Flight feather shaft structure of two warbler species with different moult schedules: a study using high-resolution X-ray imaging

T. P. Weber[1], S. Kranenbarg[2], A. Hedenström[3], J. H. Waarsing[4] & H. Weinans[4]

1 Department of Animal Ecology, Lund University, Lund, Sweden
2 Experimental Zoology Group, WIAS, Wageningen University, Wageningen, The Netherlands
3 Department of Theoretical Ecology, Lund University, Lund, Sweden
4 Orthopaedic Research Laboratory, Erasmus Medical Centre, Erasmus University, Rotterdam, The Netherlands

Abstract

Plumage constitutes a significant component of the somatic investment of birds. A detailed investigation of feathers and moult can help to uncover trade-offs involved in somatic investment decisions, the sources of some of the costs birds have to pay and the potential fitness consequences. We used micro-computed tomography imaging to study the second moment of area, a structural parameter that is one determinant of bending stiffness and the cortex volume of flight feather shafts of two sister taxa, the willow warbler *Phylloscopus trochilus*, a migratory species with two annual moults, and the chiffchaff *Phylloscopus collybita*, a migrant with one annual post-nuptial moult. Juvenile and adult willow warbler and chiffchaff feathers, all grown on the breeding grounds, are structurally very similar to each other. Willow warbler feathers grown during moult on the wintering grounds, however, have a significantly higher second moment of area and a significantly larger cortex volume than all the other feather types. We discuss the possibility that the seasonal variability of willow warbler feathers may be an adaptive structural reflection of a moult–migration strategy that has allowed this species to occupy large breeding and wintering ranges.

Introduction

Feathers make up *c*. 30% of the protein dry mass of a bird's body (Murphy, 1996) and thus constitute a significant share of the total somatic investment. A detailed investigation of feathers and moult can therefore help to reveal the trade offs involved in somatic investment decisions, the sources of some of the costs birds have to pay during their annual cycle and the associated fitness consequences. Plumage can reveal such costs and trade-offs in at least two ways. (1) Limited resources are invested in competing activities. Somatic costs are paid when resources devoted to, for example, reproduction are traded-off against demands of self-maintenance, that is, in the case of feathers moult. Thus, breeding–moult or moult–migration overlap may lead to lower energetic investment in feathers and hence, lower quality feathers. (2) High work load can directly affect the degradation of feathers through increased exposure to UV-B radiation (Bergman, 1982; Borgudd, 2003) and keratin-degrading bacteria (Burtt & Ichida, 1999), higher contact rates with abrasive vegetation and more cycles of bending during flapping flight (Weber *et al.*, 2005).

Recently, a number of mechanisms underlying trade-offs involved in moult have been investigated in some detail.

Dawson *et al.* (2000) demonstrated, for instance, that an increased rate of moult results in a lowered stiffness of flight feather shafts in starlings *Sturnus vulgaris* and McGraw, Hill & Parker (2005) showed that American goldfinches *Carduelis tristis* experiencing food restriction during moult incorporate smaller amounts of carotenoids and grow less colourful feathers. Sanz *et al.* (2004) and Martin (2005) found that there is an energetic trade-off between moult and immunity. Pap *et al.* (2008) could detect a strong effect of diet quality, but no effect of immune response on feather quality. Susceptibility to mechanical fatigue, however, remains a neglected component of the study of feather design. In materials science, fatigue refers to the damage and failure of materials under cyclic loads (Suresh, 1998). Static strength determined in tensile tests is not necessarily an appropriate measure of the strength of a structure under the cyclic imposition of small loads. One of the main reasons for this is the formation and accumulation of fatigue micro-cracks that result in the progressive degradation of mechanical properties. Cyclic loads, well below the static strength, may thus have significant biological effects. Bones can suffer from injuries caused by cyclic loading (Daffner & Pavlov, 1992; Lee *et al.*, 2003) and the repeated loading of wave-swept macroalgae can lead to complete fracture within a few

days (Mach *et al.*, 2007; Mach, 2009). In contrast to bones or algae, fully grown feathers are dead structures and incapable of repair. Therefore, any damage will accumulate.

For flight feathers, not only the risk of breakage and thus feather loss, but also the progressive degradation of bending stiffness may reduce performance. Flight feathers of long-distance migrants experience a large number of bending cycles – a small passerine migrating from Europe to Southern Africa will flap its wings *c.* 40 million times during one migratory journey. There are several reasons why reduced flexural stiffness of flight feathers may reduce flight performance. The shaft curvature and dorso-ventral flexural stiffness act passively to create appropriate pitching moments and an optimal angle of attack during the course of the downstroke (Norberg, 1985). A loss of feather stiffness may affect this mechanism adversely (away from the optimum) resulting in a reduced aerodynamic force. Also, a reduced stiffness will make the feather tip bend upwards under an increasing aerodynamic load. Because the aerodynamic lift is normal to the local flow direction, the resulting lift will tilt in a spanwise direction towards the feather attachment, with an associated reduction in the normal force component. A comparative study showed that flexural stiffness decreases with increasing body size, presumably to reduce the risk of feather failure by allowing more bending under aerodynamic load during take off and landing (Worcester, 1996). However, only scant circumstantial empirical evidence supports the prediction that lowered flexural stiffness affects flight performance. For instance, Williams & Swaddle (2003) showed for the European starling *S. vulgaris* that old, but apparently undamaged flight feathers impair escape flight performance. Bending stiffness was not measured, but this finding suggests that the mechanical properties of feathers that degrade over time might be behind the impaired flight performance.

The function of moult is to maintain plumage function. There is considerable variation in the temporal and spatial scheduling of moult for both non-migratory and migratory birds (Svensson & Hedenström, 1999; Barta *et al.*, 2006, 2008) and this variation provides us with an opportunity to study the proximate mechanisms behind life-history trade-offs and their resolution under different ecological circumstances. The old world warblers, family Sylviidae, have attracted considerable attention because they show interesting variation with respect to moult and migration schedules (Svensson & Hedenström, 1999). The adults of most species moult flight feathers once per year after breeding and embark on migration to the wintering grounds with fresh feathers. Some species moult once on the wintering grounds and willow warblers *Phylloscopus trochilus* moult twice per year, once on the breeding grounds and once on the wintering grounds (Salomonsen, 1945; Prŷs-Jones, 1991; Underhill *et al.*, 1992). Great reed warblers *Acrocephalus arundinaceus* moult on the stopover during migration (Hedenström *et al.*, 1993). The ultimate causes behind this variation are still unclear, but theoretical work suggests that temporal and spatial variations in food supply are responsible (Barta *et al.*, 2008).

Weber *et al.* (2005) have shown that flight feathers of willow warblers, a migratory species with two annual moults, fatigue faster than flight feathers of the closely related chiffchaff *Phylloscopus collybita*, which follows the more common pattern for the Sylviidae warblers of moulting only once each year immediately after breeding (Fig. 1). Weber *et al.* (2005) find that the shafts (rachis) of willow warbler flight feathers have a larger outer diameter than the shafts of the chiffchaffs' flight feathers. They argue that this co-variation between fatigue and structure suggests a possible trade-off between a material and a structural property of the rachis. Physiological stress during moult may force birds to deposit low-quality keratin in the growing feathers (see Murphy, King & Lu, 1988; Dawson *et al.*, 2000). An increased diameter stiffens the rachis and compensates for a lower keratin quality. This may, however, cause a higher rate of fatigue damage accumulation in the outer layers of the rachis because of the constant radius of curvature strains that are proportional to the distance from the unstretched and uncompressed midline (Fig. 2a). The outer diameter of the feather shaft is, though, not a reliable measure of the structural contribution to bending stiffness. The bending stiffness of the rachis is proportional to the product of a material property, the elastic modulus E (mechanical stress divided by strain) of keratin and a property of shape, the second moment of area I of the rachis. I is defined as $\int y^2 \, dA$, where y is the perpendicular distance of a cross-sectional element of the rachis from the neutral bending plane (Fig. 2b). Fatigue is mediated by the geometry of the rachis and the static strength of keratin may not accurately predict a feather's durability (for perspectives from material science, see van Paepegem & Degrieck, 2001). The web of causality between life-history decisions, feather shaft structure and mechanical fatigue is likely to be complex, but quantitative structural data are one crucial step towards developing models of structure–performance relationships.

Materials and methods

Feather samples

Intact and complete feathers were collected from birds trapped in the course of routine ringing operations during spring and autumn migrations 2002–2004 at the Ottenby Bird Observatory (Öland, Sweden). One innermost primary flight feather P1 was plucked from each bird in the sample, placed into a plastic bag and subsequently stored in a sealed container at room temperature. Only feathers without visible growth deformities were used in the tests. We used 23 feathers from willow warblers and 19 feathers from chiffchaffs.

Micro-computed tomography (μ-CT) imaging

The entire, intact feathers were placed in a vertical position inside the measuring chamber of a Skyscan®1072 μ-CT imaging system (Antwerps, Belgium). One rachis segment of each feather was scanned at 80 kV and 100 μA and with a

Phylloscopus collybita   *Phylloscopus trochilus*
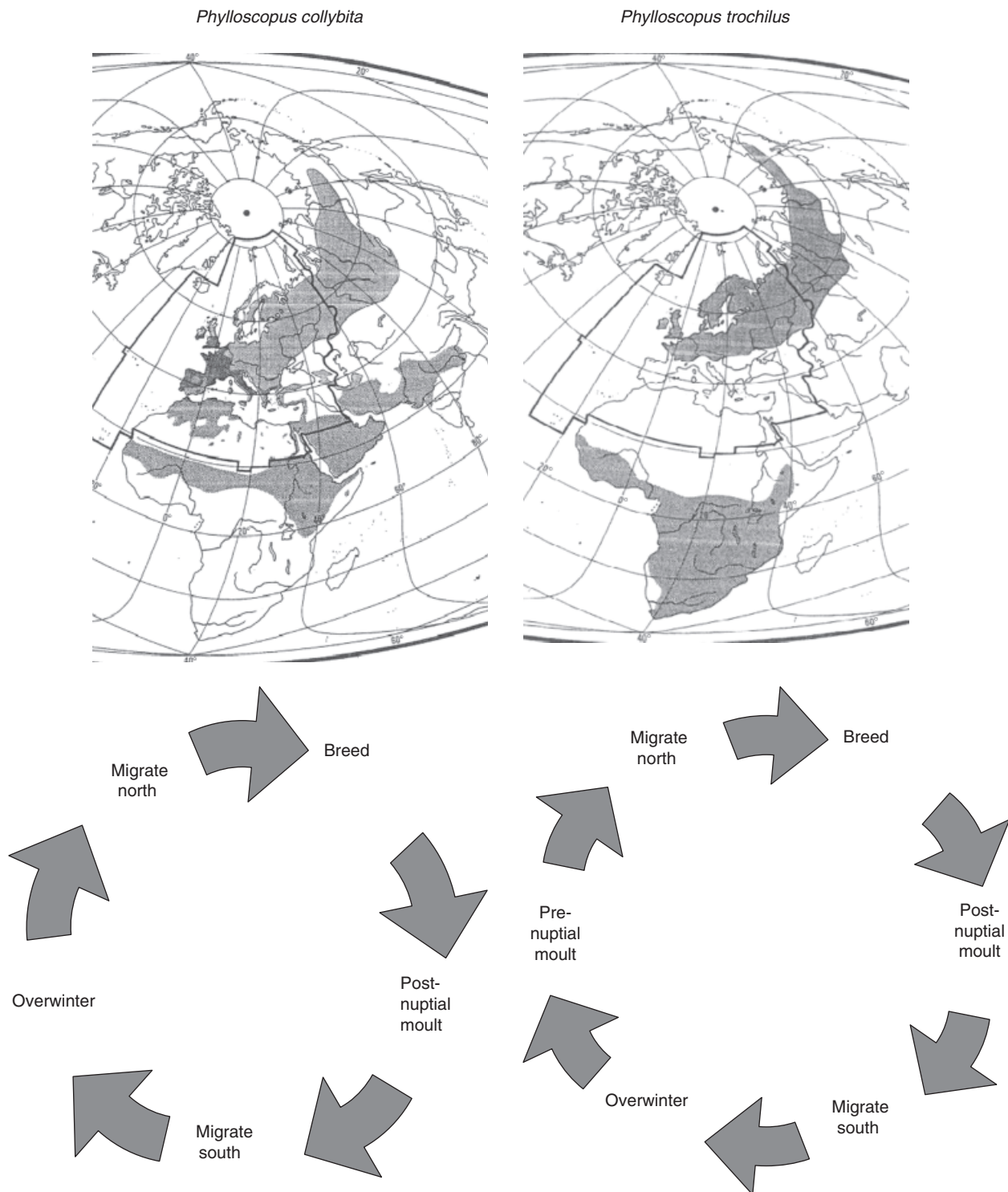
Figure 1 Geographic distribution (Cramp & Simmons, 1992) and annual routines of chiffchaffs *Phylloscopus collybita* and willow warblers *Phylloscopus trochilus*. The dark grey region in the distribution map of the chiffchaff serves as both summer and winter area.

volume element (voxel) size of 2.73 μm. The measured segment was always located approximately halfway along the length of the shaft. The tip-to-tip length of the feathers (ignoring their curvature) does not differ between the two species (in the following, results are means ± SE; willow warbler: mean length = 46.47 ± 9.69 mm; chiffchaff: mean length = 46.29 ± 10.61 mm; $t = 0.79$, d.f. = 40, $P = 0.43$). When placing the feather into the measuring chamber, we

(a)

Length, *L*

Tension
Original length, *L*
Compression

(b)

y1 y2 y3
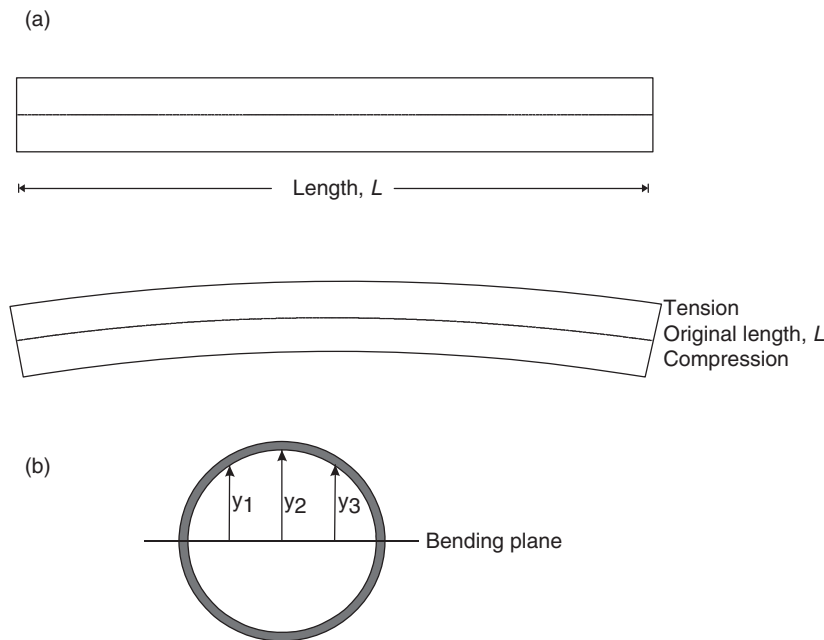
Bending plane

Figure 2 (a) Schematic lateral view of a straight and a bent rachis segment. The midline represents the neutral plane, which is neither stretched nor compressed during bending. Tension increases linearly from the midline to the top layer. (b) Schematic cross section through a rachis. The arrows y_{1-3} denote the distances of three infinitesimal cross-sectional elements on the inside of the cortex from the neutral bending plane.

could not entirely correct for variations in feather length. In longer-than-average feathers, we therefore measured segments relatively closer to the calamus and in shorter-than-average feathers segments closer to the tip. As the second moment of area varies linearly in and around the scanned regions, we therefore used feather length as a covariate in the statistical analysis.

Image processing

The scans were reconstructed using a Feldkamp cone-beam reconstruction algorithm (Feldkamp, Davis & Kress, 1984). The keratin shell of the rachis was identified using a local thresholding algorithm (Waarsing, Day & Weinans, 2004). Especially when thin structures are present in scans, this method results in better segmentations, that is, the identification of distinct regions in the original greyscale dataset, than when one global threshold value would have been applied. This segmentation procedure yielded a stack of bitmaps, representing a series of 900 cross sections along a 2.457-mm-long segment of the feather shaft. The bitmaps were subsequently hand edited to remove any parts that did not belong to the rachis. The hand editing was always done by the same investigator (T. P. W.). Figure 3a shows one reconstructed cross section of a willow warbler feather, Fig. 3b the same cross section after segmentation and Fig. 3c the cross section after editing with the two perpendicular principal axes used to calculate the second moments of area. The images sometimes showed gaps in the lateral wall of the shafts (see Fig. 3b and c). There were in fact no gaps in the shaft and this phenomenon is a result of the image reconstruction and editing process: (1) portions of the lateral walls of the shaft are in some cases so thin that they cannot be resolved in the image processing; (2) during hand editing, it often proved difficult to determine the limit of the shaft in

the regions where barbs emerge and are close to the shaft; the removal of small volumes belonging to the lateral wall of the shaft only leads to a very small underestimation of the dorso-ventral second moment of area, because these volume elements are very close to the dorso-ventral bending axis.

Structural analysis

Each stack of bitmaps representing a scanned feather shaft segment was read into a three-dimensional matrix. The volume of keratin in the scanned shell (cortex) segment was determined by counting the number of matrix elements representing keratin in the dataset, multiplied by the voxel volume of 20.35 μm^3. The dorso-ventral and lateral bending axes were determined as the two principal axes of an anterior–posterior projection of each cross section (Nash, 1977; Kranenbarg *et al.*, 2005). The second moments of area were averaged over all images of each scan. All calculations were performed in MATLAB® 7.0.

Results

The general morphology of the rachis is very similar in the two species. The rachis has an approximate shape of a box girder; it consists of a compact shell (cortex) and is filled by the substantia medullaris, which contains air-filled dead cells and which is not visible in the scans. Neither transverse septa, a ventral grove nor dorsal ridges could be observed in the scanned segments (for a comparison with pigeon primary feathers, see Purslow & Vincent, 1978); septa can, however, be seen in the more proximal parts of the shaft (data not shown). Both lateral portions of the cortex from which the feather vane projects, are very thin. The central portion of the dorsal region and both ventral corners of the rachis are reinforced. The rachis is mainly designed to

(a)

(b)

0.22 mm

(c)
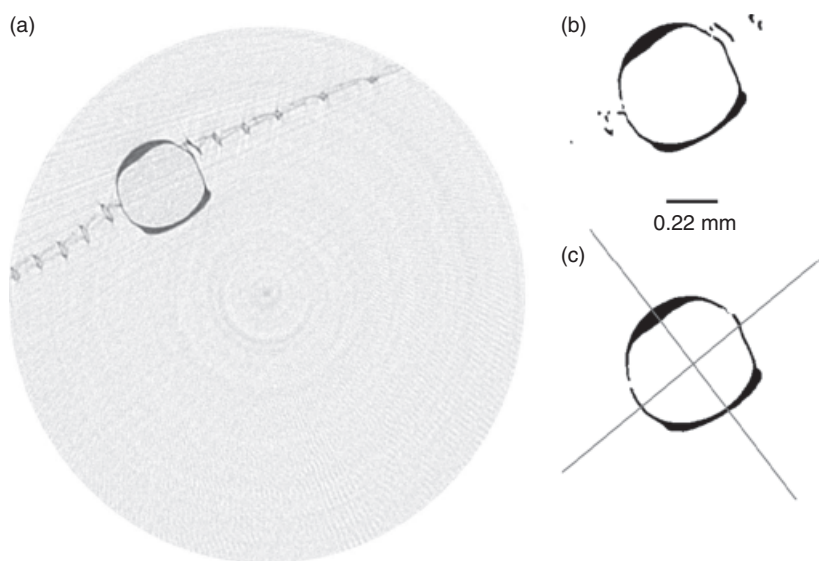
Figure 3 (a) One reconstructed scan (frame 309) of a willow warbler *Phylloscopus trochilus* flight feather. (b) Segmented scan and (c) edited scan with the two principal axes. The scale bar only applies to (b) and (c).

withstand dorso-ventral bending; generally, the second moment of area with respect to the dorso-ventral axis is roughly twice as big as the values with respect to the lateral axis (we only report values of I with respect to dorso-ventral bending).

There is a strong positive relationship between cortex volume and the second moment of area I; this applies to the pooled data ($r = 0.88$, $n = 42$, $P < 0.0001$) and for each single species (willow warbler: $r = 0.82$, $n = 23$, $P < 0.0001$; chiffchaff: $r = 0.92$, $n = 19$, $P < 0.0001$). In previous measurements, we determined the stiffness values of a subset (18 out of 42; 10 from willow warblers and eight from chiffchaffs) of the feathers in our sample (Borgudd, 2003; Weber *et al.*, 2005). There is a positive relationship between bending stiffness and the second moment of area I, which is only significant for the pooled data (Fig. 4; all individuals pooled: $r = 0.65$, $n = 18$, $P = 0.003$).

In willow warblers, we can distinguish between juvenile feathers and two adult feather groups: feathers moulted on the wintering (pre-nuptial) or on the breeding grounds (post-nuptial). The second moment of area I differs significantly between the three groups (Fig. 5a; ANCOVA, $F(2,19) = 4.85$, $P < 0.02$). I is largest for adult feathers grown during the pre-nuptial moult on the wintering grounds ($1.38 \times 10^{-3} \pm 4 \times 10^{-4}\,\text{mm}^4$); second moments of the area are smaller for both juvenile feathers ($9.7 \times 10^{-4} \pm 2.9 \times 10^{-4}\,\text{mm}^4$; Scheffé *post hoc* test, $P < 0.0002$) and adult feathers grown during the post-nuptial moult ($1.1 \times 10^{-3} \pm 2.5 \times 10^{-4}\,\text{mm}^4$; Scheffé *post hoc* test, $P = 0.0047$). Also, the amount of keratin in the cortex of the scanned rachis segment differs significantly between the three groups of willow warbler feathers (Fig. 5b; ANCOVA, $F(2,19) = 4.40$, $P < 0.027$). Only the difference between juvenile feathers ($0.065 \pm 0.02\,\text{mm}^3$) and pre-nuptial adult feathers ($0.078 \pm 0.023\,\text{mm}^3$) is significant (Scheffé *post hoc* test, $P = 0.001$).

In the chiffchaff, neither second moments of area (ANCOVA, $F(1,16) = 1.06$, $P = 0.32$) nor cortex volumes
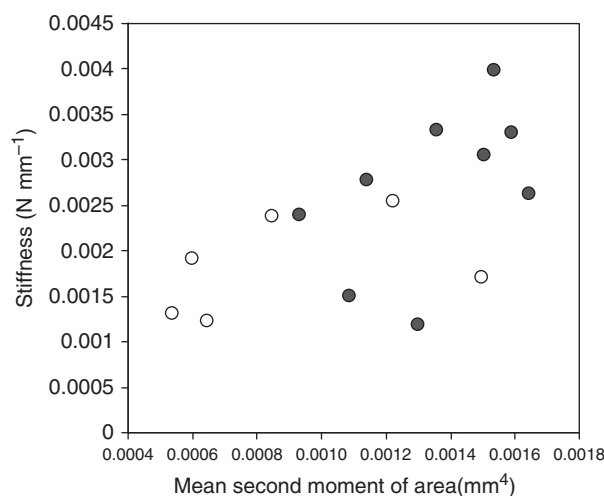
Figure 4 The relationship between second moment of area I and stiffness for a subset of the feathers used in the imaging. The open circles represent chiffchaff *Phylloscopus collybita* feathers, and the closed circles represent willow warbler *Phylloscopus trochilus* feathers.

(ANCOVA, $F(1,16) = 4.21$, $P = 0.057$) differ significantly between juvenile and adult feathers.

Feathers from juvenile willow warblers have significantly more keratin in the scanned cortex segments than feathers from juvenile chiffchaffs (0.065 ± 0.02 vs. $0.057 \pm 0.023\,\text{mm}^3$; ANCOVA, $F(1,19) = 5.92$, $P < 0.025$), but the second moments of area are not significantly different (ANCOVA, $F(1,19) = 0.84$, $P = 0.37$). Adult willow warbler feathers grown on the wintering grounds have significantly larger second moments of area than adult chiffchaff feathers grown in the northern summer after breeding ($1.38 \times 10^{-3} \pm 4 \times 10^{-4}$ vs. $1.0 \times 10^{-3} \pm 2.5 \times 10^{-4}\,\text{mm}^4$; Scheffé *post hoc* test, $P < 0.001$). Also, the cortex volume differs significantly
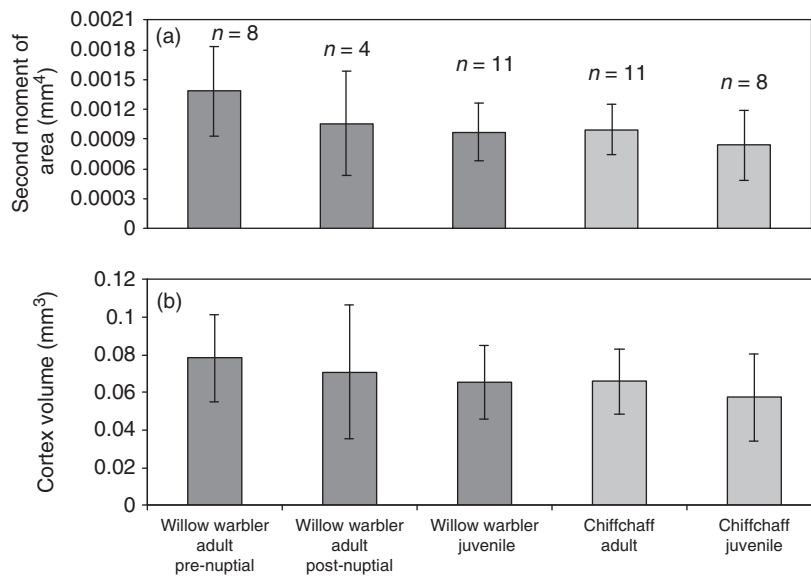
Figure 5 (a) Mean second moment of area I ($\pm$ SE) and (b) mean cortex volume ($\pm$ SE) for all classes of willow warbler *Phylloscopus trochilus* (dark grey) and chiffchaff *Phylloscopus collybita* feathers (light grey). Note that in the statistical comparison, feather length was used as a covariate that accounts for some of the variability.

between the three different types of adult feathers from the two species (ANCOVA, $F(2,16) = 6.85$, $P < 0.007$); only the volume difference between adult pre-nuptial feathers from the willow warbler and adult chiffchaff feathers is significant (0.078 ± 0.023 and $0.067 \pm 0.017 \, \text{mm}^3$, respectively; Scheffé *post hoc* test, $P < 0.001$).

Discussion

There are at least two potential adaptive explanations why willow warblers moult twice annually: (1) the metabolic cost of moult may be comparatively low allowing two moults (Barta *et al.*, 2008); (2) their annual cycle may place such high demands on their feathers that they have to moult twice – either the feathers face many insults during the year or their moult schedule is so tight that they cannot grow high-quality, fatigue-resistant feathers. We do not have information on metabolic costs of moult in willow warblers or chiffchaffs; hence, we limit our discussion to the second point.

Willow warblers are likely to experience a tighter annual routine with average longer migration episodes and shorter northerly summers than most chiffchaff populations. Underhill *et al.* (1992) showed that in some populations of willow warblers, post-nuptial moult on the breeding grounds is only half as long as the pre-nuptial moult on the wintering grounds and Hedenström, Lindström & Pettersson (1995) found an increasing incidence of interrupted post-nuptial moult (moult starts on the breeding ground, is arrested and continued in the winter quarters) the further north willow warbler populations breed. We demonstrate that willow warbler feathers grown during the post-nuptial moult on the breeding grounds incorporate less keratin in the feather shaft and have a lower second moment of area than feathers grown during the moult on the wintering grounds. This appears to suggest that time stress is occur-

ring late in summer (e.g. Dawson *et al.*, 2000) and that low-quality feathers might be the result. However, these post-nuptial feathers of the willow warbler are structurally very similar to chiffchaff feathers that are kept for an entire year. Furthermore, the large and thus apparently robust willow warbler feathers grown on the wintering grounds have high rates of fatigue (Weber *et al.*, 2005). The robustness of feathers from the pre-nuptial moult may thus be deceptive. Willow warblers may, in fact, be able to grow robust feathers in summer and not in winter. Underhill *et al.* (1992) also demonstrated that willow warblers moult during the dry season on their wintering grounds in western Africa and that the long moult duration may be a response to low food availability during this period. Feathers grown during long moults under nutritional limitation are also likely to be of low quality (e.g. Pap *et al.*, 2008). The large second moments of area of the feathers grown on the wintering grounds may thus be an expression of the possible trade-off suggested by Weber *et al.* (2005): birds could control stiffness of the feather shaft by adjusting the second moment of area to low-quality keratin and they may pay for this with high fatigue rates. In order to test this hypothesis, we need, however, to measure reliably small variations of mechanical and structural properties of feather keratin. Adapting models that originally were developed for studying fatigue damage accumulation in bones (e.g. Griffin *et al.*, 1997) to keratin will also help to investigate design principles of and possible trade-offs in feather structure.

We can, although, interpret the moult strategy of willow warblers preliminarily in the following manner: willow warblers may either be in the process of losing one moult – according to our line of argument, they should lose the pre-nuptial moult on their wintering grounds because fatigue-prone feathers are produced – or they may obtain fitness gains from keeping both. The willow warbler has exceptionally large wintering and breeding ranges. Two complete

moults could have allowed willow warblers to invade new ecological niches: new habitats may place high demands on feathers such as high UV-B levels, abrasive vegetation or increased migration distance, but the costs of two moults and of having feathers that grow under time or nutrient stress and fatigue fast may be compensated for by reaping the benefits of using new habitats and by maintaining a high average feather quality throughout the entire annual cycle (Svensson & Hedenström, 1999; Rohwer, Butler & Froehlich, 2005). The structural patterns we document here – a higher season-dependent structural variability for willow warbler feathers than for chiffchaff feather – may be an expression of this evolutionary strategy.

Acknowledgements

References

Barta, Z., Houston, A.I., McNamara, J.M., Hedenström, A., Weber, T.P. & Feró, O. (2006). Annual routines of non-migratory birds: optimal moult strategies. *Oikos* **112**, 580–593.

Barta, Z., McNamara, J.M., Houston, A.I., Weber, T.P., Hedenström, A. & Feró, O. (2008). Optimal moult strategies in migratory birds. *Philos. Trans Roy. Soc. Lond. Ser. B* **363**, 211–229.

Bergman, G. (1982). Why are the wings of *Larus f. fuscus* so dark? *Ornis Fenn.* **59**, 77–83.

Borgudd, J. (2003). *Mechanical properties of bird feathers – influence of UV-radiation and mechanical fatigue*. Report TVSM-5121, Lund Technical University.

Burtt, E.H. Jr & Ichida, J.M. (1999). Occurrence of feather-degrading bacilli in the plumage of birds. *Auk* **116**, 364–372.

Cramp, S. & Simmons, K.E.L. (1992). *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic: warblers*, Vol. 6. Oxford: Oxford University Press.

Daffner, R.H. & Pavlov, H. (1992). Stress fractures: current concepts. *Am. J. Roentgenol.* **159**, 245–252.

Dawson, A., Hinsley, S.A., Ferns, P.N., Bonser, R.H.C. & Eccleston, L. (2000). Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc. Roy. Soc. Lond. Ser. B* **267**, 2093–2098.

Feldkamp, L.A., Davis, L.C. & Kress, J.W. (1984). Practical cone-beam algorithm. *J. Opt. Soc. Am. A* **1**, 612–619.

Griffin, L.V., Gibeling, J.C., Martin, R.B., Gibson, V.A. & Stover, S.M. (1997). Model of flexural fatigue damage accumulation for cortical bone. *J. Orthop. Res.* **15**, 607–614.

Hedenström, A., Bensch, S., Hasselquist, D., Lockwood, M. & Ottosson, U. (1993). Migration, stopover and moult of the great reed warbler *Acrocephalus arundinaceus* in Ghana, West Africa. *Ibis* **135**, 177–180.

Hedenström, A., Lindström, Å. & Pettersson, J. (1995). Interrupted moult of adult willow warblers *Phylloscopus trochilus* during autumn migration through Sweden. *Ornis Svecica* **5**, 69–74.

Kranenbarg, S., Waarsing, J.H., Muller, M., Weinans, H. & van Leeuwen, J.L. (2005). Lordotic vertebrae in sea bass (*Dicentrarchus labrax* L.) are adapted to increased loads. *J. Biomech.* **38**, 1239–1246.

Lee, T.C., Mohsin, S., Taylor, D., Parkesh, R., Gunnlaugsson, T., O'Brien, F.J., Giel, M. & Gowin, W. (2003). Detecting microdamage in bone. *J. Anat.* **203**, 161–172.

Mach, K.J. (2009). Mechanical and biological consequences of repetitive loading: crack initiation and fatigue failure in the red macroalga *Mazzaella*. *J. Exp. Biol.* **212**, 961–976.

Mach, K.J., Hale, B.B., Denny, M.W. & Nelson, D.W. (2007). Death by small force: a fracture and fatigue analysis of wave-swept macroalgae. *J. Exp. Biol.* **210**, 2231–2243.

Martin, L.B. (2005). Trade-offs between molt and immune activity in two populations of house sparrows (*Passer domesticus*). *Can. J. Zool.* **83**, 780–787.

McGraw, K.J., Hill, G.E. & Parker, R.S. (2005). The physiological costs of being colourful: nutritional control of carotenoid concentration in the American goldfinch, *Carduelis tristis*. *Anim. Behav.* **69**, 653–660.

Murphy, M.E. (1996). Energetics and nutrition of molt. In *Avian energetics and nutritional ecology*: 158–199. Carey, C. (Ed.). New York: Chapman & Hall.

Murphy, M.E., King, J.R. & Lu, J. (1988). Malnutrition during postnuptial molt of white-crowned sparrows: feather growth and quality. *Can. J. Zool.* **66**, 1403–1413.

Nash, W.A. (1977). *Strength of materials. Schaum's Outline Series*, 2nd edn. New York: McGraw-Hill.

Norberg, R.Å. (1985). Function of vane asymmetry and shaft curvature in bird flight feathers; inferences in flight ability of *Archaeopteryx*. In *The beginning of birds. Proceedings of the International Archeopteryx Conference, Eichstätt, 1984*: 303–318. Hecht, M.K., Ostrom, J.H., Viohl, G. & Wellnhofer, P. (Eds) Freunde des Jura-Museums, Eichstätt.

Pap, P.L., Vágási, C.S., Czirják, G.Á. & Barta, Z. (2008). Diet quality affects postnuptial molting and feather quality of the house sparrow (*Passer domesticus*): interaction with humoral response? *Can. J. Zool.* **86**, 834–842.

Prŷs-Jones, R.P. (1991). The occurrence of biannual primary moult in passerines. *Bull. Br. Ornithol. Club* **111**, 150–152.

Purslow, P.P. & Vincent, J.F.V. (1978). Mechanical properties of primary feathers from the pigeon. *J. Exp. Biol.* **72**, 251–260.

Rohwer, S., Butler, L.K. & Froehlich, D.R. (2005). Ecology and demography of east–west differences in molt scheduling of Neotropical migrant Passerines. In: *Birds of two worlds: the ecology and evolution of migration*: 87–105. Greenberg, R. & Marra, P.P. (Eds). Baltimore: The Johns Hopkins University Press.

Salomonsen, F. (1945). Notes on the variation and moult in the willow-warbler (*Phylloscopus trochilus* (L.)). *Ark Zool.* **36**, 1–13.

Sanz, J.J., Moreno, J., Merino, S. & Tomás, G. (2004). A trade-off between two resource-demanding functions: post-nuptial moult and immunity during reproduction in male pied flycatchers. *J. Anim. Ecol.* **73**, 441–447.

Suresh, S. (1998). *Fatigue of materials*. Cambridge: Cambridge University Press.

Svensson, E. & Hedenström, A. (1999). A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *Biol. J. Linn. Soc.* **67**, 263–276.

Underhill, L.G., Prŷs-Jones, R.P., Dowsett, R.J., Herroelen, P., Johnson, D.N., Lawn, M.R., Norman, S.C., Pearson, D.J. & Tree, A.J. (1992). The biannual primary moult of willow warblers *Phylloscopus trochilus* in Europe and Africa. *Ibis* **134**, 286–297.

van Paepegem, W. & Degrieck, J. (2001). Fatigue damage modeling of fibre-reinforced composite materials: review. *Appl. Mech. Rev.* **54**, 279–299.

Waarsing, J.H., Day, J.S. & Weinans, H. (2004). An improved segmentation method for in vivo µCT scanning. *J. Bone Miner. Res.* **19**, 1640–1650.

Weber, T.P., Borgudd, J., Hedenström, A., Persson, K. & Sandberg, G. (2005). Resistance of flight feathers to mechanical fatigue covaries with moult strategy in two warbler species. *Biol. Lett.* **1**, 27–30.

Williams, E.V. & Swaddle, J.P. (2003). Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. *J. Avian Biol.* **34**, 371–378.

Worcester, S.E. (1996). The scaling of the size and stiffness of primary feathers. *J. Zool. (Lond.)* **239**, 609–624.