

## THE YOUNG'S MODULUS OF FEATHER KERATIN

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Accepted 13 December 1994

### Summary

**The flexural stiffness of the rachis varies along the length of a primary feather, between primaries and between species; the possible contribution of variations in the longitudinal Young's modulus of feather keratin to this was assessed. Tensile tests on compact keratin from eight species of birds belonging to different orders showed similar moduli (mean  $E=2.50$  GPa) in all species apart from the grey heron ( $E=1.78$  GPa). No significant differences were seen in the modulus of keratin from primaries 7–10 in any species. There was a systematic increase in the modulus distally along the length of the rachis from swan primary feathers. Dynamic bending tests on swan primary feather rachises also showed that the longitudinal elastic**

**modulus increases with increasing frequency of bending over the range 0.1–10 Hz and decreases monotonically with increasing temperature over the range  $-50$  to  $+50$  °C. The position-, frequency- and temperature-dependent variations in the modulus are, however, relatively small. It is concluded that, in the species studied, the flexural stiffness of the whole rachis is principally controlled by its cross-sectional morphology rather than by the material properties of the keratin.**

Key words: feather keratin, Young's modulus, longitudinal variation, viscoelastic behaviour, interspecific variation, bird.

### Introduction

The primary feathers of birds bend under the aerodynamic forces generated during flight. The rachis of these feathers is a cantilever beam structure whose bending behaviour is controlled by the flexural stiffness along its length. For bending in the dorsoventral plane, the flexural stiffness is the product of the longitudinal Young's modulus ( $E$ ) and the second moment of area for dorsoventral bending,  $I$ , of the rachis; control of the flexural stiffness along the length of the rachis could be achieved by variations in  $I$ , in  $E$  or in both. The cross-sectional shape of the rachis varies along its length and shows differences between species, as detailed by Rutschke (1966). Purslow and Vincent (1978) quantitatively modelled the role of variations in  $I$  along the length of the rachis of pigeon primaries in determining their bending behaviour, concluding that flexural stiffness was largely controlled by the morphology of the outer (cortical) region. Rutschke (1976) and Macleod (1980) have reported variations in the modulus along the rachis. Macleod (1980) also presents some evidence of intraspecific differences in the Young's modulus of the rachis from contour feathers. The role of variations in Young's modulus in determining the inter- and intraspecific variability of bending properties of rachises therefore needs to be clarified.

The five published estimates of the Young's modulus of compact feather keratin allow little to be deduced about

patterns of inter- or intraspecific differences in mechanical properties, as the investigators used different methods to obtain their results. Hertel (1966) used tension tests and found that the elastic modulus of feather rachis was  $920 \text{ kg mm}^{-2}$  (9.02 GPa). Rutschke (1976) states that the elastic modulus of feather keratin is  $300 \text{ kg mm}^{-2}$  (2.94 GPa) and that the bending strength of feather keratin increases towards the tip of the feather. Purslow and Vincent (1978) estimated the stiffness of the cortex of pigeon rachis as 7.75–10 GPa by best fit to a bending model. Crenshaw (1980) found the stiffness of pigeon rachis was 2.52 GPa (tension tests). Fraser and Macrae (1980) cite unpublished data of E. G. Bendit, who found the stiffness of Laysan albatross feather keratin to be 5.2 GPa. Macleod (1980) found the stiffness of keratin from contour feathers to be 0.045–0.682 GPa in tension. The apparently wide range of Young's modulus (three orders of magnitude) could indicate a high degree of interspecific heterogeneity in keratin properties; alternatively, it may be the result of differences in testing methodology. Since  $\beta$ -keratin is biochemically highly conservative (see Brush, 1976a,b; Busch and Brush, 1979), one might expect that feather keratin from different species should have somewhat similar mechanical properties.

Hair keratin shows time- and temperature-dependent recoil after extension (Spearman, 1977). Such viscoelastic behaviour

is common to biological materials (Dorrington, 1980) and may also be expected in feather keratin. Tao and Postle (1989) also suggest that keratin composite materials are viscoelastic. Strain rate or frequency dependence in the elastic modulus of feather keratin may place constraints on the aerodynamic performance of the feather in flight. The occurrence of time- or frequency-dependent variations in  $E$  would require standardisation of testing conditions for meaningful comparisons of moduli measured in different studies. The *in vivo* performance of feather keratin will, of course, be influenced by fluctuating temperatures and loading rates.

The principal aim of this paper is to quantify any variations in the longitudinal Young's modulus of keratin from the cortical layer of the rachis that may occur between species, between primary feather positions on the wing and along the length of the rachis. The objective of this is to determine any role for variations in Young's modulus in the control of flexural stiffness of feathers. This will prove useful in any future attempts to model the aeroelastic behaviour of feathers. The frequency and temperature dependence of flexural stiffness is also examined to determine whether these factors significantly affect the mechanical properties of feather keratin.

#### Materials and methods

Sections of keratin measuring 25 mm in length were cut from the dorsal surface of flight feathers. All of the carcasses from which feather material was examined had been stored frozen at  $-20^{\circ}\text{C}$  in sealed bags prior to thawing and use. Sections were cut just distal to the calamus, an obvious ring of tissue on the shaft marking the insertion point into the skin. The sections had parallel sides and were cut to a sufficiently narrow width to prevent significant curvature being present in the cross section (specimens were no wider than approximately 40% of the shaft diameter). The medullary material and the ridges on the inner surface of the specimens were carefully scraped away. Each end of these strips was held between two strips of thin, stiff steel to which it was attached by cyanoacrylate adhesive (Loctite 'Prism' space-filling adhesive). Mean gauge length of the specimens was  $9.5 \pm 0.103$  mm (S.E.M.,  $N=51$ ). Small pieces of 'wet and dry' abrasive paper were glued to the surface of the steel to provide a good purchase for the pneumatic grips of an Instron testing machine. All mechanical tests were performed on an Instron model 6022 (Instron Ltd, High Wycombe, Bucks) test frame. Material was tested from a total of eight species from eight separate orders: grey heron (*Ardea cinerea* Linnaeus), mute swan [*Cygnus olor* (Gmelin)], Eurasian sparrowhawk [*Accipiter nisus* (Linnaeus)], willow ptarmigan [*Lagopus lagopus* (Linnaeus)], black-headed gull (*Larus ridibundus* Linnaeus), rock pigeon (*Columba livia* Gmelin), tawny owl (*Strix aluco* Linnaeus) and common starling (*Sturnus vulgaris* Linnaeus). The specimens were conditioned at room temperature and humidity for at least 24 h before use. Tension testing was performed with a crosshead speed of  $1 \text{ mm min}^{-1}$ . The three outermost primaries were used, permitting an

analysis of differences between feathers. The longitudinal variation in stiffness of keratin was determined by serially cutting test pieces from along the length of the rachis of a primary feather from a mute swan. 25 mm keratin strips were prepared as detailed in the previous experimental procedures. A crosshead speed of  $1 \text{ mm min}^{-1}$  was used for the tests.

To investigate the effect of strain rate and temperature on Young's modulus, a series of dynamic tests was performed. Two short lengths (approximately 20 mm) were cut from the rachis of a mute swan primary feather, one with its proximal end 40 mm distal to the point on the rachis where the vane begins (mid-section specimen) and the other with its proximal end 140 mm from the beginning of the vane (distal specimen). Each segment was subjected to dorsoventral oscillatory bending by means of a dynamic mechanical thermal analyser (Polymer Labs Ltd, Loughborough, UK). Sinusoidal displacements of  $64 \mu\text{m}$  amplitude were applied to each section held as a single cantilever beam 14 mm long and of measured width and depth. The second moment of area of the beam was calculated assuming the cross section to be rectangular. Oscillations of 0.1, 1 and 10 Hz were applied to the specimen at intervals as its temperature was raised from  $-50$  to  $+50^{\circ}\text{C}$  at  $1.5^{\circ}\text{C min}^{-1}$ . From the dynamic response of the rachis, the tensile storage modulus ( $E'$ ) and the viscous loss function ( $\tan\delta$ ) were calculated.

Statistical analysis was performed using Minitab 7.1 software.

#### Results

##### *Inter- and intraspecific variation*

The mean Young's modulus of keratin from the eight species of bird examined was 2.50 GPa (Table 1). Analysis of variance revealed some interspecific differences in the modulus ( $F=3.55$ ,  $P=0.004$ , 50 d.f.). Using Tukey's multiple-range test, it was found that the Young's modulus of keratin from the grey heron was significantly lower than that of the willow ptarmigan, tawny owl and common starling (5% confidence level). No other significant differences were found. No significant differences were found between the stiffness of keratin from the three outermost primaries

Table 1. Young's modulus ( $E$ ) of feather keratin

Species	Young's modulus (GPa)	S.E.M.	$N$
Rock pigeon	2.42	0.073	9
Willow ptarmigan	2.71	0.124	11
Mute swan	2.39		1
Eurasian sparrowhawk	2.41	0.157	9
Black-headed gull	2.04	0.075	3
Tawny owl	2.76	0.167	6
Grey heron	1.78	0.156	3
Common starling	2.67	0.160	9
Mean	2.50	0.064	51

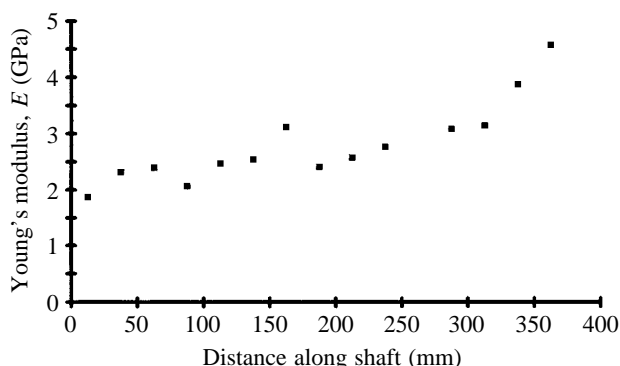


Fig. 1. Longitudinal variation in Young's modulus along the length of a mute swan's primary feather.

( $F=1.23$ ,  $P=0.301$ , 50 d.f.) (excluding grey heron,  $F=1.25$ ,  $P=0.296$ , 47 d.f.).

*Longitudinal variation*

The Young's modulus of the keratin was found to increase along the length of the rachis of a swan feather (Fig. 1). The data appear to fit a linear regression model [ $E=1.80+0.00547L$ ;  $N=14$ ;  $r^2=74.7\%$  (72.5%);  $P\ll 0.001$ , where  $E$  is in GPa and  $L$  is the length along the rachis in mm] better than they do a logarithmic one [ $\ln E=0.028+0.198\ln L$ ;  $N=14$ ;  $r^2=63.0\%$  (60.0%);  $0.01>P>0.001$ ]. There is approximately a twofold increase in Young's modulus from the base of the calamus to the tip of the rachis.

*Viscoelastic variations*

The storage modulus,  $E'$ , of the swan rachis decreases monotonically with temperature over the temperature range  $-50$  to  $+50$  °C (Fig. 2), which roughly brackets the full range

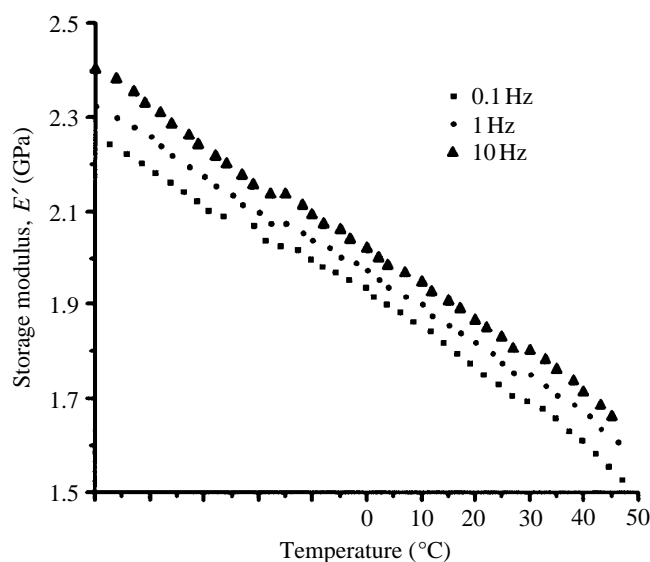


Fig. 2. Storage modulus ( $E'$ ) in a section of keratin from a mute swan rachis, over a range of temperatures and loading frequencies.

of working temperatures the rachis may experience, from body temperature at its point of insertion down to the low air temperatures a swan may encounter flying at altitude in winter. At all temperatures in this range,  $E'$  at 10 Hz was higher than that at 1 Hz, which in turn exceeded  $E'$  at 0.1 Hz, by roughly constant amounts. The apparent modulus derived from bending of the whole section, which is computed on the assumption of a homogeneous rectangular prismatic beam, is lower for the mid-section specimen of the swan primary rachis than for the distal section, but shows the same pattern of variation with temperature and frequency. The longitudinal stiffness of the cortex increases slightly in the distal region of the rachis of this bird, but the higher apparent modulus of the distal rachis segment in bending could also reflect a higher overall contribution of the cortical material to the true flexural stiffness ( $EI$ ) of the rachis at this point. The damping factor ( $\tan\delta$ ) for bending of the swan rachis was very low (in the range 0.03–0.07), indicating that the rachis is principally acting as an elastic structure at low strains.  $\tan\delta$  did increase with temperature by approximately a factor of 2 over the temperature range studied.

**Discussion**

There are only minimal inter- and intraspecific differences in the Young's modulus of compact keratin in the region of the rachis tested in these experiments. This confirms the biochemical evidence that the  $\beta$ -keratin composite is indeed conservative (see Brush, 1976a,b; Busch and Brush, 1979). This finding contradicts that of Macleod (1980), who suggested that feather keratins showed a great degree of interspecific heterogeneity. Whether the similarity in mechanical properties is due to developmental constraints or simply to mechanical optimality remains to be seen. Perhaps we can now understand why there is such diversity in the architecture of the rachis (see Chandler, 1916; Rutschke, 1966, 1976; Purslow and Vincent, 1978). Lack of variation in basic material properties means that changes in the mechanical behaviour of feathers may only be accomplished by altering the size and shape of the rachis cross section. The species examined show a wide range of body masses (0.06–10 kg), so we can be fairly confident that the mechanical properties of feather keratin do not scale with body mass.

The increasing longitudinal modulus in distal regions of the swan primary rachis shown in Fig. 1 is in agreement with the observations of Macleod (1980) on contour feathers. The twofold increase reported here is somewhat lower than the average 4.5-fold increase found in Macleod's (1980) study. One possible explanation for this is that the forces experienced by contour feathers are considerably different from the forces experienced by flight feathers, which arguably results in different patterns of mechanical properties. A comparative study of the bending behaviour and material properties of primary and contour feathers from the same species would no doubt resolve this problem.

The increase in longitudinal modulus along the rachis may

be explained by changes in the composite structure of the cortex. Astbury and Bell (1939) reported that the rachis of feathers exhibited two distinct layers. The orientation of keratin fibres in the inner layer was parallel to the axis of the feather. There was also a distinct outer layer, composed entirely of circumferentially orientated fibres. Earland *et al.* (1962*a,b*) reported that the two layers described by Astbury and Bell (1939) were biochemically identical, both being composed almost entirely of  $\beta$ -keratin. Furthermore, they found that this outer layer constituted approximately one-seventh of the thickness of the rachis wall at the base. Sectioning further along the rachis revealed that this outer layer became thinner. This helps to explain the observed longitudinal increase in keratin stiffness as the proportion of longitudinally aligned keratin filaments increases distally.

Why should Young's modulus increase markedly along the rachis when variability between feathers and species is so small? If we consider a primary feather acting as a simple aerofoil in a laminar airflow, the profile drag of the feather will be proportional to the dorsoventral thickness of the rachis (Hoerner, 1951). An increase in Young's modulus towards the feather tip would allow a reduction in the second moment of area, and hence the thickness of the rachis, for a required level of flexural stiffness ( $EI$ ); however, the savings in thickness are quite small. During flapping flight, the leading primaries are not acting simply as aerofoils in laminar flow (Rayner, 1979*a,b*). The effects of possible drag reduction on the power requirements for flapping flight can be modelled; not surprisingly, profile drag contributes to increased power requirements (Rayner, 1993). Whether the contribution of increased profile drag is important for power requirements at low flight speed is debatable (Rayner, 1979*a,b*).

It is interesting to consider why the published estimates of Young's modulus of feather keratin vary so much. The mechanical properties of feather keratin vary appreciably along the length of the rachis. It is for this reason that the inter- and intraspecific comparisons in this study were made using specimens cut from the same region of the rachis (i.e. just distal to the calamus). Although the effects of room temperature and strain rate on the elastic properties of the rachis are small, there is a trend towards lower stiffness and slightly more viscous dissipation of elastic energy at higher temperatures. These changes with frequency and temperature are qualitatively expected from a viscoelastic solid (Wainwright *et al.* 1976; Ferry, 1960). Similar trends in  $E'$  with changes in frequency and temperature were observed from longitudinal strips cut from the cortex of the swan primary rachis dynamically tested in tension and also from the rachis of a grouse primary feather tested in bending (data not shown). It is unlikely that testing temperature alone can account for the differences previously reported in the literature; it is far more likely that the differences are the result of the longitudinal variation in properties, the strain rate dependence of Young's modulus or, possibly, differences between types of feathers (e.g. contour feathers *versus* primary remiges).

The results of the dynamic tests have some interesting

implications for feather aeroelasticity. Pennycuik and Lock (1976) proposed that primary feathers may act as stores of elastic energy that could be used to decelerate the wing at the end of the downstroke. As we have shown, the Young's modulus increases somewhat as wingbeat frequency increases. For a linearly elastic system the strain energy,  $SE$ , stored is:

$$SE = \sigma^2/2E, \quad (1)$$

where  $\sigma$  is the stress and  $E$  is the Young's modulus. Hence, the strain energy decreases, with increasing Young's modulus, as wingbeat frequency increases.

This may explain why there is no evidence in the literature of such action in the wake of a flying bird. If we consider the temperature gradient along a rachis of a bird flying in very cold air, the effect of this would be to exacerbate the gradient of stiffness along the rachis seen in measurements at room temperature; this would result in further losses in the potential of the rachis to store elastic energy. Both effects, however, are quite small.

R.H.C.B. wishes to thank Dr J. M. V. Rayner for his support and encouragement. R.H.C.B. was funded by an SERC studentship. P.P.P. is supported by a grant from the AFRC (now BBSRC).

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