

# Vane macrostructure of primary feathers and its adaptations to flight in birds

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The selection pressures that drive flight feather morphology are poorly understood. Using a phylogenetic comparative approach and data from 178 species of birds, we investigated whether both position along the wing length and flight feather length affected vane structure. We found that barb density was lower on distal primaries than on proximal primaries of the leading feather vane. In contrast, on the trailing vane only mid-point barb density differed and, here, it showed denser barbs on the distal primaries. This difference was greater at the feather base than at the tip. Barb angle was higher along the full length of the leading edge vane on the proximal primaries than on the distal primaries. Overall, barb density decreased from base to tip on both trailing and leading vanes on both the proximal and the distal primaries. In general, barb angle was less acute at the feather base than at the tip. Barbs were in general denser in continuous flapping fliers than in soarers and the angle of barbs on both the proximal and the distal primaries was affected by flight type. However, we did not identify consistent differences in the pattern of barb angle change among flight style groups. These findings add new perspectives to our understanding of the functional morphology of the flight feather vane, although we still have limited knowledge on how aerodynamic forces, particularly during take-off and landing, affect the morphology of the feather vane.

**ADDITIONAL KEYWORDS:** barb angle – barb density – feather vane – flight – flight feathers – functional morphology.

## INTRODUCTION

Primary feathers are long, stiff and asymmetrically shaped feathers on the distal part of the wings of birds, and whose main function is to generate lift and thrust during flight. These primary feathers make up a large

part of the wing area, constituting approximately 50% of the total wing span depending upon the species (Nudds, 2007; Nudds *et al.*, 2011). Hence, the primaries determine the wings' ability to withstand forces during flight, which are equal to the bird's body weight during gliding flight, but are much higher when the bird is changing direction or during the flapping phases of active flight (Lees *et al.*, 2017).

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The macrostructure of the primary feather vane is a mesh formed by barbs and barbules. The barbs branch off from the shaft, are parallel to each other and are connected via hook- and bow barbules that branch off. This mesh structure ensures that feather vanes are both light and flexible and are highly resistant to aerodynamic pressure (Prum & Brush, 2002). The response of the vane to aerodynamic forces is determined by at least two traits of this mesh structure. Firstly, the density of the barbs and barbules determines the air transmissivity of the vane, which may affect flight performance (Müller & Patone, 1998; Heersiet *et al.*, 2011; Dial *et al.*, 2012). Secondly, the branching angle of the barbs determine the vane's response to in-plane and out-of-plane forces during both the down- and upstroke of the wing (Ennos *et al.*, 1995). Therefore, we expect these feather macrostructure traits to show differences at multiple levels: (1) among species that differ in flight style (wing flappers vs. soarers/gliders), (2) among primary feathers that differ in their position on the wing (proximal vs. distal) and (3) between parts of the same primary feather (basal vs. apical part or leading vs. trailing vane). The rationale behind these expectations is that the wing of birds that differ in flight type, the different feathers on the wing and the different parts of the same feather should be subject to different aerodynamic forces (see below). However, these expectations have rarely been tested in a comparison across a large variety of bird species.

Flight type (e.g. flapping, soaring/gliding or hovering flight) may be a key contributor to the diversification seen in the functional morphology of flight feathers, because different flight behaviours subject the wing feathers to different aerodynamic loads (Pennycuik, 1989). Hence, it is conceivable that the morphology and the mechanical response of the primary feathers to airflow varies with predominant flight styles among species (e.g. Nudds & Dyke, 2010; Wang *et al.*, 2011, 2012; Feo *et al.*, 2015; Pap *et al.*, 2015). Common to all species, however, is that the aerodynamic forces exerted on individual feathers vary across the wing span, with distal primary feathers needing to withstand considerably higher aerodynamic forces than more proximal primaries or secondary feathers (Ennos *et al.*, 1995; Bachmann *et al.*, 2007; Heers *et al.*, 2011; Dial *et al.*, 2012; Feo *et al.*, 2015; Pap *et al.*, 2015), particularly during downstrokes in flapping flight (Corning & Biewener, 1998). Therefore, the vane of distal feathers has to resist larger out-of-plane forces than the proximal primaries, which might ultimately result in differentiation in barb density and barb angle. Also, profile (friction) drag will exerting in-plane force, and the direction of that force relative to the vanes will change as the presentation

of the feathers differs along the span of the wing (and through the wingbeat cycle). For similar force distribution reasons, feather morphology will also differ along the shaft. This is exemplified by shaftwise changes in vane geometry and in the vane's resistance to bending (Bachmann *et al.*, 2007; Wang *et al.*, 2012; Feo *et al.*, 2015; Pap *et al.*, 2015). Vane emarginations (i.e. marked narrowing of the vane) observed in primary feathers, particularly the distal primaries, result in separation of the feather tips when the wing is spread (Norberg, 1990). These non-overlapping tips act as independent aerofoils during flight, which requires even greater resistance to aerodynamic forces, particularly at the tips of these feather sections (Tucker, 1995). Except for the most distal primary feathers, the largest pressure gradient on a fixed (non- or gentle-flapping) bird wing is toward the leading edge (Norberg, 1990) and, therefore, the base of individual feathers will experience higher pressure gradients than the tips (Müller & Patone, 1998). This probably explains why vane barb density is higher at the base than at the tip of flight feathers in the two species studied to date, the barn owl (*Tyto alba*) and the feral pigeon (*Columba livia*) (Bachmann *et al.*, 2007). Transmissivity was also found to be greater on the leading vane than on the trailing vane of each feather, perhaps indicating a greater barb density on the trailing vane (Müller & Patone, 1998). This difference in transmissivity was suggested to result in a differential pressure gradient upon the vanes, resulting in a tilting moment pushing the trailing edge of the feather against the leading edge of the adjacent more proximal feather, thereby forming a continuous smooth lifting surface (Müller & Patone, 1998). The branching angle of the barbs decreases from the base to the tip of pigeon flight feathers (Ennos *et al.*, 1995; Bachmann *et al.*, 2007). Ennos *et al.* (1995) showed that resistance to out-of-plane moments (stiffness) correlates broadly with barb angle, with the more acute angle found at the tip being associated with more resistance. It is likely that the tips of the feathers are structured to resist greater out-of-plane and hence aerodynamic forces than the bases, which are overlaid and supported by covert feathers (Ennos *et al.*, 1995). Therefore, there is evidence supporting differentiation in barb angle and barb density across the wingspan, along the feather length, and between the leading and trailing feather vanes, all probably driven by variation in the aerodynamic forces experienced at those points. To the best of our knowledge, however, no study has formally addressed how the macrostructure and geometry of primaries vary between proximal and distal feathers along the wing, along the shaft of individual feathers, and

between trailing and leading vanes among species with different flight styles. Understanding how vane morphology varies among birds with different flight styles is key to unravelling the question of how feather vanes have evolved to meet the aerodynamic requirements of flight. Such knowledge could also aid our understanding of selection pressures that drove the evolution of flight feather morphology and its variation among birds (Feo *et al.*, 2015; Pap *et al.*, 2015; Wang *et al.*, 2017). Using a phylogenetic comparative approach and data on 178 species of volant birds, we test how feather vane macrostructure varies across the wing (between proximal and distal primaries), along the axis of individual feathers, and between leading and trailing vanes in species characterized as having different flight types. We measured barb density and barb angle in distal and proximal primary feathers at three positions along the feather vanes (base, middle and tip) on both the trailing and the leading vane of the feathers (see Fig. 1). We analysed how the observed among-species variation relates to flight styles, which was assigned to one of the four categories [flapping and soaring (FS), flapping and gliding (FG), continuous flapping (CF) and passerine type (PT); following Pap *et al.* (2015)] according to the proportion of flapping flight (Pennycuick, 2008; Bruderer *et al.*, 2010).

We predicted higher barb density of the feather vanes of species using flapping (CF and PT) rather than soaring flight (FS and FG), and we expected it to be more pronounced on distal than on proximal primaries, due to greater aerodynamic forces experienced when flapping the wing. Furthermore, we predicted a decrease in barb density from the base towards the tip of the feathers because lift generation and, hence, the need for low transmissivity to air is highest at the base. In accordance with Müller & Patone (1998), we also predicted a greater density of barbs on the trailing vane than on the leading vane.

Barb angle was predicted to decrease from the base toward the tip because of the association between a lower branching angle and resistance to out-of-plane loading, which is highest at the tip. We also predicted a more acute branching angle of the barbs on the leading than on the trailing vane, with a more marked difference on the distal primary, because the outer primaries function as individual aerofoils (acting as leading edge slats) during demanding flight manoeuvres (Ennos *et al.*, 1995). We predicted a more acute branching angle for flapping flyers, and we expected it to be more pronounced on distal than on proximal primaries. However, barb angle on the leading vane is probably reduced in the serrated wings of some soaring birds, where the distal parts of distal primaries are separated and thus act as individual aerofoils.

## MATERIAL AND METHODS

### DATA COLLECTION AND FEATHER MEASUREMENTS

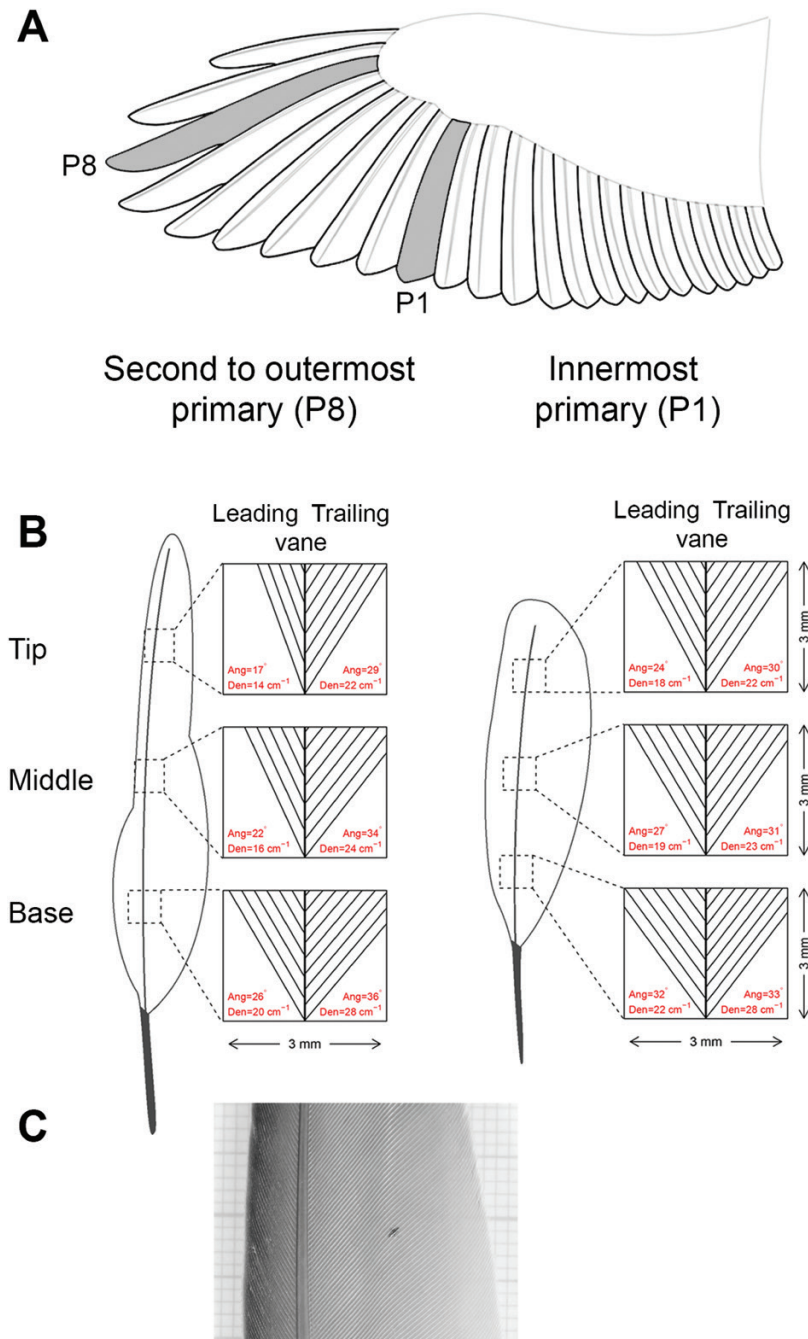
We collected feather samples from 399 adult birds of 178 species at several locations across Romania, Hungary, Norway, Sweden and Scotland between 2003 and 2017, and at the Pointe Géologie Archipelago, Terre Adélie (66°40'S, 140°01'E), Antarctica, between 2012 and 2017. All sampled individuals were dead at the time of sampling and died due to natural causes (e.g. road kill, building collision, electrocution, starvation) or were procured from authorized hunters. None of the birds were killed for the purpose of the present study. We collected a proximal primary (innermost primary, hereafter P1) and a distal primary feather (P8) from each individual (Fig. 1A). We chose to sample P8 to characterize the distal part of the wing, because it is the longest flight feather in most birds and is thus more exposed to aerodynamic forces than the more proximal P1. On each feather, we measured barb density and angle (determined by the barb axis and the distal part of the rachis) on the trailing and the leading vane sides of the rachis at three different positions along the rachis (base, middle and tip, defined as 25, 50 and 75% of the total vane length, respectively). These measurements were made on digital photographs of the feathers lying on a metric grid background, or a stage micrometer, using ImageJ v.1.37 (<http://rsb.info.nih.gov/ij/>). The density of barbs was calculated as the number of barb embranchments along a 1-cm rachis section. Barb density was measured by B.B. and barb angle by Z.S.

### EXPLANATORY VARIABLES

We obtained body mass data from Dunning (2007) for both sexes. In species for which the data of several subspecies or populations were reported, we only used European populations and subspecies with European distributions (except for species originating from Antarctica). Species-specific body mass used in the analyses was calculated as the mean of male and female body masses. Flight type was assigned to one of four categories according to the proportion of flapping flight following Bruderer *et al.* (2010) and Pennycuick (2008), with slight modification after Pap *et al.* (2015): FS, FG, CF and PT. The four flight type categories differ in wing beat frequency, with steady increase from FS to PT; the aerodynamic pressure on primaries and its effect on feather morphology was assumed to be higher in soarers than in flappers. All data are reported in Supporting Information Tables A1–A3.

### STATISTICAL ANALYSES

Large within-species variation of the studied traits can cause significant biases in comparative



**Figure 1.** Schematic drawing of the innermost (P1) and distal (P8) primaries (A), the measurement positions (B) and photograph of the mesh structure of the vane of a common buzzard (*Buteo buteo*) with parallel barbs that branch off from the shaft (C). Measurements were taken on the trailing and the leading vane sides of the rachis at three different positions along the rachis (base, middle and tip, defined as 25, 50 and 75% of the total vane length, respectively). Values in red indicate barb angle (Ang) and density (Den) for each measurement position. Wing drawing courtesy of Erzsébet Ferencz.

phylogenetic analyses. Therefore, as a first step, we tested whether feather traits were species-specific and thus suitable for multispecies comparisons. We tested the species-specificity of the measured feather morphological traits by assessing the importance

of ‘between-species’ compared to ‘within-species’ variance using the function ‘ICCest’ from R package ‘ICC’ (Wolak *et al.*, 2012). This was computed using raw, non-transformed data. The species-specificity of feather traits varied from moderate to high with

generally narrow confidence intervals, indicating that the measured feather morphological traits are species-specific (Supporting Information, Table A4) and that they adequately characterized feather traits of the studied species.

In a previous study (Pap *et al.*, 2015) we found differences in proximal and distal primary feather morphology that were related to flight style. Accordingly, here, we used a series of statistical tests to test whether feather traits differed between proximal and distal feathers (i.e. P1 vs. P8), among different sections along the shaft (i.e. base vs. middle vs. tip) and between the two sides of the shaft (i.e. leading vs. trailing vane). Firstly, using phylogenetic paired *t*-tests we investigated whether feather morphological parameters differed between P1 and P8, separately at each position along the shaft (base, middle and tip), for both the trailing and leading vanes. Secondly, we used phylogenetic paired *t*-tests (Lindenfors *et al.*, 2010) to test whether feather morphology differed between the trailing and leading vanes and between different positions (base, middle and tip) along the shaft of both P1 and P8. Thirdly, using phylogenetic generalized least squares (PGLS) models (Pagel, 1997, 1999), we investigated how flight type influenced feather morphology of P1 and P8, while controlling for the confounding effect of body mass. We chose to control for the effect of body mass instead of feather mass, because these two traits are strongly correlated, our dataset for body mass was more comprehensive than for feather mass, and we know from our previous work that body mass may affect the relationship between flight style and feather morphology (Pap *et al.*, 2015). Finally, using PGLS models, we tested how flight type influenced morphological differences between proximal and distal primaries (hereafter  $\Delta P$ ), which was computed by subtracting the value of P1 from P8 for each morphological trait.

To account for phylogeny, we used trees provided by <http://birdtree.org> (Jetz *et al.*, 2012). We generated 100 trees using the higher order phylogeny of Hackett *et al.* (2008) and derived a rooted ultrametric consensus phylogenetic tree from these using the SumTrees software (Sukumaran & Holder, 2010). Feather morphological characters were used as response variables in the PGLS models, while body mass and flight type were introduced as explanatory variables. In all analyses, we set the degree of phylogenetic dependence (Pagel's  $\lambda$ ) to the most appropriate degree evaluated for each model based on likelihood ratio statistics.

All statistical analyses were conducted using the R statistical computing environment v.3.4.3 (R Development Core Team, 2017). PGLS models were built as implemented in the package 'nlme' (Pinheiro *et al.*, 2017). All phylogenetic paired *t*-tests were two

tailed and were performed using the 'phyl.pairedttest' function of the 'phytools' package in R (Lindenfors *et al.*, 2010). We report data as means  $\pm$  standard errors (SE). Graphical presentation of paired *t*-tests is based on raw data. Graphical presentation of PGLS models is based on predicted marginal means and their contrasts, obtained using the 'lsmeans' package in R (Lenth, 2016). Barb density, barb angle and body mass were log<sub>e</sub>-transformed in all statistical models to ensure normality of residuals.

## RESULTS

### DIFFERENCES BETWEEN PROXIMAL AND DISTAL PRIMARIES

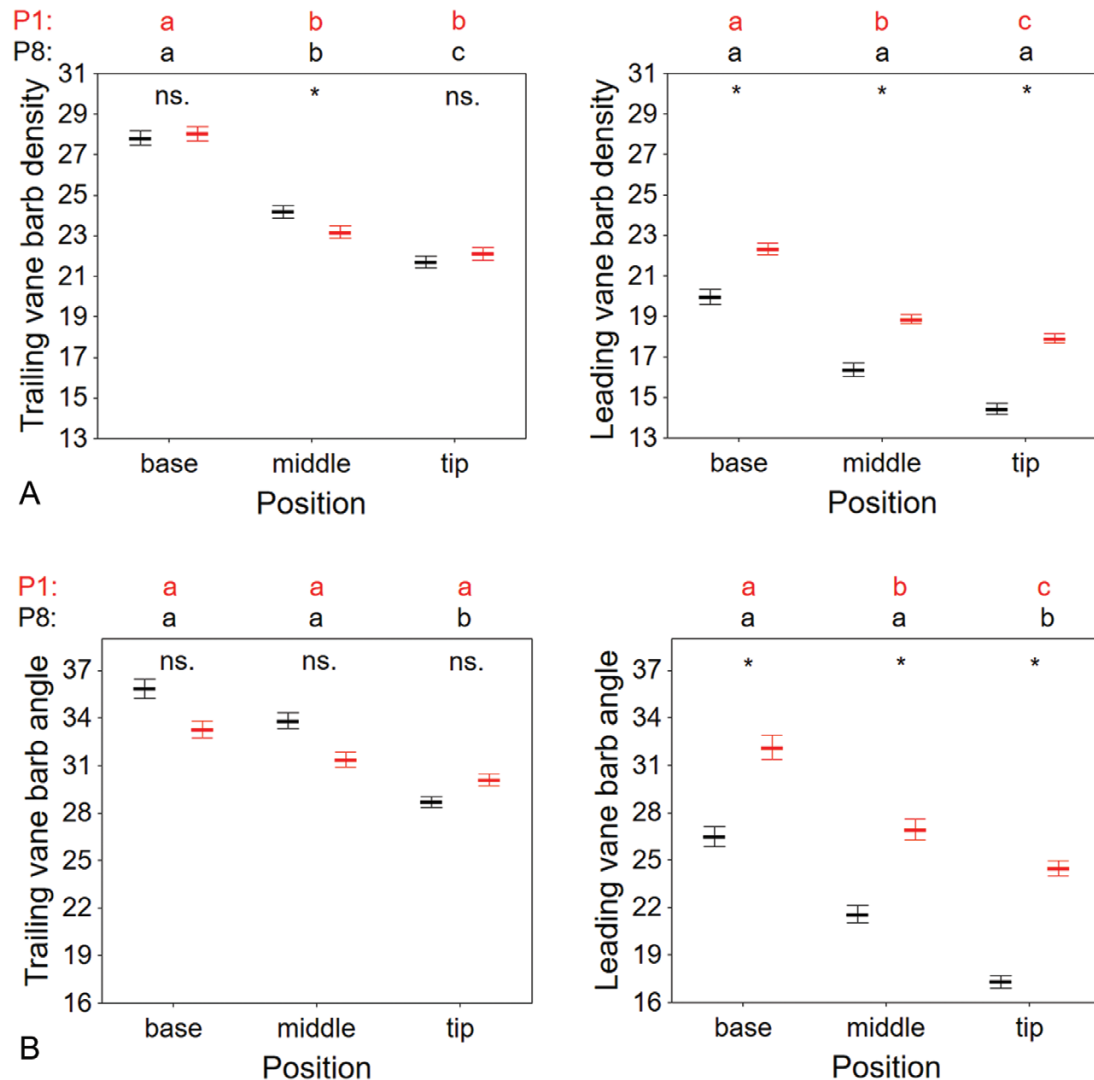
Barb density of the trailing vane was only greater on P8 than on P1 at the middle of the vane, with no differences detected between the two feathers at the base or at the tip (Table 1; Fig. 2A). In contrast, barb density of the leading vane was higher at all measurement positions along the shaft on P1 compared with P8. Barb angle was similar between P8 and P1 at all three measurement points along the shaft on the trailing vane, but higher on P1 than on P8 at all three positions on the leading vane (Table 1; Fig. 2B).

### DIFFERENCES ALONG THE SHAFT

In general, barb density decreased from the base to the tip of the feathers on both the trailing and the leading vanes of both P1 and P8. However, the degree of change along the shaft differed between P1 and P8, and also between the two sides of the vane (Table 2; Fig. 2A). For the trailing vane of P1, barb density

**Table 1.** Results of phylogenetic paired *t*-tests investigating differences in feather morphological parameters between the innermost (P1) and distal (P8) primaries measured at different positions (base, 25%; middle, 50%; tip, 75%) along the shaft on the trailing and leading vanes of the primaries ( $N = 178$  species)

|               | Barb density |          | Barb angle |          |
|---------------|--------------|----------|------------|----------|
|               | <i>t</i>     | <i>P</i> | <i>t</i>   | <i>P</i> |
| Trailing vane |              |          |            |          |
| Base          | -0.26        | 0.7915   | 1.33       | 0.1857   |
| Middle        | 2.45         | 0.0152   | 1.00       | 0.3194   |
| Tip           | -0.52        | 0.6048   | -1.58      | 0.1160   |
| Leading vane  |              |          |            |          |
| Base          | -2.98        | 0.0033   | -3.15      | 0.0019   |
| Middle        | -2.75        | 0.0065   | -2.24      | 0.0263   |
| Tip           | -2.92        | 0.0039   | -3.47      | 0.0006   |



**Figure 2.** Differences in barb density (A) and barb angle (B) between the innermost (P1) and distal (P8) primaries, measured at three positions along the feathers. Values are means  $\pm$  SE calculated from the raw data, and group-wise contrasts are extracted from the models. Different letters (a, b, c) denote significant ( $P < 0.05$ ) differences in feather traits measured at different vane positions, and asterisks denote significant differences ( $P < 0.05$ ) between P1 and P8.

decreased significantly between the base and middle positions, while for P8 the decrease was continuous and significant among all three positions along the shaft. For the leading vane of P1, barb density decreased continuously and significantly among all three positions along the shaft, while the change for P8 was non-significant. Barb angle decreased from the base to the tip on both P1 and P8, and on both sides of the vane. However, the degree of change along the shaft differed between P1 and P8, and between the trailing and leading sides of the vane (Table 2; Fig. 2B). For the trailing vane of P1, the change in barb angle was non-significant, while for P8 the decrease was sharp and significant between the middle and

tip positions. For the leading vane of P1, barb angle decreased continuously and significantly among all three positions along the shaft, while the decrease for P8 was significant only between the middle and tip (Table 2; Fig. 2B).

#### DIFFERENCE BETWEEN LEADING AND TRAILING VANES

Barb density of the trailing vane was significantly higher than that of the leading vane at each point along the vane for both P1 and P8 (phylogenetic paired  $t$ -test, P1, base:  $t = 2.15$ ,  $P = 0.0328$ ; middle:  $t = 2.47$ ,  $P = 0.0145$ ; tip:  $t = 3.46$ ,  $P = 0.0007$ ; P8, base:  $t = 4.69$ ,  $P < 0.0001$ ; middle:  $t = 4.91$ ,  $P < 0.0001$ ; tip:  $t = 5.70$ ,

**Table 2.** Results of phylogenetic paired *t*-tests investigating differences in feather morphological parameters between different positions (base, 25%; middle, 50%; tip, 75%) along the shaft on the trailing and leading vanes of the innermost (P1) and distal (P8) primaries (*N* = 178 species)

|               | Barb density |          |          |          | Barb angle |          |          |          |
|---------------|--------------|----------|----------|----------|------------|----------|----------|----------|
|               | P1           |          | P8       |          | P1         |          | P8       |          |
|               | <i>t</i>     | <i>P</i> | <i>t</i> | <i>P</i> | <i>t</i>   | <i>P</i> | <i>t</i> | <i>P</i> |
| Trailing vane |              |          |          |          |            |          |          |          |
| Base–middle   | 5.49         | <0.0001  | 6.08     | <0.0001  | 1.39       | 0.1672   | 0.96     | 0.3387   |
| Middle–tip    | 1.23         | 0.2197   | 2.36     | 0.0195   | 1.47       | 0.1439   | 3.33     | 0.0011   |
| Base–tip      | 4.87         | <0.0001  | 4.26     | <0.0001  | 1.89       | 0.0608   | 3.33     | 0.0011   |
| Leading vane  |              |          |          |          |            |          |          |          |
| Base–middle   | 3.22         | <0.0015  | 1.26     | 0.2082   | 3.93       | 0.0001   | 1.35     | 0.1783   |
| Middle–tip    | 2.95         | <0.0036  | 0.93     | 0.3535   | 2.89       | 0.0043   | 2.18     | 0.0304   |
| Base–tip      | 3.53         | <0.0005  | 1.85     | 0.0653   | 3.32       | 0.0011   | 2.59     | 0.0103   |

$P < 0.0001$ ). The barb angle of the leading vane was significantly lower than that of the trailing vane along the entire shaft of both P1 and P8, with the exception of the base of P1 (P1, base:  $t = -0.26$ ,  $P = 0.7918$ ; middle:  $t = 2.37$ ,  $P = 0.0188$ ; tip:  $t = 3.95$ ,  $P = 0.0001$ ; P8, base:  $t = 4.91$ ,  $P < 0.0001$ ; middle:  $t = 5.83$ ,  $P < 0.0001$ ; tip:  $t = 8.38$ ,  $P < 0.0001$ ).

#### FLIGHT TYPE AND FEATHER MORPHOLOGY

Flight style had a significant effect on barb density on both the trailing and the leading vane of P1 and P8, with the exception of the base of the leading vane of P1 and the tip of the leading vane of both P1 and P8 (Table 3; Fig. 3A). In general, barb density was higher in flapping (CF and PT) than in gliding flyers (FS and FG), with the largest difference observed between flight types FS and CF (Fig. 3A). However, the effect of flight type differed between P1 and P8, between the two sides of the vanes and along the shaft. The effect of flight type on barb density was most pronounced on the distal vane of P8 and less marked on the proximal vane of P1, and on the trailing side vane of both feathers.

Flight type was significantly related to barb angle on the trailing vane of P8 at all three positions along the shaft, although we did not find a clear difference between gliders (FS and FG) and flappers (CF and PT) (Table 3; Fig. 3B). In contrast, flight type had no effect on barb angle on the trailing vane of P1 (Table 3; Fig. 3B). The effect of flight type on the barb angle of the leading vane differed between P1 and P8, and along the shaft; differences were most pronounced on the tip of both P1 and P8, weaker on the middle-vane measurement of P8 and non-significant on the other measurement points. Nonetheless, the difference between gliders and flappers was unclear.

#### EFFECT OF FLIGHT TYPE ON VARIATION IN FEATHER MORPHOLOGY ALONG THE FEATHER AXIS AND ON THE DIFFERENCE BETWEEN P8 AND P1 ( $\Delta P$ )

In general, the change in barb density along the shaft on both sides of the vane was weakly associated with flight type (Table 4) and was significant in two cases only: the difference between base and tip of the trailing vane on P1, and the difference between middle and tip of the leading vane on P8 (Table 4). In both cases, the increase in barb density toward the tip of the vane was significantly higher ( $P < 0.05$ ) for CF than for FS flight styles. The change in barb angle in P8 was significantly related to flight type in three cases, but the differences did not seem to follow differences in wing beat frequency (Table 4; P8, trailing vane, base vs. middle: CF < FS; middle vs. tip: CF > FS, CF > PT; P8, leading vane, middle vs. tip: CF > FS; all  $P < 0.05$ ). Variation in barb angle along the shaft of P1 was not related to flight type.

$\Delta P$  of barb density was not related to flight type, except for the leading vane at mid-shaft (Table 5). In this case, the difference between P8 and P1 was significantly higher for CF than for FS ( $P < 0.05$ ).  $\Delta P$  of barb angle varied little with flight type, except for the trailing vane measured at the base and middle positions along the shaft (Table 5). However, group differences did not seem to reflect differences in flight type (trailing vane, base: CF < FG, PT < FG; middle: CF > FS; all  $P < 0.05$ ).

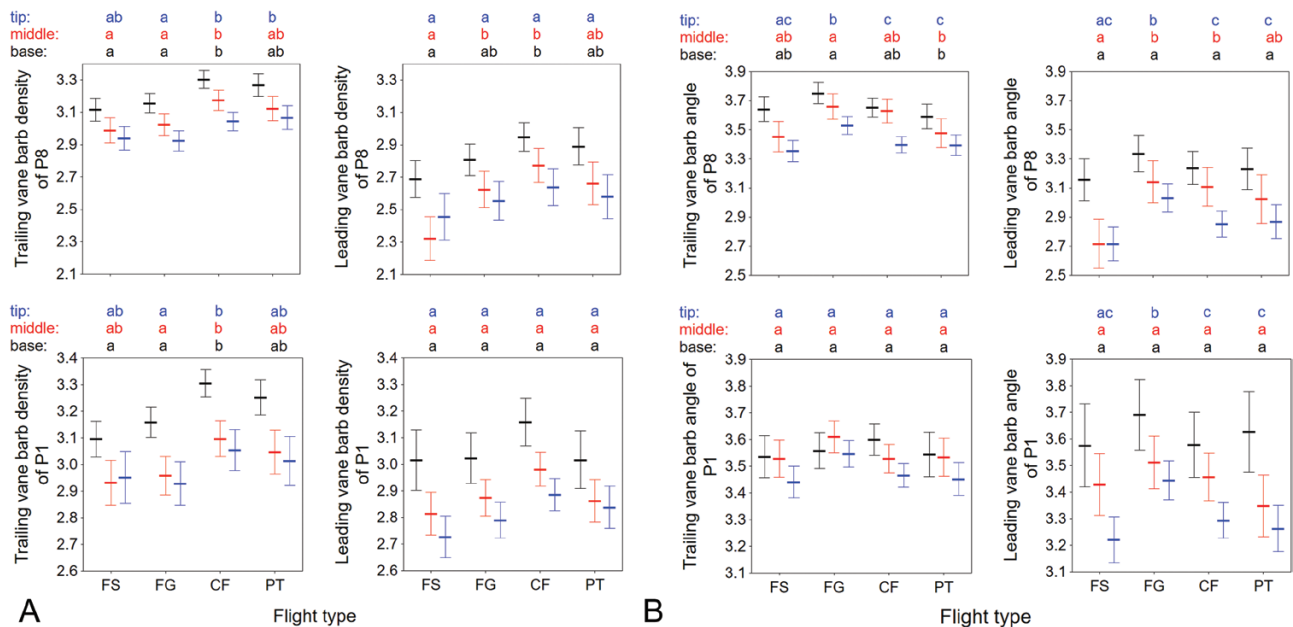
#### DISCUSSION

##### VANE MORPHOLOGY AND VARIATION WITHIN AND BETWEEN PRIMARIES

The sample of 178 species used in the current study shows that the variation in vane macrostructure (barb

**Table 3.** Results of PGLS models investigating whether the feather morphological parameters measured at different positions (base, 25%; middle, 50%; tip, 75%) along the shaft on the trailing and leading vanes of the innermost (P1) and distal (P8) primaries differed between species characterized by different flight types ( $N = 178$  species)

|               |   | Barb density |          |          |          | Barb angle |          |          |          |
|---------------|---|--------------|----------|----------|----------|------------|----------|----------|----------|
|               |   | P1           |          | P8       |          | P1         |          | P8       |          |
|               |   | <i>F</i>     | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i>   | <i>P</i> | <i>F</i> | <i>P</i> |
| d.f.          |   |              |          |          |          |            |          |          |          |
| Trailing vane |   |              |          |          |          |            |          |          |          |
| Base          |   |              |          |          |          |            |          |          |          |
| Body mass     | 1 | 26.67        | <0.0001  | 12.32    | 0.0006   | 30.82      | <0.0001  | 23.35    | <0.0001  |
| Flight type   | 3 | 8.71         | <0.0001  | 7.72     | 0.0001   | 0.60       | 0.6181   | 3.07     | 0.0292   |
| Middle        |   |              |          |          |          |            |          |          |          |
| Body mass     | 1 | 30.45        | <0.0001  | 20.01    | <0.0001  | 28.47      | <0.0001  | 6.29     | 0.0131   |
| Flight type   | 3 | 4.75         | 0.0033   | 7.23     | 0.0001   | 1.51       | 0.2055   | 4.78     | 0.0032   |
| Tip           |   |              |          |          |          |            |          |          |          |
| Body mass     | 1 | 26.27        | <0.0001  | 17.33    | <0.0001  | 13.48      | 0.0003   | 9.09     | 0.0030   |
| Flight type   | 3 | 3.08         | 0.0290   | 5.49     | 0.0013   | 2.38       | 0.0715   | 5.52     | 0.0012   |
| Leading vane  |   |              |          |          |          |            |          |          |          |
| Base          |   |              |          |          |          |            |          |          |          |
| Body mass     | 1 | 0.38         | 0.5410   | 0.02     | 0.8779   | 22.04      | <0.0001  | 7.71     | 0.0061   |
| Flight type   | 3 | 2.37         | 0.0721   | 3.14     | 0.0267   | 0.72       | 0.5409   | 1.05     | 0.3713   |
| Middle        |   |              |          |          |          |            |          |          |          |
| Body mass     | 1 | 2.45         | 0.1194   | 2.84     | 0.0936   | 30.71      | <0.0001  | 1.88     | 0.1721   |
| Flight type   | 3 | 3.19         | 0.0250   | 6.18     | 0.0005   | 1.40       | 0.2456   | 3.32     | 0.0211   |
| Tip           |   |              |          |          |          |            |          |          |          |
| Body mass     | 1 | 3.79         | 0.0533   | 5.18     | 0.0241   | 40.46      | <0.0001  | 1.48     | 0.2248   |
| Flight type   | 3 | 2.55         | 0.0572   | 1.17     | 0.3244   | 5.77       | 0.0009   | 4.37     | 0.0054   |



**Figure 3.** The relationship between flight type and barb density (A) and barb angles (B), measured at three positions along the innermost (P1) and distal (P8) primaries. Values are mean  $\pm$  SE predicted from the models, and different letters (a, b) denote significant differences ( $P < 0.05$ ), as inferred from the PGLS models. Flight types: FS, flapping and soaring; FG, flapping and gliding; CF, continuous flapping; PT, passerine type. Predicted values are on log scale (natural logarithm).

**Table 4.** Results of PGLS models investigating whether the change in feather morphological parameters along the shaft on the trailing and leading vanes of the innermost (P1) and distal (P8) primaries differed between species characterized by different flight types ( $N = 178$  species)

|               |      | Barb density |          |          |          | Barb angle |          |          |          |
|---------------|------|--------------|----------|----------|----------|------------|----------|----------|----------|
|               |      | P1           |          | P8       |          | P1         |          | P8       |          |
|               | d.f. | <i>F</i>     | <i>P</i> | <i>F</i> | <i>P</i> | <i>F</i>   | <i>P</i> | <i>F</i> | <i>P</i> |
| Trailing vane |      |              |          |          |          |            |          |          |          |
| Base–middle   |      |              |          |          |          |            |          |          |          |
| Body mass     | 1    | 0.33         | 0.5645   | 0.06     | 0.8101   | 0.36       | 0.5518   | 10.01    | 0.0018   |
| Flight type   | 3    | 1.48         | 0.2223   | 0.15     | 0.9265   | 2.65       | 0.0506   | 4.41     | 0.0051   |
| Middle–tip    |      |              |          |          |          |            |          |          |          |
| Body mass     | 1    | 0.37         | 0.5437   | 0.00     | 0.9909   | 5.46       | 0.0206   | 0.54     | 0.4619   |
| Flight type   | 3    | 1.47         | 0.2239   | 2.64     | 0.0513   | 0.23       | 0.8754   | 4.32     | 0.0058   |
| Base–tip      |      |              |          |          |          |            |          |          |          |
| Body mass     | 1    | 0.29         | 0.5923   | 0.02     | 0.8809   | 4.74       | 0.0309   | 11.54    | 0.0008   |
| Flight type   | 3    | 3.22         | 0.0242   | 2.28     | 0.0814   | 2.67       | 0.0494   | 0.37     | 0.7744   |
| Leading vane  |      |              |          |          |          |            |          |          |          |
| Base–middle   |      |              |          |          |          |            |          |          |          |
| Body mass     | 1    | 0.40         | 0.5292   | 2.72     | 0.1010   | 6.69       | 0.0105   | 4.72     | 0.0312   |
| Flight type   | 3    | 1.07         | 0.3640   | 0.44     | 0.7231   | 1.54       | 0.2065   | 1.08     | 0.3590   |
| Middle–tip    |      |              |          |          |          |            |          |          |          |
| Body mass     | 1    | 0.01         | 0.9137   | 0.20     | 0.6518   | 13.96      | 0.0003   | 0.94     | 0.3336   |
| Flight type   | 3    | 0.69         | 0.5564   | 3.82     | 0.0111   | 1.16       | 0.3271   | 3.23     | 0.0237   |
| Base–tip      |      |              |          |          |          |            |          |          |          |
| Body mass     | 1    | 0.15         | 0.7020   | 2.30     | 0.1315   | 10.91      | 0.0012   | 5.47     | 0.0205   |
| Flight type   | 3    | 0.89         | 0.4499   | 1.14     | 0.3356   | 0.31       | 0.8164   | 0.37     | 0.7779   |

density and barb angle) between P1 and P8, along the feather shaft, and between the trailing and leading vanes largely reflects the variation in aerodynamic forces along the feather and at different positions on the wing (Bachmann *et al.*, 2007; Dial *et al.*, 2012; Pap *et al.*, 2015). Specifically, the vanes of the distal primary feathers (e.g. P8), which are subject to higher aerodynamic forces during the flapping flight wing-stroke, can resist larger out-of-plane forces than proximal primaries (e.g. P1; Ennos *et al.*, 1995). The greater barb density of the trailing vane at mid-shaft of P8 compared with P1 supports this statement and also corroborates our previous findings, which showed that barb density of the trailing vane is higher in distal compared than in proximal primaries (Pap *et al.*, 2015). However, the difference in barb density between the base and the tip of the trailing vane was similar on P1 and P8, indicating that the relative distribution of forces along the feather is similar across the distal wingspan. Therefore, morphological adaptation concerning vane barb density of primary feathers is influenced by feather position, by the position along the shaft, and by the side of the vane (i.e. leading or trailing). The greater barb density of the leading vane of P1 compared with that of P8 is probably related to

the fact that peak aerodynamic forces are higher for the distal part of the wing. Barb angle of the leading vane was greater for P1 than for P8, reinforcing the role of barb angle in modulating vane width and vane asymmetry (Ennos *et al.*, 1995): P8, particularly when emarginated, generally has a narrower leading vane and greater vane asymmetry than P1.

In agreement with a study on barn owls and feral pigeons (Bachmann *et al.*, 2007), and in support of the idea of higher air pressure gradients at the base of the feather (Müller & Patone, 1998), barb density on both vanes (i.e. leading and trailing) decreased from the base to the tip of the feathers. Barb density of the leading vane, however, decreased from the base toward the tip on P1, but not on P8. Perhaps because the more distal primary (P8) orientates in the wingspan plane, whereas P1 orientates more in the chordwise plane, means that the leading edge of P8 experiences similar aerodynamic forces over its entire length. However, if this were the explanation, we might expect to see a similar result for the trailing vane of P8 too. Our results, and those of others, suggest that a major evolutionary driver of feather morphology diversity was different transmissivity needs (Müller & Patone, 1998; Heers *et al.*, 2011; Dial *et al.*, 2012; Pap *et al.*, 2015).

**Table 5.** Results of PGLS models investigating whether the difference in feather morphological parameters between the distal (P8) and innermost (P1) primaries ( $\Delta P$ ), measured at different positions (base, 25%; middle, 50%; tip, 75%) along the shaft on the trailing and leading vanes, differed between species characterized by different flight types ( $N = 178$  species)

|               |      | Barb density |          | Barb angle |          |
|---------------|------|--------------|----------|------------|----------|
|               | d.f. | <i>F</i>     | <i>P</i> | <i>F</i>   | <i>P</i> |
| Trailing vane |      |              |          |            |          |
| Base          |      |              |          |            |          |
| Body mass     | 1    | 6.50         | 0.0116   | 0.10       | 0.7496   |
| Flight type   | 3    | 0.27         | 0.8472   | 5.21       | 0.0018   |
| Middle        |      |              |          |            |          |
| Body mass     | 1    | 4.52         | 0.0349   | 3.53       | 0.0619   |
| Flight type   | 3    | 0.56         | 0.6453   | 3.43       | 0.0183   |
| Tip           |      |              |          |            |          |
| Body mass     | 1    | 4.16         | 0.0428   | 1.96       | 0.1635   |
| Flight type   | 3    | 1.13         | 0.3390   | 0.95       | 0.4191   |
| Leading vane  |      |              |          |            |          |
| Base          |      |              |          |            |          |
| Body mass     | 1    | 1.53         | 0.2178   | 1.65       | 0.2013   |
| Flight type   | 3    | 0.86         | 0.4606   | 0.43       | 0.7314   |
| Middle        |      |              |          |            |          |
| Body mass     | 1    | 0.42         | 0.5167   | 7.85       | 0.0057   |
| Flight type   | 3    | 3.07         | 0.0294   | 2.50       | 0.0610   |
| Tip           |      |              |          |            |          |
| Body mass     | 1    | 0.00         | 0.9982   | 15.50      | 0.0001   |
| Flight type   | 3    | 0.07         | 0.9751   | 0.16       | 0.9240   |

In general, the branching angle of the barbs decreased from the base to the tip on both the leading and the trailing vanes, although the change was significant only on P8. A smaller branching angle of the barbs and hence greater resistance to out-of-plane forces (Ennos *et al.*, 1995) towards the tip of the distal primary makes sense because this is the area of the feather where aerodynamic forces are likely to be highest. For example, the distal primaries can be twisted up to almost 180° to produce lift on the upstroke during take-off (Tobalske *et al.*, 2003; Crandell & Tobalske, 2011). In the case of the innermost primary, P1, the non-significant change in barb angle along the shaft on the trailing vane may reflect a more even distribution of forces resulting from the more chordwise plane of the feather (Ennos *et al.*, 1995) in comparison to that of P8.

Barb density of the trailing vane was significantly higher than that of the leading vane at all three positions along the shaft and on both primaries, suggesting that flight feathers show morphological adaptations that ensure low transmissivity to air and, therefore, high resistance to aerodynamic forces. Additionally, in accordance with Müller & Patone (1998), the difference

in transmissivities of the trailing and leading vanes may induce a pressure gradient, which pushes the less transmissive trailing vane towards the overlying, more transmissive leading vane to help maintain a continuous flight surface. Moreover, the lower branching angle of the leading edge barbs may help to produce the great degree of planform asymmetry, which allows feathers to function as independent aerofoils during flight, take-off and landing (Norberg, 1990). Lower branching angles of leading vane barbs may also increase the stiffness of the leading vane, which helps prevent barb detachment when the feather is pulled through the air (Ennos *et al.*, 1995). Currently, however, it is not possible to determine whether barb angle is driven by a need for a narrow vane, whilst maintaining structural integrity, or whether barb angle is linked directly to aerodynamic loading. Finally, it should be noted that transmissivity to air and the dynamic response of the feather vane to aerodynamic forces are determined not only by barb density and geometry, but also by the diameter and shape of the barbs, and barbules, measures which were not quantified in the present study.

#### FEATHER MORPHOLOGY AND FLIGHT TYPE

After controlling for body mass, flight type significantly affected barb density on the vanes of both proximal (P1) and distal (P8) primaries at all three positions along the axis of the feathers, except for the leading vane of P1 and the tip of the leading vane of P8. This corroborates one of our previous comparative studies, in which we found that the barb density of the trailing vane was lowest in birds with the FS flight type (Pap *et al.*, 2015). In general, barb density was higher in flappers (CF and PT) than in soarers (FS and FG), but the differences between the flight types were somewhat obscured by intermediate values for the PT group. The lack of a clear difference in barb density may indicate that feather morphology is affected by more than just steady-state flight type: e.g. the high forces generated during take-off and landing. Contrary to our prediction, flight type was not related to feather morphology differences along the shaft, and the effect of flight type was similar on both vanes of P1 and P8. This indicates that, in general, flight (regardless of flight type) affects morphological adaptation of vane barb density similarly along the shaft despite the fact that the forces acting on the feather tips during flapping flight are probably greater than during soaring flight (Müller & Patone, 1998; Pap *et al.*, 2015). This idea is further supported by the lack of a clear difference in the barb density of P1 and P8 between flappers (CF and PT) and soarers (FS and FG) (Table 5; Fig. 3A). The lack of an effect of flight type on feather vane macrostructure contrasts with our previous comparative study on a smaller number of species (Pap *et al.*, 2015). This highlights the importance

of further studies on more species with flight types not included in these studies. Additionally, there is a need for more data on the wing kinematics of different species of birds, because it is likely that the broad qualitative categorizations of flight styles currently available lack sufficient resolution to accurately define the aerodynamic forces to which any given species are subjected. In addition, further measures of the macro- and microstructure of the vane (i.e. barbule morphology and geometry) is needed to better understand the mechanic response of the feathers to flight.

Flight type affected the angle of barbs on both P1 and P8 (Fig. 3B). However, we could not find any consistent differences in the direction of change between flight type groups. Hence, adaptation of this important component of vane geometry does not seem to be driven by variation in flight style. Instead, barb angle might be more strongly affected by selective forces other than the steady-state flight type, such as the high forces generated during take-off and landing.

## CONCLUSIONS

The vanes of no two feathers are alike: the geometry of one proximal and one distal primary feather differs from each other and these fine-scale differences appear to be adaptations to the particular aerodynamic conditions to which each feather is exposed. Hence, this study adds new perspectives to our understanding of the functional morphology of flight feather vanes. To test the suggestions put forward in our paper, it would be desirable to measure other traits of the vane, such as barbule morphology and geometry, and its mechanical response to air pressure. There is also a need to investigate a wider range of birds, ranging from gliding specialists, such as albatrosses and petrels (groups which are under-represented in the present study) whose wings are mainly subjected to aerodynamic forces from below, to hovering specialists, such as hummingbirds, whose wings must withstand forces from both below and above (because of an active upstroke). Ideally, a categorization of flight styles that provides a higher resolution, more accurate description of flight behaviour would also be desirable. Furthermore, we have limited knowledge on how aerodynamic forces generated during take-off and landing affect the morphology of the feather vane and how such forces might differ between flight types, a topic that clearly deserves further investigation.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table A1.** Barb density for the innermost (P1) and second to outermost (P8) primaries. *N* is the sample size for each parameter. See Material and methods for sources.

**Table A2.** Barb angle to rachis for the innermost (P1) and second to outermost (P8) primaries. *N* is the sample size for each parameter. See Material and methods for sources.

**Table A3.** Body masses and flight types (FS, flapping and soaring; FG, flapping and gliding; CF, continuous flapping; PT, passerine-type) for the species included in the study. *N* is the sample size for each species. See Material and methods for an explanation of flight types.

**Table A4.** Repeatability of feather traits for the innermost (P1) and second to outermost (P8) primaries. ICC is the intraclass correlation and the values in parentheses denote the 95% confidence interval. Only species with at least two individuals measured are included in the analyses (*N* = 123). See Material and methods for sources.