



Research article

Ecological correlates in the evolution of moult strategies in Western Palearctic passerines

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Abstract. Moult is an important process in the life cycle of birds. Passerines differ widely in the number, seasonality and extension of moult episodes, but the incidence of birds ecology on this variation remains largely uninvestigated. We analysed the patterns of moult in European passerines in relation to their distribution, migration and sexual dichromatism. Longer migrations and southern wintering quarters were characteristic of species with complete moults in summer and an additional moult in winter. The main moult in species with larger seasonal changes in sexual dimorphism tended to be scheduled just before the start of the breeding season, suggesting a link between sexual selection and the timing of moult. These patterns strongly support the importance of migration and dichromatism on the evolution of moult strategies.

Key words: comparative analyses, migration, moult patterns, sexual dichromatism, sexual dimorphism

Introduction

Moult is considered a very expensive activity, finely timed in the life cycle of birds to avoid overlapping with other energy demanding processes such as breeding or migration (Jenni and Winkler, 1994). Moult is energetically costly in terms of the synthesis of feathers (Murphy, 1996), reduced flight performance during replacement of flight feathers (see Pennycuik, 1989; Chai and Dudley, 1999) and lowered insulation capacity of plumage during body moult (Dietz *et al.*, 1992). Experimental manipulation of moult in the collared flycatcher *Ficedula albicollis*, demonstrated a reduction of survival in individuals which started moult during the chick rearing phase (Hemborg and Lundberg, 1998; Hemborg and Merilä, 1998), and consequently delayed moult has been suggested as one of the mechanisms regulating investment in reproduction in birds (Hemborg, 1999).

Passerines differ widely in the number, season and extension of moult episodes (Jenni and Winkler, 1994). All this variation has been considered as

adaptations to different ecological characteristics of the species, mainly related to their breeding and migratory behaviour (Jenni and Winkler, 1994). However, such hypotheses have not been quantitatively tested using a phylogenetic approach. Only Svensson and Hedenström (1999) analysed the potential relationship between the evolution of moult and migratory strategies in Sylviidae.

Although migration has been considered the main factor shaping moult patterns, a number of other factors could determine moult strategies. In a theoretical analyses, Holmgren and Hedenström (1995) concluded that the higher the effect of feather quality on reproductive output, the sooner prior to breeding the moult should be scheduled. Their model also predicted an effect of migration distance on the number but not on the timing of complete moult. An interaction between plumage brightness and migration distance has been demonstrated in European passerines, with brightly coloured species migrating over larger distances than drab species (Fitzpatrick, 1994). The importance of plumage dichromatism or conspicuousness has largely been ignored in moult studies, despite the potential importance that sexual selection has in the life history of birds (for example: migration distance, Fitzpatrick, 1994, 1998; nest placement, Martin and Badyaev, 1996; survival, Promislow *et al.*, 1992).

In this paper we test the relationship between the evolution of different moult patterns in passerines and migratory behaviour and sexual dichromatism. For this purpose we choose the passerines breeding in the Western Palearctic because their biology and phylogenetic relationships are relatively well known.

Methods

For each species ($n = 147$) we registered the number of moults in the adults, considering both complete and partial moults. Complete moult refers to a whole replacement of body and flight feathers. Partial moult only affects body feathers and none or just a few of the flight feathers. We also registered the season when the complete moult occurs (summer or winter), following Svensson (1996). This variable was scored as missing in the three species with two annual complete moults, and on the species with a suspended summer complete moult completed in the winter. Although there is some individual variation within species in the timing and extension of moult, most species exhibit a relatively constant moult patterns, making justified a classification of the different European passerine species into different moult strategies (Jenni and Winkler, 1994). The mean breeding and wintering latitudes were estimated as the mean of the northern and southern extremes of the distribution during each season based on maps in the works of Cramp (1988–1992), Cramp and Perrins (1993–1994), Baker (1997), Flint *et al.* (1984) and Dement'ev and Gladkova (1954). Migration distance corresponded to the difference between

mean breeding and wintering latitude. Sexual dichromatism in summer and winter were scored separately based on plates in the same guides and descriptions of plumage in the text. Sexual dichromatism was scored from 0 to 12 based on the coding of colour dimorphism in 12 different body parts (Gray, 1996). An index of seasonal variation in sexual dichromatism was calculated as the difference between summer and winter dichromatism.

In most cases, interspecific data should not be analysed with traditional regression methods, because data of different species are not statistically independent (Harvey and Pagel, 1991), making it necessary to control the phylogenetic relationships between species. A working phylogeny for the group was compiled based on different DNA phylogenies (Sibley and Ahlquist, 1990; Blondel *et al.*, 1996; Leisler *et al.*, 1997; Price *et al.*, 1997; see Figure 1). In the case of genera with only phylogenetic information for one or two species, we included two species with different moult strategies to maximise variability on the data set. No information was available on the exact phylogenetic position of some genera with interspecific differences in moult strategies (e.g. *Saxicola*). In these cases the species were placed in the tree according to the Sibley and Monroe (1990) taxonomy. All branch lengths within the tree were set to unity.

The associations between changes in the number or season of the complete moult and the other variables analysed were tested using independent contrasts (Felsenstein, 1985). The contrast were calculated as the differences in the characters of interest between pairs of closely related taxa, and standardized in relation to the time elapsed since the separation of the lineages in the tree, by using estimated branch lengths. Under a Brownian motion model of evolution each contrast is independent of other contrasts calculated over the tree. The contrasts were calculated using the brunch procedure in the CAIC program. Associations between changes in the continuous independent variable and the discrete predictor variable were tested by determining the deviation of the contrasts from an expected mean value of zero (by using *t*-tests when contrasts were normally distributed, or Wilcoxon tests otherwise). This method is particularly adequate when the main predictor is a categorical variable (Purvis and Rambaut, 1995a).

To control the effects of migration distance on dichromatism during the breeding season and seasonal changes in dichromatism, the independent contrasts of these variables were calculated using crunch procedure in CAIC, most appropriate when analysing only continuous variables. The slope of the regression through the origin was used to calculate the residuals for each species (Purvis and Rambaut, 1995b, summer dichromatism vs. migration distance, slope = 0.0382, $F_{1,133} = 6.67$, $p = 0.01$; seasonal change in dichromatism vs. migration distance, slope = 0.0244, $F_{1,133} = 3.87$, $p = 0.05$) used as estimates of summer and seasonal changes in dichromatism corrected for migration distance. Winter dichromatism was not standardized for migration distance be-

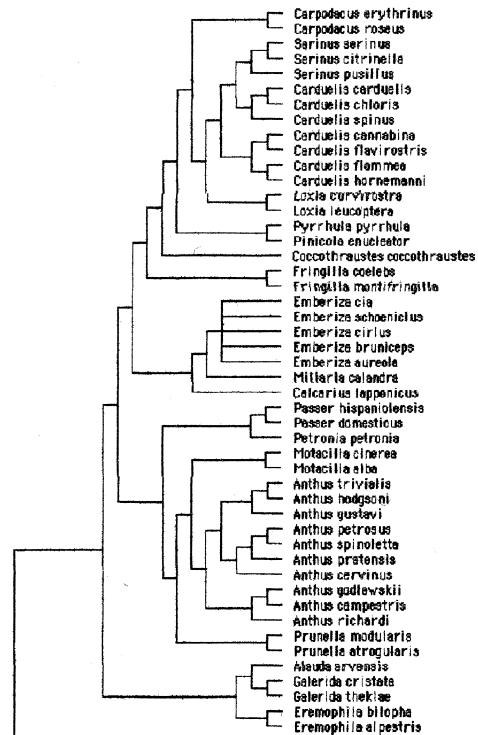


Figure 1. Phylogenetic hypothesis used in this study (continues on next page).

cause both variables were unrelated (regression through the origin of independent contrasts, $F_{1,133} = 1.01$, $p = 0.32$).

The association between the evolution of plumage dichromatism and number and scheduling of the main moult was analysed following Pagel (1994). This method is based in a markov-transition rate model of trait evolution, and since the results do not depend on the particular set of ancestral values that might be assigned by parsimony, the problems derived from ancestral character reconstruction are avoided (Pagel, 1997). However, the model assumes a constant probability of change through the tree. A model of independent evolution and another of correlated evolution were calculated and the model best fitting the data was determined by maximum likelihood statistical methods, using the DISCRETE program (Pagel, 1997, 1999). To ensure that the most stable solution was reached, analyses were repeated until four estimates of model likelihood were obtained that differed only at the second or lower decimal place. The statistical significance of differences between the evolution dependent and independent models were determined using Monte Carlo tests, because the statistic does not match any commonly used statistical distribution. The Likelihood Ratio (L.R.) obtained from the data was compared to those derived from

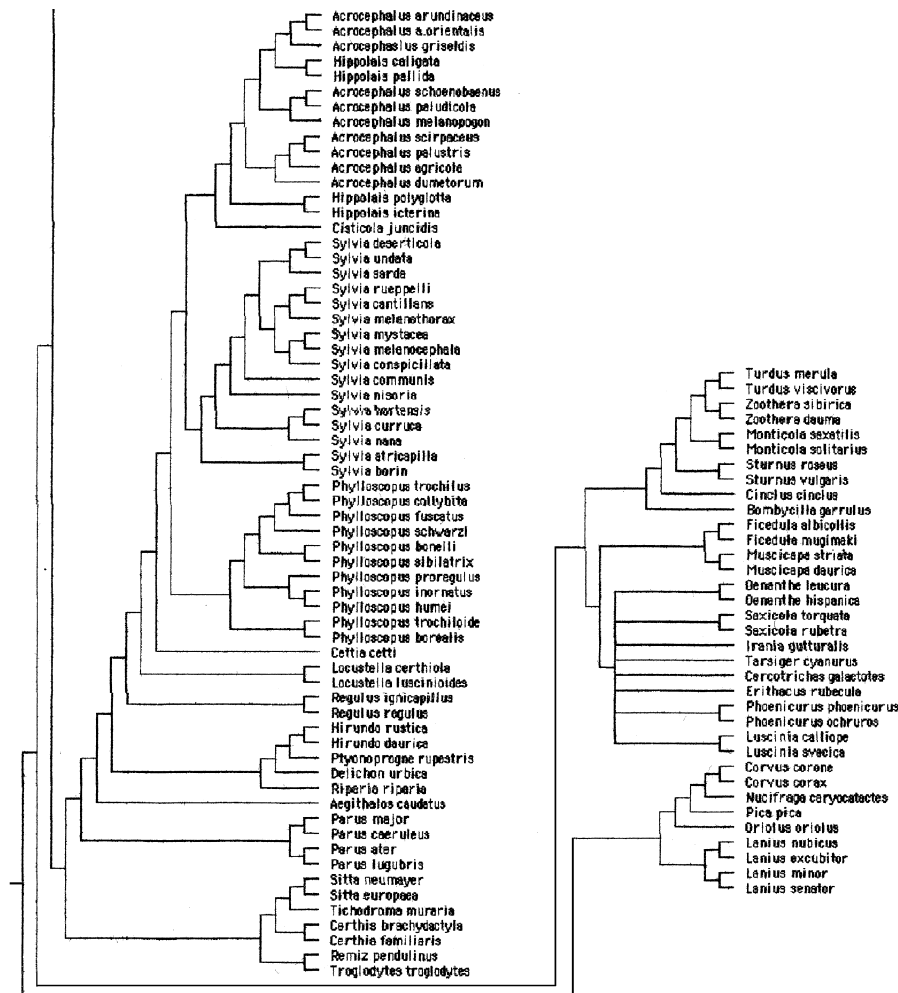


Figure 1. (Continued)

100 runs simulating the evolution of the two characters studied over the phylogeny using the independent model parameters. Each of these simulations was analysed with the models of dependent and independent changes, and the L.R. was calculated. The directionality of the significant relationships was tested by forcing the relevant parameter in the model of dependent evolution to take the same value as another related parameter in the model (Pagel, 1994). For example, to determine if double annual moults were associated with increased frequency of evolution of sexual dichromatism, the probabilities of change in dichromatism in species with one and two annual moults were forced to take the same value. If this model had a significantly reduced fit to the data, the

hypothesis of equal probability of change with respect to moult frequency was rejected. In these analyses, the statistical significance of the changes in likelihood were determined using the χ^2 distribution (1 df). For this analysis a species was considered as dichromatic if sexual dichromatism was scored as one or more during spring or winter. This method could not deal with continuous variables so migration distance could not be included in the analyses. Additionally, the method can only deal with completely bifurcating phylogenies so a reduced, but fully dichotomised version of Figure 1 was used in these second set of analyses.

Results

Migration and number of body feather moults

Species that moult their body feathers twice a year migrated over larger distances than species with a unique annual moult (mean contrast \pm SD, 9.19 ± 7.92 , $t_{23} = 5.69$, $p < 0.0001$). Species with two annual moults wintered at southern latitudes than species with a unique annual moult (-7.56 ± 7.38 , $t_{23} = 5.02$, $p < 0.0001$), but bred at similar latitudes (1.64 ± 4.75 , $t_{23} = 1.69$, $p = 0.11$).

Sexual dichromatism and the evolution of partial moults

No difference in the intensity of sexual dichromatism occurred in species with two instead of a unique annual moult (summer dichromatism, 0.46 ± 1.74 , $W_{23} = 22$, $p = 0.31$; winter dichromatism, -0.03 ± 1.54 , $W_{23} = 5.50$, $p = 0.76$). Additionally, no differences in the importance of seasonal changes in sexual dichromatism were detected according to number of moults (0.49 ± 1.33 , $W_{23} = 19$, $p = 0.10$). These results remain unchanged after controlling for the effect of migration distance (summer dichromatism, 0.11 ± 1.69 , $W_{22} = 19$, $p = 0.60$; seasonal change in dichromatism, 0.26 ± 1.35 , $W_{22} = 32$, $p = 0.37$).

When to moult: before or after autumn migration?

Species with a complete moult in winter, migrated over longer distances than species with a complete moult in summer (10.36 ± 7.28 , $t_{17} = 6.04$, $p < 0.0001$). This was because while not differing in their mean breeding latitude (1.66 ± 5.34 , $W_{17} = 36$, $p = 0.12$), species moulting in winter wintered at southern latitudes (-8.70 ± 6.56 , $t_{17} = 5.63$, $p < 0.0001$). Species with a complete moult in summer were as dichromatic as those species with a complete moult in winter (summer dichromatism, 0.30 ± 1.54 , $W_{17} = 4.50$, $p = 0.63$; winter dichromatism, 0.51 ± 1.66 , $W_{17} = 7.00$, $p = 0.38$). No differences were

detected in seasonal change in dichromatism between the two groups of species (-0.21 ± 0.48 , $W_{17} = 5.00$, $p = 0.12$). After controlling for migration distance, again no differences in seasonal change in dichromatism were found between species with a complete moult in summer or in winter (-0.09 ± 1.40 , $W_{16} = 20.50$, $p = 0.35$). However, when controlling for migration distance species with a complete moult in summer showed more reduced seasonal changes in dichromatism than species with a complete moult in winter (-0.47 ± 0.47 , $W_{16} = 76.50$, $p < 0.0001$).

Evolutionary correlation between dichromatism and moult strategies

The evolutionary changes in the number of annual moults and plumage dichromatism are strongly correlated (LR = 14.23, $p < 0.01$). Likelihood analyses of the evolution of correlated changes in dichromatism and moult patterns suggest that sexual dichromatism evolved more frequently in taxa with a unique annual moult ($\chi^2 = 12.04$, $p < 0.001$). We found no evidence that the evolution of sexual dichromatism facilitated the evolution of double annual moults ($\chi^2 = 2.44$, $p = 0.13$).

The changes in dichromatism and scheduling of the main moult were also correlated (LR = 13.88, $p < 0.01$). One of the reasons for this association was that the frequency of changes in dichromatism depend upon the scheduling of moult, the transitions to monomorphism in species with the main moult in winter being less frequent than expected ($\chi^2 = 11.58$, $p < 0.0001$). The loss of dichromatism tended to be more frequent in species with the main moult in summer ($\chi^2 = 3.88$, $p = 0.05$). No dependence of changes in dichromatism on changes in moult scheduling was detected ($\chi^2 = 1.44$ and 3.08 , $p = 0.49$ and 0.08).

Discussion

Our results confirm the importance of migration and sexual dichromatism on the evolution of moult strategies. Although partial moults are associated with seasonal changes in the intensity of sexual dichromatism of some species (otherwise a general expectation of ornithologists), our results indicate that sexual dichromatism *per se* did not appear as a selective factor favouring the evolution of partial moults. To understand such apparent incongruency, it should be remembered that in many species seasonal changes in coloration are not due to feather moult, but related to the abrasion of feather tips revealing parts of the feathers with different coloration (Jenni and Winkler, 1994).

Species that undertake the complete moult in winter migrated over larger distances and were more sexually dichromatic during the breeding season, after

controlling for migration distance. Our results contrast with the conclusions of Svensson and Hedenstrom (1999), that related the evolution of complete moult in winter with the colonisation of northern breeding areas. We did not detect such an effect of breeding latitude, probably because the species considered in our study were restricted to a specific breeding area (Western Palearctic), while no restriction was set on winter distribution. Additionally, in our analysis, the association with migration distance was due to lower wintering latitudes. Consequently the relationship between winter moult and migration distance could arise by two additional mechanisms unrelated to migration distance *per se*. If early arrival to wintering areas is advantageous, for example, in terms of obtaining a better wintering territory (Alerstam and Högstedt, 1982), there could be a strong selection favouring an early start of migration, delaying moult until arrival at the wintering area. Second, species with two annual moults wintered at lower absolute latitudes ($t_{23} = 3.85$, $p = 0.0008$), and consequently could be more exposed to plumage abrasion due to sunlight and UV damage upon feathers (Bergman, 1982). Under these circumstances, renewing the feathers before starting northward migration could be favoured in terms of survival.

Sexual dichromatism (and the diverse sexual and natural selection pressures related to it) could have intensified selection favouring winter moult to present a fresh plumage during the mating season. Moult close to the start of northwards migration could probably increase plumage brightness during the mating season and consequently being favoured by intrasexual competition and intersexual selection (see review in Andersson, 1994). Our results indicate a trend to retain dichromatism in species that make the main moult before breeding and a trend to lose dichromatism in species that moult after breeding. This supports the conclusions of Holmgren and Hedenström's (1995) models indicating the potential importance of sexual selection on the evolution of winter moult, given that sexual dichromatism is positively correlated with intensity of sexual selection as estimated from frequency of extrapair paternity in monogamous passerines (Møller and Birkhead, 1994). In conclusion, changes in moult strategies appear closely related to migration and dichromatism in European passerines.

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