



Factors influencing the evolution of moult in the non-breeding season: insights from the family Motacillidae

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The number of moults per annual cycle and their final spatial pattern (i.e. topography) show high interspecific variation in the order Passeriformes. Factors behind this variability remain obscure, especially for variability in spatial pattern among species. Here, we explored the relative influence of ten ecological, ontogenetic, social and sexual factors on the evolution of autumn moult (feather replacement largely undertaken by migratory species, which is not necessarily an independent episode within their moult cycle) and prealternate moult among Northern Hemisphere species of the family Motacillidae using phylogenetically controlled analyses, ancestral state reconstruction and analyses of correlated evolution. The results strongly support the presence of prealternate moult and absence of autumn moult as ancestral states in this family. A high rate of change between related species indicates phylogenetic independence among prealternate moult patterns and examined factors. Migration distance and gregariousness are the most important factors influencing prealternate moult evolution, and point toward natural selection and sociality as the most important evolutionary drivers of prealternate moult in Motacillidae. Breeding latitude, seasonal plumage change, winter plumage conspicuousness, sexual dichromatism, plumage maturation and extent of preformative moult show a minor influence, and suggest that ontogeny and sexual selection may have played a limited role in shaping prealternate moult in Motacillidae. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 774–785.

KEYWORDS: autumn moult – gregariousness – moult strategies – moult topography – pipits – prealternate moult – wagtails.

INTRODUCTION

Moult is the process that allows the maintenance and adjustment of plumage functionality throughout the annual cycle (Jenni & Winkler, 1994). A high amount of variability in moult strategy within and among species (Svensson, 1992; Pyle, 1997a, b) is achieved through many elements that integrate a species' moult strategy (Barta *et al.*, 2006): topography (the spatial configuration of the replaced feathers after a moult; Guallar *et al.*, 2014), energetic requirements, feather quality, number and timing of moults per cycle, intensity, duration and order of replacement. Moult strategies may affect survival and fitness (Holmgren & Hedenström, 1995), and have probably evolved in response to shifts in natu-

ral history and environmental parameters (Rohwer *et al.*, 2009; Pap *et al.*, 2015).

Until now, most studies have emphasized the evolution of the preformative and definitive prebasic moults (equated to the postjuvenile and postnuptial moults, respectively; terminology follows Howell *et al.*, 2003), while other moults have received less attention. The presence of a single moult within the annual cycle, the prebasic moult, is the ancestral state in passerines, and the addition of the prealternate moult (equivalent to the prenuptial moult) is considered an autapomorphy with multiple independent evolutionary origins (Figueroa & Jovani, 2001; Howell *et al.*, 2003). The prealternate moult is largely undertaken by migratory species before departing their wintering grounds. However, the existence of other moult episodes is controversial. In particular, the replacement of feathers upon arrival at the winter grounds – usually in early autumn – is rarely

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acknowledged as an independent episode (Howell *et al.*, 2003; Newton, 2008: 305–306). Autumn feather replacement of migratory passerines has been routinely reported in their winter grounds (Shirihai, Helbig & Gargallo, 2001; Alström & Mild, 2003; Guallar *et al.*, 2009), but it usually involves only body feathers, suggesting the end of a previous ‘true’ moult episode, suspended or not (birds may migrate while still replacing part of their body plumage, even the juvenal one, which may affect aerodynamics; Butler, Donahue & Rohwer, 2002). Some migratory species are known to suspend their prebasic/preformative moult until they finish migration (e.g. Alström & Mild, 2003), although some clearly have an autumn moult episode (e.g. *Passerina* buntings and Bell’s Vireo *Vireo bellii*; Guallar *et al.*, 2009). Regardless, autumn moulting may constitute an individual- or species-level strategy to cope with tight complex annual cycles (Wingfield, 2008). Besides taking place outside the breeding grounds, prealternate and autumn moults neither overlap in time nor interact directly with reproduction. For these reasons, we categorize them as ‘non-breeding moults’. Migration is a strong selective factor that influences the evolution of non-breeding moult strategies (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001), but other factors may also affect the timing and duration of moult. For example, depletion of food resources and presence of predators may affect the schedule of primary moult (Voelker & Rohwer, 1998; Rohwer, Butler & Froehlich, 2005; Ydenberg, Butler & Lank, 2007), and moult duration is related to wing size (Bridge *et al.*, 2007; Rohwer *et al.*, 2009).

Evolution of moult may have not only been affected by natural selection, but also by sexual selection (Simpson & Campbell, 2013). Birds use different plumage characteristics for mate choice (Zahavi, 1997), and the emergence of the prealternate moult in a species annual cycle could have been targeted by sexual selection to produce a brighter plumage during the mating season (Figuerola & Jovani, 2001; Peters, 2007). The extent of the preformative moult may also serve as an indicator of health status (Senar, Copete & Martin, 1998; López *et al.*, 2005).

For these reasons, natural and sexual selection appear to be drivers of moult evolution. Here, we use phylogenetically controlled comparative analyses to evaluate the relative influence of different ecological, social and sexual factors on the evolution of non-breeding moult among species of the family Motacillidae, which has a well-documented and highly diverse natural history (Cramp, 1988; Alström & Mild, 2003). We focused on the 25 of the 31 species of this family breeding in the Northern Hemisphere with published descriptions of non-breeding moult.

We test six hypotheses on the potential factors mentioned above. First, migratory behaviour may have favoured the evolution of non-breeding moults. If this is the case we can expect more extensive non-breeding moults as migratory distance increases. This hypothesis has already received support from previous studies analysing the number, seasonality and extent of moult in some European passerines (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001) although it has not been tested for the autumn moult. One mechanism proposed to explain this effect is a reduction in feather quality induced by time constraints (de la Hera, Pérez-Tris & Tellería, 2009) arising from ever tighter moult schedules, so that birds have less time available to grow high-quality feathers (Hall & Fransson, 2000; Dawson, 2004). Species under strong time constraints before departing the breeding grounds tend to present more moult episodes and more extensive ones than those that do not face time constraints (Holmgren & Hedenström, 1995). Exposure to increased solar radiation in winter grounds as migration distance increases is also thought to explain this effect (Bergman, 1982; Figuerola & Jovani, 2001).

Latitude may have influenced the evolution of non-breeding moult episodes as well. This second hypothesis suggests that time for moult is constrained by climatic conditions at northern latitudes (Dawson, 2008). According to this hypothesis, species breeding at higher latitudes may experience increasing time constraints and may grow lower quality feathers (Hall & Fransson, 2000; Kiat & Izhaki, 2016) which they would tend to renew as soon as possible after departing the breeding grounds. Consequently, autumn moult will be more frequent and also will tend to be more extensive in these species. Extreme time constraints before migration would tend to cause very reduced prebasic or preformative moults (Barta *et al.*, 2006). However, sexual selection would not exert pressure on this moult in Motacillidae, as autumn moult in species of this family does not involve changes in coloration, and autumn plumage is overridden by the prealternate moult before the onset of the breeding season.

The third hypothesis states that the prealternate moult may have evolved to allow plumage coloration changes. Seasonal changes can be achieved through wear (e.g. in Common Reed Bunting *Emberiza schoeniclus*; Cramp & Perrins, 1994) and photo-oxidation (e.g. in Common Linnet *Carduelis cannabina*; Blanco *et al.*, 2005), but most species achieve them through moult. The prealternate moult may become more extensive to allow larger plumage changes. The same effect could be found in conspicuous species to allow the acquisition of brighter alternate plumages. Note that seasonal changes in plumage coloration

are not necessarily associated with sexual dichromatism (e.g. Water Pipit *Anthus spinoletta*).

The fourth hypothesis posits that the evolution of prealternate moults may have been driven by sexual selection. Molt is an energetically costly process (Murphy, 1996), and as such may honestly signal physical condition; therefore, individuals with more extensive prealternate moult may have an advantage as potential breeding mates. Sexual selection also predicts more extensive prealternate moult as sexual dichromatism becomes greater: species with sexual marks restricted to an area of the body – such as the eyebrow of Blue-gray Gnatcatcher *Poliptila caerulea* (Guallar *et al.*, 2009) – would tend to replace fewer feathers than species with overall dichromatic plumage such as Summer Tanager *Piranga rubra* (Pyle, 1997a, b). Here, we test the second prediction of this hypothesis: the influence of dichromatism on moult evolution.

The fifth hypothesis posits that social selection may have influenced the evolution of non-breeding moults through the acquisition of new functions such as status signalling. Gregarious species display badges of status (Tibbets & Safran, 2009; Chaine *et al.*, 2013) and their signal phenotype probably expresses other aspects of their social environment (Dey, Dale & Quinn, 2014), which can be mediated through non-breeding moults. This hypothesis predicts more extensive non-breeding moults in more gregarious species (probably associated with higher social complexity).

Finally, the sixth hypothesis posits that ontogenetic factors may have contributed to shaping non-breeding moults. Plumage maturation is delayed in first-cycle individuals of many species until the prealternate moult (Rohwer, Fretwell & Niles, 1980; Hill, 1996). This delay may have selected for a more extensive first prealternate moult in order to acquire an alternate plumage as similar to the definitive alternate plumage as possible. Partial preformative moults could have influenced non-breeding moult evolution, as plumage gaps should be filled and formative feathers of potentially lower quality (Butler, Rohwer & Speidel, 2008; Echeverry-Galvis & Hau, 2013) are replaced as soon as possible.

MATERIAL AND METHODS

DATASET AND PHYLOGENETIC RELATIONSHIPS

We obtained information on moult strategies, plumage characteristics, gregariousness, habitat occurrence and latitudinal distribution of Motacillidae of the Northern Hemisphere from Alström & Mild (2003; see Supporting information, Table S1, Data S1). When intraspecific variation in the variable of

interest exists, we discarded infrequent values and calculated the arithmetic mean of the remaining ones. We completed gaps on gregariousness using information from Étchecopar & Hüe (1983) and Ali & Ripley (1993).

We visually scored dichromatism, conspicuousness and seasonal plumage change for each species using illustrations in Alström & Mild (2003). To reduce subjectivity, we averaged the scores of three observers for each of these variables.

We included body mass as a surrogate of size (data from Dunning, 2007). Because no information on body mass of the recently described Mekong Wagtail *Motacilla samveasnae* is available, we took it as the mean of White Wagtail *Motacilla alba* and African Pied Wagtail *Motacilla aguimp*, due to the similarity to these two species (see Diagnosis in Duckworth *et al.*, 2001).

Species range maps were downloaded from BirdLife International and NatureServe (2014). Migration distance was computed as the kilometres between the centroid of the wintering range and the centroid of the breeding range using QGIS (QGIS Development Team, 2015). Centroids were weighted by the area of polygons. Latitudinal distances between the breeding and wintering centroids were calculated using Geographic Distance Matrix Generator (Ersts, 2015).

We created four categories of mass and breeding latitude from the computation of three quartiles on our dataset (Supporting information, Table S1). Likewise, we created three categories of migration distance by computing two quartiles for migratory species and added a fourth category for non-migrant species. The purpose of using the same scale for all covariates was to allow direct comparisons among the model estimates.

For our working phylogeny we downloaded 10 000 trees for our set of species from birdtree.org (Jetz *et al.*, 2012), and then derived a consensus tree, assigned all internode branches equal to 1 and forced tips to be contemporaneous (Pagel, 1992). We used Slate-throated Redstart *Myioborus miniatus* as the outgroup (data from Guallar *et al.*, 2009).

To check sensitivity to phylogeny, we replicated all our analyses using published phylogenetic trees for this family (Voelker, 1999; Alström & Ödeen, 2002). As results only show minor differences, we included our replicates in the Supporting Information (Figs S4, S5, Table S5).

INFLUENCE OF NATURAL HISTORY FACTORS

To control for the phylogenetic relationship among the sampled species we used phylogenetic generalized least squares regression (PGLS; Pagel, 1997,

1999) models as implemented in the R statistical environment (The R Foundation for Statistical Computing, 2015) and the libraries *ape*, *geiger* and *nlme*. The PGLS approach controls for non-independence among species by incorporating a matrix of the covariances based on their phylogenetic relationships (Martins & Hansen, 1997; Pagel, 1997, 1999).

We estimated the phylogenetic signal (λ) using the unpublished function *pglm3.3.r* (R. Freckleton, University of Sheffield). The phylogenetic signal represents the importance of phylogenetic correlation within the data (Freckleton, Harvey & Pagel, 2002) and varies between 0 and 1. We then tested the statistical significance of λ against theoretical values of 0 and 1 using likelihood ratio tests. Finally, λ was incorporated in the correlation structure of the PGLS models to control for the effect of phylogenetic relationship (Harvey & Pagel, 1991; Martins & Hansen, 1997).

We first explored the relative importance of nine covariates on the prealternate and the autumn moults in two sets of PGLS models: migratory strategy, mean breeding latitude, seasonal plumage coloration change (only in prealternate models as autumn moult are not associated with changes in plumage coloration), male basic plumage conspicuousness, sexual dichromatism in alternate plumage, gregariousness in the non-breeding season, non-breeding moult pattern (autumn on models with prealternate moult as response and vice versa), habitat and body mass (Supporting information, Table S1). Each set of models contains all combinations among the covariates (2048 models for the prealternate moult as response, and 512 models for the autumn moult as response).

We also investigated the possible influence of ontogeny on prealternate and autumn moults by including two age-specific covariates, plumage maturation and preformative moult, in two new sets of models. Again, each of these two sets of PGLS models contains all possible combinations among the covariates.

We ranked the models according to their Akaike information criterion corrected for small sample size (AICc) values, and calculated the relative importance of each covariate based on its Akaike weight using the zero method implemented in package *MuMIn*. In the zero method (Burnham & Anderson, 2002), all covariates absent from models are substituted by zeros, and estimates are obtained by averaging over all models in the top model set (Grueber *et al.*, 2011). This method is recommended in studies aiming at determining which factors have the strongest effect on the response variable (Nakagawa & Freckleton, 2011). As we standardized our covariates, we assessed their relative magnitude and direction

directly. Each estimated coefficient in the average model equates to effect size of its corresponding covariate (Grueber *et al.*, 2011). We expressed parameter uncertainty by means of the estimated standard error (Burnham & Anderson, 2002), and model uncertainty as the percentage of models used to create the 95% confidence sets of models (McAlpine *et al.*, 2008).

We compared migration distance and breeding latitude among species with or without non-breeding moults, using phylogenetic ANOVA (Garland *et al.*, 1993) using the *phytools* package.

ANCESTRAL STATE RECONSTRUCTION AND CORRELATED EVOLUTION

We first tested for differences in transition rates between states using default settings in *BayesTraits* (Pagel, 1999; Pagel, Meade & Barker, 2004). The significant differences between transition rates were incorporated in subsequent analyses. Next, we checked whether the evolution of non-breeding moult was directional. Model selection was based on Bayes factors (BFs) (Kass & Raftery, 1995).

We reconstructed the ancestral state of non-breeding moults in our replicate phylogeny (Supporting information, Fig. S1) calculating state likelihoods at each node to determine final maximum likelihood of the ancestral state (Schluter *et al.*, 1997). We dealt with the polytomy by averaging the values of the involved species (all absences for the autumn moult, two presences and two absences for the prealternate moult).

Reliable statistical inference could not be drawn for the autumn moult because of the low number of species that present it ($N = 7$). Nevertheless, we show the output of correlated evolution and relative importance analyses for this moult in the Supporting Information (Data S1).

RESULTS

Phenology of non-breeding moults in Motacillidae of the Northern Hemisphere is synthesized in Figure 1. Only four species (16%) do not show non-breeding moults, all of which are non-migratory except the Japanese Wagtail *Motacilla grandis* (a short-distance migrant). The remaining species undergo either prealternate moult or autumn plus prealternate moults (only seven species show autumn moult, 28%). There were no species that underwent only autumn moult. Alström & Mild (2003) state that in species with two non-breeding moults the same feathers are replaced in both episodes.

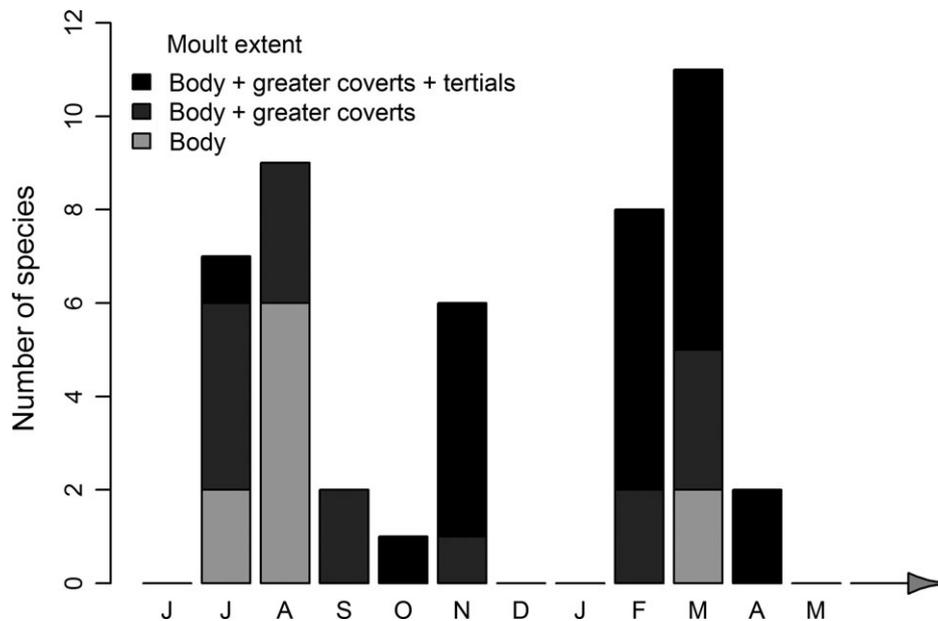


Figure 1. Annual moult cycle of Northern Hemisphere Motacillidae (prebasic moult is not shown). Preformative moult shows the widest range of moult extent values. Autumn moult takes place immediately after migration from the breeding grounds and prealternate moult before migration to the breeding grounds. It is important to bear in mind that autumn moulting could actually be the completion of suspended or protracted prebasic/preformative moults in some cases. Moult extent values were rounded to the nearest integer. Each species' moult was assigned to the second month of the period recorded by Alström & Mild (2003) because this probably coincides with moult peak (highest overlap of individuals and highest moult intensity). Prealternate moult phenology of paddyfield pipit *Anthus rufulus* and Mekong wagtail have not been documented yet and are not included here. The key refers to categories defined in Supporting Information (Table S1).

RELATIVE IMPORTANCE OF NATURAL HISTORY FACTORS

Migration distance, gregariousness and seasonal change are the most important factors influencing prealternate moult, with maturation ranking fourth in first-cycle birds (although the latter two factors with much lower relative importance values; Fig. 2). However, only migration reached statistical significance in the averaged model. Breeding latitude, sexual dichromatism, plumage conspicuousness and preformative moult had little influence. Coefficients of the covariates had the expected signs: positive for all the previously mentioned covariates except preformative moult, conspicuousness, dichromatism and habitat (Table 1). Model and parameter uncertainty are moderately high (Fig. 2, Table 1).

The phylogenetic signal $\lambda < 0.001$ for all models was significantly different from 1 (loglik > 8.43 , $P < 0.004$) but not from 0 (loglik < -0.001 , $P = 1$), which implies phylogenetic independence due to a very high rate of change between related species.

Species with autumn moult (mean \pm SE migration distance 3158.58 ± 2064.08 km, $N = 7$) and species without it (2856.23 ± 2463.72 km, $N = 18$) did not show significant differences ($F_{1,24} = 0.08$, $P = 0.88$).

We did not find significant differences between the number of migratory and non-migratory species with autumn moult (chi square test $\chi^2 = 0.30$, $P = 0.58$). Species with prealternate moult (mean \pm SE migration distance = 3426.78 ± 2195.46 km, $N = 21$) undertook significantly longer migrations than species without it (389.96 ± 799.92 km, $N = 4$; $F_{1,24} = 7.26$, $P = 0.007$).

Species with autumn moult (mean \pm SE breeding latitude = $35.55 \pm 21.05^\circ$, $N = 7$) bred farther south than species without it ($43.63 \pm 19.88^\circ$, $N = 18$). Again, differences were not significant ($F_{1,24} = 0.81$, $P = 0.60$).

Migration distance did not influence the occurrence of non-breeding moults, and no differences in migratory distance were found between species with prealternate moult (3560.87 ± 2321.85 km, $N = 14$) and species with both prealternate and autumn moult (3158.58 ± 2064.08 km, $N = 7$; $F_{1,24} = 1.84$, $P = 0.21$).

ANCESTRAL STATE RECONSTRUCTION AND CORRELATED EVOLUTION

Evolutionary gains of prealternate moult were more frequent than losses (log BF = 7.88) and transitions

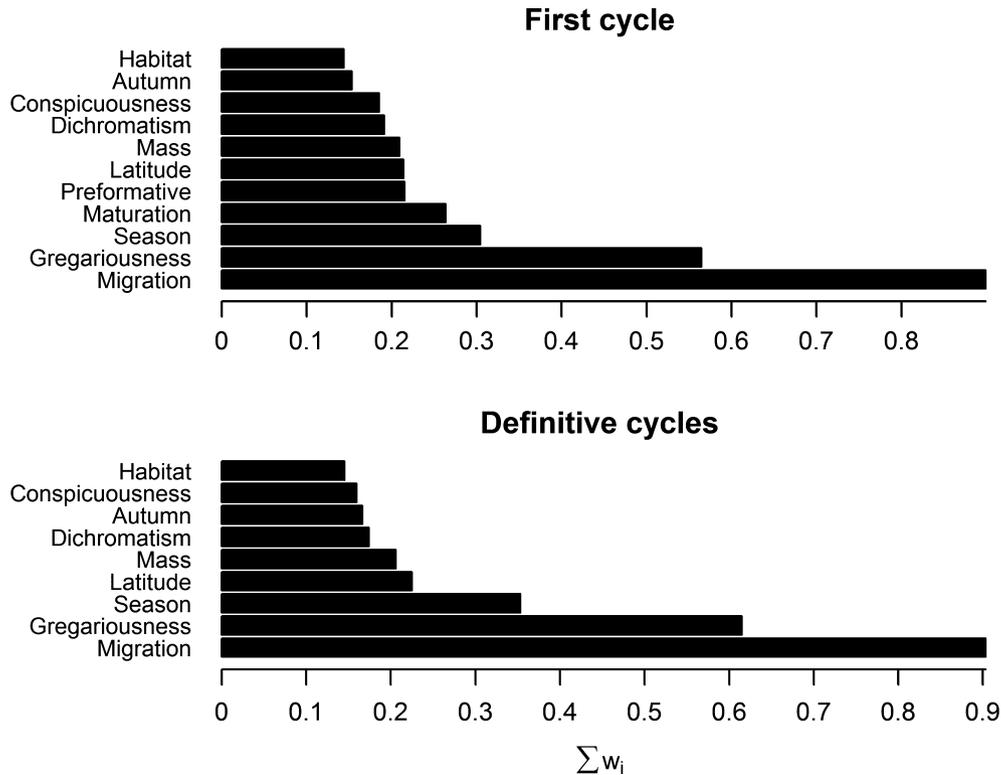


Figure 2. Relative importance of covariates used for prealternate moult models based on the subset whose accumulated Akaike weights reached 95% of the total averaged models: 529 and 154 for first and definitive cycles, respectively, which corresponds to 25.8 and 30.1% model uncertainty. The scale indicates the sum of Akaike weights.

towards autumn moult were also more frequent than losses (log BF = 2.54).

We found no support for directionality in the evolution of non-breeding moults (log BF = 0.45 for prealternate moult; log BF = 1.12 for autumn moult).

Our reconstruction of non-breeding moult strongly supports the presence of prealternate moult as an ancestral state (likelihood = 0.96) of Motacillidae breeding in the Northern Hemisphere but not autumn moult (likelihood = 0.82) (Fig. 3).

The four wagtails included in the polytomy plus the clade encompassing the seven species from Long-billed Pipit *Anthus similis* to Upland Pipit *Anthus sylvanus* contain all non-migratory species that breed in more southern latitudes (Fig. 3). Unexpectedly, the latter clade contains 71% (five) of all species with autumn moult (Fig. 3).

We found very strong support for the correlated evolution of the prealternate moult and the two most important covariates that influence it: migration and gregariousness (Table 2). Species without autumn moult have a plumage throughout the winter that is acquired in either the prebasic or the preformative moult. As the prebasic moult is always complete in this family, variation in the extent of the preformative

moult might be influenced by some of these natural history factors. As 16 of the 18 species which did not present autumn moult showed winter gregariousness, we also checked the correlation between preformative moult and winter gregariousness and found a strong association (log BF = 2.65), which suggests an influence of sociality on the evolution of this moult episode.

We found a direct relationship between migration distance and breeding latitude in Motacillidae [in accordance with Outlaw & Voelker (2006) but contrasting with the results obtained from a broad taxonomic group by Figuerola & Jovani (2001); Supporting information, Fig. S7). We also found a positive but weak correlation between breeding latitude and extent of prealternate moult (log BF = 1.93). This could be an additive effect which would enhance the effect of migration distance, especially in species without autumn moult.

DISCUSSION

To examine evolutionary pressures that underlie non-breeding moult strategies, we tested multiple

Table 1. Results of PGLS analyses of ten natural history covariates on prealternate moult

	Autumn	Conspicuousness	Dichromatism	Gregariousness	Habitat	Latitude	Mass	Maturation	Migration	Preformative	Season
First cycle	0.01 (0.07)	-0.04 (0.19)	-0.05 (0.21)	0.25 (0.29)	-0.01 (0.08)	0.04 (0.20)	0.03 (0.10)	0.08 (0.21)	0.59 (0.30)	-0.05 (0.15)	0.09 (0.20)
Definitive cycles	0.01 (0.07)	-0.02 (0.13)	-0.03 (0.17)	0.28 (0.29)	-0.01 (0.08)	0.05 (0.20)	0.03 (0.10)		0.61 (0.30)		0.11 (0.21)

Coefficients (adjusted standard error) with shrinkage are based on the subset of total averaged models whose accumulated Akaike weights reached 95%. Significance is indicated by bold type. Only migration distance and gregariousness had noticeable effect sizes.

hypotheses for the evolution of non-breeding moult using broad-scale natural history information of the Motacillidae breeding in the Northern Hemisphere.

In agreement with previous studies (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001), we found that migration distance is the most important factor influencing non-breeding moults. Species that undertake longer migrations are also likely to be exposed to more intense solar radiation in the wintering grounds, a factor that may increase plumage deterioration (Lennox & Rowlands, 1969; Surmacki, Sieffermann & Yuan, 2011; but see Willoughby, 1991). While the evolution of prealternate moult is highly correlated with migration distance, the occurrence of non-breeding moults was not related to migration distance.

The relationship between non-breeding moults and breeding latitude does not support the hypothesis predicting more extensive autumn moult as species breed at higher latitudes, suggesting phylogenetic inertia.

Seasonal plumage change is an important life-history trait in the annual cycle of many bird species, including Motacillidae, as it involves behavioural changes (Ruff *Philomachus pugnax* and Rock Ptarmigan *Lagopus mutus* are extreme cases; Hogan-Warburg, 1966; Montgomerie, Lyon & Holder, 2001) and physiological changes (Brush, 1990) with fitness consequences mediated by variation in predation rates (Montgomerie *et al.*, 2001) and mating success (Andersson, 1994). Seasonal change was the third most important factor but was weakly correlated to prealternate moult. This low influence on the evolution of prealternate moult is probably due to the limited seasonal plumage changes that species of this family undergo (only four of 25 species presented changes that were scored as moderate). Seasonal plumage changes may take place to a greater extent in males than in females (e.g. they are very conspicuous in the migratory species of the genus *Piranga* in the family Cardinalidae). As few sex-specific differences in moulting strategies are mentioned in the literature (Pyle 2007), it is thus not surprising that seasonal change was only weakly correlated with prealternate moult extent. It again points to the occurrence and extent of prealternate moults being driven by the need to replace feathers due to loss of functionality, at least partially. Any increase in colour change in males based on sexual selection would then have occurred after the moult had evolved in both sexes due to other factors.

In agreement with Figuerola & Jovani (2001), sexual dichromatism showed a small influence on prealternate moult. Sexual dichromatism is associated with losses of female ornamentation in other passerine families (Friedman *et al.*, 2009; Simpson,

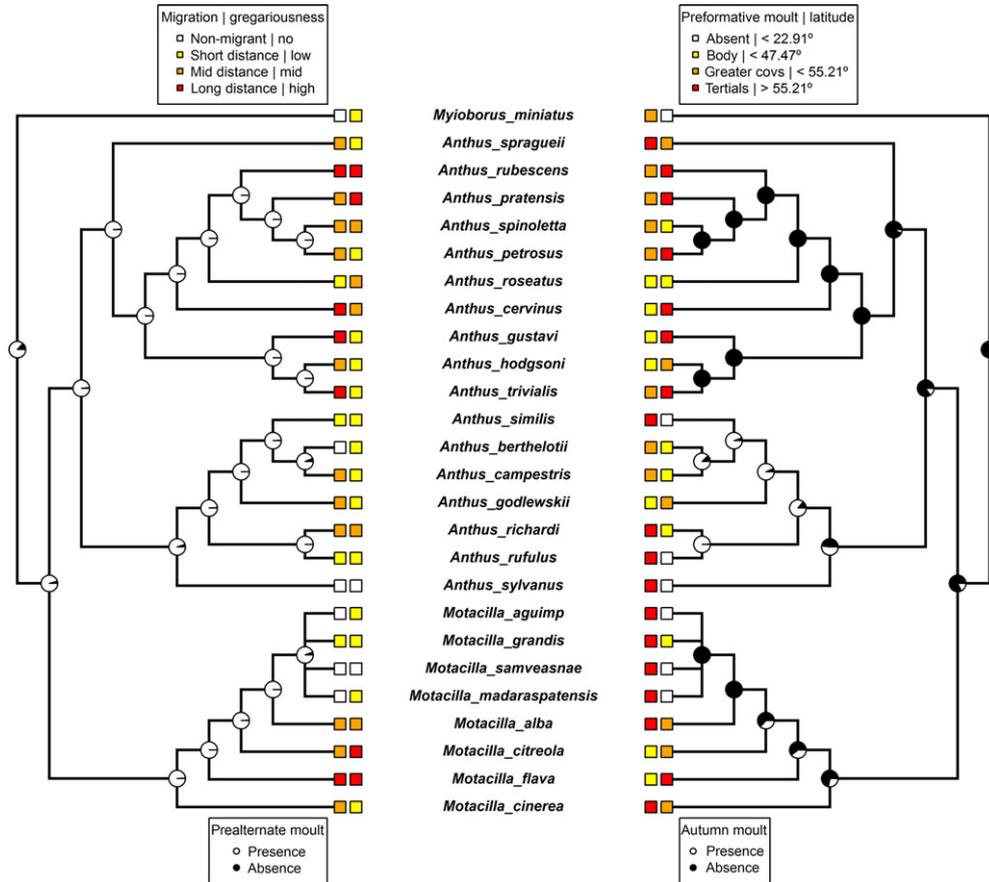


Figure 3. Phylogenetic reconstruction of non-breeding moults. Pie charts on internal nodes depict likelihood of presence/absence for prealternate moult on the left tree, and for autumn moult on the right tree. The four tip nodes depict, from left to right: migration distance, gregariousness, preformative wing-moult extent (categorization in Supporting Information, Table S1) and breeding latitude.

Table 2. Evidence of correlated evolution between prealternate moult and influential covariates

	log BF	Evidence
Conspicuousness	-0.96	Weak against
Dichromatism	2.80	Positive
Gregariousness	10.29	Very strong
Breeding latitude	1.93	Weak
Habitat	1.17	Weak
Mass	0.70	Weak
Maturation	1.29	Weak
Migration distance	10.88	Very strong
Preformative moult	1.97	Weak
Seasonal change	1.08	Weak

Johnson & Murphy, 2015), so that prealternate moult is not necessarily linked to an increase in sexual dichromatism. Thus, sexual selection seems to

have played a limited role in the evolution of prealternate moult in Motacillidae.

Sociality had a remarkable influence on the evolution of prealternate moult as shown by its very strong correlation with gregariousness and by the fact that this covariate is the second most important one explaining variation of prealternate moult. Gregariousness characterizes the winter social behaviour of many species of Motacillidae but, contrary to predictions from our hypothesis, of nine species that showed mid to high gregariousness only Yellow Wagtail *Motacilla flava* and Citrine Wagtail *Motacilla citreola* presented autumn moult. Given this, why might gregariousness exert its influence at the end of the winter period? February to April, the peak of prealternate moult in our study species (Fig. 1), coincides with depletion of food resources in many regions (Lack, 1966; Karr, 1976; Sherry, Johnson & Strong, 2005), which can influence prealternate moult (Danner *et al.*, 2015). In this context, prealternate moult (and partic-

ularly extent and feather quality) could constitute an honest signal of physical condition. Premigratory roosts (López *et al.*, 2005) also take place at the end of this period, in which signal of a higher status could be advantageous for example to claim the safest places in the roost (Beauchamp, 1999).

As expected, higher scores of delayed plumage maturation were associated with more extensive prealternate moults, and prealternate moult extent decreased with extent of preformative moult. The prealternate moult was weakly correlated with these two factors, which were the fourth and fifth most influential ones in first-cycle birds. Altogether, these ontogenetic factors do not seem to have played an important role in the evolution of prealternate moult, although preformative moult may have had a stronger influence on autumn moult (see Supporting Information, Data S1).

We have studied the effect of multiple natural history factors on the evolution of non-breeding moults in the family Motacillidae. Lack of information for many species reduces the scope of our conclusions but we can still provide insight into the fact that non-breeding moult may have evolved under different selective forces in different taxonomic groups. We found that migration distance is the most influential force in Motacillidae, although gregariousness has also been an important driver of moult evolution. However, we still lack detailed information on other essential factors that may have played an even more important role in the evolution of non-breeding moult strategies in Motacillidae, such as feather quality and variation of feather coloration throughout the year. Differences in feather quality among species and even within individual feathers (especially in nestlings) are important drivers of the extent of the preformative moult of passerines (Weber *et al.*, 2005; Kiat & Izhaki, 2016).

There was a remarkable versatility in the evolution of moult strategies as suggested by the lack of phylogenetic inertia. This capacity for rapid change highlights their adaptive character, which introduces a great deal of flexibility in the moult strategies of passerines, and also has contributed to diversification of their natural histories by taking up new functions such as social signalling under selective pressures conditioned by changes in the state of other traits. For example, the gain of a prealternate moult might subsequently be targeted by sexual selection to originate sexual dichromatism. Phylogenetic analyses may help to elucidate the selective forces at work, but the genetic basis of moult evolution remains virtually unexplored. Future research should investigate which genes are involved and how differences in gene regulation relate to different moult strategies in birds.

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REFERENCES

- Ali S, Ripley D. 1993. *Handbook of the birds of India and Pakistan, Vol. 9, 2nd edn*. Oxford: Oxford University Press.
- Alström P, Mild K. 2003. *Pipits and wagtails of Europe, Asia and North America. Identification and systematics*. London: Christopher Helm.
- Alström P, Ödeen A. 2002. Incongruence between mitochondrial DNA, nuclear DNA and molecular data in the avian genus *Motacilla*: implications for estimates of species phylogenies. Unpublished DPhil Thesis, Uppsala University.
- Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.
- Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TP, Feró O. 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* 112: 580–593.
- Beauchamp G. 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behavioral Ecology* 10: 675–687.
- Bergman G. 1982. Why are the wings of *Larus f. fuscus* so dark? *Ornis Fennica* 59: 77–83.
- BirdLife International and NatureServe. 2014. *Bird species distribution maps of the world*. Cambridge and Arlington, VA: NatureServe and BirdLife International.
- Blanco G, Frias O, Garrido-Fernández J, Hornero-Méndez D. 2005. Environmental-induced acquisition of nuptial plumage expression: a role of denaturation of feather carotenoproteins? *Proceedings of the Royal Society of London Series B, Biological Sciences* 272: 1893–1900.
- Bridge ES, Voelker G, Thompson CW, Jones AW, Baker AJ. 2007. Effects of size and migratory behavior on the evolution of wing molt in terns (Sternae): a phylogenetic-comparative study. *Auk* 124: 841–856.
- Brush AH. 1990. Metabolism of carotenoid pigments in birds. *FASEB Journal* 4: 2969–2977.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn*. New York: Springer.
- Butler LK, Donahue MG, Rohwer S. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): age effects, aerodynamics, and conservation implications. *Auk* 119: 1010–1023.
- Butler LK, Rohwer S, Speidel MG. 2008. Quantifying structural variation in contour feathers to address func-

- tional variation and life history trade-offs. *Journal of Avian Biology* **39**: 629–639.
- Chaine AS, Roth AM, Shizuka D, Lyon BE. 2013.** Experimental confirmation that avian plumage traits function as multiple status signals in winter contests. *Animal Behaviour* **86**: 409–415.
- Cramp S, ed. 1988.** *The birds of the Western Palearctic, Vol. 5: tyrant flycatchers to thrushes*. Oxford: Oxford University Press.
- Cramp S, Perrins CM, eds. 1994.** *The birds of the Western Palearctic, Vol. 9: buntings and New World warblers*. Oxford: Oxford University Press.
- Danner RM, Greenberg RS, Danner JE, Walters JR. 2015.** Winter food limits timing of pre-alternate moult in a short-distance migratory bird. *Functional Ecology* **29**: 259–267.
- Dawson A. 2004.** The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starling *Sturnus vulgaris*. *Ibis* **146**: 493–500.
- Dawson A. 2008.** Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* **363**: 1621–1633.
- Dey CJ, Dale J, Quinn JS. 2014.** Manipulating the appearance of a badge of status causes changes in true badge expression. *Proceedings of the Royal Society of London Series B, Biological Sciences* **281**: 20132680.
- Duckworth JW, Alstrom P, Davidson P, Evans TD, Poole CM, Setha T, Timmins RJ. 2001.** A new species of wagtail from the lower Mekong basin. *Bulletin of the British Ornithologists' Club* **121**: 152–182.
- Dunning JB. 2007.** *CRC handbook of avian body masses, 2nd edn*. Boca Raton, FL: CRC Press.
- Echeverry-Galvis MA, Hau M. 2013.** Flight performance and feather quality: paying the price of overlapping moult and breeding in a tropical highland bird. *PLoS ONE* **8**: e61106. doi:10.1371/journal.pone.0061106.
- Ersts PJ. 2015.** *Geographic Distance Matrix Generator (v. 1.2.3)*. American Museum of Natural History, Center for Biodiversity and Conservation. Available at: http://biodiversityinformatics.amnh.org/open_source/gdmg
- Étchecopar RD, Hùe F. 1983.** *Les oiseaux de Chine. Passerelles*. Paris: Boubée.
- Figuerola J, Jovani R. 2001.** Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evolutionary Ecology* **15**: 183–192.
- Freckleton RP, Harvey PH, Pagel M. 2002.** Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160**: 712–726.
- Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009.** Correlated evolution of migration and sexual dichromatism in the New World orioles (*Icterus*). *Evolution* **63**: 3269–3274.
- Garland T, Dickerman AW, Janis CM, Jones JA. 1993.** Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**: 265–292.
- Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. 2011.** Multimodel inference in ecology and evolution challenges and solutions. *Journal of Evolutionary Biology* **24**: 699–711.
- Guallar S, Santana E, Contreras S, Verdugo H, Gallés A. 2009.** *Paseriformes del Occidente de México: morfometría, datación y sexado*. Barcelona: Museu de Ciències Naturals de Barcelona.
- Guallar S, Ruiz-Sánchez A, Rueda-Hernández R, Pyle P. 2014.** Molt topography and its application to the study of partial wing-moult in two Neotropical wrens. *Ibis* **156**: 311–320.
- Hall KSS, Fransson T. 2000.** Lesser-whitethroats under time constraint moult more rapidly and grow shorter wing feathers. *Journal of Avian Biology* **31**: 583–587.
- Harvey PH, Pagel MD. 1991.** *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- de la Hera I, Pérez-Tris J, Tellería JL. 2009.** Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. *Biological Journal of the Linnean Society* **97**: 98–105.
- Hill GE. 1996.** Subadult plumage in the house finch and tests of models for the evolution of delayed plumage maturation. *Auk* **113**: 858–874.
- Hogan-Warburg AJ. 1966.** Social behavior of the ruff (*Philomachus pugnax*). *Ardea* **54**: 108–229.
- Holmgren N, Hedenström A. 1995.** The scheduling of molt in migratory birds. *Evolutionary Ecology* **9**: 354–368.
- Howell SNG, Corben C, Pyle P, Rogers DI. 2003.** The first basic problem: a review of molt and plumage homologies. *Condor* **105**: 635–653.
- Jenni L, Winkler R. 1994.** *Molt and ageing of European passerines*. London: Academic Press.
- Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012.** The global diversity of birds in space and time. *Nature* **491**: 444–448.
- Karr JR. 1976.** Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist* **110**: 973–994.
- Kass RE, Raftery AE. 1995.** Bayes factors. *Journal of the American Statistical Association* **90**: 773–795.
- Kiat Y, Izhaki I. 2016.** Why renew fresh feathers? Advantages and conditions for the evolution of complete post-juvenile moult. *Journal of Avian Biology* **47**: 47–56.
- Lack D. 1966.** *Population studies of birds*. Oxford: Oxford University Press.
- Lennox FG, Rowlands RJ. 1969.** Photochemical degradation of keratins. *Photochemistry and Photobiology* **9**: 359–367.
- López G, Figuerola J, Varo N, Soriguer R. 2005.** White Wagtails *Motacilla alba* showing extensive post-juvenile moult are more stressed. *Ardea* **93**: 237–244.
- Martins EP, Hansen TF. 1997.** Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149**: 646–667.
- McAlpine CA, Rhodes JR, Bowen ME, Lunney D, Callaghan JG, Mitchell DL, Possingham HP. 2008.** Can multiscale models of species' distribution be generalized

- from region to region? A case study of the koala. *Journal of Applied Ecology* **45**: 558–567.
- Montgomerie R, Lyon B, Holder K. 2001.** Dirty ptarmigan: behavioral modification of conspicuous male plumage. *Behavioral Ecology* **12**: 429–438.
- Murphy ME. 1996.** Energetics and nutrition of moult. In: Carey C, ed. *Avian energetics and nutritional ecology*. New York: Chapman Hall, 158–198.
- Nakagawa S, Freckleton RP. 2011.** Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioural Ecology and Sociobiology* **65**: 103–116.
- Newton I. 2008.** *The migration ecology of birds*. London: Academic Press.
- Outlaw DC, Voelker G. 2006.** Phylogenetic tests of hypotheses for the evolution of avian migration, a case study using the Motacillidae. *Auk* **123**: 455–466.
- Pagel M. 1992.** A method for the analysis of comparative data. *Journal of Theoretical Biology* **156**: 431–442.
- Pagel M. 1997.** Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26**: 331–348.
- Pagel M. 1999.** Inferring the historical patterns of biological evolution. *Nature* **401**: 877–884.
- Pagel M, Meade A, Barker D. 2004.** Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* **53**: 673–684.
- Pap PL, Osváth G, Sándor K, Vincze O, Bãrbos L, Marton A, Nudds RL, Vágási CI. 2015.** Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat. *Functional Ecology* **29**: 746–757.
- Peters A. 2007.** Testosterone treatment of female Superb Fairy-wrens *Malurus cyaneus* induces a male-like pre-nuptial moult, but no coloured plumage. *Ibis* **149**: 121–127.
- Pyle P. 1997a.** *Identification guide to North American birds. Part I*. Bolinas, CA: Slate Creek Press.
- Pyle P. 1997b.** Molt limits in North American passerines. *North American Bird Bander* **22**: 49–89.
- Pyle P. 2007.** Revision of molt and plumage terminology in ptarmigan (Pashianidae: Lagopus spp.) based on evolutionary considerations. *Auk* **124**: 508–514.
- QGIS Development Team. 2015.** *QGIS 2.8.2 Wien*. Available at: <http://qgis.org/es/site/>
- Rohwer S, Fretwell SD, Niles DM. 1980.** Delayed maturation in Passerine plumages and the deceptive acquisition of resources. *American Naturalist* **115**: 400–437.
- Rohwer S, Butler LK, Froehlich D. 2005.** Ecology and demography of east–west differences in molt scheduling in Neotropical migrant passerines. In: Greenberg R, Marra PP, eds. *Birds of two worlds: the ecology and evolution of temperate-tropical migration*. Baltimore, MD: John Hopkins University Press, 87–105.
- Rohwer S, Ricklefs RE, Rohwer VG, Coppole MM. 2009.** Allometry of the duration of flight feather molt in birds. *PLoS Biology* **7**: e1000132.
- Schluter D, Price T, Mooers AØ, Ludwig D. 1997.** Likelihood of ancestor states in adaptive radiation. *Evolution* **51**: 1699–1711.
- Senar JC, Copete JL, Martin AJ. 1998.** Behavioural correlates of variation in the extent of postjuvenile molt in the Siskin *Carduelis spinus*. *Ibis* **140**: 661–669.
- Sherry TW, Johnson MD, Strong AM. 2005.** Does winter food limit populations of migratory birds? In: Greenberg R, Marra PP, eds. *Birds of two worlds: the ecology and evolution of temperate-tropical migration*. Baltimore, MD: John Hopkins University Press, 414–425.
- Shirihai H, Helbig A, Gargallo G. 2001.** *Sylvia warblers*. London: Christopher Helm.
- Simpson JA, Campbell L. 2013.** *The Oxford handbook of close relationships*. Oxford: Oxford University Press.
- Simpson RK, Johnson MA, Murphy TG. 2015.** Migration and the evolution of sexual dichromatism: evolutionary loss of female coloration with migration among wood-warblers. *Proceedings of the Royal Society of London Series B, Biological Sciences* **282**: 20150375.
- Surmacki A, Sieffermann L, Yuan H-W. 2011.** Effects of sunlight exposure on carotenoid-based and structural coloration of the Blue-tailed Bee-eater. *Condor* **113**: 590–596.
- Svensson L. 1992.** *Identification guide to European passerines, 4th edn*. Stockholm: L. Svensson.
- Svensson E, Hedenström A. 1999.** A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *Biological Journal of the Linnean Society* **67**: 263–276.
- The R Foundation for Statistical Computing. 2015. *Version 3.2.0 (2015-04-16)*. Vienna: The R Foundation for Statistical Computing.
- Tibbets EA, Safran RJ. 2009.** Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows. *Journal of Evolutionary Biology* **22**: 2376–2386.
- Voelker G. 1999.** Molecular evolutionary relationships in the avian genus *Anthus* (pipits: Motacillidae). *Molecular Phylogenetics and Evolution* **11**: 84–94.
- Voelker G, Rohwer S. 1998.** Contrasts in the scheduling of molt and migration in eastern and western Warbling-Vireos. *Auk* **115**: 142–155.
- Weber TP, Borgudd J, Hedenström A, Persson K, Sandberg R. 2005.** Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biology Letters* **1**: 27–30.
- Willoughby EJ. 1991.** Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. *Proceedings of the Western Foundation of Vertebrate Zoology* **4**: 247–286.
- Wingfield JC. 2008.** Organization of vertebrate annual cycles: implications for control mechanisms. *Philosophical Transactions of the Royal Society of London B* **363**: 425–441.
- Ydenberg RC, Butler RW, Lank DB. 2007.** Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. *Journal of Avian Biology* **38**: 523–529.
- Zahavi A. 1997.** *The handicap principle: a missing piece of Darwin's puzzle*. Oxford: Oxford University Press.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figure S1. Consensus trees.

Figure S2. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reached 95% of the total averaged models.

Figure S3. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reached 95% of the total averaged models.

Figure S4. Relative importance of the explanatory variables for the autumn moult based on the subset whose accumulated Akaike weights reach 95% of the total averaged models: 231 and 87 for first and definitive cycles, respectively, which corresponds to 22.6 and 34.0% model uncertainty.

Figure S5. Relative importance of the explanatory variables for the prealternate moult based on the subset whose accumulated Akaike weights reach 95% of the total averaged models: 529 and 154 for first and definitive cycles, respectively, which corresponds to 25.8 and 30.1% model uncertainty.

Figure S6. Scatterplot of migration distance versus breeding latitude.

Figure S7. Phylogenetic reconstruction of non-breeding moult episodes.

Table S1. Categorization of natural history information used in analyses.

Table S2. Results of the PGLS of ten natural history covariates on autumn moult.

Table S3. Evidence of correlated evolution between autumn moult and influential covariates.

Table S4. Results of the PGLS of 11 natural history covariates on autumn moult.

Table S5. Results of the PGLS of 11 natural history covariates on non-breeding moults.

Table S6. Categories of Bayes factors used as model selection criterion in analyses of correlated evolution.

Data S1. Values of 13 covariates for 25 species of the family Motacillidae used in analyses. In a separate spreadsheet raw scores of Conspicuousness, Dichromatism and Seasonal change given by three observers.