From partial to complete: Wing- and tail-feather moult sequence and intensity depend on species, life-cycle stage, and moult completeness in passerines

Santi Guallar

Departament de Vertebrats, Museu de Ciències Naturals de Barcelona, Barcelona, 08003, Spain

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ABSTRACT

Passerines moult during various life-cycle stages. Some of these moults involve the retention of a variable quantity of wing and tail feathers. This prompts the question whether these partial moults are just arrested complete moults or follow different processes. To address it, I investigated whether three relevant features remain constant across partial and complete moults: 1) moult sequence (order of activation) within feather tracts (e.g., consecutive outward moult of primaries) and among tracts (e.g., starting with marginal coverts, followed by greater coverts second, tertials, etc.); 2) dynamics of moult intensity (amount of feathers growing along the moult progress); and 3) protection of wing quills by overlapping fully grown feathers. To study the effect of moult completeness on these three features, I classified moults of 435 individuals from 61 species in 3 groups: i) complete and partial, ii) without and iii) with retention of feathers within tracts. To study the effect of life-cycle stage, I used postbreeding, postjuvenile, and prebreeding moults. I calculated phylogenetically corrected means to establish feather-moult sequence within tracts. I applied linear regression to analyse moult sequence among tracts, and polynomial regression to study the dynamics of moult intensity as moult progresses. Sequence and intensity dynamics of partial moults tended resemble those of the complete moult as moult completeness increased. Sequence within and among feather tracts tended to shift as moult intensity within tracts and number of tracts increased. Activation of primaries advanced in relation to the other feather tracts as number of moulted primaries increased. Tertial quills were protected by the innermost greater covert regardless of moult completeness. These findings suggest that moult is a self-organised process that adjusts to the degree of completeness of plumage renewal. However, protection of quills and differences among species and between postjuvenile- and prebreeding-moult sequences also suggest an active control linked to feather function, including protection and signalling.

1. Introduction

Moult in birds results in the restoration and adjustment of plumage functionality, although the conditions experienced by each individual may influence its output, ultimately affecting plumage performance. For example, a faster moult induced by a late start can have fitness consequences because feather properties may be altered (Nilsson and Svensson, 1996; Hemborg and Lundberg, 1998; Dawson et al., 2000), deteriorating aerodynamics, insulation, and signalling (Hall and Fransson, 2000; Hinsley et al., 2003; Serra et al., 2007; Griggio et al., 2009; Weber et al., 2010; Vágási et al., 2012). The moult process itself causes function losses that birds can compensate by increasing physiological costs and modifying behaviour (Chai, 1997; Vega Rivera et al., 1999;

Lind, 2001; Buttemer et al., 2003). Intensity of remex moult varies among bird groups, being adapted to their natural history, from the synchronous replacement in species that do not need to fly to forage (e. g., ducks, rails, and loons) to the replacement of just 1–2 remiges at a time in large raptors and aerial hunters (e.g., owls and swallows; Yuri and Rohwer, 1997; Jenni and Winkler, 2020a; Terrill, 2020), and it has likely been fine-tuned during evolution to reduce aerodynamic losses thanks to a tight control of moult sequence and intensity (Rohwer and Rohwer, 2018; Guallar and Quesada, 2023a).

However, moult does not always entail the complete replacement of a bird's plumage (complete moult), as many bird species retain part of it after finishing moult (partial moult). Passerine species typically undergo a complete moult after breeding (postbreeding moult) and a partial

moult when replacing their juvenile plumage (postjuvenile moult). Additionally, many migratory passerine species, go through a partial moult when they are away from their breeding range (prebreeding moult). While moults have traditionally been classified based on completeness, it remains uncertain whether partial and complete moults result from a single process shifting along a continuum of plumage replacement or if they exhibit unique differences. Understanding this distinction is crucial in comprehending how passerines adjust their moult strategies throughout their life-cycle. To address this question, I investigated whether completeness affects the moult sequence and intensity, and the protection of wing quills.

Retention of a variable percentage of feathers and even of entire tracts (typically primary coverts, primaries, rectrices, and secondaries) necessarily alters the order of moult activation among tracts characteristic of the complete moult, which typically starts with the inner primaries and accompanying primary coverts (Newton, 1966; Kasparek, 1979). Likewise, moult sequence within tracts might be affected in partial moults. It is known that direction of moult sequence (but not nodal primary) is conserved within the primaries in eccentric moults (partial moults characterised by the retention of a number of inner primaries and outer secondaries, and most to all primary coverts; Winkler and Jenni, 1987; Rohwer, 2008; Gargallo, 2013), although it is unclear whether sequence is conserved within upperwing secondary coverts, alula, and rectrices too, especially as moult extent varies (Newton, 1966; Kasparek, 1979). Therefore, both the sequence and the identity of the feathers that will eventually be replaced in other wing-feather tracts at the end of a partial moult remain uncertain, particularly in species which do not replace all the feathers of a given tract (e.g., greater coverts in the European Robin *Erithacus rubecula*; Svensson, 1992). However, this question can be approached from another angle: assuming that partial and complete moults share the same physiological mechanisms, moult sequence presumably remains largely constant within a species, at least within tracts (Pyle, 2022a). Considering this, my first objective was to test whether complete and partial moults differ in the sequence within and among wing-feather tracts. Based on the semiquantitative data available about partial moult sequence (summarised in Table 1), overall differences relative to completeness are expected to occur (Zeidler, 1966; de la Cruz et al., 1992), therefore, showing that partial moults are not arrested complete moults.

Due to the reduction in the quantity of replaced feather material, partial moult duration is shorter and has a lower energetic cost than the complete moult (Newton, 1966; Dolnik and Gavrilov, 1979). Additionally, most partial moults skip the replacement of the largest feathers (i. e., primaries, secondaries, and rectrices; Svensson, 1992; Pyle, 2022b). Although the moult of wing coverts has some effect on the bird's aerodynamics (e.g., altering camber; Shyy et al., 2013), retention of remiges greatly reduces the impact on flight, which could be very important during early life, when young birds do not master foraging and flight yet (Heise and Moore, 2003). Moreover, the relaxation of energetic and flight constraints of partial moults may potentially influence on the dynamics of moult intensity, which describes a parabola in the complete moult of the House Sparrow (*Passer domesticus*) (i.e., greatest during mid-moult than at either ends of moult; Guallar and Quesada, 2023a). Considering this, my second objective aimed to test whether moult intensity dynamics differs between complete and partial moults. Since fewer wing and tail feathers are moulted in the latter, it can be predicted a shift in the peak of moult intensity toward the beginning of moult. However, given the shorter duration of partial moults, wing- and tail-feather moult intensity could not have time enough to relax at the end of moult progress, therefore precluding a straightforward prediction.

The growing feather is highly vascularised (Lucas and Stettenheim, 1972). During growth, feathers are so fragile that even slight traumatisms can cause bleeding and possibly future malformations (Jovani and Rohwer, 2017). Therefore, it seems plausible that evolutionary

Table 1

Published descriptions of moult sequence for the feather tracts used in this article. Modified from Jenni and Winkler (2020b).

Tract	Partial moult [References]	Complete moult [References]
Primaries	Inward [2, 4]	Inward [16]
	Outward in most species [1, 7, 8, 15, 17]	Outward beginning by P1 [10]
	Divergent [12]	Divergent in <5% [12]
	Usually replaced together with the tertials, or shortly after, when the wing-coverts and alula feathers are already growing or full-grown (or before if many primaries are moulted) [7, 8, 10]	
Secondaries	Outward (opposite to complete moult) [2, 8]	Inward [10]
	Convergent [8]	
	Simultaneous [2]	
Tertials	Divergent [7, 8, 9, 14]	Usually T2-T1-T3 [10]
Alula	Usually A1 if only one feather is moulted; the two smallest if two are moulted (outward sequence) [10]	During the second half of primary moult [10]
Greater covs	Outward, start with GC9; GC10 last though irregular in species that rarely moult them [10]	Very variable, usually within short intervals [10]. GC10 last [18, 19]. Can be convergent or divergent [11, 18]
	May start with an outer greater covert (e.g., GC3) [6]	
	In groups starting with the outermost [2]	Inward serially or in groups [3, 19] while the new greater coverts are growing, or are full-grown [10]
Median covs	Simultaneous or highly variable [10]	
Rectrices	Centrifugal in most species [10]	Centrifugal [10]
	Divergent or convergent [6, 13]	Divergent [13]
	Inward [9]	
	Nodal feather depends on number of rectrices moulted [7]	

[1]Bensch et al. (1991); [2]de la Cruz, 1992; [3]Dhondt (1973); [4]Evans (1986); [5]Flegg and Cox (1969); [6]Flinks (1999); [7]Gargallo (2013); [8]Gauci and Sultana (1979); [9]Herremans (1988); [10]Jenni and Winkler (2020b); [11]Kasparek (1979); [12]Kiat (2017); [13]Kiat (2018); [14]Norman (1991); [15]Williamson (1968); [16]Williamson (1972); [17]Willoughby et al. (2002); [18]Winkler and Winkler (1985); [19]Zeidler (1966).

adaptations have arisen to reduce these risks during moult, especially among remiges. For example, in the complete moult of the House Sparrow, tertials and greater coverts avoid to grow simultaneously, therefore being consistent with the protection hypothesis according to which the vascularised bases of growing feathers are protected by adjacent fully grown feathers (along the bird's longitudinal axis), either old or recently moulted (Zeidler, 1966). While reduction of the number of replaced wing feathers in partial moults are likely to alter moult sequence, coordination between feather tracts may help avoid simultaneous growth of overlapping feathers. Thus, my third objective was to test whether partial moults are also consistent with the protection hypothesis. Since the need for protection of growing wing feathers is the same, I expect that partial moults would also retain the ability to keep wing quills protected.

2. Materials and methods

2.1. Dataset

The dataset comprised 310 birds undergoing a partial wing-feather moult from 61 passerine species (35 from North America and 26 from Europe), along with 125 birds undergoing a complete postbreeding moult from 21 European passerine species (all present in the partial moult subset). Birds were mist-netted between 2004 and 2023 in the
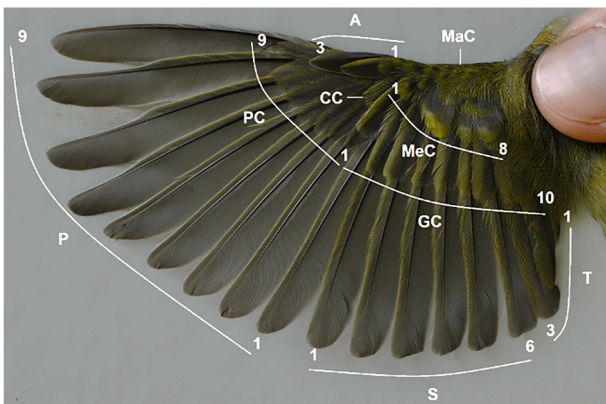
Iberian Peninsula and Mexico, with three birds from Nicaragua and Costa Rica, four from the US and Switzerland from published sources, eight museums specimens collected in Mexico during the 1980s, and two unpublished photos from North America (see location and date in Guallar, 2024). Because birds were examined only once, moult sequence could only be observed for those feathers growing at this given stage. Therefore, sample sizes for each feather were much lower than the overall sample size. I scored the growth stage of the feathers of nine tracts on the left wing and the left rectrices of each bird: six rectrices, 19 remiges, and all upper wing feathers (Fig. 1). The marginal coverts were scored as a percentage of the feathers growing in the whole feather tract (see details in Guallar et al., 2021). Before 2018, the growth of each feather was scored using the classical 0–5 protocol ($n = 111$ birds; Ashmole, 1962). From 2018 onwards, the growth stage of each feather was scored on a continuous scale to account for differences in moult progress within and among feather tracts with higher precision ($n = 324$ birds; Rohwer, 2008): 0 for old feathers, 0.5 for shed feathers not yet breaking the skin, 100 for fully grown feathers, while intermediate stages of feather growth were scored based on the linear increase in feather length (Winkler et al., 1988). For example, a feather grown up to 50% of its full length was scored 50. Since final feather length varies among feathers and individuals, scoring length is a method that relies on the observer's experience to estimate the length of the growing feather in relation to its final length when fully grown. This method was found to be highly repeatable (Guallar and Quesada, 2023a).

2.2. Moult sequence

2.2.1. Moult sequence within tracts

To study differences between the partial and complete moult sequence within feather tracts, I first separated partial postjuvenile and prebreeding moults. I then categorized postjuvenile moults based on whether species are known to replace wing-feather tracts completely or incompletely during this moult (Shirihai et al., 2001; Guallar et al., 2009; Jenni and Winkler, 2020b; Pyle, 2022b). Specifically, four species in my dataset typically (more than 50% individuals) replace all their secondary coverts (all wing coverts but the primary ones), tertials, and alula feathers during the postjuvenile moult: Sardinian Warbler (*Curruca melanocephala*), Great Tit (*Parus major*), Crested Tit (*Lophophanes cristatus*), and Blue Tit (*Cyanistes caeruleus*). In these species, retention of any greater covert or alula feather is infrequent, although they can replace S6, and 29% Sardinian Warblers in this region undergo an eccentric moult (Guallar and Jovani, 2020b).

Prebreeding moults typically occur in long-distance migrants (i.e.,

trans-Saharan and Neotropical migrants; Svensson, 1992; DeGraaf and Rappole, 1995; Pyle, 2022b), although they also occur in a number of non-migratory Neotropical species (Guallar et al., 2009). Prebreeding moults of Holarctic long-distance migrants are characterised by incomplete replacement of most wing-feather tracts. Exceptions to this rule are largely associated with species that undergo a reduced post-breeding moult before migrating south, such as many *Hippolais* or *Acrocephalus* warblers (see Svensson, 1992; Pyle, 2022b), showing larger variation among individuals of the same species than the postjuvenile moult. Moreover, postjuvenile and prebreeding moults differ in the number and, to a lesser degree, the identity of the replaced wing feathers, i.e., they are not a subset of those replaced in the other moult (e.g., European Pied Flycatcher *Ficedula hypoleuca*; Guallar and Jovani, 2020a; Jenni and Winkler, 2020b).

I determined moult sequence within feather tracts (also among tracts) only when it could be clearly established, implying that sequences from each individual were incomplete (detailed report of sample sizes used in the multiple analyses is provided in Appendix Table S1). I ordered growing feathers within tracts following Rohwer (2008): relative lengths of growing feathers indicate their sequence of replacement; when two feathers had equivalent lengths, I assigned them the same order along the sequence. From these data, I estimated mean moult sequence and 95% confidence intervals for each feather within each tract using Bayesian bootstrapping (applying 4000 iterations), as implemented in the library Bayes boot of the R environment (Bååth, 2016; R Core Team, 2022). Since moult sequence within tracts could be phylogenetically conserved, its correlation could be higher as the phylogenetic distance among species grows shorter. Therefore, I applied a phylogenetic correction to each feather's mean order of activation (i. e., position in the sequence) using the function phyloMean as implemented in package motmot (Puttick et al., 2019). To build the phylogenetic tree for the 61 species, I downloaded 100 trees from BirdTree.org (Ericson backbone; Jetz et al., 2012), derived a consensus tree with least-squares branch lengths using package phytools (Revell, 2012), and forced tips to be contemporaneous (Pagel, 1992). Subsequently, I subset the phylogeny to match the species that contributed data to each feather. I assessed moult-sequence similarity among moults differing in completeness by comparing profiles, which were built connecting the mean values computed for each feather within the tract. Additionally, I used a published dataset containing information on the feathers replaced by 3909 individuals after finishing their partial moult as an independent source to establish moult sequence within tertials and alula when only one feather was moulted in these two tracts (Guallar and Jovani, 2020b).

Finally, I studied the effect of moult intensity on the moult sequence within feather tracts that lack a clear direction. To help interpret this effect, I built three plausible null models using the greater coverts: a) fixed, where each covert starts moulting in the same order of the moult sequence regardless of the number of new or growing coverts; b) inward displacement, where order of activation of each covert slides as many positions along an inward sequence as more coverts are growing or become new: when there is only one, the carpal starts the sequence; when there are two, GC1 starts and the carpal follows, and so forth until GC10 is activated first and the carpal last; c) outward displacement, which is like the latter model but with inverted sequence.

2.2.2. Moult sequence among tracts

Analogously to the sequence within tracts, sequence among tracts was established based on relative moult progress (a detailed report of sample sizes used in the analyses is provided in Appendix Table S1). For example, if greater coverts were fully grown while median coverts were still growing, the former preceded the latter along the sequence among tracts. Since one to several wing-feather tracts are retained during partial moults, order of moult activation among them may shift as number of moulted tracts increases; alternatively, they may remain constant. Considering this, I regressed order of moult activation of every tract on

Fig. 1. Wing feather tracts and numbering used in this article. GC10, PC9 and P10 are reduced and not visible in the photograph. I adhered to the numbering system proposed by Jenni and Winkler (2020b) save for the tertials, whose moult sequence clearly differs from that of the secondaries. Hatch-year female Wilson's Warbler *Cardellina pusilla* ringed in Las Joyas, Jalisco, Mexico on 1 September 2005.

number of moulted tracts. Furthermore, given that moult intensity within tracts may also affect their order of activation, I examined this effect for primaries in eccentric moults (9-primaried species were treated as having 10 visible primaries). Since I was only interested in overall tendency, I carried out ordinary linear regressions without applying phylogenetic corrections.

2.3. Moult intensity dynamics

Moult intensity is usually measured from remiges using the raggedness index (Haukioja, 1971). Raggedness is calculated as $\sum_i 5 - s_i$, where s = score of each feather according to Ashmole's 1–5 scoring system (1962), and is highly correlated to relative wing area (Hedenström, 1998). However, partial moults are characterised by retention of these feathers, necessitating the use of a different index for comparison with the complete moult. Therefore, I employed the mass gap index, which yields very similar results to raggedness when applied to remiges (Guallar and Quesada, 2023a). Mass gap is the proportion of feather mass lacking to attain the final mass of each growing feather, and was computed as $\sum_i mass_i \cdot (100 - score_i)$, where i = growing feather (compare with raggedness). To test whether moult intensity of complete and partial moults differ, I used local polynomial regression of mass gap on moult progress in the House Sparrow (data from Guallar and Quesada, 2023b), the Great Tit, and the European Robin. Moult progress was measured as the percentage of new and growing feathers in a moulting bird of the total feather mass. I obtained the mass of every wing feather and the rectrices to the nearest 0.1 mg from two dead birds near Barcelona (NE Iberian Peninsula): one adult female Great Tit on 14 July 2005 and one second-year female European Robin on 21 May 2019. The House Sparrow undergoes a complete postjuvenile moult, whereas the Great Tit and the European Robin undergo partial postjuvenile moults. The Great Tit is a species whose population in the north-eastern Iberian Peninsula shows a remarkable postjuvenile moult repeatability, with 57% individuals moulting exactly the same wing feathers and the remaining 43% differing in only 1–2 feathers (Jenni and Winkler, 2020b; Guallar, 2024). The European Robin replaces all median and marginal coverts, a variable number of greater coverts (mean $\pm$ sd = 4.81 ± 1.73, $n = 134$), and the lesser alula (or alula covert) in 22% cases (Guallar, 2024).

2.4. Protection of wing quills

I calculated frequency at which at least one feather from each pair of overlapping feathers from longitudinally adjacent wing tracts is growing: tertials with greater covert GC10 and median coverts with GC1 to GC9 (see Fig. 1 for feather numbering). Tertials are largely arranged on top of each other presenting little lateral shift, whereby T1 protects the other two tertials and is protected by GC10. The role of GC8 and GC9 is deemed accessory since GC10 covers the insertion of T1 and the latter the insertion of the remaining tertials. For this reason, I first selected T1 growing simultaneously with another tertial and then calculated frequency of T1 and GC10 growing simultaneously. I tested whether these frequencies deviated from both 0% and 50% simultaneous growth (i.e., nil and random, respectively) in partial postjuvenile moults, whereby non-significant differences from 0% combined with significant differences from 50% between feathers of adjacent tracts indicate support for the protection hypothesis. Data for prebreeding moults were lacking due to their smaller moult extent (among the species in the dataset), which involves fewer overlapping feathers and therefore requires larger sample sizes to be detected.

3. Results

3.1. Moult sequence
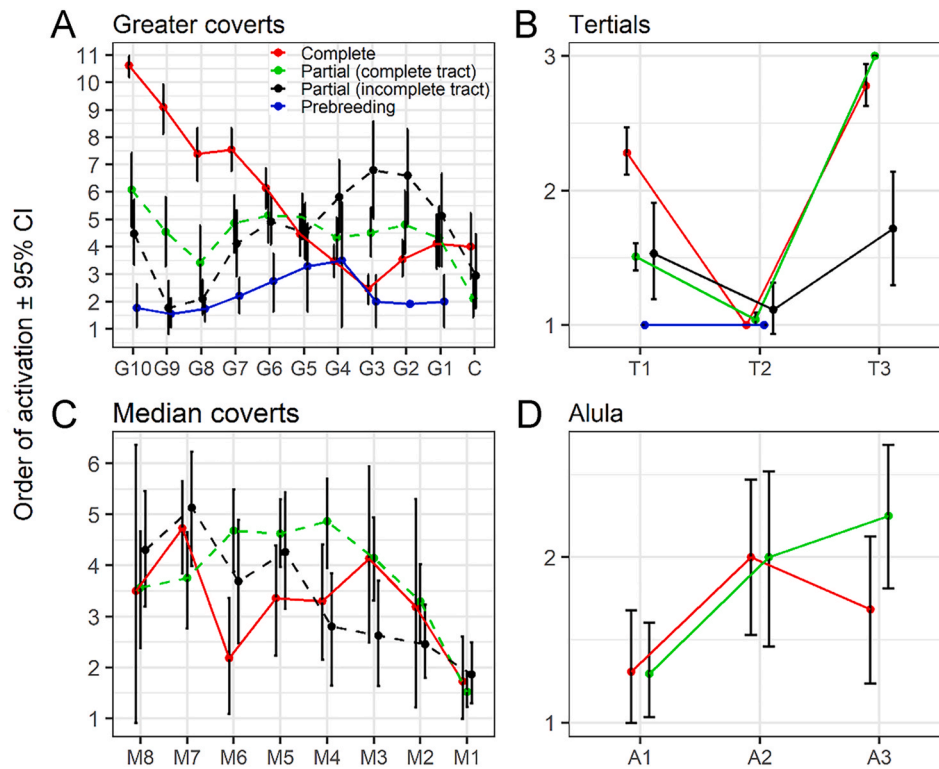
3.1.1. Moult sequence within tracts

Moult-sequence profiles of the greater coverts clearly differed among moult types. All four moults started with the outer greater coverts, although the prebreeding moult and partial moult with incomplete replacement could also start with the inner greater coverts (Fig. 2A). Moult-sequence profiles of tertials in the three partial moults were more similar to the complete-moult profile as completeness increased, diminishing the tendency to start moult with the central one (Fig. 2B; Table 2). The median coverts showed similar moult sequence regardless of moult completeness (less clearly so the central ones, MeC3 through MeC6), resembling that of the House Sparrow (Fig. 2C; Guallar and Quesada, 2023). Moult sequence of the alula tended to be distal, less distinctly in complete postbreeding moults (Fig. 2D; Table 2). Deviation from the complete moult sequence of the House Sparrow suggested species differences, although the incomplete and fragmentary information (based on 10 individuals) precluded a clear interpretation.

Moult sequence of primaries deviated more frequently from the typical consecutive (outward) sequence in eccentric moults than in the complete moult of the House Sparrows ($\chi^2_1 = 9.02$, $p = 0.003$). Concretely, four of 35 individuals with eccentric postjuvenile moult skipped up to two primaries between P2 and P5 in the sequence (see species and data in Guallar, 2024). For example, Small et al. (2013) captured a Field Sparrow (*Spizella pusilla*) with primaries exhibiting the following growth percentages P1–2 = 100%, P3–4 = 0%, P5 = 90%, P6 = 75%, P7 = 4%, and P8–9 = 0%. Moult-sequence profiles within tracts showed only small differences between phylogenetically corrected and uncorrected estimates, save for inner median and greater coverts in partial moults with complete tract replacement, indicating that moult sequence tended to differ among species, at least for these coverts (Fig. 2A and C, and Appendix Fig. S1).

The effect of moult intensity on the sequence within the greater coverts showed similarities to the null models (Fig. 3A–C). Activation of the GC1 in the postjuvenile partial moult with complete tract replacement was nearly fixed, whereas that of GC10 showed outward displacement, with the remaining coverts showing intermediate patterns (Fig. 3D). On average, this moult would start with the carpal followed by GC8, and would end by GC10 (Fig. 2A). In the partial moult with incomplete tract replacement, GC2 and GC7 showed outward displacement, while the other coverts showed intermediate patterns between the fixed and the outward displacement. On average, this moult would start with GC8–9 and end by GC2–3 (Fig. 2A). The prebreeding moult differed notably from the null models and was likely explained by a mixture of two patterns that depend on the number of greater coverts moulted: a) when moult extent ≤ 5, the inner five coverts showed an intermediate pattern between fixed and the outward displacement; b) when moult extent ≥ 5, the outer coverts were activated increasingly earlier as extent increased (Fig. 3F). The apparent fixed activation of GC6 resulted from its pivotal position between the two patterns: it was either the first or the last to be moulted.

3.1.2. Moult sequence among tracts

Analogously to null models with displacement (Fig. 3B and C), activation of most feather tracts tended to shift as number of moulted tracts increased. However, patterns varied between life-cycle stages. In the complete postbreeding moult, primaries, primary coverts, and greater coverts showed a fixed order of activation, being nearly always first, second, and third, with the remaining feather tracts being increasingly displaced as number of moulted tracts increased. Tertials and rectrices were activated only after at least two other tracts were activated, alula and secondaries after three, and median after at least five (Fig. 4A). In partial postjuvenile moults, only the marginal coverts

Fig. 2. Moult sequence within four wing-feather tracts. Greater coverts and carpal (G and C), tertials (T), median coverts (M), and alula feathers (A) obtained from 271 individuals of 22 species. Mean order of activation for each feather was corrected by phylogeny. Bars represent 95% uncorrected bootstrapped intervals, with wider confidence intervals indicating greater variation within the tract's sequence. Partial postjuvenile moults with complete tract replacement include all secondary coverts (all wing coverts but the primary ones), tertials, and alula feathers. Partial postjuvenile moults with incomplete tract replacement typically retain a variable number of secondary coverts, tertials, and alula feathers. Data from alula feathers and median coverts for the prebreeding moult were very scarce and hence excluded. Mean (range) sample sizes per feather within tracts: n_{GC} = 32 (2–41), n_T = 27 (4–54), n_{MeC} = 8 (3–27), n_A = 8 (2–17).

Table 2

Moult frequency within tertials (T) and alula feathers (A) from finished partial moults in which only one feather per tract was moulted. Feather identities in Fig. 1.

	T1	T2	T3	n	A1	A2	A3	n
Postjuvenile	75.8%	16.6%	7.7%	275	97.3%	1.6%	1.1%	982
Prebreeding	46.2%	38.5%	15.4%	12	60%	0%	40%	5
All partial moults	65.3%	25.9%	8.8%	320	97.1%	1.7%	1.1%	1044

showed a fixed order of activation, being the first one along the moult sequence, with the remaining feather tracts being increasingly displaced as number of moulted tracts increased. Alula, tertials, and rectrices were activated only after at least two other tracts were activated, and secondaries after four (Fig. 4B). Complete postbreeding moult sequence commenced with the primaries in 98.1% cases, whereas partial postjuvenile moult sequence commenced with the marginal coverts in 95.2% cases. The alula was the last to be activated in both moults in 78% cases. The scarce information on prebreeding moults indicated that tertials and marginal coverts tended to have a fixed order of activation, with secondaries and greater and median coverts being increasingly displaced as number of moulted tracts increased (Appendix Fig. S2).

Moult completeness within remiges had a large effect on its order of activation among tracts, as revealed by the decrease in the order of moult activation of primaries in eccentric moults as number of replaced primaries increased (Fig. 5). An ancillary result of this work was that moult of body-feather tracts typically started before flight-feather tracts in partial moults (see Guallar, 2024).

3.2. Moult intensity dynamics

Dynamics of postjuvenile moult intensity (measured as mass gap) in

the Great Tit did not describe a perfect parabola as in the House Sparrow. It was relatively higher during the first half of the moult. Although moult intensity peaked nearly at the same moment of the moult progress for both species (50.42% and 51.25%, respectively), it was 7.8 times lower in Great Tits than in House Sparrows (2.61% and 20.71%, respectively; Fig. 6). Moult intensity dynamics in the European Robin decreased almost linearly from the moult onset, with a peak at 0.76%, 27 times lower than that of the House Sparrow.

3.3. Protection of wing quills

Tertials and the innermost greater covert avoided simultaneous growth in partial postjuvenile moults, although partial moults with incomplete replacement of tracts did not deviate from random (Table 3). Therefore, support for the protection hypothesis was mixed: full for partial moults with complete replacement of tracts and inconclusive for those with incomplete replacement of tracts. Contrastingly, median and greater coverts did not avoid simultaneous growth, therefore refuting the protection hypothesis between these two.
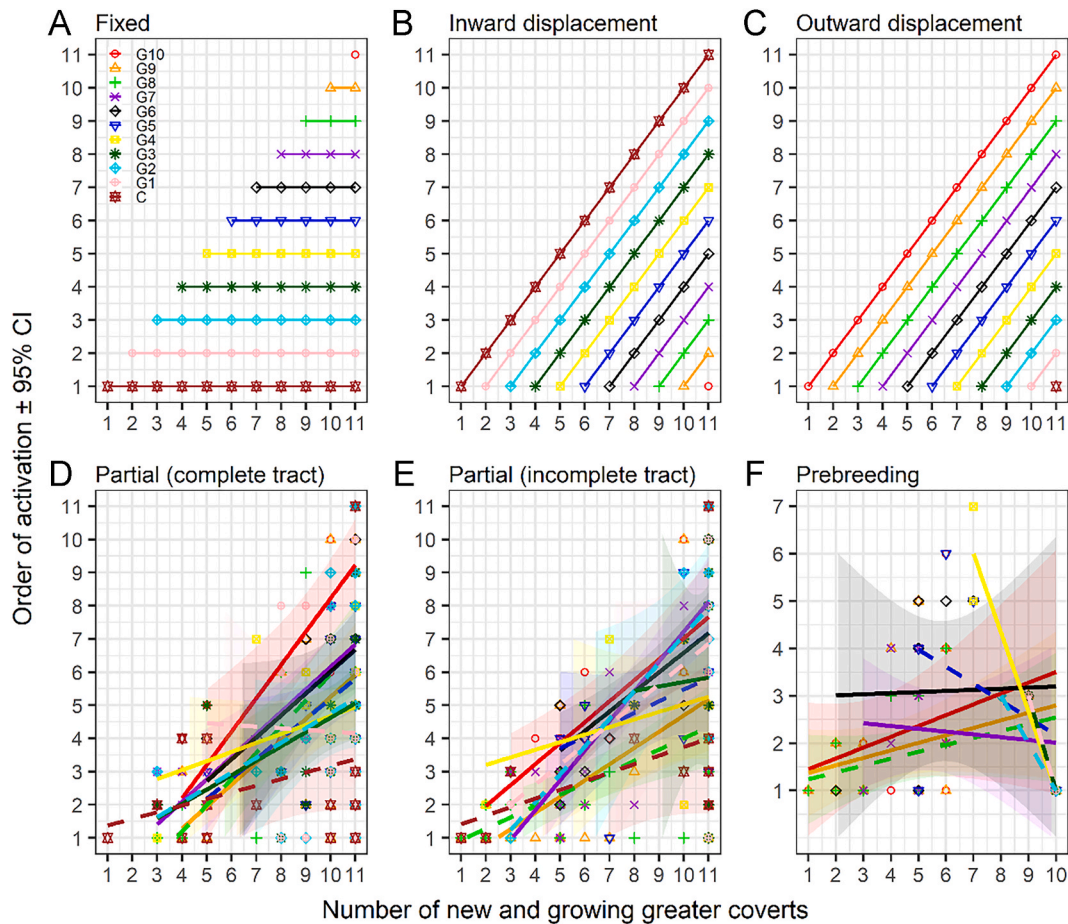
Fig. 3. Effect of moult intensity on moult sequence within the greater coverts (G) and carpal (C). Regression lines and 95% confidence intervals of the observed order of activation on number of moulted coverts. The top row displays three null models with hypothetical moult sequences. In a fixed sequence, feathers are always moulted in the same order. In the models with displacement, activation depends on the number of new and growing feathers. Partial postjuvenile moults with complete tract replacement include all secondary coverts (all wing coverts but the primary ones), tertials, and alula feathers ($n = 124$ birds, 4 Palearctic species). Partial postjuvenile moults with incomplete tract replacement typically retain a variable number of secondary coverts, tertials, and alula feathers ($n = 89$ birds, 12 Palearctic species). There were no data of the carpal covert for prebreeding moults ($n = 42$ birds, 19 species resident or wintering in Jalisco, Mexico). Mean (range) sample sizes per feather and moult type: $n_{pjcomp} = 26$ (23–31), $n_{pjincomp} = 18$ (9–35), $n_{pb} = 8$ (2–19).

4. Discussion

### 4.1. Effects of completeness, species, and life-cycle stage

Moult sequences within feather tracts tend to exhibit distinct profiles (e.g., tertials forming a V shape). They depend on moult intensity and extent within tracts, becoming more similar to the complete-moult sequence as completeness of partial moult increases (Figs. 2 and 3). The relationship between moult sequence and completeness is not linear, otherwise less complete moults would simply consist of subsets of the wing feathers replaced in moults of larger extent, i.e., they would be nested (Guallar and Jovani, 2020). This underscores that partial moults are not arrested complete moults. Furthermore, the variation in moult sequence also depends on other factors acting at the species and the individual levels.

Moult sequence within feather tracts vary among species, as evidenced by both shifts in the order of activation after applying phylogenetic corrections, differences between the overall profile and the profiles of individual species (Fig. 2, Appendix Figs. S1, S3, and S4; Table 1). This variation may stem from differences in feather function (e.g., the central rectrices of treecreepers are used as props; Fig. 7) or size as suggested by rectrix moult-sequences of the Great Tit and the House Sparrow, where the general outward sequence is blurred by the shorter R6 and R1, respectively (Fig. 7; Fig. 2D in Guallar and Quesada, 2023a).

Exposure could also induce differences in sequence. Thus, the inner more exposed greater coverts tend to be replaced earlier in partial moults (Fig. 2A). This could be especially important in partial postjuvenile moults without complete replacement of greater coverts, where the inner more exposed coverts are typically replaced during the postjuvenile moult because juvenile coverts are less durable (Pap et al., 2007).

Wear and fade deteriorate feathers over time, being greater on more exposed feathers, which has likely driven the evolution of partial prebreeding moults in passerines (Terrill et al., 2020). Thus, Nearctic warblers tend to replace inner greater coverts before departing from their winter grounds (Guallar et al., 2009), and this necessarily implies changing the complete-moult sequence, which typically starts with the outer greater coverts (Fig. 2A and 3F). The adjustment of plumage function resulting from prebreeding moults could explain changes in sequence within and among tracts. For example, sequence of tertials during the prebreeding moult deviates from the V-shape typical of the complete moult (Fig. 2B; Table 2). Similarly, the order of activation of wing-feather tracts in the European Pied Flycatcher needs to be altered because marginal coverts are nearly always moulted first during the postjuvenile moult (Fig. 4B) but are typically retained during the prebreeding moult (Jenni and Winkler, 2020b).

Although moult intensity of some individuals may be constrained by time and harsh conditions (Hall and Fransson, 2000; DesRochers et al.,
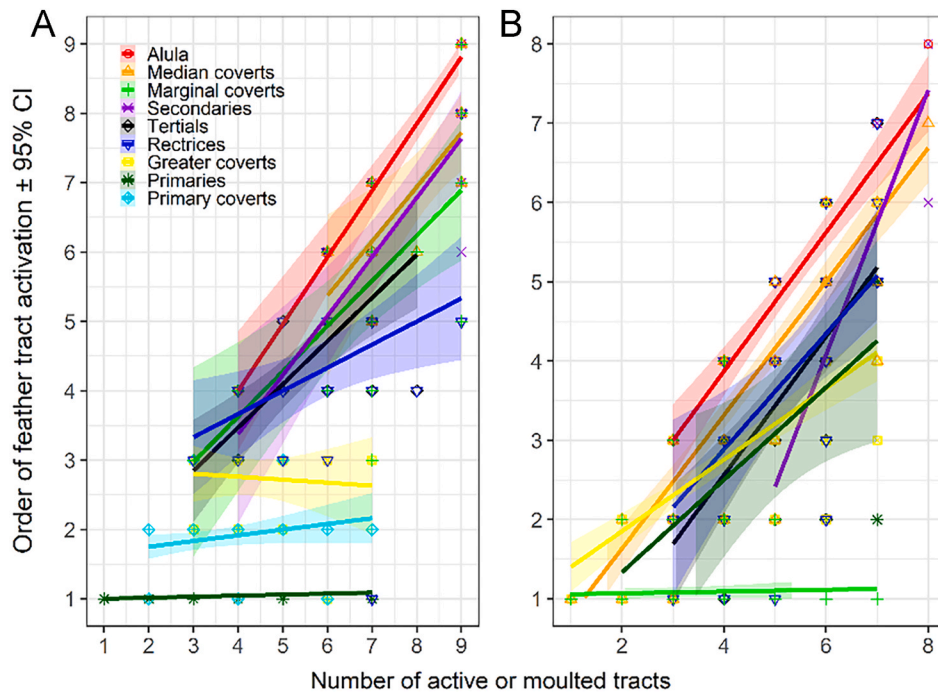
Fig. 4. Order of moult activation among wing- and tail-feather tracts in (A) complete postbreeding moults ($n = 90$, 14 species), and (B) partial postjuvenile moults (which include eccentric and abridged moult patterns; Guallar and Jovani, 2020b) ($n = 179$, 28 species). Regression lines and 95% confidence intervals of order of tract activation on number of moulted tracts. Mean (range) sample sizes per feather and moult: $n_c = 29$ (15–54), $n_{pj} = 51$ (4–146).
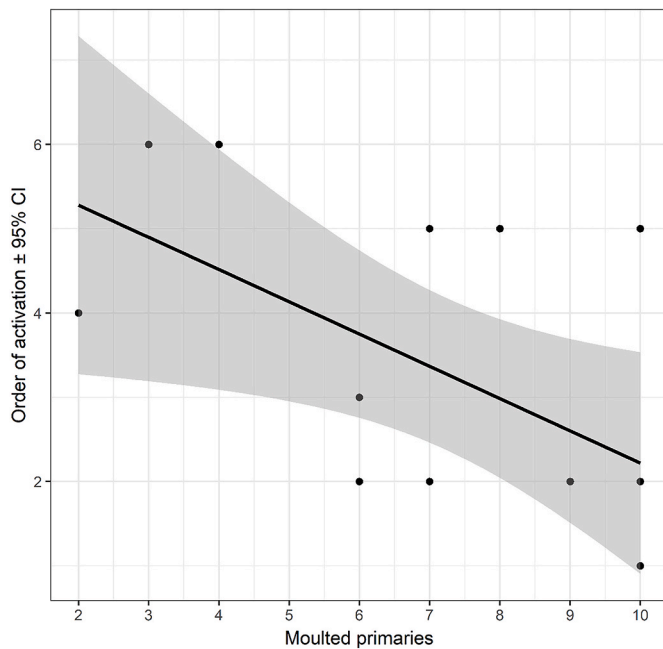
Fig. 5. Effect of completeness within tract on moult sequence among tracts. Regression line and 95% confidence interval of order of activation of the primary tract on number of moulted primaries during eccentric moults ($n = 14$, 6 species). Three individuals of 9-primaried species included here still had juvenile outer primaries, therefore could be treated as 10-primaried without affecting the results (see Guallar, 2024).

2009), the dynamics of moult intensity reveals a smooth production of feather mass and the avoidance of sudden or irregular demands (Fig. 6). The maximum of this curve is a function of the mass of the feathers moulted, which depends on their number, identity, and species-specific traits such as bird size and wing shape (Leisler and Winkler, 1985;
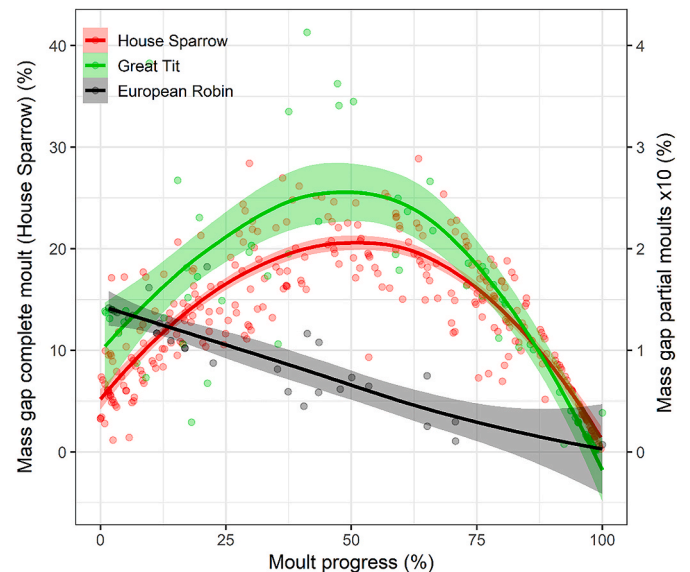

Fig. 6. Relationship between moult intensity (measured as mass gap of wing and tail) and moult progress obtained from local polynomial regression (95% confidence intervals shown as shade areas; span = 1). Comparison between the complete moult of the House Sparrow (complete moult; $n = 293$), the postjuvenile moult of the Great Tit (partial postjuvenile moult without retention of secondary coverts, tertials, or alula feathers; $n = 69$), and the European Robin (partial postjuvenile moult with retention of secondary coverts, tertials, and alula feathers; $n = 31$). To calculate the postjuvenile moult progress, I took as reference the wing and tail feathers most frequently replaced: 1) all secondary coverts, alula feathers, tertials, and rectrices for Great Tits, and 2) median, marginal coverts, and greater coverts for European Robins. To facilitate comparison, moult intensity of partial moults was multiplied by 10. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3

Summary of the chi-square tests for the protection hypothesis between feathers of longitudinally adjacent tracts in partial postjuvenile moults. In parenthesis type of hypothesis tested: deviation from nil simultaneous growth and from random occurrence of simultaneous growth.

Hypothesis	Moult type	χ_1^2	p	n
GC10 vs. TT (nil)	Complete	0	1	69
GC10 vs. TT (random)	Complete	9.296	0.002	69
GC10 vs. TT (nil)	Partial complete	2.148	0.143	95
GC10 vs. TT (random)	Partial complete	26.165	<0.001	95
GC10 vs. TT (nil)	Partial incomplete	0	1	40
GC10 vs. TT (random)	Partial incomplete	0.005	0.945	40
MeC vs. GC 1–9 (nil)	Complete	6.695	0.010	88
MeC vs. GC 1–9 (random)	Complete	16.862	<0.001	88
MeC vs. GC 1–9 (nil)	Partial complete	21.377	<0.001	102
MeC vs. GC 1–9 (random)	Partial complete	0.790	0.021	102
MeC vs. GC 1–9 (nil)	Partial incomplete	19.575	<0.001	51
MeC vs. GC 1–9 (random)	Partial incomplete	0	1	51
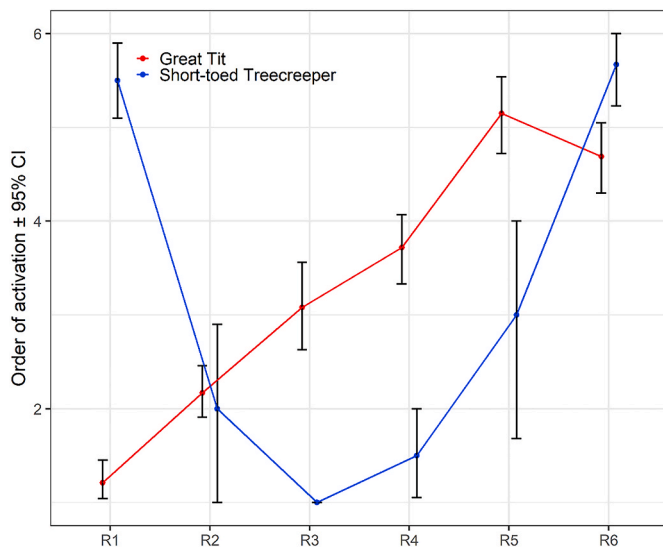
Fig. 7. Moult sequence within the rectrices of two Palearctic species. Dots show mean order of moult activation of every feather. Wider confidence intervals indicate greater variation within the tract's sequence. Rectrix number increases outwardly. Notice that R6 (the outermost and shortest rectrix) activates before R5 in the Great Tit. Sample sizes from the central rectrix outward: $n_{GT} = \{28, 25, 25, 23, 35, 35\}$, $n_{STT} = \{4, 2, 2, 2, 3, 3\}$.

Rohwer et al., 2009). However, moult-intensity dynamics also depends on moult completeness, peaking closer to the beginning of moult as completeness decreases. Thus, when the mass of the feathers moulted is low, their moult intensity may peak right at the beginning of moult, as in the European Robin (Fig. 6). This larger demand at the beginning of feather moult should have a minor impact on the smoothness of the overall feather production rate (e.g., mass of the wing and tail feathers replaced by Great Tits is about 11% of the total plumage mass; Newton, 1966; Guallar and Quesada, 2023b) and may correlate to the shift of the overall moult sequence, with moult of body tracts starting ahead of the remiges (innermost primaries start growing earlier in the complete moult; Guallar and Quesada, 2023a).

Endogenous factors may play an important role in moult sequence via moult intensity. For example, physical condition and breeding effort can constrain time and resources available for the synthesis of feather material (Hemborg and Lundberg, 1998; Hall and Fransson, 2000). Age may potentially explain differences in moult sequence and intensity. In fact, the effect of age can hardly be disentangled from the effect of completeness because they are highly correlated: postjuvenile moults are usually partial and postbreeding moults typically complete. Species

that undergo partial postbreeding and postjuvenile moults of similar extent (e.g., Garden Warbler *Sylvia borin*) might provide insights into this question. Species with complete postbreeding and postjuvenile moults may offer a better model due to their relative abundance and because they allow comparisons of know extent (the number and identity of feathers eventually replaced in partial moults are not highly predictable in most species). I did make this comparison in the House Sparrow and only found a trend to moult later some inner greater coverts in adults (Appendix Fig. S5). Further, Guallar and Quesada (2023) just found slight age-differences in moult intensity.

4.2. Implications for moult regulation and life-history

Passerines adjust moult parameters to multiple factors, including current environmental conditions (e.g., moult onset; van der Jeugd et al., 2009; Solís et al., 2021), migratory strategy (moult duration; de la Hera et al., 2010), aerodynamic loss (moult intensity; Lind, 2001; Tomotani and Muijres, 2019), and life-cycle stage (moult extent; Delhey et al., 2020; Guallar and Jovani, 2020a). While the benefit of adjusting each moult parameter may be small, lacking apparent fitness consequences (e.g., de la Hera et al., 2013; Tomotani et al., 2018), their cumulative effect likely provides an overall somatic advantage, leading to potential fixation throughout evolution. Regardless of the factors controlling sequence and intensity, these two components of the moult process exhibit enough flexibility to allow the ontogenetic and seasonal adjustments of plumage that define the diversity of moult strategies in passerine species (Jenni and Winkler, 2020a). Although intensity and moult sequence are apparently coordinated (e.g., Figs. 3–5; Dawson, 2003), the impact of the variation of moult sequence on the life-history of passerines is largely speculative. For example, it could interact with migratory strategy to allow for earlier departures after the breeding season and the replacement of feathers that tend to wear the most (Terrill et al., 2020). Some species could coapt these differences in moult sequence among life-cycle stages for social-signalling purposes (Guallar and Figuerola, 2016).

Sequence and intensity of moult have been studied from a broad perspective, with a focus on the impact of remex moult on aerodynamics (Lind, 2001; Rohwer and Broms, 2013; Tomotani et al., 2018). By focusing on the effect of completeness of plumage replacement on moult sequence and intensity, I have shown clear differences between partial and complete moults in passerines, and between moult types associated with different life-cycle stages. However, partial moults become more similar to the complete moult as investment in feather material increases, suggesting a self-organised process that depends on multiple factors, such as coordination between the moult of the innermost greater covert and tertials to protect the latter's quills. This coordination remains consistent regardless of moult completeness (Table 2; Zeidler, 1966; Guallar and Quesada, 2023a).

Noticeable variation in sequence and intensity within and among species, as well as life-cycle stages, suggests that passerines balance constraints, optimise feather-material production, and coordinate activation of feathers within and among tracts to fulfil essential functions. Changes in the budget allocated to feather production, the specific feathers replaced during a given moult (Guallar et al., 2014), and the exogenous factors that affect passerine birds during moult necessitate a flexible regulation of the moult components.

5. Conclusion

Sequence and intensity dynamics in partial moults vary with species and life-cycle stage, and tend to converge toward those of the complete moult as moult completeness increases. Moult intensity of flight-feather tracts affects moult sequence within and among tracts.

The protection of tertial quills by overlapping greater coverts is a feature shared by complete and partial moults.

Partial moults of passerines are not arrested moults (i.e., unfinished

complete moults). They may arise from a self-organised process largely contingent on the level of investment in plumage renewal.

Ethics statement

Ringing permits were granted by Departament de Territori i Sostenibilitat. Generalitat de Catalunya (permits SF/0229/2019; SF/0059/21; SF0072/22).

CRediT authorship contribution statement

Santi Guallar: Writing – review & editing, Writing – original draft, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.avrs.2024.100163.

References

Ashmole, N.P., 1962. The black noddy *Anous tenuirostris* on ascension island. Part 1. General biology. Ibis 103, 235–273.

Bååth, R., 2016. Package 'bayesboot'. An Implementation of Rubin's (1981) Bayesian Bootstrap. Version 0.2.1. https://github.com/rasmusab/bayesboot.

Bensch, S., Hasselquist, D., Hedenström, A., Ottosson, U., 1991. Rapid moult among Palaearctic passerines in West Africa- an adaptation to the oncoming dry season? Ibis 133, 47–52.

Buttemer, W.A., Nicol, S.C., Sharman, A., 2003. Thermoenergetics of pre-moulting and moulting kookaburras (*Dacelo novaeguineae*): they're laughing. J. Comp. Physiol. B 173, 223–230.

Chai, P., 1997. Hummingbird hovering energetics during moult of primary flight feathers. J. Exp. Biol. 200, 1527–1536.

Dawson, A., 2003. A detailed analysis of primary feather moult in *Sturnus vulgaris* – new feather mass increases at a constant rate. Ibis 145, E69–E76.

Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C., Eccleston, L., 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proc. Roy. Soc. Lond. B 267, 2093–2098.

de la Cruz, C., de Lope, F., Sánchez, J.M., 1992. Postjuvenile moult in the Azure-winged Magpie *Cyanopica cyanea cooki*. Ringing Migr. 13, 27–35.

de la Hera, I., Pérez-Tris, J., Tellería, J.L., 2010. Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines. J. Avian Biol. 41, 609–614.

de la Hera, I., Reed, T.E., Pulido, F., Visser, M.E., 2013. Feather mass and winter moult extent are heritable but not associated with fitness-related traits in a long-distance migratory bird. Evol. Ecol. 27, 1199–1216.

DeGraaf, R.M., Rappole, J.H., 1995. Neotropical Migratory Birds: Natural History, Distribution, and Population Change. Comstock Publishing Associates, Ithaca.

Delhey, K., Guallar, S., Rueda-Hernández, R., Valcu, M., Wang, D., Kempenaers, B., 2020. Partial or complete? The evolution of post-juvenile moult strategies in passerine birds. J. Anim. Ecol. 89, 2896–2908.

DesRochers, D.W., Reed, M., Awerman, J., Kluge, J.A., Wilkinson, J., van Griethuijsen, L. I., et al., 2009. Exogenous and endogenous corticosterone alter feather quality. Comp. Biochem. Physiol. A 152, 46–52.

Dhondt, A.A., 1973. Postjuvenile and postnuptial moult in a Belgian population of Great Tits, *Parus major*, with some data on captive birds. Gerfaut 63, 187–209.

Dolnik, V.R., Gavrilov, V.M., 1979. Bioenergetics of molt in the chaffinch (*Fringilla coelebs*). Auk 96, 253–264.

Evans, P.G.H., 1986. Ecological aspects of wing moult in the European Starling *Sturnus vulgaris*. Ibis 128, 558–561.

Flegg, J.J.M., Cox, C.J., 1969. The moult of British blue tit and great tit populations. Hous. Theor. Soc. 16, 147–157.

Flinks, H., 1999. Muster, Intensität und zeitliche Aspekte der postjuvenilen Mauser beim Schwarzkehlchen (*Saxícola torquata*). Vogelwarte 40, 11–27.

Gargallo, G., 2013. Feather selection and replacement patterns demonstrate that Goldfinches *Carduelis carduelis* fix postjuvenile moult extent prior to moult initiation. J. Ornithol. 154, 219–230.

Gauci, C., Sultana, J., 1979. Moult of the Sardinian warbler. II-Merill 20, 1–13.

Griggio, M., Serra, L., Licheri, D., Campomori, C., Pilastro, A., 2009. Moult speed affects structural feather ornaments in the blue tit. J. Evol. Biol. 22, 782–792.

Guallar, S., Santana, E., Contreras, S., Verdugo, H., Gallés, A., 2009. Paseriformes del Occidente de México: Morfometría, Datación y Sexado. Museu de Ciències Naturals de Barcelona, Barcelona.

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

Guallar, S., Figuerola, J., 2016. Factors influencing the evolution of moult in the nonbreeding season: insights from the family Motacillidae. Biol. J. Linn. Soc. 118, 774–785.

Guallar, S., Jovani, R., 2020a. Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny. Ibis 162, 778–786.

Guallar, S., Jovani, R., 2020b. Wing-feather moult phenotypes differ between: the preformative and prealternate episodes and along passerine phylogeny. Ibis 162, 778–786.

Guallar, S., Jovani, R., 2020c. Moult nestedness and its imperfections insights to unravel the nature of passerine wing-feather moult rules. J. Avian Biol. 51, e02553.

Guallar, S., Carrillo-Ortiz, J., Quesada, J., 2021. Marginal covert moult in the House Sparrow *Passer domesticus*. Ringing Migr. 36, 95–104.

Guallar, S., Quesada, J., 2023a. Moult intensity constraints along the complete-moult sequence of the House Sparrow *Passer domesticus*. Avian Res 14, 100125.

Guallar, S., Quesada, J., 2023b. Moult intensity constraints along the complete-moult sequence of the House Sparrow *Passer domesticus*. Figshare. https://doi.org/10.6084/m9.figshare.21546183.

Guallar, S., 2024. From partial to complete: wing- and tail-feather moult sequence and intensity depend on species, life-cycle stage, and moult completeness in passerines. Figshare. https://doi.org/10.6084/m9.figshare.22199491.

Hall, K.S.S., Fransson, T., 2000. Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. J. Avian Biol. 31, 583–587.

Haukioja, E., 1971. Processing moult card data with reference to the Chaffinch *Fringilla coelebs*. Ornis Fenn. 48, 25–32.

Hedenström, A., 1998. The relationship between wing area and raggedness during molt in the willow warbler and other passerines. J. Field Ornithol. 69, 103–108.

Heise, C.D., Moore, F.R., 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. Condor 105, 496–504.

Hemborg, C., Lundberg, A., 1998. Costs of overlapping reproduction and moult in passerine birds: an experiment with the pied flycatcher. Behav. Ecol. Sociobiol. 43, 19–23.

Herremans, M., 1988. Postjuvenile moult, phenology and biometry of Grey Wagtails *Motacilla cinerea* migrating over central Belgium. Ringing Migr. 9, 103–116.

Hinsley, S.A., Rothery, P., Ferns, P.N., Bellamy, P.E., Dawson, A., 2003. Wood size and timing of moult in birds: potential consequences for plumage quality and bird survival. Ibis 145, 337–340.

Jenni, L., Winkler, R., 2020a. The Biology of Moult in Birds. Helm, London.

Jenni, L., Winkler, R., 2020b. Molt and Ageing of European Passerines, second ed. Bloomsbury¸ London.

Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. Nature 491, 444–448.

Jovani, R., Rohwer, S., 2017. Fault bars in wing feathers: mechanisms, and ecological and evolutionary causes and consequences. Biol. Rev. 92, 1113–1127.

Kasparek, M., 1979. Zum Ablauf der postnuptialen Vollmauser der Rohrammer (*Emberiza schoeniclus*). J. Ornithol. 120, 247–264.

Kiat, Y., 2017. Divergent primary moult—a rare moult sequence among western Palaearctic passerines. PLoS One 12, e0187282.

Kiat, Y., 2018. Divergent rectrix moult the implications and conditions of moult sequence. J. Avian Biol. 49, e01609.

Leisler, B., Winkler, H., 1985. Ecomorphology. In: Johnston, R.F. (Ed.), Current Ornithology, 2. Springer, Boston, pp. 155–186.

Lind, J., 2001. Escape flight in moulting tree sparrows (*Passer montanus*). Funct. Ecol. 15, 29–35.

Lucas, A.M., Stettenheim, P.R., 1972. Avian anatomy, integument. In: Agricultural Handbook, 362. United States Department of Agriculture, Lansing.

Newton, I., 1966. The moult of the bullfinch *Pyrrhula pyrrhula*. Ibis 108, 41–67.

Nilsson, J.-Å., Svensson, E., 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proc. Roy. Soc. Lond. B 263, 711–714.

Norman, S.C., 1991. Post-juvenile moult in relation to dispersal and migration in the Chiffchaff *Phylloscopus collybita*. Ringing Migr. 12, 80–85.

Pagel, M., 1992. A method for the analysis of comparative data. J. Theor. Biol. 156, 431–442.

Pap, P.L., Barta, Z., Tökölyi, J., Vágási, C.I., 2007. Increase of feather quality during moult: a possible implication of feather deformities in the evolution of partial moult in the great tit *Parus major*. J. Avian Biol. 38, 471–478.

Puttick, M., Thomas, G., Freckleton, R., Clarke, M., Ingram, T., Orme, D., et al., 2019. Motmot: Models of Trait Macroevolution on Trees. R Package version 2.1.3.

Pyle, P., 2022a. Defining moults in migratory birds: a sequence-based approach. J. Avian Biol. 2022, e02958.

Pyle, P., 2022b. Identification Guide to North American Birds. Part I, second ed. Slate Creek Press, Forest Knolls.

R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Revell, L., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.

Rohwer, S., 2008. A primer on summarizing molt data for flight feathers. Condor 110, 799–806.

Rohwer, S., Broms, K., 2013. Replacement rules for the flight feathers of yellow-billed cuckoos (*Coccyzus americanus*) and common cuckoos (*Cuculus canorus*). Auk 130, 599–608.

Rohwer, S., Rohwer, V.G., 2018. Primary molt in Gruiforms and simpler molt summary tables. PeerJ 6, e5499.

Rohwer, S., Ricklefs, R.E., Rohwer, V.G., Copple, M.M., 2009. Allometry of the duration of flight feather molt in birds. PLoS Biol. 7, e1000132.

Serra, L., Griggio, M., Licheri, D., Pilastro, A., 2007. Moult speed constrains the expression of a carotenoid-based sexual ornament. J. Evol. Biol. 20, 2028–2034.

Shirihai, H., Gargallo, G., Helbig, A., 2001. Sylvia Warblers. Christopher Helm, London.

Shyy, W., Aono, H., Kang, C.-K., Liu, H., 2013. An Introduction to Flapping Wing Aerodynamics. Cambridge University Press, Cambridge.

Small, D.M., Gimpel, M.E., Gruber, J.G., 2013. Variation and extent of eccentric preformative molt in Field Sparrows. NABB (N. Am. Bird Bander) 38, 49–54.

Solís, I., Sanz, J.J., Imba, L., Álvarez, E., Barba, E., 2021. A higher incidence of moult-breeding overlap in great tits across time is linked to an increased frequency of second clutches: a possible effect of global warming? Anim. Biodivers. Conserv. 44, 303–315.

Svensson, L., 1992. Identification Guide to European Passerines, fourth ed. L. Svensson, Stockholm.

Terrill, R.S., 2020. Simultaneous wing molt as a catalyst for the evolution of flightlessness in birds. Am. Nat. 196, 775–784.

Terrill, R.S., Seeholzer, G.F., Wolfe, J.D., 2020. Evolution of breeding plumages in birds: a multiple-step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae). Ecol. Evol. 10, 9223–9239.

Tomotani, B.M., Muijres, F.T., Koelman, J., Casagrande, S., Visser, M.E., 2018. Simulated moult reduces flight performance but overlap with breeding does not affect breeding success in a long-distance migrant. Funct. Ecol. 32, 389–401.

Tomotani, B.M., Muijres, F.T., 2019. A songbird compensates for wing molt during escape flights by reducing the molt gap and increasing angle of attack. J. Exp. Biol. 222, jeb195396.

Vágási, C.I., Pap, P.L., Vincze, O., Benkő, Z., Marton, A., Barta, Z., 2012. Haste makes waste but condition matters: molt rate-feather quality trade-off in a sedentary songbird. PLoS One 7, e40651.

Van der Jeugd, H.P., Eichhorn, G., Litvin, K.E., Stahl, J., Larsson, K., van der Graaf, A.J., et al., 2009. Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. Global Change Biol. 15, 1057–1071.

Vega Rivera, J.H., McShea, W.J., Rappole, J.H., Haas, C.A., 1999. Postbreeding movements and habitat use of adult Wood Thrushes in northern Virginia. Auk 116, 458–466.

Weber, T.P., Kranenbarg, S., Hedenström, A., Waarsing, J.H., Weinans, H., 2010. Flight feather shaft structure of two warbler species with different moult schedules. J. Zool. 280, 163–170.

Williamson, K., 1968. Identification for Ringers. The Genus *Sylvia*. BTO Field Guide, 9, second ed. Tring.

Williamson, K., 1972. Reversal of normal moult sequence in the Spotted Flycatcher. Br. Birds 65, 50–51.

Willoughby, E.J., Murphy, M., Gorton, H.L., 2002. Molt, plumage abrasion, and color change in Lawrence's Goldfinch. Wilson Bull. 114, 380–392.

Winkler, R., Winkler, A., 1985. Zur jugendmauser landaufgezogener schneefinken *Montifringilla nivalis*. Ornithol. Beob. 82, 55–66.

Winkler, R., Jenni, L., 1987. Weitere Indizien für 'sektorale' handschwingenmauser bei jungen Singvögeln. J. Ornithol. 128, 243–246.

Winkler, R., Daunicht, W.D., Underhill, L.G., 1988. Die Grossgefiedermauser von Alpendohle *Pyrrhocorax graculus* und Alpenkrähe *Pyrrhocorax pyrrhocorax*. Ornithol. Beob. 85, 245–259.

Yuri, T., Rohwer, S., 1997. Molt and migration in the northern rough-winged swallow. Auk 114, 249–262.

Zeidler, K., 1966. Untersuchungen über Flügelbefiederung und Mauser des Haussperling *Passer domesticus*. J. Ornithol. 107, 113–115.