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**Morphological properties of the last primaries, the tail feathers and the
Alulae of *Falco peregrinus*, *Columba livia*, *Falco tinnunculus* and
*Accipiter nisus***

Anke Schmitz^{1*}, Benjamin Ponitz², Christoph Brücker², Helmut Schmitz¹,
Jan Herweg¹, Horst Bleckmann¹

¹ Institute of Zoology, Rheinische Friedrich-Wilhelms-University Bonn, Germany

² Institute of Mechanics and Fluid Dynamics, TU Bergakademie Freiberg, Freiberg,
Germany

The feathers of *Falco peregrinus*

*corresponding author:

PD Dr. Anke Schmitz

Institute of Zoology

Rheinische Friedrich-Wilhelms-University Bonn

Poppelsdorfer Schloss

53115 Bonn

ankeschmitz@uni-bonn.de

Phone: +49 228 735467

Abstract

During the stoop of peregrine falcons (*Falco peregrinus*) they can reach velocities of up to 320 km h⁻¹. While pulling out of the stoop from such high velocities the wing and tail feathers are likely to be exposed for a certain time-span to large mechanical forces. We investigated the mechanical properties (E-modulus, bending stiffness, barb separation forces) of the tenth primary of the wings, of the Alulae and the middle tail feathers of *F. peregrinus*. For comparison, we also investigated the corresponding feathers in pigeons (*Columba livia*), kestrels (*Falco tinnunculus*) and sparrowhawks (*Accipiter nisus*). In all four species the E-moduli of the feathers ranged from 5.9 to 8.4 GPa. The feather shafts of *F. peregrinus* had the largest cross-sections and the highest specific bending stiffness. When normalized with respect to body mass, the specific bending stiffness of primary 10 was highest in *F. tinnunculus* (16 Nmm g⁻¹), while that of the the Alula was highest in *A. nisus*. In comparison, , the specific bending stiffness, measured at the base of the tail feathers, was much higher in *F. peregrinus* than in the other three species (3.3-12.6 Nmm g⁻¹).

Key words: *Falco peregrinus*, feather morphology, nanoindentation, specific bending stiffness

44 Introduction

45 During flight manoeuvres birds experience large aerodynamic forces (Corning and
46 Biewener, 1998; Tucker et al 1998; Usherwood et al., 2005). This applies specifically to
47 the wings, but also to the tail feathers (Berg and Rayner, 1995; Corning and Biewener,
48 1998; Usherwood et al., 2005; Carruthers et al., 2007). The mechanical loads the wing
49 and tail feathers are exposed to not only depend on the flying speed and the particular
50 flight manoeuvre of a bird, but also on its body weight (e.g. Lentink et al. 2007).

51 A nose-diving peregrine falcon (*Falco peregrinus*) can reach in its stoop velocities of up
52 to 320 km/h (Tucker and Parrott, 1970; Orton, 1975; Tucker, 1990; Savage, 1992;
53 Clark, 1995; Tucker 1998; Franklin, 1999). At such velocities the wings are folded
54 around the body, which is **described by falconers** as the drop-shape (corresponding to
55 the classic falcon diamond shape) (Franklin, 1999). Moreover, the tail feathers form a
56 narrow paddle-like end in the aft part of the body(personal observation and Franklin,
57 1999). If a peregrine pulls out of a dive it starts to spread-out its wings and tail feathers
58 (National Geographic Channel 2007, **you tube video**
59 <http://www.youtube.com/watch?v=j3mTPEuFcWk>). Flight velocity is then further
60 reduced by increasing the angle of attack which results in increased drag (Franklin,
61 1999; Ponitz et al., 2014).

62 The wing and tail feathers of birds are designed to provide aerodynamic lift under
63 conditions of minimum weight and maximum structural stability (Hertel, 1966;
64 Crenshaw, 1980; Gibson and Ashby, 1988). Wing feathers can be divided into remiges
65 (or wing flight feathers) and coverts. Furthermore, flight feathers can be subdivided into
66 primaries (inserting at the hand), secondaries (inserting at the forearm), and rectrices
67 (tail feathers) (Busching, 1997). Feathers are in general composed of a central shaft and

an inner and outer vane (Sick, 1937; Rutschke, 1966, 1976). The shaft can be further subdivided into a basal calamus and a rachis. Vanes are composed of parallel oriented barbs that are interconnected via bow and hook radiates (barbules) (Hooke, 1665; Sick, 1937). This sophisticated design guarantees that vanes are light, flexible and can resist certain mechanical loads that act on the feathers during flight (Ennos et al., 1995). The calamus anchors the feather in the skin where it is attached to muscles and tendons or - in case of the flight feathers - directly to the bones. The rachis consists of a ring-like cortex and a central medulla that contains foam-like cells that support the feather further against buckling (Bonser, 2001). It has already been shown that the presence of the foam-like material within the rachis enhances the bending stiffness of a feather by 7-16% compared to the situation without the inner foam (Purslow and Vincent, 1978; Bonser, 1996). Further stabilization originates from the overlap of feathers of the wings. In primary 10 and the outermost alula, the inner vanes are partly covered by neighbouring feathers. Tail feathers typically overlap during flight and are only spread during a pull out or prior to landing.

We determined the mechanical properties of the flight feathers (primary 10), the Alulae and the tail feathers of *Falco peregrinus*. To do so we measured the Young's modulus E (sometimes also named the elastic modulus) of the rachises of the above feathers and calculated their bending stiffness by multiplying the Young's modulus with the second moment of area (see also Bachmann et al., 2012). For comparison, we also investigated the feathers of domestic rock pigeons (*Columba livia*), kestrels (*Falco tinnunculus*) and sparrowhawks (*Accipiter nisus*). All four species are excellent flyers (Mebis and Schmidt 2005) and – with the exception of the pigeon – are close relatives to *F.*

peregrinus (Jetz et al., 2012). We also determined the forces necessary to bend the rachis of the feathers as well as the forces necessary to separate the barbs. Moreover we counted the number of barbs as well as the angle between barbs and rachis.

Material and Methods

Experimental Animals

Feathers of adult males and females of four species were investigated: *F. peregrinus* (N=4), *F. tinnunculus* (N=4), *A. nisus* (N=4) and *C. livia* (N=4). All animals were obtained as frozen carcasses. Shrink-wrapped animals were kept at -20°C until further usage. All animals were thawed, weighed and photographed (Nikon Coolpix 5000). Thereafter the body dimensions (mass, wing span, body and tail length) were taken. Finally, the tenth (outermost primaries), the outermost Alulae and the middle tail feathers were removed and investigated. As the number of tail feathers differs between birds, their homology is uncertain. In the peregrine falcon the first and fifth primary were investigated, too.

Morphology of the vanes

Feathers were bilaterally removed from four specimen of each species. Each vane was photographed (Nikon Coolpix 5000) together with a ruler (resolution 1 mm). The number of barbs per cm rachis length was counted on every photo for the entire rachis. The angles between the rachis and the barbs were determined for both the outer and inner vanes.

Force gauge measurements

Feathers from one body side were investigated in four specimens of each species. All measurements were repeated four times (Fig. 1A). For force measurements feathers were fixed with the lower side up on a plastic plate that contained a 5x5 mm hole (Bachmann et al., 2007). Prior to each measurement the barbs and barbules were manually smoothed. A rod (diameter 1.5 mm), attached to a force gauge device (Sauter FK10, resolution 0.001 N), was pushed against that part of the feather that was situated right above the hole until the barbs separated (Fig. 1B). This way the forces (N) necessary to separate the barbs were determined. Although the forces acting on a feather during flight are probably rarely perpendicular to the surface of a feather our method already provided some valuable information on the feather stability by comparing the measured values between different species. Force measurements were performed on the inner and outer vanes (c.f. Fig. 1A). The outer vanes of the tenth primaries were, however, so narrow that force measurements could only be taken near the rachis.

Specific bending stiffness

In one specimen of each species the specific bending stiffness of primary 10 and one tail feather was determined with a balance (Mettler Toledo XA 105). To do so the vanes of each rachis were removed with scissors. Afterwards, each rachis was attached to a metal holder that was mounted on a micromanipulator. To take measurements, the rachis of each feather was placed on the upper edge of a vertically oriented razor blade. The firm attachment of the rachis to the micromanipulator prevented its slipping off the razor blade. The horizontal distance (d_1) between the blade and the metal holder was 30 mm. During each measurement the holder was moved downwards in 0.1 mm steps from 0.1

to 1 mm (d_2). The force values obtained were used to calculate the specific bending stiffness M (two point bending method, DIN 53121) according to:

$$M = F \times d_1^3 \times d_2^{-1} \times 3^{-1} \times w^{-1} \quad (1)$$

with F = power (N) (gram g was converted into force N , with $N = 102g$), d_1 = distance (mm) between measuring point and fixation point, d_2 = downward movement of the holder (mm), w = width of the rachis (mm).

Each measurement series was repeated three times and mean values were calculated from the 30 values obtained. The width of the rachis was obtained from the respective cross-section (see below).

If the shaft of a feather was too short (this was the case in all Alulae and primaries 10 of *A. nisus*) measurements could not be taken since we were not able to firmly attach the shaft to the metal holder. In all other feathers the first measuring point was at 25% (or 37.5%) of rachis length. Further measuring points were at 50, 62.5, 75, 87.5 and 99% of rachis length.

Cross-sections

The rachis of each feather was cut at the positions 0% (most proximal position) and 99% (most distal position) and at the intermediate positions 12.5, 25, 37.5, 50, 62.5, 75 and 87.5% (c.f. Fig. 1C). Pieces of the rachis were embedded in Epon 812 so that the surface of the requested section faced the cutting edge of the block. Blocks were polymerized for two days at 60°C and trimmed after hardening (Reichert TM60) using a diamond tip. Finally, blocks were cut with a histo-diamond knife (Diatome) to get

samples with a smooth surface. Photos were taken with a digital camera (Nikon Coolpix 5000) from each section through a binocular (Leica, MZ 16). To account for individual differences, feathers from four animals of each species were investigated.

Determination of the Young's modulus(E)

Nanoindentation can be used to determine the Young' moduls (elastic modulus) of biological materials (Oliver and Pharr, 1992; Swartz and Middleton, 2008). The Youngs's modulus of any material is defined as the slope of its stress–strain curve in the linear-elastic deformation range. The Young's modulus is a measure of the stiffness of an elastic isotropic material and is a quantity used to characterize materials (Askeland and Phulé, 2006).

For the determination of E-values of bird feather parts, blocks were glued with Stabilit[®] onto a metal disc (AFM specimen disc, 15 mm, TED PELLA, Inc.) and placed under a nanoindenter (*Hysitron Triboscope, D3100*). A Berkovich tip was used to indent the samples with a load of 2500 μ N. This resulted in a contact depth of about 500 nm.

Hardness and E-moduli of the samples were calculated from the unloading portions of the load-displacement curves following a procedure given by Oliver and Pharr (1992).

The measured value is the modulus reduced by the deformation of the diamond indenter tip itself (Oliver and Pharr, 1992; Fischer-Cripps, 2004). This effect is corrected for within the nanoindenter software using the material properties of the diamond tip (Oliver and Pharr, 1992; Fischer-Cripps, 2004). Therefore, all measured results are referred to the E-values. The contact area function was determined and the calibrations were performed using a standard reference sample of PMMA (plexiglas, *Hysitron*)

(Oliver and Pharr, 1992). For each feather, 24 indents were taken into the cortex; the indentation points are illustrated in Fig. 1C. We did not obtain values for the medullae since they were too soft for nanoindentation.

Second moment of area

The second moment of area I (mm^4), calculated according to Purslow and Vincent (1978), was determined for the transverse, lateral and dorso-ventral bending direction (Fig. 1E). In brief, we subdivided each cross section into 10 parallel segments of identical width (Fig. 1E) and determined the area of the cortex of each segment by point counting (Howard and Reed, 1998). Point counting was repeated three times per area and the mean values (A_i) for the areas A_1 - A_{10} were calculated. Two parallel lines were drawn at the upper and lower end of each section according to the intended bending direction (Fig. 1E). Between these two lines 10 segments with identical width were drawn and the midpoint of each segment was marked. The length from one of the external lines to the midpoint of the segments X_1 - X_{10} was measured. In a next step $X \cdot A$ was calculated by taking $\sum X_i \cdot A_i$ from the ten segments. X was calculated by dividing the product of $X \cdot A$ by $\sum (A_1$ - $A_{10})$. Finally for each area, Y_i was calculated according to $Y_i = X_i - X$. I (second moment of area) is the sum of all squared Y_i times A_i ($I = \sum Y_i^2 \cdot A_i$) and thus has the unit mm^4 .

We used primary 10 of *C. livia* to establish the method. We compared the measured values with the values calculated from the software package Auto-Cad (Auto-Desk). For each cross section, however, Auto-Cad calculates only the maximum irrespective of the predefined load direction as defined in our experiments. However, at least one of our calculated values (transverse, lateral, or dorso-ventral) always was similar to the

maximum calculated by Auto-Cad, therefore we continued to evaluate all I-values by point counting. This way, we obtained results for a rachis that bended homogeneously in lateral, dorso-ventral or tranverse direction.

Specific bending stiffness

The bending stiffness is defined as Young's modulus E (Nmm^{-2} , $1 \text{ GPa} = 1000 \text{ N mm}^{-2}$) times the second moment of area I (mm^4) (Bonser and Purslow, 1995). The specific bending stiffness M (Nmm) is the bending stiffness divided by the width w (mm) of the sample (taken from photos):

$$M (\text{Nmm}) = E (\text{Nmm}^{-2}) \times I (\text{mm}^4) \times w^{-1} (\text{mm}^{-1}) \quad (2)$$

Statistics

Mean values and standard deviations were calculated. Differences between species were compared using SPSS (IBM, version 22). T-test and one-way analysis of variance (ANOVA) with Bonferroni test as post-hoc evaluation were used to compare mean values of different species. We show only differences between *F. peregrinus* and one of the other species in the figures. All values obtained were normally distributed. The significance level was $p < 0.01$.

MIXED-MODEL???? Anfrage in der Statistik Bonn läuft

Results

Body mass and feather morphology

The body mass of the birds used for our study and the length of their feathers are given in Table 1. Note that feather lengths did not correlate with body mass (Table 1).

235

236 Vane morphology

237 Primary 1 and 5 of *F. peregrinus* contained 17-22 barbs per cm. Significant differences
 238 between primary 1 and 5 were not found (t-test, $p=0.1$ and 0.03 , respectively). In
 239 primary 10 the number of barbs per cm vane length was, however, lower in the outer
 240 vane than in the inner vane (12 to 22 barbs cm^{-1} , t-test, $p<0.01$). The feathers of *C. livia*
 241 had the highest number of barbs per cm rachis length (Fig. 2). In all species, inner and
 242 outer vane barb numbers were comparable for the tail feathers and the alulae (t-test,
 243 $p=0.1$ and 0.03) but differed in primaries 10 (t-test, $p<0.01$). Also, the number of barbs
 244 of the vanes of primaries 10, the tail feathers and the alulae differed across species
 245 (ANOVA, $p<0.01$) (Fig. 2). Differences between *F. peregrinus* and individuals of the
 246 other species occurred in all vanes with the exception of the inner vane of the tail
 247 feather (post-hoc Bonferroni, $p<0.01$) (Fig. 2). In all feathers and species, respectively,
 248 the number of barbs decreased from the base of the rachis towards the tip and increased
 249 again slightly for the most proximal 20% of the rachis. In all species the angles between
 250 barbs and rachis decreased from base (30° up to 88°) towards tip ($15-30^\circ$). Angles were
 251 larger for the inner vanes and differed least between species in the tail feathers.

252

253 Vane structural integrity

254 For the four species investigated the forces required to separate the barbs of primaries
 255 10, the tail feathers and the Alulae are plotted in Fig. 3. For most measuring points these
 256 forces were significantly larger in *F. peregrinus* than in the other species. An exception
 257 is the Alula: in these feathers the separation forces were highest in *A. nisus* at the
 258 measuring points 25% and 50% of the outer vane.

Nanoindentation

Young's modulus E was determined for nine cross-sections per feather (Figs. 1D and 4-6). The E -values of primaries 1, 5 and 10 of *F. peregrinus* were comparable. If averaged across all sections, the E -values of primary 10 (6.85-7.2 GPa) of the four species investigated were not significantly different (t-test, $p=0.06$ and 0.07) (Fig. 7).

Evaluation of the mean E -values of the single sections of primaries 10, the tail feathers and the Alulae revealed differences for about half of the spots (inserted tables in Fig. 7). Values ranged within 6.5 - 8.7 GPa. In all feather types values were highest for *C. livia*. In all species the E -values of the primaries 10, the Alulae and the tail feathers slightly decreased from base to tip (regression analysis). Declination was 0.112-0.26 in primaries 10, 0.079-0.21 in Alulae and 0.035-0.08 in the tail feathers (Fig. 7).

Specific bending stiffness

We calculated and measured (see material and methods) the specific bending stiffness of the rachises of primaries 10 and the tail feathers. Measured values were always slightly higher than the calculated values (Fig. 8). Furthermore, in all feathers the specific bending stiffness decreased from base to tip (Fig. 8).

In primaries 1, 5 and 10 of *F. peregrinus* the calculated specific bending stiffness was similar for the transverse bending direction in all sections. If the bending direction was lateral, however, the specific bending stiffness of primary 10 exceeded that of primary 1 and 5. If the bending direction was dorso-ventral, the specific bending stiffness of primary 5 was higher than the specific bending stiffness of primary 1 and 10 (Fig. 9).

This was most pronounced for the sections 1 to 5.

By comparing the specific bending stiffness of primaries 10, the tail feathers and the Alulae (Fig. 10) it became apparent that *F. peregrinus* had the most stiff feathers. However, plotting the specific bending stiffness with respect to average body mass (see also Worcester 1996) revealed, that the specific bending stiffness of the peregrine feathers, with the exception of the tail feathers (Fig. 11), no longer surpassed the specific bending stiffness of the feathers of the other species.

Fig. 12 gives the second moment of area divided by the width of a sample and by the body mass for the three feather types and the nine sections, respectively. Moreover, Fig. 12 also provides the statistics for these values (ANOVA, post-hoc Bonferroni). The rachises of primary 10 of *F. peregrinus* had higher or lower values than the rachis of primary 10 of all other species. Tail feather values were higher in the peregrine at most spots. In the Alula, however, feathers of *F. tinnunculus* and *A. nisus* most often had higher values than the peregrines.

Calculating the specific bending stiffness per body mass (Fig. 13) revealed that the values obtained from section one of the tail feathers of *F. peregrinus* (bending direction dorso-ventral) were much higher (mean 16.12 Nmm g^{-1}) than the values obtained from all other sections. Primary 10 of *F. tinnunculus*, if bend in a transverse or dorso-ventral direction, and the Alula of *A. nisus* had a higher specific bending stiffness than the respective feathers of all other species (Fig. 13). These feathers were especially stable in the first 3 to 5 sections.

Cross-sections

The cross-sections of the investigated feathers (Figs. 4-6) revealed almost inhomogeneous profiles. This was most conspicuous in primary 10 of *F. peregrinus* and *C. livia* (Fig. 4). Sections 2 to 5 showed pronounced protruding processes. The alulae of *F. peregrinus* and *A. nisus* were also inhomogeneous and this was particularly evident in the middle of the feather shafts (Fig. 6). In contrast, the cross sections of the tail feathers were more homogeneous in all species but the basic section in *F. peregrinus* still differed from the other species in its oval structure (Fig. 5).

Discussion

According to the present study the mechanical properties of the primaries 10, the tail feathers and the Alulae of the four species investigated were strikingly similar if related to the individual body mass. Some differences, however, do exist. For instance, at their base the tail feathers of *F. peregrinus* were significantly more stiff than the tail feathers of the other three species investigated. Peregrines probably use their tail feathers to reduce the flight velocity at the end of a dive (National Geographic Channel 2007, High velocity falcon, you tube). The specific bending stiffness of primaries was highest in *F. tinnunculus*. This falcon uses the primaries for hovering, i.e. while hovering the primaries are probably exposed to higher mechanical loads than in steady flight conditions. In *A. nisus* the Alulae were more stable than in the other species. This hints *Accipiter* might use primarily their Alulae in fast flight manoeuvres, which however needs further studies to be proven. .

Methodological considerations

The specific bending stiffness obtained with the balance was always higher than the calculated bending stiffness. This was most likely due to the fact that we neglected the medulla in our calculations, even though the medulla is known to increase the bending stiffness of vanes by 7-16% (Purslow and Vincent, 1978; Bonser, 1996). Moreover the equation used herein was derived for samples made from paperboard. Therefore the results for the balance could be higher than expected when using the rachises.

The measured Young's modulus based on nanoindentation experiments for the different species was higher than most of the E-values documented in literature so far (see below). This could be due to the anisotropy of the feather keratin since it is more aligned in the middle of the rachis and less aligned at the calamus and at the tip of the rachis (Cameron et al., 2003). These differences in alignment may result in variations in the stiffness along the rachis.

Morphology of the vanes

In terms of barb numbers the vanes of the feathers of *F. peregrinus* did not differ from the other species investigated. Therefore, the higher integrity of the peregrine feathers (with the exception of the Alulae) is most likely due to the anchoring of hooks and bows of the vanes. In general, at the most distal part of the feathers differences in their mechanical properties decreased. Moreover, the two vanes of each feather had different mechanical properties; most likely, this is an adaptation to specific aerodynamic loads.

The vanes of the outer primaries of *C. livia* are exposed to high aerodynamic loads during a down stroke in flapping flight and can resist larger out-of-plane forces than the inner primaries and the secondaries (Ennos et al. 1995). In addition the middle and distal part of each feather resist out-of-plane forces better than the proximal part, which will be covered during flight by neighbouring feathers (Ennos et al. 1995). This agrees

with the mechanical properties of primary number 10 and the Alulae of our study (Fig. 3). Moreover, the overlap of the feathers while the wings are moved plays a role in force distribution, at least in the proximal portions of most feathers. Overlapping will especially influence the forces acting on the vanes.

The structural integrity of the outer vane of primary 10 of *F. peregrinus* was comparable to that of *C. livia*. In *F. peregrinus* the inner vanes had a higher mechanical robustness than the inner vanes of *F. tinnunculus* and *A. nisus*. This may be an adaptation to the higher mass of *F. peregrinus* and/or to the higher aerodynamic forces peregrines most likely experience during fast flight manoeuvres. In *F. peregrinus*, the Alulae are not particularly exposed to the high velocities at the end of a dive (Ponitz et al., 2014). This could explain why the Alulae of *F. peregrinus* are not more robust than the Alulae of the other species. However, the vanes of the tail feathers of *F. peregrinus* were the most robust among the four species. Differences in robustness between *F. peregrinus* and the other species were especially pronounced close to the rachis. In this region stability may be of special importance. Detailed aerodynamic measurements of the forces hitting the feathers have to show which parts of the vanes are important for the flight behaviour of the four species.

Young's -modulus E

The E-values of the cortices of the feathers of various bird species range between 1.8 - 10 GPa (Hertel, 1966; Rutschke, 1976; Purslow and Vincent, 1978; Crenshaw, 1980; Fraser and Macrae, 1980; MacLeod, 1980; Bonser and Purslow, 1995, Bonser, 2001; Cameron et al., 2003; Pannkuk et al., 2010; Bachmann et al., 2012; Vincent, 2012). The

E-values obtained in the present study are within this range. Since the flexural stiffness of the rachis depends on its cross-sectional geometry to a much greater degree than the E-value (Bonser, 1996), the shape of the cross-section is likely to have a larger influence on feather stability than the material properties of the keratin (Purslow and Vincent, 1978; Corning and Biewener, 1998; Bonser and Purslow, 1995; Bachmann et al., 2012). For the four species investigated it was shown that E-values differ between species and between different areas of the feathers. As values lay between 5.8 and 8.4 GPa the Young's modulus itself has an influence on the specific bending stiffness. E.g. since the E-value of *C. livia* was higher than the E-values of the other three species. For all feathers the measured E-values of the feather rachis was higher than the values documented in literature so far. A possible for this discrepancy could be the different levels in water content of the samples. Our samples were air-dried, but in alive birds the water content of the feathers is higher and thus the actual E-values may be lower. This was shown in ostrich contour feathers in which the E-value decreased with increasing water content (0% water content 3.66 GPa to 100% 1.47 GPa; Taylor et al., 2004). Fully developed feathers are, however, no longer hydrated by blood vessels (Busching, 1997). Therefore the use of air-dried feathers seems justified.

Second moment of area and specific bending stiffness

The second moment of area of primary 10 of a 300 g *C. livia* is 0.00008-1.6 mm⁴ (Purslow and Vincent 1978). This is comparable to our values for *C. livia* (0.00004-2.33 mm⁴, 480 g). Bachmann et al. (2012) found 0.017-1.7 mm⁴ for primary 5 in the same species.

Heavier birds must generate larger forces than smaller birds to keep airborne. This in turn implies that the resistance of the rachis to bending should be greater in heavier birds (Purslow and Vincent, 1978). Therefore, we also calculated the mass-specific bending stiffness (Figs. 11, 13). The tail feathers of *F. peregrinus* had a higher mass-specific bending stiffness than the tail feathers of the other three species, especially at the base and in the dorso-ventral bending direction (natural bending direction in flight!). We suggest that this helps peregrine falcons to cope with the large aerodynamic forces that develop while pulling out of a dive.

Cross-sections

The feathers of *F. peregrinus* had larger cross-sections and more protrusions than the feathers of the other three species. This was especially striking at the base of the rachises. The size and shape of the cross-sections most likely determine the specific bending stiffness of a feather (Bachmann et al. 2012; Purslow and Vincent 1978). Differences in flexural stiffness originate most likely from differences in the shape of the cross-sections rather than differences in the material properties (e.g. varying the cross-link density of the keratin) (Purslow and Vincent, 1978). These findings are in line with our results (Figs. 4-6, 13), as in Fig. 12 and 13 the curves run in very similar manners.

Conclusions

The tested feathers show differences that can be correlated to the life style of a bird. The specific bending stiffness is highest in the feathers that birds use particularly for their special flight behaviours, at least when one simply observes the flight of the birds: Alulae in *A. nisus*, primary number 10 in hovering of *F. tinnunculus* and the tail feathers

during pull-out from a stoop in *F. peregrinus*. Aerodynamic measurements have to demonstrate the forces that the feathers have to stand and have to verify these statements.

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Table 1

Figures

Fig. 1 A. Tail feather six of *F. pergerinus*. White dots: Points of force gauge measurements. Scale bar: 1 cm. **B.** Device for the force gauge measurement. The Sauter FK10 is situated above a feather, one of the holes in the subjacent plate is marked with an arrow. For measurements the FK 10 is put downwards until it hits the feather and the power is read off when the vane gets unsealed. **C.** Primary 10 of *F. peregrinus*. Numbers 1 – 9 indicate the level of the sections used for nano-indentation. Scale bar: 5 cm. **D.** Cross-section four of primary 10 of *F. peregrinus*. White spots: Points for nanoindentation. Bar: 1 mm. **E.** Schematic drawings of the cross-section shown in C. Directions for which the second moment of area was calculated are indicated by black arrows. Thin lines separate the 10 areas in which point counting was carried out. Scale bar: 1 mm.

Fig. 2 Number of barbs per cm rachis of primary 10, a tail feather and the Alula in the four species investigated (4 specimen per species). Bars represent mean values $\pm$ one S.D. Stars indicate significant differences between *F. peregrinus* and one of the other species (ANOVA, post-hoc Bonferroni). Differences were only found in the outer vane of primary 10 and of the alula ($p < 0.01$). At the beginning of the rachis (first 1-2 cm), barbs always were soft and had no or only small barbules. Therefore these barbs were not included in the results.

Fig. 3 Forces needed for barb separation. The measuring tip of the force gauge was oriented parallel to the rachis. For primary number 10 no outer values for the position 50% could be obtained since the area was too small in this feather. S.D. of each set of measurement is given as bars in the columns. Significant differences between *F.peregrinus* and the other species are marked with a * (ANOVA, post-hoc Bonferroni, $p < 0.01$).

Fig. 4 Cross-sections at the nine rachis levels of Primary 10 indicated in Fig.1C. Primary 10 of each species is shown between the sections for size and shape comparison. In this figure and in figure 5 cross-sections are oriented such that pictures represent a feather from the right body side. Four protruding processes are marked exemplarily by arrows.

Fig. 5 Cross-sections through the rachis of the middle tail feather of the four species. Levels of cross-sections as in Fig.4 and 1C. Tail feathers of the single species are given between the sections.

Fig.6 Cross-sections through the rachis of the outermost Alula of the four species. Cross-sections are oriented such that pictures represent a feather from the left body side. The Alulae are given between the sections.

Fig.7 The E-Moduli of primary 1, 5, and 10 of *F.peregrinus* (**A**) and of primary 10, the middle tail feather and the Alula of all four species investigated (**B**). S.D. is given by

bars. In B significant differences between *F. peregrinus* and one of the other species is indicated as a X in the inserted tables (ANOVA, post-hoc Bonferroni, $p < 0.01$)

Fig. 8 Specific bending stiffness obtained with a balance (dashed lines) or calculated with equation 2 (continuous lines). Data are shown for the tail feathers of the four species investigated. Results are plotted for the lateral and dorso-ventral orientation of the rachis. E was determined with the nanoindenter, I was derived from the sections. For the balance measurements the samples were oriented such that their outer vanes (lateral orientation) or the ventral part of the rachis (dorso-ventral orientation) were aligned to the razor blade. In all cases the values obtained with the balance were slightly higher than the calculated values.

Fig. 9 Specific bending stiffness (mean $\pm$ S.D.) of primary 1, 5 and 10 of *F. peregrinus*, calculated for a transverse, lateral and dorso-ventral bending direction (c.f. Fig.1E).

Fig. 10 Specific bending stiffness (mean $\pm$ S.D.) of primary number 10, tail and Alula for the four species investigated. Bars indicate the S.D.

Fig. 11 Specific bending stiffness as a function of body mass. For each feather the average specific bending stiffness, mean of all sections, was calculated. From left to right: Values for *F.tinnunculus* (191.8 g) and *A.nisus* (202.3 g), *C.livia* (402.5 g) and *F.peregrinus* (680.8 g).

Fig.12 Second moment of area divided by the width of a sample and by the body mass. Curves for the three feather types and the three bending directions are given. Bars indicate the S.D. Inserted as tables are the statistic results for differences between *F. peregrinus* and one of the other species. Significant differences (X) are given for each section (ANOVA, post-hoc Bonferroni, $p < 0.01$).

Fig. 13 Specific bending stiffness per body mass of primary 10, the tail feathers, and the Alulae. For each section values are given for the transverse, lateral and dorso-ventral bending direction (c.f. Fig.1E). Inserted as tables are the statistic results for differences between *F. peregrinus* and one of the other species. Significant differences (X) are given for each section (ANOVA, post-hoc Bonferroni, $p < 0.01$).