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Does intestine length explain digesta retention times in birds and mammals?

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ABSTRACT

Previous studies have indicated that across birds and mammals, body mass is a comparatively poor predictor of the time digesta is retained in the digestive tract (mean retention time, MRT). Rather, MRT might be determined by gastrointestinal anatomy, which can differ considerably within and between trophic guilds. Here, we used two recent literature compilations on the intestine length and the MRT in birds ($n = 33$ species) and mammals ($n = 149$) and applied comparative statistical approaches to assess whether intestine length is more closely correlated with MRT than body mass. Regardless of the statistical model used, whether small species (< 120 g and any larger bats) were included or not, or whether birds and mammals were assessed together or separately, intestinal length generally yielded a better model fit to MRT than body mass, supporting the general concept. Nevertheless, data scatter was substantial, indicating that intestine length, though better than body mass, is still a limited explanatory factor for MRT. The intestine length-MRT relationship is an example of the direct statistical assessment of a generally presumed form-function relationship that is typically represented as a narrative. In the comparative literature, such assessments are rare.

1. Introduction

The digestive tract of animals has fascinated comparative anatomists for centuries (Mitchell, 1901, Mitchell, 1903–6, Mitchell, 1916, Stevens and Hume, 1995, Langer, 2017, Smith et al., 2017, Duque-Correa et al., 2021, Duque-Correa et al., 2022, Chapman and McLean, 2024), possibly because these complex organs presents marked differences between species that otherwise appear relatively similar in morphology. Such differences have since been linked to ecological niches, most prominently diet. For example, animals consuming a diet that is comparatively easy to digest – faunivores – are typically considered to have a digestive tract that appears less complex, less voluminous, and shorter. By contrast, animals consuming a diet that is harder to digest – herbivores – are considered to have a digestive tract that is more complex, more voluminous, and longer (Stevens and Hume, 1995; Karasov et al., 2011; Langer and Clauss, 2018; Duque-Correa et al., 2021; Duque-Correa et al., 2022; Chapman and McLean, 2024).

Yet, statistically evaluating how such anatomical differences in the digestive tract relate to the ecological niches of animals has not been easy due to challenges in morphometrically characterizing the digestive tract complex. For example, while gut volume was found to be significantly higher in herbivorous than faunivorous mammal species (De Cuyper et al., 2020), there was no consistent relationship between total gut complexity (scored from 1 to 7) and diet in placental mammals (Langer and Clauss, 2018). As a result, evaluations have typically been performed using subsections of the digestive tract that can be more easily quantified, most commonly intestine length. In birds and mammals, intestine length is statistically associated with dietary niches and other bio-ecological parameters, such as habitat aridity or mode of locomotion (Duque-Correa et al., 2021; Duque-Correa et al., 2022; Chapman and McLean, 2024).

The importance of statistically linking the digestive tract to animal ecological niches centers on the assumption that a more complex, more voluminous, or longer gut has certain physiological effects on an animal. For example, the observation that ruminants from arid habitats have longer, large intestines suggests that this gut section is important for re-

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absorbing water from the digesta (Woodall and Skinner, 1993). Plausible as this interpretation was, it lacked a direct statistical test of its functional interepretation. Later, Tahas et al. (2017) and Kihwele et al. (2020) – relying mostly on the data from Woodall and Skinner (1993) – demonstrated a significant relationship between the (body mass-corrected) length or surface area of the large intestine and the moisture content of the feces in ruminants, adding evidence that the assumed underlying process does occur. With respect to digestion, digestibility is fundamentally linked to the time it takes for digesta to pass through an animal's gut (Clauss et al., 2008; Clauss et al., 2015). Therefore, it is commonly assumed that a more difficult-to-digest diet requires a more complex, more voluminous, or longer gut (Stevens and Hume, 1995; Karasov et al., 2011; Langer and Clauss, 2018; Duque-Correa et al., 2021; Duque-Correa et al., 2022; Chapman and McLean, 2024). To date, however, there has not been a comprehensive assessment of whether gut complexity or length is linked to digesta passage time. Instead, the time it takes for digesta to pass through an organism's gut has been more crudely related to its body mass (Illius and Gordon, 1992; Clauss et al., 2007a; Yoshikawa et al., 2019; Abraham et al., 2021). Yet, mechanistically assessing such relationships is relevant for testing the assumptions underlying our understanding of animal nutritional physiology and its broader impacts on ecosystems (e.g., animal mediated dispersal of seeds and nutrients; Abraham et al., 2021).

For a very limited number of mainly domestic mammals ($n = 8$), Langer (1989) suggested a positive relationship between gut volume and digesta retention times. However, quantitative tests of the assumed relationship between gut complexity and gut passage time are rare. Instead, this principle has been considered justifiable based on theoretical expectations. The 'occupancy principle' or 'Stewart-Hamilton principle' theoretically demonstrates a necessary positive relationship between the volume of a compartment (such as the gut) and the time it takes for the material to pass through it (Holleman and White, 1989; Munn et al., 2015). Based on this principle, animals with a more capacious gut should have longer retention times (Müller et al., 2013; De Cuyper et al., 2020). However, empirical evaluation of this principle is challenging as the calculation of estimated gut fill is mathematically derived using retention time, i.e., the relationship is part of the conceptual assumptions and hence cannot be proven using the resulting data. To our knowledge, the only other studies that link a macroscopic measure of gut anatomy – intestine length – with the retention time of digesta were performed on seabirds (Jackson, 1992, 5 species) and raptors (Hilton et al., 1999, 7 species), both demonstrating longer retention in longer guts.

Here, we combined two recently published datasets to empirically test the assumption that gut length (a morphological parameter of the digestive tract) is indeed a better predictor of digesta retention times than body mass (a crude, less digestion-related parameter). Specifically, we linked a large dataset on intestine length that comprised mainly previously published data but also some new original observations (Duque-Correa et al., 2021; Duque-Correa et al., 2022), body mass and a large compilation of published data on digesta retention time (Abraham et al., 2021) in birds and mammals. These animal groups extend across vast environmental gradients (e.g., water, nutrient availability) and play important roles within ecosystems.

2. Methods

Data was obtained from published sources. Data on mammal intestine length was taken from Duque-Correa et al. (2021), and on bird intestine length from Duque-Correa et al. (2022). The mean retention time (MRT) of birds and mammals was taken from the recent data collection of Abraham et al. (2021). The final dataset included only species for which both intestine length and MRT were available (mammals = 149; birds = 33). For this dataset, the association of intestine length and body mass is displayed in Fig. 1; for a statistical evaluation of this association, the reader is referred to Duque-Correa et al. (2021) and Duque-Correa et al. (2022).

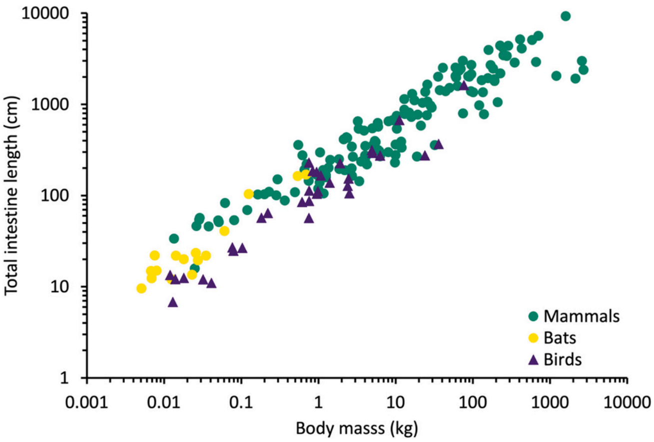

Fig. 1. Relationship between total intestine length and body mass in mammals (including bats) and birds in the dataset used for the present study.

All statistical analyses were conducted on (i) the full dataset, (ii) birds-only, (iii) mammals-only. The visual impression of the plotted data (Fig. 2) showed that patterns might be driven by small species up to ~100 g of body mass (BM). Furthermore, bats as volant animals have particularly short intestines compared to other mammals of similar body weight, most likely to reduce organ weight as a prerequisite for flight (Caviedes-Vidal et al., 2007; Duque-Correa et al., 2021). Therefore, analyses were also conducted on a fourth subset of data: (iv) heavier species only; a dataset that excluded species below 120 g, and additionally excluded the three heavier Chiropterans: *Rousettus aegyptiacus*, *Pteropus alecto*, and *Pteropus poliocephalus*. All datasets included two body mass (BM) measures per species: one corresponding to the individuals for which intestine length had been measured (BM_{IL}), and the second corresponding to the individuals for which MRT had been measured (BM_{MRT}). We ran all analyses for both versions of BM data.

For each of the four datasets (i.e., full, birds-only, mammals-only, heavy species only), we assessed which model best explained the variation in MRT across species: a model using BM-only, a model using intestine length-only, or a model using both. We selected the model that better fitted the data based on the Δ Akaike information criterion (ΔAIC), considering models with a ΔAIC of up to 2 equally matching the data (Burnham and Anderson, 2002). Furthermore, we obtained the R^2 for each model to assess the goodness of fit of each regression.

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' (Orme et al., 2013) and 'nlme' (Pinheiro et al., 2016). PGLS accounts for potential bias arising among biological traits that is caused by the phylogenetic relationships in the dataset (Symonds and Blomberg, 2014); however, for the same reason, PGLS cannot be used to test differences between birds and mammals. Models were set up as linear using log-transformed data. The strength of the phylogenetic signal was measured using Pagel's lambda (λ), which can vary from 0 (no phylogenetic signal) to 1 (strong phylogenetic signal). In all PGLS models, λ was estimated by maximum likelihood (Revell, 2010). The phylogenetic tree required for PGLS analyses was built, for birds, using two backbone trees based on Jetz et al. (2012). The mammalian phylogenetic tree was built following Upham et al. (2019). Then, a consensus tree including 33 bird and 149 mammalian species was built and used for the analyses. Branch lengths were set to describe time of divergence in millions of years (Ma). The time of divergence between birds and mammals was 319 Ma following https://timetree.org/. The significance level for all the statistical analyzes was set at 0.05.

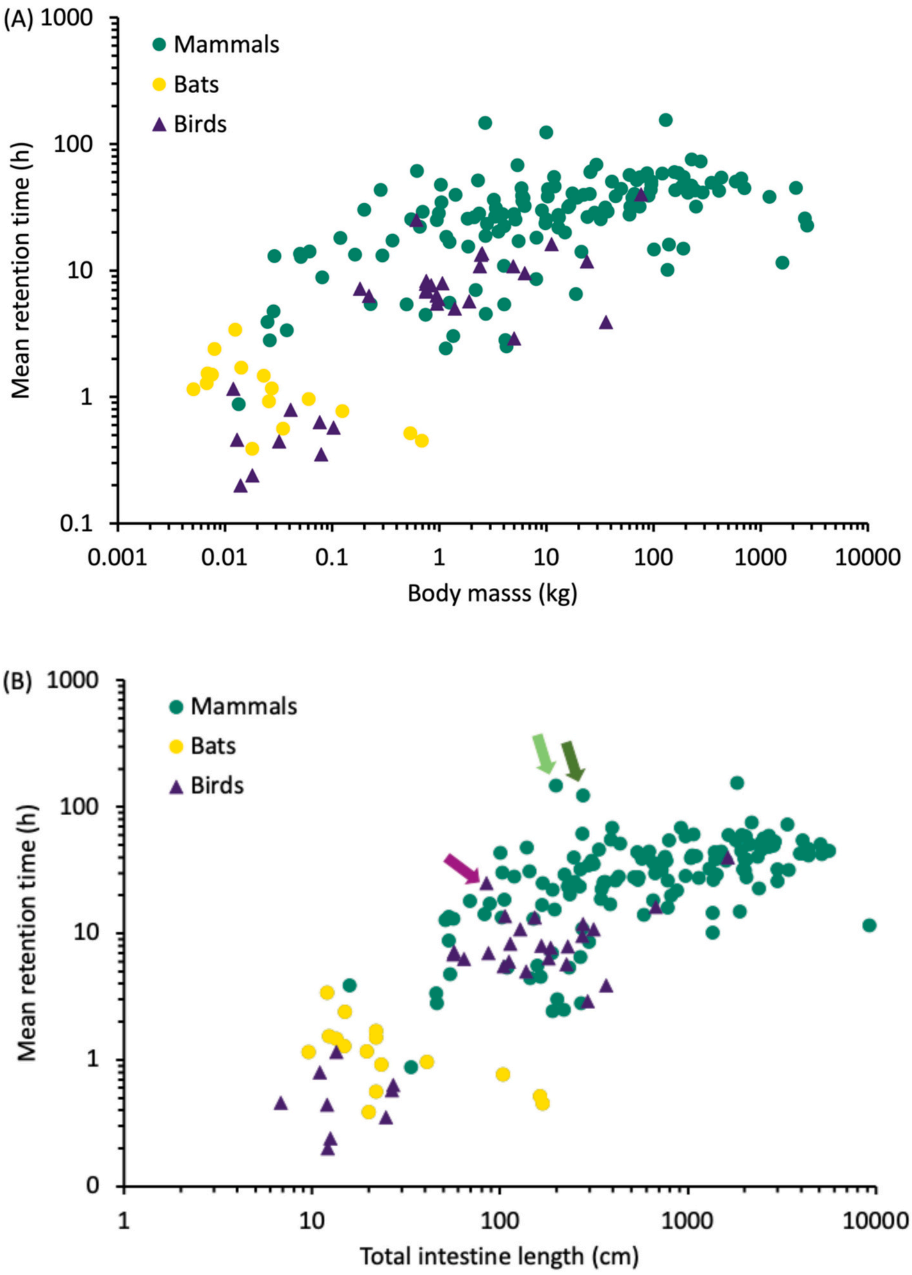

Fig. 2. Relationships in mammals (incl. bats) and birds of the digesta mean retention time in the digestive tract with (A) body mass or (B) total intestine length. In B, the bird hoatzin (*Opisthocomus hoazin,* light purple arrow) and the sloths (mammal; the three-toed sloth *Bradypus tridactylus* light green arrow and the two-toed sloth *Choloepus didactylus* dark green arrow), are marked by arrows as examples of species where a voluminous foregut fermentation chamber is associated with long mean retention times despite comparatively short intestinal tracts. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Birds and mammals

Generally, both BM and intestine length were positively related to MRT. For the full dataset, including birds and mammals, the model that achieved the best data fit for both GLS and PGLS was the one using total intestine length rather than models that included BM, regardless of which BM data were used. In GLS, all models that included intestine length performed better than those without (Table 1). In PGLS, most models had similar performance (ΔAIC $\leq$2), and in some cases, neither intestine length nor BM was significantly related to MRT (Table 1). These results support the visual impression of the data plot that there is a stronger relationship between MRT and intestine length than between MRT and BM (Fig. 2). Using intestine length and body mass as combined predictors yielded a similar data fit in PGLS compared to using intestine length as the only variable; however, body mass was not significant in the models with intestine length as an additional predictor (Table 1). In GLS, clade (mammal or bird) was a significant factor (with birds generally having shorter MRT), but clade was not a significant factor when accounting for phylogeny in PGLS (Table 1).

Visually, the positive relationships between MRT and BM or intestine length were evident across two body-size groups of organisms (roughly, those below and above 100 g BM); however, within each of these groups, the positive relationships appeared less evident or absent (Fig. 2). Correspondingly, model performance was lower (with overall reduced

Table 1
Models assessing influence on mean retention time in datasets including **mammals and birds** (significant parameters in **bold**).

	GLS					PGLS				
Model	r^2	AICc	ΔAIC		parameter (95 %CI)	lambda (95 %CI)	r^2	AICc	ΔAIC	parameter (95 % CI)
Full datase***t***[1]										
BM* + Class	0.59	212.1	21.7	a	**0.64 (0.50 to 0.78)**	0.98 (0.95 to 0.99)	0.21	67.2	6.7	0.79 (−0.52 to 2.09)
				BM	**0.30 (0.25 to 0.34)**					**0.17 (0.12 to 0.23)**
				mammal	**0.39 (0.23 to 0.55)**					0.40 (−1.41 to 2.21)
BM^{+} + Class	0.59	210.5	20.1	a	**0.64 (0.50 to 0.78)**	0.98 (0.95 to 0.99)	0.23	62.5	2.0	0.79 (−0.52 to 2.10)
				BM	**0.31 (0.26 to 0.35)**					**0.18 (0.13 to 0.24)**
				mammal	**0.38 (0.22 to 0.54)**					0.40 (−1.41 to 2.20)
Total intest. + Class	0.62	190.4	0.0	a	**−0.65 (−0.87 to − 0.44)**	0.97 (0.94 to 0.99)	0.23	60.5	0.0	−0.04 (−1.32 to 1.24)
				TI	**0.64 (0.55 to 0.72)**					**0.40 (0.29 to 0.51)**
				mammal	**0.23 (0.08 to 0.39)**					0.32 (−1.41 to 2.06)
Total intes. + BM* + Class	0.63	195.7	5.3	a	**−0.74 (−1.34 to − 0.14)**	0.97 (0.94 to 0.99)	0.23	62.5	2.0	−0.001 (−1.39 to 1.39)
				TI	**0.68 (0.39 to 0.96)**					**0.38 (0.09 to 0.67)**
				BM	−0.02 (−0.16 to 0.12)					0.01 (−0.12 to 0.14)
				mammal	**0.22 (0.05 to 0.39)**					0.32 (−1.41 to 2.06)
Total intes. + BM^{+} + Class	0.63	195.7	5.3	a	**−0.71 (−1.32 to − 0.10)**	0.98 (0.94 to 0.99)	0.24	61.2	0.7	0.26 (−1.14 to 1.66)
				TI	**0.67 (0.37 to 0.96)**					*0.26 (−0.02 to 0.53)*
				BM	−0.01 (−0.16 to 0.13)					0.07 (−0.06 to 0.21)
				mammal	**0.23 (0.06 to 0.39)**					0.35 (−1.41 to 2.11)
Species ≥ 120 g (no bats)[2]										
BM* + Class	0.36	88.3	11.2	a	**0.89 (0.76 to 1.01)**	0.94 (0.83 to 0.98)	0.07	22.4	5.8	*0.92 (−0.06 to 1.89)*
				BM	**0.14 (0.09 to 0.19)**					**0.11 (0.05 to 0.17)**
				mammal	**0.39 (0.25 to 0.53)**					0.44 (−0.91 to 1.78)
BM^{+} + Class	0.36	89.5	12.4	a	**0.88 (0.76 to 1.01)**	0.94 (0.85 to 0.98)	0.09	20.2	3.6	*0.91 (−0.07 to 1.90)*
				BM	**0.13 (0.08 to 0.18)**					**0.12 (0.06 to 0.18)**
				mammal	**0.38 (0.24 to 0.53)**					0.43 (−0.93 to 1.80)
Total intest. + Class	0.41	77.1	0.0	a	0.20 (−0.06 to 0.46)	0.93 (0.82 to 0.97)	0.11	16.6	0.0	0.31 (−0.66 to 1.28)
				TI	**0.32 (0.22 to 0.42)**					**0.29 (0.16 to 0.41)**
				mammal	**0.32 (0.18 to 0.47)**					0.39 (−0.89 to 1.67)
Total intes. + BM* + Class	0.41	82.4	5.3	a	0.03 (−0.49 to 0.56)	0.93 (0.82 to 0.98)	0.11	18.3	1.7	0.16 (−0.94 to 1.26)
				TI	**0.40 (0.16 to 0.64)**					**0.36 (0.08 to 0.65)**
				BM	−0.04 (−0.16 to 0.08)					−0.04 (−0.17 to 0.10)
				mammal	**0.31 (0.17 to 0.46)**					0.38 (−0.90 to 1.66)
Total intes. + BM^{+} + Class	0.41	81.8	4.7	a	−0.04 (−0.56 to 0.48)	0.93 (0.82 to 0.98)	0.11	18.5	1.9	0.33 (−0.76 to 1.43)
				TI	**0.43 (0.19 to 0.68)**					*0.27 (−0.04 to 0.55)*
				BM	−0.06 (−0.18 to 0.05)					0.01 (−0.004 to 0.55)
				mammal	**0.31 (0.17 to 0.45)**					0.39 (−0.89 to 1.67)

BM*: Body mass of individuals in which intestine length was measured. BM^{+}: Body mass of individuals in which MRT was measured; TI = total intestine length; Class is either bird or mammal.

[1] n = 182 species (33 birds, 149 mammals).

[2] n = 148 species (24 birds, 124 mammals).

R^2) when excluding the lighter species from the analyses (Table 1). Yet, when reducing the data to species of 120 g and heavier, the model that fitted the data best was the one with only intestine length. In PGLS, all models that included intestine length, with or without BM, fitted the data equally well (ΔAIC ≤2) (Table 1).

3.2. Birds only

Within birds only, both BM and intestine length were positively associated with retention time when assessed individually (Table 2). The models that fitted the data best, regardless of statistical method, included total intestine length only (Table 2). In PGLS, the models including BM$_{IL}$, and the models including intestine length and either of the BMs had similar data fit, again without BM being significant (Table 2). When reducing the data to species above 120 g, GLS results remained similar to the full dataset. In PGLS, the best-performing model was the one with intestine length and BM$_{MRT}$; however, the model with intestine length had a nearly identical fit, and the model with intestine length and BM$_{IL}$ was also well-supported (Table 2). Similarly to the full dataset, when birds lighter than 120 g were excluded, model performance was worse.

3.3. Mammals only

Within mammals only, both BM and intestine length were positively related to retention time when assessed individually (Table 3). In GLS, the model that fit the data best included only intestine length (Table 3). In PGLS, the best data fit was achieved by the model with BM$_{MRT}$; the model with intestine length and BM$_{MRT}$ had a similar fit. For the dataset with non-bat species of 120 g and heavier, regardless of statistical method, the best-supported model is the one with only intestine length. In PGLS, the models with BM$_{MRT}$ and those including intestine length with either BM had comparable data fit (Table 3). As was the case for the full dataset and for birds only, model performance was better when all species were included, compared to when the data was reduced to species heavier than 120 g.

4. Discussion

We evaluated whether the relationship between gut retention time, a physiological parameter, and intestine length, a morphological measurement, is tighter than the more commonly used but less digestion-related association between retention time and body mass (Illius and Gordon, 1992; Clauss et al., 2007a; Steuer et al., 2011; Müller et al., 2013; Abraham et al., 2021). As expected, we found that MRT increases with both intestine length and body mass. The expected association was demonstrated across all endotherms (i.e., birds and mammals together) and within these clades separately. However, the relationship with intestine length outperformed that with body mass statistically in almost all cases. This result corroborates the functional interpretation that a longer intestine is related – even if weakly and with quite some data scatter (Table 1) – to longer digesta retention.

Table 2
Models assessing influence on mean retention time indatasets including **birds** (significant parameters in **bold**).

	GLS					PGLS				
Model	r^2	AICc	ΔAIC		parameter (95 %CI)	lambda (95 %CI)	r^2	AICc	ΔAIC	parameter (95 % CI)
Full bird dataset[1]										
BM*	0.67	37.6	4.7	a	**0.67 (0.55 to 0.80)**	1.00 (0.82 to NA)	0.24	12.9	1.0	**0.74 (0.41 to 1.07)**
				BM	**0.49 (0.37 to 0.61)**					**0.31 (0.13 to 0.49)**
BM$^+$	0.66	38.5	5.6	a	**0.67 (0.55 to 0.80)**	1.00 (0.81 to NA)	0.17	15.7	3.8	**0.76 (0.41 to 1.11)**
				BM	**0.49 (0.37 to 0.62)**					**0.26 (0.08 to 0.45)**
Total intest.	0.71	32.9	0.0	a	**−1.18 (−1.59 to − 0.76)**	1.00 (0.81 to NA)	0.27	11.9	0.0	−0.35 (−1.09 to 0.38)
				TI	**0.90 (0.70 to 1.11)**					**0.55 (0.24 to 0.85)**
Total intest. + BM*	0.71	35.9	3.0	a	−0.89 (−2.47 to 0.68)	1.00 (0.80 to NA)	0.25	13.5	1.6	−0.001 (−1.32 to 1.31)
				TI	*0.77 (−0.001 to 1.54*)					0.36 (−0.26 to 1.00)
				BM	0.08 (−0.34 to 0.50)					0.12 (−0.25 to 0.49)
Total intest + BM$^+$	0.71	36.1	3.2	a	−0.91 (−2.35 to 0.51)	1.00 (0.80 to NA)	0.24	13.9	2.0	−0.32 (−1.48 to 0.83)
				TI	**0.78 (0.08 to 1.47)**					*0.53 (−0.01 to 1.07)*
				BM	0.07 (−0.32 to 0.47)					0.01 (−0.30 to 0.32)
Birds > 120 g[2]										
BM*	0.14	10.3	2.2	a	**0.88 (0.78 to 0.99)**	0.36 (NA to NA)	0.05	0.02	3.4	**0.89 (0.73 to 1.05)**
				BM	*0.13 (−0.007 to 0.27)*					0.12 (−0.03 to 0.29)
BM$^+$	0.10	11.1	3.0	a	**0.89 (0.78 to 0.99)**	0.99 (NA to NA)	0.01	0.3	3.7	**0.95 (0.68 to 1.23)**
				BM	0.12 (−0.02 to 0.26)					0.04 (−0.14 to 0.22)
Total intest.	0.17	8.1	0.0	a	0.27 (−0.34 to 0.88)	0.99 (NA to NA)	0.11	−3.2	0.2	0.20 (−0.60 to 1.02)
				TI	**0.29 (0.02 to 0.56)**					*0.33 (−0.003 to 0.66)*
Total intest. + BM*	0.10	12.1	4.0	a	0.32 (−0.87 to 1.53)	0.89 (NA to NA)	0.01	−1.6	1.8	−0.05 (−1.20 to 1.09)
				TI	0.26 (−0.30 to 0.82)					*0.46 (−0.06 to 1.00)*
				BM	0.01 (−0.27 to 0.30)					−0.09 (−0.38 to 0.19)
Total intest + BM$^+$	0.10	12.1	4.0	a	0.12 (−1.00 to 1.25)	1.00 (0.16 to NA)	0.14	−3.4	0.0	−0.29 (−1.35 to 0.75)
				TI	0.26 (−0.16 to 0.88)					**0.58 (0.10 to 1.07)**
				BM	−0.04 (−0.03 to 0.23)					−0.71 (−0.41 to 0.06)

BM*: Body mass of individuals in which intestine length was measured. BM$^{+:}$ Body mass of individuals in which MRT was measured; TI = total intestine length.

[1] n = 33 species.

[2] n = 24 species.

Table 3
Models assessing influence on mean retention time in datasets including **mammals** (significant parameters in **bold**).

	GLS					PGLS				
Model	r^2	AICc	ΔAIC		parameter (95 %CI)	lambda (95 %CI)	r^2	AICc	ΔAIC	parameter (95 % CI)
Full mammal dataset[1]										
BM*	0.48	169.8	14.9	a	**1.05 (0.98 to 1.13)**	0.96 (0.89 to 0.98)	0.21	39.2	2.8	**1.19 (0.56 to 1.82)**
				BM	**0.28 (0.24 to 0.33)**					**0.19 (0.13 to 0.24)**
BM$^+$	0.49	167.8	12.9	a	**1.04 (0.97 to 1.12)**	0.96 (0.90 to 0.98)	0.24	34.2	0.0	**1.19 (0.56 to 1.81)**
				BM	**0.29 (0.24 to 0.34)**					**0.20 (0.14 to 0.25)**
Total intest.	0.53	154.9	0.0	a	**−0.32 (−0.57 to − 0.07)**	0.95 (0.89 to 0.99)	0.23	36.4	2.2	0.27 (−0.41 to 0.95)
				TI	**0.60 (0.51 to 0.69)**					**0.41 (0.29 to 0.53)**
Total intest. + BM*	0.53	160.1	5.2	a	−0.31 (−1.02 to 0.41)	0.95 (0.87 to 0.99)	0.22	37.9	3.7	**0.93 (0.06 to 1.80)**
				TI	**0.60 (0.28 to 0.91)**					0.13 (−0.15 to 0.40)
				BM	0.05 (−0.08 to 0.18)					0.11 (−0.02 to 0.24)
Total intest + BM$^+$	0.53	160.0	5.1	a	0.48 (−0.16 to 1.13)	0.96 (0.88 to 0.99)	0.24	35.3	1.1	0.52 (−0.43 to 1.47)
				TI	0.31 (0.04 to 0.59)					*0.30 (−0.03 to 0.62)*
				BM	0.003 (−0.15 to 0.16)					0.06 (−0.09 to 0.21)
Mammals ≥ 120 g (no bats)[2]										
BM*	0.16	81.8	10.0	a	**1.28 (1.20 to 1.37)**	0.93 (0.78 to 0.98)	0.07	15.0	3.9	**1.36 (0.82 to 1.90)**
				BM	**0.14 (0.08 to 0.19)**					**0.11 (0.05 to 0.18)**
BM$^+$	0.15	82.4	10.6	a	**1.28 (1.19 to 1.36)**	0.93 (0.80 to 0.98)	0.10	12.1	1.0	**1.34 (0.80 to 1.88)**
				BM	**0.14 (0.08 to 0.19)**					**0.13 (0.06 to 0.20)**
Total intest.	0.16	71.8	0.0	a	**0.51 (0.20 to 0.83)**	0.92 (0.77 to 0.98)	0.11	11.1	0.0	**0.72 (0.10 to 1.35)**
				TI	**0.33 (0.22 to 0.44)**					**0.28 (0.14 to 0.42)**
Total intest. + BM*	0.22	76.8	5.0	a	0.30 (−0.32 to 0.93)	0.92 (0.77 to 0.98)	0.10	13.0	1.9	0.61 (−0.29 to 1.50)
				TI	**0.42 (0.15 to 0.69)**					**0.33 (0.01 to 0.66)**
				BM	−0.05 (0.18 to 0.08)					−0.03 (−0.18 to 0.12)
Total intest + BM$^+$	0.22	76.4	4.6	a	0.24 (−0.38 to 0.87)	0.92 (0.78 to 0.98)	0.10	12.8	1.7	**0.92 (0.03 to 1.80)**
				TI	**0.45 (0.18 to 0.72)**					0.19 (−0.13 to 0.51)
				BM	−0.07 (−0.20 to 0.07)					0.05 (−0.11 to 0.20)

BM*: Body mass of individuals in which intestine length was measured. BM$^{+:}$ Body mass of individuals in which MRT was measured; TI = total intestine length.

[1] n = 149 species.

[2] n = 124 species.

Thus, we formally verify the concept that a morphological adaptation (intestine length) has a statistically demonstrable association with, and hence putatively has an effect on, a relevant physiological performance measure (digesta retention time). However, before we discuss specifics of digestive morphophysiology of birds and mammals, we address the general heuristic value of such an approach, which is related to two different aspects. The first is the formal proof of the usually presumed link between form and function that has become the foundation of two major concepts: convergence and symmorphosis. The second is the looseness, or the data scatter, of the association.

4.1. Symmorphosis and convergence

Comparative approaches that link animal morphology and physiology are rare, even though the assumed interplay between form and function is a fundamental basis for our understanding of biology. This assumption is at the core of a very large number of comparative studies that link morphological traits to characteristics of animals' ecological niches, and corresponds to what Taylor and Weibel (1981) state as "*the firm belief that animals are built reasonably*". Examples of tests between *morphological* features and ecological niches are abundant and include: forestomach complexity and diet niche in muroid rodents (Steiner et al., 2022), beak morphology and diet niche in birds (Semprebon et al., 2019), dental complexity and diet niche in reptiles (Melstrom, 2017), or gill raker morphology and diet niche in fish (Kahilainen et al., 2011). Similarly, *physiological* measures can be related to ecological niches, such as when differences in paracellular absorption capacity are linked to a flying lifestyle (Caviedes-Vidal et al., 2007), or when differences in digesta retention are linked to specific trophic niches (Hummel et al., 2006). In both cases – when morphology or physiology are linked to niche characteristics - the other aspect that is not part of the test (i.e., physiology or morphology) as well as further physiological steps are typically assumed and part of the explanation of the pattern. Together with the relationship between large intestine length and fecal dry matter in ruminants mentioned in the Introduction (Tahas et al., 2017; Kihwele et al., 2020), other notable examples of a quantitative, statistical link between anatomy and physiology comprise the link between mammalian kidney medullary thickness and the maximum urine concentration (Beuchat, 1996), or the link between limb bone dimensions and locomotion speed (Christiansen, 2002).

When linking form and function quantitatively, the concept of *symmorphosis* (Taylor and Weibel, 1981) comes to mind. As worded by Weibel et al. (1991) when introducing the concept, "*the hypothesis of symmorphosis postulates a quantitative match of design and function parameters within a defined functional system*". Weibel, Taylor and co-authors produced a large body of data to demonstrate a link between the morphological and physiological properties of the respiratory system of mammals (Weibel et al., 1991; Weibel et al., 1992). However, interpretations of symmorphosis in this work were not based on a '*direct comparison of physiologic and morphometric measurements*,' even in cases where the title of the publication suggested this (Weibel et al., 1983), but relied on the comparison of the scaling of each of the factors with body mass. This criticism was prominently applied by Garland and Huey (1987) who showed that in the majority of statistical tests, the morphological and physiological relationships proposed for the respiratory system were not significant, basically drawing the validity of the assumed form-function association into question.

Notably, the form and function of the digestive tract were included early on in the concept of symmorphosis with a chapter on ruminant digestive tract variation with trophic niche (Hofmann, 1998) as part of an edited book on symmorphosis (Weibel et al., 1998). Although the proposed scheme in ruminants did not comprise testing of associations between the individual morphological and physiological components at the time, more recent work suggests that such associations between various morphophysiological measures can actually be found (Ehrlich et al., 2019; Przybyło et al., 2019; Hertaeg et al., 2021). But – as in the present study – the relationships, even when statistically significant, display a large degree of variability across species, and are not as tight as the wording of the explanatory concept might imply.

Thus, the second general heuristic value of studies such as the present one is a reminder that the explanations we use for the associations may be plausible, but do not merit the intuitive classification of 'rules' we might be tempted to ascribe to them. Rather, they should be considered '*a continuum of imperfection*' (Dudley and Gans, 1991) that bespeaks the concept of 'adequacy', 'sufficiency' or an just improvement compared to background levels, rather than optimal functionality, as the main criterion of natural selection (Garland and Huey, 1987).

As both of the measures linked in the present study are part of narratives of convergence, where longer intestines (Duque-Correa et al., 2021; Duque-Correa et al., 2022) and longer retention times (De Cuyper et al., 2020) are linked to more difficult-to-digest diets, their association permits us to link convergence of function to a certain degree of convergence in form.

4.2. Digestive morphophysiology

The finding that the length of the total intestine correlates positively with digesta retention time is intuitive and plausible. It also matches the finding that if a certain part of the intestine is resected, such as the caecum in rats or chickens, digesta passage is faster (Williams and Senior, 1982; Son, 2002; Kurosawa et al., 2007). Nevertheless, intestine length is clearly not the only morphological measure to link to digesta retention. For instance, it does not comprise information on the anterior part of the digestive tract, which shows a large variety of morphologies across species. In birds, this part of the digestive tract includes the crop, proventriculus and ventriculus, which all vary distinctively in complexity and volume among bird species (Kierończyk et al., 2016; Takasaki and Kobayashi, 2024). For example, among the birds, the hoatzin (*Opisthocomus hoazin*) has a particularly voluminous crop that functions as a foregut fermentation chamber (Dominguez-Bello et al., 1993), and that causes a longer MRT (Grajal and Parra, 1995) than expected based on the intestine length (Fig. 2B). In mammals, a large variety of stomach morphologies have been described including large, complex structures (Langer, 1988; Langer, 2017) that can retain digesta for extended periods and thus affect MRT measurements (e.g., Schwarm et al., 2008; Schwarm et al., 2009). For example, the two-toed (*Choloepus didactylus*) and the three-toed sloth (*Bradypus tridactylus*), with their voluminous forestomachs, also have longer MRT (Foley et al., 1995; Vendl et al., 2016) than expected based on their intestine length (Fig. 2B). Due to the complex nature of these foregut structures, it is difficult to represent them by a single morphological and continuous measurement. Intestine length, in contrast, is a comparatively straightforward measurement applicable to all vertebrates whose intestines are not equipped with internal structures that lengthen the functional path of digesta beyond their external dimension (Duque-Correa et al., 2024).

Importantly, however, the 'occupancy principle' (Holleman and White, 1989) highlights that it is not the length of the intestinal tract that determines MRT as much the volume. Yet, (gastro)intestinal volume as a functional measure raises a number of methodological and conceptual issues that may be interesting on a theoretical level, but that make the actual application of this measure in comparative studies questionable. First, gastrointestinal volume is a measure that is not purely anatomical, because it requires either ingestion of food by the animal prior to its dissection (i.e., the presence of digesta, which is quantified), or the filling of the gastrointestinal tract by an investigator, for example with water up to a certain hydrostatic pressure. Notably, these two methods do not yield identical results (Demment, 1982; Luna and Weckerly, 2013). Evidently, the gut fill due to the prior ingestion of food will depend crucially on the time that has passed since the last meal; a factor that not only applies to faunivores in which gut fill may range from empty (before a hunt) to 22 % (or more) of their body mass (Stahler et al., 2006), but also to herbivores in which the level of gut fill may vary due to season, hour of the day, or time since the last feeding (Barboza et al., 2006; Weckerly, 2010; Munn et al., 2012; Luna and Weckerly, 2013). As for true morphological measurements, such as dimensions (including surface) or mass of a gastrointestinal compartment, these cannot capture the degree of expandability of the structure, and hence its capacity to contain a volume, across species. Secondly, as mentioned above, the measure of digesta fill is physically linked to the measure of digesta retention, based on the occupancy principle that a quantity of food will be retained longer in a compartment of larger volume (Holleman and White, 1989; Munn et al., 2015). Therefore, a statistical relationship between volume and retention measures can automatically be expected.

These considerations raise a serious question for comparative morphophysiology: which measurements to include in an analysis to yield a result that is heuristically valuable not only for the sheer corroboration of a statistical form-function association, but also for additional functional insights. Considering physiological variables, for example, one can postulate that the negative relationship between intake and digesta retention (i.e., the more food is ingested, the shorter the overall mean retention time) is the default expectation, again due to the 'occupancy' principle. Then, the degree to which certain taxa correspond to this expectation or not can be used as an indication of how flexible their gut volume can react to an increased intake (Clauss et al., 2007b), including possible speculations about the selective pressures that lead to the evolution of this flexibility. As another example, the association between the physically unrelated measures of chewing efficacy and digesta retention (Clauss et al., 2009; Clauss et al., 2015) can illuminate different evolutionary digestive strategies that achieve digestive efficiency by increased particle size reduction during chewing, by increased exposure to digestive processes during longer retention times, or both. In this respect, our study confirms the concept that longer intestines are – somewhat – related to longer retention times and support previous claims that body mass is a poor predictor of digesta retention times (Clauss et al., 2007a; Steuer et al., 2011; Müller et al., 2013; Abraham et al., 2021). There are probably several reasons for this, including the fact that animals of similar body mass may have different gastrointestinal anatomies.

5. Outlook and conclusion

Whether a positive relationship between intestine length and digesta retention can be demonstrated across vertebrates remains to be investigated. In reptiles, such a comparison may be possible, given quantitative data on intestine length (Hoppe et al., 2021) and on digesta retention measurements (Lillywhite et al., 2002; Franz et al., 2011; Sadeghayobi et al., 2011; Wehrle and German, 2023). In ectothermic animals, temperature plays an integral role in determining metabolic rates, food intake and hence retention times, and thus would have to be controlled for. Given the low degree of intestine length differentiation between reptilian herbivores and faunivores (Hoppe et al., 2021) and the enormous range of retention times (e.g., ranging from 2 to 180 days in snakes) (Lillywhite et al., 2002), the relationship between intestine length and retention times may be even less clear than those in birds and mammals. For fish, a large number of intestine measures exist (Duque-Correa et al., 2024), but digesta retention measurements are particularly challenging and, to our knowledge, do not exist for large numbers of species (Horn, 1989; Clements et al., 2014).

In conclusion, the present study supports a general concept that longer intestines are related to longer digesta retention in birds and mammals. While the results underline that body mass is a poorer predictor of retention time than a physiologically more relevant measure related to the digestive tract, the remaining large degree of data scatter indicates that intestine length alone does not provide ultimate constraints on digesta passage time in endothermic animals. Further explanation is required for additional insight and implications for digestive physiology.

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CRediT authorship contribution statement

María J. Duque-Correa: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Marcus Clauss:** Writing – original draft, Supervision, Project administration, Conceptualization. **Carlo Meloro:** Writing – review & editing, Methodology, Conceptualization. **Andrew J. Abraham:** Writing – original draft, Data curation, Conceptualization.

Declaration of competing interest

The authors declare no potential conflict of interest.

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Data availability

The data is taken from open access repositories, anyone can access them.

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