



## Moult topography and its application to the study of partial wing-moult in two neotropical wrens

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During partial moults birds replace a variable number or percentage of old feathers. This quantity, known as moult extent, has been a primary variable used in comparative studies. However, different spatial configurations of feather replacement may result from an equal number of renewed feathers. Few studies have addressed spatial aspects of moult, which may vary among species, among individuals of the same species and between episodes at the individual level. We present a novel approach to quantify the spatial configuration of a wing-moult episode, hereafter referred to as moult topography, which comprises two elements, namely extent and vector, the latter condensing the spatial configuration of the replaced feathers on the wing plane. We apply this method to investigate preformative (post-juvenile) wing-feather moult pattern in the Spot-breasted Wren *Pheugopedius maculipectus* and the White-breasted Wood-Wren *Henicorhina leucosticta*. We specified a null model of wing-moult topography by which feather replacement follows a discrete anterior–posterior (vertical) axis between tracts and a discrete proximal–distal (horizontal) axis within tracts, and whereby wing feathers from a new tract are replaced only if all the feathers from the previous (anterior) tract have been replaced. Our sample of Spot-breasted Wrens showed a strict single pattern of replacement that did not differ significantly from the null model. Our sample of White-breasted Wood-Wrens, however, differed significantly from the null model, showing prioritization of proximal wing feathers closer to the body. These differences might have biological relevance, for example in mate selection or in response to different environmental stressors, and might reveal the influence of these factors on the evolution of moult strategies. Overall, moult topography provides a new approach to future ecological and evolutionary studies of moult.

**Keywords:** moult effort allocation, moult extent, moult vector, Spot-breasted Wren, White-breasted Wood-Wren.

Important gaps remain in our understanding of bird moult regarding the sequence (the order in which new feathers emerge during active moult), extent (the number or percentage of feathers replaced in a moult episode) and individual variation of moult (Bridge 2011), in particular for Neotropical birds (Ryder & Wolfe 2009). The first step towards filling these gaps necessarily includes descriptive work. This information can be gathered

in the field and in museums, and has immediate applications in studies of avian biology as related to constraint trade-offs between moult and both reproduction (Dawson *et al.* 2000, Flinks *et al.* 2008, Rohwer *et al.* 2011) and migration (Bridge *et al.* 2007, De la Hera *et al.* 2009).

Research on moult sequence (e.g. Rohwer & Wang 2010, Junda *et al.* 2012, Pyle 2013) and extent (e.g. Gosler 1994, Deviche 2000, Okahisa *et al.* 2013) has focused primarily on wing feather tracts and rectrices, although there has been important work on moult other than remiges and

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rectrices, especially in passerines (e.g. Rymkevich 1990, Jenni & Winkler 1994) but also in non-passerines (e.g. Williamson 1956, Pyle 2008). Sequence and extent do not maintain a straightforward relationship as can be easily seen by comparing the nodal feathers of prebasic (equivalent to post-nuptial; new nomenclature follows Howell *et al.* 2003) and preformative (equivalent to pre-juvenile) moults of passerines: the former commences with the innermost primary in most species, although nodal primaries can occasionally vary, even within species (Junda *et al.* 2012), and the latter can commence with other primaries within the tract (Jenni & Winkler 1994, Pyle 1998). Moulting extent has been assessed by feather tract for many species (e.g. Rymkevich 1990, Jenni & Winkler 1994) and the dependence between tracts has also been studied (Jenni & Winkler 1994, Gargallo 1997, Guallar *et al.* 2009, Butler 2013).

To outline the geometric properties of moulting, we introduce a novel metric called moulting topography that defines the spatial configuration of feathers replaced at the end of a partial moulting episode. Moulting topography describes how many and which feathers have been renewed at the individual level once the moulting process has finished, as synthesized in wing diagrams (Jenni & Winkler 1994, Shirihai *et al.* 2001). We stress that moulting topography is solely concerned with finished moulting episodes and therefore should not be confused with active moulting sequence. Moulting topographies have thus far been classified into broad qualitative categories including, for instance, 'eccentric' (partial episodes that include remiges) and 'in block' (partial episodes that include all the wing coverts except primary coverts). To our knowledge, however, moulting topographies have never been assessed quantitatively.

By including additional information on the geometric arrangement of the renewed feathers, moulting topography provides a new approach to the study of moulting strategies from ecological, social and evolutionary perspectives. For example, two hypothetical sister species may show the same preformative moulting extent, but one may favour replacement of distal greater coverts while the other prioritizes the tertials. Such variation in topographical patterns suggests that different specific factors may shape the spatial configuration of a partial wing-feather moulting. For example, migratory passerine species such as *Setophaga* warblers (Pyle 1997b) and *Passerina* buntings (Guallar *et al.* 2009) can undergo more than one moulting episode during their first

moulting cycle, each of which potentially serves a different function (Figuerola & Jovani 2001).

Few studies have attempted to describe how moulting topography varies as extent increases (Guallar *et al.* 2009, Gargallo 2012); however, it is generally reported that when birds renew only a few wing feathers these are often the coverts closest to the body and, conversely, when they replace many wing feathers the last ones to be replaced in most species are certain remiges and the primary coverts (Jenni & Winkler 1994, Pyle 1997a, 2008). As extent increases we would expect that new tracts accumulate from the leading edge of the wing caudally and feathers within tracts are replaced proximal–distally. However, such modes of wing-moulting pattern variation have been little studied and might not be fixed.

Quantitative studies of preformative moulting have analysed extent in relation to variables such as social status of yearlings (Senar *et al.* 1998) and time elapsed since hatching (Bojarinova *et al.* 1999). Other studies have used mass of replaced feathers as a measure of physiological effort invested (Gargallo 1996, 2012). However, none has considered the importance of the spatial arrangement of the replaced feathers following a partial moulting episode. Here we propose moulting topography as an appropriate quantitative descriptor for these and other moulting studies.

Moulting topographies examine both the extent and the precise spatial arrangement of feather replacement. The method we propose incorporates vectors, as has previously been applied to the biomechanics (Bock 1964, Winkler & Bock 1976) and aerodynamics of birds (Tucker & Parrott 1970, Thomas 1993, Spedding *et al.* 2003). We use vectors to represent the geometric arrangement of moulted feathers and to define the direction and magnitude (equivalent to the module of a vector; see Methods for a numerical definition) of a finished moulting episode on the plane of the wing. To check the application of our method, we compare the patterns of feather replacement in two Neotropical wrens, describing the relationship between spatial configuration and extent of wing-moulting.

## METHODS

### Moulting data

We gathered moulting data from 34 study specimens in formative plumage (19 Spot-breasted Wrens

*Pheugopedius maculipectus* and 15 White-breasted Wood-Wrens *Henicorhina leucosticta*), and eight live birds, six that were mist-netted at Los Tuxtlas Biosphere Reserve in Veracruz state (two Spot-breasted Wrens and four White-breasted Wood-Wrens), Mexico (18°35'7"N, 95°4'30"W) in October 2010, and two White-breasted Wood-Wrens at Las Cruces Biological Station, Costa Rica (8°47'7"N, 82°57'32"W) in March 2008.

Age was determined by the identification of moult limits between replaced formative and retained juvenile wing feathers, the latter of which are paler and have ill-defined blackish barring in wrens (Ruiz-Sánchez *et al.* 2012). Preformative moult is incomplete and prebasic moult is complete for both species (Ruiz-Sánchez *et al.* 2012).

### Quantification of wing-moult topography

We scored each primary, secondary, tertial, alula, median covert, greater covert (including the carpal) and primary covert on the upper surface of the left wing as juvenile or formative, and did the same for the 18 blocks into which we divided the lesser coverts (Fig. 1). We then quantified two elements: extent and direction of moult. First, we scored extent as the sum of the replaced upper left wing feathers, assigning a 1 to each individual feather or block of lesser coverts that was moulted and a 0 to each of these that was

retained. We excluded the scapulars, as well as the innermost greater covert and the innermost median covert because these feathers have a transitional character with the scapulars in small passerines. This restriction could be modified in other groups of birds if required. Then we mapped the replacement of each feather on a wing diagram and arranged the feathers of the upper wing tracts in rows and columns on an orthogonal plane (Fig. 1), replicating the wing pterilia (Aldrich 1956, Proctor & Lynch 1993). Next, we calculated its centroid  $C$  and derived the moult vector  $\vec{M}$  from it:

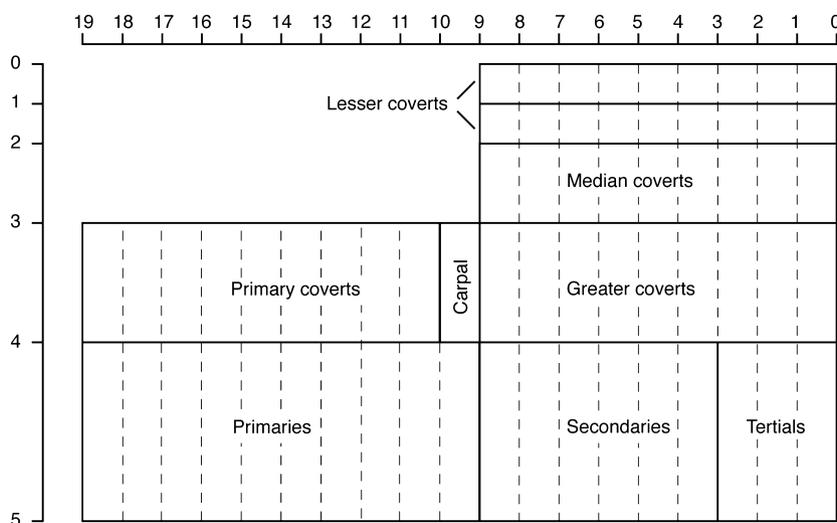
$$C = (C_X, C_Y) = \left( \frac{\sum_{i=1}^{i=N} w_i x_i z_i}{\sum_{i=1}^{i=N} w_i z_i}, \frac{\sum_{i=1}^{i=N} w_i y_i z_i}{\sum_{i=1}^{i=N} w_i z_i} \right)$$

$$\vec{M} = (M_X, M_Y) = C - O = (C_X, C_Y) - (O_X, O_Y)$$

where  $x_i, y_i$  denote the coordinates of feather  $i$ ,  $w_i$  denotes the weight attributed to feather  $i$ ,

$$z_i = \begin{cases} 0 & \text{if feather } i \text{ has not been replaced} \\ 1 & \text{if feather } i \text{ has been replaced} \end{cases}$$

and  $N$  denotes the total number of replaced feathers (moult extent). The origin of the moult vector  $O = (7.92, 3.46)$  is set at the centroid of the wing for a complete moult.



**Figure 1.** Arrangement of the feathers of the upper surface of the left wing on an orthogonal plane. Lesser, median and greater coverts, as well as secondaries and tertials are inserted in the forearm, the rest in the carpal region. We have deformed the vertical scale (positions are not equidistant) for graphical purposes.

The moult vector represents a simplification of the real warped topography of the avian wing. Its angle  $\alpha = \arctan\left(\frac{M_Y}{M_X}\right)$  gives a measure of moult direction, and its module  $|M| = \sqrt{M_X^2 + M_Y^2}$  gives a measure of magnitude in that direction.

This procedure is sensitive to the weight  $w$  given to each feather. In our example we assigned  $w = 1$  to every feather (i.e. a pure geometric approach) but weighting could, for example, take into account the mass of each individual feather to control for mass effort allocation and differences in morphology between individuals and species. This procedure is also sensitive to the coordinates given to the alula feathers. Because the alula feathers are directly inserted neither in the carpal region nor in the forearm, we did not place them on our wing diagram and left them out of the analyses, but they could be included if necessary.

## Statistical analyses

To compare differences in moult topographies, we first defined a null model based on simple geometric rules ( $w = 1$ ) applied to the general mode of wing-feather replacement reported in the literature for passerines (e.g. Jenni & Winkler 1994, Pyle 1997a). In our null model, feathers are replaced from the body in a proximal to distal direction, starting with the most anterior row of feathers (i.e. the lesser coverts; Fig. 1) caudally; only when a row of feathers is completely renewed do the feathers of the next row begin to be replaced. Primary coverts, despite being placed on the fourth row of our wing plane (Fig. 1), are an exception in partial moults: they are only replaced after most or all remiges are renewed, if at all (see *Myiarchus* flycatchers in Pyle 1997a, 1998). In accordance, our null model takes 40 values (which correspond to 40 different levels of extent), starting from 0 (no feathers replaced) and 1 (only the uppermost, innermost block of lesser coverts is replaced), following sequentially in a posterior-caudal direction, to finish with 40 (the entire lesser, median and greater coverts, as well as the tertials are replaced). Moult direction is calculated following the quantitative procedure described in the preceding section.

To evaluate the relationship between moult direction and moult extent, we fitted two regression models: linear and local polynomial using direction as dependent variable and extent as independent

variable. Confidence intervals (95%) were obtained from the standard errors of the fitted values. We first assessed whether moult directions derived under our null model and our two case species violated linear regression assumptions. We checked whether they deviated from normality using the Shapiro–Wilk test and plotted residuals vs. fitted values to check whether they were homoscedastic. Independence and deterministic condition of the explanatory variable were reasonably met. Next, we selected the models with the lowest second-order Akaike information criterion, AICc. We used AICc instead of AIC to avoid overfitting (Burnham & Anderson 2002) potentially caused by the small sample sizes, and in the local polynomial regression models by the equivalent number of estimated parameters.

Finally, we checked for differences between the null model and the model fitted to our case species by comparing the slopes between lines using parametric analysis of co-variance (ANCOVA) in cases where the final selected model was linear; or equality between curves using non-parametric ANCOVA in cases where the local polynomial model was selected. Comparisons were carried out after matching the extent ranges (e.g. if the range of the extent for one species is 20–40, we compared it with the subset of the null model corresponding to this same range).

Wilcoxon rank sum tests were used to compare means of moult directions and of extents. We adopted this non-parametric approach because of the small sample sizes and because this test does not require normality. Means are given  $\pm 1$  sd throughout.

Power tests were carried out with G\*POWER 3.1.2 (Faul *et al.* 2007). The remaining analyses were carried out with R 2.15.3 (The R Foundation for Statistical Computing 2013). Local polynomial regressions were fitted using the built-in function `loess()` in the base package. We also used libraries `ggplot2`, `fANCOVA` and `AICcmodavg`. AICc from local polynomial regression models were computed by extracting the coefficients from the output of the model.

## RESULTS

The extent of the preformative moult of the Spot-breasted Wren was significantly larger than that of the White-breasted Wood-Wren ( $35.76 \pm 2.12$  vs.  $27.48 \pm 6.07$ ;  $W = 18.5$ ,  $P < 0.001$ ), whereas the

White-breasted Wood-Wren has a larger vertical component than the Spot-breasted Wren due to its tendency to retain more outer coverts (Supporting Information, Table S1). Consequently, the latter has a larger  $\alpha$ , i.e. a more obtuse angle ( $14.57 \pm 1.34^\circ$  vs.  $18.23 \pm 3.62^\circ$ ;  $W = 55.5$ ,  $P < 0.001$ ). Examination of the raw data (Table S1) shows that Spot-breasted Wrens replace wing feathers without leaving gaps within or between tracts (which can be visualized as zeros inserted within the long series of ones), with only one slight deviation involving the carpal covert. On the other hand, White-breasted Wood-Wrens showed gaps in the coverts, presenting a more proximal feather replacement pattern. Within the latter species, there is indication of heterogeneity, suggesting two separate groups within the dataset, those showing gaps in their coverts (White-breasted Wood-Wren 0;  $n = 14$ ) and those without gaps (White-breasted Wood-Wren 1;  $n = 7$ ).

As individuals in our dataset have very heterogeneous origins (Table S1), we assessed intraspecific geographical differences. Due to our small sample sizes ( $n = 21$  for each species) we only classified birds into two groups, those from Veracruz state (mostly within the Los Tuxtlas region) and those from the remaining areas. Neither extent ( $W = 63.5$ ,  $P = 0.563$ ,  $n = 11$  for Spot-breasted Wren;  $W = 57$ ,  $P = 0.574$ ,  $n = 7$  for White-breasted Wood-Wren) nor direction ( $W = 36$ ,  $P = 0.183$ ,  $n = 11$  for Spot-breasted Wren;  $W = 62$ ,  $P = 0.360$ ,  $n = 7$  for White-breasted Wood-Wren) differed significantly between geographical areas. Inspection of the raw data indicates that these variables take values along the whole sample range in both groups (Table S1), which suggests small and little biases for geographical differences. Our small sample sizes, however, result in low test powers ( $1 - \beta_{\text{extent}} = 0.053$ ,  $1 - \beta_{\text{direction}} = 0.226$  for the White-breasted Wood-Wren;  $1 - \beta_{\text{extent}} = 0.099$ ,  $1 - \beta_{\text{direction}} = 0.113$  for the Spot-breasted Wren) so there is a risk of Type II error.

The model selection process showed that local polynomial regression had a better fit than linear regression in all cases except the subset 'White-breasted Wood-Wrens 0' (Table 1, Table S1), this latter case probably being driven by small sample size ( $n = 7$ ).

Non-parametric ANCOVA indicated that the pattern of wing-feather replacement did not deviate from our null model for Spot-breasted Wren (Fig. 2a) but did deviate for White-breasted

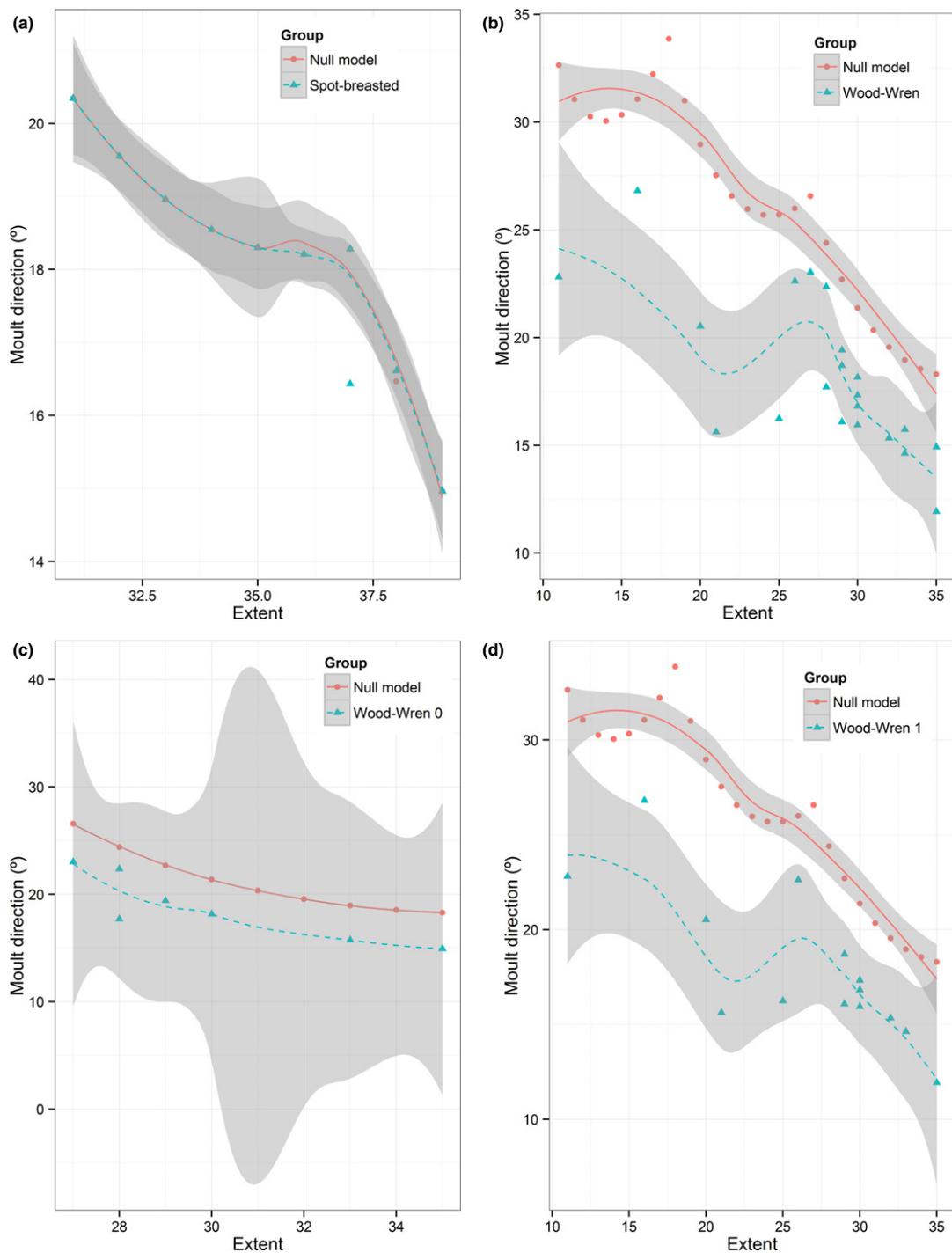
**Table 1.** AICc calculated for each regression model and dataset. We also calculated the AICc for each range of the null model used in the direct comparison with the case species as well (results not shown). In all cases, the local polynomial model had lower AICc values except for the White-breasted Wood-Wren 0. Selected models are shown in bold type. White-breasted Wood-Wren 1 are the individuals of this species with gaps in their wing coverts (Table S1), and White-breasted Wood-Wren 0 are the individuals without these gaps.

	Linear model	Local polynomial model
Null model	245.06	<b>28.10</b>
Spot-breasted Wren	50.45	<b>-42.78</b>
White-breasted Wood-Wren	105.96	<b>27.12</b>
White-breasted Wood-Wren 0	<b>39.10</b>	45.06
White-breasted Wood-Wren 1	72.59	<b>26.60</b>

Wood-Wren (Fig. 2b). This was largely due to the subset with gaps (Wood-breasted Wood-Wren 1; Table S1, Fig. 2d). The curve for these individuals differed significantly from that of the null model, whereas neither the slope nor the curve of the individuals without gaps (Wood-breasted Wood-Wren 0) differed significantly from that of the null model (Fig. 2c). Although the best fit for our null model was achieved by the local polynomial regression, direct comparisons can only be carried out either between lines or between curves. We chose to plot curves in Figure 2c but parametric ANCOVA leads to the same conclusions ( $F_1 = 0.161$ ,  $P = 0.695$ ).

## DISCUSSION

Consideration of moult strategies has focused on nearly all of its components: phenology and number of episodes per year (Svensson & Hedenström 1999), resultant plumages (Figuerola & Jovani 2001), sequence (Pyle 2013), duration and overlap with reproduction (Bridge 2006), variation in moult extent in the greater coverts or in the remiges and rectrices (Senar *et al.* 1998, Willoughby 2007), and frequency of feather replacement (Jenni & Winkler 1994, Shirihai *et al.* 2001). There have been previous attempts to study the spatial distribution of replaced wing feathers, notably by Rymkevich (1990) and Jenni and Winkler (1994) but, to our knowledge, this is the first time that the spatial configuration of replaced feathers following a moult episode (moult topography) has been quantified.



**Figure 2.** Fitted regression curves of moult direction vs. moult extent. Panels show plots comparing the null model with our two case species (in parentheses are the results of non-parametric ANCOVA tests to check for differences in equality between the regression curves fitted): (a) Spot-breasted Wren ( $T = 0.029$ ,  $P = 0.289$ ). (b) White-breasted Wood-Wren (complete dataset;  $T = 8.335$ ,  $P = 0.015$ ). (c) White-breasted Wood-Wren 0 (individuals with gaps in their wing coverts;  $T = 3.051$ ,  $P = 0.194$ ). (d) White-breasted Wood-Wren 1 (individuals without gaps in their wing coverts;  $T = 10.26$ ,  $P = 0.005$ ). We used default settings for the local polynomial regression (smoothing parameter  $\alpha = 0.75$ , polynomial degree = 2) except for (c), where we applied  $\alpha = 0.9$  to reduce the large deviance produced by the insufficient data that falls for  $\alpha = 0.75$ . Shaded areas correspond to 95% confidence bands obtained from the standard errors of the fitted values.

Our method simplifies the real geometry of the wing to a plane whose elements (the feathers) are placed according to a system of Cartesian coordinates. It sets the origin of vectors at the centroid defined by a complete moult, and groups the lesser coverts in two rows of nine blocks each. Different grouping of the lesser coverts would yield different numerical outputs but the qualitative results would remain unaltered. This grouping was driven by the need to be as coherent as possible with the other tracts (which include a number of feathers that can be counted easily), and to reduce the difficulties of counting every single lesser covert and assigning it to a row within this tract. Overall, this simplification introduces some imprecision but eases data gathering and calculations.

The vector method described here is just one variant. For example, origin of moult vector could be set at the insertion of the anterior-proximal lesser covert (this approach would contract the range of angles, from the whole circumference to just 180–270°). Moult topographies could be categorized by classifying moult direction into each quarter of the circle. Feather overlap in both the folded and the unfolded wing could be quantified and incorporated. Weightings could be adapted to diverse aims to control for pigment content, hue, feather surface, exposed area, patch area, dry mass, insulation or relative contribution to lift. Finally, true insertion of each wing feather could be projected on a Cartesian plane. Likewise, statistical methods, such as principal component analysis, could also be implemented as an alternative approach to quantify moult topography.

We designed our method to quantify moult topography of passerine wings, which have relatively simple moult patterns. Furthermore, the invariant feather-wing structure within the Passeriformes allows for direct comparisons between families or genera. Quantification of moult topography might not be as simple for other avian orders, especially of large-sized taxa, and species which re-start moult from where they have previously arrested it, such as some terns (Sternidae; Bridge *et al.* 2007). However, moult topography could be applied *a priori* to the study of any partial moult episode regardless of the avian order, as it is concerned with the pattern observed at the end of a moult episode and not with the process (i.e. the sequence) that leads to this pattern.

Different moult topographies can have the same moult vector. For example, one individual that has

replaced the outermost primary and the inner tertial will show the same vector as another individual that has replaced the second outermost primary and the central tertial (given that  $w = 1$ ; Supporting Information, Table S2), or two birds that replaced all coverts plus four remiges and four secondaries only will show the same moult vector if the centroid also had identical horizontal coordinates ( $C_x$ ). However, partial wing-moult topographies are a restricted subset (for unknown biological reasons) of all possible geometric configurations. For example, passerine species studied thus far generally replace remiges sequentially (Jenni & Winkler 1994, Pyle 1997a) in blocks attached to the outermost (i.e. outer primaries) and innermost positions (i.e. inner secondaries and tertiaries; Gargallo 2012), leading to a very low probability that two different real moult topographies would have the same moult vector. This problem would also be solved using individual feather-weighting procedures, as described above.

Although with a low frequency in our sample (one of 42 individuals), birds can skip feathers during the preformative moult, leaving a discontinuity in a given tract; we have more frequently observed this phenomenon within the tertiaries and greater coverts. During prealternate (equivalent to pre-nuptial) moults, however, wing-moult topography can be patchy and discontinuous, as in the Pied Flycatcher *Ficedula hypoleuca* (Jenni & Winkler 1994) and Nutting's Flycatcher *Myiarchus nuttingi* (Guallar *et al.* 2009). Our method can be also applied to these situations. The application of a topographical method to the body plumage would require a more complicated projection or the use of cylindrical coordinates.

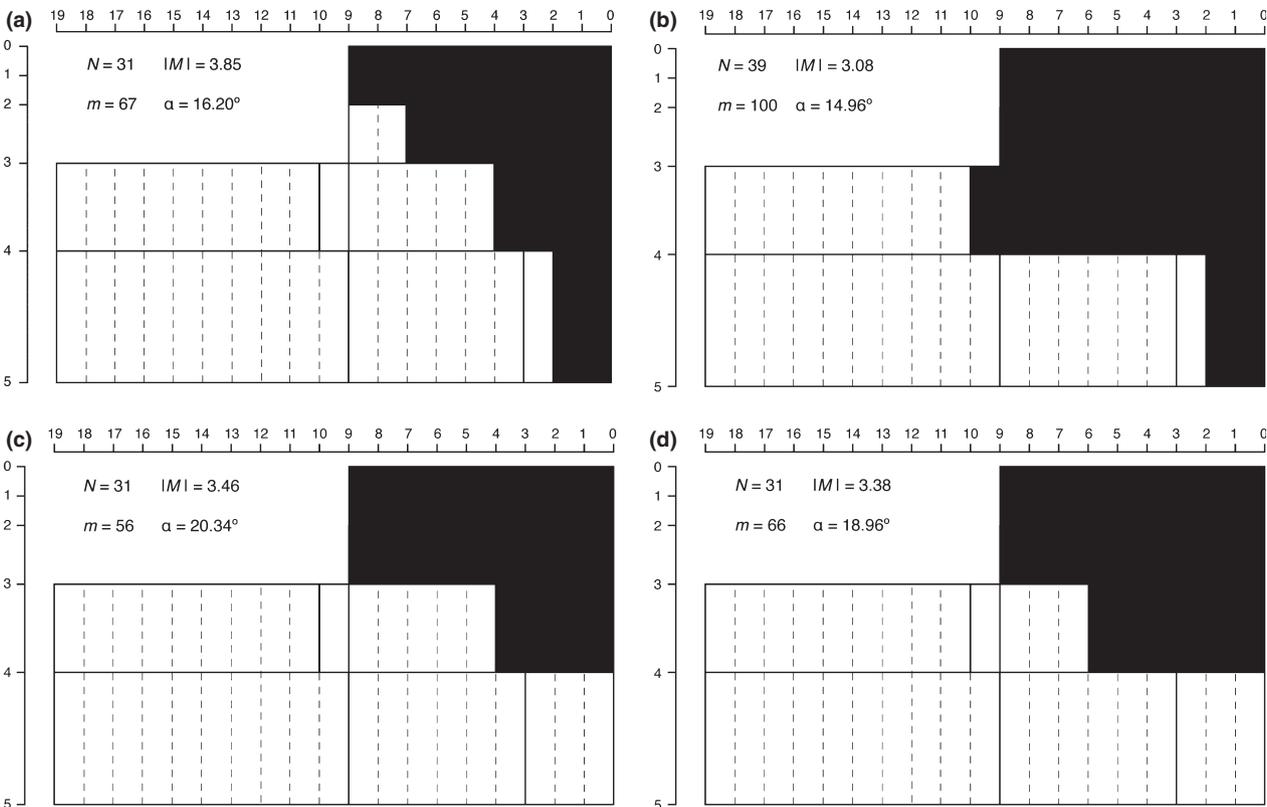
Regardless of the precise method used, the study of moult topography constitutes a promising approach to investigate interspecific and intraspecific variations in moult strategies. To the best of our knowledge, this is the first time in which polymorphism in moult topography within a species has been quantified. This polymorphism has been verbally suggested in several passerine species, for example the Northern House Wren *Troglodytes aedon*, Common Yellowthroat *Geothlypis trichas* and Song Sparrow *Melospiza melodia*, in which most individuals replace wing coverts and one or more tertiaries, but some engage in eccentric moults (Pyle 1997a,b). We showed that the moult topography of the White-breasted Wood-Wren follows these two modes:

- General: filling of an entire tract before proceeding with the next tract of feathers. It matches the null model we used as standard.
- Proximal: prioritization of the feathers closer to the body before finishing the replacement of anterior tracts.

To assess the relevance of this dimorphism we can fix a parameter and compare the resulting moult patterns under the two modes of feather replacement. For example, we may impose the replacement of the inner and the central tertials, and then define a pattern with extent  $N = 31$  under the proximal mode (Fig. 3a), which is equivalent to a unique pattern with  $N = 39$  in the general mode (Fig. 3b). In this case the general mode for  $N = 31$  would produce a moult pattern with the entire lesser and median coverts replaced plus four greater coverts (Fig. 3c). From a purely geometric point of view, it is easy to see that birds replace fewer feathers under the proximal mode. We can then take

feather mass  $m$  into account by applying arbitrary weightings; for example, for  $w =$  (lesser coverts = 1; median coverts = 2; greater coverts = 5; carpal covert = 4; inner tertial = 6.5; central tertial = 8) we obtain  $m = 100$  under the general mode and  $m = 67$  under the proximal mode. Now, the resulting moult topography under the general mode for  $m = 66$  (the nearest value we can get) would replace the entire lesser and median coverts plus six greater coverts. The proximal mode therefore allows a mass saving of 33 units in each wing over the general mode.

We lack data to assess whether this saving involves important physiological costs for White-breasted Wood-Wrens, and therefore we cannot establish a direct association between the proximal mode and a need to minimize investment in new feathers. However, the fact that other species distributed across the phylogenetic tree of the family Troglodytidae (Mann *et al.* 2006), including Sinaloa



**Figure 3.** (a) A possible moult topography fixing the replacement of the central and inner tertials under the proximal mode ( $N = 31$ ). (b) The equivalent configuration that would be obtained under the general mode. (c) Resulting configuration with extent  $N = 31$  under the general mode. (d) Moult topography corrected for the mass arbitrarily given to each feather under the general mode.  $N$ , extent;  $m$ , mass;  $\alpha$  and  $M$ , angle and module of moult vector.

Wren *Thryophilus sinaloa*, Brown-throated Wren *Troglodytes aedon brunneicollis*, Northern House Wren and Grey-breasted Wood-Wren *Henicorhina leucophrys*, also present the proximal mode (Gualtar *et al.* 2009) suggests that this mode of feather replacement may have a strong phylogenetic signal within this taxon.

Moult topography, the spatial configuration of replaced feathers following a moult episode, is a descriptor that may prove highly useful in comparative and experimental studies to test hypotheses on environmental predictors of incomplete moult episodes and mating success in monochromatic bird species. Moult topography should be considered and quantified to improve our understanding of moult strategies, especially in Neotropical passerines.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Localities and moult scores for all the individual feathers and block of feathers ordered from the lesser coverts caudally and from the feather closest to the body distally within each tract.

**Table S2.** Example of calculation of the centroid  $C$  and moult vector  $\vec{M}$  of two individuals that have replaced all their lesser, median and greater coverts plus the carpal but different tertials and primaries: A has replaced the outermost primary plus the inner tertial and B the second outermost primary plus the central tertial.