Merycism and Rumination – a comparative view of an evolutionary adaptation and a behavioural disorder

Marcus Clauss

Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Switzerland
5. Zürcher Dyphagietagung, 24.-25.01.2014
Joh. Conradí Peyeri
cognomento Pythagore
Merycologia
Sive de Ruminantibus
et Ruminatione
Commentarius.
Quo primum exponuntur
Ruminantium Species et Differrentia, per omnia animalium genera; deinde organisorum
ruminations interiores et exteriorum admiranda structura describitur. Et iambus
ari incisit ante oculos pullurus: denique de ruminatione ipsa
ejusque causis de utilitate differitur.

Basileæ
Apud Joh. Ludovicum Köenig
& Joh. Brandmyllervm,
CM DC LXXVII.
from Stevens und Hume (1995)
• Digestion
  • mechanical and chemical breakdown of food into smaller components that can be absorbed
  • takes place during the retention in, and passage through, the digestive tract
• Coprophagy

• ingestion of regular faeces
  => normal feeding behaviour (‘detritivores’)  
  => behavioural mechanism to ensure inoculation of GIT with symbiotic microbes (rare) 
  => abnormal behaviour

• ingestion of special faeces (‘caecotrophs’) 
  => separation mechanism in the hindgut 
  => recycling of bacterial protein 
  => near-obligatory in many rodents and lagomorphs

Definitions

Photo: A. Tschudin
from Stevens und Hume (1995)
from Stevens und Hume (1995)
• **Vomiting**
  - involuntary (forceful) expulsion of stomach contents
    => linked to aversive condition (gastritis, poisoning)
    => ‘does not stop in the mouth’
Definitions

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  • involuntary (forceful) expulsion of stomach contents
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• **Regurgitation**
  • voluntary/intentional expulsion of material from mouth/pharynx/esophagus/stomach
    => transport: feeding young/sharing food
    • production of special products in GIT (crops milk in pigeons, bee honey)
    => elimination: indigestible products (pellets/‘casting’ in carnivorous/piscivorous birds; stomach eversion in sharks)
Shark stomach eversion
Eagle pellet
Shrike pellet
Owl pellet
Owl pellet
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    => ‘regurgitating artists’
Regurgitators

- 1621 ‘nail-vomiting boy of Boston’
- 1642 Catharina Geisslerin, the ‘toad-vomiting woman of Germany’
- 1694 Theodorus Döderlein (vomiting newts and frogs)
- 1834 Henriette Pfenning (vomiting frogs)

- compulsive swallowsers (1927 patient with toothbrushes and disposable razor handles in his stomach)

- Stevie Starr – the ‘professional regurgitator’
Regurgitators

Stevie Starr
The Regurgitator
Unofficial Fan Site

Stevie Starr Swallows and Then Regurgitates Things in the Most Amazing Way

Stevie Starr on Czech and Slovak Got Talent (October 2011)

Stevie is in another "Got Talent" competition, this time in the Czech and Slovak Republics. He is in the first round and "everyone loves him," according to fan Václav C.

In 2010, Stevie made it to the semi-finals on "Britain's Got Talent" as well as on "Das Supertalent," Germany's version of the show.

About The Regurgitator

I first saw "The Regurgitator" (Stevie Starr) on a rerun of the Tonight Show with Jay Leno in 2005, and I decided I needed to make a fan site for him.

Stevie Starr is amazing. I have no idea how he does it and I couldn't find out any more information in a google search.
Human regurgitators
from Stevens und Hume (1995)
from Stevens und Hume (1995)
Definitions

• Rumination / Merycism
  • “to turn over in the mind”
  • “to chew the cud”
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  => maladaptive in humans as well as certain zoo animals
     ‘rumination syndrome’ / ‘RR’
Gorilla R/R
Gorilla R/R
A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (Gorilla gorilla gorilla)

Kristen E. Lukas *


Despite findings that provision of browse and removal of fruit from the diet reduces R/R (Loeffler, 1982; Gould and Bres, 1986a; Ruempler, 1992; Wiard, 1992; Velderman, 1997), no one has yet documented the elimination of this behavior from an individual’s repertoire. Ruempler (1992), however, reported that one gorilla’s R/R had completely ceased for over a year after removing all but huge portions of vegetables and browse (18 kg per adult animal per day) from the diet at Cologne Zoo in Germany. For comparison, an adult male gorilla consumes approximately 6 kg/day at Zoo Atlanta (G. Hamor, personal communication), 13 kg/day at Brookfield Zoo (C. Demitros, personal communication), and 30 kg/day in the wild (G.g. beringei, Goodall, 1977). Unfortu-
**Removing Milk from Captive Gorilla Diets: The Impact on Regurgitation and Reingestion (R/R) and Other Behaviors**

Kristen E. Lukas,†,‡,§, Gloria Hamor,∥ Mollie A. Bloomsmith,∥§, Charles L. Horton,∥ and Terry L. Maple∥§

Zoo Biology 18:515 - 528 (1999)

**TABLE 6. Comparisons of gorilla behavior between conditions in Phase 2**

<table>
<thead>
<tr>
<th></th>
<th>Baseline (32 oz milk)</th>
<th>Treatment (32 oz diluted (fruit juice)</th>
<th>Baseline (32 oz milk)</th>
<th>Hypothesis test: baselines vs. treatment</th>
<th>Probability (α = 0.05)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scan data (percentage of time)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R/R</td>
<td>5.9%</td>
<td>3.7%</td>
<td>6.3%</td>
<td>F = 8.508</td>
<td>P = 0.010</td>
</tr>
<tr>
<td>Eat hay</td>
<td>1.3%</td>
<td>1.6%</td>
<td>0.3%</td>
<td>F = 0.767</td>
<td>ns</td>
</tr>
<tr>
<td>Inactive</td>
<td>45.5%</td>
<td>46.6%</td>
<td>46.3%</td>
<td>F = 0.115</td>
<td>ns</td>
</tr>
<tr>
<td>Drink water</td>
<td>3.4%</td>
<td>3.3%</td>
<td>2.9%</td>
<td>F = 0.011</td>
<td>ns</td>
</tr>
<tr>
<td>Social (affiliative)</td>
<td>8.4%</td>
<td>8.0%</td>
<td>11.7%</td>
<td>F = 1.221</td>
<td>ns</td>
</tr>
<tr>
<td>Other undesirable</td>
<td>1.0%</td>
<td>1.2%</td>
<td>2.0%</td>
<td>F = 0.594</td>
<td>ns</td>
</tr>
<tr>
<td>Self-directed behavior</td>
<td>17.1%</td>
<td>17.5%</td>
<td>13.9%</td>
<td>F = 1.681</td>
<td>ns</td>
</tr>
<tr>
<td>Social (agonistic)</td>
<td>0.1%</td>
<td>0.3%</td>
<td>0.4%</td>
<td>F = 0.136</td>
<td>ns</td>
</tr>
<tr>
<td>Other active behavior</td>
<td>16.0%</td>
<td>16.7%</td>
<td>15.0%</td>
<td>F = 0.605</td>
<td>ns</td>
</tr>
<tr>
<td>All-occurrence data (no. per 5 min)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R/R attempts</td>
<td>0.022</td>
<td>0.017</td>
<td>0.011</td>
<td>F = 0.000</td>
<td>ns</td>
</tr>
<tr>
<td>R/R bouts</td>
<td>0.428</td>
<td>0.256</td>
<td>0.422</td>
<td>F = 4.684</td>
<td>P = 0.045</td>
</tr>
<tr>
<td>Feed on another’s regurgitant</td>
<td>0.061</td>
<td>0.061</td>
<td>0.072</td>
<td>F = 0.239</td>
<td>ns</td>
</tr>
<tr>
<td>Examine another engaging in R/R</td>
<td>0.056</td>
<td>0.056</td>
<td>0.072</td>
<td>F = 0.221</td>
<td>ns</td>
</tr>
<tr>
<td>Agonistic behavior</td>
<td>0.089</td>
<td>0.111</td>
<td>0.233</td>
<td>F = 1.342</td>
<td>ns</td>
</tr>
</tbody>
</table>
Chimpanzee R/R
Chimpanzee R/R
An analysis of regurgitation and reingestion in captive chimpanzees

Kate C. Baker a,*, Stephen Phillip Easley b


of cagemates or housing history; nor were sex differences detected. Meal composition was not found to effect the time devoted to R/R. Statistical tests did show a strong positive relationship between rates of R/R and elapsed time since feeding. These results suggest that increasing meal frequency or providing consistently available edible material may prove more broadly effective than altering meal composition. Temporal distributions of R/R differed from those of abnormal old male) (Morgan et al., 1993). That study found that R/R occurred within minutes of each meal, and was most frequent following meals consisting of fruit. Reductions in R/R occurred during behavioral training sessions and when more browse was provided.
Orangutan R/R
Orangutan R/R
Prevalence of Regurgitation and Reingestion in Orangutans Housed in North American Zoos and an Examination of Factors Influencing its Occurrence in a Single Group of Bornean Orangutans

Christine M. Cassella,1,2* Alyssa Mills,1 and Kristen E. Lukas1,2

* Corresponding author
Special Articles

Regurgitation in Gorillas: Possible Model for Human Eating Disorders (Rumination/Bulimia)

EDWIN GOULD, PH.D.
Department of Mammalogy, National Zoological Park, Smithsonian Institution, Washington, D.C.

MIMI BRES, M.S.
Department of Biological Sciences, The George Washington University, Washington, D.C.
Rumination disorder in man

Merycism or Ruminations in Man.
By J. Grant Millar, M.B., Ch.B. Glasg.,

Habitual rumination: a benign disorder
D F Levine, D L Wingate, J M Pfeffer, P Butcher

Merycism or Ruminations Disorder
A Historical Investigation and Current Assessment
Brenda Parry-Jones
Rumination disorder in man

- Historically: linking to bovine ancestry (incl. autopsies to check for chambered forestomach)
  => ‘the mark of the beast’ (primitive impulse)

- 6-10% of institutionalized persons with severe mental retardation

- Complications: malnutrition, weight loss, aspiration/choking
  => aspiration cause of death 5-10% of ruminators

- Social isolation

- Treatment option: ad libitum feeding/satiety
BRIEF REPORT: EFFECTS OF SUPPLEMENTAL FEEDINGS OF WHITE BREAD ON CHRONIC RUMINATION

Christopher J. Masalsky* and James K. Luiselli

Behavioral Interventions
DECREASING RUMINATION USING A STARCHY FOOD SATIATION PROCEDURE

Laura L. Dudley\textsuperscript{1,2}, Cammarie Johnson\textsuperscript{1,2} and R. Scott Barnes\textsuperscript{1}
## Special Articles

**Regurgitation in Gorillas: Possible Model for Human Eating Disorders (Rumination/Bulimia)**

**EDWIN GOULD, Ph.D.**

Department of Neurology, National Zoo, Washington, D.C.

**R. R. BRES, M.S.**

Department of Biological Sciences, The George Washington University, Washington, D.C.

### TABLE 1. Comparison of Regurgitation and Reingestion with Two Human Disorders

<table>
<thead>
<tr>
<th></th>
<th>Bulimia</th>
<th>Ruminator</th>
<th>r/r Gorilla</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ontogeny</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Failure to engage mother to interact</td>
<td>O</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Age at onset</td>
<td>11–22 yr</td>
<td>3–6 mo</td>
<td>&gt; 5 yr</td>
</tr>
<tr>
<td>Parental separation</td>
<td>X</td>
<td>O</td>
<td>X</td>
</tr>
<tr>
<td>Lacks control of eating</td>
<td>X(05)</td>
<td>O</td>
<td>X</td>
</tr>
<tr>
<td><strong>Motor pattern</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neck swaying</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Chews</td>
<td>O</td>
<td>X^2,7</td>
<td>X</td>
</tr>
<tr>
<td>Mouth fills</td>
<td>O</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Reingest</td>
<td>O</td>
<td>X^7,47–49</td>
<td>X</td>
</tr>
<tr>
<td>Valsalva maneuver</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Mueller maneuver</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Rhythmic chest, neck movement</td>
<td>O</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Induced with finger</td>
<td>X(05)</td>
<td>X^36</td>
<td>X</td>
</tr>
<tr>
<td>No effort required</td>
<td>X(05)</td>
<td>O</td>
<td>X</td>
</tr>
<tr>
<td>Bends deeply prior to vomiting</td>
<td>X</td>
<td>X^0,47,48</td>
<td>X</td>
</tr>
<tr>
<td><strong>Timing</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Interval between eating and regurgitation</td>
<td>&gt; 1 min</td>
<td>0–30 min</td>
<td>0–8.3 hr</td>
</tr>
<tr>
<td>Interval between regurgitations</td>
<td>O</td>
<td>2–4 min</td>
<td>1.5–3 min</td>
</tr>
<tr>
<td>Duration of bouts</td>
<td>–</td>
<td>30–60 min</td>
<td>2 min–6 hr</td>
</tr>
<tr>
<td>Frequency/day</td>
<td>1^6</td>
<td>15–20/30–60^6</td>
<td>1–175</td>
</tr>
<tr>
<td><strong>Context</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Do it alone</td>
<td>X</td>
<td>O</td>
<td>X</td>
</tr>
<tr>
<td>Favorite foods</td>
<td>O</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Enjoy the taste</td>
<td>O</td>
<td>X^2,49</td>
<td>X</td>
</tr>
<tr>
<td><strong>Treatment</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Reduced if more food</td>
<td>O^6</td>
<td>X</td>
<td>(one study)^35</td>
</tr>
<tr>
<td>Increased mother contact</td>
<td>–</td>
<td>X^36</td>
<td>(browse)</td>
</tr>
</tbody>
</table>

Definitions: X, inferred; X, observed; –, unknown; O, doesn't occur.
Definitions

• Rumination / Merycism
  • “to turn over in the mind”
  • “to chew the cud”
    => implies regurgitation, chewing, re-swallowing

  => maladaptive in humans as well as certain zoo animals
  ‘rumination syndrome’ / ‘RR’
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=> ‘bubbling’ in certain flies
Fly bubbling
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  => ‘bubbling’ in certain flies

  => obligatory mechanism in functional ruminants
  => probably facultative mechanism in several herbivores
Rumination in ruminants
Rumination in ruminants
Rumination in camelids
Why rumination?
Why rumination?

- Anti-predation strategy
  - "Rumination seems to allow herbivores to ingest in haste and masticate at leisure" (Karasov & Del Rio 2007)
  
  => Ruminants should ingest similar amounts of food as other herbivores and just ‘chew later’ - or become time-constrained in intake
Why rumination?

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• Energy-saving mechanism
  • Rumination occurs in a state of ‘drowsiness’ similar to rest; may represent an energy-saving strategy - less time spent ‘wide awake’ (Gordon 1968)
    => Ruminants should have lower energy requirements/higher productivity than other herbivores
Why rumination?

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● Enhancement of digestive efficiency
  ● Rumination reduces particle size and hence allows faster digestion at constant intake
    => Ruminants should have smaller digesta particle sizes (and higher intakes) than other herbivores
Hindgut Fermentation - Caecum

from Stevens und Hume (1995)
Hindgut Fermentation - Caecum

from Stevens und Hume (1995), Fotos J. Fritz/M. Clauss
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: 3.3 m

from Stevens & Hume (1995)
Foregut Fermentation

from Stevens & Hume (1995)
Foregut Fermentation

Kangaroo (Macropus giganteus)
Body Length: 115 cm

Sloth (Bradypus tridactylus)
Body Length: 55 cm

Colobus Monkey (Colobus abyssanicus)
Body Length: 50 cm

Hippopotamus (Hippopotamus amphibius)
Body Length: 4 m

Photos A. Schwarm/ M. Clauss
Foregut Fermentation - Ruminant

Llama (Lama glama)
Body Length: 193 cm

Sheep (Ovis aries)
Body Length: 110 cm

Photo Llama: A. Riek

aus Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

from Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

Fermentation after enzymatic digestion and absorption:

from Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

Fermentation after enzymatic digestion and absorption:

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

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Foregut vs. Hindgut Fermentation

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from Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

Fermentation after enzymatic digestion and absorption:

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

Use of easily digestible substrates

from Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:

Fermentation after enzymatic digestion and absorption:

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

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Foregut vs. Hindgut Fermentation

**Fermentation prior to enzymatic digestion and absorption:**
- Use of bacterial protein, bacterial products (B-Vitamins)

**Fermentation after enzymatic digestion and absorption:**
- ‘Loss’ of bacterial protein, bacterial products (B-Vitamins?)
- (coprophagy)
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from Stevens & Hume (1995)
Fermentation prior to enzymatic digestion and absorption:

- Use of bacterial protein, bacterial products (B-Vitamins)
- Bacterial detoxification?

Fermentation after enzymatic digestion and absorption:

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- (coprophagy)
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from Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

Fermentation prior to enzymatic digestion and absorption:
- Use of bacterial protein, bacterial products (B-Vitamins)
- Bacterial detoxification?
- ‘Loss’ of easily digestible substrates and bacterial modification

Fermentation after enzymatic digestion and absorption:
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from Stevens & Hume (1995)
Foregut vs. Hindgut Fermentation

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- Use of bacterial protein, bacterial products (B-Vitamins)
- Bacterial detoxification?
- ‘Loss’ of easily digestible substrates and bacterial modification

particulary suited for fibre fermentation

Fermentation after enzymatic digestion and absorption:
- ‘Loss’ of bacterial protein, bacterial products (B-Vitamins?)
- (coprophagy)
- Use of easily digestible substrates

from Stevens und Hume (1995)
European Mammal Herbivores in Deep Time

from Langer (1991)
European Mammal Herbivores in Deep Time

from Langer (1991)
Conceptualizing herbivore diversity

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

\[ R^2 = 0.9497 \]

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

Data from Savage et al. (2004)

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

\[ R^2 = 0.9497 \]
Conceptualizing herbivore diversity

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

metabolic intensity

\[ rDMI \ (g \ kg^{-0.75} \ d^{-1}) \]

from Clauss et al. (2010)
Conceptualizing herbivore diversity

metabolic intensity

\[ r\text{DMI} \text{ (g kg}^{-0.75}\text{ d}^{-1}) \]

from Clauss et al. (2010)
Conceptualizing herbivore diversity

metabolic intensity

$r_{DMI}$ (g kg$^{-0.75}$ d$^{-1}$)

from Clauss et al. (2010)
Conceptualizing herbivore diversity

metabolic intensity

\[ r\text{DMI} \text{ (g kg}^{-0.75}\text{ d}^{-1}) \]

from Clauss et al. (2010)
Conceptualizing herbivore diversity

Metabolic intensity

$r_{DMI} \ (g \ kg^{-0.75} \ d^{-1})$

from Clauss et al. (2010)
Intake and Passage in Primates

from Clauss et al. (2008)
Intake and Passage in Primates

from Clauss et al. (2008)
Hindgut fermenters can have either - high or low intake and (hence) short or long ingesta retention

from Clauss et al. (2008)
Nonruminant forms appear limited to a low food intake and (hence) long ingesta retention.

Intake and Passage in Primates

from Clauss et al. (2008)
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)
<table>
<thead>
<tr>
<th>Digestive Strategies</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Low intake</strong></td>
</tr>
<tr>
<td>⇒ long passage</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td><strong>High intake</strong></td>
</tr>
<tr>
<td>⇒ short passage</td>
</tr>
<tr>
<td>Low intake</td>
</tr>
<tr>
<td>------------</td>
</tr>
<tr>
<td>⇒ long passage</td>
</tr>
<tr>
<td>Autoenzymatic digestion followed by thorough fermentative digestion</td>
</tr>
</tbody>
</table>
Digestive Strategies

| High intake  | Low intake  
|-------------|-------------
| Autoenzymatic digestion followed by cursory fermentative digestion | Autoenzymatic digestion followed by thorough fermentative digestion |
Digestive Strategies

<table>
<thead>
<tr>
<th>Low intake</th>
<th>Autoenzymatic digestion followed by thorough fermentative digestion</th>
<th>Fermentative digestion followed by autoenzymatic digestion of products (and remains)</th>
</tr>
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<tbody>
<tr>
<td>⇒ long passage</td>
<td>✅</td>
<td>✅</td>
</tr>
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**Digestive Strategies**

<table>
<thead>
<tr>
<th>Low intake ⇒ long passage</th>
<th>Autoenzymatic digestion followed by thorough fermentative digestion ✓</th>
<th>Fermentative digestion followed by autoenzymatic digestion of products (and remains) ✓</th>
</tr>
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<tbody>
<tr>
<td>High intake ⇒ short passage</td>
<td>Autoenzymatic digestion followed by cursory fermentative digestion ✓</td>
<td>Cursory fermentative digestion mainly of autoenzymatically digestible components followed by ineffective autoenzymatic digestion of undigested fiber?</td>
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## Digestive Strategies

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</table>
Intake and Passage

ungulates from Foose (1982)
mammal herbivores Clauss et al. (2007)
**Intake and Passage**

- **OMI (g/kg^{0.75}/d)** vs. **MRT (h)**
  - Simple-stomached
  - Nonruminant ff

- **DMI (g/kg^{0.75}/d)** vs. **MRT (h)**
  - Simple-stomached
  - Nonruminant ff

- **Ingestive and Passage**
  - Ungulates from Foose (1982)
  - Mammal herbivores from Clauss et al. (2007)
Intake and Passage

Nonrum. ff appear limited to a low food intake and (hence) long ingesta retention
while hindgut fermenters can cover the whole range

ungulates from Foose (1982)
mammal herbivores Clauss et al. (2007)
## From Digestive to Metabolic Strategies

<table>
<thead>
<tr>
<th>Low intake</th>
<th>Long passage</th>
<th>Low BMR</th>
<th>High BMR</th>
</tr>
</thead>
<tbody>
<tr>
<td>High intake</td>
<td>Short passage</td>
<td>high BMR</td>
<td></td>
</tr>
</tbody>
</table>
European Mammal Herbivores in Deep Time

from Langer (1991)
How can you increase fermentative digestive efficiency?

- Digestion of plant fibre by bacteria is the more efficient ...
  - the more time is available for it
    = the longer the mean gastrointestinal retention time.
  - the finer the plant fibre particles are
    = the finer the ingesta is chewed.
How can you increase energy intake?

- higher food intake
- higher digestive efficiency
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

higher gut volume
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

sorting !
If you do not sort ...
If you do not sort ...
If you do not sort ...
If you do not sort ...
If you do not sort ...
If you do not sort ...
If you do not sort ...
If you do not sort ...
The power of sorting
The power of sorting
The power of sorting
The power of sorting
The power of sorting
The power of sorting
Ruminant vs. Nonruminant Foregut Fermentation

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

Schwarm et al. (2008, 2009)
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How can you increase energy intake?

- higher food intake
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→ sorting!
Intake and Passage

ungulates from Foose (1982)
mammal herbivores Clauss et al. (2007)
**Intake and Passage**

- **OMI (g/kg\textsuperscript{0.75}/d)**
- **MRT (h)**

- Simple-stomached
- Nonruminant
- Ruminant

**Intake and Passage**

ungulates

from Foose (1982)

mammal herbivores

Clauss et al. (2007)
Intake and Passage

ungulates
from Foose (1982)

mammal herbivores
Clauss et al. (2007)
Intake and Passage

Ruminants expand the intake range of foregut fermenters (while retaining long retention times)

ungulates from Foose (1982)
mammal herbivores Clauss et al. (2007)
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing
“Mammals are the definite chewers”
“Mammals are the definite chewers”

aus Jernvall et al. (1996)
“Mammals are the definite chewers”

aus Jernvall et al. (1996)
“Mammals are the definite chewers”
Ingesta particle size (chewing efficiency)

from Fritz (2007)
Ingesta particle size (chewing efficiency)

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Ingesta particle size (chewing efficiency)

from Fritz (2007)
“Mammals are the definite chewers”
Ingesta particle size (chewing efficiency)

from Fritz (2007)
Ingesta particle size (chewing efficiency)

from Fritz (2007)
Why can’t everyone just chew more?
Chewing in ruminants and nonruminants
Chewing in ruminants and nonruminants
Chewing in ruminants and nonruminants
Chewing in ruminants and nonruminants

Photo A. Schwarm
Chewing in ruminants and nonruminants
Chewing in ruminants and nonruminants

Photo A. Schwarm
How can you increase energy intake?

- higher food intake
- longer retention
- finer chewing

→ sorting!
Conceptualizing herbivore diversity

metabolic intensity

rDMI (g kg^{-0.75} d^{-1})

from Clauss et al. (2010)
Conceptualizing herbivore diversity

from Clauss et al. (2010)
Digestive and Metabolic Strategies

Low intake
⇒ long passage  
⇒ *low* metabolism  

High intake
⇒ differentiated passage  
⇒ *high* metabolism
### Digestive and Metabolic Strategies

<table>
<thead>
<tr>
<th>Low intake</th>
<th>High intake</th>
<th>Differentiation</th>
<th>Metabolism</th>
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<tbody>
<tr>
<td>long passage</td>
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<td>✓</td>
<td>✓</td>
</tr>
<tr>
<td>low metabolism</td>
<td>✓</td>
<td>✓</td>
<td>✓</td>
</tr>
</tbody>
</table>

- **Low intake**:
  - long passage
  - low metabolism
- **High intake**:
  - differentiated passage
  - high metabolism
Digestive and Metabolic Strategies

Low intake
⇒ long passage
⇒ *low* metabolism

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High intake
⇒ differentiated passage
⇒ *high* metabolism

<table>
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<tr>
<th></th>
<th>✓</th>
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<th>✓</th>
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European Mammal Herbivores in Deep Time

from Langer (1991)
European Mammal Herbivores in Deep Time

from Langer (1991)
**Digestive and Metabolic Strategies**

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<td>✓</td>
<td>✓</td>
</tr>
<tr>
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Conceptualizing herbivore diversity

metabolic intensity

from Clauss et al. (2010)
The case of the proboscis monkey
The case of the proboscis monkey

from Stevens und Hume (1995)
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

[Graph showing time spent feeding (% of day) vs. R/R and no R/R]
Faecal particle size in free-ranging primates supports a ‘rumination’ strategy in the proboscis monkey (*Nasalis larvatus*).

Ikki Matsuda · Augustine Tuuga · Chie Hashimoto · Henry Bernard · Juichi Yamagiwa · Julia Fritz · Keiko Tsubokawa · Masato Yayota · Tadahiro Murai · Yuji Iwata · Marcus Clauss

<table>
<thead>
<tr>
<th>mm</th>
<th>16</th>
<th>8</th>
<th>4</th>
<th>2</th>
<th>1</th>
<th>0.5</th>
<th>0.25</th>
<th>0.125</th>
<th>0.063</th>
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Faecal particle size (dMEAN, mm)

Body mass (kg)

Oecologia
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![Graph showing faecal particle size (dMEAN, mm) against body mass (kg) for different species.](image-url)
The case of the kangaroos
The case of the kangaroos

from Stevens und Hume (1995)
The case of the kangaroos

Food Regurgitation in the Macropodidae

S. Barker,* G. D. Brown† and J. H. Calaby*

BIOLÓGICOS ZENTRALBLATT

Vergleichende Untersuchung des Wiederkauverhaltens

Von Hubert Hendrichs¹)

Dagegen sah ich folgende Marsupialier wiederkauen:

Thylagale eugenii (Desmarest, 1817)
Setonix brachyrurus (Quoy et Gaimard, 1830)
Dendrolagus ursinus (Temminck, 1836)
Dendrolagus ursinus integus (Müller, 1840)
Protejennodon agilis (Gould, 1842)
Protejennodon rufogrisea (Desmarest, 1817)
Macropus gigantea (Zimmermann, 1777)
Macropus (Megaleia) rufus (Desmarest, 1822)
Macropus (Osphranter) robustus (Gould, 1841).
The case of the kangaroos
The case of the kangaroos

No distinct stratification of ingesta particles and no distinct moisture gradient in the fore-stomach of non-ruminants: The wallaby, peccary, hippopotamus, and sloth

Angela Schwarm\textsuperscript{a,b,*}, Sylvia Ortmann\textsuperscript{a}, Julia Fritz\textsuperscript{c}, Edmund Flach\textsuperscript{d}, Wolfram Rietschel\textsuperscript{e}, Marcus Clauss\textsuperscript{f}

Mammalian Biology 78 (2013) 412–421
The case of the capybara
The case of the capybara

from Stevens und Hume (1995)
Regurgitation and Coprophagy. – A significant new finding of this study was observations of capybaras regurgitating and masticating their food while resting, a parallel of rumination among the ruminants such as cattle.

Regurgitation and mastication of food by capybaras was seen only while resting on land, throughout the day, unlike coprophagy which is practised primarily in the morning (Lord 1991, Herrera 1985). Regurgitation is frequently proceeded by a gaping yawn, followed by stretching of the neck, then about a minute of mastication. Sometimes the food material could been seen in the mouth and on occasion spilled out. A young capybara was videotaped eating some spilled regurgitation material from an adult female. The gape yawn may be proceeded by a half role on one side, and/or sitting up. Videotape analysis of this practice has shown the pattern to be somewhat ritualized. It is practised much more frequently than coprophagy, but was probably overlooked because it appears to be a simple yawn.
The case of the hyrax
The case of the hyrax

from Stevens und Hume (1995)
The case of the hyrax

Rock Hyrax - Irac coneys

Questi animali sono citati tre volte nella Bibbia:

Lv 11:5, Pr 30:26, Sal 104:18

These animals are quoted three times in the Bible
11 The Lord said to Moses and Aaron, "Say to the Israelites: 'Of all the animals that live on land, these are the ones you may eat: 3 You may eat any animal that has a divided hoof and that chews the cud. 4 'There are some that only chew the cud or only have a divided hoof, but you must not eat them. The camel, though it chews the cud, does not have a divided hoof; it is ceremonially unclean for you. The hyrax, though it chews the cud, does not have a divided hoof; it is unclean for you.
Vergleichende Untersuchung des Wiederkauverhaltens

Von Hubert Hendrichs

VI. Entdeckung von Wiederkauen bei einer Säugetierordnung

bereiste, schreibt vom „Aschkoko“, dem Klippschliefer: „Ich hörte nie einen Laut von ihm, aber er käuet zuverlässig wieder: um dies zu untersuchen unterhielt ich ihn hauptsächlich eine Zeitlang lebendig“. 
The case of the hyrax
The case of the koala
The case of the koala

from Stevens und Hume (1995)
Evidence for the occurrence of rumination-like behaviour, or merycism, in the koala (Phascolarctos cinereus, Goldfuss)

M. Logan
EFFECT OF TOOTH WEAR ON THE RUMINATION-LIKE BEHAVIOR, OR MERYCISISM, OF FREE-RANGING KOALAS (PHASCOLARCTOS CINEREUS)

M. LOGAN*

The case of the koala

The effects of lactation on the feeding behaviour and activity patterns of free-ranging female koalas (Phascolarctos cinereus Goldfuss)

M. Logan and G. D. Sanson

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*Australian Journal of Zoology, 2003, 51, 415–428*
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M. Logan and G. D. Sanson

*Australian Journal of Zoology, 2003, 51, 415–428*
Why rumination?

- **Anti-predation strategy**
  - “Rumination seems to allow herbivores to ingest in haste and masticate at leisure” (Karasov & Del Rio 2007)
    => Ruminants should ingest similar amounts of food as other herbivores and just ‘chew later’ - or become time-constrained in intake

- **Energy-saving mechanism**
  - Rumination occurs in a state of ‘drowsiness’ similar to rest; may represent an energy-saving strategy - less time spent ‘wide awake’ (Gordon 1968)
    => Ruminants should have lower energy requirements/higher productivity than other herbivores

- **Enhancement of digestive efficiency**
  - Rumination reduces particle size and hence allows faster digestion at constant intake
    => Ruminants should have smaller digesta particle sizes (and higher intakes) than other herbivores
Regurgitation / Reingestion as a behavioural disorder appears limited to great apes /humans
Rumination has evolved repeatedly in mammals.
Rumination is most powerful if coupled with a sorting mechanism.
thank you for your attention

outlook: cheek pouches // coprophagy