RESEARCH ARTICLE

Partial or complete? The evolution of post-juvenile moult strategies in passerine birds

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Abstract

1. Moulting strategies in birds have evolved to avoid overlap with, or prepare for, other demanding parts of the annual cycle, such as reproduction or migration. When moulting for the first time after leaving the nest, young birds replace their typically poor-quality plumage during the post-juvenile moult. The extent of this moult varies between species from partial to complete.

2. Earlier studies, restricted to Western Palearctic birds, suggest that in most species a complete post-juvenile moult may not be possible simply because young birds are constrained by not having the same access to resources as adults, unless environmental conditions are favourable. These studies also show that complete post-juvenile moult is more common in species with poor-quality nest-grown plumage.

3. We expanded the spatial and taxonomic scope of previous studies to 1,315 species of passerines from across the world and considered both the role of constraints, plumage quality and other selective pressures favouring a complete post-juvenile moult. Thus, we test whether complete moult is more prevalent in species where nest-grown feathers are presumably of poor quality (shorter nestling period), that live in environments that foster quick plumage degradation (open habitats, high insolation and humidity), and where males are under strong sexual selection.

4. Our data reveal that 24% of species carry out a complete post-juvenile moult, and that this trait has a strong phylogenetic signal. Complete moult is more common in species that inhabit warmer regions and open habitats, show no delayed plumage maturation and have higher levels of sexual dichromatism (indicative of strong sexual selection). Neither the presumed quality of the nest-grown plumage nor living in regions with high insolation correlates with complete moult.

5. In conclusion, the evolution of complete post-juvenile moult not only depends on whether birds can perform a complete moult (i.e. suitable environmental conditions) but also on the strength of selection associated with the need of a complete moult. In particular, the necessity to keep the plumage in good condition in challenging environments and the benefits associated with producing adult-like plumage colours to attract mates or deter rivals seem to play an important role.

1 | INTRODUCTION

Feathers are an essential feature of birds, fulfilling a variety of key functions, such as flight, thermoregulation, communication and camouflage. They are also extremely complex integumentary appendages composed of keratin which, when fully grown, are dead structures that deteriorate over time. This requires their regular replacement through moults. Moulting is considered an energetically expensive process that involves substantial physiological changes and often affects the performance of the plumage, hampering flight or reducing insulation (Newton, 2009). Hence, variation among species in the timing, speed, sequence and extent of moult has been shaped by natural selection (a) to coincide with periods when resource availability is high (Barta et al., 2006), (b) to avoid interference with other demanding life-history events such as reproduction and migration (Newton, 2009) and (c) to ensure that the plumage is in optimal shape for these events (Kiat, 2018). As a result, in most bird species, moult episodes follow a predictable sequence during their annual and life cycles (Barta et al., 2006).

In most passerine species, adults replace the entire plumage at least once per year, and this moult—which is referred to as prebasic or post-nuptial moult—generally takes place shortly after breeding (Howell et al., 2003; Jenni & Winkler, 1994). For young birds, the first moult after leaving the nest is the preformative or post-juvenile moult (Howell et al., 2003; Jenni & Winkler, 1994). Juvenile individuals commonly have plumage of lower quality than that of adults (Callan et al., 2019; Fogden, 1972) and to successfully face the challenges of early independent life their feathers will most likely need to be replaced (Kiat & Izhaki, 2016; Kiat & Sapir, 2018). However, this moult is also challenging because young birds are not as proficient as adults at obtaining food and evading predators (Heise & Moore, 2003; Hoy et al., 2015; Naef-Daenzer & Gruebler, 2016). It is no surprise then that in the majority of passerine birds the first moult leading into adulthood is partial. Commonly, most of the body plumage is replaced, but varying numbers of wing and tail feathers are retained. Nevertheless, a sizeable proportion of species carry out a complete post-juvenile moult (Ginn & Melville, 1983; Jenni & Winkler, 1994; Pyle, 1997), raising the question why not all species follow this strategy. To answer this question, we need to identify not only the constraints and costs that prevent a complete moult but also the factors that favour a complete post-juvenile moult, and establish how these vary across species.

One important constraint limiting the occurrence of complete post-juvenile moult is simply the time available for moulting. Accordingly, previous analyses (Kiat & Izhaki, 2016) show that complete post-juvenile moult is more prevalent among (a) smaller and medium-sized species compared to larger ones because larger species moult more slowly (Rohwer et al., 2009) and (b) resident species,

presumably because migratory species have less time to moult before departing to their wintering grounds. These time constraints should be most marked for species living in highly seasonal environments, where favourable conditions for moulting deteriorate rapidly after the summer. Furthermore, Kiat and Izhaki (2016) show that complete post-juvenile moult is more common at lower latitudes, where temperatures are higher and seasonality lower. The type of resources exploited also matter since species that feed on highly seasonal resources such as insects and other invertebrates are less likely to show complete post-juvenile moult than seed-eating species (Kiat & Izhaki, 2016). The latter presumably have a more stable food supply, especially towards the end of summer and autumn when moulting takes place (Barta et al., 2006; Faccio, 2018). These recent efforts exploring the evolution of moult strategies are largely restricted to passerines that occur in temperate regions and it remains to be shown whether environmental constraints can explain the occurrence of complete post-juvenile moult in a more diverse sample of species.

While resource availability may lead to a partial post-juvenile moult in many species (Kiat & Izhaki, 2016), species with ecological and life-history characteristics that require a highly functional post-juvenile plumage will be under stronger selection to moult the entire juvenile plumage. Because the post-juvenile moult replaces the plumage grown in the nest, species in which nest-grown feathers are of poorer quality—such as species with a short developmental time in the nest (Callan et al., 2019)—should be more likely to perform a complete moult. Indeed, previous studies showed that Western Palearctic species with a complete post-juvenile moult grew poorer-quality plumage in the nest (Kiat & Izhaki, 2016; Kiat & Sapir, 2018). In addition, a complete post-juvenile moult should be more likely in species that live in environmental conditions that foster feather degradation. Feathers degrade rapidly by being exposed to sunlight (Bergman, 1982; Test, 1940). Hence, species that are more exposed to strong sunshine, such as those that live in open environments and in regions with high levels of insolation should be more likely to have a complete post-juvenile moult. Feathers also degrade due to keratinolytic bacteria, which are more active in humid and warm conditions (Burtt & Ichida, 2004). Thus, species living in these conditions should also be more likely to evolve complete post-juvenile moult.

Furthermore, the occurrence of complete post-juvenile moult may be linked to the intensity of sexual selection. A complete post-juvenile moult eliminates the differences in feather wear and colouration between new and old feathers that characterize first-year birds in species with partial post-juvenile moult. Such subtle cues of age—when available—may be used by conspecifics to gauge the age of a rival or potential mate (Crates et al., 2015). Age is an important determinant of breeding success in many species (Cleasby & Nakagawa, 2012), with older males being preferred as mates and better at competing for

resources (Brooks & Kemp, 2001). It could thus be hypothesized that in species in which males are under strong sexual selection, juvenile birds should be more likely to have evolved complete post-juvenile moult to conceal their age and display the most elaborate colours possible during their first breeding season (Kiat et al., 2019). This effect, however, should mainly apply to species where the plumage of first-year males resembles that of older males because a complete post-juvenile moult would make no difference in species where young males clearly differ from older males, that is, in species with delayed plumage maturation (Hawkins et al., 2012). Moreover, species with delayed plumage maturation are often under stronger sexual selection (Beauchamp, 2003), and thus statistically accounting for delayed plumage maturation is essential to assess the effects of sexual selection intensity on the extent of post-juvenile moult.

Here we undertake a large-scale analysis of the evolutionary and ecological correlates of complete post-juvenile moult in passerine birds. We collated information on the extent of post-juvenile moult (partial vs. complete) for the species of passerine birds that inhabit three well-known avifaunas (Western Palearctic, Nearctic and Australasia) and we complemented this survey with information from the primary literature on species from other regions. Following the two key hypotheses that the extent of post-juvenile moult is shaped by constraints and by variation in selective pressures associated with plumage performance, we predict that complete post-juvenile moult should be more prevalent in (a) species that are less time-constrained, such as smaller species that are resident or migrate short distances; (b) species that live in environments with less seasonal fluctuation of resources such as tropical regions; (c) species that exploit less-seasonal resources (seed-based diet); (d) species with short developmental periods in the nest, that fledge with lower-quality plumage, (e) species that live where feather deterioration is more rapid, that is, in open habitats and regions with high levels of insolation or rainfall (which promote the activity of feather-degrading bacteria) and (f) species that are under strong sexual selection such that males may benefit from achieving similar colouration to adults during their first year (species with reduced delayed plumage maturation).

2 | MATERIALS AND METHODS

2.1 | Post-juvenile moult scoring and species included

We scored each species of passerine with available moult data mentioned in the three main regional handbooks where information on moult is consistently listed [Birds of the Western Palearctic, BWP (Cramp & Simmons, 1977), Birds of North America Online, BNA (Poole, 2005) and the Handbook of Australian, New Zealand and Antarctic Birds, HANZAB (Marchant & Higgins, 1990)]. We complemented and updated this dataset with information from the primary literature (see the Data sources section) and from own unpublished field data. In total, we compiled data for $N = 1,593$ taxa.

Species for which we could obtain moult data were classified into the following categories: (a) complete post-juvenile moult, species

that moult all feathers during the post-juvenile moult; (b) partial post-juvenile moult, species that moult some but not all feathers (including species classified as having incomplete, partial and limited post-juvenile moult; Johnson & Wolfe, 2017; Pyle, 1997) and (c) partial or complete post-juvenile moult, species where some individuals or populations show complete and some partial post-juvenile moult. Migratory species that initiate their post-juvenile moult in the breeding area and complete it after arriving in the wintering grounds (e.g. many Hirundinidae) were included as having a complete post-juvenile moult, following the classification provided in our sources. However, the strategy of completing the post-juvenile moult in the wintering quarters is hard to distinguish from that of species which undergo a partial post-juvenile moult, but then perform a complete nuptial (pre-breeding) moult in their wintering grounds (e.g. many *Acrocephalus* sp.). In our first classification, these species were assigned to the partial post-juvenile moult category because post-juvenile and nuptial moult were considered as separate moulting events. However, given the difficulty of separating moult events in some cases (Jenni & Winkler, 1994), and the fact that from a functional point of view all these species perform a complete moult before their first breeding season, we computed a new response variable (complete moult before first breeding: yes/no). Species were considered to have a complete moult before the first breeding season if they had either a complete post-juvenile moult or if we had evidence that they performed a complete nuptial moult. We note that the extent of nuptial moult is often not well known. Nevertheless, using this new response variable allowed us to assess whether results differed compared to the original post-juvenile moult classification. For each species, we also estimated data quality by recording whether or not the moult type assessment was based on limited data (usually reported in text by indicating that limited information was available and/or that only few specimens have been examined).

After classifying moult patterns, we matched the scientific names used in our moult data sources with the species names used by our source of phylogenetic information: www.birdtree.org (Jetz et al., 2012). After matching species names, we ended up with 94 species for which we had more than one source of information on post-juvenile moult, and the classification agreed for 81 species. In the remaining cases, we either used the more recent or comprehensive source ($N = 2$ species), or we assigned 'complete or partial' ($N = 11$ species for which one source assigned one population as having complete post-juvenile moult and another source assigned a different population as having partial post-juvenile moult). This resulted in a final sample of 1,315 species for which we had data on post-juvenile moult.

2.2 | Explanatory variables

2.2.1 | Variables based on distribution ranges

We used distribution ranges (as vectorized polygons) from Birdlife International (http://datazone.birdlife.org/) and overlapped these

with raster layers of annual mean temperature (BIOCLIM BIO 1, resolution 0.0083 decimal degrees), annual precipitation (BIOCLIM BIO12, 0.0083 decimal degrees), mean annual insolation, and the amount of solar energy received by a given surface (W/m², 0.25 decimal degrees). Annual mean temperature and annual precipitation were obtained from Karger et al. (2017) while insolation was obtained by averaging monthly estimates for the years 2006–2019 obtained from https://neo.sci.gsfc.nasa.gov/. Using the function 'exact_extract' from the R package 'EXACTEXTRACTR' (Baston, 2020), we averaged climatic and insolation values for all raster cells covered by a species' distribution. We computed climatic and insolation estimates separately for the breeding and year-round distribution ranges and for the non-breeding distribution range of migratory species. Subsequently, we averaged data for the breeding or year-round resident and non-breeding distribution to obtain overall estimates for the entire species distribution. This procedure may not be entirely accurate when quantifying the climate experienced by migratory species because they do not experience the winter in their breeding grounds. Therefore, climatic variables may be biased in migratory species, particularly in long-distance migrants. To determine whether this potential bias drives some of the climatic effects that we detect (see Section 3), we re-ran analyses excluding long-distance migrants (species with migratory distances >2,000 km; Dufour et al., 2020). Finally, we computed absolute latitude as the distance in degrees between the centroid of each species' breeding or year-round resident distribution (avoiding the non-breeding distribution) and the equator using function 'sf_centroid' from the package 'SF' (Pebesma, 2018). This information was available for 1,311 species.

2.2.2 | Other explanatory variables

(a) Body mass ($\log_{10}$-transformed, $N = 1,287$ species) was obtained mainly from Dunning et al. (Dunning, 2008) and Wilman et al. (2014) as collated by Mcqueen et al. (2019). (b) Migration distance (in km, data for $N = 1,315$ species) was obtained from Dufour et al. (2020) (variable called 'distance_quanti_ALL' in their dataset). In this dataset, migration distance was missing for 10 resident species and these were assigned migration distance of 0 (Dufour et al., 2020). (c) Diet, the percentage of the diet composed by seeds, obtained from Wilman et al. (2014, data for $N = 1,315$ species). (d) Length of the nestling period (in days, $N = 860$ species), collated from the Handbook of the Birds of the World (HBW; del Hoyo et al., 2018) and Cooney et al. (2020). (e) Habitat openness ($N = 1,311$ species). Based on the habitat use data from Birdlife International (http://datazone.birdlife.org/), we assigned each major habitat used by each species an openness score that varies from 1 (forests) to 4 (coastal and marine environments) and averaged these scores for each species. For more details on the scores assigned to each type of habitat, see Supporting Information. (f) Sexual dichromatism, as an estimator of the strength of sexual selection on males, scored based on scanned book plates from the HBW. Sexual dichromatism was computed for each species as the average difference in Red–Green–Blue (RGB)

values between males and females across nine plumage patches as described in Mcqueen et al. (2019; $N = 1,293$ species). Book plates provide good approximations of colour variation measured directly on museum specimens (Dale et al., 2015; Delhey et al., 2019). (g) Delayed plumage maturation ($N = 1,297$ species), scored on a three-level scale (0 = species where first-year males are identical or very similar to second-year adult males, 1 = species where first-year individuals are similar but on average less ornamented than second-year males, and 2 = species which have a clearly distinct first-year plumage and often take several years to reach adult plumage).

2.3 | Statistical analyses

All analyses were carried out within the R statistical environment (R Development Core Team, 2019). We used the package BTW (Griffin, 2018) to interact with the program BayesTraits V3 (http://www.evolution.rdg.ac.uk/BayesTraitsV3.0.2/BayesTraitsV3.0.2.html) from within R. We used the Multistate module in BayesTraits to estimate the rates of evolutionary shifts between the different types of post-juvenile moult using maximum likelihood across a sample of 100 phylogenies. We considered two alternative transition models: a model where gains of complete post-juvenile moult happen at a different rate than losses, and a model where both rates are set to be equal. We compared the performance of both models using a likelihood-ratio test. As BayesTraits allows polymorphic traits, species with both partial and complete post-juvenile moult were considered polymorphic. All other analyses require binary traits and hence we classified all species with partial/complete post-juvenile moult as being able to carry out a complete moult.

We quantified the phylogenetic signal of post-juvenile moult using Fritz and Purvis' D (2010) for binary traits using the function 'phylo.d' from the R package CAPER (Orme et al., 2018) computed across 100 phylogenies (see below for justification). D values close to 0 indicate a strong phylogenetic signal as expected from a Brownian motion type of evolution (equivalent to lambda = 1 for a continuous trait), while values close to 1 indicate random evolutionary patterns (essentially little phylogenetic signal, equivalent to lambda = 0 for a continuous trait; Fritz & Purvis, 2010). We also used a permutation procedure implemented in the same function (1,000 permutations) to test whether values of D are statistically different from 0 and 1. For visual purposes, we also reconstructed ancestral states for the different types of post-juvenile moult using stochastic mapping across 100 phylogenies as implemented by function 'make.simmap' in the package PHYTOOLS (Revell, 2012) using the model that allows different rates for gains and losses (the best supported model identified by BayesTraits, see Section 3).

To quantify the associations between our explanatory variables and the occurrence of complete post-juvenile moult, we used logistic phylogenetic regression (Ives & Garland, 2010) as implemented in the function 'phyloglm' from the package PHYLOLM (Tung Ho & Ané, 2014). The phylogenetic structure in the residual distribution is estimated and corrected by the parameter alpha, which reflects

the overall rate of transition between binary states. Small values of alpha (close to zero) correspond to stronger phylogenetic effects (Ives & Garland, 2010). All models were run across a sample of 100 phylogenies (see justification below) using the Ericsson backbone obtained from www.birdtree.org (Jetz et al., 2012) to account for phylogenetic uncertainty. These phylogenetic supertrees include nearly all bird species and have been obtained using available genetic data in combination with taxonomic information to randomly place species without genetic data using a birth–death polytomy resolver (Rabosky, 2015). Based on simulations, Rabosky (2015) suggested that this random placement of species may bias comparative analyses by reducing the phylogenetic signal in trait data. However, this conclusion was based on simulations with closely related groups of species, within taxonomic families, and Rabosky (2015) suggests that biases should be much less marked if the analyses are focused on taxonomically broad and sparse datasets. Given that our data include most passerine families with relatively sparse sampling within families, we expect biases to be minor. Moreover, most of the species included in our samples have been placed in the phylogeny using genetic data ($N = 1,176$ species).

In each case, results from the 100 models were summarized using Rubin's rules (Nakagawa & de Villemereuil, 2019). This approach enabled us to compute average estimates, their standard errors, associated test statistics (t values), degrees of freedom and p-values that incorporate phylogenetic uncertainty adjusting for sample sizes (Nakagawa & de Villemereuil, 2019). We also computed 'relative efficiency' which reflects, for each parameter, the efficacy of the process of accounting for phylogenetic uncertainty by comparing the used number of phylogenies with the theoretical efficacy achieved using an infinite number of phylogenies. This value varies between 0 and 1, and achieving values above 0.99 is recommended (Nakagawa & de Villemereuil, 2019). We achieved this level with 100 phylogenies for all models and parameters, adequately capturing phylogenetic uncertainty in our analyses. In some cases (see Tables S1–S14), a few models (all <10) failed to converge and were discarded, but relative efficiency values were still >0.99.

Because some of the explanatory variables had missing values, sample sizes differed between datasets. We therefore compiled two main datasets. For dataset 1 ($N = 1,266$ species), we subset the data to include the following: body mass, latitude, temperature, precipitation, insolation, habitat openness, delayed plumage maturation, sexual dichromatism and migration distance. For dataset 2 ($N = 860$ species), we included the variables mentioned above plus time nestlings spent in the nest. For each dataset, we ran models including each explanatory variable as sole predictor and one model with all variables together. However, we could not fit all covariates in the same model due to high levels of collinearity between latitude and temperature ($r = -0.83$), latitude and insolation ($r = 0.60$) and temperature and insolation ($r = 0.77$). We therefore fitted three alternative models: one with latitude, one with temperature and one with insolation. Finally, we re-ran these three multivariate models for a subset of dataset 1, eliminating species for which moult information was more limited ($N = 245$) to check whether results changed.

All explanatory variables were centred and scaled. For all models, we computed two values of R^2 using function 'R2.lik' from the package 'rr2' (Ives & Li, 2018). This function compares the likelihood of the focal model with a null model. We compared it to two different null models: (a) a simple logistic regression without covariates and without accounting for the effect of phylogeny and (b) a phylogenetic logistic regression without covariates. Thus, the first R^2 value should quantify the effects of both covariates and phylogeny (equivalent to $R^2_{conditional}$), while the second estimates the contribution of covariates independent of phylogeny (equivalent to $R^2_{marginal}$).

3 | RESULTS

We obtained information on post-juvenile moult for 1,315 species belonging to 83 of the 97 families of passerine birds. Of those, 214 species (16.3%) had complete post-juvenile moult, 105 (8.0%) had partial or complete post-juvenile moult and 996 (75.7%) had partial post-juvenile moult. The occurrence of complete post-juvenile moult was much more common in certain bird families than in others (Figure 1). The phylogenetic signal for binary traits D averaged 0.014 across 100 phylogenies (range: −0.015 to 0.046), which is indicative of a strong phylogenetic structure. Permutation tests indicated that values of D were not significantly different from 0 (Brownian motion, average $p = 0.48$, range: 0.37–0.58), but were always significantly different from 1 (random pattern, all $p < 0.001$).

The analysis of transition rates between states suggests that transitions from partial to complete post-juvenile moult occurred at a much lower rate (average: 0.0084, range: 0.007–0.01) than the reverse (average: 0.024, range: 0.019–0.03), and the model allowing different transition rates was better supported than the equal-rates model (likelihood-ratio test across all phylogenies, mean chi$^2 = 26.98$, all $p < 0.001$). This analysis also revealed that the most likely state at the root of the phylogeny was partial post-juvenile moult (probability of root being partial moult, average 0.85, range: 0.75–0.92). Similarly, stochastic mapping also suggests that the ancestral trait for passerines was partial post-juvenile moult, and that complete post-juvenile moult has been gained independently multiple times and often lost (Figure 1, e.g. Alaudidae, Hirundinidae, Furnariidae, etc.). On average, across the 100 stochastic mapping reconstructions and phylogenies, shifts from partial to complete happened 98 times and from complete to partial 88 times.

Logistic phylogenetic regressions using the most complete dataset (dataset 1, $N = 1,266$, of which 313 species are classified as having complete post-juvenile moult) revealed that complete post-juvenile moult is more prevalent in (a) species found at lower latitudes (Figure 2c,l), in warm (Figure 2d,l) and wet regions (Figure 2g,l), (b) species that inhabit open habitats (Figure 2f,l), (c) species where first-year males resemble adults in appearance (species without delayed plumage maturation, Figure 2j,l) and (d) species with higher levels of sexual dichromatism (Figure 2i,l). Full model results are provided in Tables S1–S3.
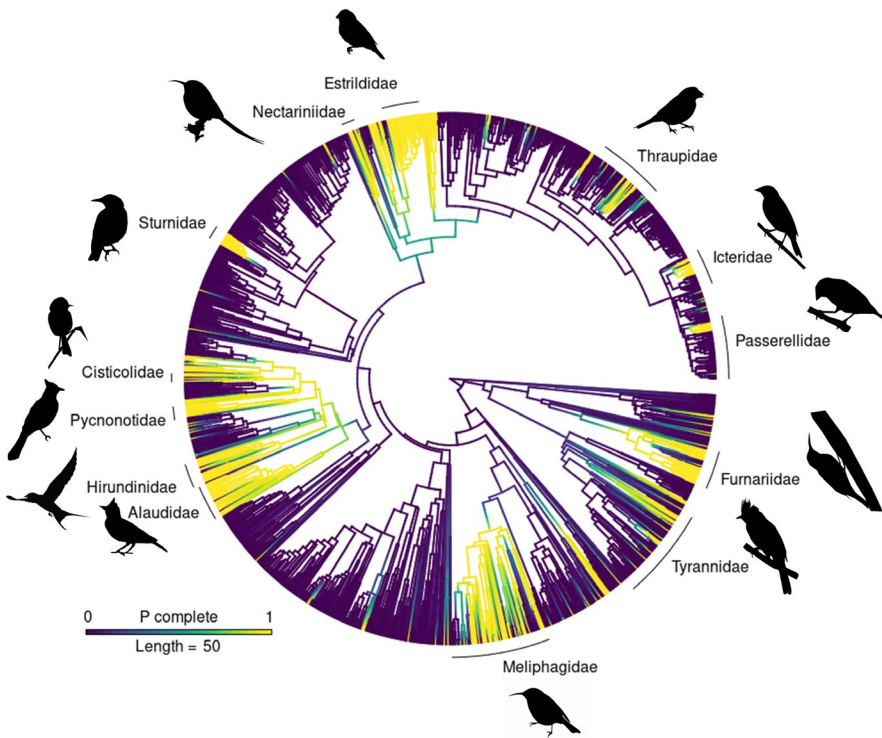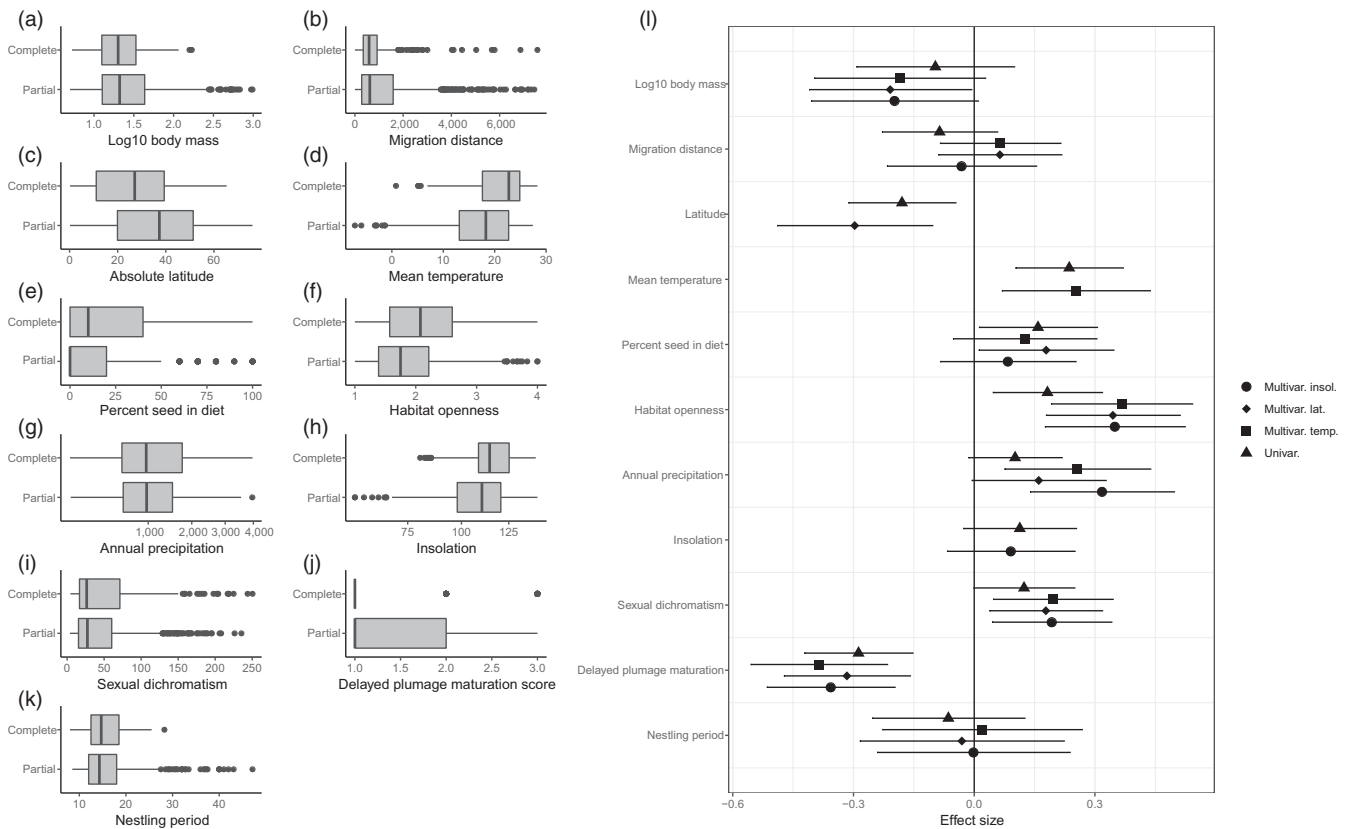
FIGURE 2 Boxplots (a–k) of raw data without phylogenetic correction showing differences between species with partial and complete post-juvenile moult, and a forest plot (l) depicting effects and 95% CIs of explanatory variables included in the phylogenetic logistic regression models. Because there were many missing values in one covariate (nestling period), we carried out the analyses on two datasets: dataset 1 (N = 1,266 species), included all covariates except for the duration of the nestling period, and dataset 2 (N = 860 species) which also included nestling period. In addition, due to collinearity, latitude, insolation and annual mean temperature could not be included in the same model and were fitted in three separate models. Full model results and output can be found in Tables S1–S7. Boxplots show median and interquartile ranges and outliers (black dots); in the forest plots 95% CIs that do not overlap 0 correspond to statistically significant effects ($p < 0.05$)

Smaller species, and species that feed on seeds were more likely to have complete post-juvenile moult, but these effects were generally not statistically significant (Figure 2l). There were no statistically significant effects of insolation or migration distance (Figure 2l). The phylogenetic signal was strong in all cases, as indicated by the small values of alpha (0.02–0.03, see Tables S1–S14). Multivariate models accounted for ~54% of the variation in post-juvenile moult type (multivariate models with latitude or temperature, $R^2_{conditional} = 0.54$), but most of this is due to shared phylogenetic history. The explanatory variables together explained 12%–14% of the variation in moult pattern. Out of the three multivariate models tested, the one with latitude had the lowest AICc value (860, Table S1), followed by the model with temperature (AICc = 864, Table S2) and the insolation model (AICc = 873, Table S3). Fitting explanatory variables as single predictor variables yielded qualitatively similar effects, but these were not always statistically significant (e.g. sexual dichromatism, Figure 2l, Table S4). Restricting the dataset to include species for which there was also information on the length of the nestling period (dataset 2, N = 860, of which 213 species with complete post-juvenile moult) revealed that species with fast-growing nestlings were not more likely to have complete post-juvenile moult (Figure 2k,l, full model results are shown in Tables S5–S7).

We assessed the robustness of our results through three additional analyses: (a) using an alternative moult classification, (b) excluding species where moult data are more limited and (c) excluding long-distance migratory species to assess whether potential inaccuracies in the computation of their climatic variables is driving climatic effects in the analyses. (a) We used an alternative classification of moult by scoring whether there is complete moult before first breeding regardless of moult type. This analysis shows similar results (Tables S8–S10), except for the migration distance effect, which becomes statistically significant, suggesting that a complete moult before the first breeding season is more likely in species with longer migration distances. (b) We eliminated species for which moult information was based on limited information (N = 1,021 species, 245 species excluded). The results were similar (Tables S11–S13), except for the sexual dichromatism effect, which became statistically non-significant. (c) We excluded long-distance migratory species to assess the effect of potential inaccuracies in the climatic variables. However, the effects of temperature and rainfall did not change (Table S14), suggesting that our conclusions are robust.

4 | DISCUSSION

Our survey across >1,300 species, which includes members of most families of passerines, revealed that nearly 25% of the species have at least some individuals or populations that carry out a complete post-juvenile moult. Ancestral trait reconstructions indicate that complete post-juvenile moult has been gained and lost multiple times and is highly phylogenetically conserved (Figure 1a). Our comparative analyses identified several ecological, environmental and life-history predictors that together account for >10%
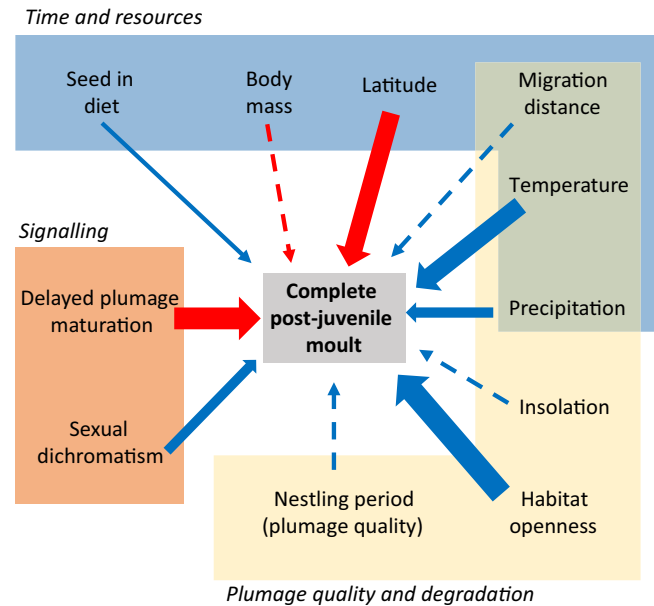

Time and resources

Signalling

Plumage quality and degradation

FIGURE 3 Summary of effects associated with complete post-juvenile moult in passerine birds. Arrow thickness represents the strength of the effect (blue positive effects and red negative effects) and dashed lines represent non-significant effects based on Figure 2l. Effects have been grouped into three broad categories: constraints imposed by available time and food resources (light blue), selective forces associated with plumage quality and degradation (light yellow) and selective forces associated with the ornamental signalling functions of plumage (orange)

of the variation in the extent of the post-juvenile moult (considered as a binary trait: partial vs. complete; Figure 2). Our results show an increased prevalence of complete moult in warm, favourable environmental conditions with low-resource seasonality, confirming earlier work (Kiat & Izhaki, 2016), and indicating the importance of constraints. However, our study also indicates the important roles of plumage degradation and visual signalling, highlighting the selective pressures that favour complete post-juvenile moult (Figure 3).

We hypothesized that lower-quality juvenile plumage and conditions that foster rapid plumage degradation should constitute strong selective factors favouring a complete post-juvenile moult. The quality of plumage in young birds varies greatly and is positively correlated with the time they spend in the nest (Callan et al., 2019). However, our data clearly show that species with shorter nestling periods are not more likely to have a complete post-juvenile moult (Figure 2), despite their presumed poorer quality plumage. This is surprising given that previous work detected clear associations between feather quality and post-juvenile moult (Kiat & Izhaki, 2016; Kiat & Sapir, 2018). By necessity, due to data availability, we used a proxy of feather quality (nestling period) rather than feather quality itself and this could have weakened our inference. Moreover, it is possible that the direction of causation is reversed, meaning that increased quality of nest-grown plumage is an evolutionary response to partial post-juvenile moult (Kiat & Sapir, 2018). Rigorous tests of these ideas, which allow general conclusions beyond Western

Palearctic species (Kiat & Izhaki, 2016; Kiat & Sapir, 2018), will require more data on feather quality.

Plumage degradation is continuous and starts already in the nest, in part through the action of feather-degrading bacteria (Azcárate-García et al., 2020), which are more active and prevalent in warm and humid environments (Burtt & Ichida, 2004). Accordingly, we found that both temperature and, to a lesser extent, precipitation correlated positively with the likelihood of complete post-juvenile moult (Figure 2). Our study thus suggests that increased risk of feather degradation may favour the evolution of complete post-juvenile moult. Feathers also degrade through exposure to sunlight (Bergman, 1982; Surmacki et al., 2011; Test, 1940), and our analyses revealed that species living in open environments, which are more exposed to sunlight, are more likely to have a complete post-juvenile moult (Figure 2k). Following this logic, we also expected that species living in regions with higher levels of solar radiation would be more likely to undergo a complete post-juvenile moult. However, this was not the case: the effect of insolation was positive but clearly not statistically significant (Figure 2). Because the effect of insolation may apply mainly to species living in open habitats, we further tested for a positive interaction between insolation and habitat openness, but the interaction was negative and not statistically significant ($t = −1.045$, $p = 0.29$). Alternatively, the association between complete post-juvenile moult and habitat openness may not only be caused by faster feather degradation in open habitats but also because birds inhabiting such environments rely more on their flying abilities to escape predators, display (Menezes & Santos, 2020) or forage, than species living in closed environments (Guallar et al., 2009). A complete post-juvenile moult would ensure a less worn plumage ready to cope with these challenges during their first year.

The lack of an insolation effect was unexpected, in particular, because insolation strongly correlated with temperature and latitude (see Section 2), two covariates that are linked to complete post-juvenile moult in previous (Kiat & Izhaki, 2016) and in our analyses (Figure 2). Latitudinal gradients in the prevalence of complete post-juvenile moult have been interpreted as evidence that warmer, tropical climates with lower seasonality impose less stringent temporal constraints on post-juvenile moult because environmental conditions do not deteriorate as rapidly as in temperate regions after the summer (Kiat & Izhaki, 2016). Our results are consistent with this interpretation, as are studies of intraspecific variation in moult extent, which reveal that individuals from populations living at lower latitudes and in warmer regions often show more extensive post-juvenile moults (Chabot et al., 2018; Christmas et al., 1989; Ginn & Melville, 1983; Jenni & Winkler, 1994; Rockey, 2016). Furthermore, Kiat et al. (2019) showed that the extent of post-juvenile increased over time in several species of passerines, most likely as a result of climate warming. Warmer or milder climatic conditions allow for earlier breeding (one of the best-documented effects of climate change; Scheffers et al., 2016), resulting in earlier fledging which leads to an earlier start of the post-juvenile moult. Both correlational and experimental data show that birds that start moulting earlier

in the year moult slower and achieve more extensive post-juvenile moults (Rymkevich & Bojarinova, 1996; Ryzhanovskiy, 2017; Serra et al., 2007).

Our results provide macro-evolutionary support for the hypothesis that time constraints constitute an important factor explaining variation in the completeness of post-juvenile moult. We also predicted that species that eat mostly seeds—a resource that should decline less rapidly in late summer than insects or fruit—should be more likely to evolve complete post-juvenile moult (Kiat & Izhaki, 2016). While the effect was in the predicted direction, it was not statistically significant in all models (Figure 2). Two other factors associated with time constraints, namely body size (large species moult slower; Rohwer et al., 2009) and migration distance (long-distant migrants are under stronger time constraints; Kiat & Izhaki, 2016; Kiat & Sapir, 2017) did not show statistically significant effects (Figure 2). While the body mass effect was in the expected direction (negative), the effect of migration distance tended to be positive in the multivariate models (Figure 2l). Thus, rather than acting as a constraint, longer migration distances tend to favour the evolution of complete post-juvenile moult. One possibility is that species that migrate farther require plumage in top condition to complete their journeys, and this should apply to flight feathers in particular. Hence, we further tested this idea by focusing on whether species moult all primaries during their post-juvenile moult (obviously, all species with complete post-juvenile moult all primaries, but 97 species with partial post-juvenile moult do so as well). Repeating the analyses in Figure 2 using complete primary moult (no/yes) as response variable revealed that the effect of migration distance was clearly not statistically significant. However, the effect of migration distance became statistically significant when we used an alternative moult classification that indicated whether or not a species carries out a complete moult before their first breeding season (either a complete post-juvenile moult or a complete nuptial moult; Tables S8–S10). We note that the main difference between the two moult classifications stems from the fact that many long-distance migratory species that carry out only a partial post-juvenile moult, perform a complete nuptial moult in their tropical wintering grounds. A complete moult in these species might be more likely because of favourable conditions (reduced constraints; Kiat & Sapir, 2018) while new plumage may be advantageous to successfully complete the spring migration (selective advantage). Thus, although the effect is not clear in all analyses, our results suggest that migration distance may play a role in shaping moult strategies during the first year.

Beyond the constraints imposed by the available resources (food and time) and the feather-degradation potential of the environment, our results also suggest that the signalling functions of the plumage may have played a role in the evolution of complete post-juvenile moult. One of the strongest predictors of complete post-juvenile moult was the occurrence of delayed plumage maturation (DPM), whereby species with DPM were less likely to have a complete post-juvenile moult (Figure 2). In species with DPM, first-cycle males differ markedly in colouration from older males,

and these young males usually have lower mating success or forego reproduction entirely, but benefit from reduced aggressive interactions with older males (Greene et al., 2000; Hawkins et al., 2012; Senar et al., 1998). If there is less pressure to look attractive in the first breeding season, replacing all juvenile feathers (often differently coloured from the adult plumage) during the post-juvenile moult may not be beneficial, and hence sexual selection on the extent of post-juvenile moult would be relaxed. In some species, a partial post-juvenile moult may also provide a flexible mechanism for individuals to signal lower status in the same way as DPM, but allowing other—presumably higher-quality individuals—to achieve a more extensive moult and more adult-like plumage, possibly at the expense of increased aggression by older males (López et al., 2005; Senar et al., 1998).

In species without DPM, on the other hand, first-year males may benefit from erasing any subtle cues of age (e.g. moult limits, the differences between old and newly moulted feathers), associated with partial post-juvenile moult. Resembling adults may be more important if the potential rewards are high, for instance, when sexual selection on males is stronger. Indeed, we found that sexual dichromatism—a proxy for the intensity of sexual selection on male birds (Dale et al., 2015; Dunn et al., 2001)—correlates positively with the likelihood of a complete post-juvenile moult (Figure 2). Because the effects of sexual selection intensity should be more marked in species without DPM, one could also predict a negative interaction between DPM and sexual dichromatism. However, our analyses do not support this idea: the interaction term was positive and not statistically significant ($t = 1.16$, $p = 0.24$). Thus, the effects of DPM and of sexual dichromatism seem largely independent of each other, although the sexual dichromatism effect is only statistically significant after accounting for the effects of DPM and other covariates (Figure 2l).

Consistent with the hypothesis that sexual selection affects moult, males moult more extensively than females in many (Bojarinova et al., 1999; Crates et al., 2015; Illera & Atienza, 2002; Jenni & Winkler, 1994; Kiat et al., 2019; Senar et al., 1998) but not all (Jenni & Winkler, 1994; Kiat et al., 2019; Pérez-Granados, 2020) species with partial post-juvenile moult. This suggests that stronger sexual selection on males may have led to sexual dimorphism in moult extent. Thus, we could envision a scenario where strong sexual selection favours more extensive post-juvenile moult, possibly because moulting more feathers signals higher quality (Gosler, 1991; Minias & Iciek, 2013; Minias et al., 2015; Pagani-Núñez & Hernández-Gómez, 2013; Vagasi et al., 2012, but see Crates et al., 2015). Within species, individuals that moult earlier in the season usually moult more slowly and more extensively (Rymkevich & Bojarinova, 1996; Ryzhanovskiy, 2017; Serra et al., 2007), which, in turn, may produce both higher-quality plumage (Dawson et al., 2000) and more colourful feathers (Ferns & Hinsley, 2008; Griggio et al., 2009; Serra et al., 2007). As a consequence, strong directional selection on ornamental plumage may result in complete post-juvenile moult in males, and also in females, either due to genetic correlation or through sexual or social selection acting directly on females (Tobias et al., 2012). Puzzlingly, the extent of post-juvenile moult increased more in females than in males in response to historical climate warming trends, at least in a few sexually dichromatic species (Kiat et al., 2019), suggesting that moult in females may be more sensitive to environmental variation. Finally, while many species develop their first-year plumage colours during the post-juvenile moult, some species do so in a different moulting event, referred to as the nuptial or pre-breeding moult. Interestingly, species that change into breeding colours by means of a nuptial moult show remarkable parallels with those that undergo a complete post-juvenile moult: nuptial moult is also more prevalent in species with more marked sexual dichromatism (Mcqueen et al., 2019).

In sum, our analyses show that a combination of multiple, fundamentally different mechanisms, explain sizeable amounts of variation (>10%) in the extent of post-juvenile moult between species (Figure 3). Our results clearly highlight that constraints faced by young birds during their first independent moult (time and food) are important, but are not the only factors that determine whether a species undergoes a complete post-juvenile moult. Variation between species in the strength of natural and sexual selection acting on functional or ornamental roles of plumage has important effects as well, and suggests that the extent of post-juvenile moult is not simply the outcome of a best-of-a-bad-job situation. In particular, we provide evidence for the surprisingly strong effects of delayed plumage maturation and sexual selection, which seem to have pervasive effects shaping the evolution of different types of moult in birds (Fig uerola & Jovani, 2002; Mcqueen et al., 2019; Peters et al., 2013).

AUTHORS' CONTRIBUTIONS

B.K. and K.D. conceived the study; K.D., S.G., R.R.-H., M.V. and D.W. collected the data; K.D. and M.V. analysed the data; K.D. and B.K. wrote the manuscript with input from all co-authors.

DATA AVAILABILITY STATEMENT

The data are available at https://doi.org/10.6084/m9.figshare.12925 895.v1 (Delhey et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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