Introduction to herbivore digestive physiology

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Wildlife Digestive Physiology Vienna 2013
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
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Primary consumers
Herbivory
Herbivory
Vertebrates cannot digest plant fibre by their own enzymes (aut-enzymatically); they have to rely on symbiotic gut microflora (allo-enzymatic digestion).

Bacterial digestion = fermentation

The host has to supply this microflora with a habitat (so-called fermentation chambers).
Carnivory ...

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

• **Digesting prey is easy - catching prey is the hard part!**
Herbivory ...

• ... is no logistical challenge
• ... but a digestive one!

• Catching plants is easy - digesting plants is the hard part!
Food chains
Food chains

A terrestrial food chain
- Quaternary consumers: Hawk
- Tertiary consumers: Cod
- Secondary consumers: Herring
- Primary consumers: Grasshopper
- Producers: Flower

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

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

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
  - Zooplankton
- Producers
  - Flower
  - Phyttoplankton

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

no shortcut
Food chains - and shortcuts

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

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

No shortcut
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

ADF

NDSF

NDF

Non-starch polysaccharides

NFC

from Hall (2003)
Photosynthesis
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

O₂
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?
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)

\[ \downarrow \]

Hydrolysis
(soluble sugars)

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

\[\rightarrow\]

Hydrolysis
(soluble sugars)

\[\rightarrow\]

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

H₂, CO₂

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

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

H₂, CO₂

Methanogenesis
(CH₄, H₂O)

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

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

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis
($C_2H_3O_2$, $H_2$)

Acetogenesis
($C_2H_3O_2$, $H_2O$)

Methanogenesis
($CH_4$, $H_2O$)

$H_2$ $CO_2$

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\(_2\)H\(_3\)O\(_2\), H\(_2\), H\(_2\)O)

**Methanogenesis**
(CH\(_4\), H\(_2\)O)

**Acetogenesis**
(C\(_2\)H\(_3\)O\(_2\), H\(_2\))

**Methanogenesis**
(CH\(_4\), HCO\(_3\))

---

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
(C₂H₃O₂, H₂)

Methanogenesis
(CH₄, HCO₃)

Methanogenesis
(CH₄, H₂O)

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 (C₂H₃O₂, H₂)
      - Methanogenesis (CH₄, HCO₃)
      - Methanogenesis (CH₄, H₂O)

- Acetogenesis (C₂H₃O₂, H₂)
- Methanogenesis (CH₄, HCO₃)
- Microbial biomass

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

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

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

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

→ Microbial biomass

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 (C₂H₃O₂, H₂O)

Methanogenesis (CH₄, H₂O)

Acetogenesis (C₂H₃O₂, H₂)

Methanogenesis (CH₄, HCO₃⁻)

H₂, CO₂

Herbivore

Microbial biomass

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

Organic polymers (cellulose, hemicellulose)

Hydrolysis (soluble sugars)

Primary fermentation (lactate, succinate)

Secondary fermentation

Acetate, propionate, butyrate

H₂, CO₂

Acetogenesis (C₂H₃O₂, H₂O)

Methanogenesis (CH₄, H₂O)

Microbial biomass

Herbivore

Sewer Detritus

Acetogenesis (C₂H₃O₂, H₂)

Methanogenesis (CH₄, HCO₃)
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 ($C_4H_2O_2, H_2O$)
  - Methanogenesis ($CH_4, H_2O$)
  - Acetogenesis ($C_2H_3O_2, H_2$)
  - Nonruminant

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 ($CH_4$, $H_2O$)
- Methanogenesis ($CH_4$, $HCO_3$)
- Acetogenesis ($C_2H_3O_2$, $H_2$)

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?
Two fundamental questions

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
Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera

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Refractory food item
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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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“external rumen”

\begin{itemize}
\item Microbes
  \begin{itemize}
  \item transient or digested
  \item gut fauna
  \end{itemize}
\item Refractory food item
\item Metabolites, exoenzymes
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**Diagram Notes:**
- **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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**Text:**
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
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
Two fundamental questions

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

From Karasov & Martinez del Rio (2007)

Organic polymers
(cellulose, hemicellulose)

Hydrolysis
(soluble sugars)

Primary fermentation
(lactate, succinate)

Secondary fermentation

acetate, propionate, butyrate

Acetogenesis
($C_2H_3O_2$, $H_2$)

Methanogenesis
($CH_4$, $HCO_3$)

Methanogenesis
($CH_4$, $H_2O$)

H$_2$ CO$_2$

Microbial biomass

from Karasov & Martinez del Rio (2007)
Fibre digestion

Organic polymers (cellulose, hemicellulose)

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

6:1

... affects all surface-related processes

24:8 = 3:1

heat loss  ---  energy requirements  ---  food intake

from Clauss & Hummel (2005)
Surface/volume geometry

... affects all surface-related processes

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

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

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

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

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

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Body mass (kg)

DMClin (kg)

WMC (kg)

from Müller et al. (2013)
Gut moisture content

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

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

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

6:1

24:8 = 3:1

... affects all surface-related processes

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
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Two fundamental questions

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- bacterial digestion after auto-enzymatic digestion allows more efficient use of those substrates that can be digested auto-enzymatically
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
Cellulolytic Systems in Insects
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Annu. Rev. Entomol. 2010. 55:609–32

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

Peter Holter\textsuperscript{1*} and Clarke H. Scholtz\textsuperscript{2}

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1 Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045, USA
2 School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia


\textbf{Scarabaeus} spp. (fresh dung)

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

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

Herbivorous fish

© Kendall Clements
Hindgut Fermentation - Reptiles

from Stevens & Hume (1995)

Photo: J. Fritz
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

from Stevens & Hume (1995)
Herbivores - Colon fermenters

Common Wombat
*(Vombatus ursinus)*
Body Length: 98 cm

Woolly Monkey
*(Lagotricha lagotricha)*
Body Length: 60 cm

Orangutan
*(Pongo pygmaeus)*
Body Length: 64 cm

from Stevens und Hume (1995)
Herbivores - Colon fermenters

from Stevens und Hume (1995)
Photo: M. Clauss
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 - Colon

from Stevens & Hume (1995)
Hindgut Fermentation - Colon

from Stevens & Hume (1995)
White rhino photo: D. Müller
Foregut Fermentation

from Stevens & Hume (1995)
Foregut Fermentation

Photos A. Schwarm/ M. Clauss
Foregut Fermentation

Photo M. Clauss
Foregut Fermentation

Photo M. Clauss
Herbivores - Foregut fermenters

from Schwarm et al. (in prep.)
Photo: A. Schwarm
Foregut Fermentation - Ruminant

Llama
(Lama glama)
Body Length: 193 cm

Sheep
(Ovis aries)
Body Length: 110 cm

aus Stevens & Hume (1995)
Photo Llama: A. Riek
Foregut/Hindgut Fermenters

With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.

 Demon mole rat
(*Tachyoryctes daemon*)
papillated forestomach
Foregut/Hindgut Fermenters

With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.

Laotian rock rat
(Laonastes aenigmamus)
kangaroo-like forestomach

from Scopin et al. (2011)
Foregut/Hindgut Fermenters

With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.

Maned (crested) rat
(Lophiomys imhausi)
complex forestomach

from Vrontsov (1967)
Foregut/Hindgut Fermenters

With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.

White-tailed antsangy (Brachytarsomys albicauda) complex forestomach

from Vrontsov (1967)
Foregut/Hindgut Fermenters

With the majority of rodent species un-studied, we have not grasped the variability, and adaptive significance, of foregut and hindgut fermentation yet.

Malagasy giant rat
(Hypogeomys antimena)
complex forestomach

from Vrontsov (1967)
Herbivores - Hyrax

from Stevens und Hume (1995)
Herbivores - Hyrax

from Stevens und Hume (1995)
Analysing for energy in plant material

*in vitro fermentation (gas production)*

- May give a more biological estimation (compared to bomb calorimetry) of digestibility of energy - but higher variability
- Based on the use of enzymes (in vitro digestion) or gut microbes (in vitro fermentation), or a combination of both
- In vitro fermentation can be used to simulate foregut fermentation or other sections of the GIT with fermentative capacity
Forage fermentation patterns

Cumulative gas production (ml/200 mg DM)

Duration of fermentation [h]

Browse + PEG
Browse

from Hummel et al. (2006)
Forage fermentation patterns

Cumulative gas production (ml/200 mg DM) vs. Duration of fermentation [h]

- Browse + PEG
- Browse
- Twigs

from Hummel et al. (2006)
Forage fermentation patterns

Cumulative gas production (ml/200 mg DM) vs. Duration of fermentation [h]

- Herbs
- Legumes
- Browse + PEG
- Browse
- Twigs

from Hummel et al. (2006)
Forage fermentation patterns

From Hummel et al. (2006)

Cumulative gas production (ml/200 mg DM)

Duration of fermentation [h]
Fibre composition of forages

from Hummel et al. (2006)
Lignin is a major constraint on digestibility

\[ y = -0.19x + 60.4 \]

\( R^2 = 0.96 \)

from Hummel et al. (2006)
Forage fermentation patterns

from Hummel et al. (2006)
thank you
for your attention