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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*

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The feathers of *Falco peregrinus*

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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}).

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 pergerinus*. 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 (Mebs 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              $$M = F \times d_1{}^3 \times d_2{}^{-1} \text{ x } 3^{-1} \times w^{-1}$$ (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 µN. 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 (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 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 (tranverse, 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 (Nmm^{-2}, 1 GPa = 1000 N mm^{-2})

217   times the second moment of area I (mm^4) (Bonser and Purslow, 1995). The specific

218   bending stiffness M (Nmm) is the bending stiffness divided by the width w (mm) of the

219   sample (taken from photos):

220

221   $M (Nmm) = E (Nmm^{-2}) \times I (mm^4) \times w^{-1} (mm^{-1})$ (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. pereginus* 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. pereginus* 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°). 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 rachisis 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 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 allmost

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 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^4

398   (Purslow and Vincent 1978). This is comparable to our values for *C. livia* (0.00004-2.33

399   mm^4, 480 g). Bachmann et al. (2012) found 0.017-1.7 mm^4 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 finding 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 particular 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.

430 NOCH ETWAS SCHREIBEN, DASS DIE FEDERN WAHRSCHEINLICH NICHT

431 DIE HAUPTLAST BEIM STURZFLUG ODER DEM ABBREMSEN TRAGEN UND

432 DASS ALS NÄCHSTES DIE KNOCHEN UND MUSKELN UNTERSUCHT

433 WERDEN.

434

435

436 Acknowledgements

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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 ± 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 ± 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 ± 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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