Introduction to digestive physiology

Marcus Clauss

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland

Bio 122 2013
getting the food

the availability of sufficient amounts of available packages
Getting the food

• Catching prey is (often) the hard part!

• Catching plants is (mostly) easy!
Sufficient amounts of available packages

from Hiiemae (2000)
Sufficient amounts of available packages

from Hiiemae (2000)
Sufficient amounts of available packages

from Hiiemae (2000)
Sufficient amounts of available packages

- ANIMAL = high protein
  - Larger Mammals
  - Fish
  - Crustacea
  - Mollusca
  - Krill
- INSECTIVORES
  - Other vertebrates
  - Small mammals, birds
  - Insects
- CARNIVORES
- OMNIVORES
  - Eggs
  - Generalized Mammal e.g. Opossum
  - Pollen
- FRUGIVORES
  - Fruit
  - Nectar
- HERBIVORES
  - Mature leaves, Grasses
  - Buds, Shoots
  - Seeds, Nuts
  - Aquatic herbivores

from Hiiemae (2000)
Sufficient amounts of available packages

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Sufficient amounts of available packages

- **CARNIVORES**
  - Larger Mammals
  - Fish
  - Crustacea
  - Mollusca
  - Marine mammals/large fish

- **INSECTIVORES**
  - Other vertebrates
  - Krill
  - Small mammals, birds

- **OMNIVORES**
  - Carrion
  - Insects

- **HERBIVORES**
  - Mature leaves, Grasses
  - Fruit
  - Nectar
  - Seeds, Nuts
  - Buds, Shoots
  - Aquatic herbivores

**BODY SIZE**

- Generalized Mammal e.g. Opossum

*from Hiiemae (2000)*
Herbivory and Carnivory - Physiological Challenge and Physiological Opportunity
Carnivory ...

- ... is no physiological challenge
- ... but a biomechanical and logistical one!

- **Digesting prey is easy - catching prey is the hard part!**
Carnivores

from Stevens und Hume (1995)
Carnivores
Food Organism
Food Organism

Essential food components (minerals, vitamins, amino acids, fatty acids)
Food

Organism

- Essential food components (minerals, vitamins, amino acids, fatty acids)
- Non-essential food components (fuels and precursors of self-synthetized substances)
Food Organism

Ecophysiological challenge

- **Essential food components** (minerals, vitamins, amino acids, fatty acids)
- **Non-essential food components** (fuels and precursors of self-synthetized substances)
Food Organism
Many enzymes can be spared!
Food Organism

but: more essential food components (minerals, vitamins, amino acids, fatty acids)!
Idiosyncratic nutrient requirements of cats appear to be
diet-induced evolutionary adaptations*

James G. Morris
Idiosyncratic nutrient requirements of cats appear to be diet-induced evolutionary adaptations

James G. Morris

Ecological opportunity adaptation
Particularities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency

  similar enzyme patterns in trout, alligators, vultures, barn owls
Particularities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency
- Arginine is essential

also in mink and ferrets
Particularities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency
- Arginine is essential
- Taurine is essential: cannot be synthesized in sufficient amount from cysteine and methionine

deficiencies observed in zoo felids, maned wolves, foxes, merkats, anteaters
Particularities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency
- Arginine is essential
- Taurine is essential: cannot be synthetized in sufficient amount from cysteine and methionine
- Arachidonic acid is essential: cannot be synthetized in sufficient amount from linoleic acid; docosahexaenoic acid also essential

also in lions, cheetahs and mosquitoes
Particularities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency
- Arginine is essential
- Taurine is essential: cannot be synthetized in sufficient amount from cysteine and methionine
- Arachidonic acid is essential: cannot be synthetized in sufficient amount from linoleic acid; docosahexaenoic acid also essential
- Limited tolerance of carbohydrates: CH-digesting enzymes have low activity and cannot be up-regulated
Particularities of the cat

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- Limited tolerance of carbohydrates: CH-digesting enzymes have low activity and cannot be up-regulated; in intermediary metabolism, monosaccharides are metabolised very slowly
- β-carotene has no effect: vit. A cannot be synthetized from β-carotene

Also in foxes
Particularities of the cat

- High protein requirement: amino acid catabolism cannot be reduced even in deficiency
- Arginine is essential
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- β-carotene has no effect: vit. A cannot be synthesized from β-carotene
- Vitamin D is essential: no synthesis even in UV-light
Particularities of the cat

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- Arachidonic acid is essential: cannot be synthesized in sufficient amount from linoleic acid; docosahexaenoic acid also essential
- Limited tolerance of carbohydrates: CH-digesting enzymes have low activity and cannot be up-regulated; in intermediary metabolism, monosaccharides are metabolized very slowly
- \(\beta\)-carotene has no effect: vit. A cannot be synthesized from \(\beta\)-carotene
- Vitamin D is essential: no synthesis even in UV-light
- Niacin is essential: cannot be synthesized from tryptophane

Also in trout and salmon
Food chains
A green world
Primary consumers
Primary consumers

from Akin & Amos (1975)
Primary consumers

from Amos & Akin (1978)
Primary consumers

from Akin & Benner (1988)
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Primary consumers
Food chains

A terrestrial food chain

A marine food chain

Producers

Flower    Phytoplankton
Food chains

A terrestrial food chain

A marine food chain

Primary consumers
Grasshopper
Zooplankton

Producers
Flower
Phytoplankton
Food chains

A terrestrial food chain

A marine food chain

- Secondary consumers: Mouse, Herring
- Primary consumers: Grasshopper, Zooplankton
- Producers: Flower, Phytoplankton
Food chains
Food chains
Food chains - and shortcuts

A terrestrial food chain:
- Quaternary consumers: Hawk
- Tertiary consumers: Snake
- Secondary consumers: Mouse
- Primary consumers: Grasshopper
- Producers: Flower

A marine food chain:
- Quaternary consumers: Killer whale
- Tertiary consumers: Cod
- Secondary consumers: Herring
- Primary consumers: Zooplankton
- Producers: Phytoplankton
Easy-to-harvest packages of tiny invertebrates – krill clouds
Food chains - and shortcuts

- A terrestrial food chain: Quaternary consumers (Hawk), Tertiary consumers (Snake), Secondary consumers (Mouse), Primary consumers (Grasshopper), Producers (Flower/Phytoplankton)
- A marine food chain: Quaternary consumers (Killer whale), Tertiary consumers (Cod), Secondary consumers (Herring), Producers (Zooplankton)

no shortcut
Productive yet minute packages of plant food in marine systems
Productive yet minute packages of plant food in marine systems
Rare large marine herbivores
Rare large marine herbivores
Food chains - and shortcuts

A terrestrial food chain:
- Quaternary consumers: Hawk
- Tertiary consumers: Snake
- Secondary consumers: Mouse
- Primary consumers: Grasshopper
- Producers: Flower

A marine food chain:
- Quaternary consumers: Killer whale
- Tertiary consumers: Cod
- Secondary consumers: Herring
- Primary consumers: Zooplankton
- Producers: Phytoplankton

no shortcut
Ubiquitous dense large packages of plant food in terrestrial systems
Food chains - and shortcuts

A terrestrial food chain:
- Quaternary consumers: Hawk
- Tertiary consumers: Snake
- Secondary consumers: Mouse
- Primary consumers: Grasshopper
- Producers: Flower

A marine food chain:
- Quaternary consumers: Killer whale
- Tertiary consumers: Cod
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no shortcut
Food chains - and shortcuts

A terrestrial food chain:
- Quaternary consumers: Hawk, Killer whale
- Tertiary consumers: Snake, Cod
- Secondary consumers: Mouse, Herring
- Primary consumers: Grasshopper, Zooplankton
- Producers: Flower, Phytoplankton

A marine food chain:

no shortcut
No easy-to-harvest packages of tiny invertebrates
Herbivory

- Principles
  (fibre digestion)
Competition for light ...
Competition for light...
Competition for light ...

... results in a struggle against gravity in terrestrial systems:
Competition for light ... results in a struggle against gravity in terrestrial systems: the evolution of ‘fibre’
Fibre analysis

Plant carbohydrates

Cell contents
- Organic acids
- Mono-oligosaccharides
- Starches
- Fructans
- Pectic substances
  - Galactans
  - β-glucans

Cell wall
- Hemicelluloses
- Cellulose

NDF
- Non-starch polysaccharides

NFC

from Hall (2003)
Photosynthesis

1. Chloroplasts trap light energy
2. Water enters leaf
3. Carbon dioxide enters leaf through stomata
4. Sugar leaves leaf

WATER + LIGHT = CHEMICAL ENERGY

CHEMICAL ENERGY + CARBON DIOXIDE = SUGAR
Photosynthesis

WATER + LIGHT = CHEMICAL ENERGY

1. Chloroplasts trap light energy
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4. Sugar leaves leaf

CHEMICAL ENERGY + CARBON DIOXIDE = SUGAR

O₂
First fundamental question

Do you want to use plant fibre or only the plant cell contents?
Do you want to use plant fibre or only the plant cell contents?
First fundamental question

Do you want to use plant fibre or only the plant cell contents?
Fibre digestion

Organic polymers (cellulose, hemicellulose)

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

\[\text{Hydrolysis}
\text{(soluble sugars)}\]
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

↓

Hydrolysis
(soluble sugars)

↓

Primary fermentation
(lactate, succinate)

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

$H_2$, $CO_2$

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

[\rightarrow]

Hydrolysis
(soluble sugars)

[\rightarrow]

Primary fermentation
(lactate, succinate)

[\rightarrow]

Secondary fermentation
acetate, propionate, butyrate

\[ \text{H}_2 \quad \text{CO}_2 \]

Removal ('sinks')?

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

Methanogenesis (CH₄, H₂O)

H₂, CO₂

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

Acetogenesis ($C_2H_3O_2, H_2O$)

Methanogenesis ($CH_4, H_2O$)

acetate, propionate, butyrate

$H_2, CO_2$
Fibre digestion

Organic polymers (cellulose, hemicellulose) →

Hydrolysis (soluble sugars) →

Primary fermentation (lactate, succinate) →

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis (C₂H₃O₂, H₂) →

H₂ CO₂

Acetogenesis (C₂H₃O₂, H₂O) →

Methanogenesis (CH₄, H₂O)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

↓

Hydrolysis (soluble sugars)

↓

Primary fermentation (lactate, succinate)

↓

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis (C\textsubscript{2}H\textsubscript{3}O\textsubscript{2}, H\textsubscript{2})

Methanogenesis (CH\textsubscript{4}, HCO\textsubscript{3})

Acetogenesis (C\textsubscript{2}H\textsubscript{3}O\textsubscript{2}, H\textsubscript{2}O)

Methanogenesis (CH\textsubscript{4}, H\textsubscript{2}O)

H\textsubscript{2} CO\textsubscript{2}

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation
acetate, propionate, butyrate

Acetogenesis
($C_2H_3O_2$, $H_2$)

Methanogenesis
($CH_4$, $HCO_3$)

from Karasov & Martinez del Rio (2007)
Fibre digestion

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Hydrolysis (soluble sugars)

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acetate, propionate, butyrate

Acetogenesis ($\text{C}_2\text{H}_3\text{O}_2$, $\text{H}_2$)

Methanogenesis ($\text{CH}_4$, $\text{HCO}_3$)

Methanogenesis ($\text{CH}_4$, $\text{H}_2\text{O}$)

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis ($\text{C}_2\text{H}_3\text{O}_2$, $\text{H}_2\text{O}$)

Methanogenesis ($\text{CH}_4$, $\text{H}_2\text{O}$)

from Karasov & Martinez del Rio (2007)
Fibre digestion

from Karasov & Martinez del Rio (2007)

Organic polymers (cellulose, hemicellulose)

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Hydrolysis (soluble sugars)

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Primary fermentation (lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis ($C_2H_3O_2$, $H_2$)

Methanogenesis ($CH_4$, $HCO_3$)

$H_2$ $CO_2$

Microbial biomass
Fibre digestion from Karasov & Martinez del Rio (2007)

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

Acetogenesis ($\text{C}_2\text{H}_3\text{O}_2$, $\text{H}_2\text{O}$)

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$\text{H}_2$ $\text{CO}_2$

Microbial biomass

Herbivore
Fibre digestion

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

Acetogenesis ($C_2H_3O_2$, $H_2$)

Methanogenesis ($CH_4$, $H_2O$)

Herbivore

Sewer Detritus

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis
($C_2H_3O_2$, $H_2$)

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Methanogenesis
($CH_4$, $HCO_3$)

Herbivore

Microbial biomass

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

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acetate, propionate, butyrate

Acetogenesis ($C_2H_3O_2$, $H_2$)

Methanogenesis ($CH_4$, $H_2O$)

Herbivore

Microbial biomass

from Karasov & Martinez del Rio (2007)
Methane allometry in herbivores

from Franz et al. (2011)
Methane allometry in herbivores

from Franz et al. (2011)
Methane allometry in herbivores

from Franz et al. (2011)
Herbivory

- Principles (body size)
Two fundamental questions

1. ‘In-house’ or outsourcing of fibre digestion?

2. What sequence of fibre digestion and auto-enzymatic digestion?
1. ‘In-house’ or outsourcing of fibre digestion?

   ‘In-house’ fibre digestion necessitates anatomical and physiological adaptations that might be costly in some circumstances.

2. What sequence of fibre digestion and auto-enzymatic digestion?
Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera

C. A. Nalepa¹, D. E. Bignell² and C. Bandi³

Insectes soc. 48 (2001) 194–201
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“external rumen”

**Microbes**
- transient or digested
- gut fauna

**Refractory food item**

**Metabolites, exoenzymes**
- of free living microbes
- of resident gut fauna
- of host
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THE EVOLUTION OF AGRICULTURE IN INSECTS

Ulrich G. Mueller,1,2 Nicole M. Gerardo,1,2,3 Duur K. Aanen,4 Diana L. Six,5 and Ted R. Schultz6

Most biologists consider body mass the most important characteristic of an organism. It is also (mostly) easy to measure.

All morphological and physiological traits scale somehow with body mass.

"Scaling is interesting because, aside from natural selection, it is one of the few laws we really have in biology." John Gittleman
1. ‘In-house’ or outsourcing of fibre digestion?

‘In-house’ fibre digestion necessitates anatomical and physiological adaptations that might be costly in some circumstances.

Outsourcing is only feasible at small body sizes where you have high encounter rates with nutritionally relevant amounts of microorganisms.

(although there are billions of microorganisms in this room, their mass is not enough to meet the daily energy requirements of a single member of the audience)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

Acetogenesis ($\text{C}_2\text{H}_3\text{O}_2, \text{H}_2$)

Methanogenesis ($\text{CH}_4, \text{H}_2\text{O}$)

$\text{H}_2, \text{CO}_2$

Microbial biomass

from Karasov & Martinez del Rio (2007)
Fibre digestion

Herbivore

Organic polymers (cellulose, hemicellulose)

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$\text{H}_2$ $\text{CO}_2$

from Karasov & Martinez del Rio (2007)
Surface/volume geometry

... affects all surface-related processes

heat loss $\rightarrow$ energy requirements $\rightarrow$ food intake

from Clauss & Hummel (2005)
Surface/volume geometry

6:1

... affects all surface-related processes

24:8=3:1

from Karasov & Martinez del Rio (2007)
Surface/volume geometry

... affects all surface-related processes

from Karasov & Martinez del Rio (2007)
Surface/volume geometry

... affects all surface-related processes

6:1

24:8 = 3:1

from Karasov & Martinez del Rio (2007)
Gut moisture content

\[ y = 0.028x^{0.93} \]

Body mass (kg)

DMClin (kg)

WMC (kg)

from Müller et al. (2013)
Gut moisture content

$y = 0.028x^{0.93}$

$y = 0.108x^{1.06}$

from Müller et al. (2013)
Gut moisture content

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from Müller et al. (2013)
Gut moisture content

\[ y = 0.028x^{0.93} \]

\[ y = 0.108x^{1.06} \]

from Müller et al. (2013)
Surface/volume geometry

... affects all surface-related processes

6:1

short
long
diffusion ways

24:8=3:1

from Karasov & Martinez del Rio (2007)
Herbivory - Principles (digestive tracts)
2. What sequence of fibre digestion and auto-enzymatic digestion?

- fibre digestion prior to auto-enzymatic digestion allows the use of bacterial biomass
- bacterial digestion after auto-enzymatic digestion allows more efficient use of those substrates that can be digested auto-enzymatically
Two fundamental questions

2. What sequence of fibre digestion and auto-enzymatic digestion?

- fibre digestion prior to auto-enzymatic digestion allows the use of bacterial biomass
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Hindgut fermentation - ‘the conventional approach’
Cellulolytic Systems in Insects

Hirofumi Watanabe¹ and Gaku Tokuda²

Annu. Rev. Entomol. 2010. 55:609–32

Periplaneta americana

Panesthia angustipennis spadica

MG  MT  HG

10 mm
Cellulolytic Systems in Insects
Hirofumi Watanabe¹ and Gaku Tokuda²
Annu. Rev. Entomol. 2010. 55:609–32

scheme from Karasov & Martinez del Rio (2007)
Elongated Hind guts in Desert-Living Dung Beetles (Scarabaeidae: Scarabaeinae) Feeding on Dry Dung Pellets or Plant Litter

Peter Holter¹* and Clarke H. Scholtz²


Scarabaeus spp. (fresh dung)

Pachysoma spp. (plant litter)
Hindgut Fermentation in Three Species of Marine Herbivorous Fish

Douglas O. Mountfort,¹* Jane Campbell,² and Kendall D. Clements²

Hindgut Fermentation - Reptiles

from Stevens & Hume (1995)
Herbivores - Birds

Hoatzin (Opisthocomus hoazin)
Body Length: 65 cm

Chicken (Gallus domesticus)
Body Length: 46 cm

Ostrich (Struthio camelus)
Body Length: 80 cm

from Stevens und Hume (1995)
Herbivores - Birds

from Stevens und Hume (1995)
Photo: J. Fritz
Herbivores - Birds

Photos: J. Fritz
Hindgut Fermentation - Caecum

Greater Glider
(Petauroides volans)
Body Length: 40 cm

Capybara
(Hydrochoerus hydrochaeris)
Body Length: 140 cm

Rabbit
(Oryctolagus cuniculus)
Body Length: 48 cm

from Stevens & Hume (1995)
Hindgut Fermentation - Colon

from Stevens & Hume (1995)
Hindgut Fermentation - Colon

Zebra (Equus burchelli)
Body Length: 2 m

Rhinoceros (Diceros bicornis)
Body Length: 3.2 m

African Elephant (Loxodonta africana)
Body Length: 3.2 m

from Stevens & Hume (1995)
Foregut Fermentation

from Stevens & Hume (1995)
Foregut Fermentation
Foregut Fermentation - Ruminant

aus Stevens & Hume (1995)
Photo Llama: A. Riek
With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.
Foregut vs. Hindgut Fermentation

from Stevens & Hume (1995)
Fermentation prior to enzymatic digestion and absorption:

Foregut vs. Hindgut Fermentation

from Stevens & Hume (1995)
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Use of bacterial protein, bacterial products (B-Vitamins)

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Use of easily digestible substances prior to fermentation

‘Loss’ of bacterial protein, bacterial products (B-Vitamins?)

from Stevens & Hume (1995)
Herbivory

- Principles
  (coprophagy)
Fermentation after sites of enzymatic digestion and absorption:

Use of easily digestible substances prior to fermentation

Loss of bacterial protein

Coprophagy / Caecotrphy

from Stevens und Hume (1995)

Photo: B. Burger
Coprophagy/Caecotrophy

Photos: B. Burger
Coprophagy/Caecotrophy

Photos: B. Burger
Coprophagy/Caecotrophy

Photos: B. Burger
Coprophagy/Caecotrophy

Photos: B. Burger, M. Clauss
Coprophagy/Caecotrophy

Photo: A. Tschudin
Sorting of ingesta for caecotroph formation

from Sakaguchi (2003)
Sorting of ingesta for caecotroph formation

Wash back mechanism (Rabbit)

Mucus trap mechanism (Guniea pig, Chinchilla)

from Sakaguchi (2003)
The colonic groove / furrow

from Besselmann (2005)
The colonic groove / furrow

Mara

Photo: M. Clauss
Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera

C.A. Nalepa¹, D.E. Bignell² and C. Bandi³

Insectes soc. 48 (2001) 194–201
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C. A. Nalepa¹, D. E. Bignell² and C. Bandi³
Insectes soc. 48 (2001) 194–201

ASOCIAL

DETRITIVORY, GENERAL COPROPHAGY
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Insectes soc. 48 (2001) 194–201
The question is not so much why such a large variety of hindgut fermenters practice coprophagy, but rather why there is a certain group of large hindgut fermenters that does not.
Herbivory - diversity concepts
Conceptualizing herbivore diversity

metabolic intensity
Conceptualizing herbivore diversity

metabolic intensity
Conceptualizing herbivore diversity

To achieve a high metabolic intensity, you need
To achieve a high metabolic intensity, you need

- a high food intake
To achieve a high metabolic intensity, you need

- a high food intake
- a high digestive efficiency
To achieve a high metabolic intensity, you need

• a high food intake

• a high digestive efficiency
  - long retention times
  - intensive particle size reduction
  - (high feeding selectivity)
Conceptualizing herbivore diversity

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from Clauss et al. (2009; data from Foose 1982)
Conceptualizing herbivore diversity

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Compensation via gut capacity?
Conceptualizing herbivore diversity

Gut capacity is relatively constant across metabolic intensities
Conceptualizing herbivore diversity

Gut capacity is relatively constant across metabolic intensities

from Franz et al. (2009)
Conceptualizing herbivore diversity

Gut capacity is relatively constant across metabolic intensities

from Franz et al. (2009)

from Franz et al. (2011)
Conceptualizing herbivore diversity

metabolic intensity

Body mass (kg)

Basal metabolic rate (kJ/d)

after Kirkwood (1996)
Conceptualizing herbivore diversity

from Franz et al. (2011)

metabolic intensity

Body mass (kg)

Basal metabolic rate (kJ/d)

after Kirkwood (1996)
Conceptualizing herbivore diversity

from Franz et al. (2011)
Conceptualizing herbivore diversity

**metabolic intensity**

- **from Franz et al. (2011a)**

  - Figure showing the relationship between body mass (kg) and DMI (kg d\(^{-1}\)) for mammal and reptile herbivores with corresponding equations:
    - Mammals: \( y = 0.047x^{0.76} \)
    - Reptiles: \( y = 0.005x^{0.76} \)

- **from Franz et al. (2011b)**

  - Figure showing the relationship between body mass (kg) and methane production (L d\(^{-1}\)) with the equation:
    - \( y = 0.014x^{1.03} \)
Conceptualizing herbivore diversity

metabolic intensity

from Franz et al. (2011)

from Fritz et al. (2010)
Conceptualizing herbivore diversity

metabolic intensity

from Franz et al. (2011) and Fritz et al. (2010)
Conceptualizing herbivore diversity

metabolic intensity
Conceptualizing herbivore diversity
Conceptualizing herbivore diversity

**Metabolic Intensity**

\[ y = 239.05x^{0.7098} \]

\[ R^2 = 0.9497 \]

Data from Savage et al. (2004)
Conceptualizing herbivore diversity

\[ y = 239.05x^{0.7098} \]

\[ R^2 = 0.9497 \]

Data from Savage et al. (2004)
Conceptualizing herbivore diversity

Data overlap from Savage et al. (2004) and Clauss et al. (2007)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Conceptualizing herbivore diversity

**metabolic intensity**

![Graph showing metabolic intensity](image)

from Clauss et al. (2010)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Two Preconditions

1. It is energetically favourable to digest ‘autoenzymatically digestible’ components autoenzymatically, not by fermentative digestion.

2. Autoenzymatically digestible components are fermented at a drastically higher rate than plant fiber.

from Hummel et al. (2006ab)
Digestive Strategies

Low intake ⇒ long passage

High intake ⇒ short passage
<table>
<thead>
<tr>
<th>Low intake</th>
<th>Autoenzymatic digestion followed by thorough fermentative digestion</th>
</tr>
</thead>
<tbody>
<tr>
<td>long passage</td>
<td></td>
</tr>
<tr>
<td>High intake</td>
<td></td>
</tr>
<tr>
<td>short passage</td>
<td></td>
</tr>
</tbody>
</table>
# Digestive Strategies

<table>
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<tr>
<td>Autoenzymatic digestion followed by thorough fermentative digestion</td>
<td>Autoenzymatic digestion followed by cursory fermentative digestion</td>
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</tbody>
</table>
## Digestive Strategies

<table>
<thead>
<tr>
<th>Intake Level</th>
<th>Digestive Process</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>Autoenzymatic digestion followed by thorough</td>
</tr>
<tr>
<td></td>
<td>fermentative digestion</td>
</tr>
<tr>
<td>High</td>
<td>Autoenzymatic digestion followed by cursory</td>
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<td>fermentative digestion</td>
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<tr>
<td></td>
<td>Fermentative digestion followed by</td>
</tr>
<tr>
<td></td>
<td>autoenzymatic digestion of products (and remains)</td>
</tr>
</tbody>
</table>
Digestive Strategies

- **High intake**  
  ⇒ short passage  
  - Autoenzymatic digestion followed by cursory fermentative digestion

- **Low intake**  
  ⇒ long passage  
  - Autoenzymatic digestion followed by thorough fermentative digestion
  - Fermentative digestion followed by autoenzymatic digestion of products (and remains)
  - Cursory fermentative digestion mainly of autoenzymatically digestible components followed by ineffective autoenzymatic digestion of undigested fiber?
Digestive Strategies

<table>
<thead>
<tr>
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<th>Autoenzymatic digestion followed by thorough fermentative digestion ✓</th>
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<td>Autoenzymatic digestion followed by cursory fermentative digestion ✓</td>
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<tr>
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<td>Fermentative digestion followed by autoenzymatic digestion of products (and remains) ✓</td>
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<tr>
<td></td>
<td>Cursory fermentative digestion mainly of autoenzymatically digestible components followed by ineffective autoenzymatic digestion of undigested fiber?</td>
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### From Digestive to Metabolic Strategies

<table>
<thead>
<tr>
<th>Low intake</th>
<th>High intake</th>
</tr>
</thead>
<tbody>
<tr>
<td>⇒ long passage</td>
<td>⇒ short passage</td>
</tr>
<tr>
<td>⇒ low metabolism</td>
<td>⇒ high metabolism</td>
</tr>
</tbody>
</table>

- **Low intake (long passage):** ✓
- **High intake (short passage):** ✓
- **Low intake (low metabolism):** ✓
- **High intake (high metabolism):** ✗
Herbivory
- the ruminant revolution
Conceptualizing herbivore diversity

metabolic intensity

from Clauss et al. (2010)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
<table>
<thead>
<tr>
<th>Digestive and Metabolic Strategies</th>
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<tr>
<td>⇒ long passage</td>
</tr>
<tr>
<td>⇒ low metabolism</td>
</tr>
<tr>
<td>High intake</td>
</tr>
<tr>
<td>⇒ differentiated passage</td>
</tr>
<tr>
<td>⇒ high metabolism</td>
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## Digestive and Metabolic Strategies

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  - Low metabolism: ✔

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<tbody>
<tr>
<td>Low intake</td>
<td><img src="image" alt="Digestive System" /> <img src="image" alt="Omnivore" /> <img src="image" alt="Herbivore" /></td>
</tr>
<tr>
<td>⇒ long passage</td>
<td>![ ✓ ] ![ ✓ ] ![ ✓ ]</td>
</tr>
<tr>
<td>⇒ low metabolism</td>
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  - (high feeding selectivity)

Sorting!
Ruminant vs. Nonruminant Foregut Fermentation

Schwarm et al. (2008)
Ruminant vs. Nonruminant Foregut Fermentation

Schwarm et al. (2008, 2009)
Ruminant vs. Nonruminant
Foregut Fermentation

Schwarm et al. (2008, 2009)
Ruminant vs. Nonruminant Foregut Fermentation

Schwarm et al. (2008, 2009)
Ingesta particle size (chewing efficiency)

from Fritz et al. (2009)
Ingesta particle size (chewing efficiency)

Ingesta particle size (chewing efficiency) from Fritz et al. (2009)
Ruminant vs. Nonruminant Foregut Fermentation

Schwarm et al. (2008,2009)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Detailed function: solutions of different efficiency
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Matsuda et al. (2011)
Regurgitation and remastication in the foregut-fermenting proboscis monkey (Nasalis larvatus)

Ikki Matsuda¹,*, Tadahiro Murai¹, Marcus Clauss², Tomomi Yamada³, Augustine Tuuga⁴, Henry Bernard⁵ and Seigo Higashi⁶

Matsuda et al. (2011)
1. Fibre digestion with the help of symbiotic microbes is widespread in the animal kingdom
2. So is the direct use of microbial biomass - either via coprophagy, farming, or foregut fermentation
3. Reasons for different proportions of acetogenic and methanogenic hydrogen sinks in ruminants and nonruminants remain unclear
4. Due to its relevance for food encounter rates, harvesting mechanisms and surface/volume geometry, body size has an important influence on foraging strategies and digestive morphophysiology
6. Different merits of foregut and hindgut fermentation (at similar metabolic intensity) remain to be fully elucidated

7. Rather than classifying herbivores according to body size or digestion type, classifying herbivores according to metabolic intensity is a promising novel approach

8. Whereas the hindgut fermenter system allows a large range of metabolic intensities, the (nonruminant) foregut fermenter system appears to restrict animals to the low metabolic intensity side of the spectrum
thank you for your attention