



Variation in the mechanical properties of flight feathers of the blackcap *Sylvia atricapilla* in relation to migration

Iván de la Hera, Anders Hedenström, Javier Pérez-Tris and José Luis Tellería

I. de la Hera (correspondence), J. Pérez-Tris and J. L. Tellería, Dept. of Zool. and Physic. Anthropol., Fac. of Biol., Compl. Univ. of Madrid, ES-28040 Madrid, Spain. – A. Hedenström, Dept. of Theor. Ecol., Ecology Building, Lund Univ. SE-223 62 Lund, Sweden. – Current address I. de la Hera: Dept. of Anim. Ecol., Neth. Inst. Ecol. (NIOO-KNAW), NL-6666 ZG Heteren, The Netherlands. E-mail: i.delahera@nioo.knaw.nl

Migration causes temporal and energetic constraints during plumage development, which can compromise feather structure and function. In turn, given the importance of a good quality of flight feathers in migratory movements, selection may have favoured the synthesis of feathers with better mechanical properties than expected from a feather production constrained by migration necessities. However, no study has assessed whether migratory behaviour affects the relationship between the mechanical properties of feathers and their structural characteristics. We analysed bending stiffness (a feather mechanical property which is relevant to birds' flight), rachis width and mass (two main determinants of variation in bending stiffness) of wing and tail feathers in migratory and sedentary blackcaps *Sylvia atricapilla*. Migratory blackcaps produced feathers with a narrower rachis in both wing and tail, but their feathers were not significantly lighter; in addition, bending stiffness was higher in migratory blackcaps than in sedentary blackcaps. Such unexpected result for bending stiffness remained when we statistically controlled for individual variation in rachis width and feather mass, which suggests the existence of specific mechanisms that help migratory blackcaps to improve the mechanical behaviour of their feathers under migration constraints.

Birds that have less time and resources for moulting because they have to migrate twice a year might pay a cost in the form of reduced plumage functionality (Berthold 1975, Bonier et al. 2007, de la Hera et al. 2009a). This may involve a reduced structural complexity or a smaller size of important elements of feathers (Dawson et al. 2000, de la Hera et al. 2009b). For example, birds produce feathers with reduced mass and narrower rachis when forced to moult fast in experimental manipulations of the photoperiod, that mimic a constrained moult (Dawson et al. 2000, Dawson 2004, Serra et al. 2007), a detrimental effect on feather quality which has been used to infer the consequences of migration constraints on feather function (Hall and Fransson 2000, de la Hera et al. 2009b). However, it remains unclear whether reduced feather mass or rachis width affect the mechanical properties of the feathers. In fact, given the importance of a suitable mechanical behaviour of feathers during long flights, migratory birds might have developed specific adaptations to maintain feather performance to a suitable level despite their time-constrained moult. In turn, a proper analysis of the relationships between feather structural traits and feather performance is important for understanding the mechanical consequences of time-constrained moult in migratory birds.

We analysed the bending stiffness (Borguud 2003, Weber et al. 2005) of tail and wing flight feathers of blackcaps *Sylvia atricapilla*. Bending stiffness is a main mechanical property of feathers, because it transmits the aerodynamic forces to the musculoskeletal system during flight (Videler 2005, Weber et al. 2005). In blackcaps, a previous study has shown that tail feathers of sedentary individuals are heavier and also have a wider rachis than the feathers of migratory individuals (de la Hera et al. 2009b), a difference that can affect the bending stiffness of feathers (Corning and Biewener 1998, Dawson et al. 2000, Tubaro 2003, Weber et al. 2005). Therefore, we specifically tested whether migratory blackcaps have less stiff feathers than sedentary blackcaps, which would represent a cost of migration in terms of plumage functionality. Alternatively, the feathers of migratory blackcaps could be as stiff, or even stiffer than the feathers of sedentary blackcaps, which would suggest the existence of adaptations to maintain a suitable feather performance despite of time constraints. To do so, we evaluated if variation in bending stiffness of feathers between migratory and sedentary blackcaps could be explained by differences in rachis width and feather mass (de la Hera et al. 2009b). Such comparison is expected to shed light on the implications of migration in relation to feather function.

Material and methods

Study area and field methods

Blackcaps were mist-netted monthly from Sept. 2006 to March 2007 at four different sites in the Campo de Gibraltar region, southern Iberia (36° 01'N, 5° 36'W). In this area, local sedentary blackcaps, and migratory blackcaps that breed at higher latitudes, live together during migration and wintering periods (Pérez-Tris and Tellería 2002). We plucked a second outermost tail feather and an innermost primary feather from each individual (Jenni and Winkler 1994), which were stored in dry paper envelopes until laboratory analyses. Additionally, we measured the length of the eighth primary feather, the length of the tail, and the distances from the tip of the primaries 1 and 9 to the wing tip (Svensson 1992). These morphological variables were used in a discriminant function analysis to assign the migratory behaviour of each individual, a method which correctly classifies the migratory behaviour of nearly all blackcaps (over 90%; Pérez-Tris et al. 1999, de la Hera et al. 2007). It is important to note that any incorrectly classified bird only would lower the statistical power of our comparisons, making the study conservative.

During the study period, we also distinguished between blackcaps wearing juvenile flight feathers (juvenile plumage) and blackcaps having a set of feathers produced during the post-breeding complete moult (adult plumage). For this, we aged birds by iris colour, skull pneumatization and the presence of two generations of feathers, a diagnostic character of juvenile blackcaps, which perform a partial moult after fledgling (Jenni and Winkler 1994, Shirihi et al. 2001). We distinguished between juveniles and adults because they produced flight feathers under different developmental conditions (e.g. a simultaneous synthesis of flight feathers in juveniles compared to the sequential growth in adults; Jenni and Winkler 1994), which could have different implications on feather structure and quality.

In all, we captured 553 blackcaps. In order to optimize resources while capturing all possible sources of variation in this sample, we randomly selected 30 individuals of each population and age class for feather measurements, which produced a final sample size of 120 individuals.

Feather measurements

We measured the dorsoventral bending stiffness of feathers using a test device mounted in a MTS® 810 machine, and following similar procedures described in Weber et al. (2005). Each test took 3 min per feather and provided measurements of the force necessary every 1.5 s to bend the feather 0.05 mm (6 mm of overall feather deformation). This technique provided 120 measurements for each feather, which allowed us to estimate the bending stiffness from the slope of the force-displacement line. Thus, the steeper the force-displacement slope, the higher the value of bending stiffness. To obtain such information, the proximal part of each feather shaft (calamus) was inserted into the clamp of the test device until the beginning of the rachis. The clamp was filled with silicon to avoid damage on the calamus. The force was applied at 26 and 31 mm from

the rachis base for primary and tail feathers, respectively. We evaluated the repeatability of bending stiffness by blindly measuring twice 20 randomly selected individuals (both primary and tail feathers were measured for each one). Repeatability was high and statistically significant both for primary ($r_i = 0.78$, $F_{19,20} = 8.22$, $P < 0.001$) and tail feathers ($r_i = 0.80$, $F_{19,20} = 8.96$, $P < 0.001$).

The overall size of the rachis has been suggested as the main determinant of bending stiffness (Corning and Biewener 1998, Tubaro 2003). In fact, Dawson et al. (2000) found a significant correlation of rachis width and feather mass with bending stiffness and other important properties of feathers (e.g. feather resistance to wear) in the European starling *Sturnus vulgaris*, which suggests that these feather traits could be good surrogates of feather quality. In order to explore the contribution of these feather traits to variation in bending stiffness, we measured the dorsoventral width of the rachis at its base using a Mitutoyo 500 digital calliper (0.01 mm resolution). Rachis width was measured twice to estimate its repeatability, which was very high and statistically significant for both feathers (primary feathers: $r_i = 0.92$, $F_{119,120} = 27.41$, $P < 0.001$; tail feathers: $r_i = 0.95$, $F_{119,120} = 41.36$, $P < 0.001$). We used the average value of both rachis width measurements in our analyses. We also obtained feather mass using a Mettler Toledo AG-245 digital balance (0.01 ± 0.02 mg instrumental repeatability), a measurement which is correlated with the size and complexity of the main structural traits of the feather (i.e. feather vane and rachis; de la Hera et al. 2009b). Additionally, to control for the potential confounding effect of feather size on feather traits or on the bending stiffness tests, we also measured feather length using the same digital calliper. To avoid any source of personal bias, all feather traits were measured by the same person (IH).

Statistical analyses

We used 'General linear models' (StatSoft 2002) to analyze the variation between migratory and sedentary blackcaps in rachis width and feather mass for tail and primary feathers respectively, but controlling for the effect of sex, age (adult vs juvenile) and feather length. Secondly, we also assessed if the bending stiffness of both tail and primary feathers together are affected by the migratory behaviour of blackcaps. For this, we performed a multivariate analysis of variance (MANOVA) including the bending stiffness of primary and tail feathers as dependent variables; and sex, age and migratory behaviour as factors. Finally, bending stiffness was analyzed separately for each type of feather (primary and tail feather) in order to evaluate the contribution of their corresponding feather structural traits to variation in bending stiffness. In each analysis, age, migratory behaviour and sex were included as factors; while feather length, rachis width and the residuals of feather mass on feather length were used as covariates. These residuals were used instead of feather mass because they provide a size-independent measure, while feather size was already represented by feather length. Thus, positive residuals indicate a greater feather structural complexity of the feather than negative residuals (de la Hera et al. 2009b). In the regression analyses used to calculate these residuals,

feather mass and feather length were significantly correlated to each other, in both tail ($F_{1,118} = 100.13$, $P < 0.001$, $\beta = 0.678$) and primary feathers ($F_{1,118} = 106.57$, $P < 0.001$, $\beta = 0.689$).

Results

After controlling for the significant effect of feather length, adult and sedentary blackcaps showed wider rachis than juvenile and migratory ones, respectively, in both tail and primary feathers (Table 1, Fig. 1A–B). Furthermore, we also detected that males produced feathers with wider rachis than females, an effect which only was significant for tail feathers (Table 1). Accordingly, the analysis of feather mass showed heavier feathers in adult blackcaps in relation to juveniles, but this effect was only significant in tail feathers (Table 1, Fig. 1C–D). However, the observed differences in rachis width did not result in significant variation in feather mass between migratory and sedentary blackcaps (Table 1).

Bending stiffness of feathers depended on age, with adult blackcaps having more stiff tail (univariate result: $F_{1,112} = 29.71$, $P < 0.001$) and primary feathers (univariate result: $F_{1,112} = 13.64$, $P < 0.001$) than juvenile ones (Table 2), as we expected according to differences between age classes in rachis width and feather mass. However, we observed a somewhat counterintuitive pattern of variation in bending stiffness between migratory and sedentary blackcaps: although the feathers of migratory blackcaps had thinner rachis and tended to be lighter (if anything) than the feathers of sedentary blackcaps, they showed higher values of bending stiffness in both tail (univariate result: $F_{1,112} = 4.28$, $P = 0.041$) and primary feathers (univariate result: $F_{1,112} = 5.55$, $P = 0.02$; Table 2).

Overall, long feathers with wide rachis and positive residuals of feather mass on feather length, had higher values of bending stiffness in both tail and primary feathers (Table 3). These feather structural traits accounted for most of the variation that had previously been observed between adult and juvenile blackcaps (Table 3). However, once these effects were controlled for, adult blackcaps still maintained significantly higher values of bending stiffness in tail feathers (Fig. 2). Interestingly, migratory behaviour greatly increased its significance as a factor explaining variation in bending stiffness after controlling for structural feather traits and other effects (Table 3), with migratory blackcaps having much more stiff feathers than sedentary blackcaps (Fig. 2).

Discussion

Migratory blackcaps produced feathers with thinner rachis than their sedentary counterparts, probably as a consequence of constraints imposed by fast plumage development because of the need to migrate (Dawson et al. 2000, de la Hera et al. 2009b). Assuming that feather keratin of all bird species has the same Young's modulus (a physical property that is intrinsic to each material and affects its bending properties; see Bonser and Purslow 1995, Bonser 1996, Dawson et al. 2000 for the case of keratin), bending

Table 1. Results of the GLM analysing the variation in rachis width and feather mass of tail and primary feathers between migratory and sedentary blackcaps in relation to sex, age and feather length.

	Tail feathers						Primary feathers					
	Rachis width			Feather mass			Rachis width			Feather mass		
	β	$F_{1,111}$	P	β	$F_{1,111}$	P	β	$F_{1,111}$	P	β	$F_{1,111}$	P
Feather length	0.229	7.73	0.006	0.632	78.68	<0.001	0.236	6.71	0.011	0.660	83.23	<0.001
Sex		5.20	0.025		0.00	0.949		0.99	0.321		0.26	0.609
Age		22.56	<0.001		4.92	0.029		7.90	0.006		3.00	0.086
Migration		4.92	0.029		1.86	0.176		4.12	0.045		1.04	0.311
Sex × Age		0.45	0.504		0.12	0.730		1.91	0.170		0.16	0.693
Sex × Migration		0.44	0.506		0.54	0.464		0.78	0.380		0.98	0.325
Age × Migration		0.93	0.338		0.00	0.991		0.46	0.501		0.31	0.576
Three way interaction		0.35	0.553		0.37	0.544		1.62	0.206		0.34	0.560

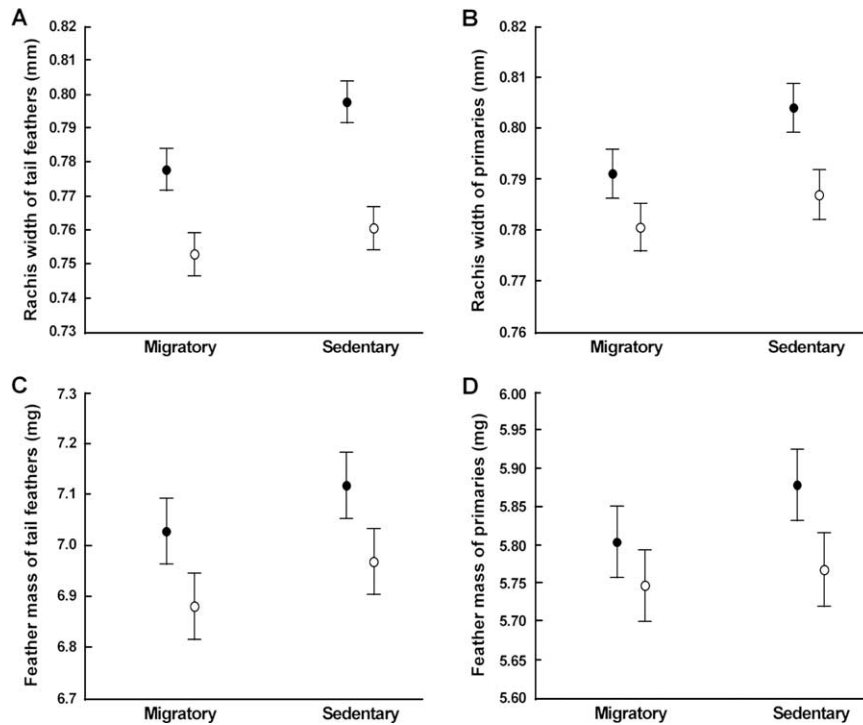


Figure 1. Variation in rachis width (A)–(B) and mass (C)–(D) of tail and primary feathers, in relation to migratory behaviour (migratory vs sedentary) and age (filled dots: adults; open circles: juveniles) of blackcaps. Graphs show the means (\pm SE) adjusted for the effects shown in Table 1.

stiffness of feathers should be directly proportional to the width of the feather rachis (Wainwright et al. 1976, Corning and Biewener 1998, Tubaro 2003). However, although we found a positive correlation between rachis width and bending stiffness across individual blackcaps, migratory individuals (which had feathers with narrower rachis) produced more stiff feathers than sedentary individuals, a difference which even increased controlling for rachis width and other feather traits.

Our results revealed that rachis width and feather mass explain much variation in the mechanical performance of feathers within populations, a widely accepted assumption which remained to be explicitly tested (Dawson et al. 2000, de la Hera et al. 2009b). More interestingly, our results revealed a link between migratory behaviour and the structure and mechanical properties of feathers, which suggested the existence of additional mechanisms that may improve bending stiffness in migratory blackcaps, possibly because natural selection favouring a suitable

mechanical performance of feathers is very high in birds that face two migratory flights (Berthold et al. 2003, Piersma et al. 2005). Given that feather mass and rachis width were controlled for, migratory blackcaps could only improve bending stiffness if they differed from sedentary blackcaps in the allocation of material into different feather structures. With an equal amount of feather material, migrants may increase the thickness of the rachis cortex, although this is unlikely because the reduction of the second moment of area associated with decreasing rachis width would be greater than the gain associated to increasing cortex thickness. Therefore, differential investments by migrants are likely to involve costs. For example, migrants might have reduced the investment of material in other feather structures, such as barbs, which would explain their light and stiff feathers, but would also involve higher susceptibility to feather wear. The existence of such a cost might explain the maintenance of the difference in feather structure and properties between migratory and sedentary blackcaps, a possibility that deserves a more detailed study.

Arguably, the observed patterns could be affected by variation in mechanical fatigue of the feathers between populations or age classes. In the case of differences between migratory and sedentary blackcaps, this confusion is unlikely; one would expect greater mechanical fatigue of feathers in migrants, because the feathers were collected when the latter had already undergone autumn migration. However, mechanical fatigue of feathers could be greater in juvenile than in adult blackcaps, because adult flight feathers develop between one and two months later than juvenile feathers (Shirihai et al. 2001). Whether variation between adult and juvenile blackcaps is caused by a

Table 2. Results of the multivariate analysis of variance MANOVA analyzing the joint variation of tail and primary feather stiffness in relation to sex, age and migratory behaviour.

	Wilks lambda	F _{2,111}	P
Sex	0.960	2.32	0.103
Age	0.779	15.72	<0.001
Migration	0.942	3.40	0.037
Sex × Age	0.984	0.92	0.401
Sex × Migration	0.975	1.43	0.243
Age × Migration	0.989	0.63	0.537
Three way interaction	0.998	0.09	0.918

Table 3. Results of the GLM analysing separately the variation in tail and primary bending stiffness (BS) of feathers, in relation to sex, age, migration and feather traits (feather length, rachis width, and the residual of feather mass on feather length).

	BS of tail feathers			BS of primary feathers		
	β	$F_{1,109}$	P	β	$F_{1,109}$	P
Feather length	0.201	6.68	0.011	0.392	40.30	<0.001
Rachis width	0.291	10.49	0.002	0.167	5.13	0.026
Residual feather mass	0.231	9.23	0.003	0.510	57.38	<0.001
Sex		2.64	0.107		3.28	0.073
Age		6.25	0.014		1.55	0.216
Migration		10.21	0.002		13.01	<0.001
Sex \times Age		1.47	0.228		0.30	0.582
Sex \times Migration		0.29	0.592		0.91	0.341
Age \times Migration		0.02	0.891		0.00	0.973
Three way interaction		0.50	0.481		0.14	0.705

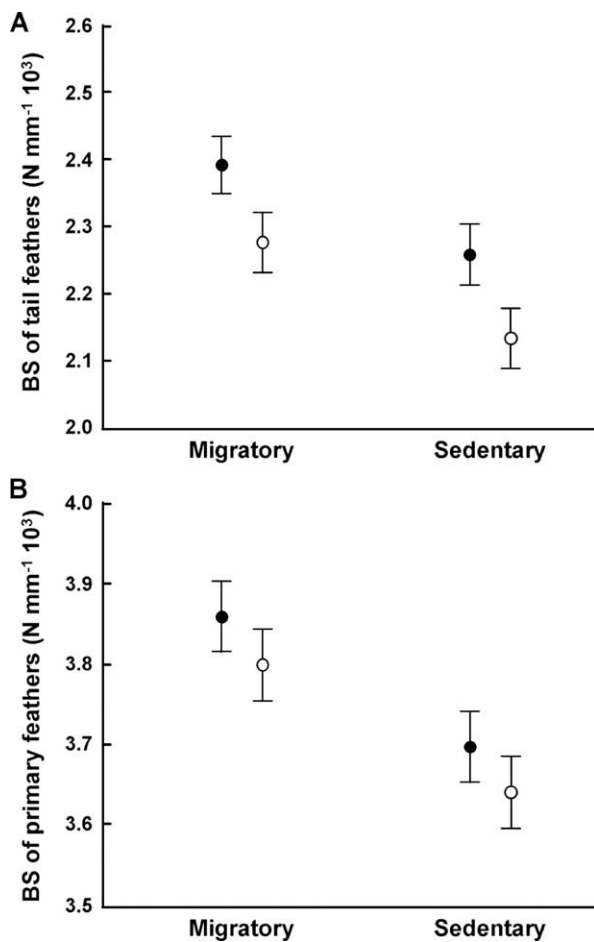


Figure 2. Variation in bending stiffness (BS) of tail (A) and primary feathers (B) between migratory and sedentary blackcaps, and age classes (filled dots: adults; and open circles: juveniles). Graphs show means (\pm SE) adjusted for the effects shown in Table 3.

systematic age-dependent difference in mechanical fatigue, or because of intrinsic differences in the structure of adult and juvenile feathers, the fact that adults and juveniles differ in bending stiffness is an important finding that may contribute to explain age-dependent survival probabilities in natural bird populations.

Acknowledgements – This study was funded by the Spanish Ministry of Science and Technology (projects CGL2004-02744/BOS and CGL2007-62937/BOS) and the Dept of Education, Univ. and Research of the Basque Government (a PhD studentship to IH). We are particularly indebted to Thord Lundgren and Kent Persson (Div. of Struct. Mechan., Lund Inst. of Technology, Lund Univ.) for their invaluable help during the analyses of bending stiffness.

References

- Berthold, P. 1975. Migration: control and metabolic physiology. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds), *Avian biology*. Vol. 5. Academic Press, pp. 77–128.
- Berthold, P., Gwinner, E. and Sonnenschein, E. 2003. *Avian migration*. – Springer.
- Bonier, F., Martin, P. R., Jensen, J. P., Butler, L. K., Ramenofsky, M. and Wingfield, J. C. 2007. Pre-migratory life history stages of juvenile arctic birds: costs, constraints, and trade-offs. – *Ecology* 88: 2729–2735.
- Bonser, R. H. C. 1996. The mechanical properties of feather keratin. – *J. Zool.* 239: 477–484.
- Bonser, R. H. C. and Purslow, P. P. 1995. The Young's modulus of feather keratin. – *J. Exp. Biol.* 198: 1029–1033.
- Borguodd, J. 2003. Mechanical properties of bird feathers: influence of UV-radiation and mechanical fatigue. – Lund Techn. Univ., report TVSM-5121.
- Corning, W. R. and Biewener, A. A. 1998. In vivo strains in pigeon flight feather shafts: implications for structural design. – *J. Exp. Biol.* 201: 3057–3065.
- 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 starlings *Sturnus vulgaris*. – *Ibis* 146: 93–500.
- Dawson, A., Hinsley, S. A., Ferns, P. N., Bonser, R. H. C. and Eccleston, L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. – *Proc. R. Soc. B* 267: 2093–2098.
- de la Hera, I., Díaz, J. A., Pérez-Tris, J. and Tellería, J. L. 2009a. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. – *J. Avian Biol.* 40: 461–465.
- de la Hera, I., Pérez-Tris, J. and Tellería, J. L. 2007. Testing the validity of discriminant function analyses based on bird morphology: the case of migratory and sedentary blackcaps *Sylvia atricapilla* wintering in southern Iberia. – *Ardeola* 54: 81–91.

- de la Hera, I., Pérez-Tris, J. and Tellería, J. L. 2009b. Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird. – *Biol. J. Linn. Soc.* 97: 98–105.
- Hall, K. S. S. and Fransson, T. 2000. Lesser whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. – *J. Avian Biol.* 31: 583–587.
- Jenni, L. and Winkler, R. 1994. Moulting and ageing of European passerines. – Academic Press.
- Pérez-Tris, J. and Tellería, J. L. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. – *J. Anim. Ecol.* 71: 211–224.
- Pérez-Tris, J., Carbonell, R. and Tellería, J. L. 1999. A method for differentiating between sedentary and migratory blackcaps *Sylvia atricapilla* in wintering areas of southern Iberia. – *Bird Study* 46: 299–304.
- Piersma, T., Pérez-Tris, J., Mouritsen, H., Bauchinger, U. and Bairlein, F. 2005. Is there a 'migratory syndrome' common to all migrant birds? – *Ann. NY Acad. Sci.* 1046: 282–293.
- Serra, L., Griggio, M., Licheri, D. and Pilastro, A. 2007. Moulting speed constrains the expression of a carotenoid-based sexual ornament. – *J. Evol. Biol.* 20: 2028–2034.
- Shirihai, H., Gargallo, G. and Helbig, A. J. 2001. *Sylvia* warblers. – Princeton Univ. Press.
- StatSoft Inc. 2002. STATISTICA (data analysis software system), ver. 6. – StatSoft Inc., Tulsa.
- Svensson, L. 1992. Identification guide to European Passerines. – L. Svensson, Stockholm.
- Tubaro, P. L. 2003. A comparative study of aerodynamic function and flexural stiffness of outer tail feathers in birds. – *J. Avian Biol.* 34: 243–250.
- Videler, J. J. 2005. Avian flight. – Oxford Univ. Press.
- Wainwright, S. A., Biggs, W. D., Currey, J. D. and Gosline, J. M. 1976. Mechanical design in organisms. – Princeton Univ. Press.
- Weber, T. P., Borgudd, J., Hedenström, A., Persson, K. and Sandberg, G. 2005. Resistance of flight feathers to mechanical fatigue covaries with moulting strategy in two warbler species. – *Biol. Lett.* 1: 27–30.