

Interspecific variation in the structural properties of flight feathers in birds indicates adaptation to flight requirements and habitat

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Summary

1. The functional significance of intra- and interspecific structural variations in the flight feathers of birds is poorly understood. Here, a phylogenetic comparative analysis of four structural features (rachis width, barb and barbule density and porosity) of proximal and distal primary feathers of 137 European bird species was conducted.

2. Flight type (flapping and soaring, flapping and gliding, continuous flapping or passerine type), habitat (terrestrial, riparian or aquatic), wing characteristics (wing area, S and aspect ratio, AR) and moult strategy were all found to affect feather structure to some extent. Species characterized by low wing-beat frequency flight (soaring and gliding) have broader feather rachises (shafts) and feather vanes with lower barb density than birds associated with more active flapping modes of flight. However, the effect of flying mode on rachis width disappeared after controlling for S and AR , suggesting that rachis width is primarily determined by wing morphology.

3. Rachis width and feather vane density are likely related to differences in force distribution across the wingspan during different flight modes. An increase in shaft diameter, barb density and porosity from the proximal to distal wing feathers was found and was highest in species with flapping flight indicating that aerodynamic forces are more biased towards the distal feathers in flapping flyers than in soarers and gliders.

4. Habitat affected barb and barbule density, which was greatest in aquatic species, and within this group, barb density was greater in divers than non-divers, suggesting that the need for water repellency and resistance to water penetration may influence feather structure. However, we found little support for the importance of porosity in water repellency and water penetration, because porosity was similar in aquatic, riparian and terrestrial species and among the aquatic birds (divers and non-divers). We also found that barb density was affected by moult pattern.

5. Our results have broad implications for the understanding of the selection pressures driving flight feather functional morphology. Specifically, the large sample size relative to any previous studies has emphasized that the morphology of flight feathers is the result of a suite of selection pressures. As well as routine flight needs, constraints during moulting, habitat (particularly aquatic) and migratory requirements also affect flight feather morphology. Identifying the exact nature of these trade-offs will perhaps inform the reconstruction of the flying modes of extinct birds.

Key-words: barb density, barbule density, flight, flight feathers, functional morphology, moult, rachis width, vane porosity, water repellence, wing morphology

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Introduction

Primary feathers are positioned distally on the wings of birds, and their morphology may vary depending upon the aerodynamic forces they are subject to, which in turn is influenced by their spanwise position upon the wing (Pennycuik 1989; Svensson 1992; Jenni & Winkler 1994; Linde-Norberg 2002; Nudds & Dyke 2010). Species differ in the amount of time they spend flying, their flight speeds and flight type (flapping vs. soaring–gliding) all of which expose the wing feathers to different amounts of aerodynamic forces (Pennycuik 1989). Consequently, the quantity of keratin invested in flight feathers and their structure varies with flying behaviour and life history (Worcester 1996; Aparicio, Bonal & Cordero 2003; Weber *et al.* 2005; Lingham-Soliar, Bonser & Wesley-Smith 2010; Bachmann *et al.* 2012; Wang *et al.* 2012).

The primary feathers of larger birds are relatively more flexible than those of smaller birds due to relatively narrower rachises, which is thought to reflect exposure to lower forces and bending moments in flight (Wang *et al.* 2012). These reduced forces and bending moments are a consequence of relatively shorter primary feathers (Nudds, Kaiser & Dyke 2011; Wang *et al.* 2012) and flight styles that tend to be less demanding (i.e. that generate proportionately less forces on the wings) (Pennycuik 1989). The ‘flexible shaft’ hypothesis predicts that species with mostly non-flapping flight (soaring and gliding) have more flexible wing feathers and narrower rachises than birds with flapping flight because rachis width and flexural stiffness are positively correlated (Worcester 1996; Wang *et al.* 2012; Pap *et al.* 2013). Additionally, the aerodynamic forces are less demanding on more proximal than on more distally positioned primary feathers, meaning that rachises should become more robust outwards (Corning & Biewener 1998). The spanwise distribution of forces upon the wing is also likely influenced by flight type, which in turn should influence the difference in rachis width between the proximal and distal primary feathers (Ennos, Hickson & Roberts 1995). Therefore, as well as a general proximal–distal increase, we would also predict that the increase in distal feather rachis width over that on proximal feathers to be greater in species with more demanding flight styles (i.e. flapping flyers). However, wing area (S) and wing shape (i.e. aspect ratio, AR) must also be considered when investigating feather morphology, because they should also affect the distribution of aerodynamic forces upon the wing (Pennycuik 2008), and are likely to correlate with flight type.

Feather vanes are formed by parallel barbs that are connected via hook and bow barbules and are light, flexible and resistant to damage (Prum & Brush 2002). Barbule density increases the feather vane’s resistance to air transmissivity (Heers, Tobalske & Dial 2011; Dial, Heers & Tobalske 2012). Therefore, we predict a positive association between barbule density and wing-beat frequency, with an increase in density from soaring and gliding to flapping

flight. Because not only the flight type, but the migratory behaviour may also affect the material and structural properties of flight feathers, migration distance must also be taken into account (de la Hera, Pérez-Tris & Tellería 2009; de la Hera, DeSante & Milá 2012).

Besides the main aerodynamic function of the primary feathers, water repellency and resistance to water penetration is also essential for the maintenance of an effective flight surface (Rijke 1968, 1970; Elowson 1984; Rijke & Jesser 2011). Water repellency is determined by the porosity of the vanes, which is a function of $(r + d)/r$, where $2r$ is the width, and $2d$ is the spacing of the barbs and of barbules (Rijke 1968, 1970). Water repellency increases with larger values of $(r + d)/r$ of the barbs, whereas smaller values (of barbs and barbules) increase resistance to water penetration. Hence, the structural characteristics compatible with optimal water repellency are in conflict with the requirements of resistance to water penetration. Previous studies have shown that the density of flight feather vanes differs between species living in different habitats and between diving and non-diving aquatic birds, but the differences are less than those observed in body contour feathers (Butler, Rohwer & Speidel 2008; Rijke & Jesser 2011). Further, the porosity (which is a function of barb and barbule density) of the vane of flight feathers might be determined primarily by aerodynamic forces and only secondarily by habitat. The effect of habitat on the porosity of primary feathers has only been tested in a narrow range of mainly aquatic bird species without accounting for phylogenetic dependence (Rijke 1968, 1970; Rijke & Jesser 2011). Despite concerns about the validity of the textile model (Elowson 1984), which postulates that high water repellency of textiles is ensured by high values of porosity, the application of the model for feathers is still accepted in the literature. To test the relationship between waterproofing and feather structure, we analysed the barb and barbule density of the proximal and distal primaries in relation to habitat type and diving behaviour of aquatic birds. Additionally, we calculated the porosity of the primary feather vanes and related these values to habitat in order to test the textile model.

Feathers lose structural integrity with time, and therefore, birds must moult periodically to replace them with new, undamaged ones. Moult is aerodynamically costly and requires a great quantity of resources and time (Chai & Robert 1999; Hedenström & Sunada 1999; Dawson *et al.* 2000; Lind 2001; Pap *et al.* 2008; Vágási *et al.* 2012), since the feathers compose about 30% of the total protein mass of the birds (Murphy, King & Lu 1988). Thus, overlapping moult with other energetically demanding activities is generally avoided, and as a consequence, the duration of moult is constrained by breeding and migration within the annual cycle of birds (Jenni & Winkler 1994). Previous studies show that migratory species moulting on the winter grounds have a longer moulting duration, while birds moulting immediately after breeding are more limited in terms of time available for feather replacement (de la Hera,

Pérez-Tris & Tellería 2010). The time and nutritional limitation imposed by food quality and parasites may affect the structural development of feathers (DesRochers *et al.* 2009; Vágási *et al.* 2012; Pap *et al.* 2013). While there is consensus about how limited time and nutrition reduce the amount of keratin invested in feathers (rachis width, feather mass/feather length), conflicting results were found for the effects on vane density (Dawson *et al.* 2000; Pap *et al.* 2008, 2013; DesRochers *et al.* 2009; Vágási *et al.* 2012; Danner *et al.* 2014). Therefore, to determine whether moulting and nutritional limitation constrains the development of primary feathers, we compared the feather structure of species with different moult strategies and differing amounts of protein included in their diets.

Here, we used the phylogenetic comparative approach and data from 137 temperate European bird species to test whether flight type and migration distance affects the structure of primary feathers. We test the validity of the 'flexible shaft' hypothesis for explaining the material and functional response of primary feathers to increased aerodynamic loads as a function of flight type (soaring or flapping). Further, we test for effects of the need for water repellency on primary feather structure by comparing data across species living in different habitats and between diving and non-diving aquatic birds. Finally, we analyse whether moulting and nutrition influence feather structure.

Materials and methods

FIELD DATA COLLECTION AND FEATHER MEASUREMENTS

We collected feather samples from 661 adult birds belonging to 137 species between 2003 and 2013 at several locations across Romania. The birds were captured throughout the year using mist nets (Eco-tone, Poland). Upon capture, the innermost primary (P1) was plucked from one wing. In addition, P1 and primary 8 (P8) feathers were collected from dead birds. P8 was chosen, because it is generally the longest distal flight feather in birds and is more exposed to aerodynamic forces than the more proximal P1. Therefore, we expected that traits related to flight type would have a larger effect on the structure of P8 than that of P1. Rachis width, barb density and barbule density were measured for each feather. We measured the diameter of barbs ($2r$) and interbarbs' distance ($2d$) in a subset of randomly selected individuals (2 to 4) per species, unless the original sample size was one or feather damage did not allow measurement. Rachis width was measured across the dorsoventral plane with a digital calliper to the nearest 0.01 mm at the base of the vane. Digital photographs of the feathers laying on a metric grid background or a stage micrometre were imported into IMAGEJ version 1.37 (<http://rsb.info.nih.gov/ij/>) to allow measurements of barb and barbule density. Barb and barbule density were measured on the inner feather vane, at a point corresponding to half of the length of the vaned rachis section. The density of barbs and barbules were calculated as the number of embranchments of barbs and proximal barbules in the middle of the vane along 1 cm of rachis and a 1 mm barb length section, respectively. At the same position of the vane, we measured the diameter of five barbs and five interbarb distances, and the mean values were used for further analyses. Our measure of vane porosity is measured as the porosity of the barbs only, that is barbule porosity was not measured.

The feather quality parameters of P1 were similar for live and dead birds (Wilcoxon matched pairs test: feather length: $Z = 1.77$, $N = 36$, $P = 0.0772$; feather mass: $Z = 0.21$, $N = 37$, $P = 0.8327$; paired sample t -test; rachis width: $t = 1.04$, $N = 37$, $P = 0.3080$; barbs density: $t = 0.76$, $N = 36$, $P = 0.4513$; barbule density: $t = -0.44$, $N = 37$, $P = 0.6661$). Therefore, it is unlikely that the results are biased by degradation of feathers collected from dead individuals. Rachis width was measured by GO, barb and barbule density, and the diameter of barbs and interbarb distances by KS.

BODY MASS AND WING MORPHOLOGY

We obtained body mass data from Dunning (2007). In the case of species for which the data of several subspecies or populations were reported, we only used European populations and subspecies with a European distribution. We calculated an overall mean body mass of the sexes. To quantify wing shape and proportions across the broad size range of birds in the data set, wing area (S) and aspect ratio ($AR = b^2/S$, where b denotes the wingspan) were quantified (Norberg 1990; Pennycuik 2008). Measurements were taken from the photographs using ImageJ. Wing areas were measured as the surface of both wings plus the area of the body: the distance between the wing roots multiplied by wing chord (see Pennycuik 2008).

The body was not fully visible in some of the photographs, and hence, we could not calculate b and S , which are necessary to calculate AR . In these instances, we measured reduced wingspan (b_{red}) and reduced wing area (S_{red}), which do not include the body width and body area, respectively (see also Andrews, Mackenzie & Gregory 2009). Reduced aspect ratio (AR_{red}) was calculated as b_{red}^2/S_{red} . Note, however, that there is a very strong correlation between the measures with and without the body both when individual-level data and species averages were correlated (phylogenetically uninformed ordinary least squares regression: b , β (SE) = 1.09 (0.00), $t_{583} = 363.10$, $R^2 = 1.00$, $P < 0.0001$; S , β (SE) = 1.11 (0.00), $t_{583} = 783.75$, $P < 0.0001$, $R^2 = 1.00$; phylogenetic generalized least squares regression: b , β (SE) = 1.08 (0.01), $t_{95} = 182.00$, $R^2 = 1.00$, $P < 0.0001$; S , β (SE) = 1.10 (0.01), $t_{95} = 155.92$, $R^2 = 1.00$, $P < 0.0001$). Therefore, we used the reduced measures in subsequent analyses to increase the sample sizes, but use the standard nomenclature (i.e. S and AR). The above measurements were carried out blindly with respect to the tested hypothesis by CIV.

LIFE-HISTORY, ECOLOGICAL VARIABLES AND FLYING BEHAVIOUR

Species were classified into one of three habitat groups (Cramp & Perrins 1977–1994): terrestrial (rarely encountering water), riparian (living in wetland habitats, e.g. marshes and sedges) or aquatic (species that locomote on the surface of or in water). Aquatic species were further categorized as divers and non-divers. Migratory behaviour was quantified by calculating the geographical distance between the latitudinal mid-point (centroid) of the breeding and wintering ranges (found by the 'gCentroid' function of the R package 'rgeos'; Bivand & Rundel 2013), which are situated between longitudes 20W and 60E. Distribution maps (shape files) were retrieved from <http://www.bird-life.org/datazone/info/spcdownload> (BirdLife International & NatureServe 2012). Migration distance was then calculated as the geographic distance between the breeding and wintering centroids using a custom function written in R (R Development Core Team 2013). The result is the mid-point of a species migration distance range. Diet during moult was assigned to one of the two categories: high or low protein content. High defined as

exclusively feeding on invertebrates and/or vertebrates and low as omnivorous and/or species feeding on plants. Dietary information for each species was obtained from Cramp & Perrins (1977–1994). We also assigned species to three different moulting categories following Baker (1993), Cramp & Perrins (1977–1994), Jenni & Winkler (1994) and Svensson (1992): species that moult after breeding while within their breeding range during the summer period (summer moult), species that moult on their wintering grounds after the completion of their autumn migration (winter moult) and species that moult continuously, but sometimes with small interruptions (continuous moult) at least during two life-history phases (breeding, migration and wintering). Flight type was assigned to one of the four categories according to the proportion of flapping flight following Bruderer *et al.* (2010) and Pennycuik (2008): flapping and soaring, flapping and gliding, continuous flapping and passerine type. All the mentioned variables are reported for each species in Appendices S1, S2 and S3 in Supporting Information.

STATISTICAL ANALYSES

First, we investigated the relationship between feather morphological variables of P1 and P8 (individually) and the body mass, moult, diet, habitat, migratory and flight type categories, with and without wing parameters included in the models. Wing parameters were included in the models separately in order to test how wing architecture affects the relationship between feather traits and explanatory variables. Secondly, we performed phylogenetic paired *t*-tests (Lindenfors, Revell & Nunn 2010) to test whether feather morphology differed between P1 and P8. Thirdly, the relationship between the difference in feather morphology between the proximal and distal remiges ($\Delta P = P8 - P1$) of the same species and whether ΔP was influenced by wing morphology or life-history variables was tested. Sample size for these ΔP analyses is reduced because we had limited samples for P8. Rachis width, barb and barbule density and body mass were log_e-transformed in all statistical models to ensure the data were normally distributed.

Large within-group (i.e. within species) variation of studied traits can cause significant biases in phylogenetic comparative analyses. To find out whether feather quality traits are species specific and thus suitable for multispecies comparison, we tested the repeatability of these traits by assessing the importance of between- compared to within-species variance (function 'ICCest' from R package 'ICC'; Wolak, Fairbairn & Paulsen 2012). However, since precision of true variance estimate is dependent upon sample size, the estimation of repeatability across species in comparative studies with unbalanced sample sizes is not equivocal. To overcome this limitation, we measured repeatability by randomly picking two out of all the measurements for a species with at least two individuals measured and partitioning variance to within- and between-group components. This was iterated 1000 times, so repeatabilities are the average of the 1000 repeatability estimates. Repeatability was tested using raw, non-transformed data.

To account for phylogeny, we used trees provided by <http://birdtree.org> (Jetz *et al.* 2012). This website does not provide one unique consensus tree, but samples trees from a pseudoposterior distribution. We generated 1000 trees using two different higher level phylogenies (Ericson *et al.* 2006; Hackett *et al.* 2008) as a backbone tree and derived two consensus trees from these, using R statistical software ('consensus' function from the 'ape' package). Two different branch length transformations for both trees were used (Grafen's method and all branch lengths assigned to 1). The tree out of the four that best fitted our full models based on Akaike information criteria (AIC) was then selected. This was the phylogeny with the backbone tree taken from Hackett *et al.* (2008) with branch lengths equal to 1. We

used a phylogenetic generalized least squares (PGLS) model (Pagel 1997, 1999) using backward stepwise deletion of non-significant predictors from the full model based on the largest *P*-value. The PGLS approach controls for the non-independence among species by incorporating a matrix of covariances among species, based on their phylogenetic relationships (Martins & Hansen 1997; Pagel 1997, 1999) and also estimates the importance of phylogenetic corrections in the analyses (Freckleton, Harvey & Pagel 2002). In all analyses, we set the degree of phylogenetic dependence (Pagel's λ) to the most appropriate degree evaluated for each model by likelihood ratio statistics. A value of λ close to zero indicates phylogenetic independence, while larger values indicate that closely related species are more similar to each other than expected by chance (Pagel 1997, 1999). Habitat, diet, moult category and flight type were entered into the models as fixed factors, whereas all other (continuous) variables were included as covariates.

We report the minimal models. Our sample sizes differed among species, and such variations in sampling effort are known to be sources of bias because different estimates are not estimated with similar precision (Garamszegi & Møller 2010, 2011). However, if within-species variance is particularly small compared to between species variance, then ignoring this measurement error has no effect on type I error in phylogenetic analyses (Harmon & Losos 2005). Conspecific feather quality measures were highly similar in species for which at least two individuals were available (see Results); therefore, we present the weighted models. Additionally, we tested whether weighting models by the sample size or log-transformed sample size of the dependent variable increases model fit by comparing full models based on their Akaike information criteria (AIC). Models weighted by log-transformed sample size had the lowest AIC values in the case of all four feather morphological characters used here. Therefore, we present the results of weighted models.

All statistical analyses were conducted using the R statistical computing environment version 3.0.2 (R Development Core Team 2013). PGLS models were built as implemented in the package 'nlme' (Pinheiro *et al.* 2014). To test for differences in the feather morphology of P1 and P8, we used phylogenetic paired two tailed *t*-tests, using the 'phyl.pairedttest' function of the 'phytools' package in R (Lindenfors, Revell & Nunn 2010). Means are reported as $\pm$ standard errors. Sample sizes differ across statistical tests because data are incomplete for some species. Model predictions and associated standard errors for the graphical presentation of the data have been obtained using the 'predictSE.gls' function of the 'AICc.modavg' package in R (Mazerolle 2013).

Results

REPEATABILITY OF FEATHER TRAITS

Feather quality traits were highly (and moderately for the vane porosity of P8) repeatable with generally narrow confidence intervals, indicating that the traits are species specific (P1: rachis width: ICC = 0.98, 95% CI 0.98–0.99; barb density: ICC = 0.82, 0.76–0.88; barbule density: ICC = 0.73, 0.64–0.82; vane porosity: ICC = 0.66, 0.55–0.77; P8: rachis width: ICC = 0.99, 0.99–1.00; barb density: ICC = 0.83, 0.71–0.95; barbule density: ICC = 0.90, 0.82–0.97; vane porosity: ICC = 0.36, 0.00–0.73). Hence, species included in the data set are adequately characterized in terms of their feather quality traits, and small sample sizes are unlikely to bias the analyses.

THE VARIATION OF WING PARAMETERS WITH FLIGHT AND HABITAT

In general, S differed between habitat categories and AR between flight types (Table 1). S was largest in terrestrial species, lowest in aquatic birds and intermediate in riparians. Within aquatic species, S was smaller in diving than in non-diving birds. Although AR differed between flight categories, no clear pattern emerged in terms of flapping frequency (Table 1), with flap gliders having the highest AR , followed by continuous flapping, flap soaring and passerine-type flyers.

FLIGHT FEATHER MORPHOLOGY OF P1 AND P8

With the exception of the porosity of P8 feathers, flight type significantly affected all of the feather quality parameters for both P1 and P8 (Table 2, Fig. 1a–h). In general, the rachis width of P1 was broadest in species characterized by flight types with low wing-beat frequency and narrowest in species that engage in flapping flight more (Fig. 1a). Conversely, the rachis width of P8 was less clearly defined by flight type with no obvious change between groups (Fig. 1b). Barb density of both P1 and P8 was lowest for flap soarers and similar among species belonging to the other three flight-type groups (Fig. 1c–d). In contrast, there was no clear pattern in the effect of flight type on barbule density for P1 and P8 and vane porosity for P1 (Fig. 1e–g), and no effect on vane porosity for P8 (Fig. 1h) feathers was detected.

Because of the association between AR and flight type (Table 1), we reran the PGLS models for both P1 and P8 feathers this time including AR , while also controlling for the other wing parameter S . Inclusion of the wing parameters removes the effect of flight type on rachis width for both P1 and P8 and barbule density for P8, with AR and S both affecting the former and AR alone the latter. AR also influences barb density for P8, but its inclusion on the PGLS model does not remove the effect of flight type. AR is also correlated with vane porosity for P8 (Table 2).

AR was positively correlated with rachis width of P8 (β (SE) = 0.09 (0.02)) and S positively correlated with rachis

width of P1 (β (SE) = 0.42 (0.03)) and P8 (β (SE) = 0.34 (0.06)), respectively (Table 2). AR was positively correlated with barb density of P8 (β (SE) = 0.06 (0.02)), barbule density of P1 (β (SE) = 0.03 (0.01)) and P8 (β (SE) = 0.05 (2.74)) and vane porosity of P8 (β (SE) = 1.46 (0.39); Table 2).

Habitat was found to affect each of the measured quality parameters except vane porosity (Table 2, Fig. 2a–h). Although not as clearly defined in P8, for both flight feathers, rachis width was lowest and barbule density highest in aquatic species, (Fig. 2a–h). For P1, barb density was also distinct in aquatic species being higher than that measured for terrestrial and riparian species, which were similar to each other (Fig. 2c, e). Indeed, for all feather morphological measures, riparian and terrestrial birds had similar values (Fig. 2a–h). Inclusion of the wing parameters (AR and S) removed the effect of habitat only on rachis width for both P1 and P8 and barbule density for P8 (Table 2).

Among the aquatic species, after controlling for the effect of body mass, the rachis width of P1 was significantly narrower in diving than in non-diving birds (Table 3). The density of barbs of P1 was significantly higher in divers than in non-divers, whereas no difference was found for barbule density (Table 3). No difference was found between divers and non-divers in the porosity of the vane. The effect of diving behaviour on feather quality parameters remained unchanged after including S (which was significantly related to habitat; see Table 1) in the models, except the rachis width, which became only marginally related to diving behaviour (Table 3). The reduced sample size for P8 ($N \leq 9$) did not allow us to investigate the effects of habitat and wing parameters within the aquatic bird category.

Moult category was only found to affect barb density of P1 (Table 2), with winter moulting species having the highest, continuous moulters the lowest and the summer moulting group intermediate barb densities (Fig. 3). The effect of moulting strategy on barb density remained after controlling for wing morphological parameters (Table 2). Only rachis width for P8 was affected by migration strategy, increasing with migration distance (Table 2). The

Table 1. Results of the PGLS models investigating the relationship between wing parameters (wing area, S and aspect ratio, AR), flight type and habitat in birds. In all models, body mass was included to control for size effects

	d.f.	S			AR		
		F	P	Ranking between groups	F	P	Ranking between groups
Flight type	3	0.94	0.4216	FS = FG = CF = PT	5.97	0.0008	FG > CF > FS > PT
Body mass	1	512.39	<0.0001		7.94	0.0056	
Habitat	2	12.68	<0.0001	T > R > A	0.42	0.6590	A = R = T
Body mass	1	709.83	<0.0001		8.92	0.0034	
Diving vs. non-diving	1	8.85	0.0070	ND > D	0.44	0.5159	ND = D
Body mass	1	139.62	<0.0001		3.20	0.0875	

FS, flapping and soaring; FG, flapping and gliding; CF, continuous flapping; PT, passerine type; T, terrestrial; R, riparian; A, aquatic; ND, non-diving; D, diving.

Table 2. Results of the minimal PGLS models investigating whether the feather morphological parameters of primaries 1 and 8 differ between life-history and ecological traits. The minimal models were obtained by eliminating non-significant predictors from the full models in a backward stepwise manner based on the largest *P*-value.

		Minimal models without wing parameters				Minimal models with wing parameters			
		Primary 1		Primary 8		Primary 1		Primary 8	
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>
Rachis width									
Body mass	1	726.97	<0.0001	393.69	<0.0001	13.71	<0.0001	8.78	0.0045
Flight type	3	6.09	0.0007	5.08	0.0035	0.38	0.7700	0.96	0.4199
Habitat	2	9.40	0.0002	3.62	0.0332	0.89	0.4147	2.25	0.1156
Migration	1	—	—	7.59	0.0079	—	—	0.00	0.9948
Wing area	1	—	—	—	—	146.70	<0.0001	28.50	<0.0001
Aspect ratio	1	—	—	—	—	0.23	0.6350	15.71	<0.0001
Barb density									
Body mass	1	38.88	<0.0001	1.01	0.3190	0.63	0.4303	0.55	0.4607
Flight type	3	4.10	0.0082	7.14	0.0004	3.30	0.0227	4.22	0.0092
Habitat	2	10.12	0.0001	—	—	5.88	0.0036	—	—
Moult	2	7.25	0.0010	—	—	7.01	0.0013	—	—
Wing area	1	—	—	—	—	3.56	0.0615	2.99	0.0891
Aspect ratio	1	—	—	—	—	0.88	0.3513	8.92	0.0042
Barbule density									
Body mass	1	8.44	0.0043	2.47	0.1218	0.05	0.8288	0.18	0.6708
Flight type	3	3.27	0.0233	3.46	0.0221	3.01	0.0330	2.40	0.0782
Habitat	2	12.45	<0.0001	3.02	0.0568	7.25	0.0010	1.29	0.2841
Wing area	1	—	—	—	—	1.87	0.1737	0.05	0.8244
Aspect ratio	1	—	—	—	—	5.95	0.0161	7.52	0.0083
Vane porosity									
Body mass	1	0.30	0.5840	0.14	0.7081	0.10	0.7485	0.60	0.4419
Flight type	3	2.95	0.0353	—	—	2.42	0.0692	—	—
Wing area	1	—	—	—	—	0.01	0.9323	0.01	0.9431
Aspect ratio	1	—	—	—	—	0.55	0.4589	13.94	<0.0001

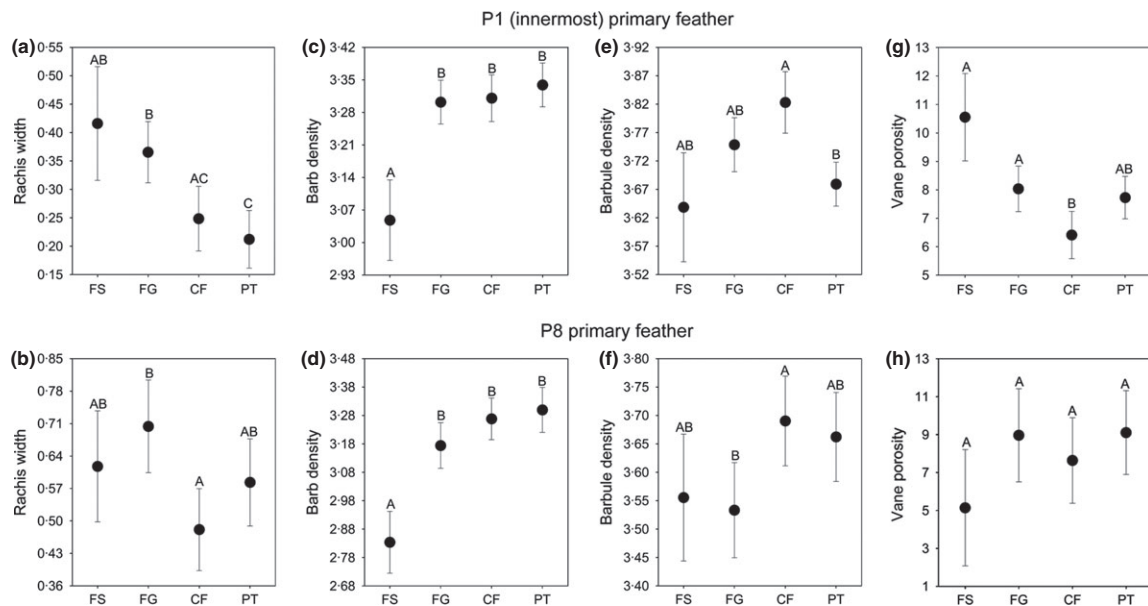


Fig. 1. The relationship between flight type and the feather morphological variables. Different letters denote significant differences at $P < 0.05$, as indicated by the PGLS models. The values are mean $\pm$ SE predicted from the models. The abbreviations are as follows: FS, flapping and soaring; FG, flapping and gliding; CF, continuous flapping; PT – passerine type.

effect of migration distance on rachis width, however, was removed when wing parameters were included in the PGLS model (Table 2).

The effect of diet on the structural properties of P1 and P8 was non-significant and was excluded during the model simplification procedure (Table 2).

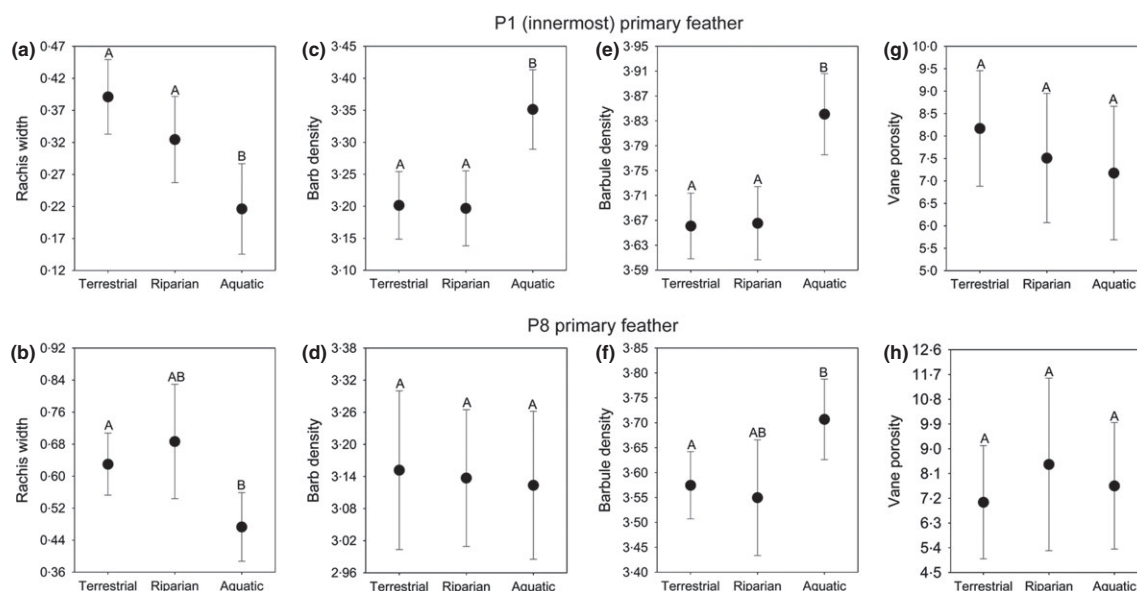


Fig. 2. The relationship between habitat type and the feather morphological variables. Different letters denote significant differences at $P < 0.05$, as indicated by the PGLS models. The values are mean $\pm$ SE predicted from the models.

Table 3. Results of the PGLS models investigating whether the feather morphological parameters of primaries 1 differ between diving and non-diving bird species.

	<i>N</i>	Models without wing area included		Models with wing area included	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Rachis width	25				
Body mass		149.30	<0.0001	6.45	0.0191
Diving behaviour		14.45	0.001	3.98	0.0591
Wing area		—		23.43	<0.0001
Barb density	25				
Body mass		36.58	<0.0001	0.91	0.3516
Diving behaviour		25.00	0.0001	12.38	0.002
Wing area		—		5.02	0.036
Barbule density	25				
Body mass		1.01	0.3255	0.00	0.9726
Diving behaviour		0.07	0.7973	0.00	0.9955
Wing area		—		0.16	0.6972
Vane porosity	23				
Body mass		0.46	0.5038	0.01	0.9303
Diving behaviour		3.36	0.0819	1.76	0.1998
Wing area		—		0.03	0.8712

DIFFERENCES IN FEATHER MORPHOLOGY BETWEEN THE P8 AND P1 FEATHERS (ΔP)

Across all species, the rachis width was broader in P8 feathers than for P1 feathers (phylogenetic paired t -test, $t = 4.45$, $N = 61$, $P < 0.0001$; Fig. 4a). Similarly, barb density was higher in P8 feathers ($t = -2.63$, $N = 61$, $P = 0.0107$; Fig. 4b). Barbule density and porosity, however, were similar between P1 and P8 feathers (barbule density: $t = 0.15$, $N = 61$, $P = 0.8802$; porosity: $t = -0.18$, $N = 58$, $P = 0.8573$; Fig. 4c, d).

EFFECTS OF LIFE-HISTORY AND ECOLOGICAL TRAITS ON ΔP

Habitat type did not affect any of the morphological parameters for ΔP . In contrast, ΔP for barb density and vane porosity differed between flight types (Table 4), with a tendency for both to increase with flight styles in terms of flapping frequency, that is flap soarer < flap gliders < continuous flappers < passerine-type flyers (Fig. 5b, d). Although a similar trend was evident for rachis width ΔP , the effect was statistically non-significant (Fig. 5a). ΔP

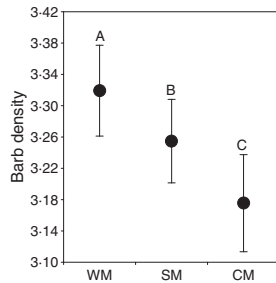


Fig. 3. The effect of moulting on the number of barbs of P1. Different letters denote significant differences at $P < 0.05$, as indicated by the PGLS models. The values are mean $\pm$ SE predicted from the models. The abbreviations are as follows: WM, winter moul; SM, summer moul; CM, continuous moul.

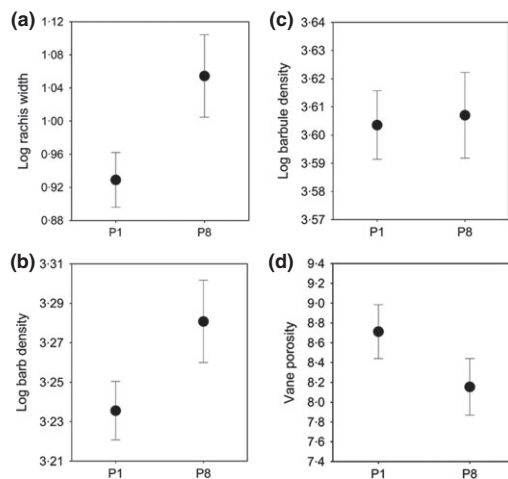


Fig. 4. Differences in the feather morphological variables between the innermost (P1) and distal primaries (P8). The values are mean $\pm$ SE.

vane porosity was significantly and positively related to migration distance (Table 4), while the diet was eliminated from all minimal models.

After controlling for the effect of S and AR on ΔP for each feather parameter, the effect of flight type only remained for vane porosity (Table 4). AR significantly and positively affected ΔP for rachis width (β (SE) = 0.09 (0.03)), barbule density (β (SE) = 1.31 (0.49)) and vane porosity (β (SE) = 0.70 (0.34)), but not barb density (β (SE) = 0.54 (0.44); Table 4).

Discussion

FEATHER STRUCTURE AND FLIGHT

The sample of 137 European bird species used in this current study suggests that flight type, habitat and moulting strategy affect the functional morphology of the flight feathers. These effects, however, are often more prominent in the proximal (P1) than in the more distal primary feathers (P8). Feathers, particularly the remiges, of flying birds have to withstand aerodynamic forces during flight (Pennycuik

1989; Lindhe Norberg 2002; Wang *et al.* 2012). Here, species characterized with flight types associated with low wing-beat frequency (flapping and soaring, and flapping and gliding flight) generally have proximal wing feathers with broader rachises than those of continuous flappers and passerine-type flyers. This observation does not support the 'flexible shaft' hypothesis and is consistent with the idea that stiffer feathers (with broader rachises) allow birds to generate more lift and better lift to drag ratios by increasing the effective surface area of the aerofoil (Heers, Tobalske & Dial 2011; Dial, Heers & Tobalske 2012). The effect of flight type on distal wing feathers, however, is less clear, because the change in rachis width with flight type does not appear to relate to levels of flapping flight. It may be that the selection pressures acting on feather morphology differ subtly between proximal and distal feathers. It is not surprising that P8 feathers generally have a more robust construction than P1 feathers (Fig. 4) because during all types of flight, including flapping, the distal feathers are loaded more heavily than the proximal feathers. It is possible, that a similar distal primary rachis morphology is optimal for all flight types. Whereas the optimum proximal feather morphology differs between vigorous flapping flyers and soaring/gliding birds, because these inboard feathers are subject to greater forces during flapping flight and a more flexible (narrower) feather is required to sustain these. Congruent with this idea, is the fact that, here, we found the increase in rachis width between the proximal and distal wing feathers was significantly larger in species characterized with passerine-type flight than in flap soarers, with intermediate values for continuous flappers and flap gliders (Fig. 5a). If the aerodynamic forces on wing feathers change little along the proximal–distal axis, because the aerodynamic forces are generated more evenly across the span as is the case in soaring and gliding flight, the rachis width and hence the stiffness of the wing feathers, should remain more similar along the wing. Conversely, in the case of flapping flyers where thrust is generated largely from the distal part of the wings (Lindhe Norberg 2002), the aerodynamic forces are much greater distally than proximally. Hence, the P8 feather would be expected to have a larger diameter than P1 feathers in flapping flyers as found in this current study. The positive relationship between P8 rachis width and migration distance (Table 2) suggests that besides the aerodynamic force generated during flapping, the amount of time spent flying also influences the stiffness of the distal wing feathers.

It is not surprising that when wing morphologies S and AR are incorporated into the statistical models, they often show a significant correlation with feather morphological variables, sometimes reducing or negating the effect of flight type and migration strategy (Tables 2–4). AR and S are likely to define flight type at a higher resolution than discrete categories. Previous work has shown strong correlations between wing morphology and both flight type and migratory strategy (Rayner 1988; Norberg 1990; Wang, McGowan & Dyke 2011). Here, S was shown to differ

Table 4. Results of the minimal PGLS models investigating whether the difference in feather morphological parameters between the primary 8 and 1 (ΔP) differ between life-history and ecological traits. The minimal models were obtained by eliminating non-significant predictors from the full models in a backward stepwise manner based on the largest P -value.

	d.f.	ΔP Minimal models without wing parameters		ΔP Minimal models with wing parameters	
		F	P	F	P
Rachis width					
Body mass	1	36.30	<0.0001	5.21	0.0262
Flight type	3	2.46	0.0712	2.33	0.0838
Wing area	1	—	—	0.11	0.7451
Aspect ratio	1	—	—	9.53	0.0031
Barb density					
Body mass	1	12.01	0.0010	2.28	0.1369
Flight type	3	2.85	0.0453	1.28	0.2894
Wing area	1	—	—	0.17	0.6810
Aspect ratio	1	—	—	1.48	0.2287
Barbule density					
Body mass	1	5.81	0.0189	0.11	0.7464
Wing area	1	—	—	0.68	0.4129
Aspect ratio	1	—	—	7.22	0.0093
Vane porosity					
Body mass	1	4.26	0.0443	1.58	0.2149
Flight type	3	9.38	<0.0001	8.77	<0.0001
Migration	1	4.33	0.0426	2.05	0.1589
Wing area	1	—	—	0.69	0.4107
Aspect ratio	1	—	—	4.27	0.0443

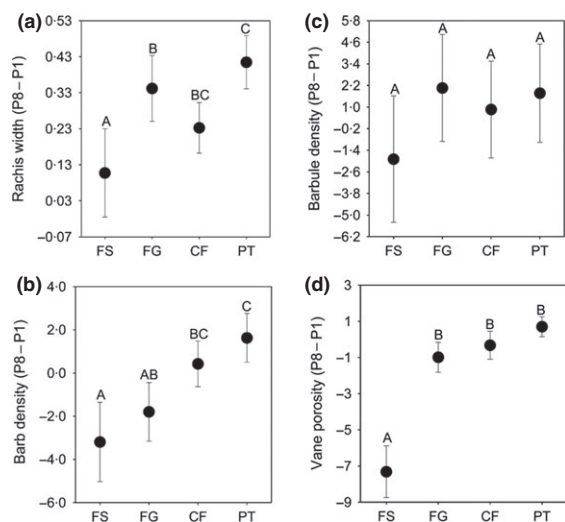


Fig. 5. The increase in the feather morphological variables between P1 and P8 feathers in relation to flying type. Different letters denote significant differences at $P < 0.05$, as revealed from PGLS models. The values are mean $\pm$ SE predicted from the models. The abbreviations are as follows: FS, flapping and soaring; FG, flapping and gliding; CF, continuous flapping; PT – passerine type.

between habitat and diving strategy (within aquatic birds) and AR , with flight type.

The pattern of variation in S found with habitat type is understandable (Table 1). The terrestrial category contains species that soar or glide, where high S is advantageous. Whereas the riparian category is predominantly comprised

of fast flapping species, where high wing-loading (i.e. smaller S relative to body mass) and a faster flight speed are favoured. Diving birds have the lowest wing areas, because of the conflict between the needs of underwater propulsion and aerial locomotion (Elliott *et al.* 2013). The much higher density of water favours shorter and less extensive wings. A high AR is associated with more economic flight, but less manoeuvrability (Norberg 1990). Therefore, we would expect to see high AR wings in soaring birds and birds that fly over long distances and low AR wings in birds engaging in flapping flight within more cluttered environments or requiring manoeuvrability for prey capture. Consequently, although the ranking of the AR of three of the flight types here is as expected, the flap soarers only having the 3rd highest AR is not (Table 1). This, however, is explained by the fact that most of the species in the flapping and soaring group are, in fact, birds of prey (Appendix S3), which require some manoeuvrability, and hence, their wing shape is a compromise (Rayner 1988). Our results suggest that differences in feather morphology, at least for P8 feathers, are better defined by AR than flight type. Yet, flight type defines feather morphological variation better for the more proximal P1 feathers than wing morphology.

Previous work has suggested that flight feathers are impervious or have limited transmissivity to air because of the enlarged ventral margins of the barbules and transmissivity differences between species are small (e.g. Heers, Tobalske & Dial 2011; Dial, Heers & Tobalske 2012), which is mirrored in the low interspecific variation in the distance between barbules (see Müller & Patone 1998). Enlargement

of the ventral margins of the barbules and their apposition to the bases of adjacent barbules reduces the size of these gaps allowing the vanes to function as a relatively impervious surface. Our results indicate that flight type affects barb density, barbule density and vane porosity (except the porosity of P8 feathers) and the change in barb density and vane porosity between the P1 and P8 feathers (Tables 2–3, Fig. 1c–h, Fig. 5b, d). Barb density, but neither barbule density nor vane porosity, differed between the proximal and distal primary feathers (Fig. 4b–d). Transmissive vanes might reduce flight performance (Barbosa *et al.* 2002) and, because of the higher forces generated upon the wings of flapping flyers, those species flapping most vigorously may require more dense feather vanes. That forces during flight shape the feather vane is further supported by, first, the significantly lower barb density for P1 and P8 in flap soarers related to the other 3 flight groups. Secondly, the higher barb density found in the P8 relative to the P1 feathers (Fig. 4b), as forces will be highest upon the wing more distally. Finally, the increasing difference in barb density between the P8 and P1 feathers with flapping flight demands (Fig. 5b), even after controlling for wing parameters, shows that the density of barbs is likely to be under strong selection for aerodynamic performance. In agreement with Müller & Patone (1998), however, the effect of flight type on barbule density and vane porosity is not clear, nor consistent, since in most cases only one flight group differed from the other 3. One possible explanation for this is that the barbule overlap and the number of barbicels on barbules are more important in determining transmissivity than the density of barbs and barbules *per se* (Heers, Tobalske & Dial 2011; Dial, Heers & Tobalske 2012).

FEATHER STRUCTURE, HABITAT AND WATER RESISTANCE

Narrower shaft widths in aquatic birds for both the P1 and P8 feathers (Fig. 2a–b) suggest that they have more flexible flight feathers than terrestrial birds. The rachis width of P1 was also significantly narrower in diving than in non-diving birds. The direct cause of the observed pattern in rachis width with habitat, however, is likely to be related to *S* and not to habitat. *S* is lower in aquatic than in riparian and terrestrial species, and within aquatic species, divers have smaller *S* than non-divers. Indeed, including *S* in the statistical models negated the significant relationship between habitat type and rachis width for both P1 and P8 feathers (Table 2).

Water repellency is a phenomenon that occurs at the interface between a surface and water, while the ability of the feather coat to keep water away from the body is determined by its resistance to water penetration (Rijke 1968, 1970; Elowson 1984; Rijke & Jesser 2011). While rigid feather vanes primed with a waxy coating may be effective in repelling water, they may still be vulnerable to water penetration. Experimental evidence to verify the validity of the porosity equation ($(r + d)/r$) is lacking

(review in Rijke & Jesser 2011), but despite concerns (Elowson 1984), it is widely accepted in the literature. Our results show that aquatic species have flight feathers with a higher density of barbs (P1 feathers only) and barbules than terrestrial birds. Also, the density of barbs of the innermost primaries were significantly higher in divers than in non-divers, which strongly indicates selection for higher barb and barbule density in aquatic habitats. The change in barb and barbule density between P8 and P1 feathers was not affected by habitat, which might be expected because the exposure to water is uniform across the wingspan. The absence of a difference in the density of the barbs of P8 between habitats, contrary to the significant habitat effect in case of P1, may be due to the reduced sample size for P8. Our results, however, question the validity of the textile model (Rijke 1968, 1970) for predicting the water resistance of feathers, because vane porosity did not differ between habitats, nor between divers and non-divers. These results are in line with Elowson's (1984) conclusions, namely that the textile–feather analogy is not realistic, because feather structure is considerably more complex and variable than the simple geometric model that is fundamental to the textile equation. Our results suggest that the water resistance of the flight feathers is primarily explained by the density of the barbs and is not affected by the diameter of the barbs. This is expected, because of the disproportionally high interbarb distance related to the diameter of the barbs (see Appendix S2). It is important to mention, however, that our conclusion stands only for the porosity of the barbs, but not for barbules. We could not measure the *r* and the *d* of the barbules on such a large number of feathers, which would necessitate scanning electron micrographs. Therefore, the validity of the textile model for barbules was not tested.

THE EFFECTS OF MOULT AND NUTRITION UPON FLIGHT FEATHERS

Smaller birds generally replace all their flight feathers annually, while larger birds often extend the primary moult over two or more years and continue to fly when renewing their primaries (Rohwer *et al.* 2009). For these latter species, moult must be traded off against competing needs, such as aerodynamic performance, energy expenditure and nutrition (Hemborg & Lundberg 1998; Hemborg, Lundberg & Siikamäki 1998; Chai & Robert 1999; Lind 2001; Lind & Jakobsson 2001; Moreno *et al.* 2001; Barta *et al.* 2006). The trade-off between moulting and other life-history traits was evident in this current study, where the density of barbs was found to be the lowest in continuously moulting species (see Echeverry-Galvis & Hau 2013). Whereas the density of barbs was highest in winter moulting species, which have the longest time available for feather growth during which no other costly activities occur (i.e. migration and breeding) and hence are probably less constrained (Dawson *et al.* 2000; Vágási *et al.* 2012). Furthermore, barb density was intermediate for summer moulters, which have limited time

available for feather growth, at least in the case of migratory species (de la Hera, Pérez-Tris & Tellería 2010; de la Hera, DeSante & Milá 2012). Assuming that a higher barb density equals a superior quality of feather, our results support the hypothesis that moulting is energetically and/or nutritionally limited (Dawson *et al.* 2000; Pap *et al.* 2008; Vágási *et al.* 2012; but see Buttemer, Nicol & Sharman 2003). The finding that moult strategy did not relate to rachis width and barbule density is in contrast to previous intraspecific experimental studies on house sparrows (*Passer domesticus*), where the increased growth rate within a short time window of moult and/or nutritional constraints resulted in a general decrease of feather quality (Vágási *et al.* 2012; Pap *et al.* 2013).

It is clear that our present understanding of the selection pressures that drive flight feather morphology is limited. Our results have broad implications for understanding the evolution of flight feather structure and function. Specifically, the optimum structures for flight and habitat appear to conflict resulting in compromise, for example flapping and soaring flight selects for low barb density of the vane, while aquatic habitat and diving selects for an increase in density. Further work, however, with a larger data set, a broader range of flight feathers (not just P1 and 8), and improved resolution measurements of vane structure (e.g. SEM measurements of barbule structure) are required before the exact nature of the interactions between, flight and ecological, and life-history traits can be identified fully. In addition to illuminating our understanding of extant bird flight feather form and function, the results of this current study may help in the reconstruction of the flight and habitat of extinct birds where flight feathers are preserved.

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Data accessibility

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1538t> (Pap *et al.* 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Morphological parameters for the primary 1 and primary 8 feathers. *N* is the sample size for each parameter. See Material and methods for sources.

Appendix S2. Summary data for barb radius (*r*), inter-barbs distance (*2d*) and $(r + d)/r$ for primary 1 and primary 8. *N* denotes the sample size for each category. See Material and methods for sources.

Appendix S3. Summary of data showing species-specific body mass, habitat (T – terrestrial, R – riparian, A – aquatic), diving behaviour (D – diving, ND – non-diving), migration distance, food type (1 – food composed mainly of insects and vertebrates, 2 – large proportion of the food composed of plant materials), flight type (1 – continuous flapping, 2a – flapping and soaring, 2c – flapping and gliding, 3 – passerine-type) and sample size for wing measurements (*N*_{wing}).