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Evolutionary trade-off between male colouration and feather moult extent also indirectly determines female moult

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Abstract

Males and females are often influenced by different selective forces, frequently resulting in diverging phenotypes, for example in colouration. Since an animal's colouration may strongly influence its fitness, causes and consequences of sexual dichromatism in birds could aid in understanding important factors affecting sexual and natural selection. Variation in plumage ornamentation may affect mate attraction or intraspecific antagonistic behaviour. In most passerines, body plumage colouration of juveniles is obtained through the process of feather moult. The number of moulted wing and tail feathers, which also influences the bird's appearance, may affect its fitness. Here, we show that body plumage colouration of male, but not female, passerines is correlated with the number of moulted wing and tail feathers in the early stage of the bird's life for both sexes. Thus, the extent of wing and tail moult in females is not modulated by the female's colouration and can prevent females from reaching their sex-specific optima. This result could be explained by high intersexual genetic correlations, which might make it impossible for the sexes to reach their own trait fitness optima. Our findings may indicate that species-specific, rather than sex-specific, internal correlations shaped bird moult strategy, an important avian life-history trait.

KEYWORDS
feather moult, genetic correlation, life-history transitions, passerines, sexual conflict, sexual selection

1 | INTRODUCTION

Animal colour ornamentation has attracted much attention in evolutionary research due to the strong relationship between colouration and fitness (Andersson, 1994). Animal colour patterns are determined by multiple and often measurable selection forces and consequently constitute a highly suitable model system for understanding evolutionary processes using a comparative approach. Birds are a group characterized by extraordinary interspecific variation in colouration (Figure 1), and as such, they may provide important inferences for the evolution and ecology of animal ornamentation (Dale et al., 2015; Jawor & Breitwisch, 2003). Bird plumage colouration involves several pigment groups, for example, carotenoids, melanins and porphyrins. Notably, plumage colouration may bear several costs such as the higher metabolic cost of the synthesis of ornamented feathers (Hill, 2000; Siefferman & Hill, 2005) and higher predation risk due to more conspicuous plumage (Götmark, 1993; McQueen et al., 2019; Ruiz-Rodríguez et al., 2013). Although many studies discussed the factors affecting male and female plumage ornamentation (e.g. Amundsen, 2000; Badyaev & Hill, 2003; Dale et al., 2015; McQueen et al., 2019), the consequences of plumage colouration for avian moult strategies are largely overlooked (but see Delhey et al., 2020; Jenni & Winkler, 2020; McQueen et al., 2019).

The evolution of male ornaments is traditionally been explained by the sexual selection, which operates through two mechanisms: mate choice and intrasexual competition (Andersson, 1994; Darwin, 1871). Male ornaments may act as honest signals of quality that are selected by females, indicating the individual's quality (Cooney et al., 2019; Dale et al., 2015; Dunn et al., 2015; Seddon et al., 2013). Highly ornamented male plumage is thus expected to be beneficial for obtaining mating opportunities, and consequently, immature males will be under selection to replace as many juvenile feathers as possible with the more colourful adult-type male feathers in order to resemble an adult. Yet, immature colourfulness may alternatively favour a delayed plumage maturation in males, including delayed acquisition of a breeding plumage colours until after the first potential reproductive season (Hawkins et al., 2012). Indeed, many studies have found evidence that plumage colour plays an important role in various social interactions, including male–male competition (Clutton-Brock, 2007; Hoi & Griggio, 2008; Leitão et al., 2019; Senar et al., 1998; Tarof et al., 2005). The two mentioned consequences of immature male colourfulness, choice by females and competition between males and specifically asymmetrical antagonistic interactions by adult males on immature males, may occur simultaneously or sequentially within populations (Hunt et al., 2009).

Nevertheless, females of many species are highly ornamented, which is peculiar since, in most bird species, female plumage is not used for sexual attraction but rather as camouflage to reduce the risk of predation when female birds incubate and care for their young (Dale et al., 2015). Therefore, an ornamented female plumage is disadvantageous both because it attracts predators and due to the high metabolic cost of producing colourful plumage (Andersson, 1994; Dunn et al., 2015). Hence, ornamented female plumage may be a result of a correlated genetic response to selection forces affecting only the male (Kraaijeveld, 2014; Poissant et al., 2010; Potti & Canal, 2011). This situation may be a result of the shared genome preventing females from reaching optimal trait values and subsequently reducing their fitness (Pennell & Morrow, 2013). Alternatively, ornamented female plumage may be also adaptive and includes a directly socioecological benefit to females, in contrast to the indirect relationship, as a non-adaptive by-product resulting from selection on males, as described above (Diamant et al., 2021; Fitzpatrick & Servedio, 2018; LeBas, 2006; Rubenstein & Lovette, 2009). This selection may include also a female–female intrasexual competition. Hence, sexual selection may be one component of a more general form of selection resulting from all social interactions, including intrasexual competition for mating and the competition for other ecological resources (Tobias et al., 2012).

Plumage ornamentation is acquired during the moult process in which old feathers are replaced by new ones (Jenni & Winkler, 2020). Several external and internal factors may affect the ornamentation of the plumage through the moult process. For example, differences in the time available for moulting could affect the extent of moult because moulting more feathers requires more time (Kiat & Sapir, 2017). Also, limited time for moulting may induce less ornamented plumage due to the production of less colourful feathers (Griggio et al., 2009; Serra et al., 2007).

In most passerine species, juvenile nest-grown body plumage is substantially duller in colour than that of adults and is of poorer quality (Jenni & Winkler, 2020). Notably, juveniles of many passerine species change their appearance in early life stages by replacing their body plumage in a process called ‘post-juvenile moult’ or ‘preformative moult’ (Howell et al., 2003; Jenni & Winkler, 2020). Through this process, the birds gain adult-like, colourful plumage one to three months after fledging. This moult regularly includes a limited, partial or complete replacement of the wing's coverts, as well as the flight feathers of the wing and the tail, which are mostly not characterized by much colouration. Several factors were found to limit the extent of moult of the wing and tail feathers among juvenile birds, including hatching date (Bojarinova et al., 1999), migration distance (Kiat, Izhaki, et al., 2019; Pérez-Granados et al., 2020), latitude (Jenni

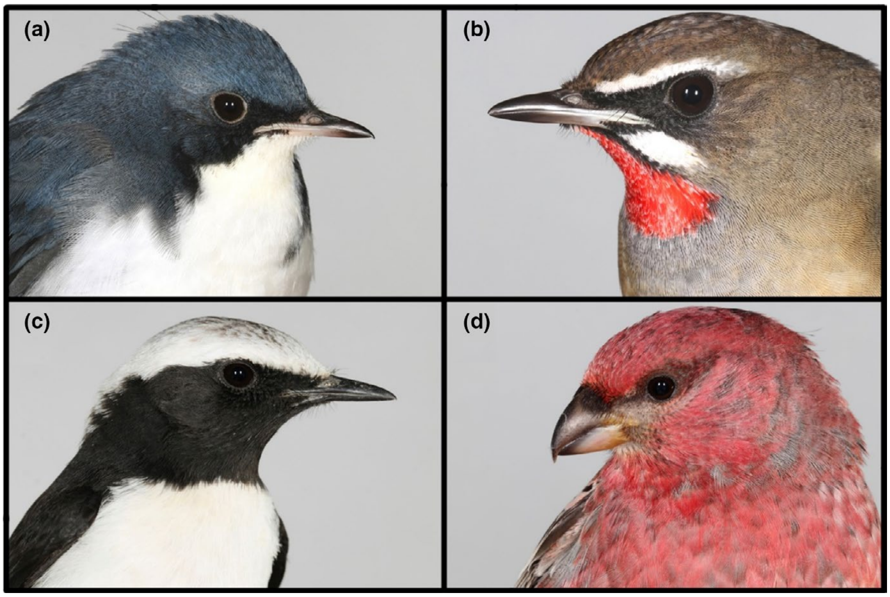

FIGURE 1 Interspecific variation in body plumage colouration among male passerines: (a) Siberian Blue Robin, *Larvivora cyane*, (b) Siberian Rubythroat, *Calliope calliope*, (c) Mourning Wheatear, Oenanthe lugens, and (d) Pine Grosbeak, *Pinicola enucleator*

& Winkler, 2020; Kiat & Sapir, 2017), longitude (Kiat et al., 2020; Ryzhanovsky, 2017), climatic conditions (Kiat, Vortman, et al., 2019), body mass (Kiat & Izhaki, 2016) and sexual dichromatism level (indicative of sexual selection level; Delhey et al., 2020).

In this study, we examined the hypothesis that body plumage colouration influenced the number of moulted wing and tail feathers (moult extent) among juvenile passerines. In species characterized by highly ornamented plumage, the extent of wing and tail feather moult in juveniles may be relatively low as a result of higher metabolic costs involved in the synthesis of a more colourful body plumage. Alternatively, in these species, moult could be more extensive in order to gain adult-like appearance before the first breeding period to increase bird attractiveness and thus mating potential and higher competitive ability. We specifically predict that post-juvenile moult will be correlated with the plumage colourfulness and will be determined mainly by the time that is available for moulting (environmental conditions; e.g. migration distance or latitude) and by the strength of the selection that is related to the need to moult extensively (Delhey et al., 2020).

2 | METHODS

2.1 | Study species and feather moult data collection

In order to examine the research hypothesis, we used data from Old-World passerine species, a clade which is characterized by low variation in the number of wing and tail feathers (e.g. Ginn & Melville, 1983) and high variation in body plumage colouration (Dale et al., 2015) and wing and tail moult extent (e.g. Jenni & Winkler, 2020). In total, our data consisted of 83 Old-World passerine species (7877 individuals) from 12 families: Laniidae (2 species), Paridae (2 species), Remizidae (1 species), Scotocercidae (1 species), Sylviidae (5 species), Sturnidae (1 species), Turdidae (7 species), Muscicapidae (36 species), Passeridae (1 species), Motacillidae (2 species), Fringillidae (20 species) and Emberizidae (5 species). For these species, we collected data on the extent of the species' post-juvenile moult, of the wing and tail feathers, in males and females. This moult is undertaken at or near the birds' breeding areas one to three months after fledging. We included species for which we were able to measure the moult extent of at least five individuals from each sex (Table S1). We used all species for which we had moult data, as well as information about the birds' sex. No species for which we had data were removed from the analysis.

Data were obtained from bird skins stored in the collections of nine natural history museums (totalling 3,316 specimens): (I) the Steinhardt Museum of Natural History, Tel-Aviv University (Tel-Aviv, Israel), (II) the Natural History Museum (Tring; UK), (III) the Museo Nacional de Ciencias Naturales (Madrid, Spain), (IV) the Museum National d'Histoire Naturelle (Paris, France), (V) the Museum für Naturkunde (Berlin, Germany), (VI) the Finnish Museum of Natural History (Helsinki, Finland), (VII) the Naturhistoriska Riksmuseet (Stockholm, Sweden), (VIII) the National History Museum of Denmark (Copenhagen, Denmark) and (IX) the Natural History Museum Vienna (Vienna, Austria). We additionally collected moult data from live birds trapped during bird ringing sessions in several sites in Israel (a total of 4561 individuals), chiefly Beit-She'an Valley (32.45°N/35.54°E) and the Jerusalem Bird Observatory (31.78°N/35.21°E).

The sex of sexually dichromatic species was determined using published plumage characteristics (most species; Del Hoyo et al., 2019), whereas the sex of two sexually monomorphic species was determined using between-sex biometric differences (Cetti's Warbler *Cettia cetti*) and using incubation patch and cloacal protuberance during breeding (Pale Sparrow *Carpospiza brachydactyla*; Svensson, 1992). We determined bird age by its plumage features according to information in the literature (e.g. Jenni & Winkler, 2020; Svensson, 1992). Overall, the nest-grown juvenile wing and tail feathers are duller, poorer in texture and have higher wear compared with feathers that were developed during the post-breeding moult of adult birds or the post-juvenile moult of first-year individuals. We used species-specific features (Jenni & Winkler, 2020; Svensson, 1992) to age each bird as either an adult or a first-/second-calendar year (post-juvenile) bird. Data were collected from all first-/second-calendar year specimens and live birds that already completed their partial post-juvenile moult, but did not start their next moult (a complete moult, undertaken in the first post-breeding period). Consequently, we do not expect that the ordinal date of the measurement of live birds or the collection of the specimens will affect the moult extent measurements. All data were collected by the first author during 2012–2020.

We quantified the extent of moult by classifying each wing and tail feathers of the individuals as being either not moulted (score 0) or moulted (score 1) in the post-juvenile moult. We included in this study only individuals whose moult had ended, confirmed by the absence of signs of moult in each feather through visual inspection. The presence of growing short-sized feathers or those characterized by having protective peripheral sheath remains indicated that the birds are undergoing active feather moult. We documented a total of 48 feathers for each examined individual, as follows: primaries ($P_{1–10}$), secondaries ($S_{1–6}$), tertials ($T_{7–9}$), primary coverts ($PC_{1–9}$), alula ($Al_{1–3}$), carpal covert (CC), greater coverts ($GC_{1–10}$) and rectrices ($R_{1–6}$). Based on the estimated proportion of the area consisting moulted feathers, we additionally measured the proportion of the feathers that have been moulted in two feather tracts: the lesser coverts (LC) and the median coverts (MC), since these tracts have numerous small and difficult to distinguish feathers. The average post-juvenile moult extent was calculated for each sex of each of the 83 study species (Table S1).

2.2 | Quantification of plumage colouration

Plumage ornamentation score data were provided by Dale et al. (2015). The method used for quantifying plumage colouration for male and female included colour measurements in three dorsal (nape, crown and forehead) and three ventral (throat, upper breast and lower breast) body patches. The plumage colouration was computed for each species based on values of the RGB colour space across the six patches as calculated by Dale et al. (2015; Table S1). This calculation is based on measurements from scanned book plates which provide good approximation of colour measured directly on museum specimens (Dale et al., 2015; Delhey et al., 2019, 2020).

2.3 | Quantification of factors that may influence the extent of wing and tail moult

We calculated the mid-breeding latitude (which we considered as the mid-moulting latitude since moulting in these species takes place at their breeding areas) and the average migration distance for each species using the distribution maps generated by BirdLife International (version 2019.1). The mid-wintering latitude and the mid-breeding latitude were calculated as the averages of the northernmost latitude and the southernmost latitude of a specie's over-wintering and breeding distribution ranges respectively. We calculated the average migration distance by calculating the distance between the mid-wintering and the mid-breeding distribution ranges. We calculated the breeding and wintering ranges latitudes at 0.5° accuracy and calculated the migration distance at 50 km accuracy. The average body mass of the study species was collected from published data with 0.5 g accuracy (Dunning, 2007; Table S1).

2.4 | Statistical analysis

We used a comparative approach to test the effects of five independent variables that may affect the extent of post-juvenile wing and tail moult (dependent variable), separately for each sex. These variables included (1) male plumage colouration score, (2) female plumage colouration score, (3) migration distance, (4) mid-moulting latitude and (5) body mass. We used average values for all variables for each species (Table S2). We also included in the analysis the moulting year as an independent variable due to possible effects of changes in climatic conditions over the years (Kiat, Vortman, et al., 2019). Since species traits could be phylogenetically related, data from species that are closely related may not be statistically independent. Consequently, we alleviated this concern by analysing the data using the independent contrasts method. This method identifies evolutionarily independent comparisons (Felsenstein, 1985). To take phylogenetic non-independence into account, we undertaken this analysis by applying phylogenetic generalized least square (PGLS) regression (Freckleton et al., 2002). We explored the extent of phylogenetic non-independence by calculating the maximum likelihood value of Pagel's λ, a scaling parameter (Pagel, 1997) using the R package 'caper' (Orme, 2013). Pagel's λ ranges between zero (no phylogenetic signal) and one (phylogenetic signal that depends on branch lengths as in the analysis of phylogenetically independent contrasts) and is a multiplier of the off-diagonal elements of the variance–covariance matrix, which provides the best fit of the Brownian motion model to the tip data. Then, we corrected for the effects of shared ancestry by the maximum likelihood value of λ. We obtained the phylogenetic tree (Figure S1) from a global analysis of bird diversity (Jetz et al., 2012, 2014) using 10,000 trees that we generated by BirdTree.org version V2.iii (Rubolini et al., 2015). We used Beast version 1.8.4 to build the consensus tree. We used the Akaike information criterion, modified for small sample sizes (AICc; Akaike, 1987) for model selection through the R package 'MuMIn' (Barton & Barton, 2019). We selected a specific model only if its ΔAICc was larger than 2.00, compared with other models. The main disadvantage of using PGLS is the elimination of the natural variance in the tested sample (individuals) using the variables averaging (for each species), as required in this analysis, and hence, we repeated the analysis using generalized linear mixed model (GLMM) using the R package 'lme4' (Bates et al., 2012; species as a random factor and other variables same as in the above PGLS). We performed our analyses (two-tailed, critical $\alpha = 0.05$) using R (version 4.1.1; R Core Team 2021).

3 | RESULTS

We measured the extent of wing and tail feathers moult in male and female birds belonging to 83 passerine species ($n = 7877$ individuals; Table S1 and Figure S1). We found a strong positive correlation between the moult extent of males and females of the same species (Spearman's correlation; $\rho = 0.97$, $p < 0.001$; Figure S2). By applying PGLS regression, we found that the best model explaining the variation in the extent of wing and tail moult among males and among females (separately for each sex) included the male body plumage colouration score (ΔAICc = 2.23 in the male moult extent model and 4.58 in the female moult extent model; Figures 2 and 3 and Table 1). More extensive wing and tail moult among both male and female passerines was evident in species whose male body plumage was less colourful. Interestingly, the effect of male plumage colouration on male and female moult was very similar (Table 1 and Figures 2 and 3). Female body plumage colouration did not affect the extent of wing and tail moult among either males or females. An additional factor affecting male moult extent was the species' breeding latitude ($p < 0.01$), whereas the extent of female moult was affected by both the species' breeding latitude ($p < 0.01$) and the year ($p < 0.01$; Figure 3 and Table S3). Similar findings were found in the GLMM analysis (Table S4).

4 | DISCUSSION

Animal colouration may affect fitness in different ways, including by influencing important behavioural, physiological and life-history properties. In this study, we examined the relationship between bird plumage colouration and the wing and tail feathers moult, a critically important process in the avian yearly cycle with implications for

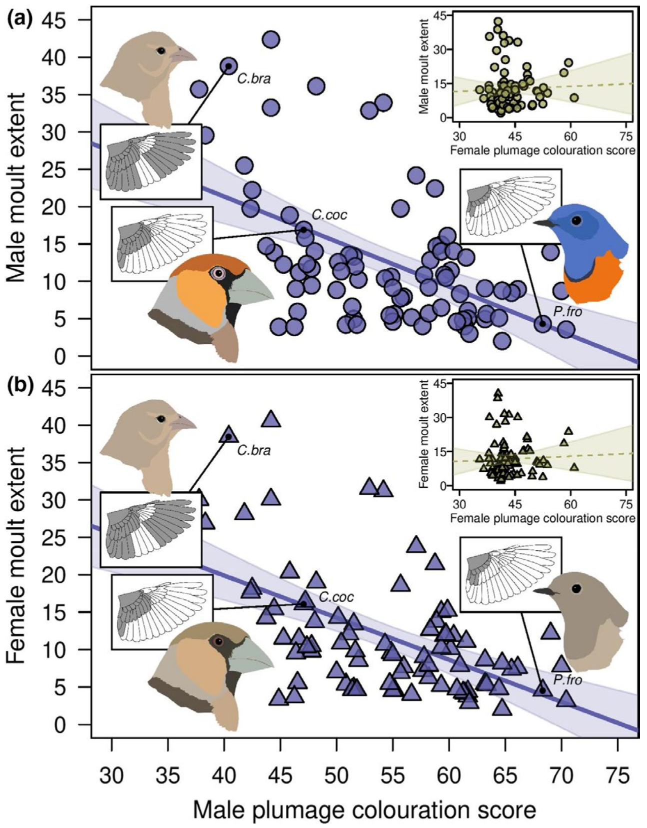

FIGURE 2 Effects of the variation in male and female body plumage colouration scores on the variation in male (a) and female (b) post-juvenile moult extent of wing and tail feathers (±95% confidence intervals). The results indicate an effect of male body plumage colouration on wing and tail moult extent of both males ($t = -2.19$, $p = 0.032$) and females ($t = -2.62$, $p = 0.011$), but no effect of female body plumage colouration ($p > 0.05$). The rectangular insets depict examples of male (a) and female (b) wing moult extents. The wing areas that are shaded grey depict the wing's moulted feathers, whereas non-coloured areas represent non-moulted feathers. An example is shown for three different species: Pale Rockfinch, *Carpospiza brachydactyla* (*C. bra*), Hawfinch, *Coccothraustes coccothraustes* (*C. coc*), and Blue-fronted Redstart, *Phoenicurus frontalis* (*P. fro*)

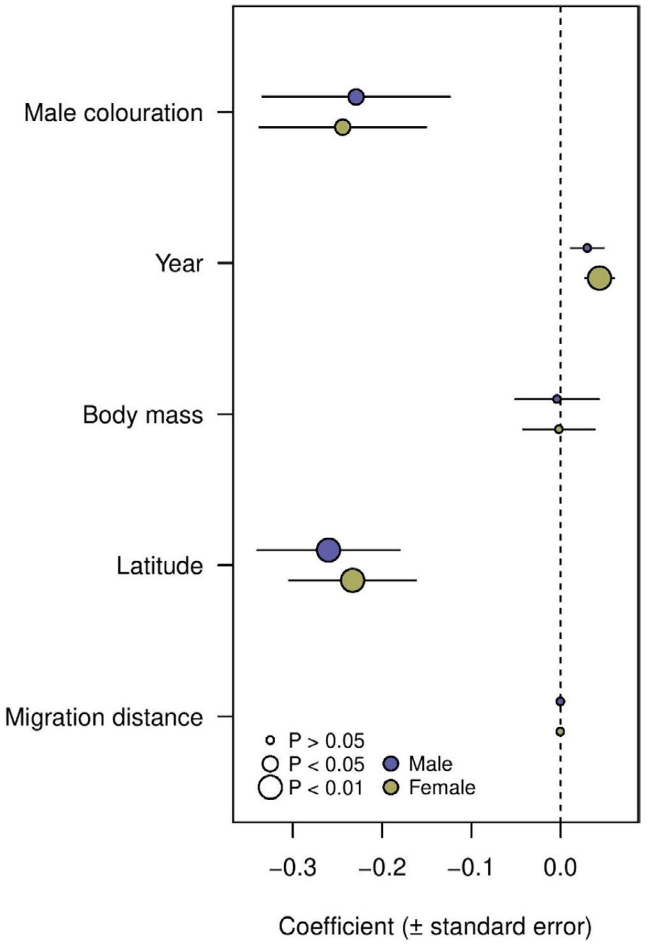

FIGURE 3 Model coefficients (± standard error) of each of the five tested independent variables and their significance levels for males and females. The results suggest that male body plumage colouration and latitude predict the extent of wing and tail feathers moult for both sexes. The year is another predictor for female moult extent (see Table S3 for the complete statistical models)

bird behaviour and flight performance (Jenni & Winkler, 2020; Senar et al., 1998; Serra et al., 2007). We found that more colourful male body plumage, but not female body plumage, is negatively related to the number of moulted wing and tail feathers in juveniles and that this relationship was similar in males and females. Therefore, male plumage colourfulness can be regarded as a selection factor that reduces the extent of wing and tail feathers moult in passerines, suggesting that extensive feather moult either induces costs that are elevated in colourful birds or provides more benefits for less ornamented species. For example, this could be the case if in a colourful species the main signalling of quality is made through the colourfulness of the body plumage whereas in a less ornamented species the main signalling of quality is done through the wing and tail feathers (e.g. to the wing coverts, as demonstrated by Senar et al., 1998). Future research may consequently benefit from assessing the signalling potential of the wing and tail feathers in addition to that of the body plumage which is discussed in this study. This can be done for understanding how individual quality is determined during sexual selection and hence also whereas males compete for females.

4.1 | The influence of male plumage colouration on male feather moult

Our results may indicate a cost involving the renewal of ornamented feathers. This cost may be a direct metabolic cost of the synthesis of more colourful body plumage (Hill, 2000; Serra et al., 2007; Siefferman & Hill, 2005) or an indirect cost related to high aggression inflicted by other males on colourful juvenile male birds (Senar et al., 1998). A higher metabolic cost for the synthesis of colourful feathers likely requires the acquisition of more resources (Hill, 2000; Siefferman & Hill, 2005). Hence, we suggest a trade-off between the allocation of resources to body plumage and wing and tail feathers

TABLE 1 Effects of migration distance, breeding latitude, body mass, year, and male and female plumage colouration scores on the variation in male and female post-juvenile moult extent of wing and tail feathers: list of statistical models (PGLS), statistics and Akaike information criterion (AICc; see the full models in Table S3)

						Male plumage coloration score	Female plumage coloration score			
Model	λ	r^2	*F*	**df**	**logLik**	**Coefficient**	**Coefficient**	**AICc**	**ΔAICc**	**Akaike weight**
Male post-juvenile moult extent										
~ migration distance +latitude + body mass +year + male plumage coloration score	0.85	0.29	6.32	6	−266.82	−2.29e−01 ± 1.05e−01	–	546.78	0.00	0.69
~ migration distance +latitude + body mass +year	0.90	0.24	6.00	5	−269.10	–	–	549.01	2.23	0.23
~ migration distance +latitude + body mass +year + female plumage coloration score	0.91	0.24	4.77	6	−270.00	–	−6.00e−02 ± 1.35e−01	551.13	4.35	0.08
Null Model	0.95	0.00	–	1	−279.93	–	–	561.94	15.16	0.00
Female post-juvenile moult extent										
~ migration distance +latitude + body mass +year + male plumage coloration score	0.79	0.36	8.61	6	−256.62	−2.44e−01 ± 9.33e−02	–	526.31	0.00	0.88
~ migration distance +latitude + body mass +year	0.84	0.30	8.18	5	−260.07	–	–	530.89	4.58	0.09
~ migration distance +latitude + body mass +year + female plumage coloration score	0.85	0.30	6.52	6	−259.90	–	−7.08e−02 ± 1.23e−01	532.87	6.56	0.03
Null Model	0.91	0.00	–	1	−274.27	–	–	550.56	24.25	0.00

during the moult process: Given the limited capabilities of juveniles to acquire resources (Marchetti & Price, 1989), and given that the juveniles of most study species are characterized by at least an extensive replacement of body plumage (post-juvenile moult), the outcome could be a smaller number of wing and tail feathers that are produced during the moulting period. Additionally, in case of partial wing and tail moult and given that synthesis of more colourful body plumage is more energetically expensive, a smaller number of wing and tail feathers can be renewed in the time window during which the bird is able to replace its feathers. According to this explanation, the time needed for moulting each ornamented feather is higher than for non-ornamented feather, resulting in an overall smaller number of replaced wing and tail feathers during the moulting period (Figure 4, Option I). Alternatively, highly ornamented males may bear a cost that includes aggression from competing adults, for example during territorial disputes, foraging and mate acquisition (Senar et al., 1998). According to this explanation, the reduced extent of wing and tail moult among highly ornamented juveniles is the result of fitness costs through involvement in antagonistic interactions with conspecifics during the first year of the bird's life (Figure 4, Option II).

4.2 | The influence of male plumage colouration on female feather moult

In addition to the relationship between male post-juvenile moult extent and body plumage colouration, we found a similar correlation between male plumage ornamentation and the extent of female wing and tail moult, resulting in consistent between-sex moult extent in each species (Figure S2). Notably, the females' wing and tail moult extent was correlated with the colourfulness of males body plumage and not with their own body plumage colourfulness (Figure 2b). We propose that this correlated effect may indicate a correlated response of males and females to factors that shape the extent of their wing and tail moult at the genomic levels (Figure 4). Such sexually correlated phenotypes were documented for several morphological and chromatic traits among animals (Kraaijeveld, 2014; Poissant et al., 2010), for example, the long outermost tail feathers in many swallow species (Cuervo et al., 1996), female canine tooth size in primates (Plavcan, 1998) and body size (Tigreros & Lewis, 2011). We consequently propose that our findings point to evolution of phenotypic monomorphism for this specific trait (the extent of moult of wing and tail feathers).

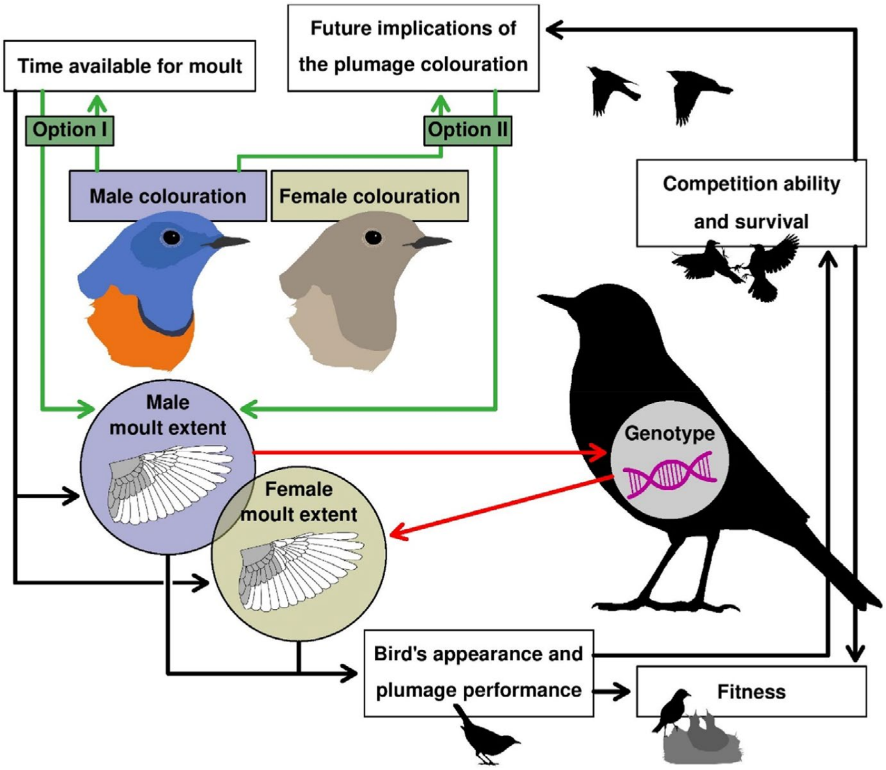

FIGURE 4 Proposed framework explaining the correlation between male body plumage colouration and moult extent of wing and tail feathers through costs involved in plumage synthesis or future implications of the plumage colouration, and female moult extent through intersexual genetic correlations. We portray the presumed relationships among components and influencing factors that affect each other with arrows indicating the direction of impact. The link between male body plumage colouration and post-juvenile moult extent of wing and tail feathers may be explained by two mechanisms: (1) The cost related to the higher metabolic cost of ornamented feather synthesis which in turn may limit the number of wing and tail feathers renewed in the time available for moult (green arrows; option I), and (2) by future implications of plumage colouration, mainly an intraspecific competition, that could strongly reduce the fitness of juvenile males that moulted wing and tail extensively, but likely mostly among species with relatively highly ornamented plumage (green arrows; option II). In addition, female moult extent was also affected by male plumage colouration, likely through a genetic link which is may prevent females from reaching their optimal wing and tail moult extent (red arrows)

Importantly, the correlated evolution of males and females likely interferes with optimal adaptation of females which are being selected through selection on male traits (Pennell & Morrow, 2013). This may complicate our understanding of the adaptive significance and evolution of colourfulness and sexual dimorphism. In addition, since sex-specific selection on a given trait in one sex will compromise the adaptive evolution of the same trait in the other sex, loosening the genetic bound between males and females may permit sexual dimorphism and could allow both sexes to approach their distinct adaptive peaks (Arnqvist & Tuda, 2010; Bonduriansky & Rowe, 2005; Innocenti & Morrow, 2010). Therefore, our study exemplifies the importance of animal colouration in shaping, including limiting, the evolution of sex-specific life-history traits.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

YK and NS conceived the ideas and designed methodology; YK collected and analysed the data and led the writing of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/jeb.13977.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available as Supplementary files.

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