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A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines

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Birds moult to maintain plumage function through life, but the factors that determine moult duration are poorly understood. In temperate areas, variation in moult duration could be largely associated with between-species differences in migratory behaviour (migrants have less time for moulting after breeding), and body mass (because the aerodynamic cost of rapid moult increases allometrically with body size). Moreover, if the energetic cost of transport favours a smaller body size in migratory species, then the effects of migratory behaviour and body mass on moult duration could be confounded. We conducted a comparative study of the duration of adult complete moult in 48 European passerine species, in relation to body mass and migratory behaviour (sedentary, short-distance migrants and long-distance migrants). Lighter and more migratory species moulted faster than heavier and more sedentary species, but migration was not associated with body mass. If accelerated moult compromises the success of migration, changes in the physiology or phenology of moult in migratory birds are better interpreted as adaptive responses to compensate for such costs.

Moult is essential for birds to maintain plumage function through life (Jenni and Winkler 1994). In the temperate zone, most passerines undergo a complete post-breeding moult each summer since their second year of life, which lasts from 28 to 182 days depending on the species (Ginn and Melville 1983, Jenni and Winkler 1994). However, the factors that may explain such a wide variation in moult duration among species are far from being identified (Kjellén 1994), a gap in our knowledge which is especially relevant because moult duration can greatly affect the structure and function of feathers (Dawson et al. 2000, Hall and Fransson 2000).

It is common knowledge that migratory behaviour and body mass of birds are two major determinants of moult duration. Migration is costly in terms of both energy and time (Alerstam 1990, Berthold et al. 2003), and therefore birds tend to separate migration from other costly activities, such as moult (Jenni and Winkler 1994). As a consequence, migratory birds have less time available for post-breeding summer moult before migration, which might select for rapid moult in migratory but not in sedentary species (Kjellén 1994, Piersma et al. 2005). Besides, larger bird species may take longer to complete their moult than smaller ones, because their larger feathers may take longer to reach full size, and the aerodynamic costs of moult increase allometrically with increasing body mass (Jenni and Winkler 1994). The latter is particularly important because wing gaps formed during moult impair flight performance (Williams and Swaddle 2003), and fast-moulting birds have larger wing gaps than slow-moulting birds (Bensch and Grahn 1993). Interestingly, heavy species will face larger flight costs than lighter species with equivalent wing gaps given their size (Jenni and Winkler 1994, Carrascal and Polo 2006), which might select for slow moult in heavy species.

Although the existence of relationships among moult duration, migratory behaviour and body mass of birds seems intuitive, the shape of such relationships is far from being explicitly evaluated. In particular, it is important to determine how migratory behaviour and body mass interact as possible determinants of moult duration. For example, heavy birds might face an increased cost of transport during migratory flights (Hedenström and Alerstam 1998, Bowlin and Wikelski 2008), which might have favoured the evolution of reduced body mass in migratory species (Calmaestra 2000). In turn, a detailed knowledge of the relationships among body size, migratory behaviour, and moult duration is required for understanding the evolution of different moult durations observed among bird lineages.

We conducted a comparative analysis of 48 species of European passerines for which data of moult duration, migratory behaviour and body mass were available from the literature. We tested for differences in moult duration and body mass among three groups of species with different migratory behaviours (sedentary, short-distance migration, and long-distance migration), with specific interest in the effect of migration on moult duration controlling for variation in body mass.

Material and methods

We used data of moult durations of European passerines reported by Ginn and Melville (1983), who summarized the moult cards from the BTO's collection and other sources. Ginn and Melville (1983) estimated individual moult durations by regressing date of capture on moult score (a parameter that represents the degree of progression of the moult through the sequence of feather replacement), which allows a reasonable approximation to the average duration of primary moult of an individual. The duration of primary moult can be used as a proxy to total moult duration because the complete moult of passerines follows a strict sequence: it starts with the drop of the innermost primary feather, and finishes when the outermost primary feather reaches full size (there are few exceptions to this rule, none of which was included in the study; for further details see Jenni and Winkler 1994). Moult durations estimated from moult cards are sensitive to sample size and, more importantly, to the estimation method used. To increase the reliability of our analyses, we used species with moult durations estimated from data on at least 20 individuals (which only excluded the black redstart *Phoenicurus ochruros*, $n = 13$). We also excluded four species of corvids whose moult durations were reviewed from the literature by Ginn and Melville (1983), who made a cautionary note on the reliability of such estimates. The method used by Ginn and Melville (1983) has itself been criticized (Jenni and Winkler 1994), but moult durations can be directly compared only if they have been obtained using standardized methods. Because of this reason, we did not use other potential sources of data available in the literature, such as estimates of moult speed (Bensch and Grahn 1993).

We restricted our analyses to species that undergo an adult complete moult in the breeding grounds (i.e. summer moult; Svensson 1992, Jenni and Winkler 1994), because the species that moult after migration (i.e. winter moult) are not expected to face equivalent time constraints in relation to the onset of migration. The willow warbler *Phylloscopus trochilus* is an exceptional species because it undergoes two complete moults per year (one in breeding grounds and one in wintering grounds). For this species, we used data of the summer moult only. We considered median moult durations of species for which Ginn and Melville (1983) reported different moult durations for early and late moulters.

We further improved the reliability of our comparative analysis by removing between-population variation from the study, for which we used data of British populations only. For example, many species vary in the extent of their migration across the Palaearctic (sometimes spanning the whole range from sedentary to long-distance migratory; Alerstam 1990, Berthold et al. 2003), which may blur the link between migration and moult duration estimated on different populations of the same species. Therefore, we determined the migratory behaviour of each species according to the winter distribution of ringing recoveries of British populations (Wernham et al. 2002). We distinguished between sedentary species (which do not migrate), short-distance migrant species (which migrate within the Palaearctic, typically towards the Mediterranean Basin), and long-distance migrant species (species that cross the Sahara desert to winter in tropical Africa). The average body mass of each species was obtained from Dunning (1993). All data were log-transformed to meet the requirements of statistical tests.

Species are part of a hierarchically structured phylogeny, which renders species data statistically non-independent (Felsenstein 1985, Harvey and Pagel 1991). Because of this reason, we conducted phylogenetic analyses of (co)variance (Garland et al. 1993). The method is based on F statistics computed using conventional (i.e. phylogenetically uncorrected) AN(C)OVA, but estimates 'phylogenetically correct' significance values using null distributions of F statistics obtained from empirically scaled computer simulation models of traits evolving along known phylogenetic trees. It is important to note that phylogenetic and non-phylogenetic analyses often render similar results (Price 1997), and the non-phylogenetic approach may avoid the drawbacks of using comparative methods when models of evolutionary change or phylogenetic topologies are uncertain. Because of this we also reported conventional, non-phylogenetic results of our analyses.

We used the program STATISTICA (Statsoft 2002) to analyse variation in moult duration among species with different migratory behaviour, using body mass as a covariate. We also tested for differences in body mass in relation to variation in migratory behaviour. Then, we used the "Phenotypic diversity analysis programs" (PDAP; Garland et al. 1993) to determine the phylogenetically correct statistical significances of the above effects. Our phylogenetic hypothesis (Fig. 1) was based on an earlier tree (Figuerola and Jovani 2001), which we updated with later data of the families Emberizidae (Grapputo et al. 2001), Paridae (Gill et al. 2005), and Corvidae (De Kort and Clayton 2006). We established politomies for groups with unknown phylogenies, or well established clades whose members had ambiguous phylogenetic relationships (such as the genus *Turdus*; Pan et al. 2007). Due to uncertainties with respect to branch lengths in units of expected variance of change (Felsenstein 1985, Martins and Garland 1991), all branch lengths were set equal, thereby assuming a speciational model of evolutionary change in which most change is expected to occur in association with speciation events (Rohlf et al. 1990).

We used the program PDANOVA to create phylogenetically correct null distributions of F statistics, using 1,000 sets of tip values generated by PDSIMUL (Garland et al. 1993). In the simulations, body mass was bounded between the mass of the lightest living bird *Mellisuga helenae* (2 g; Dunning 1993) and an arbitrary measure (1,500 g) well above the mass of the heaviest passerine in the Palaearctic (*Corvus corax*, 1,200 g). Likewise, moult duration was bounded between the shortest moult duration recorded in birds (28 d of *Plectrophenax nivalis*) and the longest value registered in passerines (182 d; Jenni and Winkler 1994). We used the between-species means of real data as both starting values and expected means of simulated tip values. The expected variances of the simulated tip data were set equal to the variances of the real data. Correlations between the simulated changes for traits were set to 0. Because all branches in the phylogeny were set equal, our analyses assumed a speciational Brownian motion model of evolutionary change.

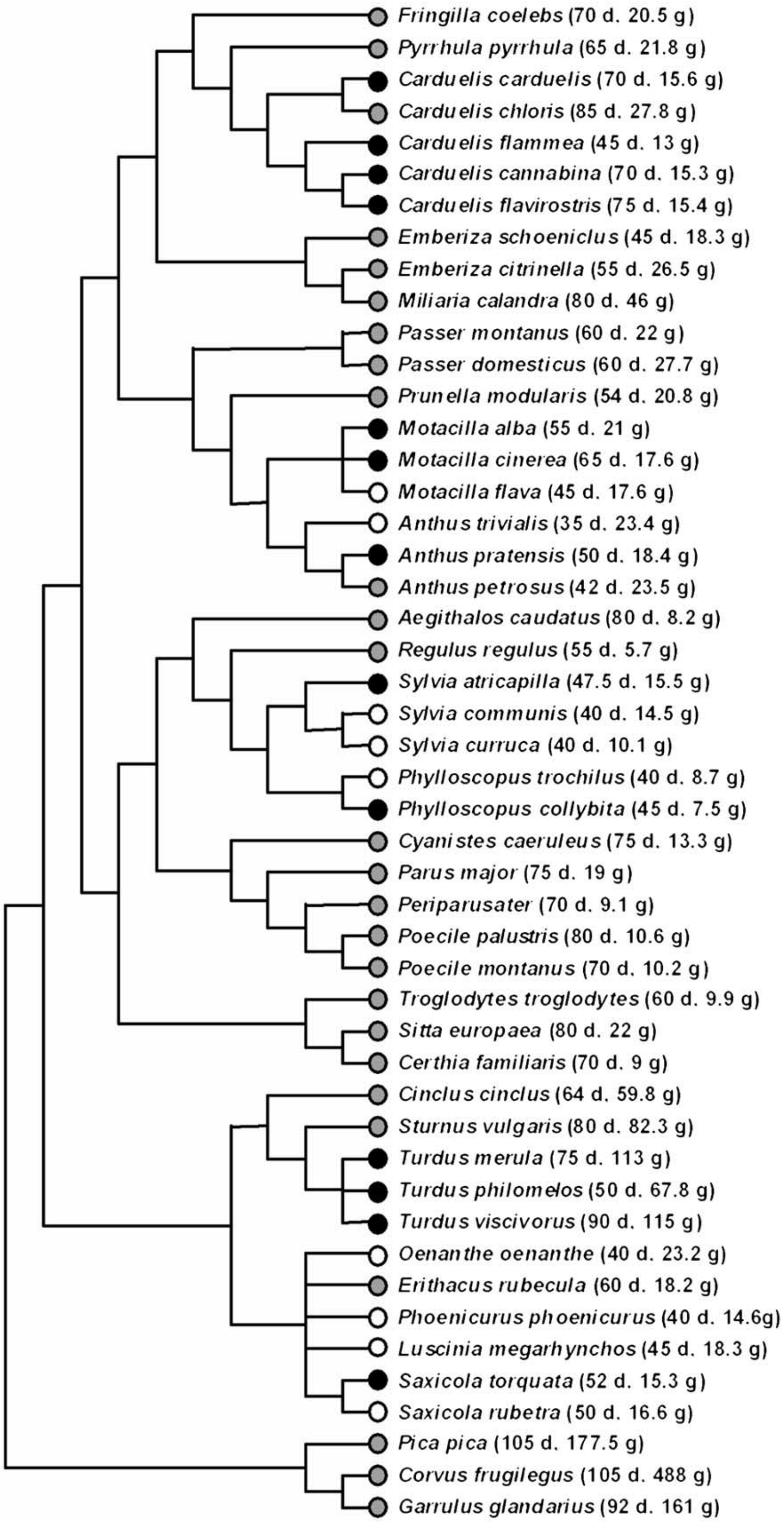

Figure 1. Putative phylogenetic relationships among the 48 passerine species included in the study. Grey dots, black dots, and open circles represent bird species which are sedentary, short-distance migrants, and long-distance migrants respectively. Moult duration (d) and body mass (g) are shown in parentheses.

Results

Both body mass and migratory behaviour had a significant effect on moult duration. Larger species took longer to moult than smaller ones (Fig. 2, effect of body mass as a covariate: $F_{1,44} = 15.71$; both conventional and phylogenetically correct $P < 0.001$). Controlling for the effects of body mass, moult duration depended on the intensity of migratory behaviour (Fig. 3, effect of migratory behaviour as a factor: $F_{2,44} = 19.53$; both conventional and phylogenetically correct $P < 0.001$): the longer the distance of migration, the shorter the duration of moult.

The effect of body mass on moult duration did not vary between groups (test of homogeneity of slopes: $F_{2,42} = 0.28$; conventional $P = 0.757$; phylogenetically correct $P = 0.846$). Interestingly, body mass did not differ significantly among species with different migratory behaviour, specially in the phylogenetic analysis ($F_{2,45} = 0.95$; conventional $P = 0.396$; phylogenetically correct $P = 0.589$).

Discussion

Migratory behaviour and body mass have long been thought to influence variation in moult duration among species (Jenni and Winkler 1994), yet such effects remained to be explicitly tested, let alone analysed in a phylogenetically explicit framework. By estimating the effects of migratory behaviour and body size in a single linear model, we confirmed that migratory behaviour and body mass have largely independent effects on moult duration. Thus, the model including both variables ($R^2 = 0.60$) explained considerably more variation than any of the two variables alone ($R^2 = 0.46$ and 0.25 for migratory behaviour and body mass, respectively). In fact, our data did not support any difference in body mass among species with different migratory behaviour ($R^2 = 0.04$).

We found similar results using conventional and phylogenetically correct methods, which is a typical outcome when the data set used is reasonably diverse and the effects are strong (Weathers and Siegel 1995, Ricklefs and Starck 1996). Therefore, the correlations between moult duration and migratory behaviour and body mass reported in this study can be regarded as robust. Large birds may benefit from slower moult because they depend more strongly on flight capability to maintain feeding ability (Carrascal and Polo 2006), or to avoid predation (Jenni and Winkler 1994, Williams and Swaddle 2003). At a given body size, migratory species may benefit from faster moult because they have less time available for moulting. Although the time available for moulting can differ between migratory species with different breeding phenology, number of broods, or duration of parental care (Jenni and Winkler 1994), time constraints on the moult of migrants have been mainly attributed to the onset of migration. Early migration may be associated with physiological costs of rapid moult (Dawson 2004), and also with other costs associated with reduced quality of fast-growing feathers (De la Hera et al. 2009). However, early migration may be selected for if early migrants accrue benefits *en route* (because they access more resources to refuel at stopover sites than late migrants), or in wintering grounds because they may occupy the best territories (Alerstam and Högstedt 1982, Marra et al. 1998). In the extreme case when migrants fail to compensate the costs of rapid moult in breeding grounds, other adaptive responses may evolve to avoid such costs. For instance, many long-distance migrants postpone their complete moult until arrival on wintering grounds (Svensson and Hedenström 1999, Hall and Tullberg 2004). In turn, a detailed knowledge of the interactions between migration patterns and other traits of the whole annual cycle of birds (not just the ones that operate on the breeding grounds) may prove essential for understanding the evolution of moult duration.

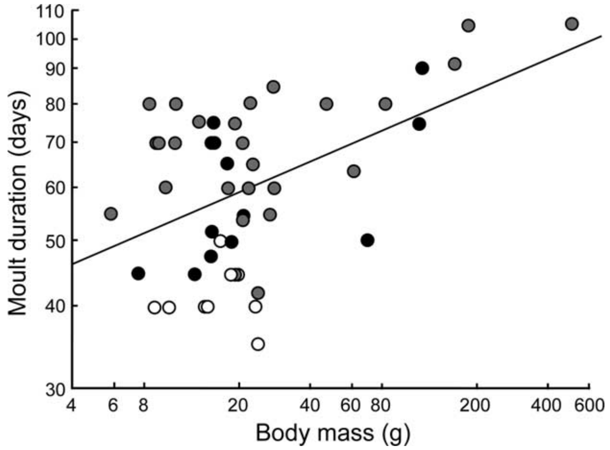

Figure 2. Variation of moult duration as a function of body mass for the 48 bird species included in the study. Symbols as in Fig. 1.

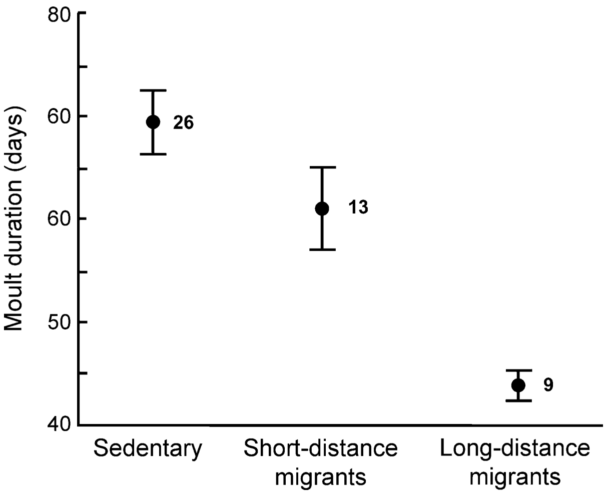

Figure 3. Variation in moult duration between species groups that show different migratory behaviour. The graph shows adjusted means (after controlling for the effects of body mass) with standard errors and sample sizes.

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