ORNITOLOGÍA NEOTROPICAL
SPECIAL ISSUE (2018) 29: S3–S10
ORIGINAL ARTICLE

Sociedad
de Ornitología
Neotropical

PREFORMATIVE WING MOLT IN 23 NEOTROPICAL RESIDENT PASSERINE SPECIES

Santi Guallar[1] · Angelina Ruiz-Sánchez[2] · Rafael Rueda-Hernández[3] · Peter Pyle[4]

[1] Department of Animal Biology, University of Barcelona, Av. Diagonal 643, Barcelona 08028, Spain.
[2] Universidad Veracruzana, Lomas del estadio S/N, Col. Zona Universitaria, Xalapa 91000, Veracruz, Mexico.
[3] Instituto de Ecología (INECOL), Carretera antigua a Coatepec 351, El Haya, Xalapa 91070, Veracruz, Mexico.
[4] Institute for Bird Populations, Point Reyes Station, CA 94956, USA.
E-mail: Santi Guallar · sguallar@yahoo.com

ABSTRACT · Quantitative descriptions of wing-feather replacement during the preformative and prealternate molts of resident Neotropical passerines are deficient: no more than 100 species possess adequate information. Here, we present quantitative molt data for 23 Neotropical passerines in three blocks: wing and tail molt extent, frequency of wing-molt pattern, and frequency of wing-feather replacement. We used Bayesian bootstrapping to estimate mean and 95% credible intervals of wing- and tail-molt extent. We found four molt patterns in the preformative molt, of which most species present more than one. Twenty-one species undergo partial molt, being the general pattern most frequent. Only Northern Beardless-Tyrannulet (*Camptostoma imberbe*) and Black-chested Sparrow (*Peucaea humeralis*) undergo a complete preformative molt, the latter also undergoing an extensive prealternate molt. Basic life-history information may inspire hypotheses to explain molt phenomena. In this sense, our results suggest that lack of time constraints has a small influence on completeness of preformative molt, at least in Neotropical passerines.

RESUMEN · Muda preformativa de 23 especies residentes de paseriformes Neotropicales
La deficiencia de descripciones cuantitativas sobre el reemplazo de plumas del ala en las mudas preformativa y prealterna de paseriformes neotropicales es dramática: no más de 100 especies poseen información adecuada. A continuación, presentamos datos cuantitativos de muda para 23 paseriformes neotropicales en tres bloques: extensión de muda en ala y cola, frecuencia de patrón de muda alar, y frecuencia de reemplazo de plumas del ala. Utilizamos "bootstrapping" bayesiano para estimar la media e intervalos de credibilidad del 95% de la extensión de muda en ala y cola. Encontramos cuatro patrones de muda en la muda preformativa, de los cuales la mayoría de las especies presentan más de uno. Veintiuna especies mostraron patrones parciales, siendo el patrón general el más frecuente. Sólo *Camptostoma imberbe* y *Peucaea humeralis* realizan una muda completa (este último también presenta una extensa muda prealterna). La información básica sobre historia natural puede inspirar hipótesis que expliquen los fenómenos de muda. En este sentido, nuestros resultados sugieren que la ausencia de limitaciones temporales tiene una influencia limitada sobre la compleción de la muda preformativa, al menos en paseriformes neotropicales.

KEY WORDS: Bayesian bootstrapping · Molt extent · Molt pattern · Pattern signature

INTRODUCTION

Of the three main life-history stages, molt has received far fewer publications in the last five decades than breeding or migration (Bridge 2011). Therefore, it comes as no surprise that important gaps in the study of feather molt still exist. Bridge (2011) reviewed some of these gaps, among which sparsity and inadequacy of basic molt data on timing (Freed & Cann 2012, Cristol et al. 2014), intensity (Rohwer 2013, Rohwer & Rohwer 2014), number of molt episodes in the annual cycle (Barta et al. 2008, Newton 2008), replacement sequence (Rohwer 2008, Pyle 2013), and their topography (Jenni & Winkler 1994, Guallar et al. 2014) stood out. Quantitative descriptions of feather replacement in the preformative and prealternate molts of Neotropical passerines represent one such deficiency. Of the 2,412 passerine species listed for the Neotropics (Gill & Donsker 2016), this information exists for fewer than 100 (see Guallar et al. 2009, 2016; Ruiz-Sánchez et al. 2012, Johnson & Wolfe 2014, Guallar et al. 2016). This knowledge would not only enhance our ability to age individuals in moni-

Receipt 25 September 2016 · First decision 7 November 2016 · Acceptance 22 December 2016 · Online publication 8 May 2018

Communicated by Maria Echeverry-Galvis

toring projects (DeSante et al. 2002), it could be directly used to test ecological and evolutionary hypotheses such as the factors influencing molt extent across and within species (Guallar & Figuerola 2016), the evolution of complete molts in relation to feather quality (Kiat & Izhaki 2016), or sex determination (e.g., juvenile males of the Cinnamon-bellied Flowerpiercer *Diglossa baritula* cannot be identified to sex until preformative feathers grow in; Guallar et al. 2009).

Here, we document quantitative molt data for 23 resident passerine species that breed throughout the Neotropical region, from the southwestern United States to Argentina (Table 1). This range lies within the subtropical and tropical regions (Hess & Tasa 2014). Resident birds within these regions show more relaxed annual cycles, since they are neither constrained by migration (Barta et al. 2008) nor by a strongly marked seasonality (Wikelski et al. 2000). We propose summarizing this information in three blocks to facilitate its use for hypothesis testing and age determination:

i) Estimates of wing- and tail-molt extent;

ii) Observed frequencies of wing-molt pattern;

iii) Observed frequencies of wing-feather replacement.

METHODS

We gathered preformative molt data for 23 species of 10 passerine families (Table 1). We selected species for which little or no information on preformative molt was available. This broad selection covers 25% of the passerine families breeding in the Neotropics (Gill & Donsker 2016), and ranges from southern Arizona to Argentina (Table 1). Our dataset contains molt information from 129 specimens (62% were collected in Mexico) in three museum collections (Museum of Vertebrate Zoology, Berkeley, California, USA; Museo de Zoología Alfonso Herrera, Mexico, DF, Mexico; and Museu de Ciències Naturals in Barcelona, Spain; see Supplementary Online Material for a list of specimens) and from 52 mist-netted birds in Jalisco and Veracruz states, Mexico between 2004 and 2010. Additionally, we described the prealternate molt of the Black-chested Sparrow (*Peucaea humeralis*) because it is similar to, and can be mistaken for, a preformative molt, especially given that coloration of basic, formative, and alternate plumages do not vary. We also included information on skull pneumatization and iris color in mist-netted birds. These characters vary as birds mature and are widely used for aging birds (Sweijd & Craig 1991, Jenni & Winkler 1994, Pyle 1997a, Nogueira & Alves 2008).

Terminology used. Molt terminology is multifarious and not consistent across authors. Here, we used many terms, some introduced recently (e.g., topography), or for the first time (e.g., limited wing-molt pattern). In order to help the reader, we included definitions of relevant terms used here. In alphabetical order:

Molt episode: each separate molt event in the annual molt cycle of passerines. Here, we only considered the preformative and the prealternate.

Molt extent: quantity of replaced feathers.

Molt topography: number and identity of feathers replaced after a molt episode. This metric informs about the spatial configuration of molt. It is restricted to the wing in this article.

Pattern signature: observed frequency of wing-molt patterns in a given species.

Wing-molt patterns: categories of wing-molt topographies sharing particular rules of similarity. The different patterns here considered should not be confused with other uses given by other authors. For example, Pyle (1997a: 31) uses “limited molt” to refer to body feathers only.

Molt extent. We scored non-active molt data, specifying which wing feathers and rectrices were replaced or not, using established aging criteria, based on feather coloration, shape, and wear (Jenni & Winkler 1994, Pyle 1997a; Figure S1, Supplementary Material online). Replaced feathers belonging to the most recent molt episode were scored 1, retained feathers were scored 0. The 10 primaries, nine secondaries, three alula feathers, 10 greater coverts, nine primary coverts, eight median coverts, and 12 rectrices were scored individually. For standardization purposes, the tenth primary of species with nine visible primaries was given the same score as the ninth primary (Hall 2005). Replaced lesser coverts were scored as the fraction of the feathers of the tract, and the final score was 1 for replacement ratios ≥ 0.85, 0 otherwise (we used a cut-off sufficiently close to 1 to acknowledge the difficulties of assessing the exact replacement ratio). Wing-molt extent was computed as the sum of feather scores for one wing, and ranged from 1 to 51 (the latter corresponding to the complete molt). All individuals of each species were pooled regardless of sex and locality due to small sample sizes. This may cause biases even in non-migrant species (Jenni & Winkler 1994, Crates et al. 2015). However, our assessment of the overall effects of sex and latitude on wing-molt extent in our dataset suggests that such biases are small (Figures S2–S3, Supplementary Material online) in accordance with other studies showing that the degree of sex and geographic differences in molt extent within species tend to be negligible (Bojarinova et al. 1999, Guallar et al. 2016).

Wing-molt pattern. We considered seven patterns (definitions in Table 2), including complete (Dwight 1902), general and proximal (Guallar et al. 2014), inverted and limited (Jenni & Winkler 1994). Briefly, the complete pattern consists of full replacement of the wing feathers (the remaining patterns are partial); eccentric pattern consists of an almost complete molt with retention of inner primaries, outer second-

Species	Family	English name	N	Wing extent	Tail extent	Complete	General	Proximal	Inverted	Limited
Preformative molt										
†*Camptostoma imberbe*	Tyrannidae	Northern Beardless-Tyrannulet	5	50.8 (50.4–51)	6	5	0	0	0	0
Mionectes oleagineus	Tyrannidae	Ochre-bellied Flycatcher	6	12.8 (9.1–16.4)	0.3 (0–0.7)	0	4	1	0	1
Contopus pertinax	Tyrannidae	Greater Pewee	11	13.6 (10.2–17.1)	0	0	2	9	0	0
Empidonax fulvifrons	Tyrannidae	Buff-breasted Flycatcher	5	8.2 (6.5–9.9)	0	0	0	5	0	0
Attila spadiceus	Tyrannidae	Bright-rumped Attila	9	13.0 (10.6–16.5)	0	0	3	6	0	0
Corapipo altera	Pipridae	White-ruffed Manakin	4	8.8 (6.4–10.9)	0	0	1	3	0	0
Ceratopipra mentalis	Pipridae	Red-capped Manakin	10	16.0 (14.6–17.2)	0	0	9	1	0	0
Tunchiornis ochraceiceps	Vireonidae	Tawny-crowned Greenlet	2	22.5 (22.0–23.0)	0	0	2	0	0	0
Pachysylvia decurtata	Vireonidae	Lesser Greenlet	2	22.0 (21.0–22.9)	0	0	2	0	0	0
Vireo huttoni	Vireonidae	Hutton's Vireo	11	20.4 (18.6–22.0)	0.1 (0–0.3)	0	10	1	0	0
†*Cyanocorax sanblasianus*	Corvidae	San Blas Jay	12	13.1 (10.4–15.9)	0.2 (0–0.4)	0	4	4	0	4
**Turdus chiguanco*	Turdidae	Chiguanco Thrush	2	19.0 (17.2–21.0)	0	0	1	1	0	0
**Turdus ignobilis*	Turdidae	Black-billed Thrush	2	19.0 (14.5–24.0)	1.0 (0.1–2.0)	0	2	0	0	0
†*Ptiliogonys cinereus*	Ptiliogonatidae	Gray Silky-flycatcher	15	23.0 (22.2–23.8)	0.1 (0–0.2.0)	0	13	2	0	0
†*Euphonia elegantissima*	Fringillidae	Elegant Euphonia	4	19.0 (14.1–23.6)	0	0	2	2	0	0
Arremon aurantiirostris	Emberizidae	Orange-billed Sparrow	9	20.4 (17.9–22.5)	0.4 (0.2–0.8)	0	7	2	0	0
**Arremon torquatus*	Emberizidae	White-browed Brushfinch	3	21.0 (20.2–21.7)	0	0	3	0	0	0
**Atlapetes tricolor*	Emberizidae	Tricolored Brushfinch	2	15.7 (7.8–23.8)	0	0	1	1	0	0
†*Peucaea humeralis*	Emberizidae	Black-chested Sparrow	5	51	6	5	0	0	0	0
Piranga flava	Cardinalidae	Hepatic Tanager	16	21.6 (21.1–22.0)	0	0	16	0	0	0
†*Piranga bidentata*	Cardinalidae	Flame-colored Tanager	7	20.4 (18.7–22.3)	0	0	6	1	0	0
†*Amaurospiza concolor*	Cardinalidae	Blue Seedeater	4	22.0 (21.4–22.7)	0	0	3	1	0	0
†*Cassiculus melanicterus*	Icteridae	Yellow-winged Cacique	14	9.1 (5.9–12.5)	0	0	4	3	0	7
Presence						8.7	87.0	69.6	0	13.0
Prealternate molt										
Peucaea humeralis	Emberizidae	Black-chested Sparrow	11	16.7 (13.9–19.8)	1.5 (0.2–2.7)	0	3	7	1	0

Table 1 (see previous page). Wing and tail preformative and prealternate molt extent and pattern signature for 23 resident Neotropical passerine species for which n > 1. Extent estimates correspond to Bayesian bootstrapped means (95% credible intervals). Pattern signature corresponds to observed frequencies for five molt patterns (five columns on the right). Presence indicates the percentage of study species showing a particular molt pattern. * indicates exclusive South American geographic distribution. † indicates exclusive Central American geographic distribution. Greater Pewee, Buff-breasted Flycatcher, Hutton's Vireo, and Hepatic Tanager also occur in southwestern United States.

aries, and primary coverts; general and proximal patterns consist of a partial replacement that prioritizes feathers from the leading edge (secondary coverts, alula, less frequently tertials) over those of the trailing edge of the wing (secondaries, primaries, or primary coverts); inverted pattern consists of a partial replacement that prioritizes feathers from the trailing edge over those of the leading edge of the wing (tertials, secondaries, and greater coverts); limited pattern consists of a partial replacement that only affects the lesser and median coverts; and reduced pattern consists of only the replacement of a few secondaries or greater coverts near the body.

Wing-feather replacement. For each species, we calculated the arithmetic mean score of every individual wing-feather, including the block of lesser coverts.

Statistical analyses. Mean and 95% credible intervals of wing- and tail- molt extent for each species were estimated applying Bayesian bootstrapping. 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. For example, 95% Bayesian credible intervals say that the true mean will lie within these intervals with a 95% probability. These estimates can be easily carried out in R (R Core Team 2016) using libraries bayesboot and BayesianFirstAid (Bååth 2014, 2016).

RESULTS

Molt extent. Buff-breasted Flycatcher (*Empidonax fulvifrons*), White-ruffed Manakin (*Corapipo altera*), and Yellow-winged Cacique (*Cassiculus melanicterus*) presented the lowest wing-molt extent, whereas Black-chested Sparrow and Northern Beardless-Tyrannulet presented the highest (Table 1). The Northern Beardless-Tyrannulet undergoes a complete preformative molt as already documented by Pyle (1997a); however, its extent is not 51 because of occasional retention of inner secondaries. Complete preformative molts were confirmed with iris color (which shifts from pale brown to reddish brown in Black-chested Sparrows during the first months of life) and skull pneumatization in mist-netted birds. Mean molt extent for the remaining 18 species is 18.2, which would equate to replacement of all secondary coverts except the carpal in the general pattern.

Only six species with partial preformative wing-molts replaced 1–2 central rectrices (Table 1), of which the Orange-billed Sparrow (*Arremon aurantiirostris*) renewed them at moderately high frequency (44.4%). All 23 species replaced their whole body feathers during the preformative molt (also the prealternate molt of the Black-chested Sparrow).

Wing-molt pattern. We did not find the eccentric and reduced patterns in our study species (Table 2). Pattern signature varied with species, with most presenting more than one pattern: only eight showed one pattern, 12 showed two patterns, while three species showed three patterns. The complete pattern was the least frequent among the 23 study species, being present in two (8.7%) of our study species (Table 1); Bayesian binomial test: $P < 0.001$). Moreover, it was not associated to any other patterns. The general pattern was the most frequent molt pattern, it was observed in 20 of the 23 study species, and was only absent from the two species undergoing complete preformative molt as well as in the Buff-breasted Flycatcher. The proximal pattern was present in all but seven species, and it always appears associated to the general pattern except again in the Buff-breasted Flycatcher. The inverted pattern only appeared in the prealternate molt of the Black-chested Sparrow. Finally, the limited pattern appeared associated to the general and proximal patterns, and was only found in three species, the two largest ones (San Blas Jay *Cyanocorax sanblasianus* and Yellow-winged Cacique) along with the Ochre-bellied Flycatcher (*Mionectes oleagineus*).

Wing-feather replacement. Priority of replacement is depicted in the wing diagrams of Figure 1. It is worth mentioning that the lesser coverts have lower priority than inner median and greater coverts in Ochre-bellied Flycatcher, Bright-rumped Attila (*Attila spadiceus*), and Gray Silky-Flycatcher (*Ptiliogonys cinereus*). Also the innermost greater covert has lower priority than adjacent greater coverts in Greater Pewee (*Contopus pertinax*), Flame-colored Tanager (*Piranga bidentata*), and Yellow-winged Cacique. Frequency of replacement are annexed as an excel file in Supplementary Online Material to facilitate its use in further molt research.

DISCUSSION

We documented molt extent, frequency of wing-molt patterns, and frequency of wing-feather replacement for 23 Neotropical resident passerine species.

Table 2. Molt patterns considered for describing pattern signature in our dataset (based on Guallar & Jovani in prep.). Mode of replacement is the hypothetical underlying physiological mechanism of control, which switch on or off certain areas of the wing allowing or excluding the renewal of the involved feathers.

Pattern	Mode of replacement (MR) Example (Ex)	Notes
Complete	**MR:** Full feather replacement. **Ex:** Preformative molt of the House Sparrow (*Passer domesticus*).	Conserved molt sequence: start at primary 1, replacement of primaries accompanied by respective primary coverts.
Eccentric	**MR:** All tracts are affected. Inner primaries, secondaries, and most to all primary coverts are retained. **Ex:** Preformative molt of *Passerina* buntings.	Nodal remiges differ from those of complete molts; coverts may grow in before primaries, which are not accompanied by their corresponding primary coverts (except for outermost coverts in some birds).
General	**MR:** Replacement of secondary coverts. Tertials are replaced only if all coverts are molted. Might be extended with 1–2 adjacent secondaries. It does not include primaries nor primary coverts. **Ex:** Preformative molt of *Turdus* spp.	There is a prioritization from leading to trailing edge of wing: filling of an entire feather tract before proceeding with the next.
Proximal	**MR:** Same as the general pattern but tertials (and adjacent inner secondaries) are replaced with retention of outer secondary coverts. **Ex:** Preformative molt of Wood-Wrens *Henicorhina* spp.	From leading to trailing edge of wing: prioritization of feathers closer to the body before finishing replacement of anterior tracts.
Inverted	**MR:** Replacement of inner secondaries and secondary coverts. May include primaries and primary coverts in extreme cases. **Ex:** Prealternate molt of several trans-Saharian migrants including the Pied Flycatcher (*Ficedula hypoleuca*)	From trailing to leading edge of wing: prioritization of feathers closer to the body of tertials, secondaries, and greater coverts over median and lesser coverts (the latter usually at low percentages).
Limited	**MR:** Replacement of lesser and or median coverts, including the carpal covert. **Ex:** Preformative molt of dippers, nuthatches, treecreepers, and kinglets.	Prioritization of replacement from leading to trailing edge of area and from inner to outer feathers within it.
Reduced	**MR:** Replacement of one to a few tertials and or greater coverts. Strongly asymmetrical molts are considered accidental. **Ex:** Prealternate molt of some *Myiarchus* flycatchers.	Activation of follicles from a small wing area near the body. Unlike the other patterns, it may not be accompanied by replacement of body feathers.

Molt extent and wing-molt pattern. Although small sample sizes increase uncertainty in the molt estimates (McCarthy 2007), and may leave some patterns undetected within species, our results do not depart from what we know from closely related species. Similarity among closely related resident Neotropical passerine species suggests phylogenetic inertia and hence constraints on the evolution of different molt strategies. However, major changes in molt strategies may be associated to evolutionary novelties such as adaptation to a new habitat (Guallar et al. 2016). As expected, extent and pattern of wing feather replacement during the preformative molt of the study species are very similar to those for close Neotropical relatives with available quantitative information. For example, molt extent of Clay-colored Thrush (*Turdus grayi*) and Chestnut-capped Brush-Finch (*Arremon brunneinucha*) overlap with the extent of their congenerics here documented (mean [95%CI]: 15.6 [13.5–17.8] and 18.5 [16.8–20.2], respectively; Guallar et al. 2016). Likewise, pattern and extent of molt in the Hutton's Vireo in the Neotropics are nearly identical to those documented for four Neotropical resident congenerics (Guallar et al. 2009). Gómez et al. (2012) also found (partial) molt strategies consistent with seven genera we included in this study: *Attila*, *Ceratopipra*, *Turdus*, *Vireo*, *Arremon*, *Atlapetes*, and *Piranga*. Furthermore, the molt strategy of the Black-chested Sparrow is nearly identical to that of the congeneric Stripe-headed Sparrow (*Peucaea ruficauda*) (Guallar et al. 2009), which consists of a complete preformative molt in late autumn and a spring prealternate molt. It is also worth noting that wing-molt patterns of resident Neotropical passerine genera (e.g., *Camptostoma*, *Contopus*, *Empidonax*, *Vireo*, *Cyanocorax*, *Turdus*, *Peucaea*, *Piranga*), are similar to those of the same or congeneric species in the Nearctic (Pyle 1997a, 1997b; Wolfe & Pyle 2012).

Most study species showed more than one molt pattern during the preformative molt, with the general pattern being prevalent (Table 1), as documented elsewhere (Guallar et al. 2016). The meaning of molt pattern variation is poorly known and understudied at the species level (Pyle 1997a, Guallar et al. 2014). This variation might reflect the ability of individuals of a given species to meet different plumage requirements (Gill 1995) under time and energetic con-

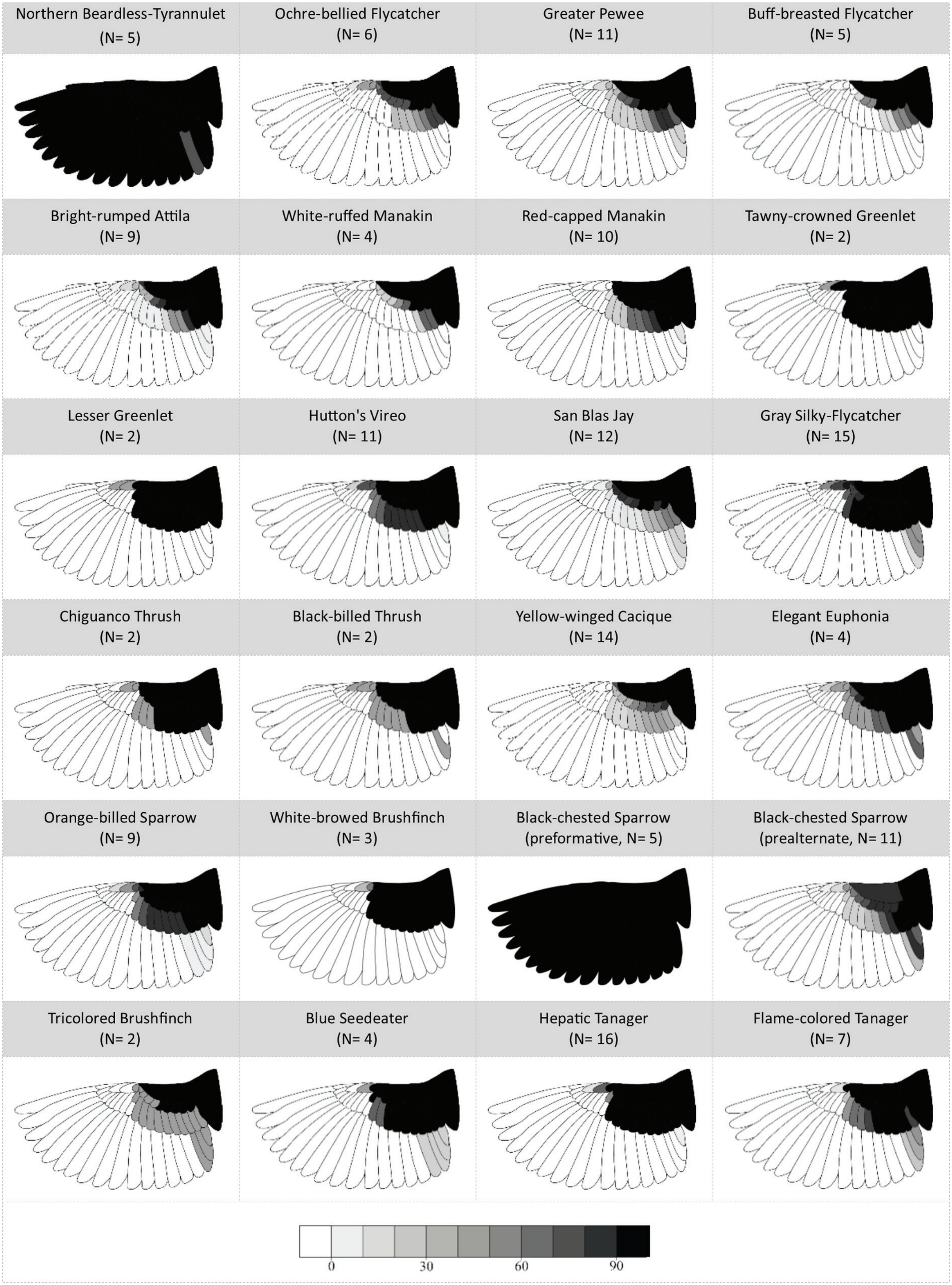

Figure 1. Frequency of wing-feather replacement resulting from preformative molts in 23 resident Neotropical passerine species, and prealternate molt of the Black-chested Sparrow. Gray scales represent observed replacement frequencies. Wing diagrams of species that retain lesser coverts show a small distal compartment which depicts that retention within this tract usually takes place at its distal end.

straints (Gosler 1991, Barta et al. 2008). For example, a hypothetical species might have adapted replacement of juvenile remiges during the preformative molt because it inhabits an abrasive environment (Willoughby 1991, Greenberg & Marra 2005) or is subject to extensive solar exposure on an annual basis (Pyle 1998); however, scheduled restrictions due to the onset of migration or change in climate (Coppack & Both 2002, Cristol et al. 2014) would impede a complete molt, and this species would eventually replace just part of its remiges in an eccentric pattern, or even in a general pattern in the case of stronger time constraints. In such cases, fledglings from later broods may show more-constrained molt patterns than those of earlier broods (Pyle 1997a).

The complete pattern is only shown by two of our 23 resident species, Northern Beardless-Tyrannulet and Black-chested Sparrow. Since resident birds have more relaxed annual cycles (Barta et al. 2008), we would have expected more species to show the complete pattern; therefore time constraints do not seem to have played an important role in the completeness of the preformative molt in Neotropical passerines, as has been suggested for their Palearctic counterparts (Kiat & Izhaki 2016). Northern Beardless-Tyrannulet and Black-chested Sparrow are the only inhabitants of arid habitats in our dataset (Howell & Webb 1995). Birds that occur in arid habitats are likely more exposed to solar radiation, which is known to accelerate feather deterioration (Bergman 1982, Burtt 1986, Pyle 1998). The fact that species occurring in nearby closed habitats do not undergo complete preformative molts (e.g., Tyrannidae, Emberizidae; Guallar et al. 2016, this study) suggests the importance of habitat and/or solar exposure as driver of molt completeness (Pyle 1998, Greenberg & Marra 2005; but see Willoughby 1986, 1991). This hypothesis awaits experimental evidence to be adequately tested, however.

Wing-feather replacement. Wing diagrams are not only useful aging tools (Jenni & Winkler 1994), they also depict priority of wing-feather replacement. In agreement with previous studies (e.g., Jenni & Winkler 1994; Pyle 1997a, 1997b), wing feathers closer to the leading edge and to the body show higher priority of replacement than feathers closer to the trailing edge and the wing tip. However, detailed examination reveals several deviations from this rule:

1) Species with a complete preformative molt replace all wing feathers, although some medial secondaries may be retained (e.g., Northern Beardless-Tyrannulet). This retention can happen in individuals of other passerine species and may reflect time or energy constraints (Pyle 1997a).

2) Median and lesser coverts in species with proximal wing-molt patterns have lower replacement frequencies than inner greater coverts (e.g., Bright-rumped Attila).

3) Lower priority of replacement of the innermost greater covert in relation to adjacent greater coverts (e.g., Greater Pewee). Retention of this feather, which is largely covered by the scapulars, might reflect the ability of some individuals to skip the general rule of replacement and renew more exposed feathers.

4) Tertials and innermost greater coverts have higher priority of replacement than lesser and median coverts in the prealternate molt of the Black-chested Sparrow, which also present an inverted wing-molt pattern. This has also been observed for example in tyrannid flycatchers (Pyle 1997a, 1997b) and could relate to the need to replace these exposed feathers.

Quantitative descriptions of molt are essential to start filling the enormous gap of knowledge that exist on the life-history of Neotropical passerines, to provide useful aging tools for studies that rely on capturing and marking individuals, and to answer ecological and evolutionary questions such as which factors influence the evolution of wing-molt patterns, what functions carry out each wing-feather tract or why pattern signatures vary among species and between molt episodes within species. We encourage ornithologists in the Neotropical region to gather this type of information, such that we may fill species gaps and eventually have a fuller picture of variation in molt strategies among Neotropical birds.

ACKNOWLEDGMENTS

We are deeply grateful for the comments of Wayne Arendt, Miguel Moreno-Palacios, and one anonymous reviewer. We thank Carla Cicero, Museum of Vertebrate Zoology, Berkeley, California; Dr. Adolfo Navarro and M.C. Fanny Rebón, Museo de Zoología Alfonso Herrera, Mexico City; Dra. Patricia Escalante and M.C. Marco Gurrola, Colección Nacional de Aves, Mexico City; and Dr. Javier Quesada, Museu de Ciències Naturals, Barcelona, for assistance and access to specimen collections. Anna Gallés drew the wing diagrams.

REFERENCES

Bååth, R (2014) *Bayesian First Aid: a package that implements Bayesian alternatives to the classical *.test functions in R*. *In* Proceedings of UseR! 2014 - the International R User Conference. Downloaded on 20 August 2016 from https://github.com/rasmusab/bayesian_first_aid

Bååth, R (2016) *Package 'bayesboot'. An implementation of Rubin's (1981) Bayesian bootstrap*. Version 0.2.1. Downloaded on 20 August 2016 from https://github.com/rasmusab/bayesboot

Barta, Z, JM McNamara, AI Houston, TP Weber, A Hedenström & O Feró (2008) Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society B* 363: 211–229.

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

Bojarinova, JG, E Lehikoinen & T Eeva (1999) Dependence of postjuvenile moult on hatching date, condition and sex in the Great Tit. *Journal of Avian Biology* 30: 437–466.

Bridge, ES (2011) Mind the gaps: what's missing in our understanding of feather molt. *The Condor* 113: 1–4.

Burtt, EH (1986) An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs* 38: 1–126.

Coppack, T & C Both (2002) Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* 90: 369–378.

Crates, RA, BC Sheldon & CJ Garroway (2015) Causes and consequences of individual variation in the extent of post-juvenile moult in the Blue Tit *Cyanistes caeruleus* (Passeriformes: Paridae). *Biological Journal of the Linnean Society* 116: 341–351.

Cristol, DA, KM Johnson, KD Jenkins & DM Hawley (2014) Timing of feather molt related to date of spring migration in male White-throated Sparrows. *Journal of Experimental Zoology A* 321: 586–594.

DeSante, DF, KM Burton, P Vélez & D Froehlich (2002) *MAPS manual*. Institute for Bird Populations, Point Reyes Station, California, USA.

Dwight, J (1902) Plumage-cycles and the relation between plumages and moults. *The Auk* 19: 248–255.

Freed, LA & RL Cann (2012) Changes in timing, duration, and symmetry of molt of Hawaiian forest birds. *PLoS ONE* 7: e29834.

Gill, FB (1995) *Ornithology*. 2nd ed. W.H. Freeman and Company, New York, New York, USA.

Gill, FB & D Donsker (eds) (2016) *IOC World Bird List*. Version 6.3. doi: 10.14344/IOC.ML.6.3. Downloaded on 30 August 2016 from http://www.worldbirdnames.org/.

Gómez, C, E Botero-Delgadillo, NJ Bayly, MI Moreno & CA Páez (2012) Documentando estrategias de muda en aves neotropicales: ejemplos de la Sierra Nevada de Santa Marta, Colombia. *Ornitología Neotropical* 23: 129–138.

Gosler, AG (1991) On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major. Bird Study* 38: 1–9.

Greenberg, & P Marra (eds) (2005) *Birds of two worlds: the ecology and evolution of migration*. The Johns Hopkins Univ. Press, Baltimore, Maryland, USA.

Guallar, S & J Figuerola (2016) Moulting in the non-breeding season: insights from the family Motacillidae. *Biological Journal of the Linnean Society* 118: 774–785.

Guallar, S, E Santana, S Contreras, H Verdugo & A Gallés (2009) *Paseriformes del Occidente de México: morfometría, datación y sexado*. Museu de Ciències Naturals de Barcelona, Barcelona, Spain.

Guallar, S, A Ruiz-Sánchez, R Rueda-Hernández & P Pyle (2014) Moult topography and its application to the study of partial wing-moult in two Neotropical wrens. *Ibis* 156: 311–320.

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

Hall, KSS (2005) Do nine-primaried passerines have nine or ten primary feathers? The evolution of a concept. *Journal of Ornithology* 146: 121–126.

Hess, D & DG Tasa (2014) *McKnight's physical geography: a landscape appreciation*. 11th ed. Pearson Education Limited, Harlow, Essex, UK.

Howell, SNG & S Webb (1995) *A guide to the birds of Mexico and northern Central America.* Oxford Univ. Press, Oxford, Massachusetts, USA.

Jenni, L & R Winkler (1994) *Moult and ageing of European passerines.* Academic Press, London, UK.

Johnson, EI & JD Wolfe (2014) Thamnophilidae (antbird) molt strategies in a Central Amazonian rainforest. *Wilson Journal of Ornithology* 126: 451–462.

Kiat, Y & I Izhaki (2016) Why renew fresh feathers; advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology* 47: 47–56.

McCarthy, MA (2007) *Bayesian methods for ecology.* Cambridge Univ. Press, Cambridge, UK.

Newton, I (2008) *The migration ecology of birds.* Academic Press, London, UK.

Nogueira, DN & MAS Alves (2008) Iris colour as an indicator of age feature in female Brazilian tanagers (Passeriformes: Emberizidae) confirmed by a molecular sexing technique. *Revista de Biología Tropical* 56: 1629–1633.

Pyle, P (1997a) *Identification guide to North American birds. Part I Columbidae to Ploceidae.* Slate Creek Press, Bolinas, California, USA.

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

Pyle, P (1998) Eccentric first-year molts in certain Tyrannid flycatchers. *Western Birds* 29: 29–35.

Pyle, P (2013) Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconidae) and parrots (Psittaciformes). *The Condor* 115: 593–602.

R Core Team (2016) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/ [Accessed 19 August 2016].

Rohwer, S (2008) A primer on summarizing molt data for flight feathers. *The Condor* 110: 799–806.

Rohwer, S (2013) Molt intensity and conservation of a molt migrant (*Passerina ciris*) in northwest Mexico. *The Condor* 115: 421–433.

Rohwer, V & S Rohwer (2014) How do birds adjust the time required to replace their flight feathers? *The Auk* 130: 699–707.

Ruiz-Sánchez, A, R Rueda-Hernández, S Guallar & P Pyle (2012) Age determination of the Spot-breasted Wren and the White-breasted Wood-Wren using preformative molt patterns. *North American Bird Bander* 37: 93–100.

Sweijd, N & AJFK Craig (1991) Histological basis of age-related changes in iris color in the African Pied Starling (*Spreo bicolor*). *The Auk* 108: 53–59.

Willoughby, EJ (1986) An unusual sequence of molts and plumages in Cassin's and Bachman's Sparrows. *The Condor* 88: 461–472.

Wikelski, M, M Hau & JC Wingfield (2000) Seasonality of reproduction in a Neotropical rain forest bird. *Ecology* 81: 2458–2472.

Willoughby, EJ (1991) Molt of the genus *Spizella* in relation to ecological factors affecting plumage wear. *Proceedings of the Western Foundation of Vertebrate Zoology* 4: 247–286.

Wolfe, JD & P Pyle (2012) Progress in our understanding of molt patterns in Central American and Caribbean landbirds. *Ornitología Neotropical* 23: 169–176.