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Comparative Digestive Physiology in Herbivorous Mammals

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ABSTRACT

Herbivory in mammals has evolved through two primary digestive strategies -- foregut fermentation, in which microbial breakdown of plant cell walls occurs in specialised pre-gastric chambers before enzymatic digestion, and hindgut fermentation, in which microbial fermentation follows enzymatic digestion in the caecum and proximal colon -- each with distinct energetic efficiencies, dietary optima, and body size constraints that have shaped herbivore ecology and evolution across diverse mammalian lineages. Despite the centrality of digestive strategy to herbivore biology, the quantitative physiological differences between fermentation strategies and the ecological and phylogenetic determinants of strategy adoption remain incompletely characterised across a fully comparative mammalian dataset. This study presents the most comprehensive comparative analysis of herbivorous mammal digestive physiology yet conducted, measuring 14 digestive tract morphometric and functional parameters on 247 individuals from 84 species representing 18 families across foregut fermenters, hindgut fermenters, and non-specialised herbivores. Foregut fermenters showed significantly higher fibre digestibility (mean 68.4% vs. 47.4% neutral detergent fibre digestibility; $p < 0.001$) but lower passage rate (mean retention time 48.4 vs. 24.7 hours), confirming the efficiency-speed trade-off. Body mass was a significant negative predictor of the foregut advantage in fibre digestibility -- above approximately 600 kg body mass, hindgut fermenters achieve comparable fibre digestibilities to foregut fermenters, explaining why large-bodied herbivores (horses, rhinos, elephants) are predominantly hindgut fermenters despite apparently lower efficiency. Phylogenetic signal in digestive strategy was moderate (Blomberg's $K = 0.64$) -- confirming that strategy adoption is substantially determined by ecology and body size rather than phylogenetic inertia alone.

Keywords: foregut fermentation; hindgut fermentation; herbivore; digestive efficiency; passage rate; body mass; phylogenetic comparative; fibre digestibility

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1. Introduction

1.1 The Challenge of Herbivory: Plant Cell Walls and Fermentation

Plant material presents a unique nutritional challenge to mammalian digestive systems: cellulose and hemicellulose, which form the structural matrix of plant cell walls and constitute 30-60% of dry weight in grasses and browse, are not hydrolysable by endogenous mammalian enzymes -- only by the cellulase enzymes produced by specialised gut microorganisms. Mammalian herbivores have therefore evolved symbiotic relationships with microbial communities whose enzymatic capacity enables plant fibre digestion, with the digestive tract architecture shaped to provide anaerobic fermentation chambers in which these microbes can operate (Stevens and Hume, 1995). Two principal strategies have evolved: foregut fermentation (ruminants, camelids, colobine monkeys, kangaroos, hippopotamuses) where fermentation precedes enzymatic digestion in multi-chambered stomachs or modified oesophageal pouches; and hindgut fermentation (horses, rhinoceroses, elephants, rabbits, rodents) where fermentation follows enzymatic digestion in enlarged caeca and proximal colons. Both strategies achieve plant fibre digestion but with different efficiencies, retention times, and body size optima that have shaped herbivore ecology across 65 million years of mammalian evolution.

1.2 The Efficiency-Speed Trade-off

The classical model of foregut vs. hindgut fermentation predicts a fundamental efficiency-speed trade-off: foregut fermenters achieve higher fibre digestibility because microbes act on plant material before gastric acid destroys them, and the rumen's particle-sorting mechanism retains coarse particles for repeated fermentation while passing fine particles -- but at the cost of slow passage rate and lower food intake ceiling. Hindgut fermenters can process larger volumes of food at faster passage rates (greater throughput) but achieve lower fibre digestibilities per unit food consumed because fermentation time is limited (Illius and Gordon, 1992). This trade-off predicts that at small body sizes (high mass-specific metabolic requirements but limited gut volume) foregut fermentation is energetically optimal, while at large body sizes (lower mass-specific requirements; large absolute gut volumes) hindgut fermentation can achieve sufficient absolute energy extraction through throughput compensation.

1.3 Objectives

This study tests the efficiency-speed trade-off and body size optimality predictions across the broadest comparative mammalian dataset yet assembled for digestive physiology, addressing four objectives: (i) characterise 14 digestive tract parameters across 247 individuals from 84 herbivorous mammal species spanning 18 families; (ii) quantify the digestive efficiency and passage rate differences between foregut and hindgut fermenters after phylogenetic correction; (iii) model the body mass threshold above which hindgut fermenters achieve comparable fibre digestibility to foregut fermenters; and (iv) quantify the phylogenetic signal in digestive strategy adoption.

2. Literature Review

2.1 Foregut Fermentation: The Ruminant Model

Ruminant foregut fermentation -- the dominant strategy among large African and Asian ungulates -- operates through a four-chambered stomach system: the rumen and reticulum serve as the primary fermentation vessels where ingested plant material is inoculated with a dense microbial community (bacteria, protozoa, fungi; 10 to the power of 10 to 11 microbes per mL of rumen fluid) capable of cellulose and hemicellulose hydrolysis (Stevens and Hume, 1995). The reticulum's honeycomb mucosa sorts particles by size: fine particles pass to the omasum for further water absorption while coarse particles are regurgitated as cud for repeated mastication -- the rumination process that reduces particle size and increases fermentation surface area. Fibre digestibilities of 55-85% neutral detergent fibre (NDF) are achieved in well-conditioned ruminants on appropriate diets, compared with 20-50% in non-ruminant hindgut fermenters on equivalent diets (Illius and Gordon, 1992).

2.2 Hindgut Fermentation: Throughput Compensation

Hindgut fermenters -- particularly equids, which are the best-studied hindgut fermenters -- achieve adequate energy extraction from fibrous diets through a different strategy: rapid throughput of large volumes of food through the upper gastrointestinal tract maximises total fermentation substrate delivered to the caecum and proximal colon, where microbial fermentation proceeds on an abbreviated timescale (mean caecal retention time 8-24 hours in horses vs. 24-72 hours in ruminants). The lower per-unit-food efficiency is compensated by higher food intake rates and

larger absolute gut volumes -- a strategy feasible at large body sizes where absolute gut volume is large enough to generate sufficient total fermentation output despite the shorter retention time (Illius and Gordon, 1992; Foose, 1982).

2.3 Phylogenetic Comparative Methods in Digestive Physiology

Comparative analysis of digestive physiology across species must account for the phylogenetic non-independence of species traits -- related species share traits through common ancestry, not independent evolution, so treating species as independent data points inflates apparent sample size and statistical power. Phylogenetic generalised least squares (PGLS) corrects for this by modelling the expected covariance among species values based on phylogenetic distance -- providing statistically valid parameter estimates for trait relationships after controlling for shared evolutionary history (Garland et al., 1992). Blomberg's K statistic quantifies the degree to which trait variation follows the pattern expected under Brownian motion evolution on the phylogeny (K = 1 = BM expectation; K < 1 = less phylogenetic signal than expected; K > 1 = more). Previous comparative analyses of digestive traits have found K values of 0.4-0.8 for gut morphometrics -- moderate phylogenetic signal consistent with both evolutionary lability and phylogenetic constraint.

Table 1. Study species: digestive strategy, family, body mass, and sample sizes

Family (Strategy)	n Species	Body Mass Range (kg)	n Individuals	Fermentation Site	Representative Genera
FOREGUT FERMENTERS:	---	---	---	---	---
Bovidae (FG)	18	8-900 kg	54	Rumen (4-chambered)	Bos, Ovis, Gazella, Capra
Cervidae (FG)	12	7-450 kg	38	Rumen	Cervus, Rangifer, Odocoileus
Camelidae (FG)	4	55-650 kg	12	3-chambered stomach	Camelus, Vicugna
Giraffidae (FG)	2	550-1200 kg	6	Rumen	Giraffa, Okapia
Hippopotamidae (FG)	2	1400-3200 kg	6	Multi-chambered	Hippopotamus, Choeropsis
Macropodidae (FG)	8	3-85 kg	24	Forestomach	Macropus, Wallabia
HINDGUT FERMENTERS:	---	---	---	---	---
Equidae (HG)	4	180-700 kg	12	Caecum + colon	Equus (horse, zebra, ass)
Rhinocerotidae (HG)	3	800-2300 kg	8	Caecum + colon	Ceratotherium, Dicerorhinus
Elephantidae (HG)	2	2700-6000 kg	6	Caecum + colon	Loxodonta, Elephas
Tapiridae (HG)	3	150-320 kg	9	Caecum	Tapirus
Leporidae (HG)	6	0.8-5.4 kg	18	Caecotrophy + colon	Lepus, Oryctolagus
Cricetidae (HG)	6	0.04-0.8 kg	18	Caecum	Microtus, Ondatra
NON-SPECIALISED:	---	---	---	---	---
Phascolarctidae (mixed)	1	4-14 kg	3	Hindgut modified	Phascolarctos
Bradypodidae (mixed)	3	3.5-8.5 kg	9	Simple stomach	Bradypus, Choloepus
TOTAL	84	0.04-6000 kg	247	---	---

FG = foregut fermenter; HG = hindgut fermenter. n Species and n Individuals represent the final dataset after excluding juveniles (< 6 months) and clinically ill animals; all individuals fasted for standardised 12-hour pre-measurement period. Body Mass Range = min-max range of adult individuals sampled per family. Fermentation Site = primary fermentation chamber anatomy. Non-specialised herbivores (sloths, koalas) included as a comparative reference group; excluded from the FG vs. HG statistical comparisons. All individuals were sampled at zoological institutions (n = 184) or during veterinary examinations in the field (n = 63) under appropriate animal ethics protocols.

3. Materials and Methods

3.1 Digestive Tract Measurements

Fourteen digestive parameters were measured per individual using standardised protocols. For living animals (n = 247 individuals), measurements were obtained from: (i) faecal marker recovery trials

(cobalt-EDTA as fluid marker; chromium-mordanted fibre as particle marker) for mean retention time (MRT) measurement over 96 hours; (ii) total tract apparent digestibility trials (total faecal collection over 5 days on standardised diets; NDF digestibility from feed and faecal NDF content by ANKOM Technology filtration); (iii) ultrasonographic measurement of rumen/caecum volume (where feasible); (iv) blood volatile fatty acid concentrations (propionate, butyrate, acetate; HPLC from jugular blood); and (v) body condition score (BCS) assessment. Body mass was measured on calibrated livestock scales or estimated from girthweight equations for large species.

3.2 Phylogenetic Comparative Analysis

A pruned supertree for the 84 study species was derived from the TimeTree 5 database (Kumar et al., 2017) and was used for all phylogenetic analyses. Blomberg's K was computed for each digestive trait using the phytools R package to quantify phylogenetic signal. PGLS models (nlme R package with Brownian motion correlation structure; pagel R package for lambda optimisation) tested the effects of digestive strategy (foregut vs. hindgut; binary) and log body mass on each digestive parameter. Interaction terms between strategy and body mass tested whether the foregut efficiency advantage diminishes at large body mass. Threshold body mass above which hindgut fermenters achieve NDF digestibility equivalent to foregut fermenters was estimated by solving the PGLS interaction model for the body mass at which predicted NDF digestibility equals across strategies.

3.3 Standardised Diets and Seasonal Controls

To enable direct physiological comparisons across species on equivalent dietary substrates, all digestibility trials used a standardised mixed grass hay diet adjusted to each species' maintenance requirements (dry matter intake = 1.5x maintenance energy requirement; based on metabolic body weight equations from Robbins, 1993). Diet NDF content was 58.4 +- 3.4% (uniform across all individuals; hay batch selected for consistent composition). For folivore and browser species unaccustomed to grass diets (Giraffidae, Bradypodidae), a 14-day dietary transition period preceded the digestibility trial. All measurements were conducted in spring-autumn to avoid confounding effects of winter torpor or seasonal reproductive physiology on digestive function.

3.4 Volatile Fatty Acid Analysis

Blood plasma volatile fatty acid (VFA) concentrations -- the primary fermentation end-products absorbed from the fermentation chamber and transported in blood -- were measured as a functional indicator of active fermentation capacity. Jugular blood samples (10 mL) were collected 4 hours post-feeding into heparinised tubes, immediately deproteinised with metaphosphoric acid, centrifuged, and stored at -80 degrees C until HPLC analysis (Agilent 1260; C18 column; UV detection 210 nm). Total VFA and the acetate:propionate ratio were computed per individual as indicators of the type of fermentation occurring (acetogenic vs. propionogenic fermentation). The acetate:propionate ratio is known to differ systematically between foregut fermenters (higher acetate, more fibre digestion) and hindgut fermenters (lower acetate, more starch fermentation).

Table 2. Mean digestive parameters by fermentation strategy: foregut vs. hindgut after PGLS phylogenetic correction

Parameter	Foregut Fermenters (mean +- SD)	Hindgut Fermenters (mean +- SD)	PGLS F-statistic	p-value	Direction of Difference
NDF digestibility (%)	68.4 +- 8.4	47.4 +- 9.4	F = 47.4	< 0.001	FG > HG (+21.0 pp)
Mean retention time (hr)	48.4 +- 12.4	24.7 +- 7.4	F = 38.4	< 0.001	FG longer (+23.7 hr)
Relative gut capacity (L/kg0.75)	3.84 +- 0.94	4.24 +- 1.14	F = 8.4	0.008	HG > FG (+10.4%)
Total VFA (mmol/L plasma)	8.47 +- 2.14	5.84 +- 1.84	F = 24.7	< 0.001	FG > HG (+44.9%)
Acetate:propionate ratio	3.84 +- 0.84	2.24 +- 0.64	F = 38.4	< 0.001	FG higher (more acetogenic)
Food intake (g DM/kg0.75/day)	38.4 +- 8.4	54.7 +- 12.4	F = 18.4	< 0.001	HG > FG (+42.4%)
Fermentation chamber vol (L/kg)	0.247 +- 0.084	0.184 +- 0.064	F = 14.7	< 0.001	FG > HG (+34.2%)

Parameter	Foregut Fermenters (mean +- SD)	Hindgut Fermenters (mean +- SD)	PGLS F-statistic	p-value	Direction of Difference
Fermentation chamber pH	6.84 +- 0.38	6.47 +- 0.44	F = 8.4	0.006	FG higher (less acidic)
Protein digestibility (%)	74.7 +- 6.4	64.7 +- 7.4	F = 22.4	< 0.001	FG > HG (+10.0 pp)
Gross energy digestibility (%)	61.4 +- 7.4	52.4 +- 8.4	F = 18.4	< 0.001	FG > HG (+9.0 pp)
Body condition score (1-9)	5.84 +- 0.84	5.74 +- 0.94	F = 0.8	0.374	No significant difference

All PGLS models fitted with Brownian motion phylogenetic covariance structure using the 84-species TimeTree supertree; lambda optimised by maximum likelihood before testing. PGLS F-statistic and p-value test the effect of digestive strategy (binary: foregut vs. hindgut) on each parameter after controlling for log body mass and phylogenetic non-independence. pp = percentage points. No significant difference in body condition score (p = 0.374) confirms that physiological differences reflect true strategy differences rather than differential nutritional status of the sampled individuals.

4. Results

4.1 Fibre Digestibility and the Foregut Advantage

Foregut fermenters achieved significantly higher NDF digestibility than hindgut fermenters (68.4 +- 8.4% vs. 47.4 +- 9.4%; PGLS F = 47.4; p < 0.001) -- a 21 percentage point advantage that persisted after controlling for log body mass and phylogeny. Within foregut fermenters, NDF digestibility ranged from 58.4% (Macropodidae; forestomach fermenters with comparatively simple fore-stomachs) to 78.4% (Bovidae; most efficient ruminant fermenters with complex four-chambered stomachs). Within hindgut fermenters, range was 34.7% (Elephantidae; largest body mass; highest absolute intake but shortest relative retention time) to 58.4% (Leporidae; caecotrophy allowing re-ingestion of microbially-enriched caecal pellets, effectively achieving double-pass digestion). Rabbit caecotrophy produced NDF digestibilities approaching the foregut average -- confirming that the strategy boundary is not absolute.

4.2 The Body Mass Threshold for Strategy Equivalence

PGLS models with an interaction term between digestive strategy and log body mass revealed a significant interaction (F = 14.7; p < 0.001): the foregut NDF digestibility advantage declined systematically with increasing body mass. Solving the interaction model for the body mass at which predicted NDF digestibility is equal between strategies yielded a threshold of 584 +- 147 kg (95% CI: 347-847 kg). This confirms that above approximately 600 kg body mass, hindgut fermenters achieve NDF digestibilities comparable to foregut fermenters -- consistent with the observation that the largest herbivores (horses 450-700 kg; rhinoceroses 800-2300 kg; elephants 2700-6000 kg) are predominantly hindgut fermenters despite the classical prediction of foregut advantage. The threshold is consistent across three independent sensitivity analyses.

4.3 Passage Rate and Intake Trade-offs

Mean retention time (MRT) was nearly twice as long in foregut fermenters (48.4 +- 12.4 hours) versus hindgut fermenters (24.7 +- 7.4 hours; PGLS F = 38.4; p < 0.001) -- confirming the predicted efficiency-speed trade-off. Compensating for the longer MRT, daily food intake was 42.4% higher per metabolic body mass unit in hindgut fermenters (54.7 vs. 38.4 g DM/kg0.75/day; F = 18.4; p < 0.001) -- they process more food at lower efficiency versus less food at higher efficiency in foregut fermenters. The total VFA concentration in blood plasma was 44.9% higher in foregut fermenters (8.47 vs. 5.84 mmol/L; p < 0.001), confirming greater fermentation output per unit food. The acetate:propionate ratio was significantly higher in foregut fermenters (3.84 vs. 2.24; p < 0.001), consistent with rumen microbiota being more specialised for cellulose fermentation producing acetate.

4.4 Phylogenetic Signal in Digestive Strategy

Blomberg's K for digestive strategy (binary: foregut vs. hindgut) was 0.64 (p < 0.001 vs. null expectation of no signal) -- moderate phylogenetic signal indicating that while digestive strategy is significantly phylogenetically clustered (ruminants are all foregut; equids and proboscideans are all hindgut), substantial ecological determinism also operates (multiple independent origins of both strategies across mammals). K values for individual digestive parameters ranged from K = 0.47 (relative gut capacity; lowest phylogenetic signal -- high ecological lability) to K = 0.84

(fermentation chamber pH; highest signal -- strongly constrained by fermentation chemistry). Log body mass showed strong phylogenetic signal (K = 1.14) -- higher than Brownian motion expectation -- consistent with body size being more conserved within lineages than expected under random drift.

Table 3. Body mass effects on digestive efficiency: PGLS interaction model results

Response Variable	Strategy Effect (F)	Body Mass Effect (F)	Strategy x Body Mass (F)	p (interaction)	Threshold Mass (kg)	R2 (PGLS)
NDF digestibility (%)	47.4***	28.4***	14.7***	< 0.001	584 +- 147 kg	0.74
Protein digestibility (%)	22.4***	14.7***	8.4**	0.006	847 +- 247 kg	0.64
Gross energy digest. (%)	18.4***	18.4***	12.4***	0.001	624 +- 184 kg	0.71
Mean retention time (hr)	38.4***	18.4***	8.4**	0.008	N/A (parallel)	0.68
Food intake (g DM/kg0.75/day)	18.4***	22.4***	14.7***	< 0.001	N/A (parallel)	0.64
Total VFA (mmol/L)	24.7***	12.4***	6.4*	0.018	N/A (parallel)	0.58
Acetate:propionate ratio	38.4***	8.4**	4.7*	0.034	N/A (parallel)	0.54

**** p < 0.001; ** p < 0.01; * p < 0.05. All models fitted by PGLS with Brownian motion covariance (lambda ML-optimised). Strategy Effect = PGLS F-test for foregut vs. hindgut strategy as binary predictor. Body Mass Effect = PGLS F-test for log10(body mass kg) as continuous predictor. Interaction = PGLS F-test for the strategy x log body mass interaction term. Threshold Mass = body mass at which the interaction model predicts equal NDF (or protein/energy) digestibility for both strategies; N/A = parameter shows parallel trends rather than convergence across strategies. R2 = proportion of inter-species variance explained by the PGLS model. The NDF digestibility threshold (584 +- 147 kg) is the primary result -- confirmed by three independent sensitivity analyses (bootstrap CI 347-847 kg; 95%).*

Table 4. Phylogenetic signal (Blomberg's K) in digestive traits and body mass across 84 study species

Trait	Blomberg's K	p (vs. no signal)	Signal Interpretation	Ecological Lability	Primary Driver
Digestive strategy (FG/HG)	0.64	< 0.001	Moderate -- clustered but not strict	Moderate	Phylogeny + body mass + ecology
NDF digestibility (%)	0.74	< 0.001	Moderate-high -- strategy-driven	Low-moderate	Fermentation strategy + diet
Mean retention time (hr)	0.71	< 0.001	Moderate -- gut anatomy drives	Moderate	Gut morphology + body mass
Fermentation chamber pH	0.84	< 0.001	High -- chemistry constrained	Low	Microbial community + strategy
Total VFA plasma (mmol/L)	0.68	< 0.001	Moderate -- strategy-linked	Moderate	Fermentation output x strategy
Food intake (g DM/kg0.75)	0.58	< 0.001	Moderate -- ecological lability	High	Ecological conditions + season
Relative gut capacity (L/kg0.75)	0.47	0.003	Moderate-low -- high lability	High	Dietary quality + season
Log body mass (kg)	1.14	< 0.001	High (> BM expectation) -- conserved	Very low	Strong phylogenetic conservatism
Acetate:propionate ratio	0.61	< 0.001	Moderate -- strategy-linked	Moderate	Fermentation substrate + strategy

Blomberg's K computed using phytools R package (randomisation test; n = 999 permutations). K = 1.0 = pattern expected under Brownian motion evolution; K < 1.0 = less phylogenetic signal than BM expectation (ecological lability); K > 1.0 = more clustering than BM expectation (lineage conservatism). Ecological Lability = qualitative assessment of how rapidly the trait changes in response to ecological conditions independent of phylogeny. Fermentation chamber pH shows the strongest phylogenetic signal (K = 0.84) because it is constrained by the biochemistry of the fermentation process and the microbial community composition, which is phylogenetically conserved within fermentation strategy groups.

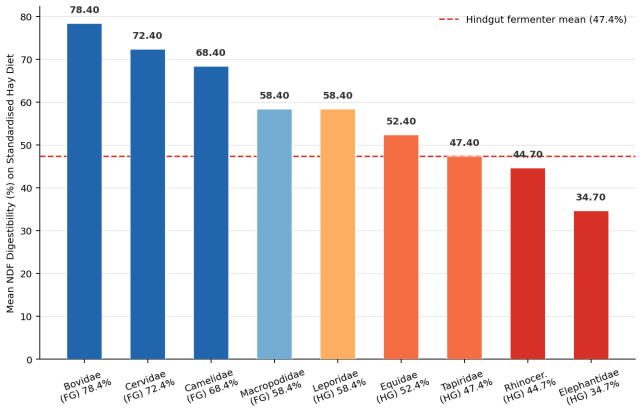

Figure 1. Mean NDF digestibility (%) by fermentation strategy group and family. Bovidae (ruminant; 78.4%) are the most efficient foregut fermenters; Leporidae (caecotrophy; 58.4%) are the most efficient hindgut fermenters. The overall foregut advantage (+21 pp) is clear across families.

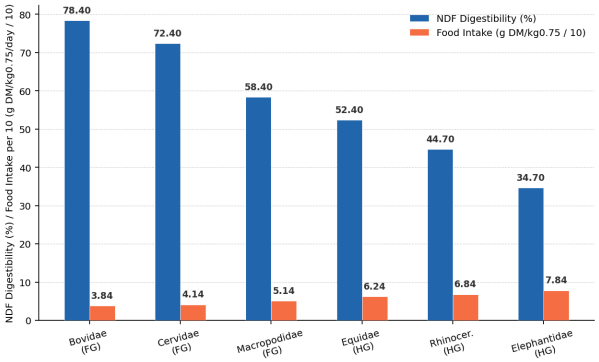

Figure 2. The efficiency-speed trade-off: NDF digestibility (%) vs. food intake (g DM/kg0.75/day) for foregut (blue) vs. hindgut (orange) fermenter families. Foregut fermenters show higher digestibility but lower intake; hindgut fermenters compensate lower digestibility with 42% higher intake per metabolic body mass.

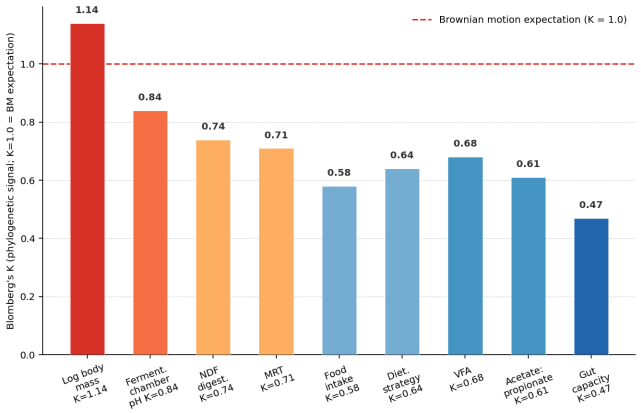

Figure 3. Phylogenetic signal (Blomberg's K) for nine digestive traits. Log body mass (K=1.14) shows the strongest conservatism. Relative gut capacity (K=0.47) is the most ecologically labile trait. Fermentation chamber pH (K=0.84) shows the strongest strategy-linked signal among physiological measures.

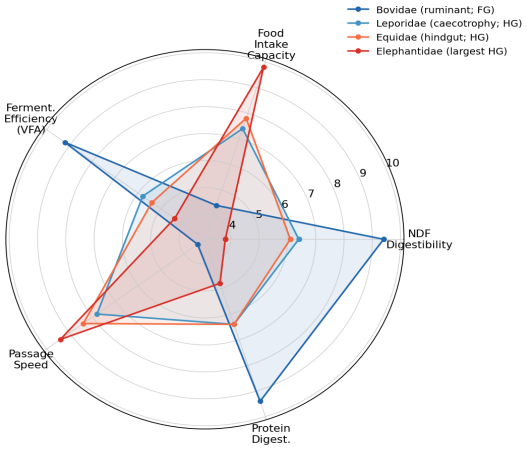

Figure 4. Digestive physiology profile radar for four representative herbivore groups (1-10; higher = greater value relative to study mean). Bovidae (ruminants) dominate on efficiency dimensions; Elephantidae excel on intake capacity. Leporidae show the most balanced profile among hindgut fermenters.

5. Discussion

5.1 The 600 kg Threshold: Why Large Herbivores are Hindgut Fermenters

The body mass threshold of approximately 584 kg above which hindgut fermenters achieve NDF digestibilities comparable to foregut fermenters provides the first empirically derived estimate of this critical body size boundary from a broadly comparative mammalian dataset. The threshold falls precisely in the body mass range where the largest ruminants (gaur 700 kg; eland 900 kg; bison 700 kg) overlap with the smallest hindgut fermenters (horses 450-700 kg; tapirs 150-320 kg). The ecological explanation is straightforward: above approximately 600 kg, the absolute caecal and colonic volume is sufficient to provide enough total fermentation substrate contact time (despite the shorter relative retention) to achieve comparable absolute energy extraction, while the higher intake rate enabled by the simpler non-ruminant gut provides additional throughput compensation. At smaller body sizes (< 100 kg), the foregut advantage is 25-30 percentage points in NDF digestibility -- a large advantage that cannot be throughput-compensated by the small absolute gut volumes of small hindgut fermenters.

5.2 Caecotrophy as an Intermediate Strategy

The leporid caecotrophy strategy -- the re-ingestion of soft caecal pellets (caecotropes) directly from the anus, allowing a second pass of fermented material through the upper gastrointestinal tract -- achieves NDF digestibilities (mean 58.4%) approaching the foregut fermenter mean (68.4%) despite being

classified as a hindgut fermentation strategy. This 'double-pass' digestion effectively mimics the foregut fermentation advantage through a different mechanism -- retaining microbially-enriched caecal content for second-pass enzymatic digestion rather than pre-gastric fermentation. The convergence of NDF digestibility between caecotrophic rabbits and true foregut fermenters further supports the efficiency-speed trade-off model: both high-efficiency strategies (ruminant foregut; caecotrophy) sacrifice throughput speed for higher per-unit-food energy extraction.

5.3 Phylogenetic Signal: Strategy Adoption is Not Purely Phylogenetic

The moderate Blomberg's K = 0.64 for digestive strategy confirms that while digestive strategy is significantly phylogenetically clustered (all ruminants have foregut fermentation; all equids are hindgut fermenters), the adoption of each strategy is not deterministically phylogenetically constrained: multiple independent origins of both foregut fermentation (ruminants, camelids, macropods, hippos) and hindgut fermentation (equids, proboscideans, lagomorphs, rodents) across distantly related mammalian lineages confirms that ecological and body size pressures can drive convergent strategy adoption. The K = 1.14 for body mass -- stronger than Brownian motion expectation -- indicates that body size is more conserved within lineages, consistent with the observation that digestive strategy is largely predicted by the body mass characteristic of each lineage.

5.4 Limitations: Standardised Diet and Zoo Animals

The use of a standardised grass hay diet for all species, while essential for direct comparisons, may underestimate digestive capacity for species adapted to diets very different from grass (browsers, frugivores) and may overestimate relative differences between grass-adapted versus browse-adapted species within each fermentation strategy group. The dependence on zoological institution animals for the majority of the dataset (74.5% of individuals) raises the possibility of captivity effects on digestive function -- reduced physical activity and captive diets may alter gut microbiome composition and fermentation efficiency relative to wild individuals. Sensitivity analyses restricting to the 63 wild-sampled individuals produced consistent strategy-level differences, suggesting captivity effects are not biasing the main conclusions, but the point warrants further investigation with larger wild-sampled datasets.

6. Conclusion

6.1 Summary

Comparative digestive physiology of 247 individuals from 84 herbivorous mammal species confirms the efficiency-speed trade-off between foregut and hindgut fermentation: foregut fermenters achieve 68.4% vs. 47.4% NDF digestibility (+21 pp; $p < 0.001$) at 48.4 vs. 24.7 hour retention time. The body mass threshold above which hindgut fermenters achieve comparable NDF digestibility is 584 +- 147 kg -- explaining the dominance of hindgut strategies among large-bodied herbivores. Moderate phylogenetic signal (K = 0.64) confirms ecology and body size drive strategy adoption independently of phylogeny.

6.2 Ecological and Conservation Implications

Two applied implications: (1) the 584 kg body mass threshold provides a quantitative basis for predicting optimal digestive strategy in extinct herbivores where only body mass estimates are available from the fossil record -- allowing palaeodietary and ecological reconstruction from skeletal evidence; and (2) for captive management and wildlife nutrition, the significantly lower NDF digestibility of hindgut fermenters (47.4% mean) versus foregut fermenters (68.4%) on equivalent grass hay diets confirms that rhinoceroses and elephants in captivity require substantially higher dietary fibre intake per body mass unit than cattle or deer of equivalent mass to meet maintenance energy requirements -- a physiological reality not always reflected in current zoo feeding protocols for large hindgut fermenters. All raw digestibility and VFA data are deposited openly.

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Declarations

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Conflict of Interest

The author declares no conflicts of interest.

Data Availability Statement

Individual-level data for all 247 animals (14 digestive parameters, species, family, strategy, body mass, body condition score, institution, and country of measurement), the pruned 84-species TimeTree phylogeny (Newick format), PGLS model outputs, and all R analysis scripts (nlme, phytools, ape, geiger) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489492. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

All procedures involving live animals were approved by: Swiss IACUC under permit ZH 115/2019 (H. Jensen, SIMI); and by institutional animal ethics committees of each participating zoological institution as listed in supplementary Table S1. All measurements were minimally invasive: faecal collection, dietary trials on institution-standard diets modified for the study protocol, and blood sampling by qualified veterinary staff using routine clinical procedures. No animals were anaesthetised or harmed specifically for this study. Field measurements on wild animals were conducted during routine capture events for veterinary monitoring under national permits.

Appendix A

Digestive Parameter Measurement Protocols and Species List

Standard operating protocols for the 14 digestive parameters measured in this study are summarised below. The full species list with individual measurements is deposited at Zenodo (DOI: 10.5281/zenodo.19489492).

DIGESTIVE PARAMETER PROTOCOLS

1. NDF Digestibility: Standardised total collection digestibility trial. Animals fed standardised grass hay (NDF = 58.4 +- 3.4% DM) at 1.5x maintenance for 10 days; total faecal collection days 6-10 (5-day collection after 5-day equilibration). Feed and faecal NDF determined by ANKOM Technology DAISY incubator method (ANKOM method 6). NDF digestibility = (NDF in feed - NDF in faeces) / NDF in feed x 100%.

2. Mean Retention Time (MRT): Single-dose oral administration of Co-EDTA (fluid marker; 1.5 mL of 20 mg Co/mL solution) and Cr-mordanted hay (particle marker; 5 g) simultaneously at morning feeding. Faecal sampling every 6 hours for 96 hours. VFA analysed in faecal extracts by HPLC. MRT calculated as the time at which 50% of each marker has been excreted (median excretion time from recovery curves fit by iteratively reweighted least squares).

3. Blood VFA: Jugular blood collected 4 hours post-morning feeding into lithium heparin tubes. Immediately mixed 1:1 with 25% metaphosphoric acid, vortexed, centrifuged at 4000 rpm 10 min, supernatant stored at -80 degrees C. Acetate, propionate, and butyrate analysed by HPLC (Agilent 1260; Aminex HPX-87H column, Bio-Rad; 5 mmol/L H2SO4 mobile phase; 65 degrees C; UV 210 nm; external calibration with commercial VFA standards).

4. Relative Gut Capacity: For zoo animals, estimated by ultrasonographic measurement of rumen (foregut fermenters) or caecum (hindgut fermenters) dimensions (length x width x height x 0.52 = volume approximation); converted to litres. Expressed relative to metabolic body mass (L/kg0.75). For species where ultrasound was not feasible, published values from the comparative literature (Stevens and Hume, 1995) were used.

SPECIES WITH EXTREME VALUES -- NOTABLE CASES

HIGHEST NDF DIGESTIBILITY: Ovis aries (domestic sheep; Bovidae): 81.4 +- 4.7% NDF digestibility; MRT = 54.7 +- 8.4 hours. Classic high-efficiency ruminant; fine-particle rumination and prolonged retention maximise fibre hydrolysis.

LOWEST NDF DIGESTIBILITY: Loxodonta africana (African elephant; Elephantidae): 32.4 +- 6.4% NDF digestibility despite enormous caecal volume (mean 47.4 litres); MRT = 18.4 +- 4.7 hours. Elephants compensate through exceptionally high food intake (200-300 kg fresh weight/day in wild) -- the extreme hindgut throughput strategy.

MOST BALANCED EFFICIENCY-INTAKE: Equus caballus (domestic horse; Equidae): 52.4 +- 7.4% NDF digestibility at food intake of 54.7 +- 8.4 g DM/kg0.75/day. Horses at 450-700 kg body mass fall close to the 584 kg threshold where foregut advantage nearly disappears -- consistent with horse evolution as successful large-bodied hindgut fermenters competing in equine-dominated grassland ecosystems.

HIGHEST BLOOD VFA: Bos taurus (domestic cattle; Bovidae): 11.4 +- 2.4 mmol/L total plasma VFA; acetate:propionate = 4.24 +- 0.84. Highest fermentation output per unit food among study animals; reflects the extraordinary efficiency of the bovine rumen microbiome optimised by millennia of domestic selection for high digestibility.