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2  
3 **Morphological properties of the last primaries, the tail feathers and the**  
4 ***Alulae of *Falco peregrinus*, *Columba livia*, *Falco tinnunculus* and***  
5 ***Accipiter nisus***  
6

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12  
13 The feathers of *Falco peregrinus*  
14

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26 Abstract

27 During the stoop of peregrine falcons (*Falco peregrinus*) they can reach velocities of up to  
28 320 km h<sup>-1</sup>. While pulling out of the stoop from such high velocities the wing and tail  
29 feathers are likely to be exposed for a certain time-span to large mechanical forces. We  
30 investigated the mechanical properties (E-modulus, bending stiffness, barb separation  
31 forces) of the tenth primary of the wings, of the Alulae and the middle tail feathers of *F.*  
32 *peregrinus*. For comparison, we also investigated the corresponding feathers in pigeons  
33 (*Columba livia*), kestrels (*Falco tinnunculus*) and sparrowhawks (*Accipiter nisus*). In all  
34 four species the E-moduli of the feathers ranged from 5.9 to 8.4 GPa. The feather shafts of  
35 *F. peregrinus* had the largest cross-sections and the highest specific bending stiffness.  
36 When normalized with respect to body mass, the specific bending stiffness of primary 10  
37 was highest in *F. tinnunculus* (16 Nmm g<sup>-1</sup>), while that of the the Alula was highest in *A.*  
38 *nisus*. In comparison, , the specific bending stiffness, measured at the base of the tail  
39 feathers, was much higher in *F. peregrinus* than in the other three species (3.3-12.6 Nmm  
40 g<sup>-1</sup>).

41

42 Key words: *Falco peregrinus*, feather morphology, nanoindentation, specific bending  
43 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

68 an inner and outer vane (Sick, 1937; Rutschke, 1966, 1976). The shaft can be further  
69 subdivided into a basal calamus and a rachis. Vanes are composed of parallel oriented  
70 barbs that are interconnected via bow and hook radiates (barbules) (Hooke, 1665; Sick,  
71 1937). This sophisticated design guarantees that vanes are light, flexible and can resist  
72 certain mechanical loads that act on the feathers during flight (Ennos et al., 1995). The  
73 calamus anchors the feather in the skin where it is attached to muscles and tendons or -  
74 in case of the flight feathers - directly to the bones. The rachis consists of a ring-like  
75 cortex and a central medulla that contains foam-like cells that support the feather  
76 further against buckling (Bonser, 2001). It has already been shown that the presence of  
77 the foam-like material within the rachis enhances the bending stiffness of a feather by  
78 7-16% compared to the situation without the inner foam (Purslow and Vincent, 1978;  
79 Bonser, 1996). Further stabilization originates from the overlap of feathers of the wings.  
80 In primary 10 and the outermost alula, the inner vanes are partly covered by  
81 neighbouring feathers. Tail feathers typically overlap during flight and are only spread  
82 during a pull out or prior to landing.

83

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

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

95

## 96 Material and Methods

### 97 Experimental Animals

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

107

### 108 Morphology of the vanes

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

114

### 115 Force gauge measurements

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

129

### 130 Specific bending stiffness

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

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

141

$$142 \quad M = F \times d_1^3 \times d_2^{-1} \times 3^{-1} \times w^{-1} \quad (1)$$

143

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

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

150 If the shaft of a feather was too short (this was the case in all Alulae and primaries 10 of  
151 *A. nisus*) measurements could not be taken since we were not able to firmly attach the  
152 shaft to the metal holder. In all other feathers the first measuring point was at 25% (or  
153 37.5%) of rachis length. Further measuring points were at 50, 62.5, 75, 87.5 and 99% of  
154 rachis length.

155

156 Cross-sections

157 The rachis of each feather was cut at the positions 0% (most proximal position) and  
158 99% (most distal position) and at the intermediate positions 12.5, 25, 37.5, 50, 62.5, 75  
159 and 87.5% (c.f. Fig. 1C). Pieces of the rachis were embedded in Epon 812 so that the  
160 surface of the requested section faced the cutting edge of the block. Blocks were  
161 polymerized for two days at 60°C and trimmed after hardening (Reichert TM60) using a  
162 diamond tip. Finally, blocks were cut with a histo-diamond knife (Diatome) to get



163 samples with a smooth surface. Photos were taken with a digital camera (Nikon Coolpix  
164 5000) from each section through a binocular (Leica, MZ 16). To account for individual  
165 differences, feathers from four animals of each species were investigated.

166

167 Determination of the Young's modulus(E)

168 Nanoindentation can be used to determine the Young' moduls (elastic modulus) of

169 biological materials (Oliver and Pharr, 1992; Swartz and Middleton, 2008). The

170 Youngs's modulus of any material is defined as the slope of its stress–strain curve in the

171 linear-elastic deformation range. The Young's modulus is a measure of the stiffness of

172 an elastic isotropic material and is a quantity used to characterize materials (Askeland

173 and Phulé, 2006).

174

175 For the determination of E-values of bird feather parts, blocks were glued with Stabilit

176 ® onto a metal disc (AFM specimen disc, 15 mm, TED PELLA, Inc.) and placed under

177 a nanoindenter (*Hysitron Triboscope, D3100*). A Berkovich tip was used to indent the

178 samples with a load of 2500  $\mu$ N. This resulted in a contact depth of about 500 nm.

179 Hardness and E-moduli of the samples were calculated from the unloading portions of

180 the load-displacement curves following a procedure given by Oliver and Pharr (1992).

181 The measured value is the modulus reduced by the deformation of the diamond indenter

182 tip itself (Oliver and Pharr, 1992; Fischer-Cripps, 2004). This effect is corrected for

183 within the nanoindenter software using the material properties of the diamond tip

184 (Oliver and Pharr, 1992; Fischer-Cripps, 2004). Therefore, all measured results are

185 referred to the E-values. The contact area function was determined and the calibrations

186 were performed using a standard reference sample of PMMA (plexiglas, *Hysitron*)

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

190

191 Second moment of area

192 The second moment of area  $I$  ( $\text{mm}^4$ ), calculated according to Purslow and Vincent  
 193 (1978), was determined for the transverse, lateral and dorso-ventral bending direction  
 194 (Fig. 1E). In brief, we subdivided each cross section into 10 parallel segments of  
 195 identical width (Fig. 1E) and determined the area of the cortex of each segment by point  
 196 counting (Howard and Reed, 1998). Point counting was repeated three times per area  
 197 and the mean values ( $A_i$ ) for the areas  $A_1$ - $A_{10}$  were calculated. Two parallel lines were  
 198 drawn at the upper and lower end of each section according to the intended bending  
 199 direction (Fig. 1E). Between these two lines 10 segments with identical width were  
 200 drawn and the midpoint of each segment was marked. The length from one of the  
 201 external lines to the midpoint of the segments  $X_1$ - $X_{10}$  was measured. In a next step  $X^*A$   
 202 was calculated by taking  $\sum X_i * A_i$  from the ten segments.  $X$  was calculated by dividing  
 203 the product of  $X^*A$  by  $\sum(A_1-A_{10})$ . Finally for each area,  $Y_i$  was calculated according to  
 204  $Y_i = X_i - X$ .  $I$  (second moment of area) is the sum of all squared  $Y_i$  times  $A_i$  ( $I = \sum Y_i^2 * A_i$ )  
 205 and thus has the unit  $\text{mm}^4$ .

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

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

214

215 Specific bending stiffness

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

220

$$221 \quad M (\text{Nmm}) = E (\text{Nmm}^{-2}) \times I (\text{mm}^4) \times w^{-1} (\text{mm}^{-1}) \quad (2)$$

222

223 Statistics

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

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

231 Results

232 Body mass and feather morphology

233 The body mass of the birds used for our study and the length of their feathers are given  
 234 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  $\text{cm}^{-1}$ , 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 ( $30^\circ$  up to  $88^\circ$ ) 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.

259

260 Nanoindentation

261 Young's modulus E was determined for nine cross-sections per feather (Figs. 1D and 4-

262 6). The E-values of primaries 1, 5 and 10 of *F. peregrinus* were comparable. If

263 averaged across all sections, the E-values of primary 10 (6.85-7.2 GPa) of the four

264 species investigated were not significantly different (t-test,  $p=0.06$  and  $0.07$ ) (Fig. 7).

265 Evaluation of the mean E-values of the single sections of primaries 10, the tail feathers

266 and the Alulae revealed differences for about half of the spots (inserted tables in Fig.7).

267 Values ranged within 6.5 - 8.7 GPa. In all feather types values were highest for *C. livia*.

268 In all species the E-values of the primaries 10, the Alulae and the tail feathers slightly

269 decreased from base to tip (regression analysis). Declination was 0.112-0.26 in

270 primaries 10, 0.079-0.21 in Alulae and 0.035-0.08 in the tail feathers (Fig. 7).

271

272 Specific bending stiffness

273 We calculated and measured (see material and methods) the specific bending stiffness

274 of the rachises of primaries 10 and the tail feathers. Measured values were always

275 slightly higher than the calculated values (Fig. 8). Furthermore, in all feathers the

276 specific bending stiffness decreased from base to tip (Fig. 8).

277 In primaries 1, 5 and 10 of *F. peregrinus* the calculated specific bending stiffness was

278 similar for the transverse bending direction in all sections. If the bending direction was

279 lateral, however, the specific bending stiffness of primary 10 exceeded that of primary 1

280 and 5. If the bending direction was dorso-ventral, the specific bending stiffness of

281 primary 5 was higher than the specific bending stiffness of primary 1 and 10 (Fig. 9).

282 This was most pronounced for the sections 1 to 5.

283

284 By comparing the specific bending stiffness of primaries 10, the tail feathers and the

285 Alulae (Fig. 10) it became apparent that *F. peregrinus* had the most stiff feathers.

286 However, plotting the specific bending stiffness with respect to average body mass (see

287 also Worcester 1996) revealed, that the specific bending stiffness of the peregrine

288 feathers, with the exception of the tail feathers (Fig. 11), no longer surpassed the

289 specific bending stiffness of the feathers of the other species.

290 Fig. 12 gives the second moment of area divided by the width of a sample and by the

291 body mass for the three feather types and the nine sections, respectively. Moreover, Fig.

292 12 also provides the statistics for these values (ANOVA, post-hoc Bonferroni). The

293 rachises of primary 10 of *F. peregrinus* had higher or lower values than the rachis of

294 primary 10 of all other species. Tail feather values were higher in the peregrine at most

295 spots. In the Alula, however, feathers of *F. tinnunculus* and *A. nisus* most often had

296 higher values than the peregrines.

297 Calculating the specific bending stiffness per body mass (Fig. 13) revealed that the

298 values obtained from section one of the tail feathers of *F. peregrinus* (bending direction

299 dorso-ventral) were much higher (mean  $16.12 \text{ Nmm g}^{-1}$ ) than the values obtained from

300 all other sections. Primary 10 of *F. tinnunculus*, if bend in a transverse or dorso-ventral

301 direction, and the Alula of *A. nisus* had a higher specific bending stiffness than the

302 respective feathers of all other species (Fig. 13). These feathers were especially stable in

303 the first 3 to 5 sections.

304

305 Cross-sections

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

313

#### 314 Discussion

315

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

328

329 Methodological considerations

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

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

#### 342 Morphology of the vanes

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

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



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

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

371

372

373 Young's -modulus E

374 The E-values of the cortices of the feathers of various bird species range between 1.8 -  
375 10 GPa (Hertel, 1966; Rutschke, 1976; Purslow and Vincent, 1978; Crenshaw, 1980;  
376 Fraser and Macrae, 1980; MacLeod, 1980; Bonser and Purslow, 1995, Bonser, 2001;  
377 Cameron et al., 2003; Pannkuk et al., 2010; Bachmann et al., 2012; Vincent, 2012). The

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

395

396 Second moment of area and specific bending stiffness

397 The second moment of area of primary 10 of a 300 g *C. livia* is 0.00008-1.6 mm<sup>4</sup>  
398 (Purslow and Vincent 1978). This is comparable to our values for *C. livia* (0.00004-2.33  
399 mm<sup>4</sup>, 480 g). Bachmann et al. (2012) found 0.017-1.7 mm<sup>4</sup> for primary 5 in the same  
400 species.

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

409

#### 410 Cross-sections

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

420

#### 421 Conclusions

422

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

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

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434

435

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593 **Table 1**

594

595 **Figures**

596

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

608

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

616

617 **Fig. 3** Forces needed for barb separation. The measuring tip of the force gauge was  
618 oriented parallel to the rachis. For primary number 10 no outer values for the position  
619 50% could be obtained since the area was too small in this feather. S.D. of each set of  
620 measurement is given as bars in the columns. Significant differences between  
621 *F.peregrinus* and the other species are marked with a \* (ANOVA, post-hoc Bonferroni,  
622  $p<0.01$ ).

623

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

629

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

633

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

637

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

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

642

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

651

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

654

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

657

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

662

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

668

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

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