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Diet, habitat, and flight characteristics correlate with intestine length in birds

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Abstract

A link between diet and avian intestinal anatomy is generally assumed. We collated the length of intestinal sections and body mass of 390 bird species and tested relationships with diet, climate, and locomotion. There was a strong phylogenetic signal in all datasets. The total and small intestine scaled more-than-geometrically (95%CI of the scaling exponent >0.33). The traditional dietary classification (faunivore, omnivore, herbivore) had no significant effect on total intestine length. Significant dietary proxies included %folivory, %frugi-nectarivory, and categories (frugi-nectarivory, granivory, folivory, omnivory, insectivory, and vertivory). Individual intestinal sections were affected by different dietary proxies. The best model indicates that higher consumption of fruit and nectar, drier habitats, and a high degree of flightedness are linked to shorter total intestine length. Notably, the length of the avian intestine depends on other biological factors as much as on diet. Given the weak dietary signal in our datasets, the diet-intestinal length relationships lend themselves to narratives of flexibility ('morphology is not destiny') rather than of distinct adaptations that facilitate using one character (intestine length) as proxy for another (diet). Compared to mammals, birds have total intestines of about 85% that of similar-sized mammals, corroborating systematic differences in intestinal macroanatomy between vertebrate clades.

Keywords: Anatomy, digestion, ecomorphology, phylogeny, scaling.

1. Background

Species differences in the anatomy of the intestinal tract have been noted in all vertebrate classes, including birds [1]. Several reasons have been put forward to explain the differences in bird intestinal length. Most commonly, diet is invoked [2]. Traditionally, relationships between diet and vertebrate intestinal length used herbivory, omnivory and faunivory as dietary categories. For birds, more detailed categories are typically used, noting several types of herbivory such as nectarivory, granivory, frugivory and folivory, and two major types of faunivory, insectivory and vertivory. Conventionally, it is assumed that herbivorous birds have the longest intestinal tract, with especially longer and more developed caeca [3, 4]. Similarly, it has been noted that faunivores (pure insectivores) have shorter intestines than herbivores such as frugivores and granivores [5]. Richardson and Wooller [6] also noted that nectarivores have shorter intestines than insectivores. As for other vertebrates, diet digestibility is the focus of explanatory narratives. High fibre levels in herbivorous diets in some species putatively require longer guts to extend gut passage to the time required for microbial fermentation [3]. However, not all herbivores consume high proportions of fibre. Nectarivory is common among birds, and since nectar is easy to assimilate, nectarivores have short intestines [7] and short digesta retention times [8]. High proportions of protein, fat and easily digestible carbohydrates in the diet could explain the shorter intestines of insectivores [5].

Most studies on avian intestinal length have focused on selected taxa. In pigeons (Columbidae and Treroninae), frugivorous species have shorter intestines than granivorous species [9]. In gallinaceous birds, it was noted that there are marked differences between folivorous and granivorous species, the former having longer caeca [3]. In corvids, Oelhafen [10] mainly focussed on the use of gastrointestinal anatomy for phylogenetic purposes, but also stated that species that are more folivorous and granivorous have longer intestines than fauni- or frugivores. There are also differences in intestinal length in parrots, where nectarivorous lorikeets have shorter intestines than non-nectarivorous parrots of similar size [11]. The findings of Ricklefs [5] and Richardson and Wooller [6] mentioned above refer to passeriformes.

A few larger studies have focused on the effect of diet on a specific section of the gut. Lavin, Karasov [12] showed a trend for an effect of diet (classified as carnivore, omnivore, herbivore, nectarivore or frugivore) on small intestine length in 220 avian species, but not when accounting for phylogenetic relationships in their sample. In contrast to the relative homogeneity of other sections of the intestine, the caeca have a highly variable anatomy across avian taxa. Most bird species have paired caeca at the junction of the small and large intestine; but notably, a few species have only a single cecum and some only vestigial or no caeca at all [13, 14]. Avian caeca can be simple, sacculated, lymphoid or glandular, and short or long [15]. Dietary relationships with caecal length are commonly assumed; several publications report longer caeca in herbivores, explained with the need for large fermentation chambers for fibre fermentation [13, 16]. This was supported to some degree by a study that included 155 avian species and used phylogenetic comparative methods [15]. However, there are several mismatches between caecal anatomy and fibre consumption, as several carnivores have very developed caeca [13, 15]. Apart from digestion and fibre fermentation, other functions like water absorption, immune reactions and nitrogen recovery from the retrogradely transported urine have been attributed to avian caeca [17, 18] and warrant further research.

Association of flight and migration with intestinal length have also been proposed, assuming flight can impose limitation on intestinal length. Species that are aerial pursuers or that feed on aerial prey should have shorter intestines to reduce weight and increase manoeuvrability [19, 20]. Furthermore, migratory species may have shortened intestines, to improve flight efficiency, or to conserve energy by supporting less of a metabolically expensive tissue during a period of increased physical activity. Empirical data to test these hypotheses are lacking [21]. In mammals, however, flight abilities have been negatively correlated with intestinal length [22-24], whereas habitat aridity had a positive relationship with large intestine length [24, 25].

In both mammals and reptiles, total intestinal length scaled more-than-geometrically with body mass at an exponent >0.33 [24, 26]. Similarly, the small intestine of birds and non-flying mammals scaled above geometric allometry, and birds had a higher scaling exponent compared to mammals [12]. Intestinal surface scales geometrically, therefore longer-than-expected intestines could compensate for a lower-than-expected scaling of intestinal diameter to keep diffusion distances short [27].

To date, Lavin, Karasov [12] and Hunt, Al-Nakkash [15] remain the only studies applying phylogeny-informed statistics to a larger dataset of avian intestine length – for the small intestine and the caeca, respectively. By combining the available data on the length of all intestinal sections in birds with biological data such as diet, migration, flight abilities, and habitat aridity, we aim to better understand the determinants of intestinal length in avian species. We hypothesize an exponent higher than geometry (positive allometry), as found previously. We expect an effect of diet on the length, especially on the large intestine and its components (the caeca and colon), with herbivores having longer structures than faunivores. We anticipate longer large intestines in birds from dryer (xeric) habitats, as a putative adaptation to water absorption, similar to what has been reported in mammals [24], and shorter intestines in particularly aerial species. We expect these features to be significant when accounting for the phylogenetic structure of the dataset, indicating true convergence due to ecological specialisation. Finally, we expected birds to have generally shorter intestines and intestinal sections than nonvolant mammals.

2. Methods

2.1 Search and data collection

Publications on bird intestinal length were searched for using Google Scholar, PubMed, and Web of Science, with taxon names and ‘anatomy’, ‘morphometry’, ‘digestive tract’ ‘intestine’, ‘gut’, ‘length’, as search terms. All search engines were last used in February 2021. Reference lists, and ‘cited by’ lists were also searched. Data were manually extracted from the publications. If the data were supplied in graphs and could be ascribed to a species, then the measures were obtained from the graphs using the ‘WebPlotDigitizer’ (https://automeris.io/WebPlotDigitizer/).

Data were only used if the publication included the species, body mass (kg) and length (cm) measurements of an intestinal section. Sections used included, if available, the small intestine (SI), the caeca/caecum, the right caecum, the left caecum, the colon-rectum-complex (‘colon/rectum’), the large intestine (LI, colon/rectum, and caeca/caecum) and/or the total intestine (TI). The scientific species name was taken as listed in the publications and (when needed) updated to the current nomenclature according to the IUCN red list of threatened species™. If the literature included data for juveniles and adults, juvenile data were excluded. Additional unpublished data were obtained from a large set of post-mortem examinations carried out by MSE (Fig. S1), and a few by MC.

Due to the differences in caecal anatomy in birds, different ways of quantifying caecal length were combined. For species for which individual data were given for the left and the right caecum, the caecal length represents the sum of these measures; in many publications, only this sum was indicated. For species with a single caecum, the data represents the length of this single structure. In case the mean caecum length was given, the value was multiplied by two.

Weighted means (correcting for sample size) were calculated of each intestinal section and the corresponding body mass. For example, if more data were available for small intestine than for caecum length of a species, then the body mass used for associations with small intestine length was different from the one used in the same species for associations with caecum length.

Information on the diet consumed in the natural habitat was obtained from the collection of Wilman, Belmaker [28]. The dataset gives quantitative information (in %) on the proportion of prey animals, fruits, nectar, seeds, and other plant parts, facilitating to investigate the effect of a single dietary factor (e.g., the proportion of seeds in the overall diet) on intestinal measures. In addition to these quantities, we used a 3-category description, classifying species into faunivore, omnivore or herbivore using two different cut-offs. One classification ascribed an extreme category (faunivore or herbivore) if 90% or more of the diet consisted of either source, with omnivores being all other species. The second classification used 70% as the respective cut-off. Finally, diet was coded as a 6-category description (frugi-nectarivore, invertivore, vertivore, omnivore, granivore or folivore) using a modified version of Wilman, Belmaker [28], splitting ‘PlantSeed’ into granivores and folivores, and ascribing a certain diet type other than omnivore if the corresponding diet constituted at least 50% of the overall diet.

Species were categorized according to several locomotion proxies. Species were classified as migratory or non-migratory based on information provided by IUCN red list of threatened species^{TM}. A dichotomic classification of volant or non-volant was based on [29]. In a more detailed approach, flight abilities, termed ‘flightedness’, were classified using a system provided by Heers and Dial [29] and information available from Billerman, Keeney [30]. Flightedness considered the species’ foraging and moving modes and represents an ordinal scale: ‘1’ was assigned to flightless birds (e.g., ratites and penguins), ‘2’ to species whose movement relies mainly on the hindlimbs (e.g., galliforms), ‘3’ to birds with both front and hind limb movement (bimodal), foraging on the ground (e.g., corvids), ‘4’ to bimodal foraging in trees mostly with more hind limb use (e.g., most Psittaciformes), ‘5’ to bimodal foraging in trees with mostly wing use (e.g., thrushes), ‘6’ forelimb-dominated movement with some hopping or climbing (most Columbiformes), ‘7’ forelimb-dominated with minimal hindlimb movement (e.g., hawks), and ‘8’ to species locomoting and feeding almost exclusively using wings (mostly, species feeding while hovering like hummingbirds).

As additional ecological proxy, ‘habitat’ was used to classify the aridity and water availability in the main habitat occupied by a species. Range maps with special attention to breeding ranges provided by Billerman, Keeney [30] were overlaid on the Köppen-Geiger classification [31] to determine the main climate zone in which the species resides. An additional factor for birds that prefer habitats with high proximity to water [30] was added to this classification. ‘1’ was assigned to hot and xeric habitats (e.g., deserts), ‘2’ to hot and mesic (e.g., steppes), ‘3’ to temperate and xeric (e.g., shrublands), ‘4’ to temperate and mesic habitats (e.g., grasslands), ‘5’ for terrestrial birds living close to open water bodies (several pigeon or dove species), ‘6’ to aquatic birds (e.g., Anseriformes and puffins).

Comparative data on mammals is from Duque-Correa, Codron [24].

2.2 Data analysis

The phylogenetic tree was built based on Jetz, Thomas [32] using two backbone trees [33, 34]. Following recent recommendations [35], the website VertLife.org was used to generate a distribution of 9,999 trees for each backbone topology inclusive of the 390 avian taxa for which comparative data were available. These were merged into a single nexus file and then a random sample of 1,000 trees was extracted to generate a consensus supertree with time calibration using scripts in package ‘phytools’ [36].The packages ‘ape’ and ‘tidyverse’ were used to ensure that the taxa within the final tree matched those in the data file. Ultimately, this procedure resulted in an ultrametric tree inclusive of 390 avian species. This was merged with that of mammals generated for [24] following topology and time of divergence presented in Fig. 1 of [37] using the software Tree Graph 2 [38].

Statistical analyses were done on (i) all available data (i.e., at different sample size for the different intestine sections – generally larger samples for the total intestine than for individual sections), and on two subsets that comprised (ii) those species for which both small and large intestine length was available and (iii) those species for which small intestine, caeca/caecum, and colon/rectum data were available, (iv) various individual taxonomic groups, (v) for only faunivores, and (vi) only herbivores. The factors migratory, volant, flightedness and habitat were assessed alone and in combination with the diet proxies for each intestinal section.

First, the allometric relationships with body mass were determined, and it was assessed which intestine section showed the best fit with body mass. Scaling exponents were termed 'more' or 'less than geometric' if they were above or below the expected isometry of 0.33. Then, the effect of diet was evaluated, using different dietary descriptors as cofactors or covariables with total intestine length, to decide which diet proxy would be used from there onwards (leading to the use of %folivory, %frugi-nectarivory and the six categories, see supplement). Then, the effect of diet proxies was analysed for all the intestinal sections in data sets i, ii and iii.

Next, the diet proxies were used to analyse their effects in different taxonomic groups (iv). For (v) faunivores (defined with the 90% cut-off) additional diet proxies were used as a continuous variable, %invertivory, %piscivory, %other-vertivory (vertebrates without fish) and %vertivory (as a distinction against insectivory). Similarly, for herbivores (vi), %frugivory, %nectarivory, %granivory, %folivory and %frugi-nectarivory (frugivory and nectarivory combined) were used as continuous variables. Finally, the locomotion and habitat proxies were analysed alone and in combination with diet proxies for all intestinal sections.

To assess the influence of flight on vertebrate intestinal length, we combined the avian data with data of 519 species of mammals and tested whether Class (bird/mammal) and/or being volant or not had an effect on the length of the various intestinal sections. Notably, this kind of data for volant mammals is extremely limited beyond a measure of total intestinal length [24].

All analyses were performed using generalized least squares (GLS) and phylogenetic generalized least squares (PGLS), recording the 95% confidence interval for parameter estimates, using the R packages 'caper' and 'nlme'. For the ease of reading, only PGLS results are explained in the main text except for the simple allometries and the bird-mammal-comparison, but readers interested in GLS results will find these alongside the PGLS statistics in the supplementary material. Allometric regressions were performed as linear regressions on log-transformed data. In all PGLS models, the phylogenetic signal lambda (λ) was estimated by maximum likelihood. Additionally, we used the R package 'phytools' to estimate the phylogenetic signals Blomberg's K (values other than 1 indicate deviation from Brownian motion) [39] and Pagel's λ (ranging from 0 to 1, with values closer to 1 indicating a stronger phylogenetic signal) for the complete datasets and the dataset of those species for which small intestine, caecum, and colon/rectum data were available. The significance level was set to 0.05. Different models applied to the same dataset (separately for GLS and PGLS) were compared using the small sample corrected Akaike's information criterion (AIC_c), considering models that differed by more than 2 ($\Delta AIC_c > 2$) as providing a different fit to the data. In total, the analyses comprised 50 different data (sub)sets and 267 models, with a maximum of 20 models applied to a single dataset in an AIC_c model selection approach. An overview over all datasets and models is given as Table S1.

3. Results

The datasets of bird intestinal length data compiled from the available literature included 390 avian species for the total intestine, 269 for the small intestine, 230 for the large intestine, 224 for caeca/caecum (with 21 species reported to have only a single caecum), 71 for the right caecum, 68 for the left caecum and 221 for the colon/rectum.

The phylogenetic signal was strong throughout; lambda was high for all intestinal sections (>0.90) when assessed individually, except for the colon/rectum (Table S2, Fig. S2). Also, in PGLS models, lambda was always significant and high (lowest at about 0.60 for models including the colon/rectum) (Tables S3-S5, S9-S13). Only when comparing the length of the right and left caecum, there was no phylogenetic signal, indicating that in paired caeca, their length is proportional (in other words: their ratio is constant) across birds, irrespective of the phylogenetic position of the species (Table S3).

The small intestine represented the longest intestinal section. The caeca showed a dichotomous distribution: in some species, they were longer than the colon/rectum, whereas in others, they were shorter (Fig. 1).

3.1 Allometry

All intestinal sections scaled more-than-geometrically (positive allometry) using simple regression models in GLS (Table 1). This was also the case for the caeca or the dataset using values for a single measured caecum. Only in the much-reduced datasets for the left and right caecum, respectively, the wide 95%CI included a geometric scaling exponent of 0.33. In PGLS, only the total and small intestine scaled more-than-geometrically. For the large intestine and its sections, caeca/caecum, and colon/rectum, geometric scaling was always included in the 95%CI of the exponent. For the reduced datasets for the left and right caecum, no significant body mass scaling was detected in PGLS (Table S3), suggesting that in these datasets, variation was mainly due to taxonomic variety. Using only species for which data for all sections are available, similar scaling relationships were found (Table S3), with all sections showing more-than-geometric scaling in GLS, but only the total and the small intestine in PGLS.

In the set with consistent data for the small, large, and total intestine, the relationship between body mass and large intestine length had the worst model fit, and the total intestine the best fit (PGLS: ΔAIC to small intestine: 8.7) (Table S3). In the set with consistent data for all intestinal sections, the models for the caeca, the whole large intestine and the colon had a poor data fit; in PGLS, the model for the total intestine was better supported than that for the small intestine (ΔAIC of 8.9) (Table S3). These analyses suggest that the length of the large intestine and its sections are particularly subject to the influence of factors other than body size.

When testing the scaling of the left caecum with its right counterpart (n= 68), the scaling exponent included linearity, as expected for symmetric anatomy, but the intercept nearly excludes zero (*P*=0.054). This would suggest that the left caecum tends to be slightly shorter (by 0.2 mm) than the right one (Table S3, Fig. S3A). Whether species have a single caecum or paired caeca did not have a systematic effect on caecum length (Fig. S3B).

3.2 Trophic level

For the ***total intestine*** length, the full set of trophic indicators was assessed. There was no significant effect of a three-level classification (faunivore, omnivore, herbivore) on total intestine length, regardless of whether the trophic cut-off was set at 70 or 90% (Table S4, Fig. S4). These models even ranked worse than the model with body mass only (PGLS: ΔAIC >2.9). The same was true for the model using %faunivory as a continuous proxy. Three trophic indicators were ever significant - %frugi-nectarivory, %folivory, and the model using the six trophic categories. In PGLS, the six categories and %frugi-nectarivory were equally supported (ΔAIC of 0.2) and better than %folivory (ΔAIC of 3.7); %folivory on its own failed to be significant; %folivory was positively and %frugi-nectarivory negatively related to intestine length.

Of the six categories, all except granivory were related to longer intestines than frugi-nectarivory in PGLS, but all other 95%CI overlapped. In all following analyses, %frugi-nectarivory, %folivory, and the six categories were used as diet proxies.

The effect of diet was not consistent across the different intestinal sections (Fig. 2). For the ***small intestine***, %frugi-nectarivory had the best fit (with a negative relationship with intestine length), followed by the body mass-only model (PGLS: ΔAIC of 6.1) (Table S5). In PGLS, %folivory and the six categories were not significant.

For the ***large intestine***, %folivory had the strongest support with a positive relationship (Table S5); %frugi-nectarivory was not significant. The six categories model was significant (with the difference between folivory and frugi-nectarivory the only significant one in PGLS).

For the ***caeca/caecum***, the models with %folivory and without diet proxy were equally supported (PGLS: ΔAIC of 1.4), but %folivory only tended towards significance. Neither %frugi-nectarivory nor the six categories were significant in PGLS (Table S5).

For the ***colon/rectum***, %folivory was the best model in PGLS, but models with the (non-significant) %frugi-nectarivory or without diet proxy were nearly as well supported (ΔAIC of 1.6 and 2.1, respectively; Table S5).

These patterns were generally similar when assessing only those species sets for which either small and large intestine length, or small intestine, caeca/caecum and colon/rectum length were available. In the first set, models with %frugi-nectarivory had the best support for total and small intestine, and models with %folivory the best support for the large intestine (Table S5). In the second set, models with %folivory were among the best supported for the total intestine, large intestine, caeca/caecum, and colon/rectum, but models with %frugi-nectarivory had the best support for the small intestine (Table S5).

When ***major avian clades*** were tested ***separately***, diet proxies were relevant for PGLS model selection for the total (and small) intestine in in Neoaves (%frugi-nectarivory negatively, frugi-nectarivory shorter than faunivory categories) and Passeriformes (%frugi-nectarivory negatively, several categories longer than frugi-nectarivory), but not in Columbaves, Galloanseres, Aequornithes, Australaves, or Psittaciformes (Table S6). Diet proxies were relevant for model selection in the large intestine and caeca/caecum in Galloanseres (Table S6).

Among faunivorous birds, %piscivory provided the best data fit for the total intestine and %vertivory was the best for the caeca/caecum in PGLS; however, the diet proxies were not significant (Table S7, Fig. S5). For the small intestine, %piscivory was positively related to length, but the respective models were less supported (ΔAIC > 2.8) than the models without diet proxy. For the caeca, %vertivory tended towards a negative relationship.

Among herbivorous birds, models with diet proxy only outperformed models without diet proxy for the small intestine in PGLS. For the total intestine, best data fit was achieved by %nectarivory, with a negative relationship. %Nectarivory was part of the best-supported model for the small intestine, again with a negative relationship (Table S8, Fig. S6).

3.3 Individual factors: Flight, Migration and Habitat

When analysed individually, the bimodal factors ‘volant/non-volant’ and ‘migratory/non-migratory’ were not significant for the total intestine, but habitat and flightedness were (Table S9). The categories ‘volant’ and ‘migratory’ were not assessed for the other intestinal sections.

Bird species from wet habitats had longer total and small intestines, while species from dryer areas had longer large intestines, caeca, and colon/rectum. However, habitat aridity was not a significant factor for the large intestine and colon/rectum when using PGLS (Tables S9-S13, Fig. S7).

Higher degrees of flightedness were correlated with shorter lengths of most intestinal sections, except for the small intestine and colon/rectum in PGLS (Tables S9–S13, Fig. S8).

3.4 Combined models

For the ***total intestine*** the best model fit was achieved including BM, %frugi-nectarivory, habitat, and flightedness in PGLS. A drier habitat, a frugi-nectarivorous diet, and a high degree of flightedness were linked to shorter total intestine length (Table S9).

For the ***small intestine***, the best data fit was achieved by the model with BM and %frugi-nectarivory; again, %frugi-nectarivory correlated with shorter small intestines. Flightedness was not significant in PGLS (Table S10).

For the ***large intestine***, the best model in PGLS included BM, %folivory and flightedness. Birds that consume high proportions of leaves had longer, and intensively flying birds shorter, large intestines, and birds from drier habitats tended towards longer large intestines (Table S11).

For the ***caeca/caecum***, the best PGLS data fit was achieved by models with BM, %folivory or %frugi-necatarivory, and habitat, or by BM and habitat alone; the diet descriptors were not significant in the combined models. Habitat aridity was negatively related to caeca/caecum length: birds from drier habitats had longer caeca (Table S12).

For the ***colon/rectum***, the model with BM, %folivory and flightedness had the best PGLS data fit. The models with BM, %frugi-nectarivory and flightedness and the one with

BM and flightedness alone were equally supported (Table S13). More flighted species had a shorter colon/rectum.

3.5 Comparison with mammals

When assessing avian and mammalian intestinal lengths together, in spite of large overlapping data ranges (Fig. 3), mammals as a class generally have longer intestines than birds when assessed in GLS (Table S14). Additionally, there was a significant interaction between body mass and class, indicating that birds had a steeper scaling, except for the colon/rectum (Fig. 3). However, as expected, the class effect was not significant in PGLS. Being volant had a similar effect in GLS models, but was additionally significant in PGLS for the total and the large intestine. In PGLS, the model with only body mass had the best support for the small intestine.

4. Discussion

The present study provides a comprehensive data collection of avian intestinal length. We find associations with trophic niche, environmental aridity, and flight abilities, and thus corroborate previous interpretations on the functional anatomy of birds. However, results change depending on whether phylogeny is taken into account, emphasizing that in the corresponding datasets, differentiation by diet, habitat or flightedness mostly occurs between phylogenetic groups and less so within them. Additionally, even for significant results, the visual impressions in scatter plots often do not suggest clear-cut category distinctions. Finally, our findings suggest that results could be influenced by sample sizes. Similarly, Lavin, Karasov [12] noted that diet effects on several intestinal metrics such as length, surface area, mass or volume changed being significant or not with varying sample size. This observation alone cautions against interpreting any results in a narrative of distinct dietary adaptations, but favours a narrative of morphological flexibility.

As with many studies based on large literature datasets, differences in how data were collected for the original publications may pose a constraint of unknown magnitude [24, 26]. For example, variety of origins of the specimens (natural habitat, captivity, unknown), differences in preservation status or methods, effects of the diets actually consumed by, or life history status (reproduction, migration) of, the dissected specimens, and variation in body condition all will contribute to an unknown degree of variation in the dataset.

Whereas it has been argued that reporting results of statistics that do not account for phylogeny in parallel to phylogeny-informed results should be avoided [40], others have pointed out the additional insight that can be gained from comparing both results. For example, differences between GLS- and PGLS-derived scaling exponents indicate differences in scaling on the level of closely related species versus deep phylogenetic nodes [41], and PGLS approaches alone will not allow a quantification of the difference between distinct clades [42], such as birds and mammals in the present study.

4.1 Allometry

As for basically all length measurements, scaling of intestine lengths with body mass was not linear, as previously noted for Spanish passerines [43] and for seabirds [20]. As for mammals and reptiles [24, 26], total and small intestine scaled at a higher exponent than the 0.33 expected by simple geometry. A positive allometry (exponent > 0.33) could be a compensatory strategy to keep short diffusion distance (gut diameter) without losing on overall absorptive surface [27]. In birds, this positive allometry only applied to the small and hence also the total intestine, but not to components of the large intestine, for which geometric scaling was excluded in the 95%CI of the exponent in GLS but included in PGLS.

This finding suggests that closely related species conform to geometric expectations in this respect, whereas this is not the case at deeper phylogenetic levels (Table 1). For the caecum, smaller datasets even showed no significant body mass scaling (left or right caecum for all available species, Table 1 PGLS), supporting the observation that avian caeca are particularly diverse [13, 15].

When comparing the scaling factors and exponents of the different taxonomic groups (Table S6, PGLS), there is general overlap in the 95%CI of the scaling exponent, but with respect to the scaling factor, Galloanseres have a longer total intestine compared to the Neoaves and Passeriformes (Fig. S2).

4.2 Trophic signal

Correlations between diet and the anatomy of the digestive tract have been commonly invoked for avian ingestive and digestive organs such as the beak and the gizzard [44, 45], or for consortia of morphological characters [46]. To some extent, our data support convergence in the length of intestine sections for diet types, conforming to the concept that frugi-nectarivores use a diet of high digestibility that facilitates particularly short intestines, and folivores with a diet containing many refractory components that require longer intestines [47]. If birds digest fibre, they do so mainly in the caeca and proximal colon aided by a microbiome, corresponding to findings of longer large intestines, caeca/caecum and colon/rectum in folivore species.

Nevertheless, our analyses also indicate a large overlap of most dietary categories in terms of intestine length, and often non-significance when controlling for phylogeny. For example, PGLS results suggest no difference in total intestinal length between the categories of folivores and faunivores, whereas that difference is significant in mammals [48]. When studying avian caeca length, Hunt, Al-Nakkash [15] found a significant diet effect, with longer caeca in herbivores, insectivores and omnivores as compared to vertivores, but notably no difference between most other groups, e.g., not between herbivores and insectivores. Our findings corroborate this lack of an expected, clear effect; for the caecum, for example, no diet proxy was significant when accounting for phylogeny. Thus, while one can use several of our findings as corroborating particular predictions on the effect of trophic niche, an overall picture emerges of a high degree of flexibility in trophic niche as related to intestine length. Similarly, recent studies testing the correlation of anatomical features of the beak with diet show that diet alone accounts for less than 20% of beak shape variation [49, 50]. Additionally, a recent study found no relationship between the microbiome and natural diets ascribed to the respective species across birds [51].

4.3 Habitat

Mammals from dry environments have a longer colon/rectum, which functions to increase water reabsorption [24]. In birds, we observed a similar relationship for the caeca/caecum and the colon/rectum. Apart from absorbing water from digesta, the avian rectum absorbs water from the urine that is emptied into the cloaca; colonic anti-peristalsis of urine allows further absorption in the colon and caeca [52]. Therefore, several intestinal locations are involved in water conservation in birds. Potentially, intestine length data could be combined with data on avian kidney function to yield a comprehensive picture of adaptations for water (and nitrogen) conservation.

Surprisingly, longer small intestines were observed in birds from more mesic habitats, and this effect was apparently stronger than the opposite effect on the large intestine, because it was also evident for the total intestine. That the small intestine should be longer under mesic, or shorter under xeric conditions has, to our knowledge, not been suggested in the literature. One reason could be that a reduced small intestine contributes to reduced overall metabolic costs of the gut [53], which may be favourable in xeric habitats. Our primary suspicion was that birds from mesic habitats are less intensive flyers, but the habitat effect remained the same for both the small and the total intestine when flightedness was included in models that also contained habitat. Whether a longer small intestine is necessary to prevent a too-expeditious passage of small particulate matter at higher water intakes remains speculative.

4.4 Flight

One of the most evident preconditions for flight is a light body, and a reduction of organs not directly involved in flight is a reasonable expectation. The simple categorisation ‘volant vs. nonvolant’ did not yield a significant difference in terms of intestine length, indicating that volant birds are very diverse in terms of intestine length (Fig. 3); additionally, some nonvolant birds have comparatively short intestines, e.g. the emu (*Dromaius novaehollandiae*). By contrast, the more detailed grading of flightedness yielded a significant effect on all intestinal sections (with the notable exception for the small intestine in PGLS), making it the most unidirectional signal in our analysis. Nevertheless, a visual inspection of the corresponding graphs (Fig. S8) indicates overlap, in particular among the higher flightedness categories, again cautioning against strong adaptive narratives.

Several previous studies showed a link between flight and reduced intestinal length. Birds have shorter guts than non-flying mammals, a finding corroborated in principle in our analysis, and flying mammals have shorter intestines than terrestrial mammals [12, 22-24]. Our combined bird-mammal-analysis, unsurprisingly, supports these findings, even though the overlap of intestine length between the classes is substantial (Fig. 3), and definitively more pronounced than the overlap between mammals and reptiles: Whereas the comparison of Hoppe, Meloro [26] suggests that reptile intestinal length is about 30-40% that of mammals, our data (from the GLS analyses, ignoring the body mass × class interaction) indicate that avian intestinal length is about 85% that of mammals of the same body size.

Flying abilities have received particular attention with respect to faunivorous birds. Hilton, Houston [54] considered areal pursuit hunters, which are typically vertivores rather than piscivores, to require shorter intestines due to their increased need for manoeuvrability. By contrast, some piscivores like penguins do not need adaptations to arial flight. Hilton, Houston [54] linked this difference to the greater digestive efficiency reported for some piscivores. Our findings when analysing faunivores individually, with longer small intestines in piscivores, support that narrative.

5. Conclusions

In conclusion, the avian digestive tract is shorter than that of mammals, which is linked to the requirement of body mass reduction for flight. Flight characteristics support this interpretation, with a tendency of shorter intestines in animals with more intensive use of flight. While relationships with both diet and habitat can be demonstrated, they are less distinct than in mammals and additionally depend on the level of detail provided by categorical variables. While a large variety of specific adaptations to diet can be reasonably expected at the level of digestive enzyme production or absorption characteristics, macroanatomy itself does not support a narrative of distinct adaptation by ecological category, but rather bespeaks a large variability in the interplay of form and function.

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Data, code and materials

Additional statistical results and figures are in the online supplement. The data collection including all individually recorded data and the species average values, together with the biological characteristics, the corresponding literature references, and the phylogenetic tree used are available at https://doi.org/10.5061/dryad.v15dv41z2. (during the review process, this is the temporary link: https://datadryad.org/stash/share/F-SM85tacScEqaH9bIfFahUJTrviylvRk8-y5Rq4ctM).

The R code used in the statistical procedures has been referenced in the method section.

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Table 1 Summary statistics for allometric scaling as log(y) = a + b log (body mass), or y = (10^a) BM^b (significant parameters in **bold**)

				GLS	PGLS	
Dependent	**Model**	**n**		**parameter (95%CI)**	**lambda (95%CI)**	**parameter (95%CI)**
Total intestine	BM	390	a	**2.14 (2.11 to 2.16)**	0.85 (0.77 to 0.90)	**2.10 (1.95 to 2.24)**
			b	**0.52 (0.50 to 0.54)**		**0.43 (0.40 to 0.46)**
Small intestine	BM	269	a	**2.05 (2.02 to 2.08)**	0.81 (0.70 to 0.88)	**2.00 (1.87 to 2.13)**
			b	**0.51 (0.49 to 0.54)**		**0.44 (0.40 to 0.47)**
Large intestine	BM	230	a	**1.29 (1.22 to 1.35)**	0.86 (0.77 to 0.92)	**1.35 (1.22 to 1.59)**
			b	**0.51 (0.45 to 0.57)**		**0.33 (0.26 to 0.39)**
Caeca	BM	224	a	**0.92 (0.82 to 1.02)**	0.92 (0.87 to 0.95)	**0.98 (0.63 to 1.33)**
			b	**0.53 (0.41 to 0.65)**		**0.33 (0.24 to 0.42)**
Caecum	BM	204	a	**0.66 (0.56 to 0.77)**	0.91 (0.85 to 0.95)	**0.68 (0.32 to 1.05)**
			b	**0.53 (0.41 to 0.65)**		**0.35 (0.25 to 0.44)**
Right Caecum	BM	71	a	**0.36 (0.20 to 0.53)**	0.97 (0.87 to NA)	**0.62 (0.22 to 1.01)**
			b	**0.34 (0.13 to 0.54)**		0.17 (-0.01 to 0.35)
Left Caecum	BM	68	a	**0.32 (0.15 to 0.49)**	1.00 (0.89 to NA)	**0.57 (0.14 to 1.00)**
			b	**0.32 (0.11 to 0.54)**		0.14 (-0.04 to 0.32)
Colon/Rect.	BM	221	a	**0.95 (0.90 to 1.00)**	0.64 (0.44 to 0.78)	**1.02 (0.83 to 1.20)**
			b	**0.39 (0.34 to 0.44)**		**0.32 (0.25 to 0.38)**

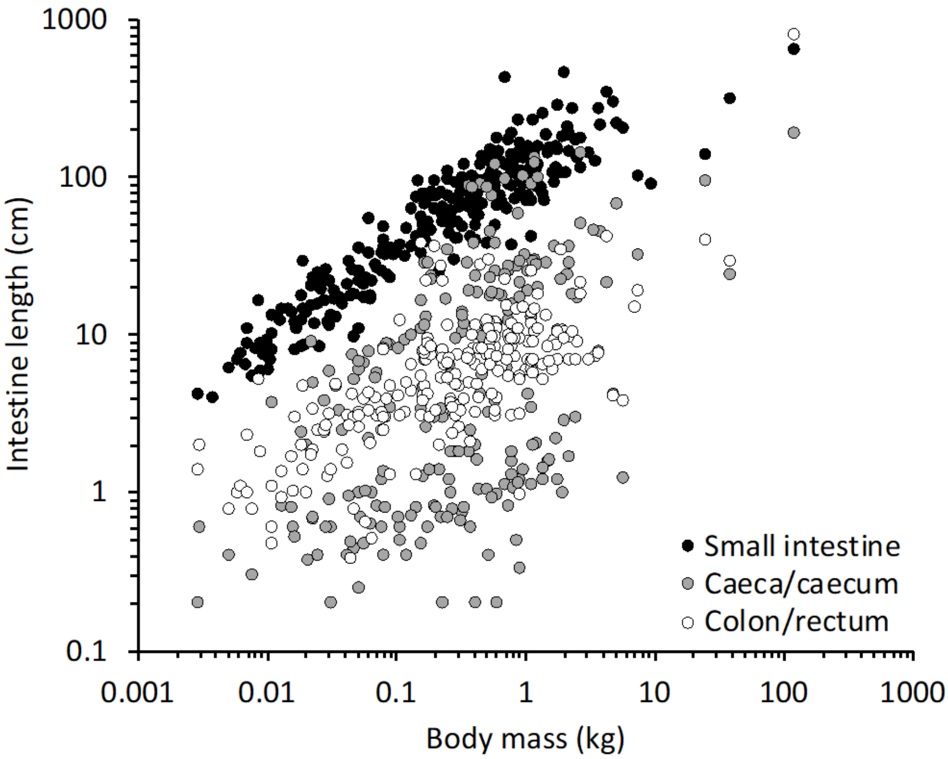

Figure 1 Comparison of the length of the small intestine (n = 269 species), the caeca/caecum (n = 225), and the colon/rectum (n = 221).

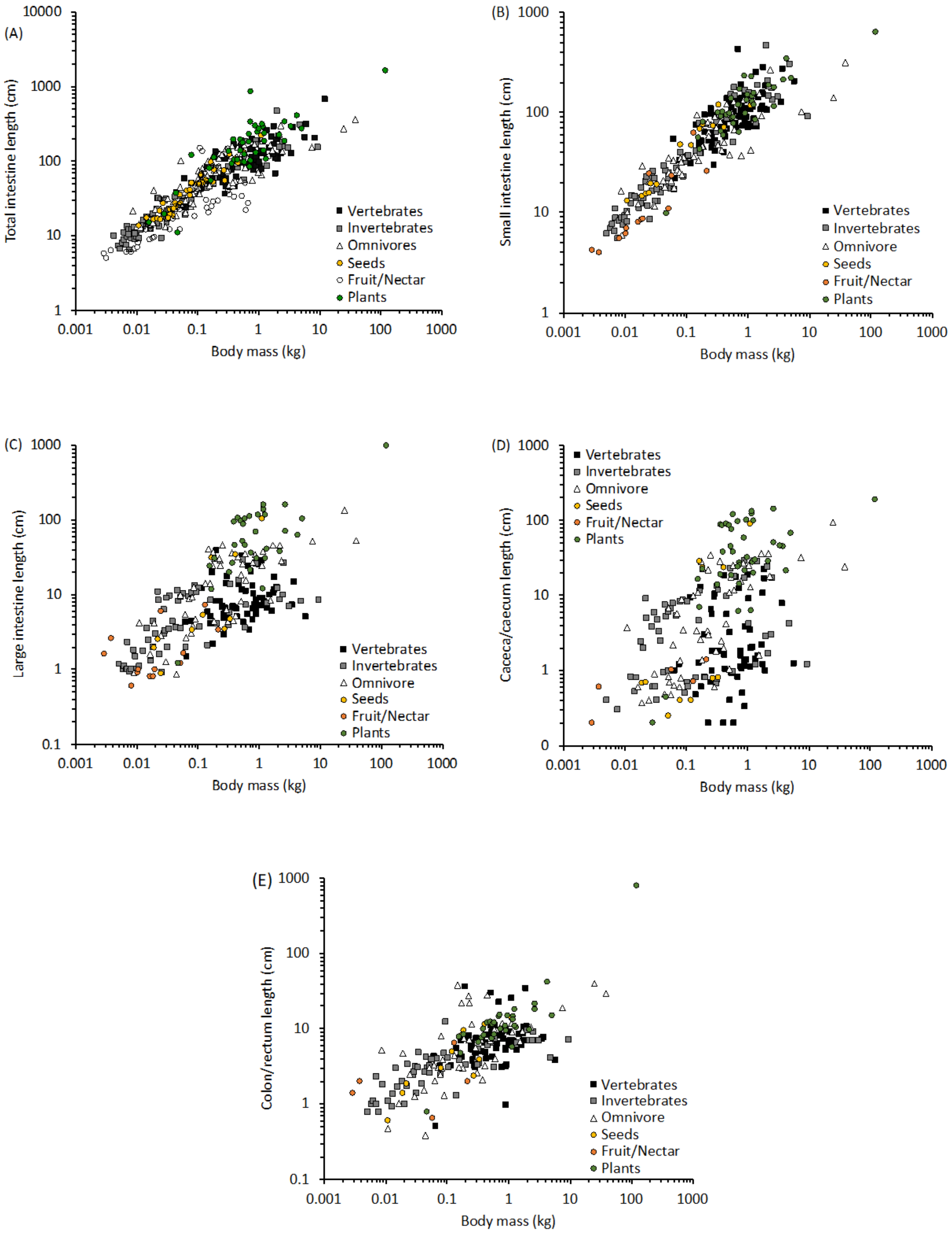

Figure 2 Relationship of body mass and intestinal length for (A) total intestine (n = 390 species), (B) small intestine (n = 269), (C) large intestine (caecum, colon, and rectum) (n = 230), (D) caeca/caecum (n = 224), (E) colon/rectum (n = 221) by trophic categories.

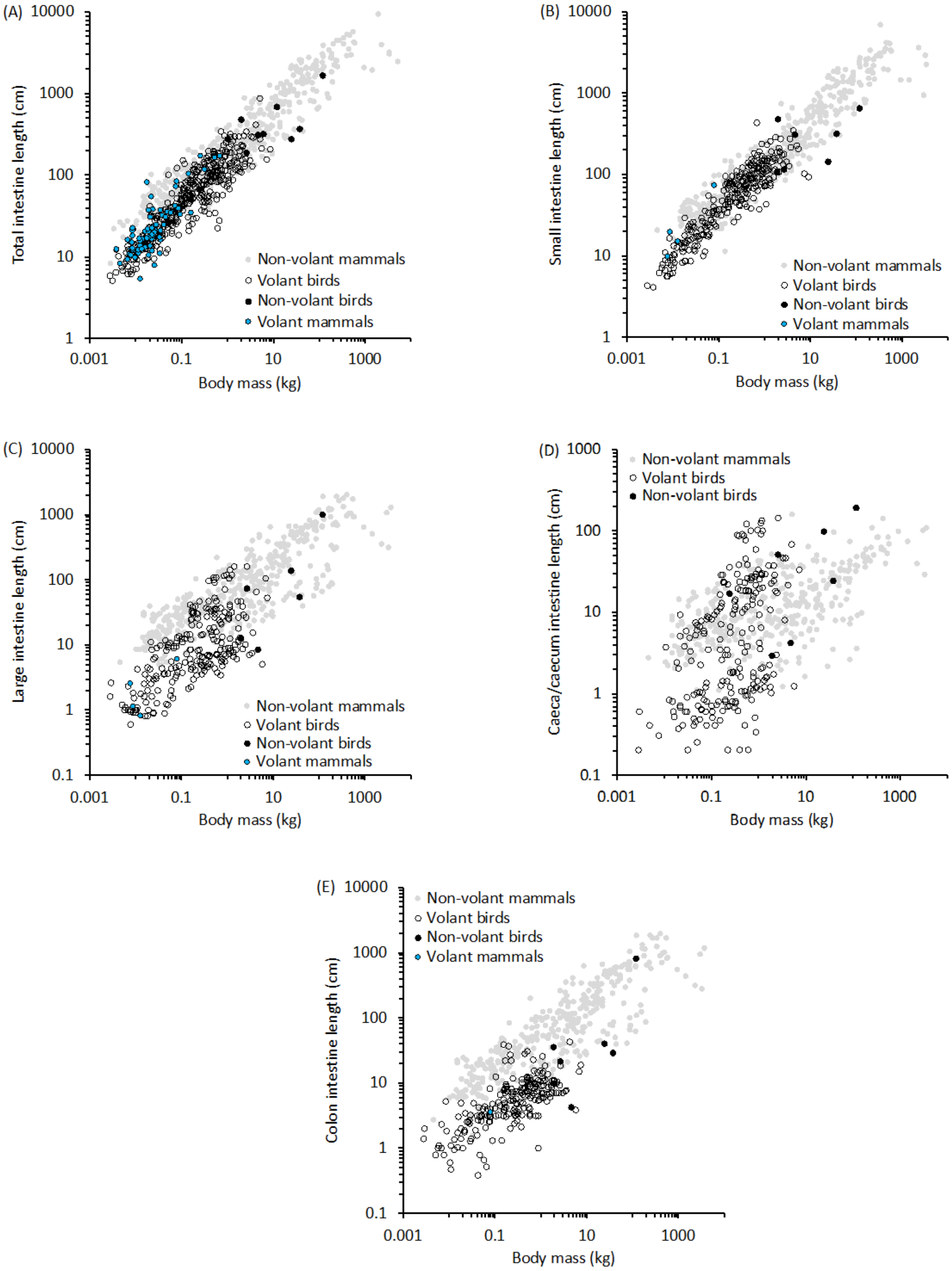

Figure 3 Relationship of body mass and intestinal length for (A) total intestine (n = 907 species), (B) small intestine (n = 664), (C) large intestine (caecum, colon, and rectum) (n = 616), (D) caeca/caecum (n = 575), (E) colon/rectum (n = 578) by for mammals and birds by volant abilities.