Comparative nutrient extraction from forages by grazing bovids and equids: a test of the nutritional model of equid/bovid competition and coexistence

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Summary. Ruminants are unevenly distributed across the range of body sizes observed in herbivorous mammals; among extant East African species they predominate, in numbers and species richness, in the medium body sizes (10–600 kg). The small and the large species are all hind-gut fermenters. Some medium-sized hind-gut fermenters, equid perissodactyls, coexist with the grazing ruminants, principally bovid artiodactyls, in grassland ecosystems. These patterns have been explained by two complementary models based on differences between the digestive physiology of ruminants and hind-gut fermenters. The Demment and Van Soest (1985) model accounts for the absence of ruminants among the small and large species, while the Bell/Janis/Foose model accounts both for the predominance of ruminants, and their co-existence with equids among the medium-sized species (Bell 1971; Janis 1976; Foose 1982). The latter model assumes that the ruminant is competitively superior to the hind-gut system on medium quality forages, and that hind-gut fermenters persist because of their ability to eat more, and thus to extract more nutrients per day from high fibre, low quality forages. Data presented here demonstrate that compared to similarly sized grazing ruminants (bovids), hind-gut fermenters (equids) have higher rates of food intake which more than compensate for their lesser ability to digest plant material. As a consequence equids extract more nutrients per day than bovids not only from low quality foods, but from the whole range of forages eaten by animals of this size. Neither of the current nutritional models, nor refinements of them satisfactorily explain the preponderance of the bovids among medium-sized ungulates; alternative hypotheses are presented.

Key words: Ruminant – Hind-gut fermenter – Intake – Digestion – Competition

All mammalian herbivores depend upon symbiotic relationships with microorganisms to digest the fibrous fractions (cellulose, hemicelluloses) of the vegetation they eat. The enlarged sections of their gastro-intestinal tracts, fermentation chambers, which house the microorganisms are in the hindgut, in an enlarged caecum and colon, in some lineages of herbivores (subungulates, perissodactyls, rodents). Three artiodactyl groups (suids, camelsids and the “ruminants”): antilocaprids, cervids, giraffids and bovids) have independently evolved systems of fermentation chambers in their forage (Moir 1968).

Ruminants are unevenly distributed across the range of body sizes observed in herbivores, Fig. 1. Among extant East African species, they predominate in the medium body sizes (10–600 kg) while the small and the large species are all hind-gut fermenters. This pattern has been explained on the basis of differences between the digestive physiology of these groups of animals, in particular the time food is retained in their digestive tracts, the extent of digestion of food particles, and the energetic consequences for the herbivores of having a (microorganism) trophic level between their food and themselves (Demment and Van Soest 1982, 1985).

Among the medium-sized grazing herbivores the artiodactyl ruminant bovids and the perissodactyls, chiefly hind-gut fermenting equids, have been the dominant species since the Palaeocene. The lineages leading to these modern groups separated some 55 million years ago, but they have evolved in parallel. Equids and bovids show convergence in key morphological characters such as elongated limbs and hypsodonty, and today occupy sim-
ages (daily digestible dry matter intake) which determines the quantity of nutrients available for maintenance, growth and reproduction. Nutrient extraction is a product of the animal's daily food intake and the digestibility of the ingested forage:

\[
\text{Nutrient extraction} = \frac{\text{Digestion coefficient}}{\text{Voluntary intake}}
\]

Very high quality plant tissues (e.g., seeds) are rare in natural ecosystems (Demment and Van Soest 1985). For medium quality forages, extraction rates of nutrients by ruminants are high because the relatively low concentrations of fibre in such foods allow high digestion coefficients and high intakes (passage rates of low fibre foods through the rumen are fast). On low quality forages nutrient extraction rates drop sharply because both digestion coefficients and intakes (Campling and Lean 1983) decline.

It has been suggested that hind-gut fermenters eat relatively more than ruminants, especially of high fibre foods, because food passes faster through hind-gut fermenters, which have no selective delaying mechanism for large particles (Alexander 1946; Balch and Campling 1965; Van Soest et al. 1983). If hind-gut fermenters can extract more nutrients per day than ruminants on very fibrous foods these could provide equids with a "ecological refuge" which would allow medium-sized hind-gut fermenters coexist with ruminants (Bell 1971; Janis 1976; Foote 1978). These arguments are summarised in a qualitative "nutritional" model (Fig. 2). On medium quality forages (i.e., 40–70% cell wall content) ruminants are assumed to extract more nutrients per day than do hind-gut fermenters, while on very high as well as low fibre forages hind-gut fermenters should achieve higher rates of nutrient extraction than do ruminants.

The two models are therefore complementary. The Demment and Van Soest model accounts for the predominance of hind-gut fermenters at the extremes of the body weight range, while the Bell/Janis/Foote model, which considers extraction rates and not simply the digestibility of forages, accounts both for the predominance of ruminants among medium-sized ungulates, and their coexistence with equids.

In this paper we provide a critical test of the Bell/Janis/Foote model by reviewing the available data on nutrient extraction rates by equids and bovids on forages of medium to high fibre concentration, typical of natural grazing-lands.

Materials and methods

Multi-species trials

The Foote data set. The first part of the results section presents data collected during feeding trials of wild and domestic ungulates at five North American zoos and Cornell University (Foote 1982). Ten species or sub-species of bovid ranging from 80 kg sheep to 800 kg African buffalo, Syncerus caffer and seven species or breeds of equids ranging from 140 kg Wild ass (Equus hemionus) to 450 kg domestic horse were used in the trials, although not all trials were done with all the species. The animals used were
of both sexes, and a variety of ages; few were lactating at the
time of the trials. Two forages were presented ad libitum: a high
fibre hay (timothy, *Phleum pratense*, or prairie grass, *Andropogon*
spp.; cell wall content 67–75%) and a medium fibre alfalfa hay
(*Medicago sativa*; cell wall content 40–53%).

The first 14 days of the 24 day trials allowed the animals to
adapt to their experimental diets. The forages were distributed once
a day on an ad libitum basis. Forages and faeces were weighed,
and then sampled. Dry and organic matter contents were deter-

Daily organic matter intake (OMI, kg d⁻¹) was calculated as
the average of the last 10 days of each trial. Total faecal collections
were made during three days in order to calculate the apparent
digestibility coefficients of organic matter (OMD %, which in-
cludes metabolic losses) and the daily digestible organic matter
intake (DOM, kg d⁻¹). Apparent digestion coefficients are used for
this comparison, rather than true digestibilities because they
take metabolic losses into account and therefore provide a better
measure of net nutrient extraction.

Mean retention time (MRT, h) was determined by staining
10% of the food provided on one way with basic Fuchsin. The
faeces were collected at known intervals after administration. MRT
(h) was calculated as:

\[
MRT = \sum \left( P_x \cdot t_x \right)
\]

where \( P_x \) is the proportion of the marker excreted in the
time interval \( x \), and \( t_x \) is the time \( (h) \) elapsed between administration
of the marker and the end of the time interval \( x \).

Other studies. Only two other trials have measured simultaneously
the nutrient extraction rates of equids and bovid fed forages with a
range of fibre concentrations. In the first of these, quarter-horse
type mares and beef cows were fed three hays, Crested wheatgrass
(*Agropyron desertorum*), Smooth broom (*Bromus inermis*), and a
mixture of Timothy and Redtop (*Agrostis alba*) whose fibre con-
 tents ranged between 70–80%. The animals were given 11 days
to habituate to the diets; collections were made over the following
ten days (Johnson et al. 1982).

In the other study growing Plains zebra (*Equus burchelli*), don-
keys and zebu steers were fed three mixtures of Red oat grass
(*Themeda triandra*) and alfalfa hays with crude fibre contents be-
tween 33–39%, crude protein contents 5–16%. The animals had
ten days to habituate followed by seven days of collection (Gakahu
1982).

Single species trials: modelling nutrient extraction rates
of equids and bovids on forages of differing fibre concentration

The three studies cited above used animals of both sexes and a
variety of ages, but for practical reasons very few were lactating.
Food intake depends to a great extent on animal requirements
for maintenance, growth and reproduction. The highest rates of
intake are found in lactating cows (A.R.C 1965). In order to esti-
mate the intake potential of the species and to extend the test
of the model beyond these three studies, in the second part of
this paper we have reviewed the results of single species feeding
trials to determine both dry matter digestibility (DDM) and volun-
tary dry matter intake (DMI) for lactating equids or cattle on
forages varying in fibre concentration. These trials can be used
for our purposes provided that they have a common measure of the
fibre concentration we chose to use the cell wall content of the
forage (NDF of the Van Soest detergent analysis, Goering and Van
Soest 1970). The range of fibre concentrations considered
(40–80% NDF) encompasses most of the forages grazed by medi-
un-sized ungulates (Van Soest 1982; Demment and Van Soest
1985).

In this part of the analysis, the procedure was to obtain regres-
sions of the digestibility and intake of forages on the fibre

![Fig. 3. The effect of dietary fibre on the digestibility of dry matter in equids (○—○ Fonsebeck 1968, Foose 1982) and in cattle (●—● NRC 1984)](image-url)
Fig. 4. The effect of dietary fibre on the voluntary dry matter intake (DMI) in equids (----- E) and in bovids (--- B)
Equids = a) 170 g·W⁻⁰.⁷³·d⁻¹
b) 119 - 3.69 NDF(%) + 32.37 ln[NDF(%)](g·W⁻¹·⁷³·d⁻¹)
Bovids = see text equation (4)

Table 1. Comparative retention times and digestibilities of alfalfa and grass hays in equids and bovids. Mean values, data from Foote (1982)

<table>
<thead>
<tr>
<th></th>
<th>Bovids</th>
<th>Equids</th>
<th>Significance of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean retention time (MRT, h)</td>
<td>grass</td>
<td>70.2</td>
<td>44.5</td>
</tr>
<tr>
<td></td>
<td>alfalfa</td>
<td>55.5</td>
<td>37.3</td>
</tr>
<tr>
<td>Digestibility of organic matter (OMD, %)</td>
<td>grass</td>
<td>55.9</td>
<td>47.0</td>
</tr>
<tr>
<td></td>
<td>alfalfa</td>
<td>71.9</td>
<td>63.5</td>
</tr>
</tbody>
</table>

In view of this uncertainty we have used two equations for the relationship between intake rate and forage fibre concentration for equids. The first keeps intake constant at 170 g·W⁻⁰.⁷³·d⁻¹ while the second, conservative, hypothesis uses the slope of the relationship between DMI and NDF for cattle, and therefore gives equids intake rates for high NDF forages which are certainly lower than the true values (Fig. 4, a versus b).

Statistical analysis. The data were analysed using least-squares regression analysis (Sokal and Rohlf 1981). We evaluated the differences between the regression intercepts using analysis of covariance after controlling for the regression slopes (Sokal and Rohlf 1981). Where regressions were non-significant the mean values were compared using t-tests, after transformation with arcsine for percentages.

Results

Multi-species trials

The Foote data set. The larger bovids tended to retain forages longer than the smaller ones, but there was no significant relationship between MRT' and body weight in either taxonomic group or forage in this data set (bovids, grass \(r² = 0.070\), alfalfa \(r² = 0.009\), \(n = 9.8\); equids \(r² = 0.211\), 0.123, \(n = 7.6\)). However, there was a clear difference between taxa, Table 1, with bovids retaining the food 50% longer than equids.

The larger animals tended to digest the days more completely than the smaller ones, but there was no significant effect of body size on the digestibility coefficients (OMD) of bovids or equids for grass or alfalfa (grass \(r² = 0.272\), 0.180, \(n = 10.9\); alfalfa \(r² = 0.048\), 0.135, \(n = 7.6\)). The digestibility of alfalfa was high, that of the grass hay low, and in each case digestibility was lower in equids than bovids (Table 1).

The pattern, therefore is that equids retained the forages for less time in their alimentary canal and digested the forages less completely.

The low MRTs allowed the equids to achieve significantly higher intakes on these forages (Fig. 5a, grass, comparison of intercepts: \(F_{1,14} = 38.1, \ P < 0.001\); Fig. 5b, alfalfa: \(F_{1,12} = 16.5, \ P = 0.002\)). As a result the extraction of nutrients was significantly higher in equids.
than in bovids (Fig. 6), both on the high fibre grass hays (F{eq}_1,14 = 14.7, P = 0.002) and on the medium fibre alfalfa hays (comparison of intercepts: F{eq}_1,12 = 7.15, P = 0.019).

Other studies. In the first study, the quarter-horse type mares ate and extracted 48–58% more dry matter than

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**Fig. 6a, b.** Relationships between extraction rates (digestible organic matter intake, DOMI) and body weight (W) in equids (○⋅⋅⋅⋅⋅⋅⋅⋅○ E) and bovids (●⋅●●●●●●●● B) fed on a) high fibre grass and b) medium fibre alfalfa hays. The relationships are:

Equids - grass: ln(DOMI) = -3.28 + 0.796 lnW (r{eq}^2 = 0.805, P < 0.01, n = 7) alfalfa: ln(DOMI) = -2.54 + 0.727 lnW (r{eq}^2 = 0.986, P < 0.001, n = 6) Bovids - grass: ln(DOMI) = -5.01 + 1.01 lnW (r{eq}^2 = 0.855, P < 0.001, n = 10) alfalfa: ln(DOMI) = -3.15 + 0.800 lnW (r{eq}^2 = 0.924, P < 0.001, n = 9) Data from Foose (1982)

**Fig. 7.** Rates of dry matter extraction (digestible dry matter intake) by horses (●, W = 429 kg) and cattle (○, W = 415 kg) on three forages. Data from Johnson et al. 1982

**Table 2.** Differences between the extraction of dry matter (DDMI, g W{eq}^{-0.75} d{eq}^{-1}) by equids and cattle on three forages varying in quality. Data from Gakahu (1982)

<table>
<thead>
<tr>
<th>Hay Quality</th>
<th>Species</th>
<th>Body (W, kg)</th>
<th>DDMI (g W{eq}^{-0.75} d{eq}^{-1})</th>
<th>Difference (%) (equid-bovid)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Good</td>
<td>Zebra</td>
<td>198</td>
<td>117</td>
<td>+46</td>
</tr>
<tr>
<td></td>
<td>Donkey</td>
<td>199</td>
<td>113</td>
<td>+41</td>
</tr>
<tr>
<td></td>
<td>Steer</td>
<td>154</td>
<td>80</td>
<td>+36</td>
</tr>
<tr>
<td>Medium</td>
<td>Zebra</td>
<td>95</td>
<td>52</td>
<td>+36</td>
</tr>
<tr>
<td></td>
<td>Donkey</td>
<td>91</td>
<td>30</td>
<td>+30</td>
</tr>
<tr>
<td></td>
<td>Steer</td>
<td>70</td>
<td></td>
<td>+28</td>
</tr>
<tr>
<td>Low</td>
<td>Zebra</td>
<td>71</td>
<td>41</td>
<td>+28</td>
</tr>
<tr>
<td></td>
<td>Donkey</td>
<td>67</td>
<td>16</td>
<td>+16</td>
</tr>
<tr>
<td></td>
<td>Steer</td>
<td>58</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Fig. 8** Model of the rates of nutrient extraction (DDMI g W{eq}^{-0.75} d{eq}^{-1}), in bovids (●●● B) and equids (○○○ E), see Methods Single species trials assuming an intake of a) 170 g W{eq}^{-0.75} d{eq}^{-1}
b) 119–3.69 NDF(%) + 32.37 / NDF(%) (g W{eq}^{-0.75} d{eq}^{-1})

the beef cows from the three hays (Fig. 7). In the second study the zebra and donkeys ingested and extracted more than the zebu steers by 16–46% (Table 2). The results from the zoo study are therefore corroborated by these two other trials where equids and bovids were fed on forages varying in fibre concentration.

Single species trials: modelling nutrient extraction by equids and bovids on forages of differing fibre concentrations

Daily rates of nutrient extraction (equation 1) were modelled using equations 2 and 4 for the bovids. For the
equids we used equation 3 and the two hypotheses for intake as described above in Methods Single species trials.

The model shows that over the range of fibre concentration considered, equids can extract more nutrients than bovids from all forages, whichever hypothesis we use for food intake in equids, Fig. 8. The lower digestibility of forages in equids is more than compensated for by the large amounts these animals eat per day.

Discussion

The evidence presented in this paper shows that equids are capable of extracting more nutrients per day from *ad libitum* forage diets than bovids. This is true across the range of fibre concentrations encountered in diets of wild herbivores of this size, and supports part of the Bell/Janis/Foose model (Fig. 2) in that the hind-gut fermenting equids extract more nutrients than do the ruminant bovids on high fibre forages. However, these data do not support a crucial part of the nutritional model, because on middle-fibre forages ruminants do not achieve higher nutrient extraction rates than hind-gut fermenters. Why then do the bovids predominate among herbivores of medium body size?

There are three obvious ways in which the nutritional model of Bell/Janis/Foose might be refined. In many forages, particularly in the tropics, protein is the limiting nutrient (Bell 1971; White 1978; Owen-Smith 1982). The digestible protein intake rather than digestible dry matter intake may therefore be the relevant measure of nutrient extraction. The apparent true digestibility of protein is similar in equids and bovids (Vander Noot and Gilbreath 1970; Foose 1982; Van Soest 1982) whereas bovids digest dry matter better. The extraction rate of protein by equids relative to bovids is therefore even higher than the extraction rate of dry matter. Moreover adult equids are no more sensitive than bovids to the quality of dietary protein because of urea recycling and microbial synthesis of amino acids (Jarrige and Tisserand 1984).

Secondly, there may be important differences in conversion efficiencies of digestible energy to metabolisable and net energy. Forages provide more metabolisable energy to cattle than to horses, but most have a higher net energy value for horses because these animals use energy more efficiently than cattle for tissue synthesis (Table 3).

Thirdly, energy requirements may differ between ruminant and hind-gut fermenters. The energy requirement for maintenance is slightly higher in equids than in bovids. Cattle require between 105–117 kcalME·W⁻⁰·⁷⁵ to meet maintenance requirements whereas horses require 120 kcalME·W⁻⁰·⁷⁵ (Vermorel 1978; Vermorel et al. 1984). This difference is much smaller than the difference in extraction rates. None of these refinements of the current nutritional models therefore alters the overall conclusion of this paper: the nutritional model does not explain why bovids are more species rich and more abundant than equids.

| Table 4. Daily intakes, digestion coefficients and extraction rates derived from Fig. 6, NDF = 60, for bovids and equids with identical diets. Equids switch to a lower quality diet to maintain intake at 170 g·W⁻⁰·₇₅·d⁻¹ and do only as well as bovids |
|---|---|---|---|---|---|
| Bovid | Equid¹ | Equid² |
| Dry matter intake (g·W⁻⁰·₇₅·d⁻¹) | 115 | 170 | 170 |
| Dry matter digestibility (%) | 58 | 55 | 29 |
| Daily extraction rate (g·W⁻⁰·₇₅·d⁻¹) | 67 | 94 | 67 |

The data presented in this study are all derived from studies of stalled animals fed *ad libitum*. It is possible that the quality and quantity of food available on the range at bottleneck times of the year are too low to allow hind-gut digesters such as equids to use their high intake strategy (Bell 1971; Langer 1987; Janis 1989).

In extreme situations the total amount of herbage in grasslands may be so low that the hind-gut fermenters are unable to harvest enough per day to achieve their potentially high intake rates. Ruminants digest forages more completely (c.f. Fig. 3) and can perhaps maintain a positive nutrient balance when the hind-gut fermenters cannot because their daily intake is too low.

In less extreme circumstances, high fibre forages may still be abundant when low fibre plant parts are sparse (c.f. Demment 1983; Demment and Van Soest 1985; Gordon 1989). Medium sized hind-gut fermenters may be compelled to eat forages more fibrous (say 80% NDF) than those eaten by sympatric bovids (say 60% NDF) in order to maintain their high rates of intake. In such circumstances the model in Fig. 8 predicts that the nutrient extraction rate of the equids would fall to the level of the ruminants (Table 4). This hypothesis is supported by a small number of studies which show that at least under some circumstances hind-gut fermenters do consume a more fibrous diet than ruminants of a similar body size (Plains zebra and Wildebeest, *Con-
Equids feed for about 15 h a day while cattle commonly feed for 8, and rarely for more than 10 h a day (Arnold and Dudzinski 1978; Duncan 1985). The extra time spent feeding by equids may impose extra costs on them, including the energy costs of activity and thermoregulation, and a higher risk of predation.

The daily energetic costs of foraging for 5 hours longer than bovids could outweigh the benefits which equids gain from their high rates of nutrient extraction. Unfortunately, the critical data to test this hypothesis are not available. No direct measures have been made of the energetic cost of grazing or of thermoregulation in equids, and there are no comparative data on the time budgets of sympatric, unmanaged equids and bovids.

The longer feeding time of equids could impose considerable costs other than energetic ones. Being forced to feed by night, for at least 3.5 h in tropical conditions and even longer during the winter in temperate latitudes, they may incur higher predation rates than bovids. Serengeti zebra do suffer more predation than wildebeest by lion (Schaller 1972), a predator that hunts by stealth though not by hyaena (Kruuk 1972), a predator that hunts by pursuit.

A further possibility is that the evolutionary success of the ruminants has been built on the ability of the rumen flora to detoxify plant secondary metabolites (Moir 1968; Freeland and Janzen 1974; Langer 1986). These are much commoner in dicots than in monocots (Freeland and Janzen 1974; Levin 1976), so this hypothesis may not explain the prevalence of bovids in the present day grazing ungulate fauna. Nevertheless it is increasingly recognised that secondary metabolites play an important role in interactions between grazers and graminoids (Georgiadis and McNaughton 1988), so this hypothesis cannot be ruled out.

From the results presented here we must conclude that there is currently not enough information available to test the alternative hypotheses above which could explain the different patterns of species richness, abundance, and resource use in these two groups of ungulates. Comparative studies of the regulation of wild populations of sympatric equids and bovids are required.

We need to know whether the food supply plays as important a role in the limitation of wild equid populations as it does in at least some bovids (c.f. Sinclair and Norton-Griffiths 1982); and particular attention should be paid to comparative nutrition:

1 What are the comparative rates of nutrient extraction by sympatric, unmanaged equids and bovids? Do equids achieve in the field the high rates of intake and extraction of which they are capable in ad libitum feeding trials?

2 What are the comparative energy/nutrient balances of unmanaged equids and bovids?

3 What are the comparative growth rates of sympatric equids and bovids?

4 Is the mortality due to predation in natural ecosystems sufficient to limit zebra populations below the food ceiling?

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