Felsenstein 1985). To account for phylogenetic nonindependence among molt extents in Cardinalidae, we fitted PGLS regression lines using the R function *phylolm* implemented in the *phylolm* package (Ho and Ané 2014). Among the eight phylogenetic models for the error term implemented in the *phylolm* function, we selected the one that minimized AIC. We assessed the strength of phylogenetic nonindependence using the maximum likelihood value of the scaling parameter Pagel's λ calculated with the same function. For the presence/

absence of primary replacement, we fitted logistic lines using the R function *phyloglm* in the same R package (Ho and Ane 2014).

To complement these results, we examined the relative importance of the five natural history factors on the preformative molt extent of Cardinalidae. We fitted PGLS models using the mean value of the preformative molt extent for each species as response variable, and migratory distance, mean breeding latitude, habitat, delayed plumage maturation, and body mass as explanatory variables. We generated one model for each combination of explanatory variables, for a total of 32 models. We ranked the models according to their Akaike information criterion corrected for small sample size values (AICc), and calculated the relative importance of each factor based on its Akaike weight using the zero method implemented in the R package *MuMIn* (Bartoń 2019, R Core Team 2019). We also ran relative importance analyses using the presence/absence of primary molt as the response variable. Since phylogenetic logistic regression models are not implemented in this package, we computed Akaike weights manually for calculating the relative importance of the presence/absence of primary replacement.

RESULTS

Ancestral State Reconstruction and Correlated Evolution

Our phylogenetic reconstruction fully supports a molt with no primary replacement as the ancestral state of preformative molt in Cardinalidae (likelihood = 0.999; Figure 1). This equates with a partial molt (sensu Pyle 1997b), whereby some or all wing coverts and tertials are replaced but not primaries or secondaries. The transition rate from the ancestral state toward primary replacement was 0.0127, whereas the reversal rate was 0.0010 ($\Delta\text{AIC}_c = 1.854$, weak evidence against equal rates). Replacement of primaries during the preformative molt in Cardinalidae was homogenous within genera: with one exception, congeneric species showed either primary replacement or primary retention. Interestingly, the sole exception to this pattern, Blue-black Grosbeak (*Cyanoloxia cyanooides*), is linked to a shift in habitat with respect to the other *Cyanoloxia* species (Figure 1). More open habitats of both the masked and blue clades (sensu Klicka et al. 2007; Figure 1) are linked to preformative molts that include the replacement of primaries. Notably, however, this shift occurred in neither the *Pheucticus* clade nor in *Spiza* of the blue clade.

Consistent with this result, we also found strong to very strong support for the correlated evolution of the preformative molt and habitat (Table 1). None of the

other four natural history factors showed strong evidence of correlated evolution to preformative molt (although delayed plumage maturation reached positive evidence for the count and mass metrics). In view of the relevance of these results, we also reconstructed the ancestral state of habitat and found solid support for a forest-dwelling ancestor of Cardinalidae (likelihood = 0.979). Thus, character reconstruction indicates that the common ancestor was forest dwelling and that it did not replace primaries.

Only species among *Cardinalis*, *Pheucticus*, and three genera in the blue clade are known to undergo auxiliary preformative molts (Appendix Table 3). We found very strong support for the correlated evolution of the auxiliary preformative molt and the preformative molt (Table 1). Preformative molt extent was significantly larger in species with auxiliary preformative molt (mean \pm SD = 35.1 ± 10.5 , $n = 14$) than in species without it (mean \pm SD = 20.7 ± 3.1 , $n = 25$; $F_{1,37} = 41.23$, $P = 0.001$; Figure 3, Online Supplemental Material Table 3 and Figure 3). However, we found only a weak support for the correlated evolution of the auxiliary preformative molt, habitat, and presence/absence of primary molt (MultiState method: log BF = -0.18 ; Pagel et al. 2004).

Relative Importance of Natural History Factors

The best fit for PGLS regression lines was achieved by the early burst model for the count and mass metrics (Online Supplemental Material Table 4), which allows the rate of evolution to slow through time, and is consistent with a rapid diversification of clades as they enter new adaptive zones, i.e. adaptive radiation (Simpson 1945). However, it was indistinguishable from the Brownian motion model since $\Delta\text{AIC}_c < 2$ (Burnham and Anderson 2002). It was the opposite for the exposure metric (now indistinguishable from the Early Burst model since $\Delta\text{AIC}_c < 2$; Online Supplemental Material Table 4), and consistent with random evolution of signaling across the family (which does not exclude natural selection; Hansen and Martins 1996, Harmon 2019). We found a phylogenetic signal $\lambda = 1$, which implies very strong phylogenetic dependence among related species likely due to phylogenetic inertia.

Based on these analyses, we conclude that habitat was the most important factor explaining preformative molt extent for all three extent metrics, and the only one reaching statistical significance, i.e. with an estimated coefficient whose confidence interval did not overlap with zero (Table 2). Preformative molt extent increased toward more open habitats (Figure 2; Online Supplemental Material Table 5), and (more weakly) with longer migration distances, increased breeding latitude, and heavier body mass. On the other hand, molt extent decreased as formative plumage increasingly differed from the definitive

TABLE 1. Evidence of correlated evolution between preformative wing-feather molt and five natural-history factors, and between preformative wing-feather molt and presence/absence of auxiliary preformative molt in Cardinalidae. Results for all three metrics were consistent, although exposure evidence was mitigated. DPM = delayed plumage maturation; logBF = logarithm of Bayes factor (Kass and Raftery 1995).

	logBF	Evidence
Extent: count		
Habitat	10.72	Very strong
Migration	-0.35	Weak against
Latitude	-0.43	Weak against
DPM	2.82	Positive
Mass	0.68	Weak
Auxiliary PF	17.06	Very strong
Extent: mass		
Habitat	9.74	Strong
Migration	0.23	Weak
Latitude	0.65	Weak
DPM	4.33	Positive
Mass	0.00	Weak
Auxiliary PF	22.48	Very strong
Extent: exposure		
Habitat	5.19	Strong
Migration	-0.21	Weak against
Latitude	-0.50	Weak against
DPM	1.23	Weak
Mass	0.62	Weak
Auxiliary PF	5.52	Strong
Primary molt		
Habitat	5.00	Strong
Migration	-1.40	Weak against
Latitude	0.83	Weak
DPM	1.03	Weak
Mass	-0.41	Weak against
Auxiliary PF	1.29	Weak

plumage (Table 2). In support of the weak effect of migration distance, we also did not find significant differences between the preformative molt extent of migratory (mean \pm SD = 26.0 \pm 7.0, n = 13) and nonmigratory species of the family Cardinalidae (mean \pm SD = 25.8 \pm 10.8, n = 26; $F_{1,37}$ = 0.002, P = 0.964; Online Supplemental Material Table 6).

Results for the presence/absence of primary molt analyses were congruous with those for extent: probability of molting primaries increased as habitat becomes more open. Body mass had a negative effect as predicted by our hypothesis on increasing time costs with increasing body size, albeit it was not significant.

DISCUSSION

Our analyses on the evolution of the preformative molt in the family Cardinalidae have yielded two main findings. First, they indicate that the ancestor of Cardinalidae was a forest-dwelling

TABLE 2. Results of the PGLS analysis of five natural history factors on three preformative wing-feather molt extent metrics and presence/absence of primary molt in Cardinalidae. 95% confidence intervals (CI) based on 100 bootstrapped samples. To make raw count directly comparable with mass and extent, we normalized this metric to range between 0 and 100. Relative importance (RI) was obtained from averaging the 32 models that can be fitted from the combination of the 5 natural history factors. Values based on the subset of models who's accumulated Akaike weights reached 95% of the total averaged models. Coefficients for the presence/absence of primary molt based on univariate models due to poor convergence of the multivariate model. Numbers in bold indicate significant effects.

	Coefficient	CI	P	RI
Extent: count				
Habitat	3.558	0.118 to 5.825	0.033	0.829
Migration	0.001	-0.001 to 0.002	0.606	0.252
Latitude	0.067	-0.120 to 0.219	0.499	0.274
DPM	-1.179	-6.528 to 4.683	0.701	0.209
Mass	0.022	-0.243 to 0.397	0.913	0.173
Extent: mass				
Habitat	6.018	1.184 to 9.887	0.016	0.924
Migration	0.001	-0.003 to 0.005	0.628	0.219
Latitude	0.053	-2.53 to 0.324	0.717	0.214
DPM	-1.524	-8.700 to 6.193	0.739	0.195
Mass	0.046	-0.390 to 0.562	0.878	0.181
Extent: exposure				
Habitat	6.470	2.885 to 10.145	0.008	1.000
Migration	-0.001	-0.004 to 0.002	0.708	0.197
Latitude	0.009	-0.127 to 0.357	0.546	0.223
DPM	-4.069	-0.104 to 2.241	0.290	0.319
Mass	-0.164	-0.579 to 0.275	0.517	0.227
Primary molt				
Habitat	1.576	0.803 to 2.554	0.005	1.000
Migration	-0.014	-0.566 to 0.838	0.944	0.385
Latitude	-0.074	-0.914 to 0.766	0.739	0.397
DPM	-0.320	-1.369 to 0.298	0.309	0.333
Mass	-0.489	-1.729 to 0.387	0.241	0.321

species whose preformative molt did not include primaries. Second, habitat has been the main force driving preformative molt evolution in Cardinalidae. Transitions from forests toward more open habitats correlated positively to preformative molt investment and exposure, which also involved the replacement of primaries in most genera (Table 1, Figures 1–2).

Although more than half of the extant species of Cardinalidae continue to inhabit forests, several species have adapted to more open habitats along their evolutionary history. According to Klicka et al. (2007), diversification of the five main Cardinalidae clades occurred very early in the history of the family (Figure 1), consistent with the best-adjusted model, the early burst model. However, this early radiation did not imply a transition to open habitats, except within the blue clade.

Species may colonize new habitats in one of three ways: through dispersal to a new area, extinction of competitors, or the evolution of a new trait or set of traits that allow them

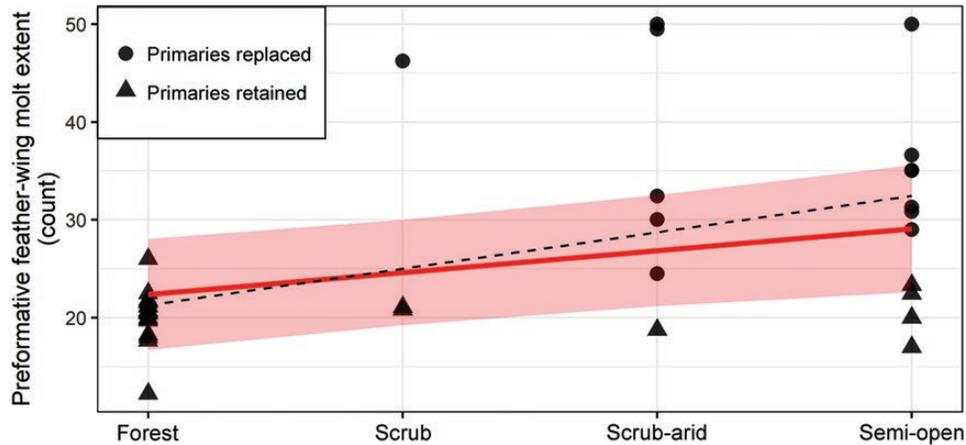


FIGURE 2. Bivariate regression of habitat category on preformative wing-feather molt extent in Cardinalidae. Habitat categories in ascending order of openness. Open habitat category lumped in the semi-open category due to its low sample size ($n = 2$). Hatched line shows ordinary least-squares regression, red line depicts phylogenetically corrected regression with shaded 95% confidence intervals computed from the variance-covariance matrix as implemented in the R package *evomap* (Smaers and Rohlf 2016).

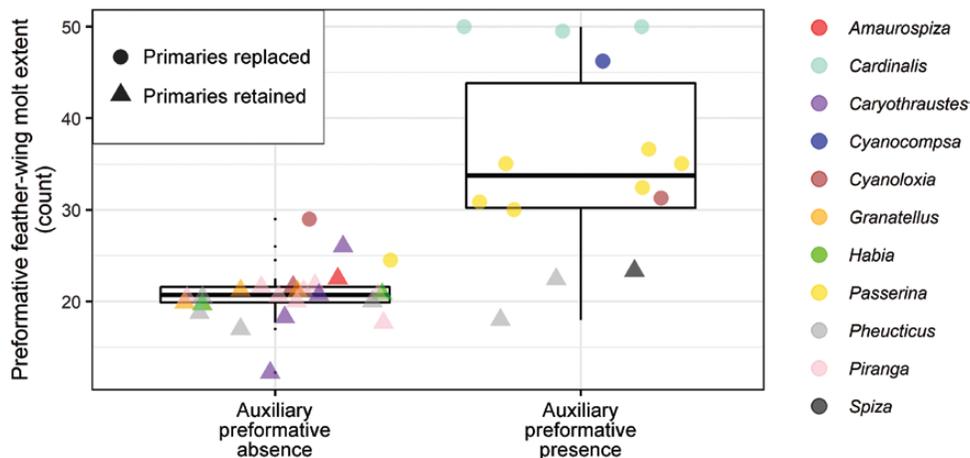


FIGURE 3. Relationship between preformative molt extent (count) and presence/absence of auxiliary preformative molt. Points represent mean preformative molt extent of each species. Note that available information on the presence of the auxiliary preformative molt is deficient in tropical species, hence, these results should be considered conservative; further study is required.

to interact with the environment in a new way (Simpson 1945). Our results suggest that transition from the ancestral forest habitat toward open habitats has triggered the increase in preformative molt extent within Cardinalidae, particularly in the evolution of primary replacement. Primaries could be under selection pressure to be replaced during the preformative molt in open-habitat species because these have more pointed wings (Keast 1996; Guallar et al. 2009, 2020), leaving juvenile primaries more exposed and therefore prone to degrade faster, which would reduce flight efficiency (Weber et al. 2010). Again, increased wear and insolation on more exposed outer than inner primaries may add to aerodynamic reasons to explain the evolution of eccentric molts in Cardinalidae species occurring in open habitats (Pyle 1998; Figure 1).

Overall, none of the 21 forest-dwelling species in our study replaces primaries during the preformative molt, while 13 of 20 nonforest dwellers do (Figure 1). Thus, one single transition outside forest habitats may have occurred in the masked clade associated with the origin of genus *Cardinalis*. Both the *Granatellus* and the *Pheucticus* assemblages contain nonforest species but none of these species undergoes primary replacement during the preformative molt (Figure 1). The absence of transition toward replacement of primaries could occur, for example, because of phylogenetic inertia (phylogenetic signal $\lambda = 1$) or because these species developed other behavioral or physiological solutions to cope with the new physical environment.

The picture gets more complex within the blue clade. This assemblage holds the largest number of species

that replace primaries during their preformative molt. However, Dickcissel (*Spiza americana*), which branched off early in the blue clade (Klicka et al. 2007), does not replace primaries despite inhabiting completely open areas. The remaining species of the blue clade inhabit open areas, with only *Amaurospiza* seedeaters and two of the four *Cyanoloxia* species inhabiting forests. This suggests a basal transition outside forest habitats, with eventual reversions in the latter two genera and a parallel reversion to the ancestral preformative molt state (retention of primaries).

Thus, both the analyses of correlated evolution and of relative importance consistently showed habitat as the main evolutionary force driving preformative molt extent of Cardinalidae. The influence of habitat has been associated with variation in preformative molt both within and among passerine species (Willoughby 1991, 2007; Guallar et al. 2016). Several elements of habitats may affect feather integrity and cause plumage abrasion: cluttered or rough vegetation such as those of xeric scrub (Willoughby 1991), the interaction of open habitats with higher temperatures in the tropics (Kiat and Izhaki 2016), or exposure to direct sunlight typical of open habitats (Bergman 1982, Pyle 1998). Contrastingly, we did not find strong support for delayed plumage maturation, migration distance, breeding latitude, or body mass to have a noticeable influence on the evolution of the preformative molt extent in this family.

Delayed plumage maturation is closely related to sexual and social factors (Senar 2006). Despite the pervasive presence of sexual dichromatism in Cardinalidae (only two *Caryothraustes* species are sexually monochromatic; Billerman et al. 2020), we did not find a significant effect of delayed plumage maturation on the preformative molt in Cardinalidae. If anything, we found a negative effect opposite to our hypothesis prediction (Table 1), likely driven by the unexpected presence of delayed plumage maturation in species undergoing extensive preformative molts. Thus, while the complete preformative molt in species with advanced plumage maturation like those in the genus *Cardinalis* was predictable under our first hypothesis, species with nearly as extensive preformative molts showed delayed plumage maturation (e.g., the entire *Passerina* and *Cyanocompsa* genera; Figures 1 and 3). This may reflect the heterogeneous strategies underlying delayed plumage maturation, which include species with first-cycle males mimicking the female plumage to reduce aggressive interactions with adult males during winter, but also to deceive them during the breeding season (Rohwer 1986, Senar 2006).

Like delayed plumage maturation, none of the variables associated with constraints showed a significant influence on the evolution of the preformative molt in Cardinalidae (Tables 1 and 2). Although considered a crucial factor in the evolution of molt strategies of Palearctic passerines (Figueroa and Jovani 2001, Kiat et al. 2019a), migration

distance was uncorrelated to preformative molt extent in Cardinalidae. This discrepancy may have arisen because of different environmental scenarios associated with different evolutionary trajectories, and consequently different evolutionary drivers (Rohwer et al. 2005, Ydenberg et al. 2007). However, we also suggest that this difference may be one of interpretation. The “post-juvenile” molt in Palearctic studies has largely been defined as molt on the breeding grounds prior to migration, whereas here we assume that the preformative molt strategy has evolved (sensu Humphrey and Parkes 1959) to include molts that are suspended for migration and completed at stopover locations (e.g., Young 1991, Rohwer et al. 2005, Pyle et al. 2009) or on the winter grounds (Pyle 1997b, Pyle et al. 2018). Preformative molt extent may be influenced by an increase in solar exposure with longer migrations, long-distance migrants being exposed to more sun on an annual basis than those that remain on or closer to northern breeding grounds because solar radiation increases toward the tropics (Pyle 1998, Mueller 2013). Analogously to open-habitat species, primaries could be under selection pressure to be replaced during the preformative molt in long-distance-migrants, because these species need to maximize the aerodynamic properties of primaries to maximize efficiency during the migratory flight (Weber et al. 2010).

Finally, the very strong positive correlation between the documented presence of an auxiliary preformative molt and the extent of the preformative molt provides evidence of their being two elements of the same early-life molt strategy (Howell et al. 2003). This view receives further support by the fact that auxiliary preformative molt is not correlated with habitat. Ephemeral, auxiliary formative plumage likely provides some benefits, for example, replacing weak juvenile feathers for migration while allowing for males to remain in a cryptic plumage until the preformative molt (Rohwer 1986, Rohwer et al. 2005, Rohwer 2013), and this could help explain the direct relation between the presence of auxiliary preformative molt and extensive preformative molts (Figure 3, Online Supplemental Material Figure 3). On the other hand, the weak correlation between this molt episode and habitat does not support a relationship between it and increased exposure to harsh vegetation or insolation. Confirmation of these results will require more documentation for the presence or absence of this molt in all species of Cardinalidae.

This study presents a comparative and functional perspective of the evolution of the preformative molt in a passerine family endemic to the American continent. Our findings indicated the existence of a strong phylogenetic signal and have pinpointed the importance of the physical environment on the evolution of the first-cycle molt strategies, at least in this passerine family. Although our results do not support those of previous analyses indicating

the influence of time constraints on the evolution of early life molt strategies (Kiat and Izhaki 2016), such analyses should be expanded in future studies to additional passerine families once large databases on preformative molt extent are built. Considering that the evolutionary histories and the environments to which each taxonomic group has adapted can diverge across passerines, we expect that future studies will find differences in the nature and strength of evolutionary drivers of their preformative molt.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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APPENDIX TABLE 3. Species names and associated natural history information used in this study. DPM = delayed plumage maturation (1 = none, 2 = slight, 3 = moderate, 4 = extensive). Primary molt and auxiliary preformative molt are presence/absence data. Information for Nearctic species on the latter episode extracted from Pyle (1997b).

Latin name	English name	Habitat	Mass (g)	Migration distance (km)	DPM	Latitude (°)	Auxiliary preformative	Primary molt	Synonyms
<i>Pheucticus chrysopleus</i>	Yellow Grosbeak	Forest	75.9	0	3	21.1184741	0	0	
<i>Pheucticus tibialis</i>	Black-thighed Grosbeak	Semi-open	62.3	0	2	9.5311658	0	0	
<i>Pheucticus chrysogaster</i>	Golden Grosbeak	Semi-open	55.8	0	3	-8.3464851	0	0	
<i>Pheucticus aureoventris</i>	Black-backed Grosbeak	Scrub-dry	49	880	4	-18.5662685	0	0	
<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	Forest	42	4299	4	48.0440801	1	0	
<i>Pheucticus melanocephalus</i>	Black-headed Grosbeak	Semi-open	45.5	1967	4	40.8885747	1	0	
<i>Granatellus venustus</i>	Red-breasted Chat	Scrub	11.1	0	4	19.21002714	0	0	
<i>Granatellus francescae</i>	Tres Marias Chat	Scrub-dry	9.9	0	4	21.5585579	0	0	<i>Granatellus venustus</i>
<i>Granatellus sallaei</i>	Gray-throated Chat	Forest	11.2	0	3	18.24616946	0	0	
<i>Granatellus peizelhi</i>	Rose-breasted Chat	Forest	26.3	0	3	-2.981812745	0	0	
<i>Spiza americana</i>	Dickcissel	Open	14.7	4040	3	39.9720859	1	0	
<i>Passerina cyanea</i>	Indigo Bunting	Semi-open	28.7	1915	4	39.1621982	1	1	
<i>Passerina caerulea</i>	Blue Grosbeak	Semi-open	15.5	2002	4	34.2541258	1	1	
<i>Passerina amoena</i>	Lazuli Bunting	Semi-open	20	2302	4	43.0318974	1	1	
<i>Passerina rositae</i>	Rose-bellied Bunting	Scrub-dry	13.2	0	4	16.6120928	0	1	
<i>Passerina leclancherii</i>	Orange-breasted Bunting	Scrub-dry	12.5	0	4	18.3227531	1	1	
<i>Passerina versicolor</i>	Varied Bunting	Scrub-dry	15.9	644	4	25.1228931	1	1	
<i>Passerina ciris</i>	Painted Bunting	Open	16.2	1731	4	32.2412822	1	1	
<i>Cyanocompsa parellina</i>	Blue Bunting	Scrub	13.1	0	4	18.82980157	1	1	
<i>Amaurospiza relicta</i>	Slate-blue Seedeater	Forest	13.1	0	4	18.36677597	0	0	<i>Amaurospiza concolor</i>
<i>Cyanoloxia cyanoides</i>	Blue-black Grosbeak	Forest	32.5	0	4	11.16805648	0	0	
<i>Cyanoloxia rothschildii</i>	Amazonian Grosbeak	Forest	24.8	0	4	-3.656139836	0	0	<i>Cyanoloxia cyanoides</i>
<i>Cyanoloxia brissonii</i>	Ultramarine Grosbeak	Semi-open	27.5	0	4	-19.43592393	1	1	<i>Cyanocompsa brissonii</i>
<i>Cyanoloxia glaucocaeerulea</i>	Glaucous-blue Grosbeak	Semi-open	18.2	735	4	-29.78297833	0	1	
<i>Habia fuscicauda</i>	Red-throated Ant-Tanager	Scrub	38	0	4	16.6372233	0	0	
<i>Habia rubica</i>	Red-crowned Ant-Tanager	Forest	32.5	0	4	-6.9665143	0	0	
<i>Piranga roseogularis</i>	Rose-throated Tanager	Forest	24	0	4	18.92595744	0	0	
<i>Piranga erythrocephala</i>	Red-headed Tanager	Forest	18.32	0	4	21.5929196	0	0	
<i>Piranga leucoptera</i>	White-winged Tanager	Forest	36.6	0	3	3.7952841	0	0	
<i>Piranga olivacea</i>	Scarlet Tanager	Forest	28.2	4825	3	41.7205083	0	0	
<i>Piranga rubra</i>	Summer Tanager	Forest	29.2	1985	4	33.4727582	0	0	
<i>Piranga bidentata</i>	Flame-colored Tanager	Forest	33.7	0	4	20.75734689	0	0	
<i>Piranga ludoviciana</i>	Western Tanager	Forest	28.1	1695	3	48.9539685	0	0	

APPENDIX TABLE 3. Continued

Latin name	English name	Habitat	Mass (g)	Migration distance (km)	DPM	Latitude (°)	Auxiliary preformative	Primary molt	Synonyms
<i>Piranga hepatica</i>	Hepatic Tanager	Forest	39.2	100	4	32.5016091	0	0	includes <i>Piranga lutea</i>
<i>Cardinalis cardinalis</i>	Northern Cardinal	Semi-open	42.6	100	1	34.85656333	1	1	
<i>Cardinalis phoeniceus</i>	Vermilion Cardinal	Scrub-dry	35	0	1	10.95500304	1	1	
<i>Cardinalis sinuatus</i>	Pyrrhuloxia	Scrub-dry	35.2	0	1	28.25550128	1	1	
<i>Caryothraustes poliogaster</i>	Black-faced Grosbeak	Forest	41.8	0	2	15.64347859	0	0	
<i>Caryothraustes canadensis</i>	Yellow-green Grosbeak	Forest	34.5	0	2	-0.74426015	0	0	
<i>Caryothraustes celaeno</i>	Crimson-collared Grosbeak	Forest	60	0	4	22.51609827	0	0	<i>Rhodothraupis celaeno</i>
<i>Caryothraustes erythromelas</i>	Red-and-black Grosbeak	Forest	48	0	4	1.444817766	0	0	<i>Periporphyrus erythromelas</i>
<i>Myioborus miniatus</i>	Slate-throated Whitestart	Forest	7.83	0	3	9.525091636	0	0	