Digestive efficiency for protein and fat in mammals of different trophic guilds and digestive strategies

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RESEARCH ARTICLE

Carnivorous Mammals: Nutrient Digestibility and Energy Evaluation

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Estimating the energy content is the first step in diet formulation, as it determines the amount of food eaten and hence the concentration of nutrients required to meet the animal’s requirements. Additionally, being able to estimate the energy content of a diet empirically known to maintain body condition in an animal will facilitate an estimation of maintenance energy requirements. We collated data on nutrient composition of diets fed to captive wild canids, felids, hyenas, mustelids, pinnipeds, and urids and the digestibility coefficients from the literature (45 species, 74 publications) to test whether differences in protein and fat digestibility could be detected between species groups, and whether approaches suggested for the estimation of dietary metabolizable energy (ME) content in domestic carnivores (NRC 2006) Nutrient requirements of dogs and cats. Washington, DC: National Academy Press.) can be applied to wild carnivores as well. Regressions of digestible protein or fat content vs. the crude protein (CP) or fat content indicated no relevant differences in the digestive physiology between the carnivore groups. For diets based on raw meat, fish, or whole prey, applying the calculation of ME using “Atwater factors” (16.7 kJ/g CP; 16.7 kJ/g nitrogen-free extracts; 37.7 kJ/g crude fat) provided estimates that compared well to experimental results. This study suggests that ME estimation in such diets is feasible without additional digestion trials. For comparative nutrition research, the study implicates that highly digestible diets typically fed in zoos offer little potential to elucidate differences between species or carnivore groups, but research on diets with higher proportions of difficult-to-digest components (fiber, connective tissues) is lacking. Zoo Biol 29:687–704, 2010.
Nutrient content and digestibility

plotting of apparent digestibility vs. nutrient content

from Clauss et al. (2010)
Lucas Plots

plotting of digestible nutrient content vs. nutrient content

from Clauss et al. (2010)
Lucas Plots

plotting of digestible nutrient content vs. nutrient content

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plotting of digestible nutrient content vs. nutrient content

intercept: endogenous losses

dig. Crude protein (% DM)

slope: ‘true digestibility’

Crude protein (% DM)

from Clauss et al. (2010)
Lucas Plots

plotting of digestible nutrient content vs. nutrient content

slope: ‘true digestibility’

intercept: endogenous losses

from Clauss et al. (2010)
Lucas Plots

plotting of digestible nutrient content vs. nutrient content

intercept: endogenous losses

slope: 'true digestibility'

endogenous losses
- per unit DM intake?
- per unit MBW?

from Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Protein digestion

dig. Crude protein (% DM)

Crude protein (% DM)

from Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Protein digestion

![Diagram showing protein digestion](image)

- **Domestic cat**
- **Domestic dog**
- **Canids**
- **Felids**
- **Hyenids**
- **Mustelids**
- **Pinnipeds**

From Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Protein digestion

from Clauss et al. (2010)
Fat digestion

from Clauss et al. (2010)
Fat digestion

[Graph showing the digestibility of ether extracts (% DM) for Domestic cat and Domestic dog.

From Clauss et al. (2010)]
Fat digestion

From Clauss et al. (2010)
Fat digestion

from Clauss et al. (2010)
Fat digestion

from Clauss et al. (2010)
Fat digestion

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Fat digestion

from Clauss et al. (2010)
Fat digestion

from Clauss et al. (2010)
... but:

How do herbivores fit in?
Material and Methods

Literature research (268 individual publications)
Data collection in EXCEL spreadsheet

Species ($n = 157$)
Trophic guild (carni-/omni-/herbivore)
Digestion type
Nutrient composition
  - Crude protein CP
  - Ether extracts EE

... and the corresponding intake and apparent digestibility (aD) data
Hindgut Fermentation - Colon

Zebra
(Equus burchelli)
Body Length: 2 m

Rhinoceros
(Diceros bicornis)
Body Length: 3.2 m

African Elephant
(Loxodonta africana)
Body Length: 3.3 m

from Stevens & Hume (1995)
Hindgut Fermentation - Caecum

from Stevens & Hume (1995)
Foregut Fermentation - Nonruminants

from Stevens & Hume (1995)
Foregut Fermentation - Ruminants

from Stevens & Hume (1995)
Predictions: Trophic Guilds

digestible nutrient (%DM)

nutrient (%DM)
Predictions: Trophic Guilds

digestible nutrient (%DM) vs. nutrient (%DM)
Predictions: Trophic Guilds

less microbial fermentation in **carnivores**, i.e. less metabolic faecal losses of protein and lipids than **herbivores**
Predictions: Trophic Guilds

less microbial fermentation in **carnivores**, i.e. less metabolic faecal losses of protein and lipids than **herbivores**

lower true digestibility in **herbivores**, e.g. due to fibre-bound nitrogen in feeds
Predictions: Trophic Guilds

because microbes consist of both proteins and lipids, parallel patterns for protein and fat are expected

less microbial fermentation in carnivores, i.e. less metabolic faecal losses of protein and lipids than herbivores

lower true digestibility in herbivores, e.g. due to fibre-bound nitrogen in feeds
Predictions: Herbivore Strategies

digestible nutrient (%DM)

nutrient (%DM)
Predictions: Herbivore Strategies

High metabolic losses in non-corpophagic hindgut fermenters
Predictions: Herbivore Strategies

- High metabolic losses in non-coprophagous hindgut fermenters
- Less metabolic losses in coprophagous hindgut fermenters

Graph showing the relationship between digestible nutrient (%DM) and nutrient (%DM).
Predictions: Herbivore Strategies

High metabolic losses in non-corpophagic hindgut fermenters.

Less metabolic losses in coprophagic hindgut fermenters.

Foregut fermenters (whether nonruminant or ruminant) in between.
Predictions: Herbivore Strategies

Because microbes consist of both proteins and lipids, parallel patterns for protein and fat are expected:

- High metabolic losses in non-corpophagic hindgut fermenters.
- Less metabolic losses in coprophagic hindgut fermenters.
- Foregut fermenters (whether nonruminant or ruminant) in between.

Digestible nutrient (%DM) vs. nutrient (%DM)
Protein digestion

- CP (%)
- dCP (%DM)

Herbivore
Omnivore
Carnivore
Protein digestion

[Graph showing the relationship between CP (% DM) and dCP (%)]

- Herbivore
- Omnivore
- Carnivore
Protein digestion

The graph illustrates the protein digestion efficiency across different percentages of dietary protein (CP) for herbivores, omnivores, and carnivores. The x-axis represents CP (% DM) and the y-axis represents dCP (%). The data points are color-coded to distinguish between herbivores (blue), omnivores (orange), and carnivores (brown). The graph shows a trend where higher CP percentages correlate with increased dCP values, indicating better protein digestion efficiency in carnivores compared to herbivores and omnivores.
Protein digestion

- dCP (%) vs. CP (%DM)
- Protein digestion graph showing the relationship between digestible crude protein (dCP) and crude protein (CP) for different dietary compositions.
Protein digestion

![Graph showing the relationship between dCP (%DM) and CP (%DM) for different dietary types: Herbivore, Omnivore, and Carnivore. The graph indicates a strong positive correlation across the dietary categories.](image-url)
Protein digestion

- dCP (%DM)
- CP (%DM)

- Herbivore
- Omnivore
- Carnivore
Protein digestion

- dCP = 0.87 [0.85, 0.88] CP – 2.9 [-3.1, -2.7]
- Herbivore
- Omnivore
- Carnivore

- dCP = 0.95 [0.94, 0.97] CP – 3.7 [-4.3, -3.1]
Protein digestion

![Graph showing the relationship between CP and dCP for different herbivorous species.](image-url)
Protein digestion

- Protein digestion is illustrated in the graph, showing the relationship between dCP (%DM) and CP (%DM) for different categories of animals, including Herbivores and Primates.
Protein digestion

![Graph showing protein digestion with different animal groups represented by different markers.](image-url)
Protein digestion

- Hindgut fermenter non-coprophagic
- Hindgut fermenter coprophagic
- Foregut fermenter non-ruminant
- Foregut fermenter ruminant
Protein digestion

- Hindgut fermenter non-coprophagric
- Hindgut fermenter coprophagric
- Foregut fermenter non-ruminant
- Foregut fermenter ruminant
Protein digestion

- Hindgut fermenter non-coprophagic
  - dCP = 0.82 [0.79,0.85] CP – 2.2 [-2.6,-1.8]

- Hindgut fermenter coprophagic
  - dCP = 0.93 [0.89,0.96] CP – 3.9 [-4.4,-3.3]

- Foregut fermenter non-ruminant
- Foregut fermenter ruminant
Protein digestion

- Hindgut fermenter non-coprophagic: $dCP = 0.82$ [0.79, 0.85] $CP - 2.2$ [-2.6, -1.8]
- Hindgut fermenter coprophagic: $dCP = 0.93$ [0.89, 0.96] $CP - 3.9$ [-4.4, -3.3]
- Foregut fermenter non-ruminant: $dCP = 0.86$ [0.82, 0.90] $CP - 2.3$ [-2.8, -1.8]
Protein digestion

- Hindgut fermenter non-coprophagic
- Hindgut fermenter coprophagic
- Foregut fermenter non-ruminant
- Foregut fermenter ruminant

- dCP = 0.82 [0.79,0.85] CP – 2.2 [-2.6,-1.8]
- dCP = 0.93 [0.89,0.96] CP – 3.9 [-4.4,-3.3]
- dCP = 0.86 [0.82,0.90] CP – 2.3 [-2.8,-1.8]
- dCP = 0.89 [0.87,0.92] CP – 3.4 [-3.7,-3.1]
Dietary CP is the main determinant of across-species CP digestibility.

Similar levels of endogenous/metabolic protein losses between herbivores and carnivores.

Lower true protein digestibility in herbivores – possibly linked to higher indigestible N levels in plant-based diets.

No evident difference between herbivore digestion types.
Fat digestion

- Herbivore
- Omnivore
- Carnivore

Fat digestion

EE (%DM)

dEE (%DM)

EE (%DM)
Fat digestion

- Herbivore
- Omnivore
- Carnivore

Fat digestion (dEE (%DM)) vs. energy efficiency (EE (%DM))
Fat digestion
Fat digestion

The graph shows the relationship between EE (Energy Expenditure) as a percentage of dry matter (DM) and dEE (Energy Efficiency) as a percentage of DM. The data is color-coded for different feeding modes:

- Green dots represent Herbivores
- Blue dots represent Omnivores
- Orange dots represent Carnivores

The x-axis represents EE (%DM) ranging from 0 to 80, while the y-axis represents dEE (%DM) ranging from -60 to 100. The graph illustrates how energy efficiency changes with energy expenditure for different feeding modes.
Fat digestion

- Herbivore
- Omnivore
- Carnivore

Graph showing the relationship between EE (%DM) and dEE (%DM) for different diet types.
Herbivore
Omnivore
Carnivore

\[ \text{dEE} = 0.87 \ [0.85, 0.88] \ EE - 0.95 \ [-1.00, -0.89] \]

\[ \text{dEE} = 0.94 \ [0.92, 0.95] \ EE - 0.22 \ [-0.55, 0.11] \]
Fat digestion

- Hindgut fermenter
  - non-coprophagic
  - coprophagic
- Foregut fermenter
  - non-ruminant
  - ruminant
Fat digestion

- Hindgut fermenter non-coprophagic
- Hindgut fermenter coprophagic
- Foregut fermenter non-ruminant
- Foregut fermenter ruminant

**Graph:

- dEE (%DM) vs. EE (%DM)
- Data points for different types of fermenters are differentiated by color:
  - Light blue for Hindgut fermenters, non-coprophagic
  - Pink for Hindgut fermenters, coprophagic
  - Cyan for Foregut fermenters, non-ruminant
  - Dark blue for Foregut fermenters, ruminant

The graph shows a trend where EE (%DM) increases with dEE (%DM), with distinct clusters for each type of fermenter.
Fat digestion

- Hindgut fermenter non-coprophagic: $dEE = 0.92 [0.87, 0.95]$ EE $= -1.55 [-1.81, -1.39$
- Hindgut fermenter coprophagic: $dEE = 0.89 [0.86, 0.92]$ EE $= -0.72 [-0.86, -0.58]$

Foregut fermenter non-ruminant
Foregut fermenter ruminant
Fat digestion

- Hindgut fermenter non-coprophagic: $d\text{EE} = 0.92 \ [0.87, 0.95] \ EE - 1.55 \ [-1.81, -1.39]$

- Hindgut fermenter coprophagic: $d\text{EE} = 0.89 \ [0.86, 0.92] \ EE - 0.72 \ [-0.86, -0.58]$

- Foregut fermenter non-ruminant: $d\text{EE} = 0.60 \ [0.50, 0.70] \ EE - 0.03 \ [-3.18, 0.27]$

- Foregut fermenter ruminant: $d\text{EE} = 0.89 \ [0.86, 0.92] \ EE - 0.72 \ [-0.86, -0.58]$
Fat digestion

- Hindgut fermenter non-coprophagic: $d\text{EE} = 0.92 \ [0.87, 0.95]$  $\text{EE} - 1.55 \ [-1.81, -1.39]$
- Hindgut fermenter coprophagic: $d\text{EE} = 0.89 \ [0.86, 0.92]$  $\text{EE} - 0.72 \ [-0.86, -0.58]$
- Foregut fermenter non-ruminant: $d\text{EE} = 0.60 \ [0.50, 0.70]$  $\text{EE} - 0.03 \ [-3.18, 0.27]$
- Foregut fermenter ruminant: $d\text{EE} = 0.78 \ [0.76, 0.80]$  $\text{EE} - 0.62 \ [-0.67, -0.56]$
Conclusions Fat

Dietary EE is the main determinant of across-species EE digestibility.

Higher levels of endogenous/metabolic lipid losses in herbivores compared to carnivores.

No evident difference between herbivore digestion types with respect to metabolic losses.

Lower true EE digestibility in foregut fermenting herbivores – possibly linked to foregut lipid production and hydrogenation.
What does the literature say?
What does the literature say?

no difference in true protein digestibility between trophic guilds
What does the literature say?

no difference in true protein digestibility between trophic guilds

no difference in true protein/fat digestion between foregut-fermenting peccaries and hindgut-fermenting pigs
What does the literature say?

- No difference in true protein digestibility between trophic guilds.
- No difference in true protein/fat digestion between foregut-fermenting peccaries and hindgut-fermenting pigs.
- No difference in metabolic faecal nitrogen between different herbivore digestion types.
What does the literature say?

- No difference in true protein/fat digestion between foregut-fermenting peccaries and hindgut-fermenting pigs.
- No difference in true protein digestibility between trophic guilds.
- No difference in metabolic faecal nitrogen between different herbivore digestion types.
- No difference in true protein/fat digestibility between coprophagic rodents/rabbits and horses.
Similar endogenous/metabolic losses of N occur across the trophic guilds, which are

- excreted as N-substances in carnivores and not ‘so much’ as microbial matter

- bound matter into microbial matter that includes also lipids in herbivores – hence their higher endogenous lipid losses.
Metabolic losses, as measured by CP and EE, do not differ between herbivore digestive strategies.

Digestive anatomy and physiology do not represent constraints with respect to CP and EE digestion, which could evolve to similar efficiencies across mammals.

Adaptations to special circumstances regarding protein or fat are more likely for metabolism/requirements, not for digestion.

Interpretation of apparent digestibility data for CP and EE always in relation to their dietary content.
thank you
for your attention
... but:

How do birds & reptiles & fish fit in?