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Source: The Wilson Journal of Ornithology, 128(3):543-555.
Published By: The Wilson Ornithological Society
DOI: http://dx.doi.org/10.1676/1559-4491-128.3.543
URL: http://www.bioone.org/doi/full/10.1676/1559-4491-128.3.543

*The Wilson Journal of Ornithology* 128(3):543–555, 2016

# MOLT STRATEGIES OF TEN NEOTROPICAL FOREST PASSERINE SPECIES

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ABSTRACT.—We describe the number of inserted molts in the annual molt cycle and topographies resulting from the preformative molt in 10 Neotropical forest passerine species. Seven species showed two annual molt peaks, one in early spring (Mar–Apr) and one in late summer (Jul–Sept). The spring molt consisted of a light replacement of body feathers in <20% of individuals in our sample, and would be most consistent with a prealternate molt. We found two modes of preformative molt feather replacement where the "general mode" included all feathers of an anterior wing-tract being replaced before proceeding to the next posterior tract; the general mode was shown by all 10 species at moderate to high frequencies (69–99%). Seven species at low to mid frequencies (1–31%) exhibited "proximal mode" to include all wing feathers adjacent to the body replaced prior to distal feathers. Mean molt angle (a measure of direction of the replaced feathers when placed on a Cartesian plane) ranged from 12° to 24° and was higher in the "general mode." An expanded phylogenetic analysis examining the extent of preformative molt that included the 10 study species plus an additional 18 Neotropical species suggested that ecological adaptations may have a greater influence over molt strategies than phylogenetic constraints at least in some of the families we examined. *Received 3 May 2015. Accepted 12 December 2015.*

Key words: annual cycle, Bayesian inference, mode of feather replacement, molt topography, prealternate molt, preformative molt.

"Molt strategy" is a term used to refer to any aspect of avian molt, including its phenology (Young 1991, Rohwer and Johnson 1992), annual cycle (Thompson 1991, Newton 2008, Pyle 2007), duration and intensity (Rohwer et al. 2009, Silveira and Marini 2012), extent (Jenni and Winkler 1994; Pyle 1997a, b), sequence (Langston and Rohwer 1995, Shugart and Rohwer 1996, Pyle 2013) and location (Butler et al. 2006, Rohwer et al. 2008). Molt strategy is thus a broad term often used to define a process or set of several processes resulting in variable patterns of molt.

Although molt in passerines has been extensively studied since the late 19th century (Dwight 1902), important gaps still exist (Bridge 2011, Pyle 2013), particularly for birds found outside of Europe and North America. The study of molt in Neotropical resident passerines has recently acquired momentum with the description of molt strategies for ~100 species in the last 15 years (Marini and Durães 2001; Pyle et al. 2004, 2015; Mallet-Rodrigues 2005; Ryder and Durães 2005; Guallar et al. 2009; Ryder and Wolfe 2009; Wolfe et al. 2009a, b; Hernández 2012; Mallet-Rodrigues and Dutra 2012; Silveira and Marini 2012, Johnson and Wolfe 2014); however, molt strategies of >90% of Neotropical passerine species remain undescribed (although crude descriptions of timing of primary molt are available for many more; see species accounts in del Hoyo et al. 2015 for instance). One important fact that emerges from the literature is that patterns of wing feather replacement during the preformative molt resemble those of their Nearctic counterparts (Pyle 1997a, Wolfe and Pyle 2012), although new patterns can potentially be found among passerines in the future (e.g., Junda et al. 2012).

Preformative molt patterns have been classified into broad qualitative categories ranging from 'limited' to 'complete' (Pyle 1997a, b). Several typical preformative molt patterns observed in passerines include 'eccentric,' resulting from an incomplete molt that includes distal primaries and proximal secondaries, and 'in block,' resulting from partial molts that include all secondary coverts but no remiges or primary coverts (Pyle 1997a, b). In an attempt to establish a more objective classification of partial molts, Guallar et al. (2014) defined two modes of wing-feather replacement in passerines based on analyses of molt topography: general and proximal, which result in distinct patterns of molt limits. Briefly, the general mode consists of replacing an entire tract of secondary coverts before proceeding to the next tract, starting with the lesser coverts and continu-

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TABLE 1. Names, sample sizes, and masses of species used in our study. Abridged names are used throughout the figures and tables. Sample size (*n*) per species includes adult birds used in description of molt phenology. Masses correspond to the mean mass (g) annotated in the specimen's labels and mist-netted birds in Xalapa, Veracruz, Mexico (sample size in parenthesis).

| Abridged name | *n* | English name | Scientific name | Family | Mass |
|---|---|---|---|---|---|
| CASMEX | 27 | Black-headed Nightingale-Thrush | *Catharus mexicanus* | Turdidae | 33 (9)[a] |
| CATDRY | 7 | Spotted Nightingale-Thrush | *Catharus dryas* | Turdidae | 37.7 (58)[a] |
| TURGRA | 50 | Clay-colored Thrush | *Turdus grayi* | Turdidae | 69.1 (18) |
| BASLAC | 70 | Fan-tailed Warbler | *Basileuterus lachrymosus* | Parulidae | 14.8 (7) |
| BASRUF | 54 | Rufous-capped Warbler | *Basileuterus rufifrons* | Parulidae | 11.3 (7) |
| BASCUL | 82 | Golden-crowned Warbler | *Basileuterus culicivorus* | Parulidae | 9.1 (32) |
| ARRBRU | 79 | Chestnut-capped Brush-Finch | *Arremon brunneinucha* | Emberizidae | 39.8 (15) |
| CHLFLA | 57 | Common Bush-Tanager | *Chlorospingus flavopectus* | Emberizidae | 16.0 (16) |
| HABRUB | 100 | Red-crowned Ant-Tanager | *Habia rubica* | Cardinalidae | 32.5 (126)[a] |
| HABFUS | 130 | Red-throated Ant-Tanager | *Habia fuscicauda* | Cardinalidae | 38.0 (11) |

[a] Values published in Dunning (2007).

ing to the median coverts, greater coverts, and tertials (see figure 1 in Guallar et al. 2014). The proximal mode, by contrast, prioritizes the wing-feathers closer to the body within each tract before completing the replacement of more anterior tracts. We would like to emphasize that other modes of replacement during the preformative molt potentially exist (e.g., eccentric molt shows distinct characteristics), although the general and the proximal modes are likely the two most frequent molts in passerines.

Intraspecific variation in preformative molt topographies has long been noticed (Jenni and Winkler 1994, Pyle 1997a) although adaptive reasons for this variation remain uncertain. Time constraints are known to explain the relationship between number of replaced feathers during the preformative molt and hatching date (Bojarinova et al. 1999, Elrod et al. 2011). Latitude also serves to influence time constraints: the shorter the time allowed to molt, the fewer the number of wing coverts replaced. This has been documented in migrants (Rymkevich 1990, Mulvihill and Winstead 1997, Deviche 2000, Johnson et al. 2013, Dietz et al. 2015), a few resident Palearctic species (Gauci and Sultana 1979, Bojarinova et al. 1999), and has been at least suggested in some resident Nearctic species (Howell 2010). Sex is another factor that may explain some variation in extent (de la Cruz Solis et al. 1991, Gosler 1991, Senar et al. 1998, Bojarinova et al. 1999), with males averaging more replaced feathers than females in some passerine species thus far studied (Gosler 1991, Senar et al. 1998, Crates et al. 2015). To date, the study of intraspecific variation in preformative molt has relied on differences in extent, largely as defined by differences in the number of replaced greater coverts and tertials for 'partial molts,' and number of replaced secondaries, primaries, primary coverts, and rectrices for 'incomplete molts' (Jenni and Winkler 1994, Pyle 1997b). In this article, we describe the annual molt cycle and preformative molt topography in 10 non-migratory Neotropical passerine forest species (Howell and Webb 1995; Table 1). We further classified topographies in a broader context, using information available on 18 species of close relatives (Guallar et al. 2009) and consider both phylogenetic and ecological factors that may have influenced the evolution of molt strategies in this group of species.

## METHODS

We gathered data for our 10 study species from 613 specimens from four museums (see Acknowledgements) and from 43 mist-netted birds in several locations of Veracruz state, Mexico. Several of our species have very wide geographic ranges throughout the Neotropics, nonetheless this dataset was restricted to 97 localities from Mexico and Central America through Panama.

Incompleteness of collections, state of study skins, missing information on labels, and inconstant capture effort resulted in sample unevenness which may cause several potential biases (Boakes et al. 2010). We therefore assessed the sex of each specimen and spatiotemporal heterogeneity in our dataset to determine possible sources of bias in our results. More data would be required to carry out adequate assessment of bias per species (see Assessment of sampling bias in the online Supplemental file). Common and scientific names of our study species as well as the sample sizes in our dataset are shown in Table 1.

To describe preformative molt and annual molt cycle, we recorded the presence of active molt, date, locality, sex, and age for all individuals. We scored non-active preformative molt data specifying which rectrices and wing feathers were formative or juvenile using established aging criteria (Pyle 1997a, Guallar et al. 2009; see Table S1 for identification of molt limits).

We quantified molt topography following Guallar et al. (2014). Briefly, we assigned x-y coordinates to each wing feather on the Cartesian plane; lesser coverts were grouped into 18 blocks organized in two rows and nine columns. Then, we calculated the centroid of every individual wing and derived its molt vector by subtracting the coordinates of the centroid for a complete molt by those of the individual's centroid. We discarded the alula feathers from calculations of molt vector to obtain a balanced Cartesian projection of the wing. We then quantified the preformative replacement frequency of each wing covert and flight feather for the two modes of replacement as well as for each species in the sample (see Supplemental material file).

Since 9-primaried species in our sample tended to be smaller than 10-primaried species, and smaller birds tend to have nine greater coverts (Guallar et al. 2009, Ruíz-Sánchez et al. 2012), we considered 9-primaried species to have nine greater coverts and 10-primaried species to have 10 greater coverts. This is a provisional criterion whose refinement needs further study.

We calculated molt extent and identified mode of replacement only for those birds with complete wing-feather scores. We also quantified frequency of replacement for each wing-feather per mode of replacement (see Supplemental material file).

*Statistical Analyses*.—We used a Bayesian framework to derive estimates of molt topography between and within species. To determine molt extent and number of replaced greater coverts we used a generalized linear model adequate for a count dependent variable:

$$C \sim \text{Poisson}(\lambda)$$

$$\log(\lambda) = a + bx$$

where $C$ is the total wing extent, $x$ is sex, $a$ is the random intercept which depends on sex, and $b$ is the common slope that measures the relation between sex and extent.

Since 95% credible intervals of molt extent for each sex overlapped widely (Table S2), we lumped all data and discarded sex in subsequent analyses.

To determine the directionality of feather replacement amongst the study species (referred to as "angle" hereafter), we used a Wrapped Cauchy model to estimate direction for continuous circular data (Kent and Tyler 1988, Jammalamadaka and SenGupta 2001):

$$\theta \sim \text{WC}(\mu, \gamma)$$

where $\theta$ is individual molt angle, $\mu$ is mean molt angle and $\gamma$ is the scale factor of the Wrapped Cauchy distribution. We specified a small scale factor ($\gamma = 0.5$) to account for the high concentration of the observed angles (see Figs. S1–S3). To determine the frequency of modes of feather replacement for each of our study species, we used a binomial model, which is a simple but appropriate way to represent a process with two possible outcomes (McCarthy 2007):

$$x \sim \text{Bin}(p, n)$$

where $x$ is the number of replaced feathers in the sample, $P$ the probability of feather replacement and $n$ the total number of each feather in the sample.

Non-informative priors were used with each model except for the Wrapped Cauchy, which we restricted to the observed range to avoid overdispersion.

We set 20,000 iterations and discarded the first 1,000 on three chains. Once the model was updated, we checked the trace of the chains and the Rubin-Gelman statistic for convergence.

We carried out analyses in WinBUGS (Lunn et al. 2000) called from R (R Core Team 2014) using package R2WinBUGS (Stutz et al. 2005). We used package CircStats (Agostinelli 2012) to obtain circular statistics, ape (Paradis et al. 2004) to

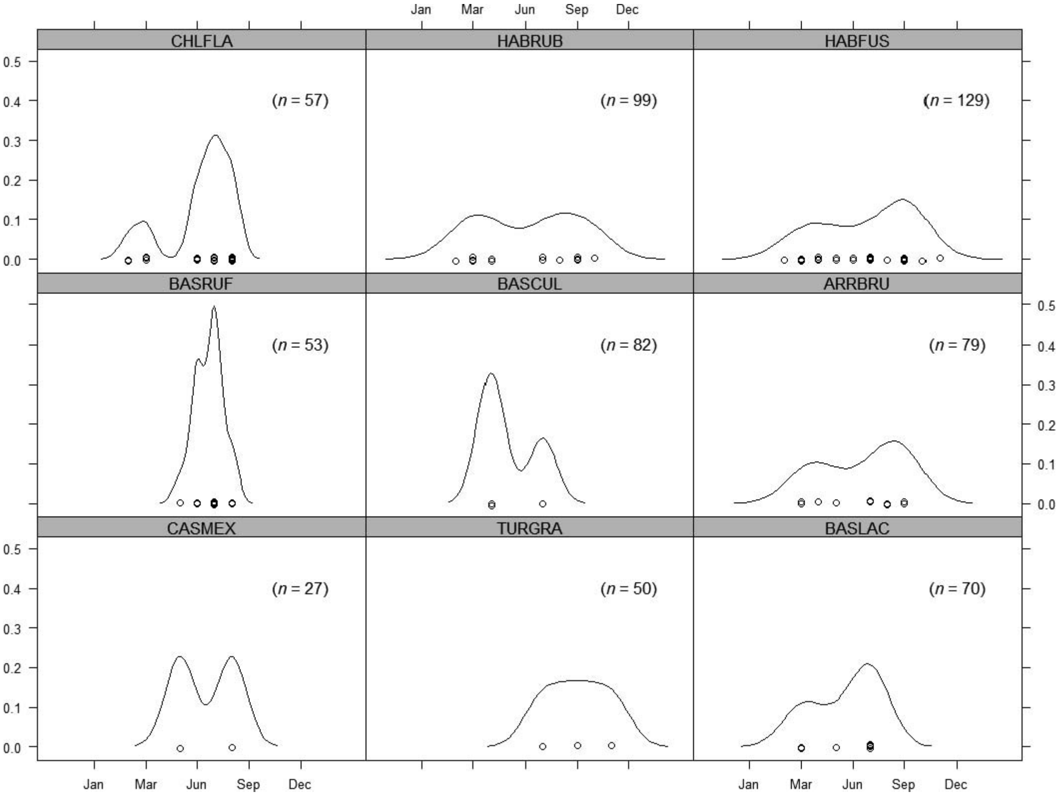

FIG. 1. Phenology of molt for nine study species (we did not find Spotted Nightingale-Thrush specimens in active molt). Circles correspond to individuals in active molt. Total sample sizes are shown on the upper right of each panel. Prebasic and preformative molts largely overlap in time, thus were combined in this panel. Kernel density plots, furnished for observed frequency of active molt per month, show relative data distribution and therefore shape may be biased by data paucity and unevenness, as evidenced in Golden-crowned Warbler (BASCUL).

manage phylogenetic trees, and ggplot2 (Wickham 2009) and lattice (Sarkar 2008) for graphics.

*Phylogenetic Analyses*.—We investigated the evolution of preformative molt topography and occurrence of spring molt in our group of 10 species plus an additional 18 close relatives previously studied (Guallar et al. 2009; Tables S3–S4) to evaluate whether these two traits are more influenced by phylogenetic inertia or ecological factors. Concentration of evolutionary changes on the tips of the phylogenetic tree suggests a larger ecological influence, whereas changes in basal branches suggests evolutionary inertia. First, we derived molt extent, molt angle, and mode of replacement metrics and standardized the observed means of these three variables. We then carried out hierarchical cluster analysis using Euclidean distances as measure of dissimilarity among species. We selected the complete linkage method, because it tends to maximize dissimilarities between clusters and yield more balanced clusters (James et al. 2013).

Finally, we mapped groups on a rooted majority-rule consensus tree obtained from 500 phylogenetic trees generated for the 28 species, plus Golden Vireo (*Vireo hypochryseus*) as an outgroup (Jetz et al. 2012).

## RESULTS

*Annual Molt Cycle*.—We obtained data on active molt for all study species except the Spotted Nightingale-Thrush (Fig. 1; see Table 1 for scientific names). Active molt periods spanned from 3 months in Clay-colored Thrush to 10 months in Red-throated Ant-Tanager. Six species showed similar timing between definitive prebasic

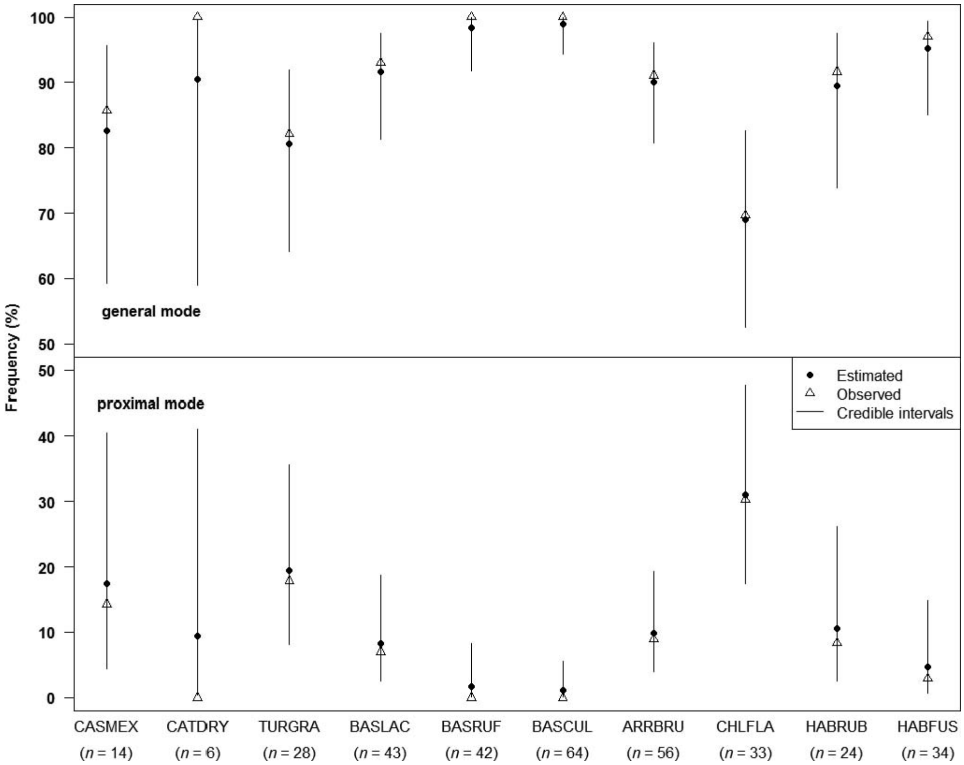

FIG. 2. Frequency of modes of replacement for 10 study species. $n$ = sample size. Note the lower plot is the specular image of the upper plot because our 10 species only present two modes of replacement.

and preformative molts, with peaks in July–August. The peaks of Clay-colored Thrush, Red-crowned Ant-Tanager, and Red-throated Ant-Tanager were in September. Seven species showed two annual molt peaks, one in late summer as described above, but a second also in spring to suggest the presence of a prealternate molt (Fig. 1). Clay-colored Thrush and Rufous-capped Warbler showed only one peak. All 10 species had a complete prebasic molt and a partial preformative molt without replacing secondaries (other than tertials), primaries, or primary coverts. The seven species with a bimodal molt peak replaced only body feathers in spring, and principally on the head; this replacement was only observed in 18% of individuals (Fig. 1). Only Clay-colored Thrush and both ant-tanagers replaced central rectrices during the preformative molt (Figs. 8–10).

*Preformative Molt Topography.*—We detected both the general and the proximal modes of preformative molt in our sample (Fig. 2). All study species showed the general mode, exclusively so in Spotted Nightingale-Thrush, Rufous-capped Warbler, and Golden-crowned Warbler, but seven species also showed the proximal mode. The general mode was the most frequently observed mode in our sample (69–100% across species); the proximal mode was present at frequencies <20% except in Clay-colored Thrush and Common Bush-Tanager (21% and 31%, respectively; Fig. 2).

Sex is one of the factors that may influence intraspecific variability in molt extent; however, we found that credible intervals of molt extent estimates for each sex overlapped 95% or more except for Black-headed Nightingale-Thrush (86%), Clay-colored Thrush (85%) and Red-throated Ant-Tanager (91%).

Of our four study families, turdids showed less extensive preformative molt particularly in the number of replaced greater coverts (frequentist correlation between extent and number of replaced greater coverts: $r^2 = 0.977$, $P < 0.001$; Table S5). Three species did not replace tertials in our

TABLE 2. Observed mean preformative molt extent, range, and lower and upper 95% posterior intervals for our 10 study species. Extent includes median and lesser coverts, the latter grouped in 18 blocks each one scoring 1 point (see Fig. 1 in Guallar et al. 2014). Alula feathers are not included.

| | | Observed | | Estimated | | |
|---|---|---|---|---|---|---|
| Sp. | *n* | Mean | Range | Mean | LCI | UCI |
| CASMEX | 14 | 28.07 | 20–31 | 28.08 | 25.37 | 30.88 |
| CATDRY | 6 | 27.50 | 27–29 | 27.50 | 23.50 | 31.83 |
| TURGRA | 28 | 33.61 | 23–41 | 33.60 | 31.49 | 35.77 |
| BASLAC | 39 | 36.33 | 24–39 | 36.34 | 34.48 | 38.26 |
| BASRUF | 37 | 37.78 | 36–38 | 37.76 | 35.81 | 39.79 |
| BASCUL | 58 | 37.84 | 32–39 | 37.84 | 36.26 | 39.41 |
| ARRBRU | 50 | 36.48 | 28–40 | 36.48 | 34.83 | 38.20 |
| CHLFLA | 28 | 34.14 | 28–38 | 34.14 | 32.04 | 36.33 |
| HABRUB | 18 | 36.22 | 30–38 | 36.23 | 33.50 | 39.07 |
| HABFUS | 28 | 38.93 | 36–49 | 38.94 | 36.66 | 41.28 |

sample: Spotted Nightingale-Thrush, Fan-tailed Warbler and Common Bush-Tanager (Figs. S5, S6, S8). Nightingale-thrushes was the only species to never replace alula feathers. Clay-colored Thrush and Fan-tailed Warbler were the only species that retained lesser coverts during the preformative molt. Along with Common Bush-Tanager and Red-crowned Ant-Tanager, they sometimes retained median coverts. Preformative molts tended to be less extensive in the proximal mode than in the general mode for each species although sample sizes were too low to make reliable inference (Tables S6–S7, Figs. S4–S13). This was especially obvious in the Fan-tailed Warbler (Fig. S6). Although we did not include alula feathers in topographical analyses, it is worth mentioning that their frequency estimates in the proximal mode were higher than in the general mode for Clay-colored Thrush, Common Bush-Tanager and Red-crowned Ant-Tanager (Figs. S8–S10).

Uncertainty in any estimate increases with dispersion and decreases with sample size. This can be detected in estimates for the proximal mode (Table S6): scarcity of data resulted in a high uncertainty as exhibited by wide 95% posterior intervals.

Observed molt angles ranged from 12° to 24° (Table 3, Fig. S2) generally higher in the proximal than the general mode of replacement, and higher in birds with more replaced greater coverts (Fig. S3). Mean angle for Spotted Nightingale-Thrush was the largest among our study species, although its 95% posterior intervals overlapped with those of Black-headed Nightingale-Thrush and Chestnut-capped Brush-Finch. The latter species

TABLE 3. Observed preformative molt direction and range and estimated mean preformative molt direction and lower and upper 95% posterior intervals for 10 study species (angles in degrees). $n =$ sample size for the global sample.

| | | Observed | | Estimated | | |
|---|---|---|---|---|---|---|
| Sp. | *n* | Direction | Range | Direction | LCI | UCI |
| CASMEX | 14 | 20.45 | 18.62–24.12 | 21.31 | 18.74 | 24.00 |
| CATDRY | 6 | 23.26 | 20.74–24.12 | 22.40 | 20.80 | 24.06 |
| TURGRA | 28 | 17.13 | 12.49–19.54 | 16.21 | 12.72 | 19.37 |
| BASLAC | 43 | 16.96 | 15.36–19.37 | 17.42 | 15.41 | 19.31 |
| BASRUF | 42 | 16.79 | 14.90–19.08 | 17.02 | 15.01 | 18.96 |
| BASCUL | 64 | 16.73 | 14.90–18.11 | 16.62 | 15.01 | 18.05 |
| ARRBRU | 56 | 16.84 | 12.03–23.43 | 18.56 | 12.61 | 23.20 |
| CHLFLA | 33 | 17.13 | 16.04–19.02 | 17.76 | 16.10 | 19.31 |
| HABRUB | 24 | 17.19 | 14.78–20.52 | 17.70 | 14.95 | 20.40 |
| HABFUS | 33 | 16.44 | 13.52–19.42 | 16.56 | 13.69 | 19.31 |

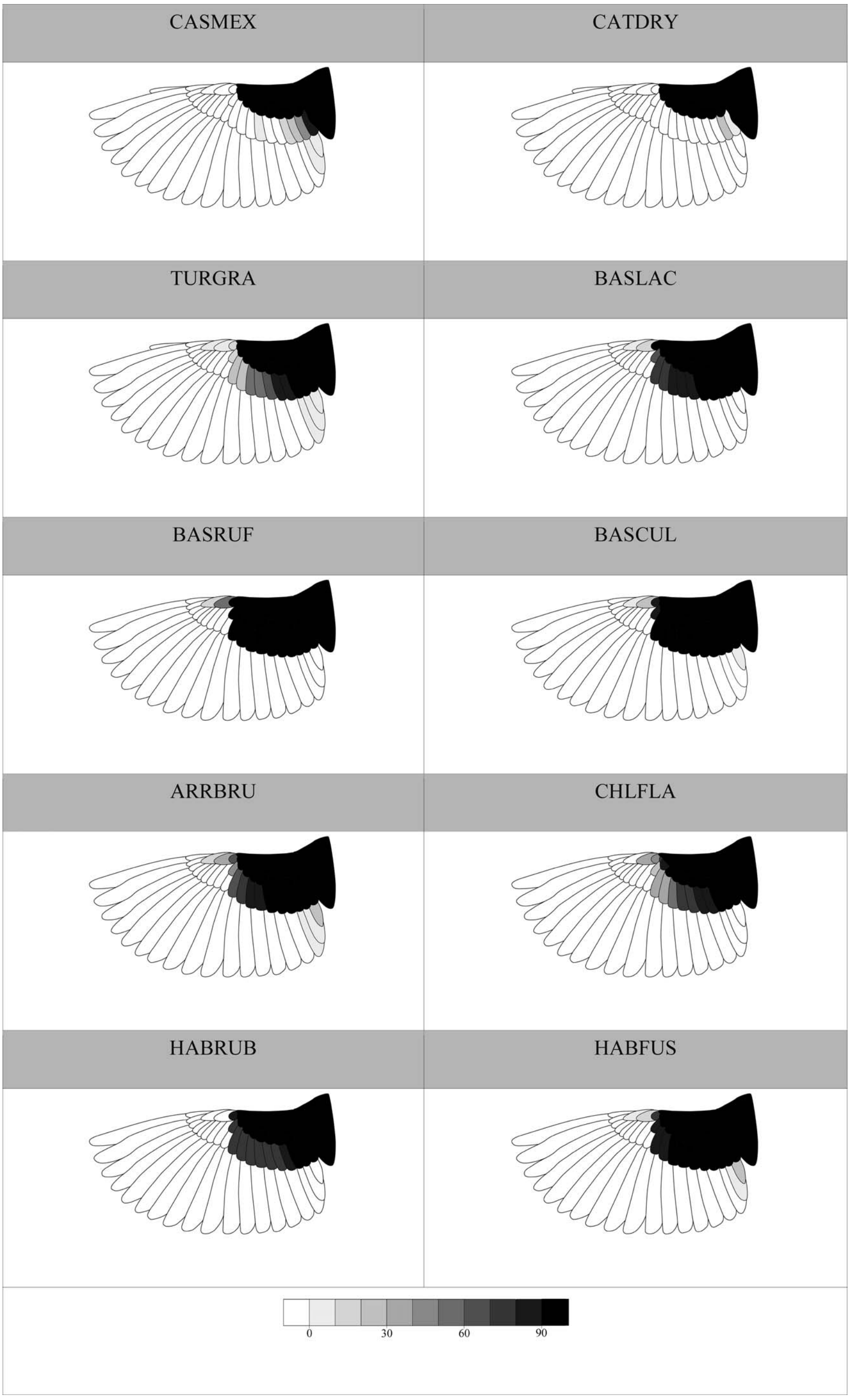

FIG. 3. Schematic representation of the frequency of feather replacement resulting from preformative molts in 10 study species. Gray scales represent observed replacement frequencies; darker shade indicates more frequent replacement. Plots with full details are included in the online Supplemental materials (Figs. S4–S13).

showed the widest range of molt angle. The 95% posterior intervals of the three turdids did not overlap with those of Golden-crowned Warbler (Table 3), which is the species that showed the narrowest range of molt angle.

*Evolution of Molt Strategies*.—Hierarchical clustering first separated species with relatively low and high frequency of the general mode of replacement (mean ± SD: 79.5% ± 6.3 vs 96.0% ± 5.3), and then each of these two clusters into two groups by preformative molt extent (mean ± SD: G1–G2: 37.2 ± 0.7 vs 28.9 ± 1.2; G3–G4: 33.3 ± 1.8 vs 40.5 ± 0.0) (Fig. 4a).

Only seven changes in the preformative molt topography were required to map the four clusters on the phylogenetic tree (Fig. 4b), the first one separates turdids from the rest. A second change separated nightingale-thrushes and Wood Thrush (*Hylocichla mustelina*) from *Turdus sp*. Within the other main branch, there was a major change that separated emberizids from parulids. The last four changes were terminal and implied reversions to the state of the common ancestor except for Swainson's Thrush (*Catharus ustulatus*) and Grey-crowned Yellowthroat (*Geothlypis poliocephala*), which implied a leap in molt topography from G1 to G4, the two most distant groups.

Spring molt appeared to be ancestral to the 28 study species belonging to four families of passerines. Only three terminal reversions of this molt have occurred, two in parulids and one in turdids (Fig. 4b).

## DISCUSSION

Here, we described the timing and peaks of molt, and preformative molt topography in a small set of Neotropical forest passerines. Furthermore, we explored phylogenetic relationships of preformative molt across the study species.

*Annual Cycle and Preformative Molt Topography.*—Two features of the annual molt cycle are particularly interesting: number of peaks and timing (Fig. 1).

The bimodal distribution of active molt during the annual cycle (Fig. 1) lends support to the presence of a prealternate molt in seven of the study species (all of them resident) as previously found in other Neotropical non-migratory species (Dickey and van Rossem 1938, Guallar et al. 2009). However, the presumed prealternate molt takes place at a low apparent frequency and usually involves a slight to moderate replacement of body feathers. The prealternate molt may be more common than previously assumed because of several reasons: difficulty of detecting feather pins and the disintegration of pins in museum specimens (Harwood 2011, Jones 2012, Erritzoe 2015). In addition, such a limited molt may proceed rapidly and may not result in substantial temperal overlap among individuals, thus may be more extensive across the sample than a maximum simultaneous measure might indicate.

The presence of prealternate molts in passerines is known to correlate with migration (Svensson and Hedenström 1999, Figuerola and Jovani 2001, Guallar and Figuerola 2016), but its occurrence in resident and especially resident Neotropical species requires further investigation. Episodes of limited body-feather replacement during non-peak times of molt could also be interpreted as part of protracted and/or suspended preformative or prebasic molts (Pyle 1997a, 2007; Howell 2010), or as adventitious in some migratory species which only replace a few body feathers (Howell 2010). Falsifying competing interpretations would require the recapture of individuals throughout the year to determine if feathers were replaced once or twice during the annual molt cycle. Our results do not support an adventitious molt explanation as we would expect the replacement of feathers to occur at the same frequency throughout the year; because we did not observe retained body feathers, and molt peaks were distinct, we found little evidence for a protracted molt scenario. We suggest that the most parsimonious explanation is the presence of a limited prealternate molt, which may be cryptic or absent in other members of the species.

The timing of definitive prebasic and preformative molts is often determined by reproductive timing, with late breeding individuals often molting later (Hahn et al. 1992). This effect has also been documented among species (Barta et al. 2006, 2008; Morrison et al. 2015). Late breeding may influence the prebasic and preformative molts if food availability and/or photoperiod impose constraints late in the season (Hau et al. 1998, Hemborg 1999, Norris et al. 2004, Barta et al. 2008). Late-molting individuals within a species might tend to show a less extensive preformative molt (Bojarinova et al. 1999, Elrod et al. 2011).

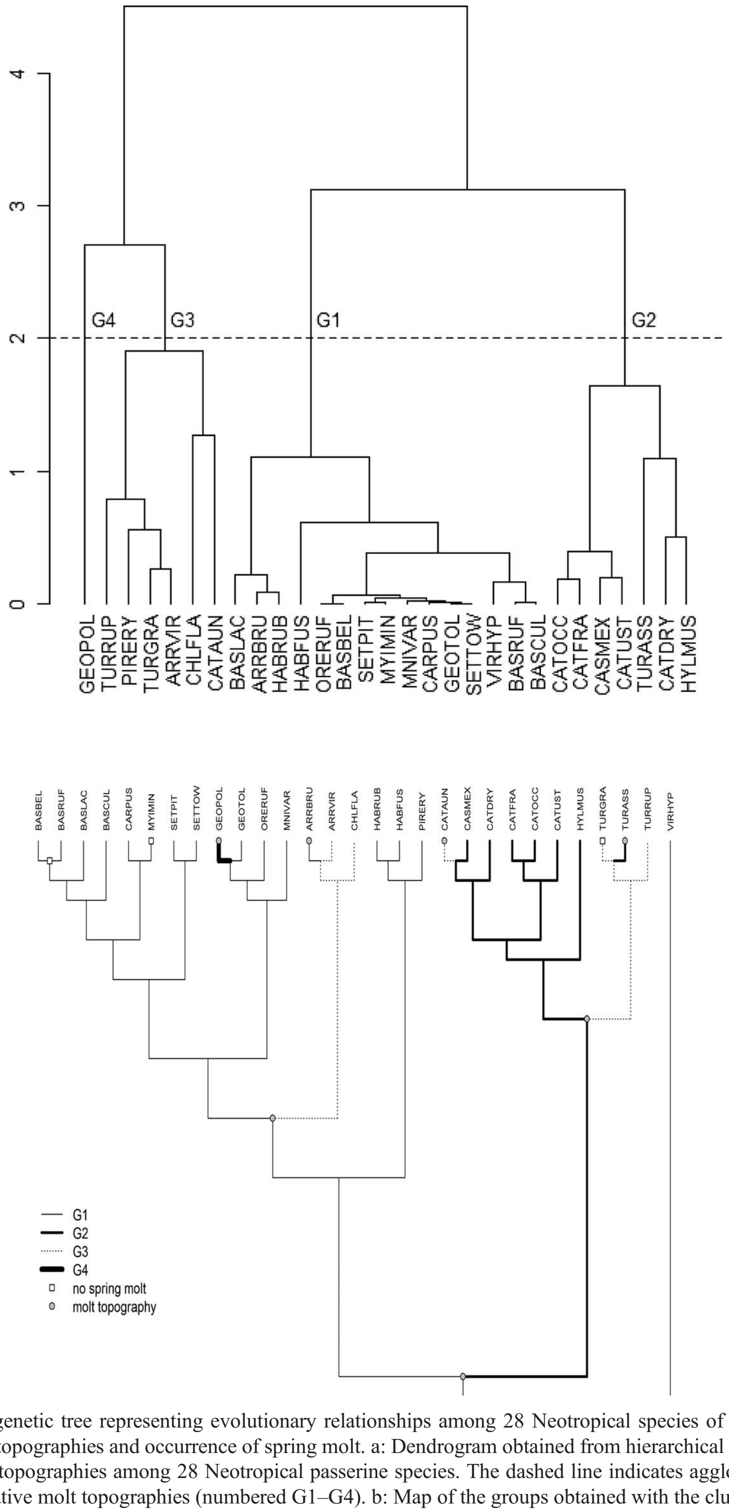

FIG. 4. Phylogenetic tree representing evolutionary relationships among 28 Neotropical species of four families, their preformative molt topographies and occurrence of spring molt. a: Dendrogram obtained from hierarchical clustering based on preformative molt topographies among 28 Neotropical passerine species. The dashed line indicates agglomeration into four groups of preformative molt topographies (numbered G1–G4). b: Map of the groups obtained with the cluster analysis on the rooted majority-rule consensus tree. Gray circles indicate changes in preformative molt topography according to the hierarchical clustering above. Line width equates group number. Blank rectangles map the changes towards absence of a spring molt (only four species lack this molt).

We found no evidence of less extensive molt in the ant-tanagers, which molt latest and have the most extensive molt among our study species (Table 2).

Preformative molt timing, intensity, duration, extent, and quality of formative feathers likely interact and trade off to determine whether an individual bird adheres to the general mode or not. Birds under greater time constraints might be expected to replace fewer feathers during the preformative molt (Jenni and Winkler 1994) but could instead compensate by shortening molt duration through increased molt intensity (Rohwer and Broms 2013) at the expense of reducing feather quality (Hall and Fransson 2000, Dawson 2004). The final topography could also be affected by the amount of resources, such as the deposition of keratin; however, relationships between resources allocated to molting feathers and subsequent topography can be further complicated by the reduction of feather mass caused by time constraints (see de la Hera et al. 2009). Variations in molt extent may also influence the mode of replacement as birds may keep extent constant, but vary which feathers are replaced (Gualler et al. 2014). Latitude is known to affect molt timing and extent in some species (Jenni and Winkler 1994, Crates et al. 2015), and could potentially be associated with mode of replacement. For example, preformative molt of Eurasian Blackcaps (*Sylvia atricapilla*) adheres to the general mode of replacement (SXG, pers. obs.), although some individuals from Iberian populations undergo a complete molt (Morganti et al. 2013). A latitudinal trend toward eccentric preformative molt patterns in southern, earlier-breeding populations is thought to occur in other Palearctic passerines (Newton 1968, Gauci and Sultana 1979). We might expect to find a parallel effect of higher relative frequency of the proximal mode in late-hatched birds in the Neotropics. Our data suggest this latitudinal trend (Fig. S15).

*Mode of Feather Replacement.*—By calculating preformative molt topography, we have revealed that proximal and general modes of replacement result in noticeable intraspecific differences, strikingly so in Fan-tailed Warbler and Common Bush-Tanager (Figs. S6, S8).

The general mode of replacement seems pervasive within passerines that have partial preformative molts, but some individuals in many species also show a proximal mode of replacement (Pyle 1997a, Guallar et al. 2014; Figs. S4–S13). Our results suggest that the proximal mode might be associated with a reduction in molt extent, at least in some species (Figs. S4–S13, Tables S3–S4). Occasionally, some individuals may show odd modes of replacement. For example, one Clay-colored Thrush presented an eccentric preformative molt in south Texas (Fig. S17; M. Grosselet, unpubl. data). Factors that drive intra- and interspecific variation in mode frequency are largely unexplained, although time constraints resulting from migration and hatching date, for example, may play important roles.

Although its significance remains unknown, modes of replacement do not seem to be errors that deviate from a "correct" pattern (Gargallo 2013) but rather represent full expressions of diverse processes acting during molt (e.g., activation of feather follicles, intensity and sequence). The preformative molt results in organized topographies of wing-feather replacement that strongly diverge from randomness. This can be rapidly assessed in our sample by dividing the number of observed combinations by all the possible feather combinations within the tracts involved (lesser, median, and greater coverts as well as tertials): 51 combinations divided by a number of 22 digits is only a tiny fraction of all the possible theoretical combinations. Even considering our sample a 0.001% of all the hypothetical real topographies, we would observe just 1 in $10^{16}$ of all possible topographies.

Differences among species in their preformative molts are noticeable and are consistent within their respective families, and even genera (Fig. 4b) suggesting phylogenetic inertia. Several deviations may be driven by ecological factors. For example, we found one terminal change within parulids which form a homogeneous group in our cluster analysis (G1 Fig. 4a) despite comprising both migrant and resident species. Gray-crowned Yellowthroat, the only non-forest parulid in our sample, is a dweller of tropical moist shrublands (Howell and Webb 1995), and the only species we documented replacing primaries, secondaries, and primary coverts. Other parulids that inhabit shrublands such as Common Yellowthroat (*Geothlypis trichas*) and Yellow-breasted Chat (*Icteria virens*, of uncertain taxonomic status; Chesser et al. 2011) also replace feathers from these tracts (Pyle 1997a, Guallar et al. 2009). On the other hand, the three changes affecting turdids and emberizids imply differences in the frequency of mode of replacement with no obvious ecological correlates that may explain them.

Our detailed examination of the preformative molt reveal subtle between-species differences that may have important implications for our understanding of the function of the preformative molt and its molt evolution, not only in Neotropical songbirds but more broadly. Whereas some molt elements such as sequence of remegial replacement and extent during prebasic molts appear fixed (Pyle 2013), other components of molt appear quite flexible. Our results suggest that ecological factors may have a stronger influence than phylogenetic inertia shaping preformative molt topography in Neotropical passerines, at least in our sample of 28 species. Different taxonomic groups may respond differently to ecological factors, showing a stronger influence of their evolutionary history and weaker capacity to adapt to new conditions, although much work is still needed. Adequate and robust assessment of the ecological and phylogenetic influences on molt topograhies of Neotropical passerines will only be possible after compiling preformative molt descriptions of a significant and representative percentage of Neotropical passerine species.

## ACKNOWLEDGMENTS

We are deeply grateful for the comments of two anonymous reviewers. We thank Carla Cicero at the Museum of Vertebrate Zoology, Berkeley, California, Maureen Flannery of the California Academy of Sciences, San Francisco, California, Dr. Adolfo Navarro and M.C. Fanny Rebón of the Museo de Zoología Alfonso Herrera, and Dr. Patricia Escalante and M.C. Marco Gurrola of the Colección Nacional de Aves in Mexico City for assistance and access to specimen collections. We are also thankful to Ángel Rueda, Manuel Grosselet, and John Woodcock for sharing their pictures, and Anna Gallés for drawing the wing diagrams

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