

## Relationships among timing of moult, moult duration and feather mass in long-distance migratory passerines

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Moult is a costly but necessary process in avian life, which displays two main temporal patterns within the annual cycle of birds (summer and winter moult). Timing of moult can affect its duration and consequently the amount of material invested in feathers, which could have a considerable influence on feather structure and functionality. In this study, we used two complementary approaches to test whether moult duration and feather mass vary in relation to the timing of moult. Firstly, we conducted a comparative study between a sample of long-distance migratory passerine species which differ in moult pattern. Secondly, we took advantage of the willow warbler's *Phylloscopus trochilus* biannual moult, for which it is well-known that winter moult takes longer than summer moult, to assess between-moult variation in feather mass. Our comparative analysis showed that summer moulting species performed significantly shorter moults than winter moulters. We also detected that feathers produced in winter were comparatively heavier than those produced in summer, both in between-species comparison and between moults of the willow warbler. These results suggest the existence of a trade-off between moult speed and feather mass mediated by timing of moult, which could contribute to explain the diversity of moult patterns in passerines.

Birds need to moult to repair the damage produced on feathers by mechanical abrasion, photochemical processes or parasites. Moult requires a great quantity of resources and time, since plumage can represent up to a fourth of the total lean dry body mass of a bird (Ginn and Melville 1983, Jenni and Winkler 1994). Thus, overlapping moult with other energetically demanding activities is generally avoided, and as a consequence both the duration and timing of moult are constrained by breeding and migration within the annual cycle of birds (Jenni and Winkler 1994, de la Hera et al. 2009a).

In the temperate region, timing of moult displays two main patterns in passerines, with the majority of species fitting the complete moult between reproduction and autumn (hereafter summer moult; Jenni and Winkler 1994). Summer moult seems to be the ancestral pattern from which other strategies have evolved (Svensson and Hedenström 1999, Hall and Tullberg 2004), while plumage renewal postponed to the winter period (i.e. winter moult) would be the main alternative option, although other minority strategies occur (e.g. suspended moult, biannual moult; Underhill et al. 1992, Hall and Fransson 2001). In the Palaearctic region, such deviations from the ancestral pattern have only evolved in some species that spend the winter in sub-Saharan Africa (i.e. trans-Saharan migrants). The evolution of winter moult has been attributed to two main circumstances: firstly, increased

migration distance may promote an early onset of autumn migration, which reduces the time available for moulting after breeding (Hall and Fransson 2001); secondly, high availability of resources for moulting in African habitats may favour the evolution of winter moult (Moreau 1972, Barta et al. 2008). However, although the factors affecting moult pattern variation in passerines have been subjected to an intense debate (Jenni and Winkler 1994, Salewski et al. 2004, Rohwer et al. 2005), the determinants of such diversification still remain poorly understood.

Some theoretical studies have suggested that the requirements associated with feather quality could determine moult schedules (Holmgren and Hedenström 1995, Barta et al. 2008), but no study has assessed whether timing of moult affects feather production. However, moult duration seems to differ markedly between summer and winter moult strategy (Ginn and Melville 1983, Underhill et al. 1992), and these variations in moult speed can affect the structure and functionality of feathers (Dawson et al. 2000, Hall and Fransson 2000, Serra 2001, Serra et al. 2007). Therefore, the analysis of the variation in moult duration and feather mass (as an estimate of the quantity of material invested in the structure of feathers; Dawson et al. 2000, de la Hera et al. 2009b) in relation to the timing of moult could shed light on the diversification of moult strategies.

In this study, we tested whether the duration of summer moult is shorter than winter moult, and if there are

differences in the mass of feathers synthesized in each moult scenario. We used two complementary approaches. Firstly, we performed a comparative study (Garland et al. 1993) to assess the differences in moult duration and feather mass among various Western Palaearctic trans-Saharan migratory bird species which differ in moult pattern (summer vs. winter moult). Secondly, we took advantage of the willow warbler's *Phylloscopus trochilus* moult strategy to test for within-species differences in feather mass in relation to the timing of moult. It is well-known that summer moult is considerably shorter than winter moult in this species (Ginn and Melville 1983, Underhill et al. 1992), but whether willow warblers produce heavier feathers during their slower African moult remains untested. Therefore, studying seasonal variation in feather mass associated to the biannual moult of willow warblers may greatly contribute to understand moult pattern evolution.

## Material and methods

### Moult duration and feather mass in long-distance migratory species

We used the data contained in Ginn and Melville (1983) to obtain the moult duration of Palaearctic trans-Saharan migratory bird species, and collected feather samples of various species to explore the relationships among moult pattern, moult duration and feather mass (Ginn and Melville 1983, Jenni and Winkler 1994). Unfortunately, we could not obtain feather samples for all species with known moult pattern and duration, and other species that could be sampled in the field lacked known estimates of moult duration. Consequently, each comparison in our study included a different subset of the 19 Palaearctic trans-Saharan migratory bird species included in the study (Fig. 1).

For 14 out of 19 species, moult duration (measured as the mean number of days that one individual needs to renew all primary feathers during a complete moult) was available from Ginn and Melville (1983; see Fig. 1). We compared moult duration of summer and winter moulting species by means of ANOVA. In a first analysis, we included body mass as a covariate, because moult duration greatly depends on body mass in passerines (de la Hera et al. 2009a). However, within our sample (which included species with little variation in body mass) the effect of body mass on moult duration was not significant and excluding it did not qualitatively change our results. Therefore, we did not further consider body mass in our analysis.

We collected feather samples for 12 of the 19 species analysed (see Appendix 1). Birds were sampled between spring 1996 and autumn 2006 in three localities of the Iberian Peninsula (for further details of these sites see Tellería and Carbonell 1999) and in a wetland located in the North of Spain (Salburua Park, Álava). Following Svensson (1992) and Jenni and Winkler (1994), each bird was aged and assigned a type of plumage: adult plumage, produced during a complete moult, or juvenile plumage, the first set of feathers produced during the fledging period (Jenni and Winkler 1994). In addition, one tail feather (one of the two fifth rectrices) was collected from each individual.

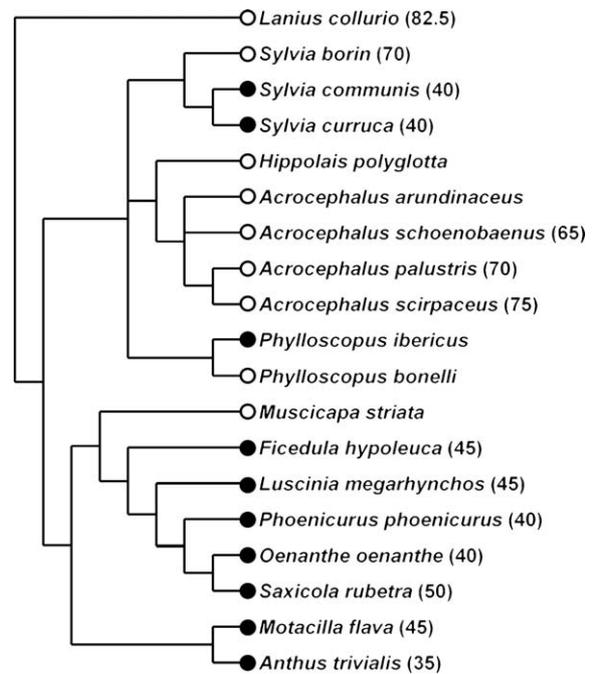


Figure 1. Phylogeny of the 19 trans-Saharan migratory bird species studied. The moult strategy of each species is represented by filled dots (summer moulters), and open circles (winter moulters). Primary moult duration in number of days is indicated in brackets.

In the laboratory, we weighed the feathers using a Mettler Toledo AG-245 digital balance (resolution of 0.01 mg). We also measured feather length from the base to tip of the feather using a Mitutoyo 500 digital calliper (resolution of 0.01 mm). It is important to note that feathers were collected between May and October, when long-distance migratory species are breeding, moulting (partially or completely depending on the species) or stopping over in the Iberian Peninsula (see median and range of collecting dates in Appendix 1). Consequently the time since feather growth can vary between individuals, which may cause variation in feather wear. To avoid that such circumstance affects the reliability of our measurements, we only used feathers in which their contour could be recognizable (i.e. feather wear was not stronger than “moderately worn”, according to Baker 1993).

Independently for each species, we performed an ANCOVA that included feather mass as dependent variable, type of plumage as factor (adult or juvenile feathers), and feather length (a measure of the size of feathers) as a covariate. These adjusted masses of tail feathers are correlated with the width of the rachis and the density and length of feather barbs (de la Hera et al. 2009b) providing a size-independent measure of feather mass. For this reason, we used these values as predictors of the quantity of material invested in feather production during moult (adults) or fledging period (juveniles). However, the conclusions of this study based only on tail feathers should be taken with caution, because previous research detected that the allocation of resources between different feather tracts can be subjected to slight variations according to their functional relevance (Jovani and Blas 2004, de la Hera et al. 2010a).

Firstly, we explored the variation between summer and winter moulting species in the adjusted mass of adult feathers (hereafter also denoted as  $m_a$ ), and including the feather length of each species as a covariate. However, such comparison is likely to be confounded by different feather requirements among species caused by a particular life style or the occupancy of different habitats. To control for such circumstance we used the adjusted mass of juvenile feathers (hereafter  $m_j$ ) as a baseline for the feather mass of each species (Rohwer et al. 2005). This decision was based on the fact that the factors affecting the incorporation of material in feathers during plumage production are expected to be more homogeneous during the fledging period of different species (for example, all juvenile flight feathers are produced simultaneously; Jenni and Winkler 1994) than during the adults' moult, when variable moult duration causes differences in moult intensity and in the demand of resources for growing feathers (Dawson 2004). According to this idea, we also explored the variation between summer and winter moulting species in the index  $m_a - m_j$ , and also including feather length as a covariate. It is expected that passerine species will show positive values of this index because adult feathers usually are more structurally complex and consequently heavier than juvenile ones (Jenni and Winkler 1994). However, we predicted that if winter moulting species undergo slower moults than summer moulting species and this circumstance allows them to incorporate more material into feathers, winter moulters will show more positive values of this index.

In order to avoid the problems associated with the absence of statistical independence in comparative studies, we analysed the effects of moult timing on moult duration and feather mass considering the hierarchical phylogenetic relationships between species (Felsenstein 1985). We used the Phenotypic Diversity Analysis Programs (PDAP) to determine phylogenetically correct statistical significance of our tests, for which we used null distributions of F statistics derived from 1000 simulations of character evolution given the phylogeny of the species, as generated by the PDSIMUL program (Garland et al. 1993). Our phylogenetic hypothesis was constructed from a larger tree of passerine species (Jönsson and Fjeldså 2006; Fig. 1). Simulations of the evolution of moult duration were bounded between the shortest and the longest moult durations recorded in passerines (28–182 days; Jenni and Winkler 1994). Possible character values for  $m_a$  and feather length were bounded between the values of one of the smallest passerine bird species in the Palaearctic (the firecrest *Regulus ignicapillus*:  $m_a = 1.93$  mg, feather length = 42.6 mm), and the values of the biggest species within the studied clade for which feathers had been measured (the blackbird *Turdus merula*:  $m_a = 46.98$  mg, feather length = 114.2 mm). Likewise, the limits for the index  $m_a - m_j$  were set between 0 as the lower limit (when adult and juvenile feathers show the same mass) and the values of the blackbird ( $m_a - m_j = 2.03$  mg). We conducted the simulations using the REPLACE option of PDSIMUL, using between-species means both as starting values and as the expected means of the generated tip values. The expected variances of the simulated tip data were set equal to the variances of the real data. The correlations between the simulated changes for each pair of traits were set to 0. We used two different models of evolutionary

change in these comparisons: *gradual Brownian* and *speciational Brownian motion*, whose significance values were denoted in the results as  $P_{grad.}$  and  $P_{spec.}$  respectively. For each analysis the original phylogeny was modified removing in each case the species for which moult duration or feather samples were not available, but maintaining the original height of the tree (Fig. 1). The program PDANOVA was used to calculate the null distribution of F statistics from the simulations.

### Feather mass and the biannual moult of the willow warbler

The willow warbler is the only species in the Western Palaearctic that performs a biannual complete moult (Underhill et al. 1992). This species breeds in the northern Palaearctic and winters in the sub-Saharan Africa (Cramp 1992). Adult birds perform a complete moult in European territories after breeding, followed by another complete moult in African wintering grounds prior to the spring migration northwards.

We collected feather samples from 45 willow warblers, which were mist-netted during their migratory passages through the Iberian Peninsula between August 2006 and March 2007. During the post-breeding migration, willow warblers can be adults, that perform a complete summer moult, or juveniles, whose flight feathers are grown during fledging period and will not be moulted until the following winter. Between mid August and the end of September 2006 (when willow warblers appear in the Iberian Peninsula from northern latitudes) we could collect one fifth rectrix feather from 19 adult birds and 14 juveniles, that were distinguished using plumage characteristics and skull pneumatization (Svensson 1992, Jenni and Winkler 1994). On the other hand, during the pre-breeding migration all willow warblers are migrating with a new set of feathers produced during the winter moult. We could capture 12 individuals in March 2007 in the Iberian Peninsula. This sample was complemented with 15 additional individuals captured early in the breeding season (May 2000 and June 2007) in Southern Sweden. These two subsamples of winter-produced feathers did not differ in their mass ( $F_{1,24} = 0.07$ ,  $p = 0.788$ ) after controlling for the effect of feather length ( $F_{1,24} = 44.51$ ,  $p < 0.001$ ,  $\beta = 0.827$ ). Therefore, they were grouped together in the analyses.

We measured the mass and length of the feathers following the methods reported above. To test for differences in the feather mass of the willow warbler, we performed an ANCOVA with feather mass as the dependent variable, type of plumage (three levels: juvenile, summer and winter feathers) as the grouping factor, and feather length as the covariate.

## Results

Summer moulting species showed significantly shorter moults than winter moulters in the conventional ANOVA ( $F_{1,12} = 106.97$ ,  $p < 0.001$ , Fig. 2). These differences were also maintained when we considered the phylogenetic

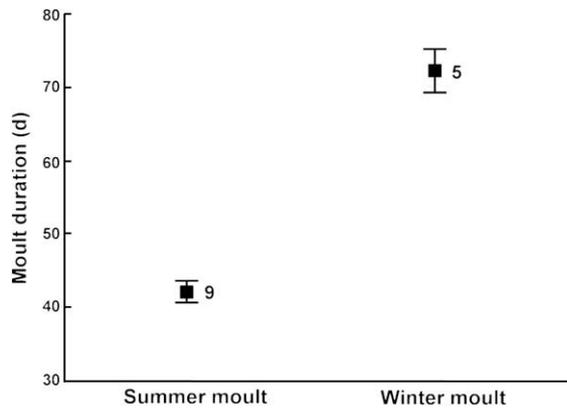


Figure 2. Variation in moult duration between summer and winter moulting species. The graph shows standard errors and sample sizes.

relationships between species both for the 14 species for which we had data of moult duration ( $p_{grad.} < 0.001$ ;  $p_{spec.} = 0.002$ ), and for a restricted analysis that only included the seven species for which we had data of moult duration and feather samples ( $F_{1,5} = 86.43$ ,  $p < 0.001$ ;  $p_{grad.} < 0.001$ ;  $p_{spec.} = 0.001$ ). Additionally, although winter moulting species showed heavier feathers ( $m_a = 6.32 \pm 0.27$  mg) than summer moulters ( $m_a = 5.78 \pm 0.32$  mg) after controlling for the effect of feather length (feather length effect:  $F_{1,9} = 134.24$ , both conventional and phylogenetically-correct  $p < 0.001$ ,  $\beta = 0.984$ ), such variation was not statistically significant (moult timing effect:  $F_{1,9} = 1.57$ ,  $p = 0.241$ ,  $p_{grad.} = 0.321$ ,  $p_{spec.} = 0.367$ ). However, the analysis of the difference between the mass of adult and juvenile feathers ( $m_a - m_j$ ) revealed greater values of this index in winter moulting species than in summer moulters (moult timing effect:  $F_{1,9} = 10.7$ ,  $p < 0.01$ ,  $p_{grad.} = 0.016$ ,  $p_{spec.} = 0.007$ , Fig. 3B; feather length effect:  $F_{1,9} = 12.2$ ,  $p = 0.007$ ,  $p_{grad.} = 0.032$ ,  $p_{spec.} = 0.020$ ,  $\beta = 0.674$ , Fig. 3A).

For the willow warbler, we detected a significant effect of the type of plumage on feather mass ( $F_{1,56} = 5.47$ ,  $p < 0.007$ , Fig. 4) after controlling for the effect of feather length ( $F_{1,56} = 230.53$ ,  $p < 0.001$ ,  $\beta = 0.833$ ). Interestingly, the observed pattern of feather mass was the same as the one detected between winter and summer moulting species (Fig. 4). Thus, feathers produced during the long winter moult of the willow warbler were significantly heavier than the feathers produced both during the summer moult (post-hoc analysis [winter vs. summer]:  $F_{1,43} = 6.24$ ,  $p = 0.016$ ; feather length effect:  $F_{1,43} = 147.41$ ,  $p < 0.001$ ,  $\beta = 0.833$ ), or during the fledging period (post-hoc analysis [winter vs. juvenile]:  $F_{1,38} = 9.12$ ,  $p = 0.004$ ; feather length effect:  $F_{1,38} = 126.13$ ,  $p < 0.001$ ,  $\beta = 0.791$ ); while juvenile and summer-produced adult feathers did not differ in feather mass (post-hoc analysis [summer vs. juvenile]:  $F_{1,30} = 0.67$ ,  $p = 0.421$ ; feather length effect:  $F_{1,30} = 198.06$ ,  $p < 0.001$ ,  $\beta = 0.922$ ).

## Discussion

This study provides empirical support to the suggested relationship between timing of moult, moult duration and

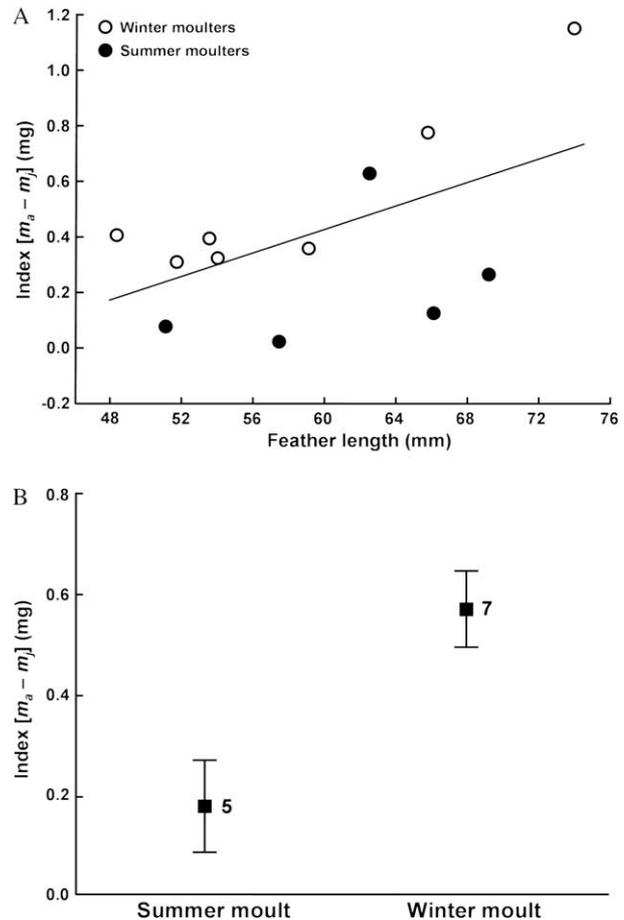


Figure 3. (A) Relationship between adult feather mass minus juvenile feather mass ( $m_a - m_j$ ) and feather length in summer (black dots) and winter moulting species (open circles). (B) Variation between summer and winter moulting species in the index  $m_a - m_j$  after controlling for the effects of feather length. The graph shows means, standard errors and sample sizes.

feather mass in Palaearctic migratory passerines. Firstly, our results corroborate the longer moult of winter moulting species compared to summer moulting birds. Although the effect of moult timing on moult duration has been widely acknowledged (Jenni and Winkler 1994, Hedenström 2008), no study had explicitly tested for such association.

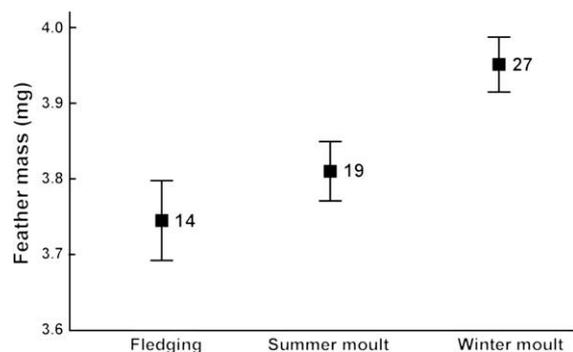


Figure 4. Variation in the feather mass of the willow warbler among feathers produced during fledging (juvenile feathers), summer moult and winter moult. The graph shows mean values adjusted by feather length, standard errors and sample sizes.

Additionally, our comparative analysis also showed variation in the difference between the mass of adult and juvenile feathers in relation to moult timing. This result suggests two complementary interpretations that are difficult to get apart, particularly because of the difficulty to avoid the confounding effect of among-species variation in feather mass. Firstly, higher values of the index  $m_a - m_j$  could be the result of relatively heavier adult feathers in winter compared to summer moulters, as it was set out above (see Methods). Alternatively, this pattern could also be caused by variation in the mass of juvenile feathers. Thus, the high values of the index  $m_a - m_j$  in winter moulters could be the consequence of having lighter juvenile feathers than summer moulters. Although the mass of juvenile feathers shows similar values in our sample (adjusted mean values and standard errors of  $m_j$  were  $5.75 \pm 0.24$  and  $5.61 \pm 0.28$  mg for winter and summer moulting species, respectively), such interpretation would be supported by the fact that the functional lifetime -and tentatively also the mass and quality- of juvenile feathers in winter moulting species is reduced compared to summer moulters. Thus, both winter and summer moulters develop the juvenile flight feathers in summer, but winter moulters take around six months to moult them in wintering grounds, while summer moulters keep them during more than one year, until the subsequent summer moult (Svensson 1992, Jenni and Winkler 1994). Opportunely, this confounding circumstance is absent in the willow warbler, for which the mass of the feathers produced during winter moult are unambiguously heavier than the feathers produced during summer. Although this result does not rule out the existence of variation in the mass of juvenile feathers, its extrapolation to the interspecific analysis supports that differences in moult duration contribute to explain variation in the mass of adult feathers between summer and winter moulting species.

The observation of faster moult in summer moulting species compared to winter moulters agrees with the idea that trans-Saharan migrants are forced to accelerate moult if they are to fit the whole process in the short gap available between breeding and autumn migration (Hall and Fransson 2001, de la Hera et al. 2009a). In contrast, such time limitations would not occur during winter, so that birds can afford a slow moult which could benefit the investment in feather mass (Dawson et al. 2000). The pattern of variation observed for feather mass in the willow warbler, together with the already known differences between seasons in moult duration (Underhill et al. 1992), supports the idea that winter moult functions as a reparation mechanism, replacing the low-quality plumage obtained during the fast summer moult (Hedenström et al. 1995). Consequently, the results of our comparative and intraspecific analyses were consistent with the existence of a trade-off between moult speed and feather quality in birds, according to which accelerated moult will occur at the expense of incorporating less material into feathers (Dawson et al. 2000, Dawson 2004).

Complementarily to this interpretation, several studies suggest that other factors could also contribute to explain variation in moult performance between summer and winter moult (such as energetic efficiency, Klaassen 1995; environmental conditions, Salewski et al. 2004; or immune response, Moreno 2004). However, whatever the relative

contribution of these factors to the variation observed in this study, the fact that feather mass is directly associated with the mechanical properties and resistance to wear of feathers (Dawson et al. 2000, de la Hera et al. 2010b), supports that timing of moult determines feather quality. Such variation in the quality of feathers had not been considered before and could contribute to explain the evolution of winter moult in the life history of birds.

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Appendix 1. Measurements of adult and juvenile feathers (mean raw values with standard errors and sample sizes) for 13 trans-Saharan migratory bird species for which feather samples were collected. The table also shows median and ranges of collection dates following a Julian day calendar.

Species scientific name	Plumage	n	Mass (mg)	Length (mm)	Median date	Range
<i>Acrocephalus arundinaceus</i>	Adult	2	12.55 ± 0.8	76.6 ± 1.5	176	136 – 215
	Juvenile	4	10.35 ± 0.65	72.6 ± 2.5	228	215 – 251
<i>Acrocephalus schoenobaenus</i>	Adult	9	3.93 ± 0.1	48.3 ± 0.6	226	136 – 229
	Juvenile	7	3.53 ± 0.05	48.3 ± 0.4	227	215 – 240
<i>Acrocephalus scirpaceus</i>	Adult	15	4.49 ± 0.09	54.9 ± 0.4	138	136 – 141
	Juvenile	11	3.85 ± 0.07	52.7 ± 0.6	249	249
<i>Ficedula hypoleuca</i>	Adult	11	5.26 ± 0.13	57.5 ± 0.5	247	246 – 248
	Juvenile	13	5.19 ± 0.08	57.3 ± 0.3	247	247 – 248
<i>Hippolais polyglotta</i>	Adult	12	4.39 ± 0.07	54 ± 0.4	154	154 – 190
	Juvenile	7	3.86 ± 0.06	52.6 ± 0.7	215	194 – 229
<i>Luscinia megarhynchos</i>	Adult	16	9.06 ± 0.2	69.4 ± 0.7	161	143 – 175
	Juvenile	19	8.64 ± 0.17	68.8 ± 0.6	177	143 – 214
<i>Muscicapa striata</i>	Adult	3	7.32 ± 0.06	65.6 ± 0.8	234	138 – 243
	Juvenile	9	6.55 ± 0.07	65.7 ± 0.4	241	235 – 245
<i>Phoenicurus phoenicurus</i>	Adult	2	7.43 ± 0.01	62.4 ± 1.5	279	267 – 291
	Juvenile	3	6.79 ± 0.1	62.5 ± 0.6	291	267 – 291
<i>Phylloscopus bonelli</i>	Adult	13	3.31 ± 0.09	51.7 ± 0.6	153	131 – 166
	Juvenile	3	2.99 ± 0.27	51.6 ± 2.2	198	174 – 199
<i>Phylloscopus ibericus</i>	Adult	5	3.19 ± 0.16	51.6 ± 1.4	178	145 – 228
	Juvenile	15	3.02 ± 0.09	50.9 ± 0.7	189	146 – 219
<i>Sylvia borin</i>	Adult	31	6.2 ± 0.08	59 ± 0.4	182	131 – 211
	Juvenile	11	5.83 ± 0.13	58.8 ± 0.7	199	194 – 242
<i>Sylvia communis</i>	Adult	5	7.1 ± 0.33	66 ± 1.1	245	244 – 254
	Juvenile	27	6.96 ± 0.08	66 ± 0.4	245	229 – 258
<i>Phylloscopus trochilus</i>	Summer moult	19	3.78 ± 0.1	54.3 ± 0.62	247	227 – 256
	Winter moult	27	4.15 ± 0.06	56 ± 0.38	123	82 – 180
	Juvenile	14	3.37 ± 0.11	51.8 ± 0.76	228	226 – 270