

## RESEARCH ARTICLE

# How feathered are birds? Environment predicts both the mass and density of body feathers

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**Abstract**

1. Studies modelling heat transfer of bird plumage design suggest that insulative properties can be attributed to the density and structure of the downy layer, whereas waterproofing is the result of the outer layer, comprised of contour feathers. In this study, we test how habitat and thermal condition affect feather mass and density of body feathers (contour, semiplume and downy feathers) measured on the ventral and dorsal sides of the body, using a phylogenetic comparative analysis of 152 bird species.
2. Our results demonstrate that feather mass and the density of downy feathers are higher in species that inhabit colder environments, whereas total feather density is higher of species breeding under intermediate temperatures compared to the ones breeding under more extreme conditions. The density of contour feathers, depending on the body region, is either quadratically related or negatively correlated with minimum winter temperature.
3. The density of contour and downy feathers, measured on both sides of the body, is higher in aquatic than in terrestrial birds. However, among the former, diving behaviour does not select for further increases in body feather mass or density.
4. The results of this study provides key insights into how the plumage of birds is adapted to different environments and lifestyles and provides a basis for understanding the diverse range and the evolution of variation in these characteristics.

**KEYWORDS**

birds, comparative analysis, feather density, feather mass, thermoinsulation, waterproofing

## 1 | INTRODUCTION

The plumage of birds functions as a critical barrier between the skin and the environment by controlling heat transfer and preventing the penetration of water, providing up to 90% of the insulation

requirements of an individual (Jarman, 1973; McCafferty et al., 2013). The high thermoinsulatory capacity of the plumage enables birds to maintain a core body temperature surpassing 40°C (Prinzinger, Preßmar, & Schleucher, 1991) over a wide range of environmental temperatures (Handrich et al., 1997; Ponganis et al.,

2003). While plumage can function to decrease heat flux between the skin and the environment by blocking radiation and trapping air near the skin, it can also increase heat flux via conduction backwards and forwards to the body (Walsberg, 1988). The thermoregulatory characteristics of body feathers are probably related to a range of attributes, including plumage depth, density and morphology (Prum & Brush, 2002; Srinivasan et al., 2014). Indeed, multiple traits of the plumage, especially body feathers, define the density and morphology of the downy plumage layer (Butler, Rohwer, & Speidel, 2008; Davenport, O'Halloran, Hannah, McLaughlin, & Smiddy, 2009; Dove & Agreda, 2007; Du, Fan, Wu, Chen, & Liu, 2007; Eadie & Ghosh, 2011; Pap et al., 2017; Wilson, Hustler, Ryan, Burger, & Noldeke, 1992), as well as the number and size of spaces that trap air adjacent to the skin (Dawson, Vincent, Jeronimidis, Rice, & Forshaw, 1999; Wilson et al., 1992). Plumage water repellence is also thought to be conferred by a layer of contour feathers that form an external barrier, whereas water resistance is further determined by plumage density. Thus, the amount of keratin, the number of feathers per unit surface and the air spaces trapped within them, comprise a multiscale air cushion at the feather–water interface. This cushion functions to prevent feathers from getting wet (Davenport et al., 2009; Eadie & Ghosh, 2011; Grémillet, Chauvin, Wilson, Le Maho, & Wanless, 2005; Grémillet et al., 2001; Kooyman, Gentry, Bergman, & Hammel, 1976; Pap et al., 2017; Rijke, 1970; Williams, Hagelin, & Kooyman, 2015). In water birds, however, alterations in insulation must occur because the thermal conductivity of this medium is about 23 times that of air, whereas further modifications are required in diving birds because increased hydrostatic pressure impinges on the plumage and compresses the air trapped among the feathers (Grémillet, Tuschy, & Kierspel, 1998; Grémillet et al., 2001; Wilson et al., 1992). Thus, in diving birds, the reduced volume of trapped air is likely partially compensated for by denser plumage (Walsberg, 1988).

Plumage in birds comprises different feather types that all have subtly different functions (Prum & Brush, 2002). This means that quantifying the densities of different feather types is essential if we are to understand how avian plumage achieves its unique thermo-insulatory and water-repellent functions. The most numerous components of avian plumage are contour feathers which cover most of the body and have multiple functions (Butler et al., 2008; Pap et al., 2017); the pennaceous distal region of these feathers form an outer water-repellent cover over the inner thermoinsulatory layer, defined by the proximal plumulaceous feather section (Pap et al., 2017; Prum & Brush, 2002; Rijke, 1970; Srinivasan et al., 2014; Stephenson & Andrews, 1997). The contour feathers of some species also have an auxiliary shaft called the afterfeather; it has been assumed that this shaft has a function in thermoinsulation, although its role in thermoregulation remains unclear (Williams et al., 2015). In addition, the plumulaceous part of contour feathers, semiplumes and downy feathers also contribute significantly to the insulating layer. Semiplumes have a central shaft which is longer than their longest barb, whereas lateral plumulaceous barbs radiate from here with barbules that do not attach to one another. Downy feathers are fluffy and have

short rachises which are shorter than the longest barbs (Lucas & Stettenheim, 1972).

The mass and the density of different body feather types vary dramatically among bird species (Cooper, 2002; Davenport et al., 2009; Hutt & Ball, 1938; Swanson, 1993; Wetmore, 1936). This variation has previously been attributed to thermal conditions as well as water repellency in aquatic birds (Dawson et al., 1999; Williams et al., 2015). However, these conclusions have been based mostly on single species, and no systematic analyses of these variations have been undertaken. Most studies completed thus far on plumage density as an adaptation to cold environments and an aquatic lifestyle have been carried out on highly specialized species which means it has been difficult to deduce the specific functions of different body feathers. For example in terrestrial species that are much less exposed to water, body plumage appears adapted to repel, rather than to withstand, water infiltration (Rijke, 1970; Srinivasan et al., 2014).

Variation in the density of avian body feathers is likely subject to a trade-off between the benefits of the plumage and costs of integument production (Butler et al., 2008; Danner, Greenberg, Danner, & Walters, 2015; Dawson, Hinsley, Ferns, Bonser, & Eccleston, 2000; Pap, Vágási, Cziráj, & Barta, 2008). Producing feathers is likely constrained by limited resources, including available protein content of food (Pap et al., 2008). While there is some consensus on how resource limitation reduces the amount of keratin invested in feathers, no studies to date have considered its effects on plumage mass and density.

We employ a phylogenetic comparative approach to investigate how habitat, diving behaviour, thermal environment and diet influence the mass and density of feathers in a dataset that incorporates dorsal and ventral plumage samples from 152 bird species. Our prediction is that body feather mass and density will be higher in aquatic birds and divers than in their terrestrial and non-diving counterparts respectively. We predict that dorsal and ventral plumage traits are variously affected by habitat because sides of the body are similarly exposed to rain and water in terrestrial species, whereas the plumage on the ventral side of aquatic birds (particularly in floaters) is subject to higher water pressure than on the dorsal side. We also predict that low ambient temperature will select for a more thermoinsulatory plumage, manifested in increased body feather mass and feather density (Dawson et al., 1999; Williams et al., 2015). Plumage may also function to facilitate heat loss (Butler et al., 2008); it is likely that looser plumage is correlated with enhanced heat loss in birds that live in hot environments. Therefore, we expect that birds that are adapted to warmer climates will have a lower mass and density of body feathers (Ward, Ruxton, Houston, & McCafferty, 2007). Heat retention and heat transfer can be ensured by low or high feather mass and density, respectively, because the number of air vacuoles vary in function of these feather traits, whereas the amount of air trapped in the plumage may remain unchanged. As a result, species living in warm or cold environments may show the same adaptation in plumage traits. Therefore, we assumed in models both linear and quadratic effect of temperature on plumage traits.

## 2 | MATERIALS AND METHODS

### 2.1 | Field data collection and feather measurements

We collected feather samples from 337 birds encompassing 152 neognath species at several locations across Romania, Hungary, Norway, Sweden and Scotland, as well as the sub-Antarctic Crozet Islands archipelago (king penguin, *Aptenodytes patagonicus*) between 2012 and 2016. Most individuals died due to natural causes (e.g. road kill, building collision, electrocution, starvation) or were procured from authorized hunters. All samples were preserved at  $-20^{\circ}\text{C}$  in a freezer until examination in 2016. The age of all specimens was recorded upon investigation that was determined based on plumage characteristics, degree of skull pneumatization and by examining flight feather moult patterns. Feathers were collected from the ventral and dorsal sides of the body, with samples used including just non-moulting individuals in good condition with clean plumage. We collected samples of ventral feathers from an area delimited by the breastbone, the contact point of the wing and leg to the body and side, including one ventral feather tract (see Appendix S1). The rectangular-shaped dorsal surface of the bird was defined as the area between the shoulder, the tail end of the synsacrum and the side. King penguin feathers were collected from a smaller area (c.  $20\text{ cm}^2$ ) on ventral and dorsal sides; however, because of the uniform distribution of feathers across the body in these birds (Dawson et al., 1999; Williams et al., 2015), this smaller sampling area probably had little effect on feather mass and density estimates of this species. Subsequent to feather collection, we photographed bare skin areas in front of a metric grid ( $1 \times 1\text{ mm}$ ) background and measured the surface using the ImageJ software, version 1.51 (<http://rsb.info.nih.gov/ij/>). Body feathers were then weighed and desiccated for 24 hr at  $37^{\circ}\text{C}$  to eliminate any moisture captured in the plumage. We weighed all body feathers (using a professional digital analytical balance Axis AGN200, accuracy class I,  $e = 0.001\text{g}$ ;  $d = 0.0001\text{g}$ ) from ventral and dorsal sides separately, and recorded the total feather mass per unit area ( $\text{g}/\text{cm}^2$ ), presenting just the mass of total feathers because the weights of different types were too low to be measured with precision. We then separated and counted different feather types in each sample to record the numbers of contour feathers, semiplumes and downy feathers per unit area ( $\text{number}/\text{cm}^2$ ). Given that the thermoinsulatory function of semiplumes and downy feathers are probably similar, and because the number of the former in most species was very low, we pooled our data for these two feather types in all analyses. We measured the length of one contour feather from each individual on both sides of the body, collected from the middle of the breastbone in case of the ventral part and from the middle of the backbone in case of dorsal part, using a ruler, and these data were completed with additional measurements from an earlier work (Pap et al., 2017); thus, our sample sizes for feather mass and density, as well as contour feather length differ slightly (Osváth et al., 2017). Feather samples from different species and individuals were randomly assigned to one of the five investigators (JP, CIV, GO, PLP and TD). Repeatability between observers was high for all parameters (total feather density:

ICC (Intra-class Correlation Coefficients) = 0.95, 95% CI 0.88–0.98; contour feather density: ICC = 0.96, 95% CI 0.91–0.99; down feather density: ICC = 0.94, 95% CI 0.85–0.98; semiplume density: ICC = 0.78, 95% CI 0.55–0.91; all  $F > 11.34$ ,  $n = 14$ , all  $p < .0001$ ).

### 2.2 | Body mass, ecological traits and habitat

We obtained body mass data from (Del Hoyo, Elliot, & Sargatal, 1992–2013; Dunning, 2007). Where mass data were available for multiple regions, we selected the one for European populations and subspecies. We then classified species into one of five habitat groups Cramp and Perrins (1977–1994); terrestrial (i.e. rarely encountering water), riparian (i.e. living in wetland habitats like marshes and sedges), waders (i.e. species that move above, and around water surface), floaters (i.e. aquatic species that float on the water but do not dive) and divers. We extracted ambient temperature data from the University of East Anglia Climate Research Unit database (<http://www.cru.uea.ac.uk/>; version 3.10.01) (Mitchell & Jones, 2005), a global dataset containing interpolated monthly average land temperatures ( $^{\circ}\text{C}$ ) in a grid of spatial coordinates ( $0.5 \times 0.5$  degrees). We used the most recent 10 years of temperature data for this study (encompassing the period between 2006 and 2015, downloaded on 3rd November 2016), and calculated average monthly mean temperature over this period for each spatial grid cell. From these monthly mean data, we created a 12-layer shape file for each grid cell, and by intersecting temperature and species distribution files, we calculated monthly temperatures for each species separately for wintering and breeding grounds (Pap et al., 2015, 2017; Vincze, 2016). Distribution maps (shape files) were retrieved from <http://www.birdlife.org/datazone/info/spcdownload> (BirdLife International & NatureServe, 2015, accessed on 27th October 2016). For breeding areas, we extracted the highest monthly mean ("maximum breeding temperature") for the period April to August as a proxy for breeding heat stress, whereas for wintering grounds we extracted the lowest monthly mean ("minimum winter temperature") for the period December to February as a proxy for winter harshness. Monthly temperatures were calculated for breeding and wintering distribution areas for species between longitudes  $20^{\circ}\text{W}$  and  $60^{\circ}\text{E}$ , although, in some cases, where breeding or wintering areas were situated outside this range, we used global ranges or other ranges specific for the sampled population (e.g. king penguin; see Osváth et al., 2017). Because African and Arabian resident populations of several species are clearly separated from their European migratory counterparts (with likely little gene flow between them), these populations and areas were not included in our analyses (Osváth et al., 2017). Furthermore, because the protein content of food can limit feather synthesis (Pap et al., 2008), we included diet type as a factor in our analyses. Diet was assigned to one of two categories, "high," or "low" protein content (Pap et al., 2015); a high protein content was defined as exclusively feeding on invertebrates and/or vertebrates, whereas low was used for species that are either omnivorous and/or species feeding on plants. Dietary information for each species was obtained from Cramp and Perrins (1977–1994). All variables for all species can be found at Osváth et al. (2017).

## 2.3 | Statistical analyses

Large within-group (i.e. within-species) variation in traits can lead to significant bias in phylogenetic comparative analyses (Freckleton, Harvey, & Pagel, 2002). Thus, in order to determine whether, or not, our feather parameters were species-specific and suitable for multi-taxon comparisons, we tested repeatability by assessing the importance of “between-species” compared to “within-species” variance using the “icc” function in the R package “irr” (Gamer, Lemon, Fellows, & Sing, 2010). As within-species sample size varies, we calculated repeatability using two randomly selected individuals per species; this test was repeated 1,000 times and ICCs and corresponding confidence intervals (CIs) were calculated as the means of 1,000 estimates (Pap et al., 2015). Repeatability was tested using raw, non-transformed values. Feather traits are highly species-specific for both ventral (total feather mass: ICC = 0.75, 95% CI 0.65–0.83; total feather density: ICC = 0.85, 95% CI 0.79–0.90; contour feather density: ICC = 0.84, 95% CI 0.77–0.89; downy + semiplume feather density: ICC = 0.58, 95% CI 0.42–0.70) and dorsal sides of the body (total feather mass: ICC = 0.71, 95% CI 0.59–0.80; total feather density: ICC = 0.84, 95% CI 0.77–0.89; contour feather density: ICC = 0.81, 95% CI 0.73–0.87; downy + semiplume feather density: ICC = 0.60, 95% CI 0.45–0.71; all  $F > 4.19$ , all  $p < .0001$ ). We therefore conclude that the species included in our datasets are adequately characterized in terms of their feather traits, and that small sample sizes in some species are unlikely to bias our results. Because feather traits can also vary over the course of a year due to changes in temperature (Cooper, 2002; Middleton, 1986; Novoa, Bozinovic, & Rosenmann, 1994; Swanson, 1991), results could also be affected by systematic bias in sampling dates among species. Thus, to test whether seasonality affects our feather traits, we compared data from birds collected in the winter (October to March) and summer (April to September) using phylogenetic paired  $t$  tests (R package “phytools”) (Revell, 2012). Note that only a subsample of the species could be used for these tests, those for which at least one individual was measured in both periods. Feather parameters were similar between the two periods (in all cases  $t < 1.87$ ,  $N_{\text{ventral side}} = 25$ ,  $N_{\text{dorsal side}} = 24$ ,  $p > .0753$ ). Furthermore, because feather traits can vary depending on the age of a bird (Butler et al., 2008), and because our sample includes birds in both immature and adult plumages, we tested differences in feather traits between age classes using phylogenetic paired  $t$  tests. All parameters remained similar between age classes (in all cases  $t < 1.62$ ,  $N_{\text{ventral side}} = 26$ ,  $N_{\text{dorsal side}} = 24$ ,  $p > .1194$ ), therefore, it is unlikely that our results are affected by either within-species seasonal differences or age-specific changes in feather traits.

We used phylogenetic paired  $t$  tests to test whether the feather parameters (mass and density) differed between ventral and dorsal sides of the body. Differences between ventral and dorsal sides of the body ( $\Delta$  = ventral minus dorsal) were analysed as response variables in multivariate models separately to test whether these differences were influenced by ecology and diet. To investigate the relationship between feather density or feather mass and body mass, diet, habitat, breeding maximum and winter minimum temperatures across

birds, we built phylogenetic generalized least squares (PGLS) models using ventral, dorsal and  $\Delta$  feather masses and feather densities as response variables. Because feather mass is largely determined by the length of individual body feathers, we additionally carried out separate analyses for the ventral and dorsal sides in which contour feather length of the respective body side was also added as an explanatory variable in models of feather mass. Total feather density and density of different feather types may also be influenced by the presence of afterfeathers on contour feathers; we therefore included this factor as an explanatory variable in feather density models. Sampling effort in our dataset differs among species, ranging between one and five individuals. Sampling inequality can cause bias in the data as measured parameters cannot be estimated with similar precision for each species (Garamszegi & Møller, 2010, 2011). Accordingly, likelihood-ratio statistics indicated that weighting phylogenetic models by log-transformed, within-species sample size significantly increases the model fit. Therefore, we present the results of models weighted by log-transformed within-species sample size in the case of each feather parameter investigated.

We accounted for phylogenetic non-independence using trees from <http://birdtree.org> (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). We downloaded 100 random trees using the Hackett backbone tree (Hackett et al., 2008), and calculated a rooted, ultrametric consensus tree using the SumTrees software (Sukumaran & Holder, 2010). We used this consensus tree in the PGLS model (Pagel, 1997, 1999) and we set the degree of phylogenetic dependence (Pagel's  $\lambda$ ) to the most appropriate value estimated by maximum likelihood in each model separately (Freckleton et al., 2002). We employed backward-stepwise elimination of non-significant ( $p > .05$ ) predictors from the full model. Habitat, the presence of afterfeathers and diet, were all entered into models as fixed factors, whereas all other (continuous) variables were included as covariates. Temperature variables were included in the model as second-order orthogonal polynomials in order to test for possible quadratic effects on feather traits. The only flightless species in our study was the king penguin. For this species, breeding temperature as well as a number of other feather traits represented outliers in our datasets (see Figure S1). We therefore re-ran all PGLS models excluding this species, but we present both model sets in the Results. Although we present the results of our models incorporating a consensus tree, we re-ran both full and minimal PGLS models using all 100 phylogenies to control for phylogenetic uncertainty. All models yielded highly consistent results across the 100 phylogenetic trees tested.  $p$ -values from these models were plotted as histograms (Figure S2).

All statistical analyses were conducted using the R statistical computing environment, version 3.3.2 (R Development Core Team, 2016), and all PGLS models were built using the “nlme” package (Pinheiro, Bates, DebRoy, & Sarkar, 2015). Sample sizes vary across models depending on the body side (i.e. ventral versus dorsal) as measurements were unobtainable for some individuals from one side of the body. Finally, all feather traits and sample sizes were  $\log_e(x + 1)$ -transformed in all statistical models to ensure model residual normality. Means  $\pm$  SE are reported throughout the text and tables. Model predictions and

associated *SE* for graphical representations of data were obtained using the “lsmeans” package in R (Lenth, 2016).

### 3 | RESULTS

#### 3.1 | Feather mass and density on the ventral and dorsal sides

Winter minimum temperature is significantly negatively correlated with feather mass on the ventral and dorsal sides of the body (Table 1a,b), indicating larger feather masses in colder than in warmer climates. This correlation remains significant after controlling for the confounding effect of feather lengths on plumage weight (Table S1). Excluding the king penguin did not change this relationship (Table 1a; Figure 1). Habitat does not affect the mass of feathers on either side of the body (Table 1a). Nonetheless, after controlling for the confounding effects of feather length on plumage weight, the effect of habitat on ventral feather mass became significant (Table S1), although there was no clear trend between groups (contrasts between groups:  $W < F$  and  $W < D$  at  $p < .01$ , all other contrasts at  $p > .05$ ). Excluding the king penguin does not affect these results (Table 1a).

Depending on feather types and body region, feather density parameters are either quadratically related or negatively correlated with maximum breeding temperature (Table 1b), indicating higher feather densities in species breeding under intermediate temperatures compared to the ones breeding under more extreme conditions, or lower feather densities in hotter compared to colder breeding climates. The latter effect holds even when the presence of afterfeathers on contour feathers is controlled (Table S1). However, the effect of breeding maximum temperature disappears in most cases, when data for the king penguin are excluded from the analyses, only showing a relatively weak but significant negative linear association with total feather density on dorsal and contour feather density on ventral sides (Table 1b). In general, feather density and winter minimum temperature are quadratically related (Table 1b), with higher feather densities in species wintering under intermediate climates compared to species wintering in colder or hotter areas. Moreover, this effect is consistent even after controlling for the presence of afterfeathers on contour feathers (Table S1). The quadratic effect of minimum winter temperature on feather density is also significant for total feather density and contour feather density measured on the ventral side after excluding the king penguin (Table 1b; Figure 2), whereas the effect turns negative and linear for contour feather density on dorsal side and downy + semiplume density on both sides of the body, indicating higher densities of these feather types in colder climates. Finally, we calculated the density of downy + semiplumes compared to total feather density; this trait measured on the ventral side of the body is significantly negatively and linearly correlated with winter minimum temperature, indicating proportionally higher number of purely insulatory than contour feathers in species inhabiting colder climates; this effect was significant both with and without the king penguin's data (data of the king penguin included:  $F = 6.61$ ,  $p = .0112$ ,  $\beta(SE) = -2.32 \times 10^{-3} (9.06 \times 10^{-4})$ ; excluded:  $F = 6.56$ ,  $p = .0114$ ,  $\beta(SE) = -2.17 \times 10^{-3} (9.92 \times 10^{-4})$ ).

Habitat affects feather density parameters, with the exception of the density of contour feathers on the dorsal side of the body, and this effect is significant both with and without the king penguin's data (Table 1b; Figure 3). Results show that the total feather density, and density of different types of body feathers increased from terrestrial to aquatic birds, with intermediate values seen for riparian and wading taxa. This change in feather density between habitat groups varied, however, as terrestrial, riparian and wading birds were similar to one another, as well as floaters and divers were similar to one another, whereas the difference between the first three and last two groups was significant (Figure 3). The effect of habitat on feather density remained significant even after we controlled for the presence of afterfeathers on contour feathers (Table S1). The density of downy + semiplume to total feather density, measured on the dorsal side of the body is also significantly related to habitat, as terrestrial, riparian and wader birds formed one cluster and floaters and divers another, whereas the difference between the two clusters was significant in the models both with and without the king penguin (with king penguin:  $F = 3.94$ ,  $p = .0046$ ; without:  $F = 3.97$ ,  $p = .0044$ ; contrasts between groups:  $T = R = W$  at  $p > .9838$ ,  $F = D$  at  $p = .6222$ ,  $F + D > T + R + W$  at  $p < .0003$ ).

Food category affects the total feather density as well as the downy + semiplume density measured on the ventral side with, or without, the king penguin data, as species with high food protein content had higher densities of these feather types than species with low food protein content (Table 1b). The effect of food on feather density remains consistent after controlling for the presence of afterfeathers on contour feathers (Table S1).

#### 3.2 | Effects of ecological traits on $\Delta_{\text{feather mass}}$ and $\Delta_{\text{feather density}}$

Overall differences in all feather traits between ventral and dorsal sides of the body are non-significant (phylogenetic paired *t* tests, feather mass:  $t = 0.00$ ,  $p = 1.0000$ ; total feather density:  $t = 0.00$ ,  $p = 1.0000$ ; contour feather density:  $t = 0.00$ ,  $p = 1.0000$ ; downy + semiplume density:  $t = 0.64$ ,  $p = .5243$ ;  $N = 147$ ), indicating no general cross-species dorsoventral difference in feather traits. Habitat influences  $\Delta_{\text{feather mass}}$  in the models with and without the king penguin, although there was no clear trend between groups (contrasts between groups:  $W < F$  and  $D$  at  $p < .01$ , all other contrasts at  $p > .05$ ). No other dorsal-to-ventral differences are influenced by habitat.  $\Delta_{\text{feather mass}}$  is related to food in the models with and without the data of the king penguin (Table 2a), indicating that species with higher protein content in their diet have higher feather mass on their dorsal than on their ventral side.  $\Delta_{\text{feather density}}$  is not influenced by any predictors (Table 2b).

### 4 | DISCUSSION

#### 4.1 | Feather traits and habitat

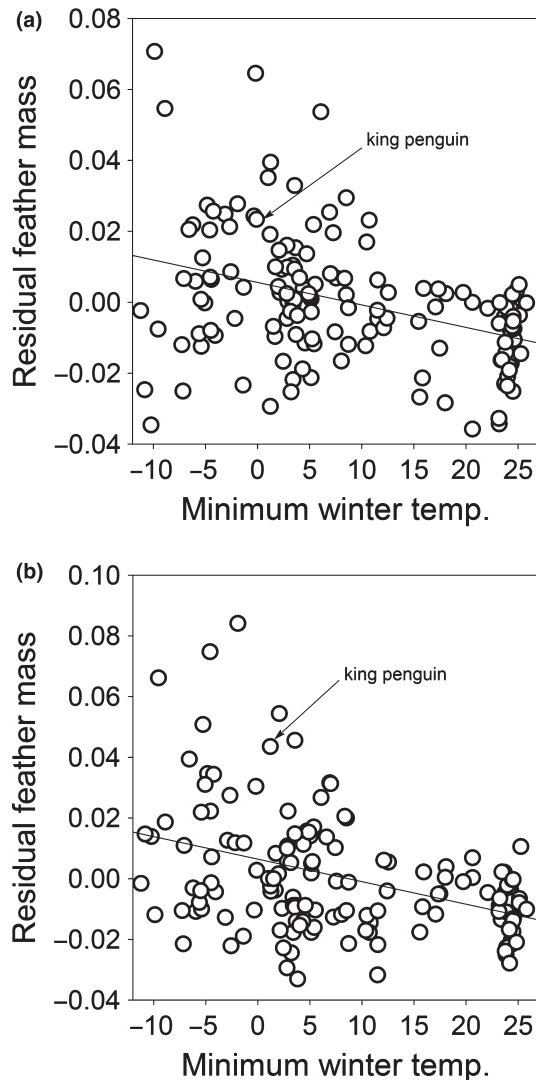
We found that habitat does not affect feather mass per unit area across species. This result is counter-intuitive as our initial

**TABLE 1** Minimum adequate PGLS models used to investigate relationships between feather mass (a), total feather density and density of different body feathers (b) on the ventral and dorsal sides of the body, in relation to body mass, life-history and ecological traits. Minimal models were obtained by eliminating non-significant predictors from full models in a backward-stepwise manner based on the largest *p*-value (see text for details). Temperature variables are included as second-order orthogonal polynomials. Exponent at the *F* value of these two variables indicate whether both the linear and quadratic (l + q) or only the linear (l) component of polynomial is retained in the minimal model after model selection

|                                                         |        | Models including king penguin                |          |                                              |          | Models without king penguin                  |          |                                              |          |
|---------------------------------------------------------|--------|----------------------------------------------|----------|----------------------------------------------|----------|----------------------------------------------|----------|----------------------------------------------|----------|
|                                                         |        | Ventral                                      |          | Dorsal                                       |          | Ventral                                      |          | Dorsal                                       |          |
|                                                         |        | <i>F</i>                                     | <i>p</i> | <i>F</i>                                     | <i>p</i> | <i>F</i>                                     | <i>p</i> | <i>F</i>                                     | <i>p</i> |
| (a)                                                     |        |                                              |          |                                              |          |                                              |          |                                              |          |
| Feather mass                                            |        | Pagel's $\lambda = 0.50$ ,<br><i>N</i> = 148 |          | Pagel's $\lambda = 0.60$ ,<br><i>N</i> = 151 |          | Pagel's $\lambda = 0.49$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.54$ ,<br><i>N</i> = 150 |          |
| Body mass                                               | 1      | 37.80                                        | <.0001   | 2.17                                         | .1432    | 32.38                                        | <.0001   | 0.43                                         | .5123    |
| Minimum winter temperature                              | 1      | 20.62                                        | <.0001   | 22.30                                        | <.0001   | 20.81                                        | <.0001   | 23.92                                        | <.0001   |
| (b)                                                     |        |                                              |          |                                              |          |                                              |          |                                              |          |
| Total feather density                                   |        | Pagel's $\lambda = 0.91$ ,<br><i>N</i> = 148 |          | Pagel's $\lambda = 0.60$ ,<br><i>N</i> = 151 |          | Pagel's $\lambda = 0.82$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.61$ ,<br><i>N</i> = 150 |          |
| Body mass                                               | 1      | 198.79                                       | <.0001   | 207.17                                       | <.0001   | 211.75                                       | <.0001   | 223.20                                       | <.0001   |
| Habitat                                                 | 4      | 7.91                                         | <.0001   | 6.82                                         | <.0001   | 10.18                                        | <.0001   | 7.36                                         | <.0001   |
| Maximum summer temperature (linear + quadratic effects) | 1 or 2 | 10.27 <sup>l</sup>                           | .0017    | 13.12 <sup>l + q</sup>                       | <.0001   | –                                            |          | 6.66 <sup>l</sup>                            | .0109    |
| Minimum winter temperature (linear + quadratic effects) | 1 or 2 | 7.00 <sup>l + q</sup>                        | .0013    | 4.35 <sup>l + q</sup>                        | .0146    | 7.81 <sup>l + q</sup>                        | .0006    | 4.75 <sup>l + q</sup>                        | .0100    |
| Food                                                    | 1      | 6.29                                         | .0133    | –                                            |          | 6.01                                         | .0155    | –                                            |          |
| Contour feather density                                 |        | Pagel's $\lambda = 0.91$ ,<br><i>N</i> = 148 |          | Pagel's $\lambda = 0.77$ ,<br><i>N</i> = 151 |          | Pagel's $\lambda = 0.90$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.79$ ,<br><i>N</i> = 150 |          |
| Body mass                                               | 1      | 296.85                                       | <.0001   | 242.64                                       | <.0001   | 322.72                                       | <.0001   | 268.86                                       | <.0001   |
| Habitat                                                 | 4      | 4.51                                         | .0019    | –                                            |          | 4.14                                         | .0034    | –                                            |          |
| Maximum summer temperature (linear + quadratic effects) | 1 or 2 | 11.29 <sup>l</sup>                           | .001     | 11.99 <sup>l + q</sup>                       | <.0001   | 4.77 <sup>l</sup>                            | .0306    | –                                            |          |
| Minimum winter temperature (linear + quadratic effects) | 1 or 2 | 4.27 <sup>l + q</sup>                        | .0158    | –                                            |          | 4.37 <sup>l + q</sup>                        | .0145    | 8.74 <sup>l</sup>                            | .0036    |
| Downy + semiplume feather density                       |        | Pagel's $\lambda = 0.60$ ,<br><i>N</i> = 148 |          | Pagel's $\lambda = 0.72$ ,<br><i>N</i> = 151 |          | Pagel's $\lambda = 0.61$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.69$ ,<br><i>N</i> = 150 |          |
| Body mass                                               | 1      | 41.56                                        | <.0001   | 45.49                                        | <.0001   | 46.22                                        | <.0001   | 50.65                                        | <.0001   |
| Habitat                                                 | 4      | 6.67                                         | .0001    | 5.18                                         | .0006    | 8.62                                         | <.0001   | 7.13                                         | <.0001   |
| Maximum summer temperature                              | 1 or 2 | 7.94 <sup>l + q</sup>                        | .0056    | 9.30 <sup>l</sup>                            | .0027    | –                                            |          | –                                            |          |
| Minimum winter temperature (linear + quadratic effects) | 1 or 2 | 7.3 <sup>l + q</sup>                         | .001     | 3.6 <sup>l + q</sup>                         | .0298    | 15.47 <sup>l</sup>                           | .0001    | 7.56 <sup>l</sup>                            | .0067    |
| Food                                                    | 1      | 16.63                                        | .0001    | –                                            |          | 14.38                                        | .0002    | –                                            |          |

prediction was that plumage should be heavier in aquatic birds, particularly in divers, because of enhanced insulatory and water resistance capabilities (Davenport et al., 2009; Williams et al., 2015). The density of all feather types was generally higher in aquatic compared to terrestrial birds, which indicates that habitat affects not

only the density of water-repellent contour feathers, but also the thermoinsulative downy layer. The water resistant outer plumage layer is composed of short, overlapping contour feathers in aquatic birds (Eadie & Ghosh, 2011; Grémillet et al., 2005; Pap et al., 2017; Rijke & Jesser, 2011), and the resistance of this layer is further



**FIGURE 1** The relationship between residual feather mass corrected for body mass and minimum winter temperature, measured on ventral (a) and dorsal (b) sides of the body. Lines are linear regressions without the king penguin's data with the equations  $y = 0.0056 - 0.0006x$  (a), and  $y = 0.0065 - 0.0007x$  (b)

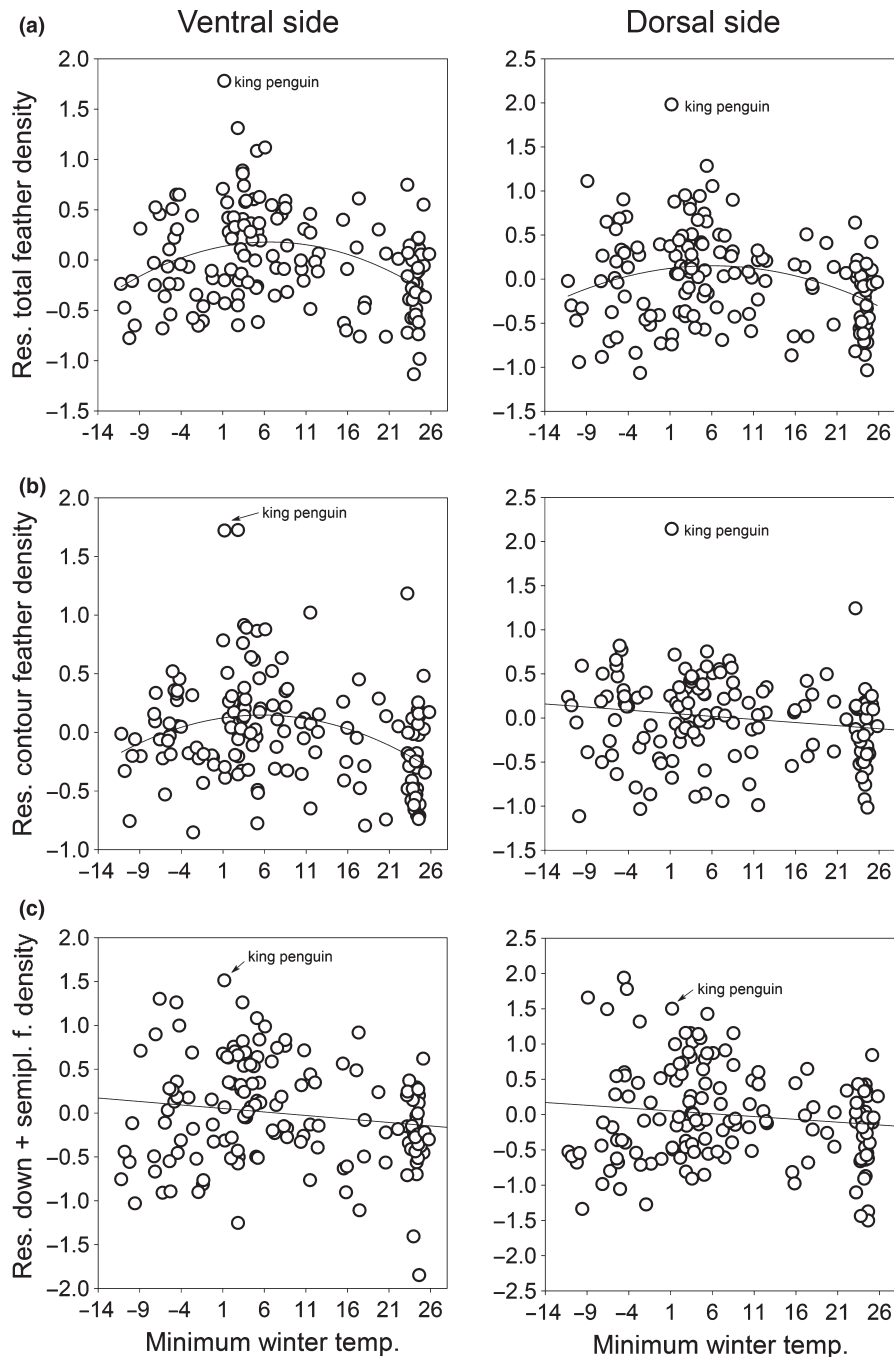
enhanced by the high vane density of the distal pennaceous parts of contour feathers, which prevents the infiltration of water into deeper plumage layers (Pap et al., 2017; Rijke, 1970; Rijke & Jesser, 2011). This result, that aquatic birds possess a higher density of contour feathers compared with their terrestrial counterparts, corroborates the earlier finding of Pap et al. (2017) regarding structural modifications of the vane of contour feathers, and further demonstrates the presence of a complex set of plumage adaptations correlated with aquatic lifestyle in birds. In line with this, we found that the density of downy feathers on both body sides, and the ratio of downy + semiplume to total feather density on the dorsal side of the body was higher in aquatic than in terrestrial species, which is also expected if we consider the high thermal conductivity of water. The high density of downy feathers and semiplumes may also enhance compression resistance of this layer during swimming

or diving (Kooyman et al., 1976), although these characteristics in aquatic birds probably replace air-filled spaces in the plumage by a keratin matrix. Because heat flow through avian plumage is the result of approximately equal contributions of thermal conduction through the feather elements and the sum of conductive and convective heat transfer through encapsulated air (Walsberg, 1988), insulating properties are likely not compromised. Furthermore, because the density of keratin is much higher than air, it follows that aquatic birds are able to minimize upthrust whilst keeping heat loss at a minimum (Grémillet et al., 1998).

Our results did not reveal any differences in feather density between divers and non-diving birds, a surprising outcome if we consider the higher thermal stress and plumage compression that is encountered when swimming underwater compared to surface feeding (De Vries & van Eerden, 1995; Grémillet et al., 2001; Wilson et al., 1992). This result implies that floaters and divers are subject to the same thermal stresses and water pressure as the functional morphology of their plumage remains unchanged irrespective of environment, and is further supported by the fact that there are no differences between the contour feather morphology of diving and non-diving birds (Pap et al., 2017). In addition, we show that there is a similar density of body feathers on the ventral and dorsal body surfaces of all species irrespective of habitat categories. However, the adaptation to diving exists at least at microscopic level of the downy feathers, in the barbule morphology, indicating that feather morphology, and less the density of the plumage ensure the enhanced repellency and insulation capacity of the diving birds (Dove & Agreda, 2007).

## 4.2 | Feather traits and temperature

Our results show that feather mass and density of downy + semi-plume feathers, and the ratio of downy + semiplume to total feather density on the ventral side of the body, were all negatively correlated with minimum winter temperature, corroborating the prediction that a dense plumage plays a role in thermal insulation (Cooper, 2002; Middleton, 1986; Novoa et al., 1994; Swanson, 1991; Williams et al., 2015). However, because we were unable to weigh different types of body feathers separately, we could not determine the specific effects of temperature. It therefore remains to be seen which specific feather types evolved to enhanced thermal insulation. The high density of downy feathers of species wintering under cold conditions support our prediction that the downy plumage layer has high insulating properties (Williams et al., 2015). The high density of contour feathers on the dorsal side of the body in species living in cold areas is also intriguing and shows that, in addition to the downy plumage layer, these may serve a similar function in thermoinsulation (Butler et al., 2008; Pap et al., 2017). Morphological adaptation of the contour feathers include the proximal plumulaceous part of the vane, in addition to a well-developed afterfeather (Osváth et al., 2017) in some species. It is thus not surprising that our results show that the density of contour feathers is higher in species that winter in colder areas; to the

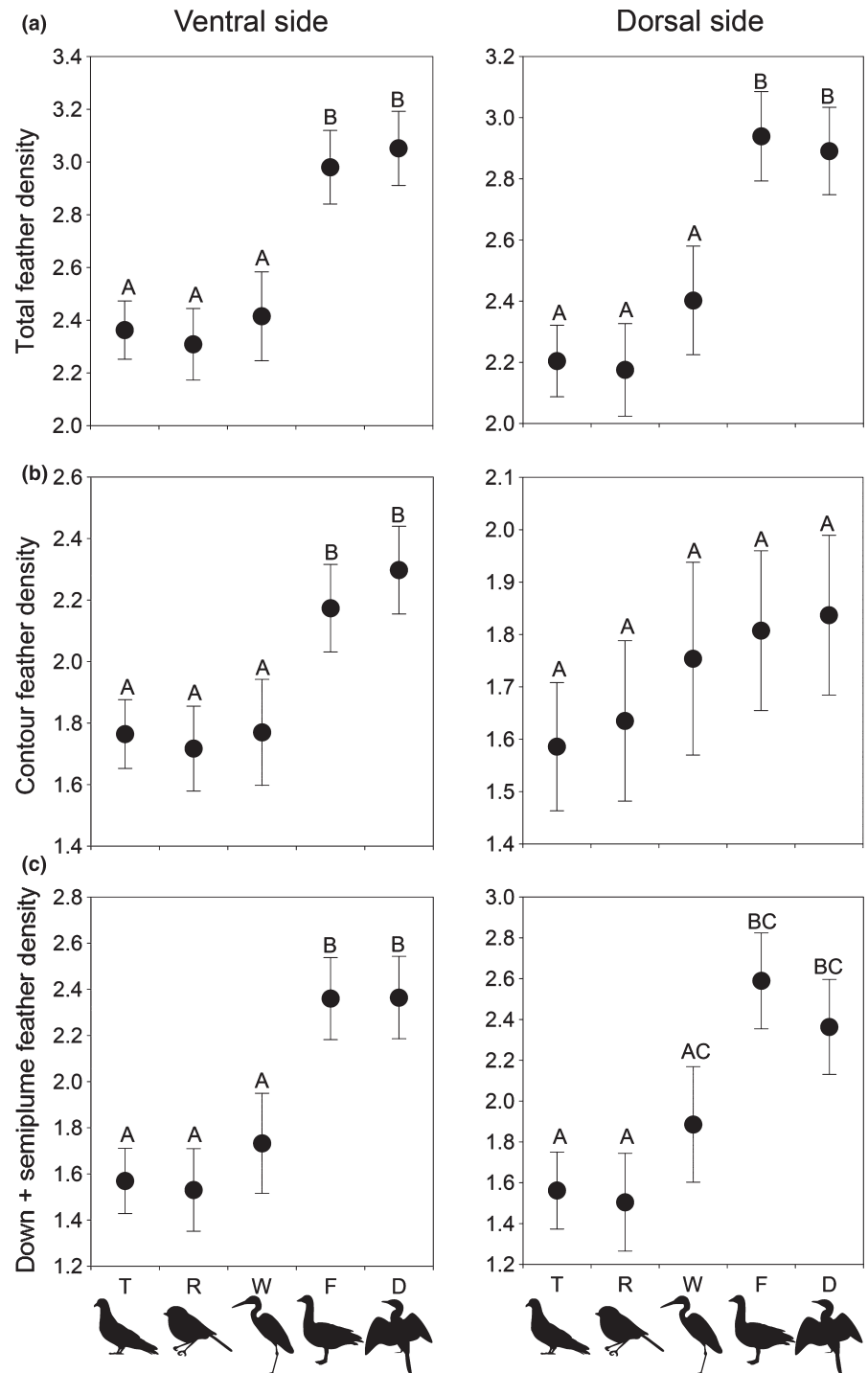


**FIGURE 2** The relationship between: total (a), contour (b), and down + semiplume (c) feather density on ventral and dorsal sides of the body and minimum winter temperature. Lines are quadratic regressions with the equations  $y = 0.1174 + 0.0185x - 0.0014x^2$  (a) and  $y = 0.1119 + 0.0126x - 0.0011x^2$  (b), and linear regression with the equation  $y = 0.0604 - 0.008x$  (c) for the ventral side of the body, and quadratic regression with the equation  $y = 0.1094 + 0.014x - 0.0012x^2$  (a), and linear regressions with the equations  $y = 0.0611 - 0.007x$  (b) and  $y = 0.0604 - 0.008x$  (c) for the dorsal side of the body. Regression lines are without the king penguin's data

best of our knowledge, this study presents the first multi-species evidence for the thermoinsulatory function of this trait. We found, however, that the total density of feathers measured on both sides of the body and the density of contour feathers on the ventral side are quadratically related with minimum winter temperature, showing higher feather densities in species wintering under intermediate climates compared to species wintering in colder or hotter climates. Our results suggest that heat retention and heat transfer can be ensured at the same time by low total feather density on the ventral and dorsal sides and by the contour feather density on the ventral side of the body. This relationship between feather density

and minimum winter temperature can be related to the variation in the number of air vacuoles in function of these feather traits, whereas the amount of air trapped in the plumage may remain unchanged. This finding indicates that species living in warm or cold environment may show the same adaptation in plumage traits, however, further measurements of feather traits and heat transfer are important to verify this assumption.

We found weak support for the prediction that birds living in warmer environments can reduce heat absorption at the surface of their plumage to prevent it from reaching the skin, or increase heat transfer from the body to the environment, at least through structural



**FIGURE 3** The relationship between residual total (a), contour (b) and downy + semiplume (c) feather density on ventral and dorsal sides of the body corrected for body mass (extracted from a single-predictor model controlled for phylogeny) and habitat type (T, terrestrial; R, riparian; W, wading; F, floating; D, diving). Different letters denote significant differences at  $p < .05$ , as indicated by PGLS models. Values are predicted  $M \pm SE$  derived from the models presented in Table 1b without the king penguin's data. Silhouettes are from PhyloPic (<http://phylopic.org>), contributed by various authors under Public domain licenses

changes of the plumage (Walsberg & King, 1978). Our results weakly support the idea that birds living in warmer areas, as characterized by maximum breeding temperature, have less dense plumage, consistent with an earlier multi-species study that showed that the morphology of individual body feathers is unrelated to the maximum breeding temperature (Pap et al., 2017). A reduced, or completely absent, role for plumage in heat dissipation might be related to the fact that avian skin has a limited capacity for evaporative heat transfer, something that is probably compensated for by other heavily vascularized

appendices, including the bill (Tattersall, Arnaout, & Symonds, 2016), and other behavioural or physiological thermoregulatory adaptations seen in birds living in hot climates (Nilsson, Molokwu, & Olsson, 2016; Nord & Williams, 2015). However, it is important to note that our species pool encompass mostly cold adapted temperate breeding birds, which limit our interpretation about the function of bird plumage to reduce heat absorption under warm conditions. Further investigation including warm adapted species will definitely clarify this issue.

**TABLE 2** Minimum adequate PGLS models used to investigate the relationships between differences in feather mass on ventral and dorsal sides of the body ( $\Delta$ ; a), and total feather density and density of different body feather types (b) on the ventral and dorsal sides of the body in relation to body mass, life-history and ecological traits. Minimal models were obtained by eliminating non-significant predictors from full models in a backward-stepwise manner based on the largest  $p$ -value (see text for details)

|                                    |   | Models including king penguin                |          | Models without king penguin                  |          |
|------------------------------------|---|----------------------------------------------|----------|----------------------------------------------|----------|
|                                    |   | <i>F</i>                                     | <i>p</i> | <i>F</i>                                     | <i>p</i> |
| (a)                                |   |                                              |          |                                              |          |
| Feather mass                       |   | Pagel's $\lambda = 0.56$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.54$ ,<br><i>N</i> = 146 |          |
| Body mass                          | 1 | 16.09                                        | <.0001   | 20.15                                        | <.0001   |
| Habitat                            | 4 | 3.84                                         | .0054    | 4.24                                         | .0029    |
| Food                               | 1 | 8.98                                         | .0032    | 10.31                                        | .0016    |
| (b)                                |   |                                              |          |                                              |          |
| Total feather density              |   | Pagel's $\lambda = 0.18$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.18$ ,<br><i>N</i> = 146 |          |
| Body mass                          | 1 | 6.21                                         | .0138    | 6.42                                         | .0124    |
| Contour feather density            |   | Pagel's $\lambda = 0.42$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.42$ ,<br><i>N</i> = 146 |          |
| Body mass                          | 1 | 0.21                                         | .6503    | 0.26                                         | .6111    |
| Downy + semi-plume feather density |   | Pagel's $\lambda = 1.01$ ,<br><i>N</i> = 147 |          | Pagel's $\lambda = 0.51$ ,<br><i>N</i> = 146 |          |
| Body mass                          | 1 | 5.17                                         | .0245    | 1.66                                         | .2001    |
| Food                               | 1 | 4.50                                         | .0356    | –                                            |          |

### 4.3 | Feather traits and diet

We found that birds that feed mainly on plants have lower feather density than those that feed on insects and vertebrates, corroborating former studies that have suggested that protein limits feather synthesis (Butler et al., 2008; Danner et al., 2015; Dawson et al., 2000; Pap et al., 2008). Intraspecific studies have also demonstrated the presence of a protein limitation on feather synthesis during growth, which shows that given the range of food compositions naturally present in avian diets, feather quality largely depends on ingested food (Dawson et al., 2000). The results of this study suggest that the density of body feathers per unit area is limited across species by food type, possibly suggesting the presence of species-level constraints on food protein content which links with keratin synthesis during feather growth. Earlier comparative studies on feather morphology (Pap et al., 2015, 2017) suggested that type of food has no effect on feather structural traits. Therefore, it appear that across multiple species food quality is associated with the amount and density of feathers but not their structural properties.

Our comprehensive study is the first to explore how natural variation in the amount and density of body feathers in birds relates to lifestyle and the environment. We present the result of a series of tests to determine how habitat and thermal condition affect feather mass,

a proxy of the amount of keratin invested per unit area, as well as the density of body feathers measured on the ventral and dorsal sides of the body, using a phylogenetic comparative analysis of 152 bird species. The results of this study demonstrate, for the first time, that body feathers mass, as well as the density of downy + semiplume feathers in birds is higher when environmental conditions are colder. Remarkably, we also show that the density of contour and downy feathers, measured on both sides of the body, is higher in aquatic than in terrestrial birds, whereas diving behaviour does not select for further increases in body feather mass and density.

This comparative study provides a basis for understanding the evolution of variation in body feather characteristics. Although our initial results are tantalizing, more work will be required if we are to understand the factors underlying the evolution of the diverse range of feathers seen in living birds. Future work will extend this study to directly measure the thermal capacity and conductivity of the plumage under various conditions, as well as in air and in water, to correlate these values with plumage traits.

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### CONFLICT OF INTEREST

The authors declare they have no conflicts of interests.

### AUTHORS' CONTRIBUTIONS

P.L.P. and G.O. designed the research; G.O., T.D., T.F., A.N., J.P., D.V. and C.I.V. collected the data; O.V., P.L.P. and G.O. analysed the data.

G.O., P.L.P. and G.D. wrote the paper with significant contribution from all co-authors. All authors discussed the results and gave final approval for publication.

## DATA ACCESSIBILITY

Data associated with this study are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.40r6p> (Osváth et al., 2017).

## ETHICAL STATEMENT

All feather data were collected from birds that died accidentally or due to natural causes.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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