

## 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 rumen 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.

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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, camelids and the “ruminants”: antilocaprids, cervids, giraffids and bovids) have independently evolved systems of fermentation chambers in the foregut (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-

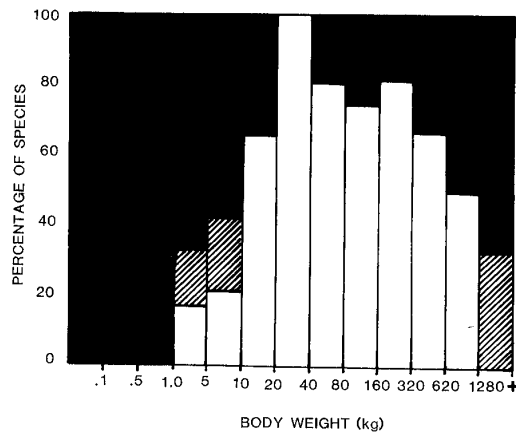


Fig. 1. Distribution of ruminants (open bars), non-ruminant foregut fermenters (cross-hatched) and hind-gut fermenters (solid) across body-sizes. Adapted from Demment and Van Soest (1985)

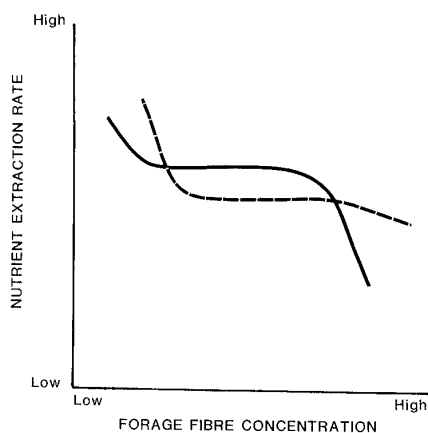


Fig. 2. Qualitative "nutritional" model which has been proposed to describe the effect of forage fibre on nutrient extraction rates in ruminants (—) and hind-gut fermenters (-----) (Foose 1982)

ilar niches. However since the late Tertiary the ruminants appear to have been more successful than the equids, at least in terms of species richness (Simpson 1953; Moir 1968; Van Valen 1971; Stanley 1974; Janis 1976; Langer 1987).

Equid species have broad ecological niches, which could account for their being less species-rich than the bovids (Owen-Smith 1985). However, not only is the number of equid species low but the most abundant medium-sized ungulate in virtually every guild of African ungulates is one of the grazing bovids (Cumming 1982). Bovids therefore predominate among medium-sized herbivores, both in species richness and in abundance.

The coexistence of these medium-sized ungulates with contrasting digestive systems has been explained by their different abilities to extract nutrients from forages of different qualities (Bell 1971; Janis 1976; Foose 1978). The Bell/Janis/Foose model emphasises that it is the animal's daily rate of nutrient extraction from for-

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:

$$\text{Nutrient extraction} = \frac{\text{Digestion coefficient}}{\text{Voluntary intake}} \times \text{Voluntary intake} \dots (1)$$

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 an "ecological refuge" which would allow medium-sized hind-gut fermenters coexist with ruminants (Bell 1971; Janis 1976; Foose 1978, 1982). 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 on 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/Foose 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/Foose 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 Foose 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 (Foose 1982). Ten species or sub-species of bovids 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 determined according to A.O.A.C. (1970) procedures.

Daily organic matter intake (OMI,  $\text{kg} \cdot \text{d}^{-1}$ ) 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 includes metabolic losses) and the daily digestible organic matter intake (DOMI,  $\text{kg} \cdot \text{d}^{-1}$ ). 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:

$$\text{MRT} = \sum (P_x \cdot t_x)$$

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 bovids 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 brome (*Bromus inermis*), and a mixture of Timothy and Redtop (*Agrostis alba*) whose fibre contents 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*), donkeys and zebu steers were fed three mixtures of Red oat grass (*Themeda triandra*) and alfalfa hays with crude fibre contents between 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 estimate 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 (DMD) and voluntary 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 medium-sized ungulates (Van Soest 1982; Demment and Van Soest 1985).

In this part of the analysis, the procedure was to obtain regressions of the digestibility and intake of forages on the forage fibre

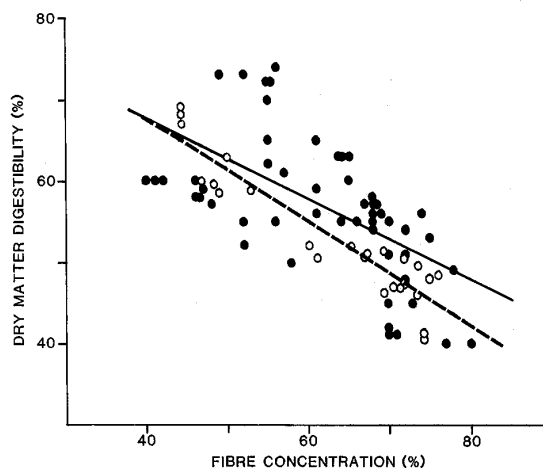


Fig. 3. The effect of dietary fibre on the digestibility of dry matter in equids (○-----○ Fonesbeck 1968, Foose 1982) and in cattle (●—● NRC 1984)

concentration for horses and for cattle. The results were then combined and the nutrient extraction rate, the digestible dry matter intake (DDMI), modelled for a range of fibre concentrations according to equation 1.

**Digestibility.** The relationship between DMD and NDF in cattle for grass and forb forages with NDF values between 40–80% is negative (Fig. 3., data from National Research Council 1984):

$$\text{DMD}(\%) = 86.6 - 0.485 \text{ NDF}(\%) \quad \dots (2)$$

( $r^2 = 0.355$ ,  $P < 0.001$ ,  $n = 54$ )

The digestibility of forages in horses also declines as the fibre content increases (Martin-Rosset et al. 1984). In the two studies where the Van Soest detergent system of analysis was used digestibility was closely and negatively correlated with the fibre concentration (Fig. 3., data from Fonesbeck 1968; Foose 1982):

$$\text{DMD}(\%) = 93.3 - 0.643 \text{ NDF}(\%) \quad \dots (3)$$

( $r^2 = 0.872$ ,  $P < 0.001$ ,  $n = 25$ )

These two regressions differ significantly ( $F_{1,76} = 4.68$ ,  $P = 0.03$ ), which is usual in equid-bovid comparisons (Hintz 1969; Martin-Rosset et al. 1984).

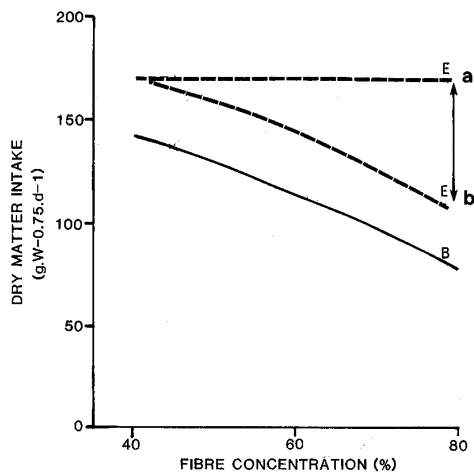
**Intake.** The intake of forages by lactating cows is negatively related to the forage fibre content (Rohweder et al. 1983):

$$\text{DMI}(\text{g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}) = 84.7 - 3.69 \text{ NDF}(\%) + 32.37 \sqrt{\text{NDF}(\%)} \quad \dots (4)$$

( $r^2 = 0.624$ ,  $P < 0.001$ ,  $n = 271$ )

As with cattle, intake in horses is clearly affected by requirements, the highest values being observed in wild-caught zebras ( $167 \text{ g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}$  and  $162\text{--}192 \text{ g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}$ , Ngethe 1976; Gakahu 1982) and lactating mares ( $139\text{--}199 \text{ g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}$ , Boulot 1987). The median of these values is  $170 \text{ g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}$ .

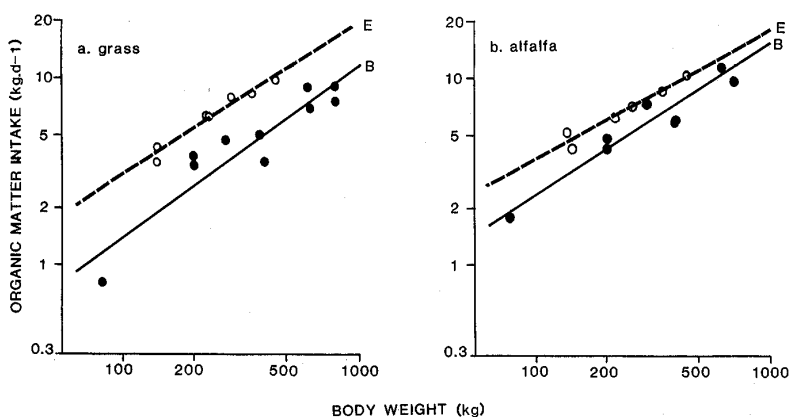
It has been suggested that equids increase their intake if forage fibre increases (Janis 1976). Geldings feeding on diets diluted with wood shavings do increase their intake as the proportion of fibre increases (Laut et al. 1985). However there is a negative relationship between intake and the fibre content of a wide range of different types of forages in non-lactating, non-growing horses (Boulot 1987). The high intake of leguminous hays and their relatively low fibre content may have biased this result: for grass hays alone the relationship is weak, and negative ( $r = -0.46$ ,  $n = 16$ ,  $P > 0.05$ ; data in Darlington and Hershberger 1968; Fonesbeck 1969; Foose



**Fig. 4.** The effect of dietary fibre on the voluntary dry matter intake (DMI) in equids (---- E) and in bovids (— B)  
Equids - a)  $170 \text{ g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}$   
b)  $119 - 3.69 \text{ NDF}(\%) + 32.37 \sqrt{\text{NDF}(\%)} (\text{g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1})$   
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 Foose (1982)

		Bovids	Equids	Significance of difference
Mean retention time (MRT, h)	grass	70.2	44.5	$t=6.78$ $df=13$ $P<0.001$
Mean retention time (MRT, h)	alfalfa	55.5	37.3	$t=4.32$ $df=12$ $P<0.001$
Digestibility of organic matter (OMD, %)	grass	55.9	47.0	$t=2.59$ $df=15$ $P<0.01$
Digestibility of organic matter (OMD, %)	alfalfa	71.9	63.5	$t=3.96$ $df=13$ $P<0.002$



**Fig. 5a, b.** Relationships between organic matter intake (OMI) and body weight (W) in equids (○-----○ E) and bovids (●-----● B) fed on a) high fibre grass and b) medium fibre alfalfa hays. Equids - grass:  $\ln \text{OMI} = -2.63 + 0.816 \ln W$  ( $r^2 = 0.953$ ,  $P < 0.001$ ,  $n = 7$ ) alfalfa:  $\ln \text{OMI} = -1.85 + 0.685 \ln W$  ( $r^2 = 0.956$ ,  $P < 0.001$ ,  $n = 6$ ) Bovids - grass:  $\ln \text{OMI} = -3.80 + 0.900 \ln W$  ( $r^2 = 0.866$ ,  $P < 0.001$ ,  $n = 10$ ) alfalfa:  $\ln \text{OMI} = -2.70 + 0.780 \ln W$  ( $r^2 = 0.924$ ,  $P < 0.001$ ,  $n = 9$ ) Data from Foose (1982)

1982). 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  $170 \text{ g} \cdot \text{W}^{-0.75} \cdot \text{d}^{-1}$  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

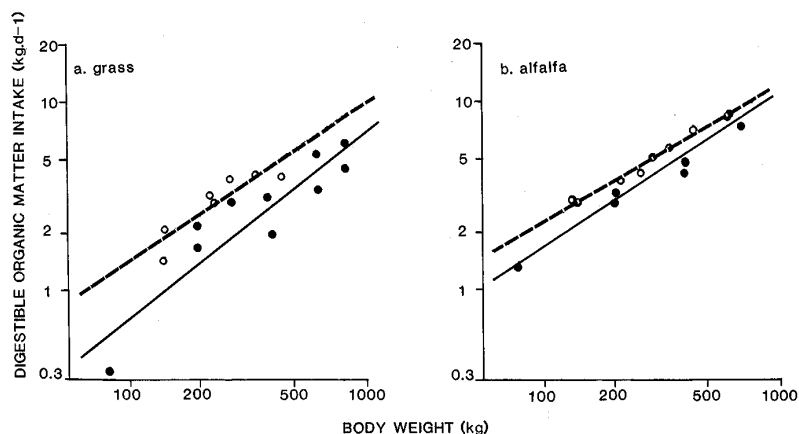
### Multi-species trials

**The Foose 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  $r^2 = 0.070$ , alfalfa  $r^2 = 0.009$ ,  $n = 9, 8$ ; equids  $r^2 = 0.211$ ,  $0.123$ ,  $n = 7, 6$ ). However, there was a clear difference between taxa, Table 1, with bovids retaining the food 50% longer than equids.

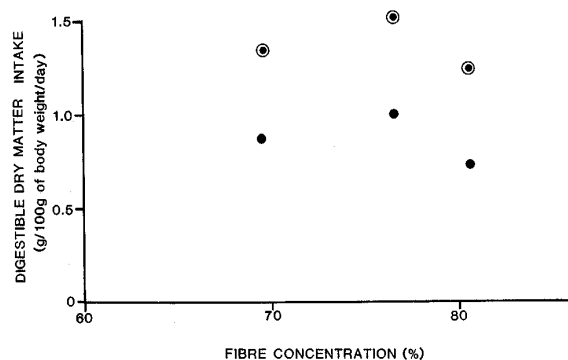
The larger animals tended to digest the days more completely than the smaller ones, but there was no significant effect of body size on the digestibility coefficients (OMD) of bovids or equids for grass or alfalfa ( $r^2 = 0.272$ ,  $0.180$ ,  $n = 10, 9$ ;  $r^2 = 0.048$ ,  $0.135$ ,  $n = 7, 6$ ). 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



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



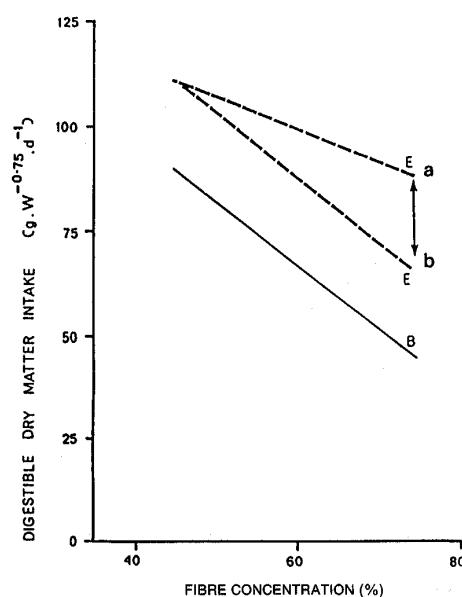
**Fig. 7.** Rates of dry matter extraction (digestible dry matter intake) by horses (●,  $W = 429$  kg) and cattle (○,  $W = 415$  kg) on three forages. Data from Johnson et al. 1982

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

Hay Quality	Species	Body (W, kg)	DDMI	Difference (%) (equid-bovid) / bovid
Good	Zebra	198	117	+46
	Donkey	199	113	+41
	Steer	154	80	
Medium	Zebra		95	+36
	Donkey		91	+30
	Steer		70	
Low	Zebra		71	+28
	Donkey		67	+16
	Steer		58	

than in bovids (Fig. 6), both on the high fibre grass hays ( $F_{1,14} = 14.7$ ,  $P = 0.002$ ) and on the medium fibre alfalfa hays (comparison of intercepts:  $F_{1,12} = 7.15$ ,  $P = 0.019$ ).

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



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

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 and 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<sup>-0.75</sup> to meet maintenance requirements whereas horses require 120 kcalME·W<sup>-0.75</sup> (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 3.** Metabolizable energy (ME; kcal/kgDM) and net energy (NE; kcal/kgDM) contents of forages varying in digestible organic matter (DOM; %) fed to horses (h) and cattle (c). Data from Vermorel (1978) and Vermorel et al. (1984)

	DOMh	DOMc	MEh	MEc	NEh	NEc
Wheat straw	35	42	1370	2270	726	709
Natural pasture						
1st cut	53	59	1840	2000	1254	1142
(flowering)						
3rd cut	69	73	2420	2580	1716	1557
Lucerne pasture						
2nd cut	53	55	1770	1820	1188	1020
4th and	68	69	2340	2390	1650	1419
5th cut						
Natural pasture hay						
50	50	56	1710	1880	1440	1055
42	42	55	1410	1820	924	1038

**Table 4.** Daily intakes, digestion coefficients and extraction rates derived from Fig. 6, NDF = 60, for bovids and equids<sup>1</sup> with identical diets. Equids<sup>2</sup> switch to a lower quality diet to maintain intake at 170 g·W<sup>-0.75</sup>·d<sup>-1</sup> and do only as well as bovids

	Bovid	Equid <sup>1</sup>	Equid <sup>2</sup>
Dry matter intake (g·W <sup>-0.75</sup> ·d <sup>-1</sup> )	115	170	170
Dry matter digestibility (%)	58	55	39
Daily extraction rate (g·W <sup>-0.75</sup> ·d <sup>-1</sup> )	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-*

*nochaetes taurinus*, Gwynne and Bell 1968; Owaga 1975, Krysl et al. 1984). Putman (1986) obtained different results comparing the diets of horses and cattle in a temperate woodland, but here the cattle were fed supplementary fodder, which may account for the different conclusion of this study. The paucity of comparative data on food intake and digestibility in wild populations of the two types of ungulates does not allow quantitative tests of this very credible hypothesis.

*Alternative hypotheses for the pattern of species diversity, body-size distribution and resource use in equids and bovids*

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 of 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 role in the limitation of wild equid populations as it does in at least some bovids (c.f. Sinclair and Nor-

ton-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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