



# Wing-feather moult phenotypes differ between the preformative and prealternate episodes and along passerine phylogeny

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Passerine wing-feather moult has been studied historically in terms of its intensity, duration, timing and extent. However, little is known about variation of wing-moult phenotypes (i.e. the identity of moulted wing feathers in a given individual) within species, among moult episodes and in relation to passerine phylogeny. Here we studied 5373 wing-moult cards from 285 Holarctic and 155 Neotropical passerine species. Variation of moult phenotypes, although high, was far below that expected by chance, and the same phenotypes were repeated among individuals within and among species, suggesting the existence of shared mechanisms of moult control. We successfully classified moult phenotypes according to nine moult patterns described in the literature and found an uneven distribution between the preformative and the prealternate moult. Moult patterns were phylogenetically conserved for the preformative but not for the prealternate moult. Our results suggest differential seasonal control of bird moult with preformative moults being associated with (evolutionarily conserved) somatic demands, whereas prealternate moults are probably associated with (rapidly evolving) signalling functions.

**Keywords:** moult patterns, moult signatures, seasonal expression.

Feather evolution eventually led to feathered wings, and these to bird flight, becoming a key innovation in the evolution of tetrapods. The concomitant evolution of feather moult was essential to maintain function of these dead, keratin structures that are prone to degradation by biotic (e.g. lice and bacteria; Goldstein *et al.* 2004, Vas *et al.* 2008) as well as abiotic factors (e.g. mechanical abrasion, sunlight; Lennox & Rowlands 1969, Surmacki *et al.* 2011). Within species, the study of bird moult ecology and its evolution has largely focused on the reasons for individual variation of moult extent (i.e. quantity of replaced feathers), such as body condition (Gosler 1994) or time available for moulting (Bojarinova *et al.* 1999, Kiat & Izhaki 2017), and the overlap with energetically costly activities such as breeding and migration

(Hemborg *et al.* 2001, Podlaszczuk *et al.* 2016). Among species, moult research has focused on differences in moult speed, duration, extent, location, and sequence as a result of the interaction of moult with specific traits such as body size (Rohwer *et al.* 2009), sexual dichromatism (Figueroa & Jovani 2001), migratory behaviour (de la Hera *et al.* 2010) and environmental factors (Dawson 2008).

## Wing-feather moult phenotypes

Much less attention has been paid to moult phenotypes, in other words the identity of feathers replaced by an individual bird in a given moult episode. Thus, the proximate and ultimate reasons explaining exactly which feathers are replaced, and why these differ among species, among individuals within species and among moult episodes, are poorly understood. This is surprising for two reasons. First, different wing feathers may have very

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different functions, e.g. status signalling by greater coverts, stall delay by alula feathers, lift by primaries. Secondly, the identity of retained and replaced feathers has been recorded for decades in moult cards (Ginn & Melville 1983), being summarized in wing diagrams showing the proportion of individuals in a given species replacing each feather (or feather track) as an age determination tool (Jenni & Winkler 1994, Guallar *et al.* 2009). However, moult cards have been largely neglected as a resource for studying the evolution of bird moult, even though these cards are for individual birds on which natural selection operates, and record data feather-by-feather, thus accounting for the distribution of functions across the wing.

Here, we focus on the wing-feather moult of passerines, arguably the bird order whose moult has been most thoroughly studied. Passerines moult in a scheduled and periodical fashion, replacing the whole plumage at least once a year (Jenni & Winkler 1994). Full plumage renewal generally occurs right after breeding, during the prebasic moult (Humphrey & Parkes 1959). However, many species undergo additional, partial moult episodes (Svensson 1992, Jenni & Winkler 1994, Pyle 1997a). These include the preformative moult of young birds (equivalent to the post-juvenile moult; Jenni & Winkler 1994), which replaces their juvenile plumage soon after fledging (Howell *et al.* 2003), and the prealternate moult of older birds (equivalent to the pre-breeding moult; Jenni & Winkler 1994), which takes place after the prebasic moult and before the onset of the breeding season (typically in the wintering grounds for migratory species; Humphrey & Parkes 1959).

We accrued a large dataset of individual moult phenotypes by gathering moult cards for birds whose moult had finished from literature and original data. First, we explored variation of moult phenotypes across individuals, species and moult episodes. Then, we tested whether moult phenotypes are random sets of replaced feathers for any given moult extent.

### Phenotypic variation and moult signatures

The study of moult phenotype variation is challenging and has been little addressed to date. Here, we tackled the complexity of moult phenotype variation by using a literature review of the so-called moult patterns, which are labels given in

order to group similar moult phenotypes. Applying this approach, we aimed to explore three aspects related to the ecology and evolution of moult phenotypes in passerines.

First, we explored whether individuals of a species during a given moult episode showed different moult patterns. As endogenous (e.g. physical condition) and exogenous (e.g. available time) factors may vary among individuals, we expected that moult phenotypes may reflect these differences and could be classified in different moult patterns.

Secondly, we examined differences in the frequency of moult patterns between moult episodes across species. Although basic plumage requirements prioritized in each moult episode are poorly understood, they may differ strongly. For instance, the preformative moult has been related to somatic performance (Middleton 1986, Minias & Iciek 2013), whereas the prealternate moult may also meet signalling functions (Fig. S1), such as social status (Guallar & Figuerola 2016) and sexual attractiveness, at least in species in which this episode takes place just before the breeding season (Lantz & Karubian 2016).

We also studied the frequency distribution of moult patterns from every species and moult episode (hereafter, moult signatures), then mapped these moult signatures to bird phylogeny and calculated their phylogenetic signal in both the preformative and the prealternate moult.

## METHODS

### Moult phenotypes

Moult cards of finished moults were retrieved from published sources and mist-netted birds from Holarctic and Neotropical bird species (Table S1). Moult state (1 replaced, 0 retained) was scored for each individual upper wing-feather, except for lesser wing coverts, which were collectively scored 1 when more than 70% of the feathers were replaced and 0 otherwise (assessment of the percentage of replaced lesser coverts is rather imprecise; to account for this fact, we defined a value high enough to indicate that nearly the whole tract was moulted). For standardization purposes, the 10th primary of species with nine visible primaries was given the same moult score as the ninth primary (Hall 2005). We removed 47 moult cards with no wing feathers replaced (or with only < 70% of lesser coverts replaced). Thus, moult

extent can range in this study from 1 to 51 (lesser coverts = 1, median coverts = 8, greater coverts = 10, carpal covert = 1, primary coverts = 9, alula = 3, tertials = 3, secondaries = 6, primaries = 10).

Although moult is conceived to be a non-random process due to the differential properties (e.g. shape, mass, position) of each feather and its associated function, as far as we know this hypothesis has never explicitly been tested. The total number of potential moult phenotypes (i.e. combinations of replaced feathers) is  $2^{51}-1$ . The number of potential moult phenotypes differs for each moult extent; for example, there are 51 combinations when moulting one wing feather, but 1275 when moulting two. Thus, for each individual in our dataset we simulated new moult phenotypes of the same moult extent, but randomizing the identity of replaced feathers. Then, we tested whether feathers are moulted randomly by comparing the number of repeated moult phenotypes across individuals between observed and simulated moult phenotypes. If moult is a non-random process, some moult phenotypes would be more repeated than expected by chance.

### Phenotypic variation and moult signatures

We reviewed the existing literature for passerine wing-moult patterns. The term moult pattern is rather vague and it has been applied to refer to features as diverse as duration (Newton & Rothery 2005), sequence of replacement (Edelstam 1984), intensity (Hall & Fransson 2000), timing (Marini & Durães 2001) and interaction of moult with other stages of the annual cycle (Giunchi *et al.* 2008). Here, we restricted the definition of moult pattern to 'classes' of observed wing-moult phenotypes (e.g. Pyle 1997b, Pinilla 2001). We then searched for the term 'moult pattern' used in this way in the specialized literature and classified the wing-moult cards in our dataset according to the currently proposed moult patterns we found.

Determination of moult homologies is an unsettled issue, with basic questions such as number of annual episodes undergone by a species still under debate (e.g. Howell *et al.* 2003, Piersma 2004, Thompson 2004, Willoughby 2004). We used two working criteria to define our moult episodes: (1) preformative moult as the first moult episode during which the juvenile plumage is

replaced (e.g. in the case of non-migratory *Acrocephalus* warblers, the preformative moult is complete, whereas it is partial for migratory species of the genus); (2) prealternate moult as the main moult episode during the non-breeding period (e.g. many species in Laniidae and Phylloscopidae show two non-breeding moult episodes, but the prealternate moult is the more extensive of the two episodes).

For each species and moult episode (preformative and prealternate), we calculated the proportion of moult phenotypes classified in each moult pattern (i.e. moult signatures). We then used hierarchical clustering with Bray–Curtis distances to group species with similar moult signatures (Fig. S2). We applied the complete linkage method because it tends to maximize dissimilarities between clusters and yield more balanced clusters (James *et al.* 2013). Given the lower abundance of prealternate moult cards in our dataset, we only included species with at least 19 moult cards for the preformative moult and at least 10 moult cards for the prealternate moult. Some species may moult more than once between the prebasic moult and before the onset of the breeding season. In these cases, we only included moult phenotypes from the most extensive of these moults as the prealternate moult (e.g. the late winter moult of Parulidae or the late autumn moult of Acrocephalidae; Salewski *et al.* 2004, Guallar *et al.* 2009).

To test for the phylogenetic signal of moult signatures, we downloaded 1000 trees for each set of bird species from birdtree.org (Jetz *et al.* 2012). Then we derived majority rule consensus trees computing mean length branches using 'phytools' (Revell 2012). From these, we estimated phylogenetic signals for moult signatures within each moult episode. Because this variable is categorical, we could not use Pagel's lambda or other methods based on continuous variables. Instead, we adopted the permutation approach proposed by Maddison and Slatkin (1991) (R code available at <https://github.com/juliema/publications/tree/master/BrueeliaMS>; Bush *et al.* 2016, R Core Team 2017). Specifically, we randomized the tree tips 999 times and compared the scores for each randomization with the empirical score. Statistical significance indicates both phylogenetic conservation and deviation from randomness. Because *P*-values vary slightly among permutation tests, we averaged *P*-values from 10 runs.

## RESULTS

### Moult phenotypes

We gathered a dataset of 5456 moult cards of birds which had finished moult (Guallar & Jovani 2019), discarding 83 moult cards either because of null extent or because they were assigned to an anomalous pattern (i.e. those that could not be assigned to any of the nine moult patterns defined in Table 1; Table S2). The final dataset used in the analyses consisted of 5373 moult cards from 440 passerine species (285 Holarctic and 155 Neotropical), 2297 of which came from

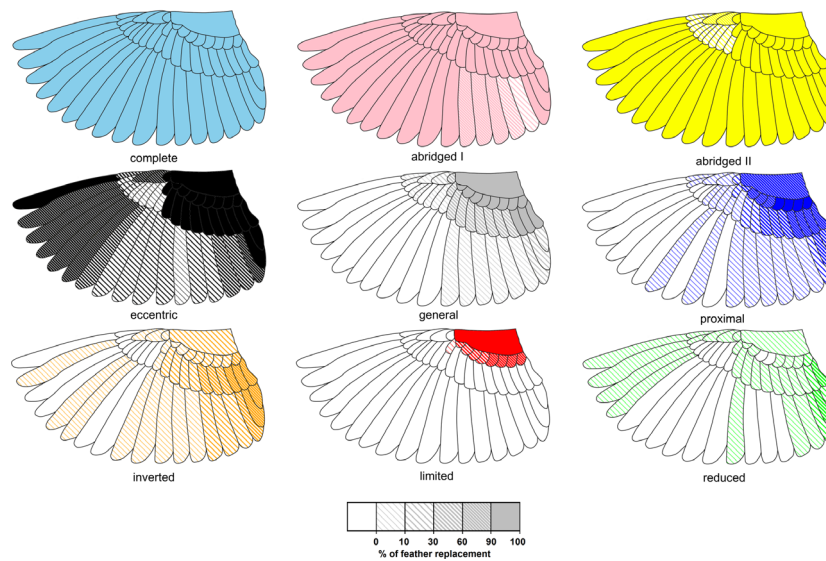
unpublished sources (Table S1). In total, 4085 moult cards were preformative, 1141 prealternate and 147 belonged to other moult episodes.

Moult phenotypes covered the whole moult extent range (i.e. from 1 to 51). In total, 20.5% of the (unique) moult phenotypes occurred at least twice in the dataset, contrasting with only 0.6% of the simulated ones (Chi-square test  $\chi^2 = 672.1$ ,  $P < 0.0001$ ; Figs S3 & S4). In terms of individual moult phenotypes, 73.9% were repeated by at least one other individual, but this only occurred in 1.5% of the randomly simulated moult phenotypes (Chi-square test  $\chi^2 = 4081.0$ ,  $P < 0.0001$ ; Fig. S3).

**Table 1.** Summary of published passerine wing-feather moult patterns.

Pattern	Description	Reference(s)
Abridged I	Complete moult aborted within secondaries: 1–6 secondaries retained. Example: Prebasic moult of Blue Bunting <i>Cyanocompsa parellina</i> .	Mead and Watmough (1976) and Norman (1991)
Abridged II	Complete moult in which primary coverts are retained. Example: Preformative moult of Graceful Prinia <i>Prinia gracilis</i> .	Pyle (1998) and Kiat and Izhaki (2017)
Complete	Full feather replacement following a highly conserved moult sequence in passerines: start at primary 1, replacement of primaries accompanied by respective primary coverts. It can be halted at any point and resumed later on (suspension) or not (arrest). Example: Preformative moult of House Sparrow <i>Passer domesticus</i> .	Zeidler (1966)
Eccentric	Retention of a variable number of (largely inner) primaries and (largely outer) secondaries, and most to all primary coverts. Example: Preformative moult of <i>Passerina</i> buntings.	Winkler and Jenni (1987) and Pyle (1998)
General	Replacement of secondary (i.e. lesser, median and greater) coverts. Tertiaries are replaced only if secondary coverts are moulted. There is a prioritization from leading to trailing edge of wing: filling of an entire feather tract before proceeding with the next. Example: Preformative moult of <i>Turdus</i> thrushes.	Pyle (1997b) and Guallar <i>et al.</i> (2014)
Proximal	Same as the general pattern but tertiaries (and adjacent inner secondaries) can be replaced with retention of outer secondary coverts. From leading to trailing edge of the wing: prioritization of feathers closer to the body before finishing replacement of anterior tracts. Example: Preformative moult of <i>Henicorhina</i> wood-wrens.	Pyle (1997b) and Guallar <i>et al.</i> (2014)
Inverted	Replacement of inner secondaries and secondary coverts. Prioritization of feathers closer to the body from trailing to leading edge of the wing: tertiaries, secondaries and greater coverts over median and lesser coverts (the latter at low percentages). Example: Prealternate moult of some trans-Saharan migrants (e.g. European Pied Flycatcher <i>Ficedula hypoleuca</i> ), and of residents of arid habitats (e.g. <i>Peucaea</i> sparrows).	Jenni and Winkler (1994) and Guallar <i>et al.</i> (2018)
Limited	Replacement of lesser and median coverts; might include the carpal covert. Prioritization of feathers from leading to trailing edge of the wing and from inner to outer feathers. Example: Preformative moult of dippers <i>Cinclus</i> spp., nuthatches <i>Sitta</i> spp., treecreepers <i>Certhia</i> spp. or kinglets <i>Regulus</i> spp.	Jenni and Winkler (1994) and Pyle (1997a)
Reduced	Replacement of one to a few tertiaries and/or greater coverts. Strongly asymmetrical moults are considered accidental. Example: 'winter' moult of some <i>Myiarchus</i> flycatchers, presupplemental ('spring') moult of Melodious Warbler <i>Hippolais polyglotta</i> .	Pinilla (2001) and Guallar <i>et al.</i> (2018)

Traditional nomenclature based on moult extent refers to these patterns as complete and partial moults (from limited to extensive).



**Figure 1.** Frequency of feather replacement by moult pattern. Definitions of moult patterns can be found in Table 1.

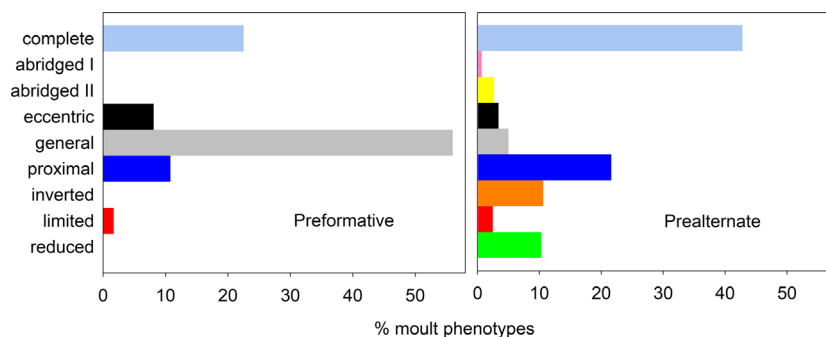
### Phenotypic variation and moult signatures

We retrieved 14 potential moult patterns from the literature, of which we retained only nine (Fig. 1, Table 1, Table S3). Note that the complete moult pattern includes arrested and suspended moults (i.e. birds that stopped a normal complete moult; Stresemann & Stresemann 1966, Norman 1991). Thus, under this definition, the complete moult pattern also comprises partial moult phenotypes. Interestingly, 99.1% of the moult phenotypes in our dataset were unequivocally classified using Table 1. Only 48 moult phenotypes (comprising 27 species) could not be classified and might either belong to minority yet

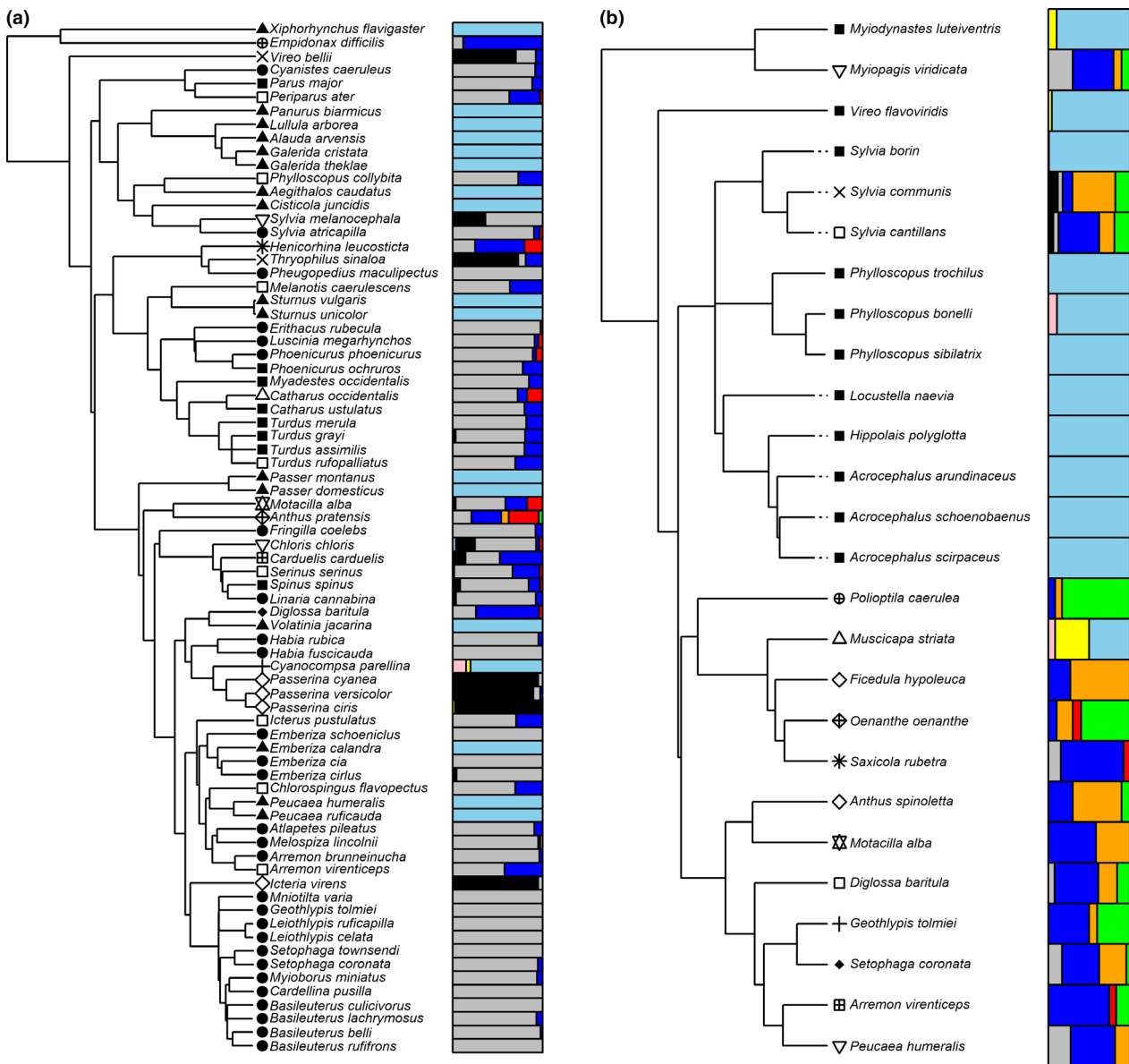
undescribed moult patterns or be simply considered as anomalies (Table S2).

Moult signatures differed strongly between moult episodes ( $G$  test  $G_8 = 1889.7$ ,  $P < 0.001$ , Fig. 2). The preformative moult was dominated by the general pattern (Table 1), whereas the prealternate episode was dominated by the complete pattern (Table 1), with the rest of the patterns more evenly distributed.

Species differed strongly in their moult signatures for both the preformative and the prealternate moults (Fig. 3, Fig. S2). Moult signatures were phylogenetically conserved for the preformative moult ( $P < 0.001$ ) and were more independent from phylogeny for the prealternate moult ( $P = 0.158$ , Fig. 3, Fig. S5).



**Figure 2.** Frequency of moult patterns (Table 1) in the preformative and the prealternate episodes, calculated as the mean percentage of moult cards per species and pattern. Bar colours follow Figure 1.



**Figure 3.** Phylogenetic trees of moult signatures: barplots show the proportion of moult cards following each moult pattern defined in Table 1. Symbols on the branch tips indicate group membership obtained through cluster analysis of similarity among moult signatures: 15 groups for the preformative moult and 13 for the prealternate moult (Fig. S2). (a) Preformative moult ( $n = 76$  species, 24 families). (b) Prealternate moult ( $n = 26$  species, 12 families). Bray–Curtis distances among species' pattern signatures were 0.57 and 0.67, respectively. Note the homogeneous pattern signatures within Phylloscopidae and Acrocephalidae. Colour of moult patterns follows Figure 1.

## DISCUSSION

### Moult phenotypes

We have shown that the identity of replaced feathers is far from random. In fact, more than

70% of moult phenotypes are repeated at least twice in the dataset, compared to the 1.5% expected by chance (Fig. S3b). In other words, individuals often share exactly the same combination of replaced feathers, which is extremely unlikely by chance alone. Moreover, most of these

repeated moult phenotypes were shared by individuals of different species and families (Fig. S2b). Therefore, passerine moult is largely a non-random process, suggesting strongly that moult is governed by some underlying rules shared across the whole order (Jenni & Winkler 1994, Kiat *et al.* 2019). These rules could, for example, be based on inherent ranks of feather-moult, energy investment or plumage exposure.

### Phenotypic variation and moult signatures

The preformative moult of fledglings showed less moult pattern variation than the prealternate moult of older birds during the non-breeding season (Fig. 2). This suggests that plumage requirements of young passerines are less diverse between species than the demands affecting the prealternate moult. A possible explanation is that the prealternate moult associates with plumage signalling functions in sexual contexts, as evidenced by the higher prevalence of prealternate moults in sexually dimorphic passerines (Omland & Lanyon 2000). More generally, the larger pattern variation in the prealternate moult might reflect more diverse plumage functions (dominance status or sexual attractiveness) and are highly species-specific (Andersson 1983). Feather tracts involved in sexual signalling may vary among species, e.g. greater coverts in Eurasian Siskin *Spinus spinus* (Senar *et al.* 2005), and greater coverts and tertials in European Pied Flycatcher *Ficedula hypoleuca* (Heij *et al.* 2011; Fig. S1). The strong homogeneity and low variation in the prealternate moult signatures of Phylloscopidae and Acrocephalidae are of note, suggesting that signalling is not important in these two families (Fig. 3). Interestingly, the 11 species with the lowest prealternate moult signature variation are sexually monochromatic (filled squares, Fig. 3; Fig. S2). These results suggest that moult patterns allow passerines to adapt to changing seasonal requirements.

Although moult patterns are shared across species and between moult episodes, species differed strongly in their moult signatures. Nevertheless, closely related species tended to show more similar moult signatures. Our data suggest that this similarity is greater in the preformative than in the prealternate moult (Fig. 3). Accordingly, only the preformative moult showed a statistically

significant phylogenetic signal. This is also consistent with the larger moult pattern variation shown in the prealternate moult, which may be correlated to the more labile evolution of sexually dimorphic plumages (Omland & Lanyon 2000). Phylogenetic conservation of preformative moult signatures further suggests that the underlying mechanisms of moult control have been shaped by natural selection, which have evolved in coordination with other key traits such as flight ability (Swaddle & Witter 1997, Pérez-Tris & Tellería 2001) and camouflage (Berggren *et al.* 2004).

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### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.9896516>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** European Pied Flycatcher after pre-ternate moult.

**Figure S2.** Cluster analysis of moult signatures per episode.

**Figure S3.** Distribution of repeated moult phenotypes.

**Figure S4.** (a) Accumulation curve of unique moult phenotypes in the dataset. (b) Frequency of repeated moult phenotypes.

**Figure S5.** Frequency of evolutionary transitions for the moult signatures in two moult episodes obtained from Maddison & Slatkin tests.

**Table S1.** Data sources.

**Table S2.** Moult anomalies in the dataset.

**Table S3.** Justification of moult pattern selection.