DIGESTIVE STRATEGIES IN RUMINANTS AND NONRUMINANTS

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STELLINGEN

I

De veelvuldig aangehangen gedachte dat paarden, wat betreft de dagelijkse opname van metaboliseerbare energie uit laagwaardig voedsel, superieur zijn aan runderen, wordt niet door alle onderzoek ondersteund en blijkt ook niet altijd uit praktijkervaringen.

P. Duncan et al. (1990). Oecologia 84:411-418.
R. Meydam. Evaluatie begrazing Meyendel. 1996.

II

Wilde zwijnen die op een dieet van uitsluitend mast leven, krijgen onherroepelijk eiwitgebrek.

III

Het concept van duurzame ontwikkeling leidt in de praktijk niet zozeer tot beperkingen aan de groei, maar meer tot de groei van de beperkingen.

B. Willers. (1994). Conservation Biology (8):1146-1148.

IV

De typisch nederlandse gedachte dat de mens verrijkend heeft gewerkt op de natuur, is een gevaarlijke misvatting.

V

Er bestaan geen uitsluitend links- of rechtsdraaiende (herkauwende) koeien. Alle koeien draaien zowel links- als rechtsdraaiend.

K. van Zomeren. NRC. 7-10-1994.

VI

De ecologie levert geen enkele reden om in natuurgebieden populaties wilde zwijnen te moeten beheren.

VII

Boerennatuur is een vorm van boerenbedrog.

VIII

Het begrip wild in de zin van de jachtwet (en ook in die van het ontwerp Flora en Faunawet) heeft een veel te beperkte strekking, en het verdient aanbeveling om het uitsluitend en eenduidig te reserveren voor 'alle in het wild levende diersoorten'.

IX

Voor een dieroecoloog is de stelling 'innovatie door observatie' van meer dan gemiddelde betekenis.

X

Het komt de democratie ten goede als de leden van de Tweede Kamer maximaal vier jaar zitten en daarna, eventueel, weer in hun oude functie kunnen terugkeren.

XI

Miles Davis en John Coltrane bewijzen dat zowel het spelen van zo weinig mogelijk noten, als het tegenovergestelde, beide gelijkwaardige wegen zijn om tot een hoge muzikale expressie te komen.

XII

De tijd leert alleen als de mensen het ook doen.

Stellingen behorende bij het proefschrift van S.E. van Wieren,
Digestive strategies in ruminants and nonruminants.

Wageningen, 3 december 1996.

CONTENTS

ABSTRACT

Van Wieren, S.E. 1996. Digestive strategies in ruminants and nonruminants. Ph.D. Thesis, Wageningen Agricultural University, Wageningen, The Netherlands. 191 pp.

Of the 176 species of ungulates in the world the great majority (146 species) are ruminants. The more recent ruminants probably have displaced the older nonruminants because of their superior digestive system in combination with the ruminantion mechanism leading to significant advantageous differences in important life history traits. Nonruminants like hippos, equids, elephants and tapirs reach sexual maturity at a later age and produce fewer young per year than ruminants, relative to body size.

Within the ruminants three different adaptive syndromes in feeding style are distinguished and expected differences in digestive physiology between members of the various feeding styles were tested. Nonruminants are poorer fibre digesters than ruminants while the large bovid 'grass and roughage feeders' have superior capacity for digesting fibre.

In some areas in the world, notably in East Africa, species-rich ungulate communities can be found. Various guilds of species occupying different habitats and feeding niches can be distinguished and the species belonging to different guilds are sufficiently dissimilar as not to compete with each other. Within guilds frequently groups of species of similar body weight and with similar ecology occur sympatrically. The apparent peaceful co-existence of these species yet has to be explained.

Keywords: ungulates, ruminants, nonruminants, grazers, browsers, horses, cattle, sheep, goats, Red deer, Roe deer, Wild boar, pigs, grazing, markers, digestion, physiology, feeding ecology, evolution, community ecology

This thesis is dedicated to the late Dr. Harm E. van de Veen

CHAPTER 1

INTRODUCTION

CHAPTER 1

Introduction

Ungulates are an important group of mammals that, like most other groups of mammals, showed an extensive evolutionary radiation from the end of the Cretaceous onwards (fig 1.1). Within the group of ungulates a few taxonomic orders are distinguished of which the Proboscidae, the Perissodactyla and the Artiodactyla are the most important. The Proboscidae comprise the two living species of elephant and are not considered here any further. The Perissodactyla (uneventooed ungulates) comprise the horses, zebras, asses and rhinos and are represented by 14 species. The Artiodactyla (eventooed ungulates) are the most diverse group with 9 families and about 165 species (fig 1.1).

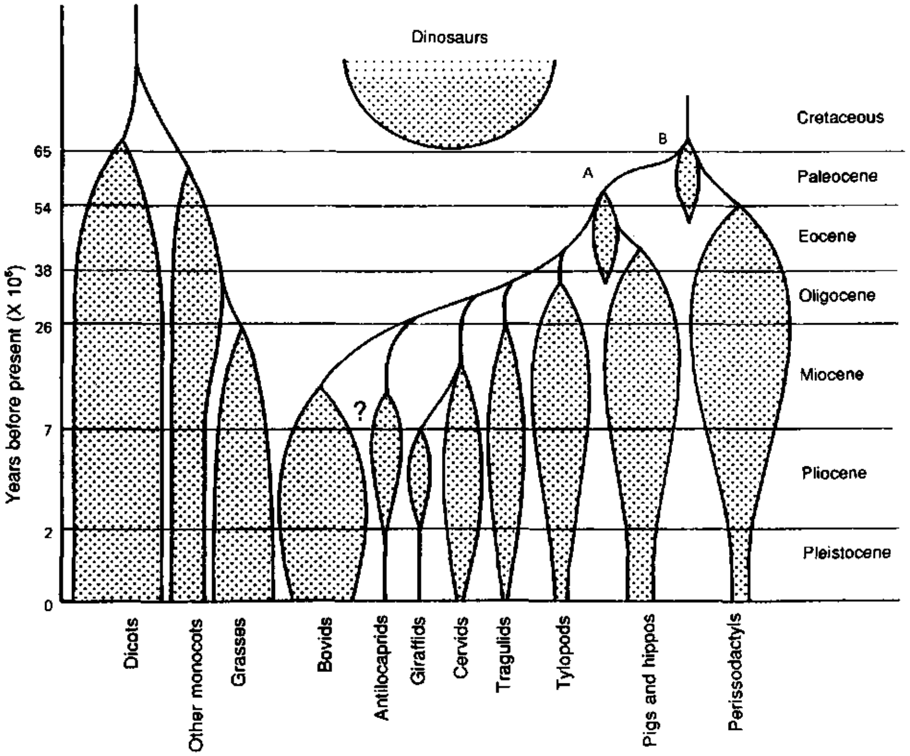


Figure 1.1. The appearance and development of ungulates and angiosperms on an evolutionary time scale. (Taken from Van Soest 1994).

The majority of the Artiodactyla are ruminants, the only nonruminants being the pigs and hippos. It is still debated whether the Tylopodae (camelids) are true ruminants but they do chew the cud (Van Soest 1994). The present-day dominance of the ruminants is a relative recent phenomenom. It were the perissodactyls that achieved dominance in the Eocene and Oligocene. They declined in the Miocene period and were largely replaced by ruminants in the Pliocene/Pleistocene (fig 1.1).

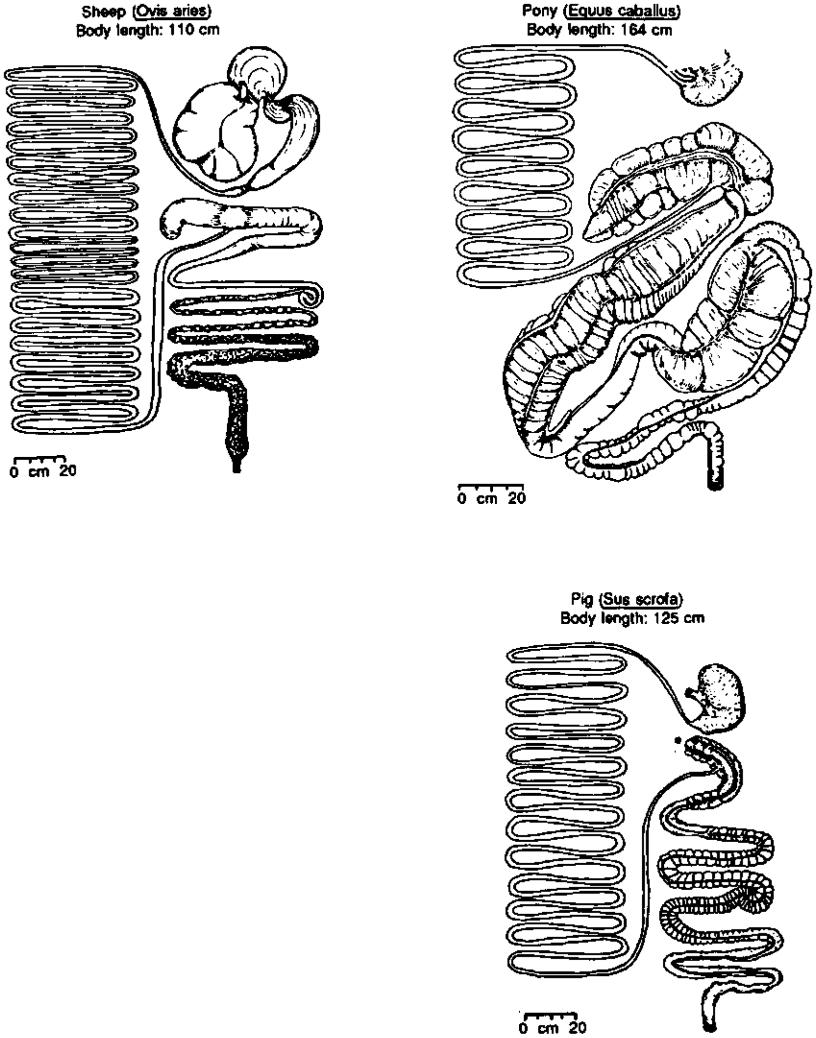
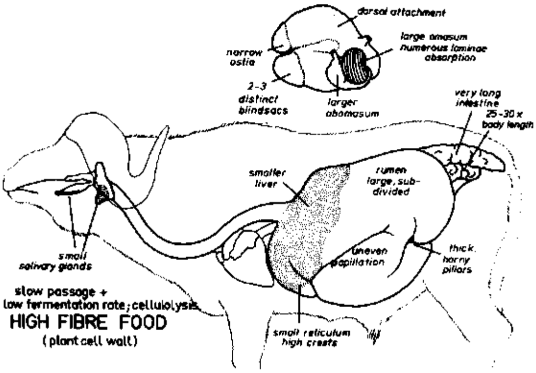
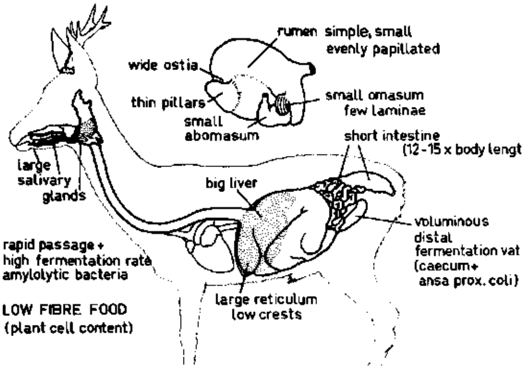


Figure 1.2. Examples of digestive tracts of a foregut fermenter and two hindgut fermenters. (From Stevens 1988).

The ancestral ruminant (and perissodactyl) probably was a small tropical forest browser. The development of the pregastric fermentation system has been associated with the rise of angiosperms which developed secondary compounds that were toxic to unadapted animals (Swain 1977). In a pregastric system these toxic substances could be detoxified. The symbiosis with micro-organisms also freed the animal for the supply of amino acids and some vitamins from external sources. The ability to use plants material rich in fibre but low in lignin did not appear before the Miocene and is clearly associated with the rise of grasslands. Grazing meant a less selective feeding pattern and a more developed cellulolytic fermentation, either in the rumen or in the ceacum/colon. Ruminants and horses became larger, an adaptation that coincided with a change to cooler and drier climates (Van Soest 1994).



The African buffalo, a non-selective roughage grazer.



The roe deer, a concentrate selector.

Figure 1.3. Example of the morphophysiological characteristics of a concentrate selector and a bulk and roughage feeder. (From Hofmann 1989).

The perissodactyls are represented by only a few lines today and seem to be declining still. The success of the ruminants seems to have been taken place at the expense of the nonruminants although the real mechanism behind this is still controversial.

Within the ungulates a distinct evolutionary diversification of digestive tracts has taken place as can be inferred from gut anatomy (fig 1.2 and 1.3). Two directions seem to have taken place from the simple stomach: elongation and sacculation of the stomach leading to complex pregastric fermentation systems (ruminants); and enlargement and modification of the cardiac region leading to complex ceacal/colonic fermentation (pigs, horses). The elaborated fermentation chambers allow for a symbiotic relationship with microorganisms which produce cellulase and hemicellulase. These enzymes are necessary to break down cellulose and cellulose-like products. Pregastric and postgastric fermentation have both advantages and disadvantages. Advantages of the pregastric system have already been mentioned above. Disadvantages include the need for conservation of essential fatty acids, the necessity of digesting protein in the form of bacteria and the constraint on passage rate (Van Soest 1994). The postgastric fermentation system does not constrain passage of feed and this may be of advantage when food quality is low. The capacity of hindgut fermenters to digest structural carbohydrates is generally lower than in the ruminant. A further disadvantage is that the time to absorp fermentation products is too short leading to excretion before absorption can take place.

Within the ruminants Hofmann (1973,1989) distinguished three types of gutmorphologies: concentrate selector, bulk and roughage feeder, and intermediate feeder. The morphology of the first two types is compared in fig 1.3, the intermediate feeder is intermediate between these two. The adaptations are related to feeding type. Concentrate selectors have a smaller rumen and a less developed omasum. The rumen structure favours less selective retention and a higher passage of carbohydrates and protein. They have a large hindgut relative to rumen size and the lower tract is more important than in bulk and rouhgage feeders (Gordon & Illius 1994). The perissodactyls (excluding the rhinos and hippos) and Suids are of intermediate size while ruminants differ in size from about 4-1000 kg. In both very small and very large animals rumination does not seem to be of any advantage (Van Soest 1994).

There are about half a billion wild ungulates in the world (table 1.1), this being a rough estimate. While some groups are quite numerous, others are rare or face extinction. Bovids are by far the most numerous. Of the about 176 species of ungulates only a limited number are domesticated. Nevertheless the domestic species outnumber the wild ones by about ten to one (table 1.1); pigs, cattle and sheep being the most numerous domestic species. Domestication started about 10,000 years ago and man has always been closely associated with herbivores ever since.

Table 1.1. Numbers of wild and domestic suids, equids and important groups of ruminants in the world. Sources: Van Soest 1994, Briedermann 1990. The numbers of wild suids and equids have to be considered rough estimates. (Numbers in millions).

	Wild	**Domestic**
suids	(10-50)	800
equids	(5-10)	115
cervids	35	2.5 (reindeer)
bovids	100-500	3032 (mainly cattle and sheep)

Herbivores are important to human societies in many ways. Eight percent of the human diet world wide is made up of animal products but this figure varies widely between countries (Borlaug & Dowswell 1994). In most societies herbivores do not really compete with humans because they consume predominantly high fibre products like grass, straw and browse which are unsuitable for man. Herbivores only compete with man to some extent in western societies when they are fed grain which also can be used by man directly. The most important non-food contributions of herbivores to human society are probably traction and dung for fuel and fertilizer (Van Soest 1994). Of less importance are fibre, skins, horns or cultural uses.

The role of large herbivores in conservation is well recognized. It is still debatable whether in the natural condition medium to large sized herbivores have played and can play a dominant role in shaping vegetation structure or if they are predominantly followers of succession (Van Wieren 1990, Chapter 2). Whatever their role in natural ecosystems it is very clear that large herbivores can be a dominant factor in semi natural landscapes. Together with man they have transformed the European landscape to produce wetlands, heathlands, grasslands and wood pastures (Van Wieren 1995). Many of these landscapes are maintained almost exclusively by grazing. A review of the importance of herbivores in conservation is the subject of chapter 2.

The remaining chapters deal predominantly with comparative digestive physiology. The inspiration for this work comes from two sources. One is Hofmann's (1973, 1989) work on the classification of ruminants into three digestive strategies. Although his work is mainly based on gut morphology there are many implications for differences in digestive physiology following differences in gut morphology. Although these implications have been hypothesized to exist, very little comparative research has been carried out in this respect. Even the claimed direct relationship between gut morphology and feeding habits has not yet been tested properly to date. A connection between gut morphology and feeding habits can be made by studying digestive capacity, voluntary intake and passage rate. The rationale for carrying out the feeding trials as described in the following chapters lies in the attempt to fill a small part of this gap. The second source of inspiration comes from the work of Van Soest (1982). Van Soest's approach to plant material whereby the plant can be distinguished and analyzed in terms of cell wall (fibre) and cell contents, has made it possible to study fibre utilization in herbivores in more detail. The claimed differences between the various species of herbivores are strongly related to the capacity to ingest and digest cell walls.

When carrying out feeding trials it is generally assumed that voluntary food intake is largely determined by the quality (digestibility) of the forage ingested. It is, however, well known that wild herbivores from the temperate and arctic zone show a voluntary drop in food intake in the winter period (Kay et al 1979). This drop in food intake can also be induced experimentally with high quality feed (Kay 1979) and acts independently from forage quality. During field work on free ranging Highland cattle it was noted that these domestic herbivores evidently also demonstrated a voluntarily drop in food intake. In chapter 3 this finding is discussed and it is hypothesized what can be the reason for this mechanism.

It is difficult to carry out feeding trials with wild herbivores like red deer and even more so with roe deer. The confinement of these type of animals to metabolic cages can produce a lot of stress and may lead to unreliable results. Therefore more space is required and this makes total faecal collection more difficult. Therefore it was tried to use a marker for estimating digestibility. One of the best internal markers is indigestible acid detergent fibre (IADF) (Tamminga et al 1989). In chapter 4 an experiment is described to test whether IADF can also be used as a marker with feeds which have not been tested earlier in this respect and which were frequently to be used in the feeding trials (e.g. browse, grass seed straw).

Chapter 5 describes a comparison between sheep and goats. Many comparisons between the two species have already been made. Tolkamp & Brouwer (1993) reviewed more than 200 feeding trials. Their analysis revealed only a very small difference in digestive capacity. Nevertheless goats and sheep are differently catagorized by Hofmann (1989). Sheep are classified as grass and roughage feeders while goats are intermediate feeders. It was hypothesized that goats might be better able to utilize browse material and browse is only seldomly used in feeding trials. The feeding trials were set up with browse as an important part of the diet.

In chapter 6 an extensive feeding trial is described with representatives of four different feeding styles: Highland cattle (grass and roughage feeder), red deer (intermediate feeder), roe deer (concentrate selector) and Konik ponies (hindgut fermenter).

A variety of feeds were tested ranging from grass seed straw to willow browse. In this way it could be studied (in a comparative way) how these 'feeding styles' were able to utilize feeds both similar and dissimilar from the normal preferred type of diet.

The possible role of fibre in the nutritional ecology of wild boar and a domestic breed of pig is investigated in chapter 7. As a result of new insights in conservation wild boar are increasingly not supplementary fed anymore in the Netherlands. Studies on not-supplementary fed wild boar show that broadleaved grasses play an important role in the winter diet in years when there is little or no mast available (Groot Bruinderink et al 1994). The extent to which wild boar are capable in utilizing fibre from different types of forages, and to compare this capacity with that of a domestic breed, is the subject of this chapter.

In chapter 8 the classification of Hofmann (1973) of ruminants in concentrate selectors, grass and roughage feeders and intermediate feeders is analyzed in a number of ways. As stated in the beginning of this chapter Hofmann (and others) claimed that the morphological specializations would have implications for various aspects related to digestive physiology and diet choice. These implications have not yet been thouroughly tested untill very recent. In these recent publications (Gordon & Illius 1994, Robbins et al 1995) Hofmann's classification has come under attack and the critics conclude that in most aspects they studied the proposed differences did not exist and that variation in body size could explain most of the differences found. In chapter 8 Hofmann's hypotheses are tested with respect to diet choice and digestive capacity. Furthermore a first statistical test is carried out with some of Hofmann's own data as such tests have not been carried out by Hofmann himself.

In the final chapter (9) various aspects of ungulate ecology are explored. Ungulates are a highly diverse group and so they have been since mid-Tertiary times. During a long epoch major changes have taken place. One of the most striking is the steady increase of the ruminants at the expense of the non ruminants. In chapter 9 some mechanisms are discussed that may have influenced the outcome of this process.

Although a diverse group, ungulates are not evenly distributed over the face of the earth. Distribution patterns are highly skewed towards the tropics and the possible reasons for this and other aspects of ungulate distribution are discussed.

Locally, ungulate communities can be very rich in species. This poses important questions as to how all these species manage to live together. How different are they and what is the smallest amount of difference needed for co-existence to take place?

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THE MANAGEMENT OF POPULATIONS OF LARGE MAMMALS

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INTRODUCTION

There are today very few, if any, populations of large mammals living under natural conditions in the temperate zone in Western Europe. Natural ecosystems have disappeared. A number of large herbivore species have become extinct (tarpan, aurochs) or have a very reduced distribution (wisent). The remaining indigenous herbivore fauna (roe deer, red deer, moose and wild boar) is present in large parts of its former range but is managed with varying degree of intensity.

Population size of those species which do remain is controlled and on the continent supplementary feeding is common practice. The main reasons for these measures are: (i) if wildlife species are present at high densities this frequently brings them into conflict with other interests (forestry, agriculture, conservation goals); (ii) because of hunting interests, densities maintained may surpass the carrying capacity of the range; (iii) supplementary feeding or population management may be undertaken to raise the quality of hunting trophies. Nevertheless, large herbivores have a major impact in natural systems and may play an important role in the dynamics of conservation areas. Further, in an increasing number of nature reserves herbivory is applied to achieve a wide variety of conservation goals.

The herbivores involved are predominantly domestic animals (sheep, cattle, horses), are regarded as management tools and managed accordingly. This is not surprising because in such a context almost all conservation goals are aimed at preserving and developing natural values that are derived from former agricultural systems and thus are side-effects of the activities of man. The management of the herbivores is so intense and arbitrary that studies on the population level are hardly rewarding.

In this chapter the possible role of large herbivores under natural conditions is indicated, a number of effects of grazing on vegetation and fauna are reviewed, and a perspective is offered on how natural self-maintaining populations of large herbivores may receive a proper place in conservation thinking.

A FRAME OF REFERENCE: THE ATLANTIC PERIOD

The Atlantic Period (7500–5000 years B.P.) can be considered as the last period with truly natural ecosystems before the influence of man became predominant (Peterken 1981). The climate was a little warmer than at present, and most of Europe was covered with dense forest dominated by shade-tolerant species like alder, elm and lime (Iversen 1973; Rackham 1980; Peterken 1981). The understorey was relatively less developed (Iversen 1973), and many plant species disappeared from the pollen spectrum (Peterken 1981). The large herbivore fauna too declined during the Atlantic period (Iversen 1973; Bottema 1988), the most abundant species being red deer and wild boar. Roe deer, moose and aurochs were rare, whereas the wild horse rapidly disappeared from Western Europe at the beginning of the Holocene (Söffner 1982). It is likely that only in habitats where abiotic conditions prevented forest growth (e.g. tidal areas, marshy areas) were conditions for large herbivores suitable. According to Heptner, Nasimovic & Bannikov (1966) most large herbivores of the temperate zone evolved in the steppe or forest/steppe zone.

All the evidence indicates that under natural conditions, when the climax vegetation is forest, the large herbivores are not able to prevent the closing of gaps in the forest. They were mere 'followers of succession' and their influence was mainly restricted to temporary gaps in the forest canopy. Only in coastal areas and possibly on very poor soils were herbivore densities probably high enough to lead to permanent structural effects on flora and fauna.

In Eastern Europe some natural forests still occur in the Karpates and Yugoslavia. The canopy is closed and gaps are filled immediately. A rather complete set of mammalian species is present (roe deer, red deer, wild boar, bear, wolf, wild cat) and yet the total density of herbivores is less than one per 100 ha (Mayer & Neumann 1981).

From 5000 years B.P. onwards human impact increased, with the overall effect that the biomas is kept on the ground and succession to climax forest ecosystems is prevented; at present grasslands, dwarf-shrublands and early forest succession stages prevail in Western Europe. In these man-induced open landscapes new plant and animal communities developed which nowadays are recognized as systems of high ecological interest.

Management of large mammals

Large herbivores have always played an important role in maintaining open landscapes but other management techniques like mowing, burning, sod-cutting were also common practice. Apart from the immediate return in exploitation these management practices were probably also necessary to prevent the succession to forest.

EFFECTS OF LARGE HERBIVORES ON VEGETATION

Forests

Forests generally serve multifunctional purposes. In small and isolated patches of ancient woodland large herbivores are frequently absent, and in the large multifunctional forest complexes the natural relationships between the large herbivores and the vegetation are disturbed. The structure and the species composition is commonly completely different from the potentially natural vegetation. Herbivore density is either artificially kept high or becomes high when man-induced early successional stages such as plantations prevail. Because of the potentially large impact and the long history of unnaturally high densities (Adams 1975), the presence of large herbivores in forests is often regarded as a negative factor.

Increasing the herbivore density beyond the natural carrying capacity can have a number of effects. The first main effect is a major shift in species composition because of preferential browsing. The regeneration of preferred species can be seriously hampered or even prevented. Preferred food plants of red deer are aspen (*Populus tremula*), willow (*Salix* sp.) and oak (*Quercus* sp.) (Mitchell, Staines & Welch 1977). Heavy grazing by domestic livestock in Scandinavia resulted in the elimination of *Salix cinerea*, *Fraxinus excelsior* and *Ulmus* sp. on a large scale (Ahlèn 1975). In the New Forest, a very high grazing intensity for a long period has led to the disappearance of shrub species (e.g. hazel) and of some palatable species on the forest floor (Tubbs 1981).

When deer numbers increased, due to human interference, regeneration of certain tree species failed and the silver fir (*Abies alba*) disappeared within 100 years from the Rothwald Forest in Austria (Mayer & Neumann 1981). In Western Europe, the succession to broadleafed forest can be retarded seriously because species of the later successional stages (e.g. oak and beech) are preferred while pioneer species like birch (*Betula* sp.) and Scots pine (*Pinus sylvestris*) are not preferred (Mitchell *et al.* 1977; Van Wieren & Borgesius 1988).

A high browse impact may lead to the spread of grazing-resistant species like gorse and holly (Putman *et al.* 1984) and *Crataegus* sp., *Rosa* sp. and *Prunus spinosa* (Ahlèn 1975).

When herbivore pressure increases even further, forest regeneration is prevented on a large scale and grasslands and dwarf-shrub heaths spread (Ahlèn 1975; Putman *et al.* 1984). Even suitable regeneration gaps in the forest can turn into grassland that are maintained for a long time (H. Koop, personal communication).

It is difficult to establish the herbivore density whereby regeneration is completely absent. In most cases man exerts additional management practices in the open areas within forest–heathland complexes. Furthermore, large differences exist between the herbivore species in the effect they have on woody species. Van Wieren & Borgesius (1988) report no regeneration at sheep densities of 22 kg ha^{-1} on dry poor soils but, with cattle and horses, regeneration of birch and Scots pine was no problem at densities at 100 kg ha^{-1}. The average deer density in Scotland of 1 deer 10 ha^{-1} allows little regeneration but, at favourite sites, densities as high as 2 deer ha^{-1} are reported (Mitchell *et al.* 1977).

There are also stimulating effects on forest growth to be mentioned. Uprooting activities of wild boar (*Sus scrofa*) increased decomposition of organic matter and increased soil nutrient mobilization, while beech showed significantly greater shoot elongation with increased exposure to rooting by wild boar (Lacki & Lancia 1983, 1986).

The above examples imply that even at relatively low (but already unnatural) densities, large herbivores can cause shifts in the tree species composition of forests. At high densities regeneration can be prevented completely. Maintaining a well-structured 'natural' forest is only possible when herbivore pressure is low.

Wood-pastures

When conditions are suitable and grazing pressure is not too high, park-like landscapes can be maintained. A good example of such a relict landscape is the wood-pasture (hudelandschaft) Borkener Paradies on the border of the river Ems in Western Germany. Here extensive grazing has been applied for more than 500 years with large herbivores (cattle and horses). A dynamic landscape has developed of pastures and woodlands with all kinds of transition zones (fringe communities) between them (Fig. 5.1, Burrichter *et al.* 1980).

The woodland is maintained because of the presence of thorny shrubs (predominantly *Prunus spinosa*) which are able to spread laterally into the pasture. In these encroachments broadleafed tree species such as oak

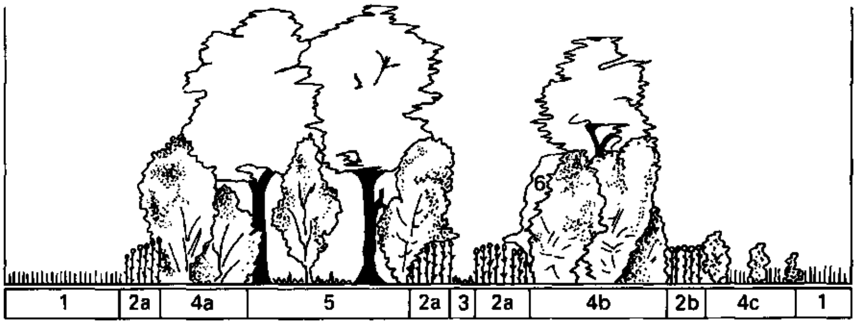

FIG. 5.1. Schematic representation of the vegetation composition of the wood-pasture Borkener Paradies, Germany. 1, Grassland (Lolio-Cynosuretum); 2, nitriphilous ecocline communities, (a) typical fringe, (b) former 'fringe' enclosed by encroaching *Prunus spinosa*; 3, wet cattle path (*Polygonum hydropiper* community); 4, shrub communities (*Prunetalia*, (a) ecocline communities (*Corno-Prunetum*) rich in woody species adjacent to old forest remnant, (b) *Prunus spinosa*-rich regeneration core of potential natural forest, (c) vegetational spread of *Prunus spinosa* in grassland; 5, heavily grazed wood-pasture; 6, vine community (*Cuscuto-convolvuletum*). (From Burrichter *et al.* 1980.)

can establish and grow up out of the reach of the herbivores. When finally the herbivores break into the encroachment a degeneration phase starts and solitary trees or patches of woodland remain. Trees do not regenerate without the protection of thorny shrubs (Burrichter *et al.* 1980). The whole system is mainly the outcome of abiotic site factors determining the potential presence of plant species and the influence of the large herbivores. Additional management consists of infrequently cutting back the encroaching *Prunus spinosa*.

Because of the presence of different successional stages and fringe communities, these kinds of wood-pastures can be rich in species (Dierschke 1974). In the case of the Borkener Paradies, however, the fringe is dominated by *Urtica dioica* as the result of heavy dung deposition by the cattle. Regeneration of woodland from bush-encroachment also occurs on a limited scale in the New Forest in Hampshire (Putman 1986).

Heathlands

The clearance of the European primeval forests and subsequent heavy use for agriculture resulted in soil impoverishment and the spreading of dwarf-shrub heaths with increasing dominance of *Calluna vulgaris*. Apart from management practices like burning, mowing and sod-cutting, large herbivores played an important role in keeping the *Calluna* in good shape. Although heathlands are species-poor communities a number of characteristic species occur which are of high ecological interest (Gimingham 1972). At present the area of *Calluna*-dominated heathland is decreasing rapidly in western Europe. Important causes are a more intensive agricultural use or the stopping of former agricultural practices. Even with proper management heathlands are threatened because of the spreading of the grass species *Molinia caerulea* and *Deschampsia flexuosa*, probably caused by a higher N-input from precipitation. Grazing with large herbivores can partly counteract the grass dominance.

In maintaining a dwarf-shrub community with a high proportion of *Calluna*, grazing intensity can act as a major determinant in shifting the balance between *Calluna* and grass species. *Calluna* declines, in favour of grasses, at about 2·7 sheep ha^{-1}, 2 deer ha^{-1} and 0·23 cattle ha^{-1} (Grant, Hamilton & Souter 1981; Welch 1984a).

The availability of grass is inversely related to the amount of heather eaten; thus, at low densities the grass is under-utilized and the heather is expected to increase, while at high utilization of the grass the heather too is heavily utilized, subsequently leading to lower productivity and less cover (Milne & Grant 1978). In the grass-heaths a number of species-specific effects were observed. Hares, rabbits and grouse had a more stimulating effect on *Calluna* growth than sheep and deer, cattle having the highest negative effect because of dung and trampling. With no grazing there was an increase of *Deschampsia flexuosa* and *Vaccinium myrtillus* (Welch 1984a).

Welch (1984b) studied changes in botanical composition of heathlands in relation to grazing pressure and soil type over a period of 4–11 years. Light grazing favoured ericoids and lichens (e.g. *Cladonia impexa*, *Erica cinerea*, *E.tetralix*) and heavy grazing favoured graminoids and forbs, e.g. *Agrostis capillaris*, *Festuca ovina*, *Poa pratensis*, *Trifolium repens*, and *Vaccinium myrtillus*. Ericoids are more vulnerable to heavy grazing and trampling than grasses.

Species diversity was higher on base-rich soils but, after 4 years of grazing, diversity rose more on base-poor soils. The trends in heather and graminoids in the thirty-two sites studied by Welch (1984b) are given in Fig. 5.2. They are plotted against dung accumulation (grazing intensity) and soil moisture.

Calluna only increased when grazing pressure was light, while *Juncus squarrosus* and *Molinia caerulea* increased significantly only where moisture content exceeded 60%. Increases of graminoids–forbs were most prominent on drier soils.

Another common problem in mismanaged heathlands, threatening

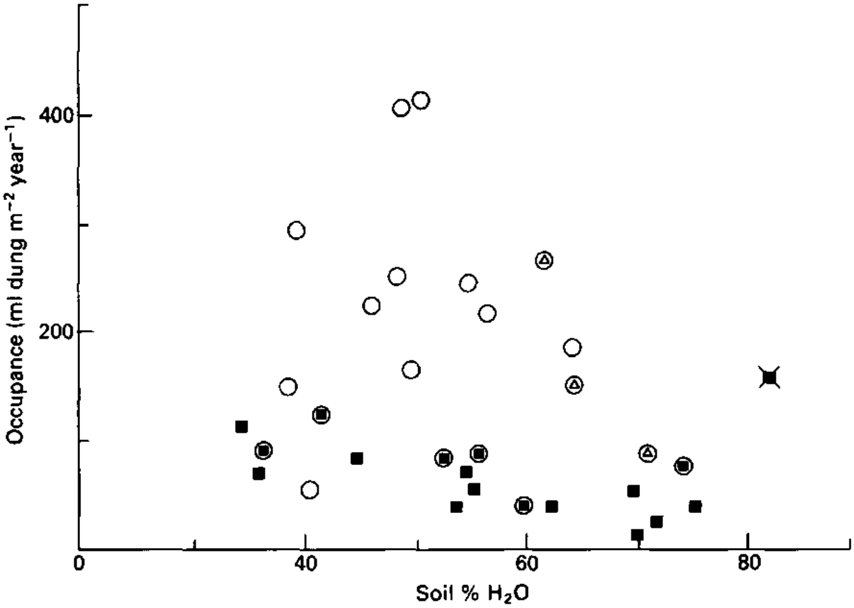

FIG. 5.2. The relationship between main vegetation trends, soil moisture content and herbivore occupance at thirty-two sites in grass-heaths (Scotland): ■ *Calluna* increase; ○ graminoids–forbs significant increase; x *Juncus squarrosus* significant increase; △ *Molinia* significant increase. (From Welch 1984b.)

their conservation, is the accumulation of litter and dead plant material. Cattle grazing reduced the amount of *dead* plant material from 4 to 1 t ha^{-1} within 2–3 years in *Deschampsia flexuosa* dominated grassland in Denmark (Büllow-Olsen 1980). Within 4 years, cattle grazing and trampling reduced the litter layer from 52 to 28 t organic matter ha^{-1} in a *Deschampsia*-dominated former heathland (Van Wieren 1988). In this grassland the biomass and productivity of *Deschampsia* was greatly reduced, gaps were created in the grass sward and *Calluna* started to regenerated from the seedbank still present. Comparable results are reported by Bokdam & Gleichman (1989).

The above examples show that large herbivores can be used as management tools to maintain and create well-developed grass-heaths. Because grass-heaths can occur on very different soils and conservation goals vary widely it is difficult to determine which herbivore density gives the best results.

Before the 'grass' problem became evident, a density of about 1 sheep ha^{-1} was applied on *Calluna*-dominated grass-heaths in the Netherlands.

This density, however, was too low to prevent forest succession and to prevent the ageing of *Calluna*, and additional management practices were always necessary. At higher sheep or deer densities (> 2 sheep/deer ha^{-1}) succession to forest may be prevented, but the proportion of grass starts to increase and the heathland becomes overgrazed.

Although cattle grazing is not considered favourable when *Calluna* is dominant (Welch 1984a), cattle can be effective when grass species start to invade and become dominant. Furthermore, cattle have less impact on regenerating *Calluna* than sheep and deer. To maintain grass-heaths with *Calluna* and grasses equally abundant a combined grazing regime with cattle and/or deer is thought to give the best results.

Grasslands

There are a number of types of grassland where grazing plays an important role in maintaining and creating ecological values. Among them are calcareous grasslands, abandoned agricultural lands, riverine grasslands, wetlands and coastal areas.

As far as the vegetation is concerned, the management of grasslands is aimed at a high diversity: a diversity both of community type and of species within each vegetation type. Species diversity is often higher in grasslands subjected to grazing, not only in ungrazed areas but also in grasslands mown mechanically. When after a period of 13 years an ungrazed, species-poor, salt-marsh is mowed or grazed, differences in species diversity occurred after 10 years (Fig. 5.3) (Bakker 1987). With mowing the number of species increased rapidly because the litter is removed for a large part in the first year. The grazers need more time to influence the litter layer but eventually a higher number of species was achieved.

On heavily fertilized chalk grasslands, Willems (1983) compared the effects of abandoning, mowing and grazing with sheep after a period of 13 years. In the abandoned area the number of species had fallen from thirty-seven to thirty-three. In the case of mowing and grazing, the vegetation had changed into a low productive chalk grassland (*Mesobromion erecti*) where the number of species increased from twenty-eight to forty with mowing and from thirty-one to forty-two with grazing.

Comparison of cattle-grazed and ungrazed (for 15 years) calcareous grassland in South Sweden showed a much higher species diversity in the grazed situation (Table 5.1) (Regnell 1980).

To obtain a high diversity, herbivore pressure should not exceed a level whereby all vegetation types are grazed very short and not be so low that a major part of the grassland degrades to rough grassland of only

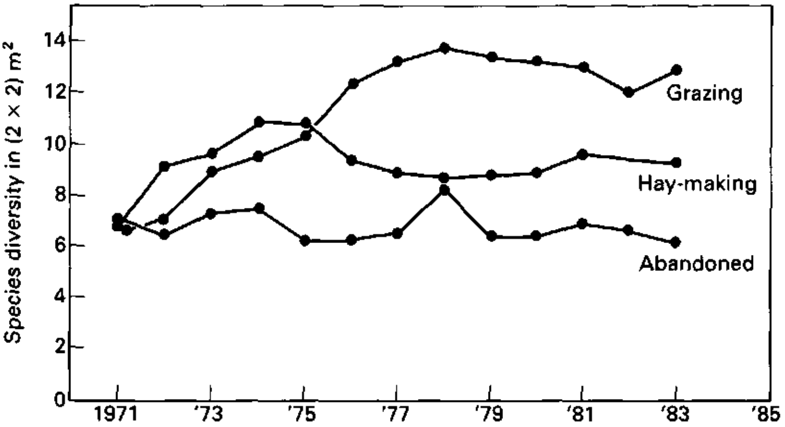

FIG. 5.3. Changes in mean species diversity with grazing, mowing and continued abandoning in various communities at the mid and upper salt-marsh of Schiermonnikoog (n=5; point quadrats (2 × 2) m²). (From Bakker 1987.)

TABLE 5.1. Main cover differences between vegetation of grazed (A,C) and ungrazed (B,D) plots in chalk grassland (Regnell 1980).

	Grazed		*Ungrazed*	
	A	C	B	D
Number of quadrats plot^{-1}	20	20	10	30
Total number of species plot^{-1}	70	66	16	11
Mean number of species quadrat^{-1}	15·5	17	5·5	5·5
Carex panicea	14	19		
Festuca ovina	32	19		
Molinia caerulea	22	11		
Centaurea jacea	7	12		
Campylium stellatum	11	2	1	
Carex flacca	5	4		
Galium uliginosum	2	3		
Potentilla erecta	12	4		
Serratula tinctoria	6	61		
Thuidium tamariscinum	15	16		
Carex nigra	10	6	13	
Filipendula ulmaria	6	47	7	83
Carex distacha	9	4	67	24
Urtica dioica				17
Galium aparine				2

coarser species. In the Netherlands, where the use of large herbivores in management of grassland systems for conservation is now widespread, a 1:1 distribution of short-grass and long-grass patches within the sward is the aim. To reach such a distribution, the grazing pressure has to vary in relation to the productivity level of the different grassland types. When grazing pressure becomes too high structural differences between vegetation types tend to disappear (Looyen & Bakker 1987).

Heavy grazing on salt-marshes may lead to a decrease or even disappearance of interesting species, e.g. *Aster tripolium*, *Limonium vulgare* and *Halimione portulacoides* (Westhof 1987). Sometimes unpalatable grasses can become dominant when grazing animals selectively feed heavily on the more palatable plant species. The spread of *Nardus stricta* in the uplands of Great Britain is a clear example (Nicholson, Patterson & Currie 1970). But, when grazing pressure is not too high, differential habitat use and selective feeding leads to structural differentiation in the vegetation and gaps are created promoting colonization of plant species. Differential treading and dunging adds further variety to the system. Intermediate grazing levels may have a mediating effect on competition between plant species resulting in the co-existence of more plant species than without grazing (Grime 1979).

The structural differences can be recognized on different scales. Well known are the macropatterns that are created on the vegetation type level. When having the choice, deer preferred grassland much more than moorland or heathland (Charles, McCowan & East 1977). Sheep removed 80% of the production of pasture and only 10% of the production of *Molinia*-dominated grassland (Job & Taylor 1978). Distinct habitat preferences exist between cattle and ponies in the New Forest.

Selective grazing, treading and dunging within vegetation types may lead to micropatterns on a smaller scale. Conspicuous are the latrine areas in the New Forest developing as the result of selective defecation behaviour of ponies. These areas are avoided by the herbivores and have a rougher appearance than the close-cropped grassland (Edwards & Hollis 1982; Putman 1986).

With a moderate grazing intensity a mosaic developed of heavily grazed and lightly grazed patches in Dutch grassland grazed by sheep (Bakker, De Leeuw & Van Wieren 1984; Bakker 1989). The micropattern was stable in time. Although no differences were found in species composition, abundancies differed substantially. However, a sowing experiment with species not present in the established vegetation nor in the seedbank revealed a higher seedling emergence in the heavily grazed than in the lightly grazed patches. More dicotyledons and fewer monocotyledons were found in the heavily grazed patches. These patches are repeatedly visited and maintained with a much higher leaf–stem ratio compared to the lightly grazed areas.

Cattle grazing in a chalk grassland in Sweden also brought about a microrelief which was absent in a comparable mowed site (Regnell 1980). In the grazed plot (and not in the ungrazed plot) tussocks and depressions could be distinguished. The tussocks had more species than the depressions (61 vs. 32). Once formed, tussocks govern the trampling pattern of the cattle: out of 117 steps, 106 were placed in depressions, 5 in an intermediate position, and only 6 on tussocks. The tussocks were preferentially grazed.

The effects of grazing often become most apparent when grazing stops. There are many examples which demonstrate a decline in species richness when grasslands are abandoned. Firstly, the mosaic of patches of different structural type caused by uneven grazing disappears. Litter also is accumulated and relationships between plant species change in favour of the more fast-growing competitive species.

The development of the vegetation of formerly grazed and/or cut grassland which has been left abandoned for 24 years was studied by Persson (1984) in Sweden. Before being abandoned there had been grazing for more than 100 years. He found that: (i) species diversity decreased, plants forming rosettes and stolons, and bryophytes decreased; (ii) equitability decreased with increasing dominance of a few species; (iii) pattern diversity decreased, fine-grained changing to coarse-grained; and (iv) the formerly grazed plot had more changes than the formerly mowed plot. It can be concluded that, within grasslands, a high diversity can be obtained when grazing intensity permits large-scale spatial heterogenity and when both heavily grazed and ungrazed patches are present.

EFFECTS ON FAUNA

Large herbivores affect other fauna either directly, e.g. by trampling, or indirectly by influencing the ground vegetation and the succession. The latter effect is considered the most important because when different successional stages are fixed by herbivory a variety of plant communities can co-exist with its typical fauna.

Invertebrates

Grassland systems which are heavily grazed experience a severe loss in number of species and in total biomass of the invertebrate fauna compared to mowing or abandoning (Morris 1967, 1968, 1969; Rahmann *et al.* 1987; Siepel & Van de Bund 1988). A negative relationship was found between grazing intensity and invertebrate biomass (Rottman & Capinera 1983).

Rahmann *et al.* (1987) compared different management systems on salt-marshes in northern Germany. The number of species decreased progressively in the sequence left abandoned for 10 years > left abandoned for 1 year > cut in July, grazed with 2 cows ha^{-1} > grazed with 5 sheep ha^{-1}. A lightly grazed grassland too (0·16 cow ha^{-1}) had fewer species and biomass than an ungrazed grassland (Siepel *et al.* 1987). The main influences of large grazing animals are summarized in Fig. 5.4. The most important negative factors on the invertebrate communities in grazed (compared to mowed or abandoned) systems are: (i) fewer flowering plant individuals; (ii) less litter; (iii) reduced standing crop; (iv) disturbance by treading; (v) less prey for predators; and (vi) a more extreme microclimate.

There are a few groups that may benefit from grazing, dung beetles (Coleoptera) being well-known examples. Some consumers of algae increased in cattle-grazed areas because suitable niches were created (bare soil, sharp edges on hoof marks) (Irmler & Heydemann 1986; Irmler, Heydemann & Wrage 1987).

Grazing may also create suitable habitats for some species of butterflies (J. A. Thomas 1980, 1983; Thomas *et al.* 1986). In particular, butterflies which require very short cropped grasses surrounded by bare ground for egg-laying sites and situated in sheltered sunspots were favoured in areas heavily grazed by sheep or rabbits. The declines of the silver-spotted skipper butterfly (*Hespera comma*), the Adonis blue butterfly (*Lysandra bellargus*) and the large blue butterfly (*Maculinae arion*) were related to the decline of sheep grazing and myxomatosis. Bink & Van der Made (1986) also found a number of species of butterflies to thrive in the very lightly grazed areas with many flowering plants within a moderately grazed park landscape.

Most studies on the invertebrate fauna are confined to grassland biotopes which are generally heavily grazed and frequently small in size. A comparison between mowed areas, abandoned areas and (large) grazing systems with low grazing intensities and containing different successional stages (fringe communities), has yet to be made.

Birds

Large herbivores in grassland and other open communities are able to maintain high quality short turfs and prevent them from developing to

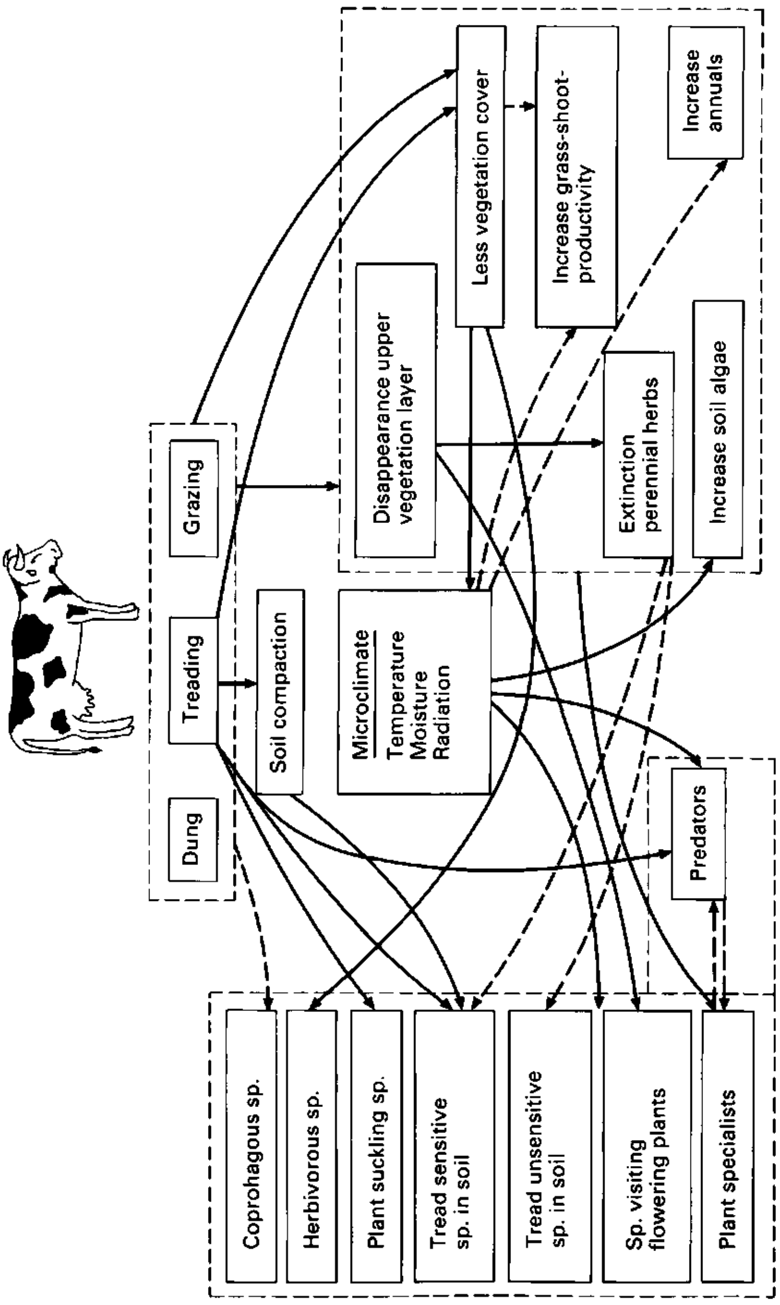

FIG. 5.4. Schematic representation of effects of cattle grazing on different parts of salt-marsh ecosystems: productivity increasing or stabilizing effects (– – –); productivity decreasing or destabilizing effects (———). (From Irmler & Heydemann 1986.)

forest. Many species of birds use these short grasslands, either for feeding or for breeding. Whether grazing is of advantage or disadvantage depends on the specific feeding and breeding requirements of the bird species involved and of their sensitivity to disturbance and trampling. Furthermore, the grazing intensity is of importance in that it will determine the precise length of the sward. Wintering wigeons (*Anas penelope*) in the Ouse Washes, for example, benefit from the effects of summer grazing with cattle at a stocking density of 2·5 cows ha^{-1}. This high grazing level prevents a succession towards dominance of the more unpalatable grasses *Glyceria maxima*, *Phalaris arundinacea* and *Agropyron repens*. Grazing thus increases the carrying capacity for wigeon (Owen & Thomas 1979). In unimproved washland at the Ouse Washes, however, nest densities of the mallard (*Anas platyrhynchos*) were highest in unused fields or lightly grazed fields, while nest densities of the shoveler (*Spatula clypeata*) and the pintail (*Anas acuta*) were positively correlated with the grazing intensity exerted in the previous year. The preferred height of the vegetation near the nest site and feeding conditions being the most likely controlling variables (G. J. Thomas 1980).

In salt-marshes the grazing pressure is often very high as salt-marshes are productive and the grazing regime is highly seasonal. Too heavy a grazing pressure can have a negative effect on bird diversity and abundance. In (heavily) grazed salt-marshes in Germany, the number of breeding pairs of all species involved was even less than in undisturbed, ungrazed areas (Table 5.2). Avocets and redshanks were particularly sensitive (Schulz 1987). In general, salt-marshes with a moderate grazing intensity (1·4–1·6 cows ha^{-1}) contained more species of breeding birds and more nests than a comparable ungrazed site, and more than heavier-grazed salt-marshes on other Dutch Wadden islands (Van Dijk & Bakker 1980). Schulz (1987) listed a number of advantages and disadvantages for birds grazing on salt-marshes also grazed by livestock. The disadvantages become greater with increasing density.

TABLE 5.2. Number of breeding pairs 10 ha^{-1} of four bird species in salt-marshes in Germany: A, 50 ha ungrazed; B, 64 ha moderately grazed; C, 100 ha intensely grazed (Schulz 1987).

	A	B	C
Avocet (*Recurvirostra avocetta*)	52·4	3·5	10·3
Redshank (*Tringa totanus*)	11·6	1·7	0·3
Oystercatcher (*Haematopus ostralagus*)	3·2	2·1	1·9
Lapwing (*Vanellus vanellus*)	1·8	1·8	0·8

Grazed salt-marshes

Advantages:
- high abundance of preferred plant species
- the presence of short dense swards
- the availability of nutrient-rich grass leaves

Disadvantages:
- competition with the grazers
- increased disturbance (by man)

Ungrazed salt-marshes

Advantages:
- no competition
- less disturbance, less visibility
- sometimes preferred species abundant (e.g. *Triglochin maritima* and *Plantago maritima*)

Disadvantages:
- high abundance of less preferred species
- lower quality forage

All the foregoing relates to studies on salt-marsh and unimproved grasslands.

In agricultural grasslands, excessively heavy grazing can be hazardous to breeding meadow birds because a large part of the nests are being trampled, the effect being related to grazing intensity (Green 1988). In Dutch grasslands hatching success of important meadow bird species was related to herbivore density and type of herbivore (Beintema & Muskens 1987). Sheep were more detrimental than heifers and dairy cattle, while hatching success was highest with heifers.

Although the grazers have negative influences on breeding success, this effect seems to be only of relative importance because the species do breed in the wet grasslands that are maintained by the large herbivores. Without grazing the wetlands would develop into marshy land.

Mammals

Little work has been done on the effects of large herbivores on other mammals in western Europe. Competitive as well as facilitative effects have been reported. In an abandoned grass-heath grazed with Icelandic ponies the rabbit density was positively correlated with the grazing pressure of the ponies. On their own, rabbits could only maintain a short sward when at very high density. When the turf became only a few centimetres high the area became less important for the rabbits (Oosterveld 1983). Also, in the same area the number of species of mice was positively correlated with pony grazing intensity (Thalen *et al.* 1987).

When grazing pressure becomes very high, however, the amount of cover and food for small rodents can decline seriously. In the New Forest, species diversity and population density of most species of mice and voles was much lower in the open communities and woodlands than in comparable vegetation types outside the Forest. An exception being wood mice (*Apodemus sylvaticus*) which appeared little affected by the heavy grazing pressure (Hill 1982).

High red deer density led to a decrease in roe deer and chamois numbers in the Swiss National Park (Schloeth 1972). In the New Forest, roe deer numbers were negatively correlated with numbers of domestic cattle and ponies suggesting competitive exclusion of roe deer by the domestic herbivores (Putman & Sharma 1987).

An interesting case of facilitation was reported by Gordon (1988) in a study on the Isle of Rhum. In 1957, all the cattle present on the island were removed and the red deer (*Cervus elaphus*) became the main herbivore species. Despite the presence of a large population of deer, the species diversity of the prevailing *Agrostis–Festuca* grasslands became reduced and the area of unpalatable *Molinia*-dominated grassland increased. In 1970 cattle were reintroduced. Cattle grazing resulted in greater biomass and a greater availability of green grass in the *Molinia* grassland than in ungrazed sites. The areas grazed by the cattle were preferentially grazed by red deer and the reproductive performance of deer in these areas was improved: the calf–hind ratio was found to be higher (Gordon 1988).

LARGE HERBIVORES, VEGETATION SUCCESSION AND BIRDS: A CASE STUDY

In 1971, the Grevelingen estuary in the south-west Netherlands was embanked and tidal movements disappeared. Because of the fixed water table the sandflats and salt-marshes became permanently dry and a new vegetation development started (desalination). In a part of the area, the 'Slikken van Flakkee', the vegetation succession and the development of the bird communities was studied (Slob 1989; Van Schaik & De Jong 1989). About half of the area (650 ha) is grazed with fifty Heck-cattle and twenty-five horses, the other half (600 ha) is left abandoned.

Summarized vegetation development

Five main vegetation types can now be distinguished (Van Schaik & De Jong 1989):

1 species-poor halophytic community (*Salicornia europea*);

2 species-rich halophytic community (e.g. *Puccinellia maritima*, *Spartina anglica*, *Spergularia salina*);

3 grassland vegetation (e.g. *Festuca rubra*, *Agrostis stolonifera*, *Calamagrostis epigejos*, and dune slack species *Centaurium littorale*, *C. pulchellum* and *Parnassia palustris*);

4 tall herb–shrub vegetation (e.g. *Cirsium arvense*, *Epilobium hirsutum*, *Sambucus nigra*);

5 woodland–shrub vegetation (e.g. *Hippophae rhamnoides*, *Rubus fruticosa*, *Salix* sp.).

In the grazed area, succession is retarded (Fig. 5.5), a large part of the short vegetation is fixed and less tall herb and shrub vegetation developed.

Breeding birds

The development of the breeding bird populations is closely related to the vegetational succession (Fig. 5.6). The number of bird species is higher in

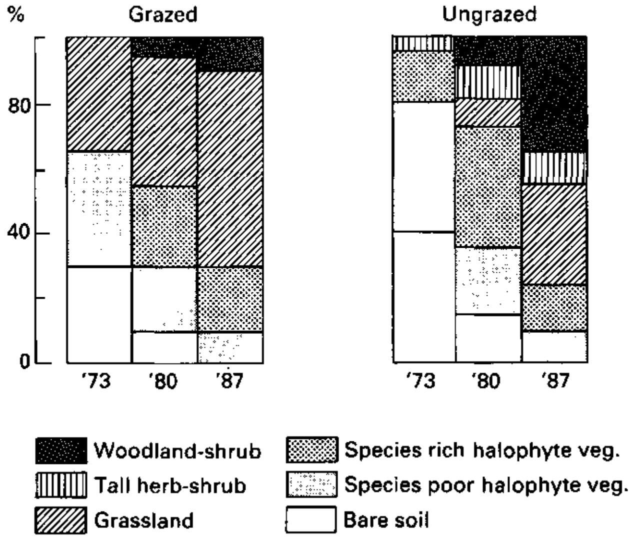

FIG. 5.5. Schematic vegetation development of (a) the grazed and (b) the ungrazed Slikken van Flakkee (the Netherlands). (Based on Van Schaik & De Jong 1989; D. J. De Jong, personal communication.)

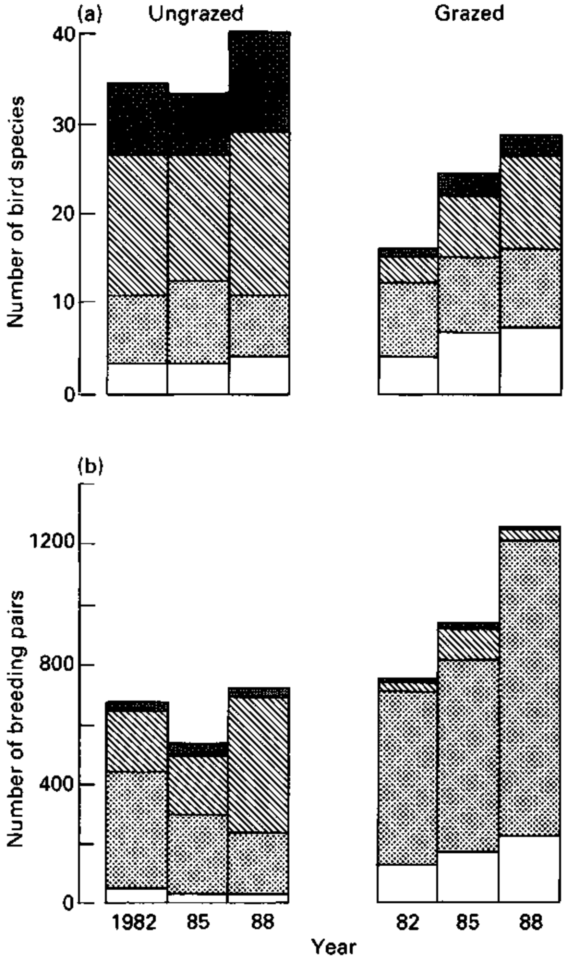

FIG. 5.6. The number of (a) bird species and (b) breeding pairs of the breeding bird community, across the main vegetation types, of the grazed and ungrazed Slikken van Flakkee in 1982, 1985 and 1988 (calculated from Slob 1989). ■ woodland shrub; ▧ tall herb–shrub; ▩ grassland; □ halophytes.

the ungrazed area because of the occurrence of shrub and woodland. The number of breeding pairs, however, is much greater in the grazed area. Although the number of species in the grassland remains about the same, the grazed grasslands become increasingly important breeding areas for the typical meadow species: oystercatcher (*Haematopus ostralegus*), lapwing (*Vanellus vanellus*), black-tailed godwit (*Limosa limosa*) and redshank (*Tringa totanus*). The relative importance of both management systems for breeding birds is indicated in Table 5.3. Both areas are important for a different group of species.

The ungrazed area is important to a limited number of species which are absent in the grazed area. Although there are no species that exclusively breed in the grazed area the total number of breeding pairs is much higher, while numbers decrease in the ungrazed area and increase in the grazed area. The presence of uniform short vegetation in the grazed area is also attractive to wintering geese (Table 5.4).

The developments in the two areas demonstrate that different communities with their own specific ecological interests are present in both management systems and that, from a conservation point of view, either community has a right to exist.

TABLE 5.3. Total number of breeding pairs of endangered or threatened species of the EEC red list for the Netherlands, in the grazed and ungrazed Slikken van Flakkee: A, species that are more abundant in the ungrazed area; B, species that are more abundant in the grazed area; number of species in parentheses (calculated from Slob 1989).

	A			B		
	Ungrazed	Grazed		Ungrazed	Grazed	
1982	22	0	(3)	138	295	(6)
1985	36	0	(3)	99	326	(8)
1988	67	0	(4)	61	708	(9)

TABLE 5.4. Total number of barnacle geese (*Branta leucopsis*) counted in the grazed and ungrazed Slikken van Flakkee in the period Nov–Feb (one count month^{-1}) (G. J. Slob, unpublished data).

	Grazed	Ungrazed
1981	7180	1200
1982	12500	0
1983	36000	370
1984	11000	0
1985	10400	2600
1986	11200	1945
1987	6000	0
1988	22400	5930

S. E. VAN WIEREN

CONSERVATION AND THE MANAGEMENT OF LARGE MAMMAL POPULATIONS

The above examples do indicate that large herbivores play an important role in nature conservation. The conservation aims, however, are generally directed towards certain plant species/communities/faunal groups and grazing pressure is manipulated. Nowhere is management aimed at the level of entire ecosystems, in which populations of large herbivores (and large predators) are present because they belong to the system, and where the system is left to its own natural dynamics. This is not surprising because we are dealing with man-made systems with ecological values that are products of former agricultural practices. This approach leaves little room for free-living populations of large mammals under more or less natural conditions. Can a place be found for this neglected conservation goal? I believe the answer could be yes, especially now the conservation goals of existing reserves are becoming increasingly difficult to achieve under the existing management.

1 A major problem is the disappearance of the former agricultural practices. Many marginal lands are abandoned for economic reasons and it is very unlikely that conservation bodies are able to continue the old management systems on a large scale. The plant and animal species connected with these systems are increasingly difficult to preserve.

2 Habitat fragmentation during this century has led to very small reserves and they have become islands in an intensely used agricultural landscape. In these isolated islands populations suffer a higher extinction rate.

3 Abiotic changes in reserves (high N input, lowered ground watertable and changed ground water quality) have led to the disappearance of highly valued species).

All these signs of degradation call for a more aggressive and ecosystem-oriented conservation strategy. Three types of nature reserves are proposed: (i) natural ecosystems; (ii) medium to large-sized semi-natural nature reserves; (iii) small to medium-sized semi-natural nature reserves.

Natural ecosystems

A natural ecosystem is large (> 100 000 ha) and contains the potential natural vegetation and fauna, while human interference is minimal. In Western Europe the vegetation will be predominantly broadleafed forest with an unknown but probably low degree of openness. The area should be large enough to contain suitable natural habitat for free-living populations of large mammals (summer and winter habitat).

The large herbivores that come into focus are initially the wild species that are still present: roe deer, red deer, wild boar, moose, wisent. Secondly, one might consider making use of primitive domestic breeds of cattle and horse and use them as replacements of the extinct aorochs and the extinct tarpan. There are two main key factors in establishing which species should play a role: (i) the species should be potentially indigenous, and (ii) there must be enough room for genetically healthy populations. If there is not enough room, a choice has to be made between the different species of herbivores. Total herbivore density will be low and should on average not exceed a threshold whereby the regeneration of the potential natural vegetation is prevented for a long time.

Management practices frequently will be needed to let the natural vegetation re-develop. The best method is natural regeneration from existing seed resources; thus, little herbivore pressure should be allowed in the first period to let the vegetation establish itself. Temporarily, exclosures might be necessary. The herbivore species are re-introduced (or populations allowed to expand) at a later stage. If the system can not be made complete, i.e. if the reintroduction of the large predators is not feasible, than population levels of the large herbivores will have to be controlled. In this way self-regulating ecosystems could be restored and, because of the high degree of naturalness and the large size (which increases the chance of habitat variety), many species could be accumulated. Almost all terrestrial plant and other animal species have evolved or have co-existed for millennia in the presence of the large herbivores.

Medium- to large-sized semi-natural nature reserves

These areas (generally exceeding 10 000 ha) are half-open landscapes with potential natural vegetation only on a limited scale and a large proportion of short vegetation (grasslands, dwarf-shrub communities). Free-living populations of large (indigenous) herbivores are present but herbivore pressure may well be higher than in natural ecosystems.

Total herbivore density should not exceed about 5–10 animals 100 ha^{-1} to ensure some regeneration of grazing-sensitive species and structural differentiation within the short vegetation communities. Because it is unlikely that these systems will keep a balanced structure by the effects of the large herbivores alone, some human interference is needed. In the short vegetation regular clearance of regenerating woodland (with species of early successional stages) is likely to be necessary while, on the other hand, short-term enclosures might be necessary to ensure regeneration of sensitive broadleafed tree species. Of the free-living populations of large herbivores only the numbers need be controlled.

Because of the fairly large scale, low grazing pressure, varied structure, and large proportion of short vegetation it is expected that these systems would contain suitable niches for a large array of species. With a much lower herbivore density than at present (and with the reintroduction of the wild boar) the New Forest in Southern England could become a fine example.

Small to medium-sized semi-natural nature reserves

Most existing nature reserves fall into this category. Management generally aims at the conservation of species and certain plant communities. It is important to note that in any reserve only a limited number of ecological objectives can be aimed at and, therefore, conservation goals have to be well defined. Because of the changes in the agricultural land use, the former agricultural practices can only be applied on a limited scale. Therefore, conservation areas have to be chosen carefully so as to obtain optimal results. In such a context the large herbivores are used as tools and their management at the population level is not important.

It has to be concluded that the real story of 'the management of *populations* of large mammals' cannot be written at the moment as far as Western Europe is concerned. Perhaps it will become possible in the near future if we establish sufficient representatives of the proposed type 1 and type 2 nature reserves.

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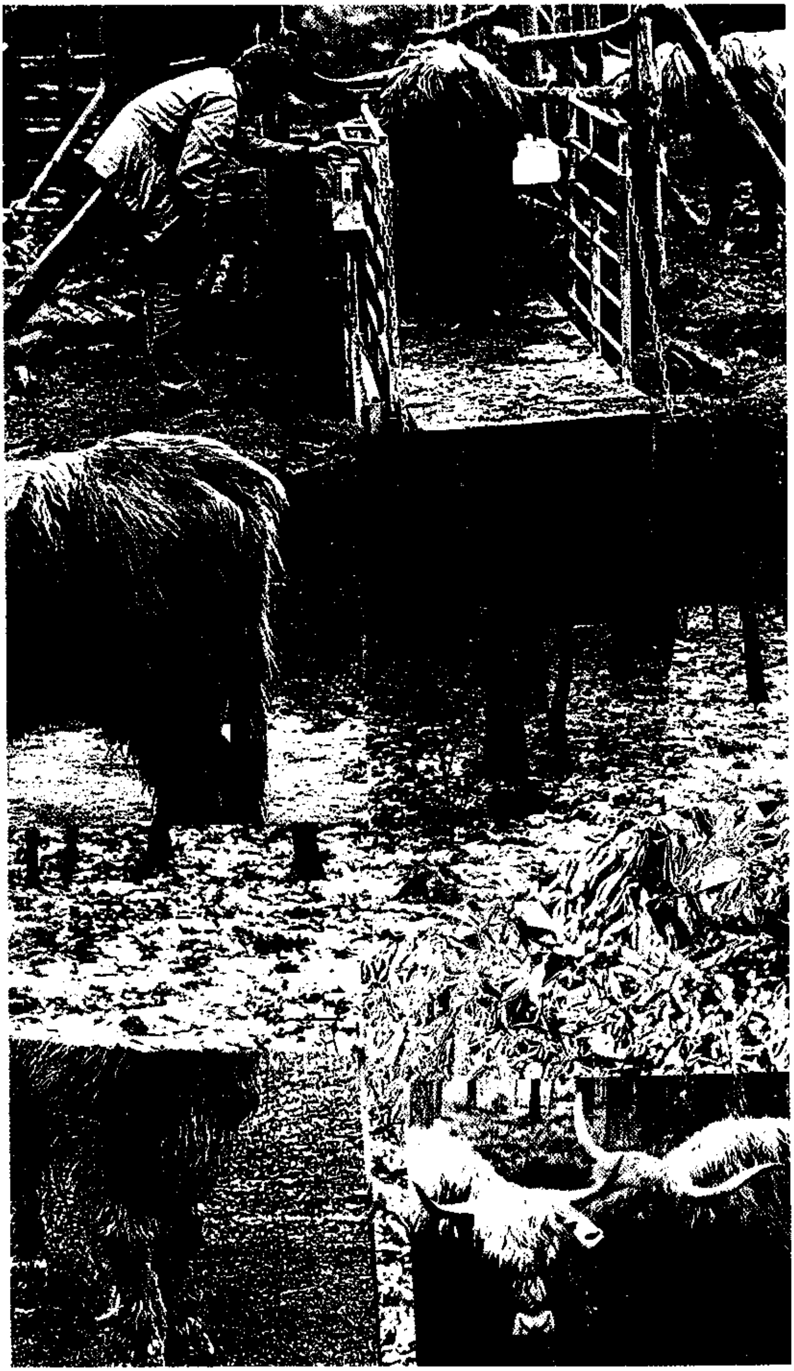

CHAPTER 3

FACTORS LIMITING FOOD INTAKE IN RUMINANTS AND NON RUMINANTS IN THE TEMPERATE ZONE

Abstract

In the temperate zone large ungulates experience a seasonal decrease in food quantity and food quality. Body weight changes in free ranging Highland cattle show that very high growth rates are possible in spring but that weight losses occur from November to March indicating that limiting factors on food intake are operating in the winter period. The digestibility of the diet appears to be the most important single factor limiting food intake but also other factors are involved. Very high intakes in April and October can be explained by compensatory growth and lactation respectively, both mechanisms being affected by the physiological state of the animal. Furthermore the realized intake in winter seems to be lower than expected from the 'maximum rumen fill hypothesis' indicating a lower voluntary food intake than is feasible. Possible reasons are discussed. It is pointed out that nonruminants are less limited by gut capacity than ruminants and, although being less efficient, they can compensate by eating more. Field evidence suggests that horses are less affected by nutritional stress in winter than cattle.

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relatively more energy is used for the maintenance of the slower growing bacteria (Hespell & Bryant, 1979, Prins & Clarke, 1980). A lower fermentation rate will have a negative effect on intake. The disappearance of food from < the rumen is the result of digestion, and subsequent absorption of fermentation products through the rumen wall, and passage of undigested food particles from the rumen to the abomasum. When digestion rate slows down, the rate of passage generally decreases too and rumen fill is likely to become a limit to food intake.

The OMI and OMD are significantly related to each other ($p < 0.001$). This linear relationship between OMD and OMI is well known (Bines *et al.*, 1969 ; Hodgson *et al.*, 1977 ; Holechek *et al.*, 1968) but, especially when the availibility and the structure of the forage play an important role, the relation is not always linear (Arnold & Dudzinsky, 1967).

In figure 3 the regression line between OMI and OMD is plotted together with the data points (months). Although the correlation is high ($r = 0.84$) not all the points do nicely fit. Especially the April and October data are noticeably higher then expected while, when leaving these two data out of the regression, the correlation is markedly increased ($r = 0.96$). It seems that although digestibility is the most important factor other factors are also into play. The very high intake in April is likely to be related to the effect of compensatory growth. It is well known that animals that went through a period of severe reduction in body weight eat much more than animals with normal weights (Balch & Campling, 1962 ; Osbourn, 1980 ; Tayler, 1959). Bines *et al.* (1969) found thin cows to eat 2.5 kg more than fat cows when the digestibility was 65%.

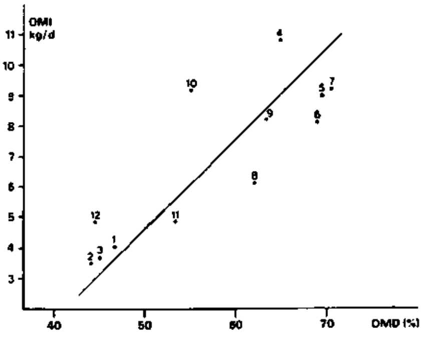


Figure 3 : Relationship between organic matter digestibility (OMD) and organic matter intake (OMI). Monthly data points are indicated ($r = 0.84$).

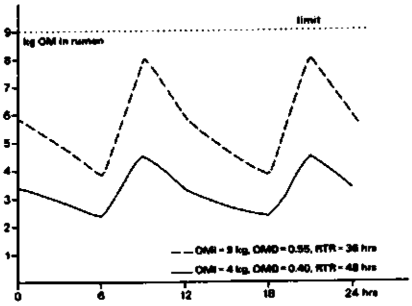
There is any reason to believe that this mechanism also (and maybe even more strongly) occurs in wild ungulates.

The very high intake in October can be explained by lactation. In ruminants during lactation the highest intakes are found (Campling, 1966 ; Weston, 1982 ; Forbes, 1986). Intake increases promptly after parturition to reach a maximum after a variable time (Weston 1982). Bines (1979) suggests this peak being reached after about 3 months in cattle. The higher intakes during lactation have a physiologically basis and are probably being made possible by an increased volume of the retico-rumen (Campling 1966, Forbes 1986). Normally intake remains high after the lactation peak for some time but this is not the case for the cow from figure 3 indicating that the requirements for normal lactation cannot be met anymore from the level of intake. Hence a calf born late in the season is less likely to be fed adequately by its mother than a calf born in spring.

A LOWER VOLUNTARY INTAKE IN WINTER?

The highly significant positive relationship between intake and digestibility suggests that digestibility is the most important factor limiting intake. As discussed a lowered rate and extend of digestion has a negative effect on the energy retention but eventually the food intake will be constrained by the physical capacity of the rumen because of the lowered disappearance rate of digesta from the rumen (through the combined effect of a slower fermentation rate and a lower rate of passage of food particles from the rumen to the abomasum) (Balch & Campling, 1962, Forbes 1986, Van Soest 1982). The physical control of intake seems to be the major factor with digestibilities up to 67-70% while at higher digestibilities intake is controlled metabolically (Conrad *et al.*, 1964). All this suggests that the main constraint is rumen fill in Highland cattle and probably in other ruminants as well.

However, doubt remains if fill is the only factor. In the first place the strong decline in intake in October/November and secondly the very low intake level in the winter period warrants further speculation on rumen fill as possible limiting factor. Diurnal variation in rumen fill at two different intake levels, representing the October intake (9 kg) and the average intake in the winter period (4 kg), were estimated (fig 4). Figure 4 suggests that the intake in October is likely to be limited by rumen fill but it is very unlikely that the very low intake in the winter is caused by physical constraints. A low amount of dry matter (DM) in the rumen on forage of low quality has been reported by Balch & Line (1957). They found that in cattle, eating good quality hay, rumen fill was 9 kg DM but that DM in the rumen fell by more than 50% (to 3.5 kg DM) when animals grazed on old pasture with low quality forage.



OMI = organic matter intake
OMD = organic matter digestibility
RTR = mean retention time of the food in the rumen

Figure 4 : Estimated rumen fill at 2 different intake levels in a Highland cow of 400 kg. The daily intake is modelled on the basis of two meals per day.

Another indication that rumen capacity is not limiting is that the capacity for ruminating does not seem to be fully exploited in winter (fig 5B). The passage rate of food from the rumen is positively influenced by rumination (Van Soest, 1982) and it is expected that rumination is increased when rate of passage is reduced and rumen fill becomes limiting. Indeed rumination intensity could be shown to increase at lower intake levels (Van Wieren unpub. res.) but total rumination time is not increased and certainly remains far below the rumination limit of 10-11 hrs/day (Bae *et al.*, 1979 ; Welch in Van Soest, 1982).

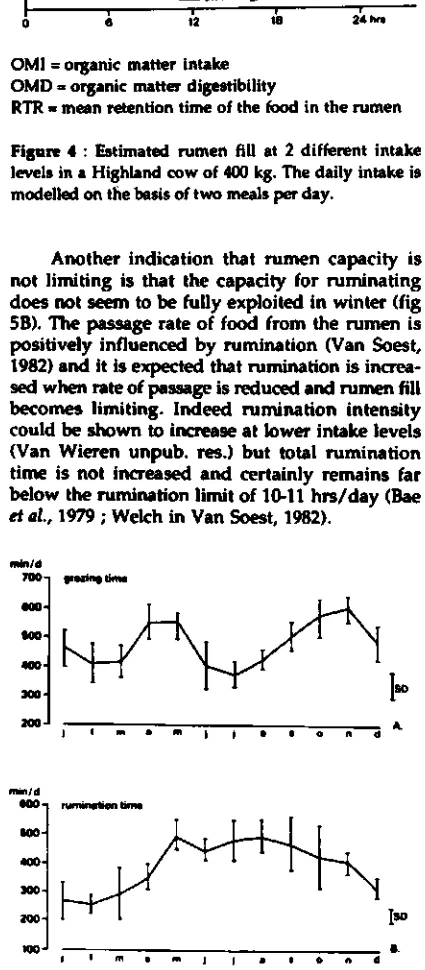


Figure 5 : Time spent grazing (A) and ruminating (B) by Highland cow

Apart from physical constraints a low food supply could have been responsible for the low intake level in winter. Forage availability may be low simply because the standing crop is below a certain minimum level (Allden & Whittaker, 1970 ; Langlands & Bennet, 1973) or because forage of a certain minimum quality is only present in limited amounts per unit area (Stobbs, 1973). In northern herbivores snow cover often acts as a logistic constraint on food intake in the winter period (Hudson & White, 1985). When less forage is available, intake rate is reduced but compensation may occur by an increase in the total daily grazing time. In ruminants, however, the total grazing time is limited and estimated to be about 800 min/day (Hudson & Nietfeld, 1985 ; Stobbs, 1970). It could be shown that in the Highland cattle the intake rate in the winter indeed was much lower than in the summer (Van Wieren unpub. res.) but this did not led to increased grazing. In fact total grazing time was low in winter (fig 5A). At any time total grazing time never reached the upper limit and hence it must be concluded that forage availibility was not limiting the total daily food intake.

The apparent voluntary reduced intake in winter can possibly be explained by seasonal variation in the voluntary food intake based on an endogenous physiological rhythm. It is well known that, even on good quality diets, herbivores of northern lattitudes exhibit seasonal variations in appetite (Kay *et al.*, 1980). This reduced appetite goes together with a reduction in metabolic rate (Argo & Smith, 1983 ; Blaxter & Boyne, 1982 ; Gordon, 1964 ; Webster, 1978). The metabolic cycle is strongly affected by changes in hormonal concentrations (Lincoln, 1985) while these are triggered by changes in photo period. According to Kay (1979) this mechanism is more pronounced in wild animals than in domestic animals. Sofar endogenous rhythms have only been reported for herbivores of northern lattitudes and if it exists in the tropics the stimulus must be something else than light.

Although a mechanism now has been found to explain the variation in voluntary intake in the winter the adaptive significance of it is not yet clear. Probably it plays an important role in the winter survival strategy but on the other hand it is not easy to see why an animal should voluntarily eat less while it could have eaten more to meet its demands better. Recently an interesting theory has been put forward which might be used as an explanation. This new theory (Ketelaars & Tolkamp, 1991) assumes that feed consumption creates both benefits to the animal (in an non reproducing animal being net energy for maintenance and gain) and costs (the total oxygen consumption of the animal). The use of oxygen by tissues indirectly causes an accumulation of damage to cell structures, a loss of vitality, ageing and a limited lifespan. Therefore these authors hypothesize that, for the animal, there exists an optimal intake level whereby the ratio between benefits and costs become maximal. In winter time when the quality of the diet is low relatively more oxygen is consumed per unit digestible dry matter intake then in the summer period. Thus, although it looks a shortsighted strategy on the short term, reducing voluntary intake in the period when food quality is low might in the long run be a more adaptable strategy because the overall benefits then are higher then the costs.

Although very little comparable field studies have been carried out on other species of ruminants in the temperate region, the results of this study together with data collected from animals held in captivity and other field evidence all point to the existence of an adaptive syndrome to a period of food stress in temperate ruminants. This adaptive syndrome can be characterized by a lower activity level, a lower metabolic rate and a lower voluntary food intake relative to other seasons.

COMPARISON WITH NON RUMINANTS

Only a few species of non ruminating ungulates live in the temperate zone and even fewer have been studied in the wild. Among them the one that is perhaps best studied in the field is the wild boar (*Sus scrofa*) but then little nutritional work has been done (Spitz 1986). More work has been carried out on free ranging horses and they are taken here as an example for comparison with ruminants (cattle). The question is if non ruminants are subjected to the same intake limiting factors as ruminants are. As a hind gut fermenting species the horse posesses an entirely different digestive system then ruminants. The results of a comparitative study by Johnson *et al.*, 1982 (table 2) summarizes the most important differences between horses and cattle in their respective ability to utilize grasses. Similar results have been reported by other workers (Hintz, 1969 ; Foose, 1982 ; Vander Noot & Gilbreath, 1970) and the trends also hold for other non ruminant species (Foose, 1982). Table 2 demonstrates that horses are less efficient than cattle (lower digestibility, lower MRT) but that they are able to realize higher intakes and that this higher intake more than compensates for the lower efficiency (higher digestible dry matter intake).

Table 2 : Comparison of the utilization of 3 grass hays (Crested Wheatgrass, Brome and Timoty) fed ad lib to mares and cows (compiled from Johnson *et al.*, 1982)

Mean	Mares	Cows
DMD (%)	54.8	61.6
MRT (hr)	8.5	20.4
DMI (kg/100 kg BW)	2.33	1.39
DDMI (kg/100 kg BW)	1.28	0.86

From these results it can be predicted that horses will experience less nutrient stress in winter, given that food quantity is not limiting, than cattle. There is field evidence that this indeed is the case. In the Netherlands there are a number of conservation areas where cattle and horses live sympatrically. In most of these situations the cattle have more problems, and frequently have to be fed, in the winter than the horses who are never fed and hardly experience severe weight loss. In table 3 the winter performance of ponies and cattle is compared. Although living in different areas it can be shown that the ponies hardly loose weight even while the quality of their diet is less than that of the cattle.

Table 3 : The winter performance of Highland cattle and Shetland ponies (period : 1 Nov. – 1 April) living in different areas

	n	average weight change	diet digestibility (range)
cattle	5	– 22%	35 – 50%
ponies	13	– 02%	27 – 35%

While cattle and other ruminants in the temperate region are less active in the winter horses certainly do not graze less and even spend more time grazing in the winter period (Duncan, 1985 ; Vulink, unpublished results).

As horses are less efficient than ruminants and especially in the winter period will have to eat a bulky diet to keep maintenance it is likely that their superiority over ruminants will depend on the presence of sufficient food. Some evidence that this could be the case comes from the New Forest in Southern England where a (very) high density of herbivores (cattle, ponies and 5 species of deer) leads to a low standing crop. The ponies here spend about 75% of their time grazing throughout the year (Putman *et al.*, 1981), which is high compared to other areas (Duncan, 1985, Vulink, unpub.res.), while their body condition generally was very low in the past when conditions were not yet improved (Pollock, 1980).

It can be speculated upon that on an evolutionary scale the displacement of non ruminants by ruminants has been made possible by the superiority of the ruminant digestive system in combination with high herbivore densities on heavily exploited short swards.

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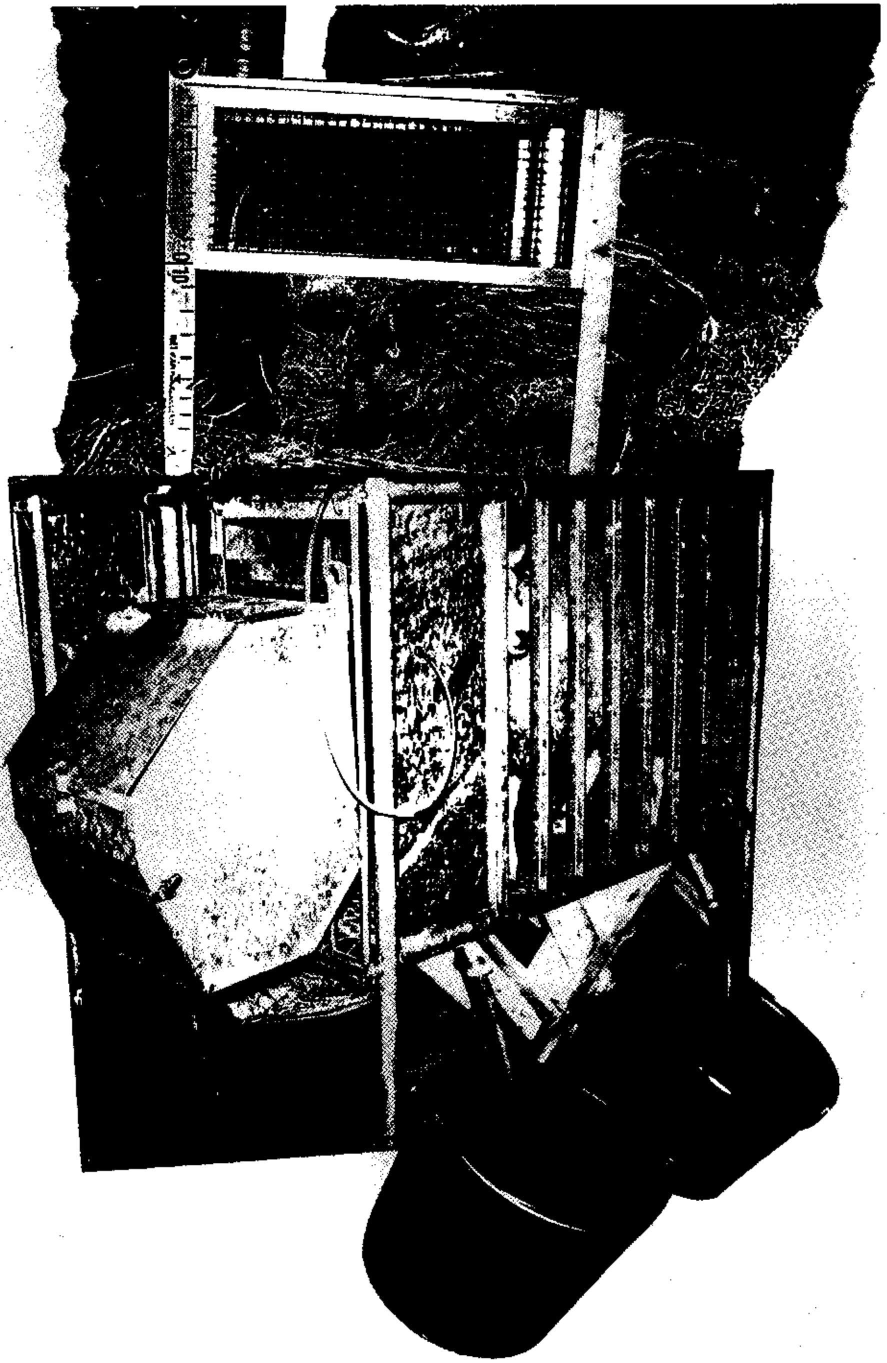

CHAPTER 4

THE USE OF INDIGESTIBLE ACID DETERGENT FIBRE TO PREDICT DIGESTIBILITY

Abstract

The potential use of cellulase indigestible acid detergent fibre (IADF) as an internal marker to predict digestibility was tested by means of 7 different feeding trials. The trials were carried out with African dwarf goats, Texel sheep, Meishan pigs and wild boar involving a wide range of different forages across a broad range of digestibilities (0.231-0.781). A good relationship was found between the in vivo digestibility and the digestibility obtained with IADF as marker. It was concluded that IADF can predict digestibility well across a wide range of forages and digestibilities but that care has to be taken with immature forages low in IADF content.

Introduction

The most accurate way to estimate diet digestibility during feeding trials is total faecal collection. However, this method is time consuming and requires quantitative separation of faeces and urine, which is often difficult especially when working with female animals or with wild species. Therefore much research effort has been devoted to trying to find suitable external and internal markers for predicting organic matter digestibility indirectly. External markers like Cr-NDF or Co-EDTA have yielded good results (Tamminga et al 1989, Uden et al 1980) but to use them oral dosing is necessary. Particularly when working with wild species like roe deer or red deer oral dosing poses problems because these animals are easily stressed when kept in cages or when they have to be handled frequently. It would, therefore, be preferable if an internal marker could be found that accurately can predict digestibility .

A number of internal markers have been tested but in general with poor or variable results. Of these can be mentioned acid insoluble ash (Penning & Johnson 1983a, Tamminga et al 1989, Uden 1984), indigestible NDF and indigestible ADF after in vitro digestion (Cochran et al 1986, Tamminga et al 1989) and methods based on indigestible lignin (Cochran et al 1986, Fahey and Jung 1983, Tamminga et al 1989).

The most promising internal marker studied so far seems to be cellulase indigestible acid detergent fibre (IADF) (Penning & Johnson 1983b, Tamminga et al 1989) although for this marker too variable and even poor results have been reported (Cochran et al 1986, Armstrong et al 1989). The potential use of IADF thus warrants further research. This far it has been tested only with grasses and legumes and in sheep and cattle. To test its potential use for a wider range of forages (including browse material) and a wider range of animal species the present study was undertaken.

Methods

The experiments were carried out with African dwarf goats, Texel sheep, Meishan pigs and wild boar (*Sus scrofa*). In the sheep/goat trials the animals were kept in cages allowing faeces and urine to be collected separately. An adaptation period of 14 days, during which animals were constantly maintained on the experimental diet, was followed by two periods of 5 days of total faecal collection. Feeding was ad lib and the animals were fed twice daily. Mixed diets were offered (table 4.1). In the first period (trial 1) diets consisted of beetpulp, poplar (*Populus canadensis*) (chopped fresh leaves and small twigs) and fresh chopped maize leaves. In the second period (trial 2) diet components were similar but the relative contribution to overall diet was changed. In trials 3 and 4 (table 4.1) the same procedure was followed but now diets consisted of chopped straw and freshly frozen chopped willow (*Salix sp.*) (leaves and small twigs). Goats and sheep weighed ca 15 kg and ca 40 kg respectively.

In the pig/boar trials the animals were kept individually in areas of 1.6x0.8 m^2. Adaptation periods were 7 days (sufficient for animals with a simple stomach) followed by 7 days of total faeces collection which was well feasible because of the clean habits of the animals. Feeding was ad lib and the animals were fed twice daily. All trials were with single feeds. Alfalfa hay, grass hay and straw was chopped at 1 cm and subsequently pelleted with 1.5% molasses. The Meishan pigs and the wild boar weighed 50-55 and 25-35 kg, respectively.

Subsamples of feed, faeces and refusals (if selection had taken place) were air dried at 60°C, milled at 1 mm and duplicate samples were analyzed for cellulase indigestible acid detergent fibre (IADF) (Penning and Johnson 1983b). Where IADF has been determined in mixed samples of faeces of animals fed the same diet the results were pooled. Regression analysis was carried out with the statistical package SAS (SAS Institue Inc. 1990), using the general model:

$Y_i = \mu + DIADF_i + e$

where Y=dependent variable; μ=overall mean; DIADF= in vitro digestibility using IADF as an internal marker; e = error.

Results

Diet composition, values for in vivo digestibility (DVIVO), digestibility using IADF as an internal marker (DIADF), and percentage recovery of IADF in the faeces (RIADF), are given in table 4.1. IADF concentration ranged from 0.061-0.288 in diets and from 0.161-0.552 in faeces. IADF was generally well recovered in the faeces (table 4.1). Recovery was incomplete in trial 1 and 2 for sheep and goats when feed components were beetpulp, poplar and maize.

There was a good overall relationship between DVIVO and DIADF (figure 4.1):

$DVIVO = 1.114\ (\pm 0.087) DIADF - 0.046\ (\pm 0.048);$

$r^2=0.9367;\ RSD=0.04;\ P<0.0001;\ n=13$

Discussion

A good relationship was found between DVIVO and DIADF, taken into account a wide range of different diets, animal species and range of digestibilities. Similar results have been reported by Pennings & Johnson (1983b) and Tamminga et al (1989).

Table 4.1. Diet composition, the in vivo digestibility (DVIVO), the digestibility using IADF as a marker (DIADF), and the recovery of IADF in the faeces (RIADF) in the various feeding trials. Tr=number of trial. (Pop=Poplar, Alf=Alfalfa).

Species (n)	Tr	%Pulp	%Pop	%Maize	%Willow	%Straw	%Alf	%Hay	DVIVO	DIADF	RIADF
Goat(3)	1	38	17	45			0	0	0.758	0.695	0.797
Sheep(3)	1	27	27	46			0	0	0.704	0.647	0.837
Goat(3)	2	56	20	24			0	0	0.781	0.764	0.923
Sheep(3)	2	44	32	24			0	0	0.762	0.681	0.747
Goat(2)	3				57	43	0	0	0.468	0.513	1.092
Sheep(3)	3				60	40	0	0	0.561	0.547	0.973
Goat(2)	4				38	62	0	0	0.512	0.571	1.145
Sheep(3)	4				41	59	0	0	0.623	0.595	0.937
Boar(2)	5						100	0	0.458	0.401	0.905
Pig(3)	6						0	100	0.411	0.457	1.091
Boar(2)	6						0	100	0.481	0.473	0.983
Pig(3)	7					100	0	0	0.231	0.259	1.035
Boar(2)	7					100	0	0	0.375	0.339	0.945

Especially the relationship found by Penning & Johnson (DVIVO=0.945DIADF + 0.0263) was very close to the one found in this study, suggesting an overall relationship of DVIVO=DIADF.

The relationship found by Armstron et al (1989) deviated markedly from simple equality: y=x: (DVIVO=0.58DIADF + 0.304; r^2; RSD=0.059; $P<0.001$; n=20) but r^2 was high indicating that such regression could nonetheless be used to

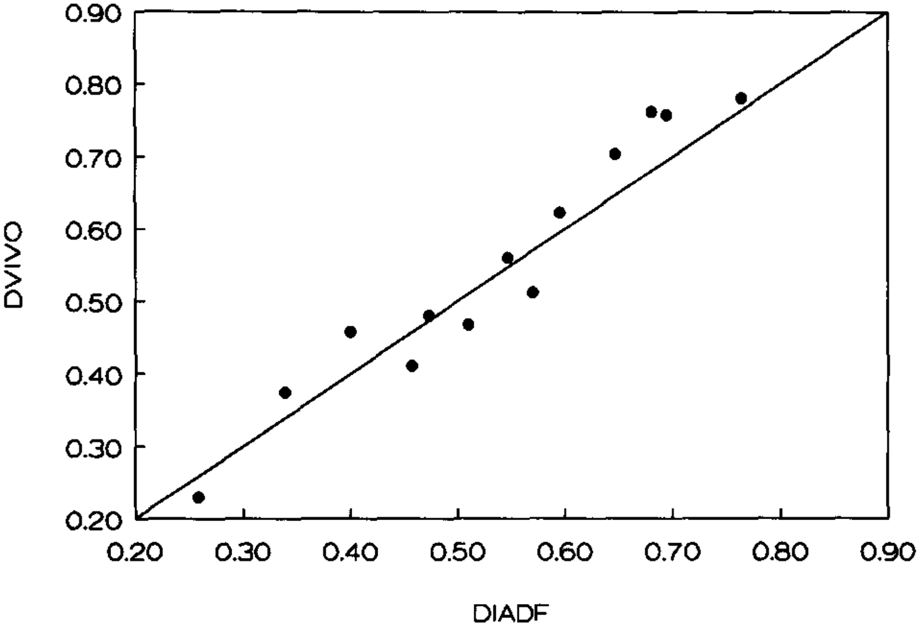

Figure 4.1. The relationship between DVIVO and DIADF; _____ : Y=X.

predict DVIVO if the goal is not necessarely a prediction close to y=x. DIADF generally underestimated DVIVO especially with lower quality herbage.

Cochran et al (1986) found variable results with the IADF technique. They tested 4 diets in 3 of which DIADF predicted DVIVO very well. These 3 data points are positioned very close to the regression lines of Penning & Johnson (1983b) and of this study. The one diet which proved to predict less precisely was a freshly harvested tall fescue in the early growth stage. Cochran et al (1986) speculated that the poor result of that feed might be due to an artificial increase of fibre content in a food high in moisture by routine drying procedures and/or to extensive disappearance of IADF during gastrointestinal transit. When comparing the results of Cochran et al (1986) with this study there is a similarity between a low proportional recovery of IADF in the faeces and a low IADF content in the diet or major diet components. IADF concentration in the tall fescue of Cochran was 5.5% which was similar to the IADF content in beetpulp (3.1%) and maize (5.1%) in the diets with the lowest recovery of IADF (table 4.1). Furthermore these IADF contents were the lowest of all diet components used in both studies. As in this and other studies drying of plant and faecal material occurred at max 70^0C, the drying process does not seem to make much difference between the different diets. In fact, all points to the partly disappearance of the marker when going through the intestinal tract leading to low recovery. It is likely that especially immature fibre has a high potential for disappearance.

It can be concluded that cellulase indigestible acid detergent fibre can well be used as a marker to predict digestibility in a wide range of digestibilities and forages but that care has to be taken with high quality forages which are low in IADF.

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CHAPTER 5

NUTRIENT EXTRACTION FROM MIXED GRASS-BROWSE DIETS BY GOATS AND SHEEP

Abstract

Voluntary food intake and digestibility by African dwarf goats and Texel sheep of mixed diets low in fibre or rich in browse content and high in fibre were compared. Goats selected a higher quality diet than sheep.

Differences between intake and digestibility of the high quality diets were small, digestibility of the goats being slightly higher than of the sheep. The browse-rich high fibre diets were better digested by the sheep while intake was much higher in the goats. No significant difference in digestible organic matter intake was found in any of the diets tested. Mean retention time of digesta was shorter in the goats on the browse-rich high fibre diet. The small goats generally passed larger food particles from the rumen to the abomasum. It was concluded that the higher intake on the browse-rich diet by the goats is facilitated by a wider reticulo-omasal orifice. The results confirm the classification of sheep as bulk and roughage feeders and of goats as intermediate feeders with a preference for browse, within the group of ruminants.

Introduction

Major anatomical and morphological differences between sheep and goats have led to the classification (on morphological grounds) of sheep as being bulk and roughage feeders and goats as intermediate feeders (Hofmann 1989). This classification is in line with preferred diet choice under field conditions; goats on average were observed to take >60% browse in the diet while for sheep this was less than 25%. With regard to digestive physiology, then, we would expect a lower digestive capacity on fibre-rich feeds in goats (Huston et al 1986), a higher intake on diets low in fibre made possible by a shorter retention time in this intermediate feeder (Hofmann 1988, Milne et al 1978), and a better utilization of lignified browse by the intermediate feeder compared to the bulk and roughage feeder (Van Wieren, unpubl. res.). Published results, however, are not in line with all of these predictions. Many studies suggest little difference in digestibility of high quality feeds (Jones et al 1972, Brown & Johnson 1984, Antoniou & Hadjipanayiotou 1985) but Arista et al (1992) found higher digestibilities by goats of high quality feeds. On low quality diets both a higher digestibility by goats (Gihad et al 1980, Alam et al 1985, Doyle & Egan 1980, Huston et al 1986) or a higher digestibility by sheep (Arista et al 1992, Brown & Johnson 1985) has been reported. Tolkamp & Brouwer (1993) carefully reviewed more than 200 datasets of goat/sheep digestibility comparisons over a wide range of diet qualities. Although the overall digestibility of goats was significantly higher than that of sheep the difference was small (< 1 unit of dig.). In a review of many published results Antoniou & Hadjipanayiotou (1985) found intake differences between goats and sheep being very variable both in high quality and low quality diets. Willow browse was much better digested and ingested by goats compared to sheep (McCabe & Barry 1988). Longer retention times in goats have been reported, both on low and high fibre diets (Doyle & Egan 1980, Huston et al 1986).

Much of the confusion and inconsistency in the results of these different studies may be attributed to differences in the experimental set up and execution of various comparative feeding trials (Van Soest 1982, Tolkamp & Brouwer 1993). Variation in digestive physiology between breeds within a species can also not be excluded as diet preferences vary widely among the various breeds of goats and sheep (Breymeyer & Van Dyne 1980), the small African dwarf goat being an example of an intermediate feeder with a high preference for browse (Wilson 1957, in Gihad et al 1980). Few comparisons between goats and sheep have been made with browse forage, while with browse as a feed notable species differences can be expected. In this study the nutrient extraction capability of goats and sheep will be compared on both diets low in fibre and lignin and diets high in fibre and lignin, all diets containing a high proportion of browse.

Methods and materials

Two different experiments were carried out, with each experiment consisting of two separate feeding trials.

Animals

In both experiments 3 wether adult African dwarf goats and 3 wether adult Texel sheep were used. In experiment 2 one goat refused to eat and was removed from the experiment. The animals were kept in balance crates and had free access to water. Urine and faeces were collected separately throughout the trials. The animals were weighed before and after each trial. The average weight of the goats and the sheep was 17.3 and 43.6 kg respectively.

Diets

Experiment 1. This experiment was carried out in the summer.

Fresh poplar leaves (*Populus x canadensis Mönch*) were collected the day before feeding and stored at 4°C. Leaves of maize (*Zea mays*) were collected daily and kept at 4°C. Shortly before feeding the maize was chopped at 5x5 mm. The poplar was offered at 8.00 hrs and the maize at 17.00 hrs. Beetpulp was given as a dry supplement together with the maize.

Experiment 2. This experiment was carried out in the winter.

Fresh willow (*Salix viminalis*) leaves and twigs (with diameter < 8 mm), previously collected in August and stored at -20 °C, were thawed shortly before feeding and chopped at ca 7 cm. Grass straw (*Lolium perenne*) was stored at room temperature and chopped at ca 5 cm before feeding. The willow was offered at 8.00 hrs and the straw at 17.00 hrs.

Procedure and analyses

Each experiment consisted of a 14 day adjustment period, followed by two collection periods of 5 days. In each collection period the composition of the diets of offer varied. Between the two collection periods a 3 day adjustment period was allowed. The orts of the diet component fed in the morning were collected before offering the diet component(s) in the afternoon. Feed residues were also collected before feeding in the morning.

All diet components were offered in an amount roughly 10% in excess of the maximum voluntary intake level which was determined before the trials. All faeces were collected.

Subsamples of feed and residues were dried at 60°C and stored for laboratory analysis. Subsamples of faeces were stored frozen at -20°C. Feed, orts and faeces were analysed for DM (Dry Matter), Ash, NDF (Neutral Detergent Fibre), ADF (Acid Detergent Fibre) and Lignin according to Goering & Van Soest (1970). N was measured after destruction with a mixture of H_2SO_4, Se and salicyclic acid with a Skalar Sanplus autoanalyzer. The in vitro digestibility the organic matter of feed residues were analyzed according to Tilley & Terry (1963).

Mean retention time (MRT) was estimated by counting stained (with basic Fuchsin) particles in faeces collected at regularly intervals after dosing (Foose 1982).
As indices of faecal particle size distribution, both the modulus of fineness (MF) and the percentage of particles > 1.25mm (LA), were used after applying a wet sieving technique as described bu Poppi et al (1980). Six sieves were used with mesh sizes of 2.5, 1.25, 0.63, 0.32, 0.16 and 0.07 mm.

Species means were evaluated statistically by ANOVA procedures as provided by the statistical package SAS (SAS Inst. Inc. 1989).

Results

The chemical composition of the feedstuffs used and the proportion of individual feedstuffs in the diets ingested in the different feeding trials are shown in table 5.1 and 5.2 respectively.

Table 5.1. Composition of feedstuffs used in the mixed diets.
DM=dry matter; NDF=neutral detergernt fibre; ADF=acid detergent fibre; N=nitrogen; OM=organic matter.

	DM %	NDF %OM	ADF %OM	LIGNIN %OM	N %DM
Maize	21	63.2	33.1	4.5	2.9
Poplar	26	40.9	28.5	13.7	2.4
Beetpulp	92	47.1	34.8	5.3	1.5
Willow	25	60.3	40.9	14.8	3.1
Straw	92	74.4	42.1	8.6	0.8

Although similar amounts of each forage type were offered there were significant differences in the actual diets selected by the goats and the sheep. In experiment one the maize was readily eaten by both species but the goats consumed relatively less of the poplar in both collection periods. In addition to these differences in the relative proportion of different species consumed, goats also showed an ability to select the higher quality components from any plant species offered. Thus table 5.3 shows that food residues left by goats were consistently of lower quality than those left by sheep. The differences were largest on willow and small on poplar, while even on the grass straw small differences could be detected.

Table 5.2. Proportions of individual feedstuffs used in the ingested diets in the feeding trials (% in diet).

	Goats		Sheep	
	Tr 1	Tr 2	Tr 1	Tr 2
Maize	45	24	45	24
Poplar	17	20	26	32
Beetpulp	38	56	29	46

	Goats		Sheep	
	Tr 3	Tr 4	Tr 3	Tr 4
Willow	56	39	59	40
Straw	44	61	41	60

Table 5.3. Chemical composition of feed residues.

Trial	Forage	Species	Ash %DM	IVOMD %	NDF %OM	ADF %OM	Lignin %OM
3	Willow	Goats	3.47	29.1	79.1	66.7	22.1
3	Willow	Sheep	5.42	35.2	71.1	60.9	24.9
4	Willow	Goats	2.71	23.9	83.3	66.6	21.8
4	Willow	Sheep	4.74	30.3	78.8	64.4	23.1
3	Straw	Goats	8.55	49.3	72.6	43.9	9.4
3	Straw	Sheep	5.72	51.5	71.1	41.3	9.3
1/2	Poplar	Goats	11.7	54.1	44.1	29.9	13.6
1/2	Poplar	Sheep	10.5	57.3	42.3	29.5	13.8

When expressed isometrically voluntary intake was higher in the goats in three of the four trials (table 5.4). When expressed relative to metabolic weight voluntary intake was higher in the goats on the straw/willow diets.

Table 5.4. Voluntary intake, digestibility of OM, NDF and N, and mean retention (MRT) of the mixed diets by goats and sheep.
MAPOPU=Maize-Poplar-Beetpulp diet, STWI=Straw-Willow diet; OMI=Organic Matter Intake; LW=Live Weight; MW=Metabolic weight; OMD=Organic Matter Digestibility; DIGNDF=Digestibility of NDF; DIGN=Digestibility of N; DOMI=Digestible Organic Matter Intake.

Exp	Tr	Diet	Spe	n	BW Kg	OMILW g/kg	OMIMW g/kg	OMD %	DIGNDF %	DIGN %	DOMI g/kg MW	MRT hrs
1	1	MAPOPU	GO	3	19.8	24.2^{ax}	38.6	75.8^{a}	74.8^{a}	73.1^{a}	38.6	
1	1	MAPOPU	SH	3	45.3	20.7^{b}	37.9	70.4^{b}	69.2^{b}	68.3^{b}	37.9	
1	2	MAPOPU	GO	3	20.4	22.3	37.1	78.2	76.2	70.8^{a}	37.1	
1	2	MAPOPU	SH	3	45.8	20.1	40.1	76.2	73.7	69.8^{b}	39.9	
2	3	STWI	GO	2	14.5	28.1^{a}	54.8^{a}	46.8^{a}	31.4^{a}	41.6^{a}	25.6	37^{a}
2	3	STWI	SH	3	41.7	15.2^{b}	38.7^{b}	56.1^{b}	46.4^{b}	49.5^{b}	21.7	48^{b}
2	4	STWI	GO	2	14.5	27.6^{a}	53.8^{a}	51.2^{a}	38.4^{a}	30.5^{a}	27.7	
2	4	STWI	SH	3	41.7	16.9^{b}	42.9^{b}	62.3^{b}	54.2^{b}	54.4^{b}	26.8	

Organic matter digestibility (OMD) was higher in the goats on one of the maize/poplar diets (table 5.4). The differences of the second trial were not significant. Sheep digested both the straw/willow diets better than the goats.
No significant difference could be detected between the digestible organic intake (DOMI) in each of the four trials but goats had a higher apparent N digestibility in one of the maize/poplar diets but in both straw/willow diets sheep had substantially higher N digestibilities than the goats.

Mean retention time could only be estimated in one trial. Goats had significantly shorter MRT on a straw/willow diet than sheep. The two indices of faecal particle size distribution are presented in table 5.5. Except for one straw/willow trial the small goats had higher MF and percentage particles >1.25mm than the larger sheep.

Table 5.5. Modulus of fineness (MF) and percentage of particles >1.25 mm (LA) in the faeces of goats and sheep. Same abbreviations as table 5.4.

Diet	Trial	Species	MF	LA
MAPOPU	1	GO	1.82	0.9
MAPOPU	1	SH	1.42	0.2
MAPOPU	2	GO	1.98	2.5
MAPOPU	2	SH	1.62	0.2
STWI	3	GO	2.31	11.2
STWI	3	SH	1.72	2.6
STWI	4	GO	1.98	12.1
STWI	4	SH	2.32	12.5

As slight differences can be expected in the quality of the ingested (maize/poplar) diets the results are presented graphically relative to NDF content of the ingested diets (Figure 5.1). Differences in OMI, OMD and DOMI between the two species are negligible at the low NDF/low lignin (maize/poplar) diets but intake was higher by the goats and digestibility higher by the sheep on the high NDF/high lignin (straw/willow) diets, while the intake of digestible organic matter was similar. Figure 5.1 also demonstrates the general negative effect of NDF content in the diet on digestibility and digestible organic matter intake.

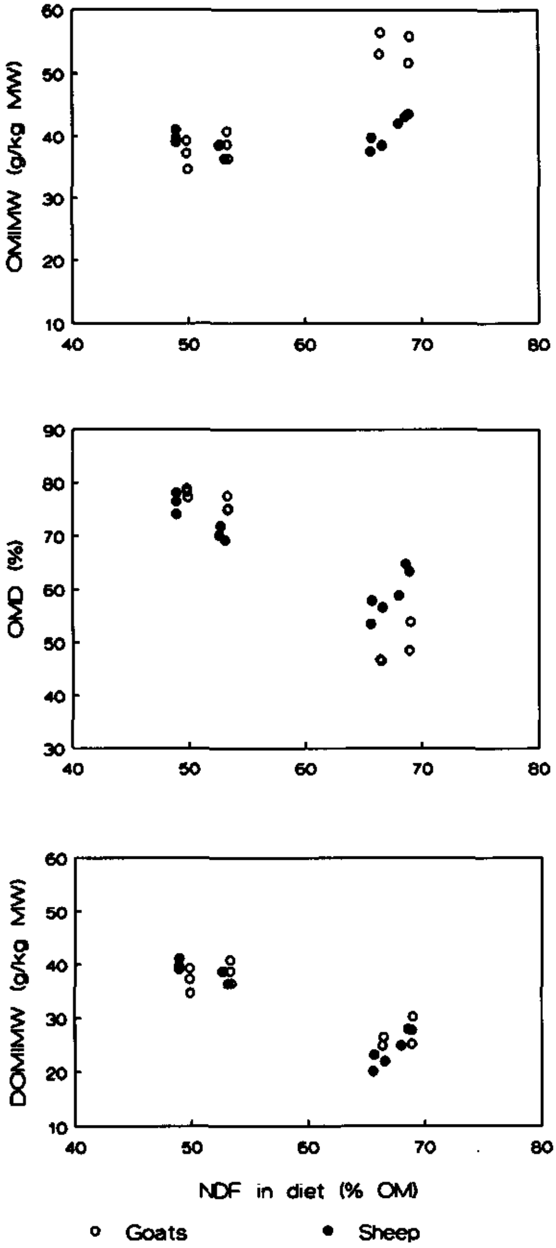

Figure 5.1. The relationship between voluntary intake (OMIMW), organic matter digestibility (OMD), digestible organic matter intake (DOMI) and NDF content of the diets ingested by goats and sheep.

Discussion

Goats were more selective than sheep both between and within forage species. Goats stripped the bark from the willow twigs while sheep took the whole twig. These differences in selection of even individual plant components stress the need to take the feed residues into account in the calculation of digestibility (Van Soest 1982).

The postulated differences in digestive physiology between goats and sheep, based on anatomy and diet preferences, were confirmed in this study. The performance on high quality diets was similar. Goats had higher OMD and cell wall digestibility in one trial but intake, expressed on metabolic weight, was not different. Yet on the low quality, highly lignified, browse-rich diet differences were large. Digestibility was much lower in the goats and intake much higher. DOMI was not different indicating that the goats could compensate for the lower digestibility by a higher intake. The higher intake of the straw/willow diets by the goats is likely made possible by a shorter retention time, which in turn is probably linked to a larger escape of large food particles through the reticulo-omasal orifice in the goats (see discussion below).

ADN (Apparent digestible nitrogen) on the high quality diets was higher in the goats but on the low quality diets this was the reverse. Both species had much lower ADN on the straw/willow diets but that of goats was more reduced than that of sheep. A lower ADN with decreasing diet quality has also been reported by other authors (Arista et al 1992, Nastis & Malechek 1981). This is in line with the general finding that ADN is positively related to N content in the diet and the amount of NDF digested (table 5.4, Tamminga pers.comm.). Osier willow contains large quantities of secondary compounds (McCabe & Barry 1988) and this may have depressed ADN. From the literature no consistent picture emerges with respect to species differences. Goats retained more N than sheep on both low fibre clover and high fibre grass diets (Doyle & Egan 1980) and goats had higher ADN on low quality browse (Wilson 1977). Antoniou & Hadjipanayiotou (1985), however, found no significant difference in ADN with grass hay, lucerne hay and Barley straw diets, like Brown & Johnson (1985) with diets with varying concentrations of wheat straw. Brown & Johnson (1984) reviewed many studies and concluded that no consistent difference in N digestibility existed between goats and sheep.

The differences between goats and sheep found in the present study can not easily be generalized, because the digestive capacity of goats has generally been found by others to be higher than of sheep, even on high fibre diets (see review by Tolkamp & Brouwer 1993). A higher digestive capacity by goats has been explained by a longer retention time of digesta in goats (Doyle & Egan 1980, Huston et al 1986) but this is not supported by the (although limited) data from the present study. Tolkamp & Brouwer

(1993) concluded that differences in voluntary intake levels between sheep and goats are a more important differentiating characteristic than digestion capability. This might well be the case, although even here differences reported in the literature are not consistent (McCabe & Barry 1988, Wilson 1977, Doyle & Egan 1980, Brown & Johnson 1985, Gihad et al 1980, Huston et al 1986, Antoniou & Hadjipanayiotou 1985). In such context it may be important to note that few of the studies reviewed by Tolkamp & Brouwer, not the studies of Doyle & Egan, or Huston et al included browse materials in the diets offered. More consistent differences between goats and sheep in VFI, retention time and digestive capacity might become apparent when a distinction is being made between predominantly browse diets and predomiantly grass diets.

Both Wilson (1977) and McCabe & Barry (1988) found a better digestion of browse by goats when compared to sheep, the difference being greater with the lowest quality browse (Wilson 1977). The reason for this difference is not clear. In the present study goats digested the high-browse diet less well than sheep.

The better performance (DOMI, expressed in relation to metabolic weight) by goats on browse diets is mainly the result of a much higher intake. A higher intake can be the result of goats having a relatively larger rumen capacity as suggested by Alam et al (1985), but the present study suggests that differences in passage rates may be more important. On the browse-rich diets goats had shorter passage rates than sheep. Passage rate is positively related to particle size reduction (Van Soest 1982) because in ruminants particles must be sufficiently reduced (by rumination) to be able to pass from the rumen to the abomasum through the reticulo-omasal orifice, which is thought to act as a sieve (Poppi et al 1985) (although this concept is now being critisized and it is now thought that functional specific gravity or 'entrapment' in the structural layer (mat) is more important (Tamminga, pers. comm.)). This critical particle size in grazer ruminants is ca 1 mm (Poppi et al 1980, 1985). Recently it has been found that in browser ruminants the critical particle size can be much larger than 1 mm (Nygren & Hofmann 1990), suggesting a wider reticulo-omasal orifice in these species. Furthermore it has been found that particle escape (to the abomasum) is enhanced by a cubical particle shape. Particles with a cubical shape (as found in highly lignified browse) pass more easily through the omasal 'sieve' than long fibrous grass particles (Troelsen & Campbell 1968). The percentage large particles > 1.25 mm as found in the faeces of goats in both the straw/willow diets might both indicate a 'browser-type' reticulo-omasal orifice and/or a higher escape potential of the cubical willow particles. In one straw/willow trial also in sheep a large percentage large particles could escape, indicating the importance of particle shape. The higher intake of browse by goats is made possible by a higher passage rate which in turn is facilitated by a high escape rate of feed particles because of a wider reticulo-omasal orifice. Maybe this escape of digesta can also explain in part the depression of both the organic matter digestibility and the apparent N digestibility in the goats.

In conclusion it can be hypothesized that species differences in nutrient extraction capability between goats and sheep do exist, at least in diets rich in browse content.

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Introduction

Within the group of ungulates four major different strategies of foodplant utilization can be distinguished. Within the ruminants Hofmann (1973) distinguished three major feeding types: Concentrate selectors (mainly browsers,(CS)), grass and roughage feeders (mainly grazers,(GR)) and intermediate feeders (IF). CS are adapted to foodplants relatively low in celllulose and are dependent primarily for nutrient intake on cell-solubles. The capacity to digest cellulose is considered to be poor (Hofmann 1973, Mould & Robbins 1982, Huston et al 1986). They have a relatively simple and small stomach. Food can pass rapidly because of a large ostium reticulo-omasicum (Hofmann 1991). Representatives of this group are Roe deer (*Capreolus capreolus*) and Moose (*Alces alces*). GR on the other hand are specialized cellulose digesters. They have a large gut capacity and retention time of food in the rumen is long permitting an extensive period of attack of the food by the rumen microbes. Representatives of this group include cattle and sheep. The gut characteristics of IF are in many respects situated in between those of CS and GR. Furthermore animals of this category seem to be very flexible with a capacity to adapt the gut morphology according to changes in diet and season (Hofmann 1991). Many representatives of this group may be found among the Cervidae e.g. Red deer (*Cervus elaphus*) and Fallow deer (*Dama dama*).

The fourth feeding stategy found among the ungulates is that of hindgut fermentation. Most non-ruminating ungulates like the Horse (*Equus caballus*) and the Wild Boar (*Sus scrofa*) are hindgut fermenters. They have a well developed caecum and colon where considerable cellulose digestion can take place although the extent of the cellulose digestion seems to be inferior to that of the ruminants (Johnson et al 1982, Smolders et al 1990, Uden & Van Soest 1982, Hintz 1969).

Although a fairly large number of feeding trials with representatives of the different feeding styles have been carried out to compare the utilization (voluntary food intake, digestibility, passage) of various food sources, no clearcut conclusions can be drawn with respect to the relative digestive capacities among the ruminant feeding types in particular. An important reason for this seems to be the confounding effect of body size. Large animals have a higher digestive capacity than small animals because of a longer retention time of the food when passing through the digestive tract and they have a higher gut capacity (Demment & Van Soest 1985, Parra 1978). Body size generally is not taken into account as a covariate in the interpretation of the results of feeding trials and anatomical/morphological specializations of the digestive tract are likely superimposed on the effect of body size.

No comparison yet has been made across all four feeding types over a wider range of forage qualities. What especially is lacking is how the different strategies 'perform' with regard to the rate of digestible energy extraction as the result of the interplay between digestive capacity, voluntary food intake and passage rate. In the present study digestibility, voluntary food intake and mean retention time of 4 diets, differing widely in chemical composition, by representatives of the four feeding types (Roe deer (CS), Red deer (IF), cattle (GR) and ponies) will be compared.

Methods

Feeding trials were carried out with 5 Scottish Highland cows (with initial body weights of 261,296,306,315,329 kg), 5 Shetland mares (123,146,152,193,200 kg), 5 Red deer hinds (68,73,77,78,79 kg) and 5 Roe deer does (12,17,17,19,21 kg) from October 1991-March 1992. For several reasons five Roe deer were lost during the trials. Three of them were replaced by others. The animals were kept indoors and individually confined to floor spaces of ca 12 m^2 (cattle, ponies) and ca 6 m^2 (Red deer, Roe deer). Ad lib water was provided. Day length was artificially kept at 16 hrs to prevent seasonal influence on feed intake.

Diets V

Willow: Leaves and twigs of current growth of osier willow (*Salix ~~f~~iminalis*) were harvested in August, cut at 10 cm, and stored at -20 °C. Shortly before feeding it was chopped at 2-3 cm.

Alfalfa hay: Medium to poor quality alfalfa hay (*Medicago sativa*) was used. The material was quite heterogeneous and dusty.

Grass hay: Hay of Perennial rye grass (*Lolium perenne*), harvested in June/July and dried on the land, was cut at 10 cm and stored until usage.

Grass straw: Grass straw of Perennial rye grass was harvested in July, cut at 10 cm and stored. The straw was not tested in the Roe deer as they refused to take it.

Grass pellets: A commercial high quality grass pellet was fed to Roe deer when the other species received the straw.

The chemical composition of the diets are given in table 6.1.

Experimental procedures

Voluntary food intake (VFI): In each experimental period the animals were accustomed to their diets for 2 weeks before the start of a measuring period of 10 days. In trials with grass hay, straw and grass pellets were fed twice daily at 08.00 and 16.00 hours. A refusal margin of ca 15% was allowed for these diets. Procedures for the willow and alfalfa measuring period were slightly different. Because of the heterogeneity of these diets substantial selection was expected. In these situations the amount offered may markedly influence voluntary food intake (Zemmelink 1980). Ideally at least 4 levels of offered feeds should be required for a reliable estimate of voluntary food intake in relation to availability. As this was not possible for technical reasons two levels of feed supply were tested to measure if an increased offer should increase intake. During the adjustment period of willow and alfalfa an average ad lib intake level was experimentally established whereby the food residues consisted of ca 10% readily edible feed and ca 90% less edible refusals. The measurement period was then divided in two periods of 5 days. In the first period 2 animals of each species received this average amount on offer (X) and 3 animals received 1.5 times this amount (1.5X). In the second period this feeding regime was reversed. During willow and alfalfa trials, experimental forages were presented three times daily. Live weights were recorded at the beginning and end of each experimental period.

Digestibility: Digestibility of ingested feed was determined by using indigestible acid detergent fibre (IADF) as an internal marker (Penning & Johnson 1983, Chapter 4). IADF was measured in representative samples of diets offered, refusals and faeces.

Mean retention time: The mean retention time (MRT) was measured after offering a single amount of 10% of the diet stained with basic fuchsin at the start of the measuring period during 4 hours. Faecal grabsamples of individual animals were then taken at 8 h intervals until at least 5 days after offering the stained material. Stained particles in the faeces were counted according to the method described by Foose (1982). MRT was calculated as the time in hrs between appearance of 5% and 80% of the marker (Van Soest 1982).

Chemical analysis: Subsamples of feed and orts were dried at 60°C and then stored at 20^0C until laboratory analysis. Subsamples of faeces were kept frozen at -20°C. Feed, orts and faeces were analysed for DM, Ash, NDF (Neutral Detergent Fibre), ADF (Acid Detergent Fibre) and Lignin according to Goering & Van Soest (1970). Nitrogen was measured, after destruction with a mixture of H_2SO_4, Se and salicyclic acid, with a Skalar San-plus autoanalyzer. The in vitro digestibility of feed offered, feed residues and faeces were analyzed according to Tilley & Terry (1963).

Differences between species means were evaluated with ANOVA procedures, and relationships between variables were analyzed with regression procedures, as provided by the statistical package SAS (SAS Inst. Inc. 1989). Because IADF was measured in mixed samples of faeces on the species level, no standard deviation could be calculated in those estimates containing digestibility as a variable.

Results

1. Effect of feeding level on VFI and selectivity of feeding on willow and alfalfa.

Table 6.1 shows the chemical composition of the willow and alfalfa offered and of the diets ingested. For all aimal species the quality (digestibility and nutrient levels) of the ingested willow diet was higher than that of the offered diet (ca 7-10 in-vitro digestion units).

Table 6.1. Chemical composition of feeds offered and feeds ingested, cell wall components and IVOMD in %OM, ash and minerals in %DM. Ro=roe deer, Re=red deer,Po=ponies, Ca=cattle.

Feed	Level of feed offered	Species	Offer/ ingested	Ash	NDF	ADF	LIG	IADF	IVOMD	N
Willow			Offered	7.4	59.7	40.9	15.1	0.336	0.442	2.81
Willow	X	Ro	Ingested	9.0	50.5	31.1	11.8	0.268	0.518	3.66
Willow	X	Re	Ingested	9.0	50.8	32.2	13.2	0.284	0.514	3.54
Willow	X	Po	Ingested	9.1	50.3	31.5	12.8	0.273	0.511	3.58
Willow	X	Ca	Ingested	8.8	51.2	31.4	12.8	0.281	0.505	3.55
Willow	1.5X	Ro	Ingested	10.0	43.5	23.2	9.4	0.225	0.541	4.26
Willow	1.5X	Re	Ingested	9.7	46.2	26.5	10.3	0.245	0.539	3.95
Willow	1.5X	Po	Ingested	9.8	45.2	25.7	11.1	0.233	0.550	3.96
Willow	1.5X	Ca	Ingested	9.6	46.9	27.4	12.2	0.242	0.541	3.85
Alfalfa			Offered	12.5	59.7	45.5	13.2	0.227	0.579	2.92
Alfalfa	X	Ro	Ingested	12.8	59.4	45.3	12.7	0.222	0.584	3.03
Alfalfa	X	Re	Ingested	11.6	58.8	45.5	12.7	0.219	0.585	2.66
Alfalfa	X	Po	Ingested	12.4	59.7	45.6	13.2	0.226	0.579	2.91
Alflafa	X	Ca	Ingested	12.1	60.4	45.5	13.3	0.227	0.576	2.87
Alfalfa	1.5X	Ro	Ingested	13.1	57.9	44.3	13.1	0.211	0.592	3.05
Alfalfa	1.5X	Re	Ingested	13.0	62.1	50.1	13.4	0.236	0.550	2.71
Alfalfa	1.5X	Po	Ingested	12.2	59.0	45.9	13.3	0.224	0.580	3.00
Alfalfa	1.5X	Ca	Ingested	11.9	58.9	46.4	13.2	0.222	0.554	2.74
Hay			Offered	9.5	65.4	31.5	6.3	0.035	0.749	2.57
Straw			Offered	7.0	76.7	48.4	9.3	0.173	0.520	0.80
Grasspellet		Ro	Offered	15.9	61.7	41.4	5.9	0.059	0.760	2.69

At the higher feeding level the quality of the ingested diets was higher than that of the lower feeding level. Although the differences between species are small, on the whole Roe deer seem to be most selective and cattle least. Differences in quality in food ingested from that offered were greater than differences in quality in dietary quality achieved at the two feeding levels. On alfalfa there was in general little difference between both the quality of the material offered and ingested, and between the two intake levels. At both intake levels Roe deer seemed to select the highest quality.

Table 6.2. Amount offered, intake and amount refused of willow and alfalfa. (Offer and intake in g OM/kg MW).

Feed	Level of feeding	Species	Offer	Intake	Residue (% offer)
Willow	X	Cattle	73	52	29
Willow	1.5X	Cattle	109	64	42
Willow	X	Red deer	76	54	29
Willow	1.5X	Red deer	113	63	45
Willow	X	Roe deer	96	63	32
Willow	1.5X	Roe deer	144	72	49
Willow	X	Ponies	80	54	32
Willow	1.5X	Ponies	120	62	47
Alfalfa	X	Cattle	76	68	11
Alfalfa	1.5X	Cattle	110	72	35
Alfalfa	X	Red deer	75	53	29
Alfalfa	1.5X	Red deer	114	58	50
Alfalfa	X	Roe deer	72	60	18
Alfalfa	1.5X	Roe deer	108	69	36
Alfalfa	X	Ponies	68	63	6
Alfalfa	1.5X	Ponies	102	77	24

In table 6.2 and 6.3 the effects of increasing the feeding levels of willow and alfalfa on intake are demonstrated. Refusals (in % of the amount offered) were greater with the highest feeding level and more variation was found on the willow diet (table 6.2). On both diets intake increases with the amount offered (table 6.3). The largest increase was found with willow. Intra-species comparison, however, revealed only a significant difference in ponies when fed alfalfa ($P<0.05$).

Table 6.3. Percentual increase in intake of willow and alfalfa when level of feed offered increased with 50%.

Feed	Willow	Alfalfa
Cattle	23	6
Red deer	16	8
Roe deer	14	15
Ponies	15	21

As there were only two intake levels the available data points to estimate intake according the Zemmelink (1980) model was not possible. Therefore the data sets associated with the highest feeding levels of willow and alfalfa were used for further analyses and comparisons.

2. Voluntary food intake

Mean VFI of tested diets are given both expressed on metabolic weight (MW) (table 6.4) and expressed isometrically with live weight (LW) (table 6.5).

Table 6.4. Mean organic matter intake (g OM/kg MW) of different feeds (s.d.).

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	64.1 (7.6)	62.5 (4.9)	72.1 (3.9)	62.4 (11.7)	63.0	65.3
Alfalfa 1.5X	71.9 (3.9)	57.8 (12.9)	69.2 (4.6)	76.9 (6.9)	68.8	69.0
Hay	76.8 (6.8)	62.4 (3.3)	50.9 (9.8)	81.5 (3.6)	73.5	67.9
Straw	49.3 (5.0)	44.1 (3.3)	-	53.5 (6.0)	48.9	-
Grass pellet	-	-	65.5 (8.2)	-		
Mean (W,A,H)	70.9	60.9	64.1	73.6		
Mean (W,A,H,S)	65.5	56.6		68.6		

When expressed on MW Roe deer had the highest VFI on the willow diet but VFI between species were not significantly different. On alfalfa Red deer had a significantly lower VFI than ponies and cattle. Cattle and ponies had significantly higher intakes of hay than Red deer and Roe deer, and Roe deer had the lowest. Red deer had the lowest intake of straw but differed significantly only from ponies. When expressed on LW differences in intake were more pronounced. Roe deer ate significantly more willow and alfalfa than the other species, about twice as much as cattle.

Table 6.5. Mean organic matter intake (g OM/kg LW) of different feeds (s.d.).

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	15.6 (2.2)	21.1 (1.9)	36.7 (3.5)	17.4 (3.3)	18.0	22.7
Alfalfa 1.5X	17.1 (0.9)	19.7 (4.6)	34.1 (3.2)	21.6 (2.9)	19.5	23.1
Hay	18.1 (1.6)	21.2 (1.4)	24.3 (2.2)	22.7 (1.4)	20.7	21.6
Straw	11.7 (1.3)	14.9 (1.1)	-	15.1 (1.9)	13.9	-
Grass pellet	-	-	31.2 (5.3)	-		
Mean (W,A,H)	16.9	20.7	31.7	20.6		
Mean (W,A,H,S)	15.6	19.2		19.2		

Cattle had lower VFI of willow than Red deer and lowest intake of straw. On average VFI of cattle was lowest and VFI of Roe deer was highest on comparable diets.

3. Digestibility of organic matter (OMD) and NDF

The organic matter digestibility of willow and alfalfa did not differ much across animal species (table 6.6).

Table 6.6. Mean organic matter digestibility (%) of the different feeds.

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	66.5	63.8	66.3	63.7	64.7	64.9
Alfalfa 1.5X	57.4	52.7	55.5	53.2	54.4	54.7
Hay	78.1	75.8	68.7	67.1	73.7	72.4
Straw	46.1	36.3	-	26.5	36.3	-
Grass pellet	-	-	63.2	-		
Mean (W,A,H)	67.3	64.1	63.5	61.3		
Mean (W,A,H,S)	62.0	57.2	-	52.6		

Roe deer and ponies digested hay less than cattle and Red deer. Cattle digested straw better

than Red deer while ponies digested straw poorly.
Ponies digested NDF of hay slightly better than Roe deer while OMD of Roe deer was slightly higher (table 6.7).

Table 6.7. Mean NDF-digestibility (%) of the different feeds.

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	40.2	33.7	36.2	35.2	36.4	36.3
Alfalfa 1.5X	43.3	41.3	42.6	41.2	41.9	42.1
Hay	83.4	78.8	66.4	68.5	76.9	74.3
Straw	42.9	31.3	-	17.9	30.8	-
Grass pellet	-	-	55.7	-		
Mean (W,A,H)	55.6	51.3	48.4	48.3		
Mean (W,A,H,S)	52.5	46.4	-	40.7		

OMD and NDF-digestibility of the hay were surprisingly similar and both were highest of all the feeds. While OMD of willow was higher than OMD of alfalfa, NDF-digestibility of willow was lower than of alfalfa in all species.

4. Digestible organic matter intake (DOMI)

Roe deer had the highest DOMI on willow and Red deer the lowest DOMI on alfalfa while differences between the other species were small on these diets (table 6.8).
On hay Roe deer performed poorly while cattle had highest digestible organic matter intake. Also on straw cattle performed best compared to Red deer and ponies.

Table 6.8. Mean digestible organic matter intake (g/kg MW) of the different feeds.

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	42.6	39.9	47.8	39.7	40.7	42.5
Alfalfa 1.5X	41.2	30.5	38.4	40.9	37.5	37.8
Hay	60.1	47.3	34.9	54.7	54.0	49.3
Straw	22.9	16.1	-	14.1	17.6	-
Grass pellet	-	-	41.4	-		
Mean (W,A,H)	48.0	39.2	40.4	45.1		
Mean (W,A,H,S)	41.7	33.4	-	37.4		

Table 6.9. Mean retention time (MRT, in hrs) of the different feeds (s.d.).

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	39.0 (2.6)	31.0 (3.6)	15.7 (1.2)	17.0 (2.3)	29.0	25.6
Alfalfa 1.5X	27.3 (3.2)	20.3 (1.9)	21.0 (3.1)	17.0 (1.9)	21.5	21.4
Hay	46.8 (6.2)	20.0 (2.6)	20.0	17.4 (3.2)	28.1	26.1
Straw	49.0 (3.5)	41.5 (5.8)	-	17.4 (2.6)	36.1	-
Grass pellet	-	-	18.0 (4.3)	-		
Mean (W,A,H)	37.7	23.8	18.9	17.1		
Mean (W,A,H,S)	40.5	28.2	-	17.2		

5. Mean retention time (MRT)

MRT of willow was significantly longer in cattle and Red deer than MRT in Roe deer and ponies (table 6.9). MRT of alfalfa and straw in ponies was significantly shorter than MRT in the other species. MRT of hay in cattle was significantly longer than MRT in the other species. On average MRT was longest for straw and shortest for alfalfa. MRT of all diets were very similar in the ponies. On average cattle had longer MRT than Red deer while Roe deer and ponies had the shortest.

Table 6.10. In vitro organic matter digestibility (% OM) of faeces in the different feeding trials.

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	-4.8	-3.8	1.4	10.0	0.5	0.7
Alfalfa 1.5X	11.2	9.4	14.3	9.7	10.1	11.2
Hay	26.6	22.1	19.0	27.2	25.3	23.7
Straw	8.9	8.0	-	8.1	8.3	-
Grass pellet	-	-	15.8	-		
Mean (W,A,H)	11.0	9.2	11.6	15.6		
Mean (W,A,H,S)	10.5	8.9	-	13.7		

Table 6.11. Mean apparent N digestibility (%) of feeds in the different feeding trials.

	Cattle	Red deer	Roe deer	Ponies	Mean (C,Re,P)	Mean (C,Re,Ro,P)
Willow 1.5X	67.8	69.2	71.6	70.1	69.0	69.7
Alfalfa 1.5X	61.0	58.1	55.0	57.8	59.0	58.0
Hay	69.0	69.0	70.6	56.9	65.0	66.3
Straw	19.8	20.3	-	11.9	17.3	-
Grass pellet	-	-	70.9	-		
Mean (W,A,H)	65.9	65.4	65.7	61.6		
Mean (W,A,H,S)	54.4	54.2	-	49.2		

6. Digestibility of faeces (IVODMF)

The IVOMDF of the willow diet was very low and that of the hay diet was rather high in all species (table 6.10). On average IVOMDF was highest in the ponies and lowest in the Red deer.

7. Apparent N-digestibility (ADN)

On average ADN of willow and hay were highest while ADN of straw was very low in all species. Species differences were small except for ponies having a very low ADN on straw.

8. Relationships

A number of potentially relevant relationships between described variables were tested for significance using regression analysis.

No significant relationship was detected between organic matter digestibility (OMD) and live weight and MRT. The relationship between OMD and VFI was positive but weak ($r^2=0.25$; $p<0.05$). OMD was significantly related to lignin content of the diet but OMD was best explained when both lignin-content and NDF-content were included in a multilinear regression model ($r^2=0.39$; $p<0.05$).

MRT was not related to OMD. Live weight explained 35% of the variance of MRT but a better relationship was found when VFI was included in a multilinear regression model ($r^2=0.48$; $F=15.8$, $p=0.01$):

$\text{MRT (hrs)}=0.06\text{LW (kg)}-0.39\text{VFI (g/kg}^{0.75})+40.93$.

Discussion

Selection was not apparent in alfalfa despite the fact that in this feed heterogeneity was enormous. Although both dust and very coarse particles were present it is likely that dust was stuck to the coarser particles so selection was minimized. When given heterogeneous willow all species selected a diet of higher quality compared to the diet offered. Roe deer, being the smallest species and hence having the smallest incisor arcade, had the highest selective ability while the large cattle had the lowest. The results make clear that when analysis of the feed residues are not taken into account when calculating digestibility, wrong conclusions can be drawn when species with very different selective capacity are compared. This can happen even if species of similar body size are compared e.g. sheep and goats (Van Soest 1982).

When the feeding level of the heterogeneous feed is increased VFI (voluntary food intake) tends to increase. This increase was less apparent in alfalfa, probably because little change in quality of offer occurred, than in willow where it was substantial. The quality of the ingested diet was also higher with willow. Although the interaction between feeding level and diet quality selected is problematic the increased intake seems to be more important than the increase in diet quality when raising the feeding level. Intake increased by more then 15% while digestibility increased on average less then 5%. While high feeding levels lead to a large percentage of refusals the frequently reported refusal allowance of 15% is probably too low when one aimes to measure VFI of heterogeneous feeds (Zemmelink 1980).

As gut contents scales linearly with body weight (Parra 1978) interspecies comparisons are best made when intake is expressed linearly (Demment & Van Soest 1985) or near-linearly ($BW^{0.9}$, Poppi et al 1989, Hendrickson et al 1981) with body weight. Energy requirements, especially of non productive animals, however, are related to metabolic weight and therefore most workers compare intake on a metabolic weight basis. Both expressions have their merits depending on the questions asked. In this study inter-species differences became more pronounced when intake was expressed on a live weight basis (table 6.4 and 6.5). Intake rates of the smaller species are seen on this basis to become relatively higher and especially emphisized the very high intakes in the small Roe deer compared to the other species. Smaller animals have been found to eat much more than large animals when intake was expressed near-linearly to body weight, while intakes were similar when expressed relative to metabolic weight when fed the same diet (Hendricksen et al 1981). When intake is considered in relation to energy requirements the lower intake of small animals (on a metabolic weight basis) has profound implications for small animals. In order to obtain the same amount of digestible energy as large species small animals have to compensate for by eating more (Batzli 1981) or by selecting a higher quality diet (Demment & Van Soest 1985). In this study Roe deer seem to be able to realize a relatively high intake on willow.

Calculated on a metabolic weight basis the intake of alfalfa by the Red deer was quite low compared to that of the other species. McCabe & Barry (1988) report a VFI of alfalfa of 75 g/kg MW by Red deer, substantially higher than found in this study. During the feeding trial it was noted that the deer were reluctant to eat from the dusty and poor looking alfalfa hay and this may have contributed to a lower intake. Higher intake of good quality alfalfa by horses when compared to bovids have been reported (Foose 1982) but there are a number of studies where intake was found to be similar (reviewed by Chenost et al 1985), as in this study. Renecker & Hudson (1990) compared VFI of alfalfa by Moose, Wapiti and cattle. They found no difference between species when compared on a live weight basis. In this study there was no difference between cattle and Red deer but VFI of the browser (Roe deer) was significantly higher.

On good and low quality grass products cattle and ponies had highest intakes, Red deer were intermediate on hay and lowest on straw, while Roe deer had the lowest intake on hay. It is well known that Roe deer can not cope with high fibrous feeds and that there is an inverse relationship between fibre content and intake (Drodz & Osiecki 1973, Perzanovski 1978). In a comparison of Red deer and sheep, Milne et al (1978) found sheep to have higher intakes of good quality hay but that the deer realized higher intakes on poor hay. In the present study the bulk and roughage feeder had high intakes both on the hay and on the straw but the differences on the straw were smaller (and not significant) than on the hay diet. Both on the hay and on the straw VFI of the ponies was a little higher than the VFI of the cattle but differences were not significant in both cases. Usually horses and ponies are reported to have higher intakes than cattle on grass products varying widely in fibre content (Johnson et al 1982, Duncan et al 1990) although the difference becomes smaller when fibre content decreases (Duncan et al 1990, Uden & Van Soest 1982).

Very few comparisons have been made with browse. In this study no significant interspecies differences were found in VFI on the willow diet, although Roe deer tended to have a higher intake. Renecker & Hudson (1990) compared moose, wapiti and cattle in their ability to ingest aspen twigs and leaves. When expressed on a live weight basis the order of decreasing VFI was Moose > Wapiti > cattle, a similar result as in this study (table 6.5).

On average hay was digested best, in decreasing order followed by willow, alfalfa and straw. Small species differences were found in the capacity to digest willow and alfalfa. Differences were much larger for hay and straw. Cattle digested all forages best. Roe deer and ponies digested hay less well than cattle and Red deer, while straw was poorly digested by the ponies. On average digestive capacity in decreasing order was cattle > Red deer > Roe deer-ponies. When compared to sheep, Red deer digested high quality diets better (Fennessey et al 1980) or less (Milne et al 1978). The reasons for these different findings are not clear. Lower quality diets were better digested by sheep than by Red deer (Milne et al 1978). These results compare well with the differences as found in this study between cattle and Red deer.

The digestive capacity of Roe deer was (surprisingly) high on all tested forages. Roe deer digested willow, alfalfa and hay better than ponies although differences were small. The digestibility by Roe deer of natural feeds was generally between 40 and 50% throughout a large part of the yearly cycle (Drodz & Osiecki 1973) but this was on highly lignified browse. Dissen (1983) compared Roe deer with goats. Fibrous feeds were well digested by Roe deer and digestibility by goats was only 5 digestion units higher. White tailed deer (a concentrate selector) digested high quality diets (including alfalfa) only slightly less than wapiti (an intermediate feeder) (Mould & Robbins 1982). The relative high digestive capacity of Roe deer found in this study compares well with other reported data.

The relative low digestive capacity of equids is well known. The digestibility by the ponies of alfalfa, hay and straw in this study is comparable with other findings (Darlington et al 1968, Smolders et al 1990). Cattle digested grasses better than horses , the difference between the species on average was about 12 digestion units. On good quality alfalfa horses performed only slightly less than cattle (difference: 3-5 digestion units). The differences between the two species became more pronounced when cell wall in the diet increased (Hintz 1969, Johnson et al 1982, Uden & Van Soest 1982, Vander Noot & Gilbreath 1970). A similar pattern was found in this study. In figure 6.1 the interspecies differences in digestibility (relative to cattle) is plotted against the cell wall content of the diets. The differences in digestive capacity increase with increasing cell wall content.

The digestibility of faeces might give some insight in the digestive capacity of herbivores. If the extent of digestion of (high quality) diets is limited within the animal it can be expected that more potentially digestible matter is present in the faeces. If the potential digestibility of the food is low the digestibility of the faeces will also be low and is then less influenced by the digestive capacity of the animal. This is likely to be the case with willow and possibly with the straw. The escape of potentially digestible matter was high on the hay diet in all species. On average the highest digestibility of faeces was found in the ponies clearly indicating a lower digestive capacity when compared to the ruminant species. Between the ruminants the differences were small.

Substantial variation was found in the apparent N digestibility (ADN) of the different diets in relation to their N content. Although the ingested willow had the highest N content of all forages ADN was very low. This is likely caused by the high content of polyphenols in the osier willow (McCabe & Barry 1988). These secondary compounds can have a profound negative effect on protein digestibility (Mould & Robbins 1982).

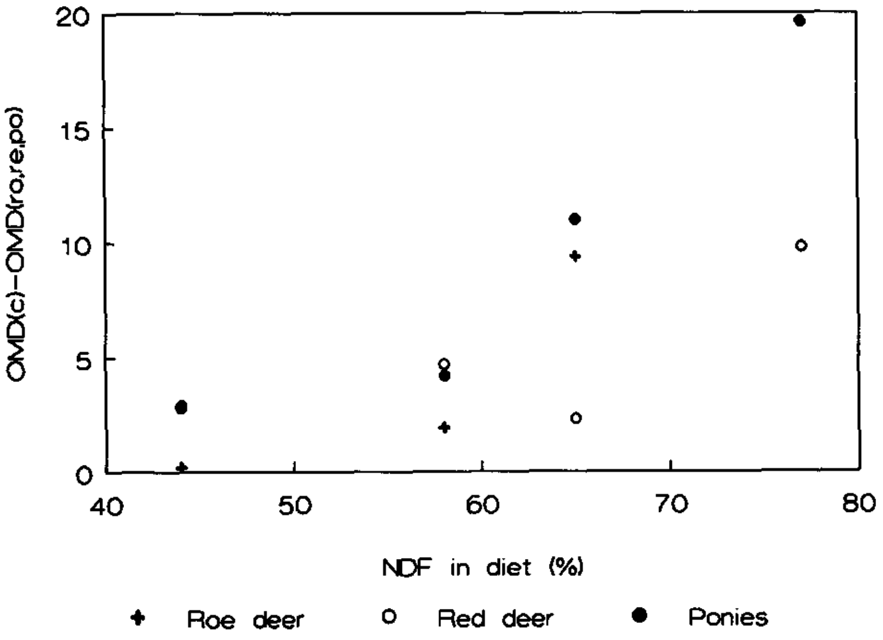

Figure 6.1. Relationship between differences in digestibility, relative to cattle, and NDF content of the diet.

Also the ADN of alfalfa was low even while the N content was quite high.
The reason of this low ADN is not clear. In high quality alfalfa ADN in ruminants and non ruminants frequently exceeds 65% (Fonnesbeck et al 1967, Chenost et al 1985, Darlington et al 1968). Cattle had the highest ADN on all forages tested while the Red deer were intermediate between cattle on the one hand and the Roe deer and ponies on the other. The last two species showed little difference. On good quality forages Red deer digested N similar (Simpson et al 1978) or 2-4 units less than sheep (Milne et al 1978). On low quality feeds the deer did better than sheep. Many comparisons have been made on N digestibility between cattle (and sheep) and horses. The results are quite variable. On good quality alfalfa and grass many workers found little difference in ADN between cattle or sheep and horses (Vander Noot & Gilbreath 1970, Hintz 1969, see review by Chenost & Martin Rosset 1985). On low quality forages horses did better than cattle (Vander Noot & Gilbreath 1970). Hintz (1969) found variable results but

generally ADN was much lower in horses (more than 13 units) than in cattle in his studies. Axelsson (1949), however, found that horses did better than cattle on 71 rations. These conflicting results warrant further study in protein digestion in ruminants and non ruminants.

When important variables related to digestive capacity of the species studied are tentatively ranked with low rank number associated with an indication of a higher digestive capacity, the following picture emerges: (if difference between variable values was less then 2 units rank numbers were treated as ties; comparisons based on mean performance on 4 diets, except for Roe deer) (table 6.12). The digestive capacity is in decreasing order cattle > Red deer > Roe deer > ponies.

Retention time (MRT) was longest in cattle on all forages, Red deer had longer MRT on willow compared to Roe deer and ponies, and longer MRT on straw than ponies. Ponies had lowest average MRT. Absolute comparisons with MRT's found in other studies are difficult to make because different markers are used and MRT is defined in different ways, but relative comparisons can be used. Dissen (1983) found Roe deer to have much shorter MRT than goats. Red deer have generally shorter MRT than sheep (Simpson et al 1978, Kay & Goodall 1976, Milne et al 1978).

Table 6.12. Ranking of species for variables related to digestive capacity.

	Cattle	Red deer	Roe deer	Ponies
OMD	1	2	3	4
NDF Dig.	1	2	3.5	3.5
IVOMDF	1.5	1.5	3	4
	-----	----	----	----
	3.5	5.5	9.5	11.5

The shorter MRT in horses compared to ruminants is well documented (Johnson et al 1982, Foose 1982, Uden et al 1982). Food retention time is considered to be an important determining factor for food intake (Demment & Van Soest 1985) and even digestibility (Mertens 1973). Indeed MRT was inversily related to intake in a number of studies (Kay & Goodall 1976, Poppi et al 1980) but in the present study the relationship was weak. No overall relationship could be detected between MRT and OMD. Over a range of animal sizes MRT increased with body size (Demment & Van Soest 1985). In the present study body weight explained 35% of the variation of MRT. A better relation was found when intake was also included in the model although the model r^2 only increased to 48%. Clearly body size played only a limited role in explaining MRT in this study. MRT's in the small Roe deer were quite similar to the larger ponies while the MRT's of the Red deer were sometimes about twice as long as in the larger ponies. Considerable variation among species was also found by Uden et al (1982), e.g. between similar sized sheep and goats, and sheep and Red deer on the same diets. Apparently body size, intake, type of diet and rumination capacity all have to be taken into account (Van Soest 1982, Demment & Van Soest 1985).

All this points to a considerable variation among the species studied in the way they are adapted to exploit different food resources by having relative different capacities for intake, digestion and food retention. How the outcome of the interaction between intake, digestion and food retention, resulting in the digestible organic matter intake rate, will be in the different species is strongly affected by the physical characteristics of the diet. The results of this study indeed indicate that 4 different strategies of nutrient extraction (expressed as DOMI) can be distinguished. The order of digestive capability of cattle > Red deer > Roe deer > ponies confirm the basic idea of ruminants having superior digestive capacity than non ruminants and that within the ruminant group the bulk and roughage feeder has the highest and the concentrate selector has the lowest digestive capacity while the intermediate feeder takes an intermediate position. A high digestive capacity means a high potential to utilize fibrous forages with a high proportion of digestible fibre (notably grasses and other monocots), as clearly is the case in the large bovid. A low digestive capacity, however, can sometimes be compensated for by an increased intake. This is presumably caused by the ability of animals to increase passage to some extend. The compensation is quite effective on high quality grass but on low quality straw ponies only come close to Red deer. Apparently compensation through VFI does not lead to an equally well or even better performance when compared to cattle when digestibility becomes very low and fibre content very high, contrary general believe (Duncan et al 1990).

Within the ruminants increasing VFI is more complicated. In this experiment Roe deer did have a much shorter MRT on willow than cattle and Red deer but on alfalfa and hay differences with Red deer were not apparent. Nevertheles, on both willow and alfalfa, Roe deer had very high intakes. Much higher than could be expected from the general relationship between body size and intake. They managed to have a high digestible organic matter intake on both those diets. Increasing intake, however, was not possible on the fibrous grass. Here intake of the browser ruminant is limited by the rumen system even when the digestibility was quite high. It seems that both the high NDF content of the diet and its physical characteristics play a role. It is suggested that browse (and possibly legume) particles are much easier fragmented into smaller particles than the long fibrous grass particles. This would facilitate passage of these food types through the concentrate selector, maybe helped by a postulated wider reticulo-omasal orifice (Hofmann, pers. comm.), although this idea has yet to be confirmed. The importance of particle size also can be illustrated by comparing the performance of Roe deer on hay and grass pellets. While the digestibility of the grass pellet was lower than that of the hay the intake was much higher. The smaller particles of the pelleted grass likely facilitated passage and hence intake. The browser ruminant is particularly well adapted to forages with relative low cell wall content even when cell wall digestibility is low. The Red deer indeed takes an intermediate position between Roe deer and cattle in many respects. When comparing Red deer with Roe deer with respect to DOMI of willow and hay, the Roe deer performed better on willow and the Red deer on the hay defining the Red deer as it has been classified: a mixed feeder or a grazer/browser.

In conclusion the three ruminant feeding types, as distinguished by Hofmann (1973) on morpho-anatomical grounds, are closely parallelled by the three different strategies of nutrient extraction as found in the representatives of the three classes in this study. The hindgut fermenter generally has lower digestive capacity when compared to the ruminants but is able to compensate for by an increased intake even on fibrous feeds. But its capacity of nutrient extraction does not surpass that of the superior large bovid, the differences becoming greater when fibre content and lignification of cell wall increase.

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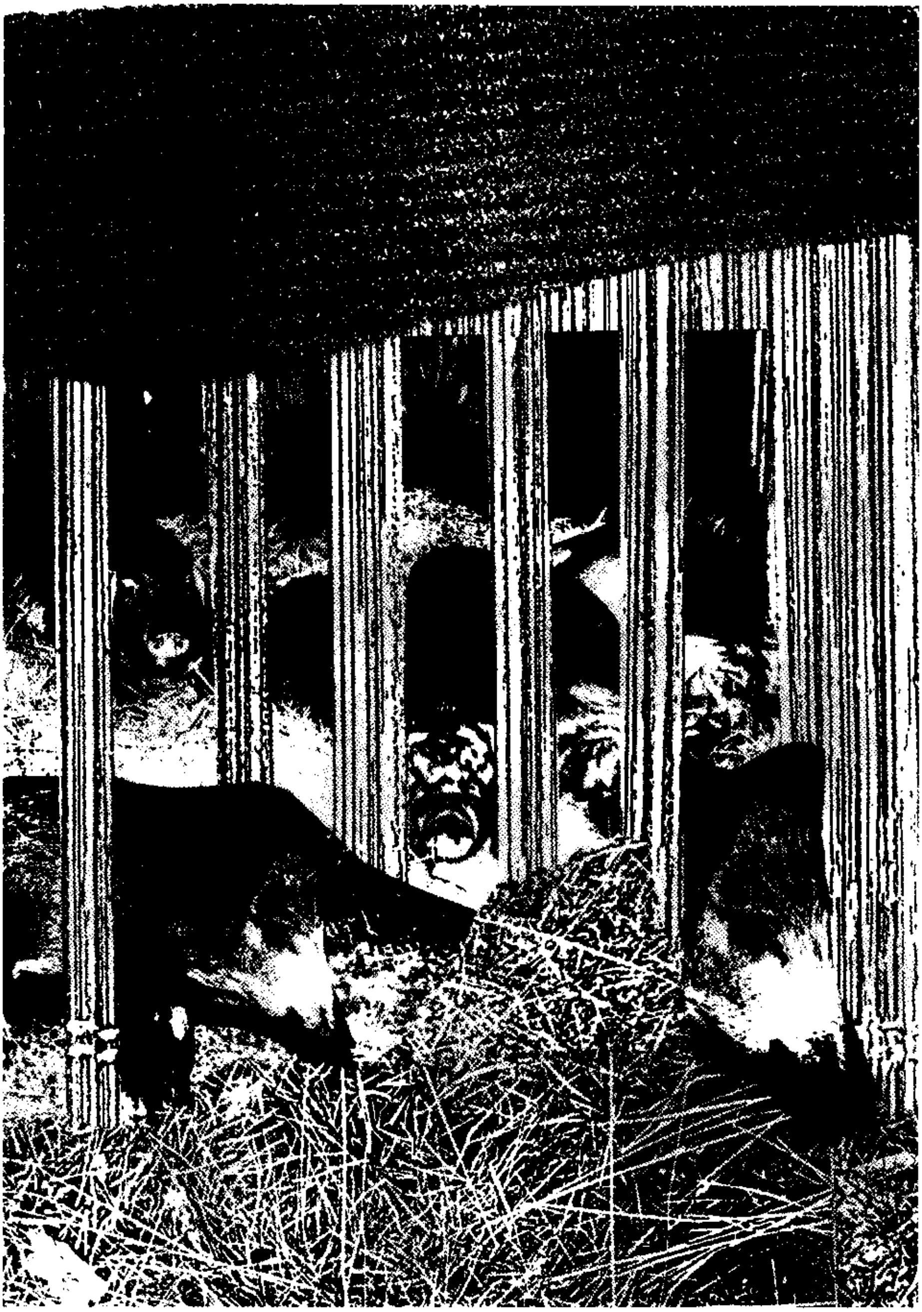

CHAPTER 7

DIGESTIBILITY AND VOLUNTARY INTAKE OF ROUGHAGES BY WILD BOAR AND MEISHAN PIGS

Abstract

The digestibility and voluntary intake of fibrous roughages and acorns was studied in wild boar and Meishan pigs. The NDF content of the diets ranged from 13.9-76.7%. Organic matter digestibility of acorns, mixed grass and wheatstraw was higher in wild boar while voluntary food intake of the Meishan pigs was higher for mixed grass, hay and wheatstraw. Organic matter digestibility and NDF digestibility were both negatively related to NDF content of the diet. No relationship existed between voluntary food intake and NDF content of the diet. The apparent N digestibility was positively related to dietary N while no relationship was found with dietary NDF.

The negative effect of NDF on digestibility could only be partly explained by the lignin content of NDF. Much more important is the lower efficiency of the carbohydrate fermentation in the caecum and colon when compared to the direct absorption of glucose from the small intestine.

It was estimated that digestible NDF at maximum contributed 34% to the metabolizable energy intake of the animals.

It was concluded that wild boar and domestic pigs should be able to maintain themselves on an all fresh grass diet when NDF content does not exceed about 55% and N content is not too low.

Introduction

It is well known that wild boar, *Sus scrofa*, are predominantly herbivorous animals (Briedermann 1990). Although the major part of the plant material selected consists of roots and mast, there are situations when a substantial proportion of the diet of wild boar is made up of vegetative plant material. On poor soils in the Netherlands stomach contents of free-ranging boar contained more than 70% leaves of broad leafed grasses in spring (Groot Bruinderink et al 1994). In mast-poor years stomach contents in autumn and winter were also high: comprising 36% and 74% grass leaves respectively (Groot Bruinderink et al 1994). Furthermore it was noted that both juveniles and adults either maintained weight or lost weight only slightly during the winter period and weight loss was more strongly related to population density than to diet composition (Groot Bruinderink et al 1994).

These observations indicate that wild boar apparently have a considerable capacity to digest and utilize fibrous plant material. For various reasons the effect of including fibre in the diet of pigs has been subject of many studies. In general fibre has a negative effect on organic matter digestibility (King & Taverner 1975, Kennelly & Aherne 1980, Just 1982, Morgan et al 1975, Frank et al 1983, Stanogias & Pearce 1985). Most studies, however, focus on digestibility and do not pay any attention to voluntary intake. Therefore it is difficult to gain insight in the effect of fibre on the potential energy contribution (DE or ME) to maintenance requirements. Furthermore, the types of fibre used in feeding trials are generally very different from those of natural feeds (hulls, purified cellulose etc.) and are normally added to a high quality basal diet, and given in the form of meal. The cell wall content of the test diets typically does not exceed 20% while cell wall content of grass leaves, as consumed by boar in the wild, in winter easily exceeds the 50% level. Because so little is known of the potential of wild boar to ingest and digest high fibrous plant species, while they are important staple food in mast poor years, a series of feeding trials were conducted with natural roughages across a range of fibre contents. To study a possible effect of domestication on digestive capacity, a comparison was made with a domestic pig breed. The Meishan breed was chosen as this race has been found to have superior capacity to digest fibre when compared to other pig breeds (Fevrier et al 1988, Kemp et al 1991).

Methods and materials

Initially the experiments started with 5 female Meishan pigs, averaging 51.2 ± 1.8 kg, aged ca 6 months, and 5 female wild boar, averaging 28.9 ± 5.2 kg, aged ca 6 months. The wild boar were taken from a small forest enclosure where they lived under semi natural conditions. One boar died of an infection at the beginning of the experiment. The animals were individually housed in small confinements (1.6x0.8 m). Water was supplied ad lib. Five test feeds were selected: Acorns (*Quercus robur*), a commercial grass pellet, alfalfa hay, grass hay (*Lolium perenne*) and wheat straw. The alfalfa hay, grass hay and wheat straw were chopped twice at 1 cm. The chopped product was then formed into a pellet with 1.5% molasses and 5% water (mesh size 1 cm). During the (first) acorn trial one Meishan refused to eat and one boar broke its leg. The boar had to be taken out of the experiment completely. With the grass pellet, the hay and the straw, a number of animals refused to eat. Therefore it was decided to give these animals a mixed diet of the test feed with some percentage of a commercial high quality baby pig diet to keep them in the trials. The resulting mixed diets were given as a wet mash. Because of the mixing with the baby pig diet this feed was also tested in a single trial. As two out of 5 wild boar were lost, 3 more female boar were included in the hay and straw trials, averaging 18.3 ± 2.1 kg, aging 5 months.

A 7 day adaptation period was followed by a 7 day measuring period. During the adaptation period the ad lib intake could be estimated approximately. The 'pure' diets were fed once daily and the mixed diets twice daily (to prevent fermentation).
All faeces and refusals were collected and weighed. Subsamples of feed offered, faeces and (if selection took place) orts were collected, frozen and stored for further analysis. The baby pig diet was not given ad lib, to prevent extensive fattening, but at approximately 1.3x maintenance.

Subsamples of feeds offered, refusals (if necessary) and faeces were analyzed for DM, ash, NDF, lignin according to Goering & Van Soest (1970).

To detect possible species differences ANOVA's were carried out on arcsin transformed data. Differences between means were analyzed with the Tukey test. Relationships between variables were evaluated with regression analysis. The calculations were carried out with the statistical package SAS (SAS Inc. 1989).

Results

The chemical composition of the diets offered is given in table 7.1. The ash content of the grass pellet was very high and indeed, the material turned out to be contaminated with ca. 30% sand. Lignin content and lignin/NDF ratio was highest in alfalfa. Acorns and straw were low in N. Because of the high ash content of the grass pellet the N concentrations were expressed on organic matter basis.

At the beginning of the acorn trial the two groups of animals treated acorns differently. Despite never having previously experienced acorns the boar immediately started to peel the acorns before ingestion of the kernels. The Meishan pigs started by ingesting whole acorns but after a few days a few of them learned how to peel off the hulls. The possibility can not be ruled out that these animals copied this behaviour from the boar. At the beginning of the measuring period all Meishan pigs had learned to peel acorns but large individual differences remained.

Table 7.1. Proximate chemical composition of diets offered.

Diet	%DM	%ASH	NDF (%OM)	Lignin (%OM)	N (%OM)	Lignin/ NDF (%)
Baby pig diet (BPD)	0.90	7.6	13.9	2.8	3.38	20.1
Acorns	0.57	2.3	37.4	4.0	1.01	10.7
Grass+40% BPD	0.94	34.3	38.4	4.4	3.41	11.4
Grass	0.94	41.1	55.8	6.0	3.43	10.8
Alfalfa	0.92	9.7	56.9	10.0	2.92	17.6
Hay+15% BPD	0.92	8.5	58.2	5.8	2.09	10.0
Hay	0.92	8.6	66.0	6.3	1.86	9.6
Straw+20% BPD	0.91	12.6	64.4	8.0	1.41	12.4
Straw	0.92	14.7	76.7	9.4	0.92	12.3

Digestibility coefficients and voluntary intakes of the different diets are presented in table 7.2. Species differences in digestibility were detected in the acorns, grass+40%-BPD, and straw diet (OM); in the acorns and straw diet (NDF); and in the grass+40%-BPD diet (N). In all cases where significant differences occurred, digestibility was higher in the wild boar.

On average the organic matter digestibilty (OMD) of the baby pig diet and of the acorns was high. Of the 'pure' fibrous feeds OMD progressively decreased from grass > alfalfa > hay > straw. Adding the high quality BPD improved the OMD of all feeds. Digestibility of NDF was highest in acorns and quite low in the baby pig diet. Of the pure roughages the grass pellet had the highest digestibility of NDF and straw the lowest. Also alfalfa had a low NDF digestibility. Adding baby pig diet only improved NDF digestibility if the NDF digestibility of the roughage was lower than the NDF digestibility of the baby pig diet. Apparent digestibility of N was quite low for the grass and alfalfa diet and very low for the acorns, hay and straw diets.

Voluntary intake of the grass+40%BPD-, the hay- and the straw diet was higher in the Meishan pigs. There were no significant differences in digestible organic matter intake. Of the feeds fed, ad lib acorns had highest voluntary intake. There is no clear intake pattern with the other diets. Adding baby pig diet improved intake of hay and straw but not of the grass pellet.

Table 7.2. Mean digestibility coefficients and voluntary intake (except BPD) of diets ingested by Meishan pigs and wild boar. Intake expressed as g/kg MW.
OMI=organic matter intake; DOMI=digestible organic matter intake. (*: $P<0.05$)

Diet	Species	n	OM	NDF	OMI	DOMI	N
Baby pig diet (BPD)	pigs	5	0.86	0.42	38.3	33.0	0.87
	boar	3	0.83	0.35	35.7	29.7	0.83
Acorns	pigs	4	0.74	0.58	47.0	35.5	0.19
	boar	3	0.89 *	0.91 *	57.6	51.2	0.32
Grass+40% BPD	pigs	2	0.59	0.50	43.7	25.8	0.58
	boar	2	0.72 *	0.56	27.8 *	20.0	0.74 *
Grass	pigs	3	0.59	0.60	34.8	20.6	0.56
	boar	1	0.54	0.62	48.4	26.3	0.46
Alfalfa	pigs	5	0.43	0.28	47.0	20.2	0.59
	boar	3	0.45	0.30	39.3	17.5	0.59
Hay+15% BPD	pigs	2	0.43	0.30	34.0	14.5	0.43
	boar	3	0.54	0.44	29.2	15.7	0.54
Hay	pigs	3	0.41	0.35	33.6	13.8	0.41
	boar	3	0.41	0.36	16.9 *	7.2	0.27
Straw+20% BPD	pigs	2	0.38	0.33	45.8	17.3	0.48
Straw	pigs	3	0.23	0.17	35.1	8.9	0.00
	boar	6	0.37 *	0.31 *	28.1 *	10.4	0.06

The effects of varying dietary NDF concentrations on intake and digestibility parameters were studied by means of regression analysis. In table 7.3 the r^2's of a number of single variable regressions are presented using the combined data from both Meishan pigs and wild boar. OMD and NDF digestibility both were negatively related to NDF content in the diet (figure 7.1 and figure 7.2), with NDF content explaining variation in OMD much better than that of NDF digestibility (table 7.3).

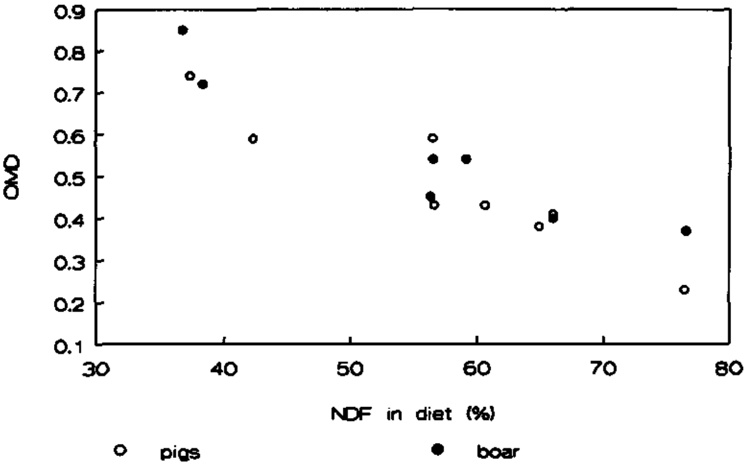

Figure 7.1 The relationship between the NDF content of the diet and the organic matter digestibility (OMD).

No clear relationship was found between intake and diet NDF (fig 7.3). Diet NDF explained only 20% of the variation of voluntary intake (table 7.3). The digestible organic matter intake was negatively related to diet NDF content (fig 7.4, table 7.3).

Apparent digestible nitrogen (ADN) was positively related to dietary N concentration (fig 7.5). Diet N explained 65% of the variation of ADN (table 7.3), the regression being:
ADN(%)= 19.9x diet N(%) - 2.3. In a simple regression a poor relationship was found between ADN and diet NDF (r^2=0.17, table 7.3).

Table 7.3. R-squares of a number of one-variable-regressions.

	Dependent variables				
Regression variables	OMD	DNDF	OMI	DOMI	ADN
NDF	0.73	0.48	0.21	0.51	0.17
OMD	-	-	0.18	-	-
DNDF	0.88	-	-	-	-
Diet N	0.09	-	-	-	0.65
Lignin/NDF	-	0.13	-	-	-

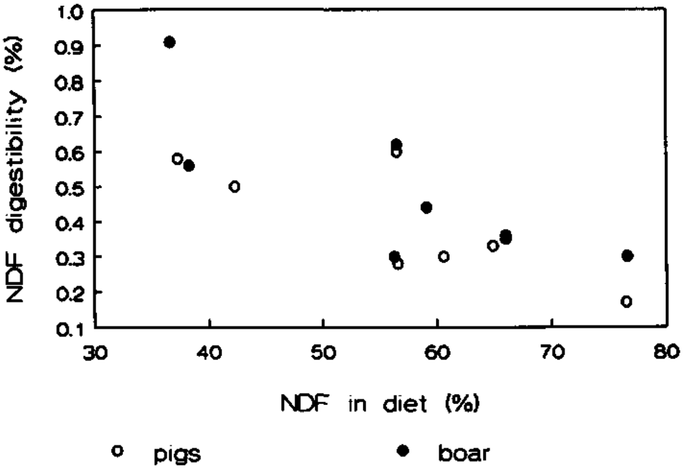

Figure 7.2. The relationship between the NDF content of the diet and the NDF digestibility.

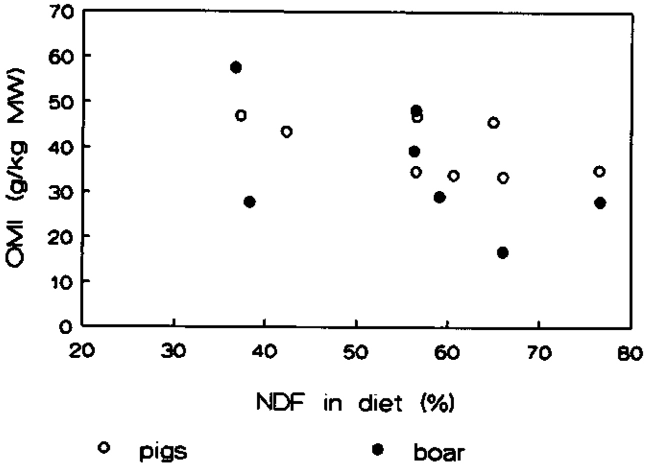

Figure 7.3. The relationship between the NDF content of the diet and the organic matter intake (OMI).

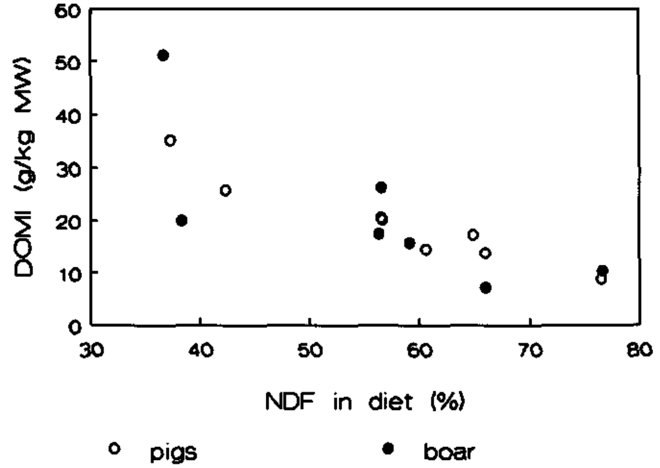

Figure 7.4. Relationship between the NDF content of the diet and the digestible organic matter intake (DOMI).

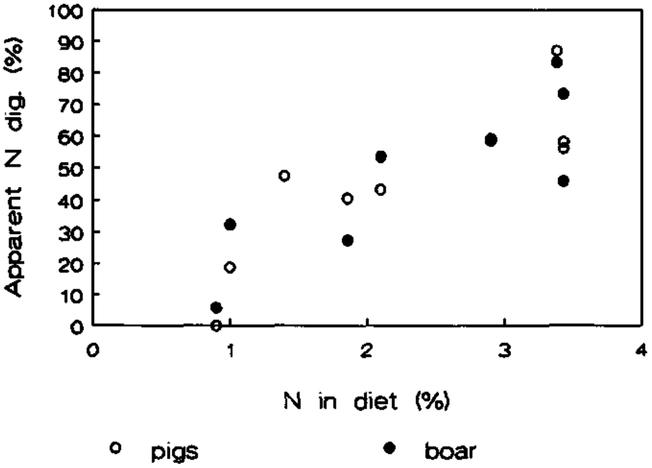

Figure 7.5. Relationship between the N content of the diet and the apparent N digestibility.

Discussion

'species' and diet differences

The differences between the two 'species' generally were small. Wild boar digested acorns, grass and straw better than the Meishans while the latter species had higher intakes of grass, hay and straw, resulting in no significant differences in intake of digestible organic matter in any of the diets tested. In a comparison of wild boar and the German Landrace pig, Schnorrenberg (1979) found comparable results, both with respect to to digestibility and voluntary intake. The wild boar in his study had 10% lower intake on the same diets. Differences however were not large. These findings are in line with the reported small anatomical differences between wild boar and domestic pigs (Briedermann 1990, Schnorrenberg 1979), while furthermore both length and wet weight of (parts of) the gastro-intestinal tract within an individual can vary considerably, dependent on the type of diet (Stanogias & Pearce 1985) which makes generalization very difficult.

The difference in NDF digestibility of acorns was very large between the two 'species'. This is the result of the greater ability of the boar to peel the acorns and thus realize a lower actual intake of NDF. The relatively large NDF content of acorns even without hulls (28%) combined with the high NDF digestibility recorded in any case raises some suspicion as to the reliability of the NDF measurement in acorns. It is not impossible that the NDF content of acorns has been overestimated as a result of the very high starch content, which in part may have 'survived' the treatment with amylase and neutral detergent reagents and thus may have been included in the NDF fraction (especially if the starch was composed of amylopectins). The relatively low NDF digestibility of the baby pig diet and alfalfa by contrast can be explained by a high lignin/NDF ratio. The depressing effect of lignin on NDF digestibility is well known (Van Soest 1982, Keys et al 1970). Despite similar NDF and lignin concentrations substantial differences in organic matter and NDF digestion were found of the remaining grass and the diets. On average the digestible organic matter intake of the 'pure' grass was more than twice that of the 'pure' hay. The reason for this difference is not clear.

N digestibility

Apparent N digestibility was positively related to dietary N concentration. This is probably the result of the rather constant endogenous N fraction, with true N digestibility remaining constant, playing an ever greater role when diet N decreases, resulting in a depression of apparent N digestibility.

No relationship was found between apparent N digestibility and dietary NDF concentration. Although similar results have been found by other workers (Eggum 1973, Kennelly & Aherne 1980) generally a negative relationship is reported (Farrell 1973, Boenker et al 1969, Pals & Evans 1978, Just 1982, Frank et al 1983). A negative relationship is expected because if diet NDF increases more NDF is fermented in the caecum/colon leading to a larger production of bacteria, resulting in a larger excretion of metabolic N in the form of bacterial residues (Just 1980, Mason & Palmer 1973, Hof 1980). Because the amount of NDF digested thus is more important than diet NDF as such, this relationship was explored by regression of output of N in the faeces (FN) on actual digested NDF (DNDF). Nitrogen intake (IN) was also included in the regression because this variable, as shown above, is also related to N digestibility:

$FN = 0.030*DNDF + 0.164*IN + 0.298$, with

part. $r^2_{DNDF} = 0.59$ and part. $r^2_{IN} = 0.14$, and where

FN = N output in faeces (g/d);

DNDF = NDF digested (g/d);

IN = N ingested (g/d).

The regression coefficient (0.030) suggets that each kg of DNDF results in the 'capture' of 189 g microbial (crude) protein, a figure agreeing reasonably well with what is known of the efficiency of N capture in microbial protein synthesis in other microbial populations in the digestive tracts of herbivores, for instance in the rumen (Tamminga, pers. comm.). The multiple regression makes clear that faecal nitrogen output indeed is well explained by the amount of NDF digested and that diet N is less important.

NDF digestibility

The negative relationship between organic matter digestibility and dietary NDF content as found in this study is in line with the findings of many other authors (King & Taverner 1975, Kennelly & Aherne 1980, Just 1982, Morgan et al 1975, Kass et al 1980, Frank et al 1983). According to King & Taverner (1975) this relationship is irrespective of weight and age of the animals. As most authors have worked with diets low in NDF, a linear relationship has now been firmly established over a very large NDF range (3-77%).

In explaining the effect of NDF on digestibility, both the NDF content as well as the source of NDF seem to be important. When an increase in diet NDF is combined with an increase in lignin content in the NDF, then the decrease can be attributed at least in part to the effect of lignin (Farrell 1973, Stanogias & Pearce 1985). In this study lignin probably played a negative role in the NDF digestibility of the baby pig diet and alfalfa. In the overall relationship, however, lignin content explained only 13% of the variation in NDF digestibility. Apparently an increase in NDF content in itself already is the most important factor, in line with other findings (Keys et al 1970, Fevrier et al 1992, Frank et al 1983). A number of reasons can be given. The most important one is that with increasing NDF more potentially energy yielding nutrients are transported to the hindgut where a part of the carbohydrates are fermented to volatile fatty acids (VFA). This fermentation process has a much lower metabolic effiency when compared with glucose being absorbed from the small intestine directly. Furthermore an increasing amount of energy is lost in gasses produced (CH_4,H_2), fermentation heat and energy in urine (Just 1980). A second reason is that an increase in NDF frequently is associated with a faster passage rate of digesta (Holzgraefe et al 1985, King & Taverner 1975, Stanogias & Pearce 1985, Van Wieren unpubl.). A faster passage rate leaves less time for biological attack of digesta leading to higher losses and a lower efficiency.

intake

In general the animals were reluctant to take the fibrous feeds, even to the extent that for some animals it was necessary to mix the roughage with a high quality pig diet. A similar finding has been reported by Fevrier et al (1992) with Meishan pigs and Large White.

In this study no relationship was found between dietary NDF content and voluntary intake. This is contrary to a frequently reported positive relationship (ARC 1981, Kennelly & Aherne 1980), likely made possible by a higher passage rate. The animals are thought to try to compensate and to maintain a certain level of digestible energy intake. As in the cited studies the NDF content never exceeded 30% it is postulated that this compensatory effect is only effective in the lower NDF range. With higher NDF contents diets tend to become unpalatable to swine resulting in depressed intake (Braude 1967) and/or the NDF content becomes so high that increasing intake is not possible because the capacity becomes limiting and that a possible increase in passage rate is levelled out by an increase in bulk content.

contribution of digestible NDF to maintenance requirements

The digestion of fibre can make a significant contribution to the metabolizable energy requirements of pigs through the production of volatile fatty acids (VFA). 90% of the total VFA production in pigs occurs in the caecum and large intestine (Just 1982). Stanogias & Pearce (1985) found a linear increase in VFA concentration in the colon with increasing NDF content. Increasing NDF content also leads to an increase in the C2/C3 ratio in VFA composition, as is the case in ruminants (Holzgraefe et al 1985, Stanogias & Pearce 1985, Van Soest 1982). There is a large variation in the reported contribution of VFA to energy requirements in pigs. Calculated contribution ranged from 5-30% with maxima of ca 30% NDF in the diet (Kass et al 1980, Farrell & Johnson 1972, Imoto & Namioka 1978, Varell 1987 in Pond 1989), depending on amount and type of NDF.

Although in this study no VFA were measured an attempt can be made to estimate the contribution of digested NDF to metabolizable energy intake (MEI). The results are presented in table 7.4. The principle of the calculation was as follows. The gross energy content of the roughages used in the experiment was estimated to be 18.5 MJ/kg organic matter (ARC 1980). ME was calculated from DE by taking ME/DE=0.82, both for the NDF fraction and for the cell content fraction (ARC 1982).
(Note: Although in pigs ME/DE generally is about 0.96, this conversion factor remaining constant with NDF ranging from ca. 8-30% (Just 1982, Drennan & Maguire 1970), here the ruminant conversion factor is taken because of the high fibre content of the feeds). The apparent NDF digestibility was calculated from the true NDF digestibility (table 7.2) by contributing the largest part (80%) of the metabolic faecal output to the NDF digestibility. The metabolic faecal output was calculated according:
MFO=(output faecal organic matter (g/d)* (1-NDF of faecal organic matter)/(organic matter intake (g/d)).

Table 7.4. Metabolizable energy intake (MJ/kg MW/d) and fractional contribution of metabolizable NDF to MEI. (st.dev.)

Diet	NDF in diet (%OM)	DOMI g/kg MW	MEI	NDF contribution to MEI
Acorns	37.0	42.3 (20.5)	0.77 (0.37)	0.24 (0.10)
Grass+40% BPD	40.3	22.9 (3.8)	0.42 (0.07)	0.20 (0.02)
Grass	56.5	22.0 (4.3)	0.41 (0.08)	0.34 (0.02)
Alfalfa	56.5	19.1 (5.6)	0.35 (0.10)	0.13 (0.12)
Hay+15% BPD	59.7	15.2 (2.9)	0.28 (0.05)	0.24 (0.11)
Hay	66.0	10.5 (5.0)	0.19 (0.09)	0.23 (0.19)
Straw+20% BPD	64.9	17.3 (4.7)	0.31 (0.09)	0.18 (0.21)
Straw	76.6	9.9 (4.3)	0.18 (0.08)	0.26 (0.22)

From these assumptions the contribution of digested NDF to MEI could be easily calculated (table 7.4). The contribution of digested NDF to MEI ranged from 13% in alfalfa to 34% in the 'pure' grass diet. The MEI of the grass diet was 0.41 MJ/kg MW which is close to the maintenance ME requirements of pigs (0.46 MJ/kg MW, ARC 1981).

A first conclusion that can be drawn is that only small differences exist between wild boar and its domestic relatives in the capacity to utilize fibrous feeds. Hence studies from the domestic pig can be used for a general understanding of the physiology of digestion of wild boar too.

Secondly the results of this study indicate that wild boar (and domestic pigs) do have the capacity to utilize plant species rich in cell wall content to a large extent, that the energy contribution of NDF digested can amount to 34% of the metabolizable energy intake and that pigs can maintain weight on an all grass diet if the NDF of the grass does not exceed 55%. Therefore fresh grass can be an important staple food for wild boar throughout the seasons.

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Introduction

It is well known that the about 150 species of ruminant show considerable variation in body weight (BW), type of diet preferred (Skinners & Smithers 1990), social organization (Jarman 1974), and other characteristics. Based on differences in anatomy Hofmann (1973) proposed three distinct feeding classes of ruminants: Concentrate selectors (CS), grass and roughage feeders (GR) and intermediate mixed-feeders (IF). In all three classes both small and large species are present and Hofmann concluded that class differences were irrespective of BW. The anatomical features Hofmann examined broadly fall into two different functional categories. One set of adaptations is related to the feeding behaviour, the other to adaptations of the gut system (Hofmann 1988, 1989). The preruminal adaptations of CS (e.g. mouth opening, torus lenght, dental pad, rostral fungiform pappillae) all point to a strong ability for selective feeding on dicotyledons, while GR are more adapted to nonselective feeding of monocotyledons. Among the features of the gut system that have been examined are stomach structure, rumen volume, rumen pillar musculature, size and structure of the four stomach compartments, maximum surface enlargement of the reticulo-rumen and width of the reticulo-omasal orifice (Hofmann 1973). GR have a larger, more muscular reticulo-rumen, reduced papillation of the dorsal rumen wall and smaller ostia between the reticulo-rumen and the omasum than CS.

The functional significance of these adaptations has been related to the exploitation of two different forage types: grass (monocots) and browse (dicots), hence the name browsers for CS and grazers for GR. Browse contains higher levels of cell solubles and has lower digestibility than grass. Grass has higher levels of cell wall components but because these cell walls generally are highly digestible the overall digestibility of grass is higher than that of browse. In the first part of the paper data on the chemical composition of browse and grass are presented because the predicted differences between browse and grass have not yet been thoroughly examined.

Based on structure and adaptations of prehensile organs and gut morphology CS are supposed to be adapted to exploit the highly fermentable browse solubles while being able to pass rapidly the undigestible cel wall fraction. GR on the other hand are better able to exploit the slower fermentable cell wall components of grasses (large stomach capacity, high capacity for long retention of digesta, unselective feeding). The predictions with respect to digestive capacity for fibre and diet choice, however, have not yet been properly tested. It can also be expected that important aspects of feeding should bear a relationship with BW. Small animals have higher energy requirements per kg body weight relative to large animals (Demment & Van Soest 1985); the digestive capacity of small animals has been suggested to be lower than of large animals (Van

CHAPTER 8

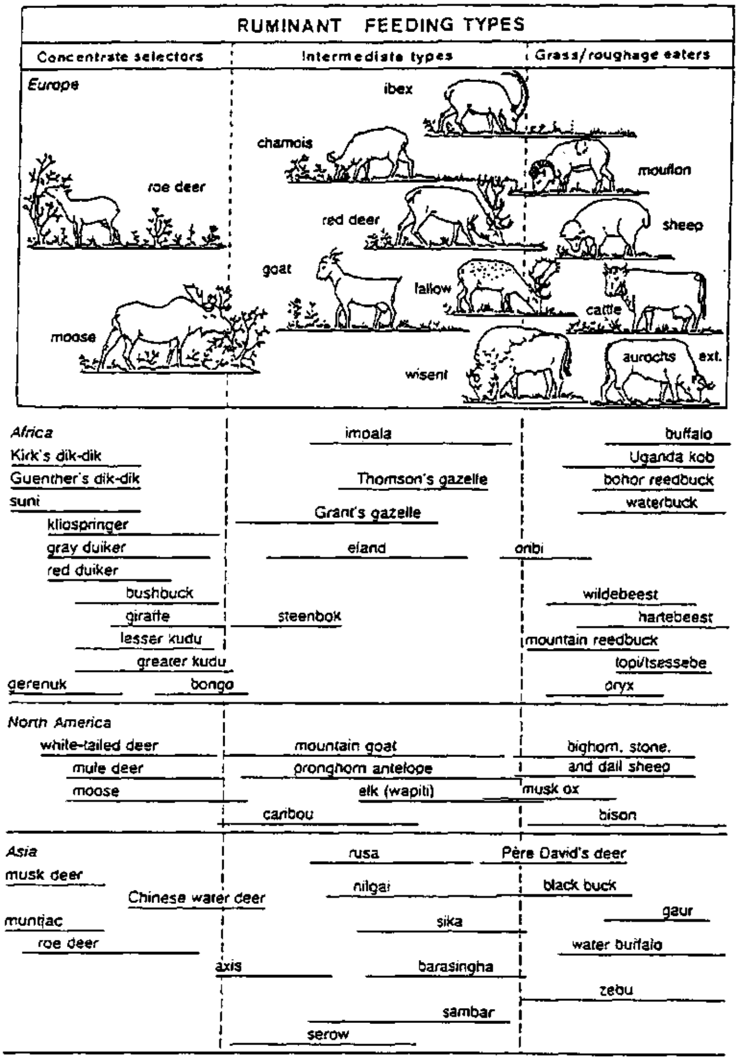

Figure 8.1. Ruminant species investigated morphologically. The farther the baseline of a species extends to the right, the greater is the species' ability to digest structural carbohydrates (plant cell wall); the farther to the left, the more selective the species. (Data from R.R. Hofmann).

Soest 1982). These two aspects combined would implicate that small animals need to select a higher quality diet and hence should rather be browsers than large animals.

Recently the Hofmann classification has come under attack. Gordon & Illius (1994) proposed that rumen fermentation rate and retention time are better explained by BW differences than by the class differences as proposed by Hofmann. In a recent paper Robbins et al (1995) did not find any class differences with respect to fibre digestion, saliva flow and ruminal liquid flow rates. Fibre digestion and parotid salivary gland weight were positively related to body weight. Saliva gland size was about 4 times larger in browsers than grazers with the Kudu as a notable exception.

A more general problem with testing Hofmann's classification is that the classes are based upon a great number of variables that together produce a class. Actually Hofmann's classes are adaptive syndromes indicating it is problematic to single out one variable to use in testing and analysing class differences. Nevertheless a number of variables have been specified by Hofmann that vary quite strictly according to class while also specific 'class' predictions have been made with respect to digestive capacity and feeding style (Hofmann 1973). Therefore a number of variables used by Hofmann for his classification can be used in comparing the body weight hypothesis and the class-approach (here termed the class-hypothesis).

In this paper an attempt is being made to test which hypothesis (the Hofmann classes or the BW relationships) does best explain variation in digestive capacity and diet composition of those species of ruminants that have been classified as CS, GR and IF based on anatomical characteristics only (Hofmann 1988, figure 8.1). Digestive capacity was analysed again as a larger data base was available than the one used by Robbins et al (1995) while a test on diet data is still lacking. As the call for rigorous tests (Robbins et al 1995) is taken up here also some of Hofmann's own data were analysed to test class differences against BW relationships for a number of variables related to inner gut structure.

Data analysis

Data on the chemical composition of food plant parts were collected during a year-round field study in enclosures of temperate mixed forests. The main plant species on which the analyses were based were: *Agrostis capilaris, Amelanchier lamarckii, Betula pendula, Betula pubescens, Calluna vulgaris, Carex arenaria, Deschampsia flexuosa, Erica tetralix, Fagus sylvatica, Frangula alnus, Holcus mollis, Molinia caerulea, Picea abies, Pinus sylvestris, Prunus serotina, Quercus rubra, Quercus robur, Rubus fructicosus, Sorbus aucuparia, Vaccinium myrtillus*. The plant parts were collected as grab samples simulating the feeding behaviour of Roe deer (*Capreolus capreolus*), Red deer

(*Cervus elaphus*) and Ox (*Bos taurus*), the size difference ensuring the inclusion of a wide range of bite sizes. The grab samples were analysed for cell wall constituents (NDF) and lignin (Goering & Van Soest 1970) and in vitro digestibility (Tilley & Terry 1963).

Data on diet composition of 53 ruminant species were compiled from the literature. A summary of the average browse and grass content of the diet is given in appendix 1.

Data on in vivo digestion by CS, IF and GR (feeds being mainly grass, browse or alfalfa) were collected from the literature (Foose 1982, Rees & Little 1980, Richmond et al 1977, Kowalczyk et al 1976, Ullrey et al 1971, Mould & Robbins 1982, Armstrong et al 1986, Kay & Goodall 1976, Poppi et al 1980, Drodz & Osiecki 1973, Uden & Van Soest 1982, Brown & Johnson 1985, Johson et al 1982, Milne et al 1987, Drodz 1979, Perzanovsky 1978, Antonio & Hajipanayiotou 1985, Wilson 1977, Dick & Urness 1991, Nastis & Malechechek 1981, Gihad et al 1980, Alam et al 1985, Staines 1969, Fennessey et al 1980, Doyle & Egan 1980, Van Wieren Chapter 5 and 6, Krausman et al 1988, Ullrey et al 1972, Huston et al 1986, Baker & Hobbs 1986, Baker & Hansen 1985, Hanley et al 1992, Dominigue et al 1991).

Digestion values were found for six concentrate selectors: Giraffe (*Giraffa camelopardus*), white-tailed, black-tailed and mule deer (*Odocoileus sp.*), moose (*Alces alces*), roe deer (*Capreolus capreolus*); five intermediate feeders: red deer or elk (*Cervus elaphus*), barasingha (*Cervus duvauceli*), gemsbok (*Oryx gazella*), eland (*Taurotragus oryx*), domestic goat; nine grass and roughage feeders: african buffalo (*Syncerus caffer*), gaur (*Bos gaurus*), bison (*Bison bison*), wisent (*Bison bonasus*), waterbuck (*Kobus ellipsiprymnus*), nilgai (*Boselaphus tragocamelus*), domestic cattle, domestic sheep, bighorn sheep (*Ovis canadensis*).

Class comparisons were performed on arcsin tranformed data when data were percentages. Analysis of variance was carried out with the GLM procedure of the statistical programme SAS (SAS inc. 1989). Differences between means were examined with the Tukey test. When an allelometric relationship was expected (taking the form $Y=aX^b$) the data were transformed using natural logarithms. Class differences in slope and intercepts were tested using analysis of covariance. As fibre digestion is related to lignin content of fibre (Robbins et al 1995, Van Soest 1982), the differences between digestion of CS, IF and GR was examined using analysis of covariance by comparing slopes and intercepts of regression of lignin content of NDF against the natural logarithm of NDF digestibility for data from CS, IF and GR.

The grass-browse distiction

With the exception of the winter period, grasses contain much more cell wall constituents than browse species (table 8.1). On average the lignin content of the browse samples was much higher than in the grass samples (table 8.1). It is well known that lignin has a depressing effect on digestibility (fig 8.2, Van Soest 1982). When lignin content exceeds the 10% level, digestibility drops to very low values. This depressing effect of lignin on digestibility is partly responsible for the on average much lower digestibility of browse (table 8.1).

That selective ability is important when exploiting browse, becomes apparent when the rate of change in quality with increasing bite size is considered (table 8.2, figure 8.3).

Table 8.1. Chemical composition of browse and grass samples. For species list see text. * = means differ significantly at $P<0.05$.

	n	NDF % DM	Lignin % DM	Dry matter digestibility	Lignin in NDF (%)
Spring					
grass	12	58.2^*	5.0^*	76.5^*	8.6^*
browse	29	39.8	13.2	58.2	33.2
Summer					
grass	12	68.5^*	6.7^*	59.4^*	9.8^*
browse	27	40.0	11.3	48.2	28.2
Autumn					
grass	11	65.3^*	5.7^*	57.0^*	8.7^*
browse	25	54.2	14.9	32.3	27.5
Winter					
grass	11	57.1	6.3^*	65.6^*	11.0^*
browse	23	56.2	17.6	38.7	31.3

In grasses quality remains relatively high over a large range of bite sizes (table 8.2) but in browse species this is different. Here abrupt changes between different plant parts (leaves vs twigs) with a corresponding large change in digestibility are apparent. As leaves are frequently small and of higher digestibility than twigs there is a quick drop in

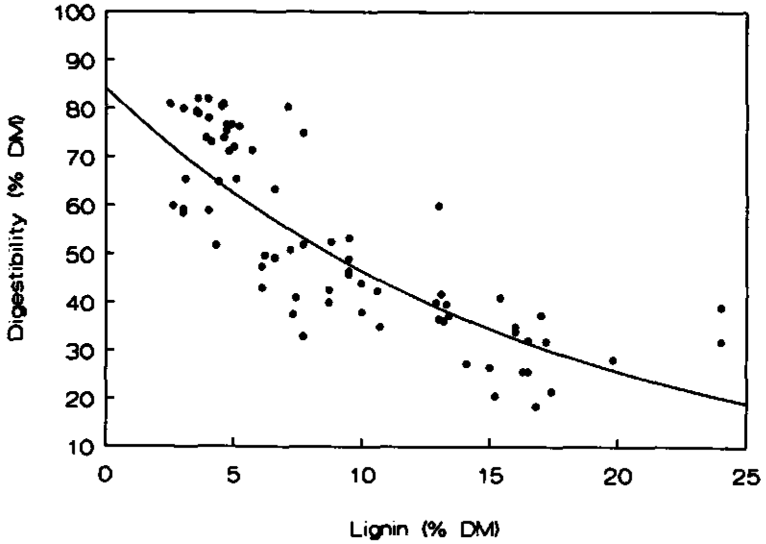

Fig 8.2. The relationship between lignin content (x) and digestibility (y) in browse and grass. $Y=84.06e^{-0.06x}$, $r^2=0.67$, $n=73$.

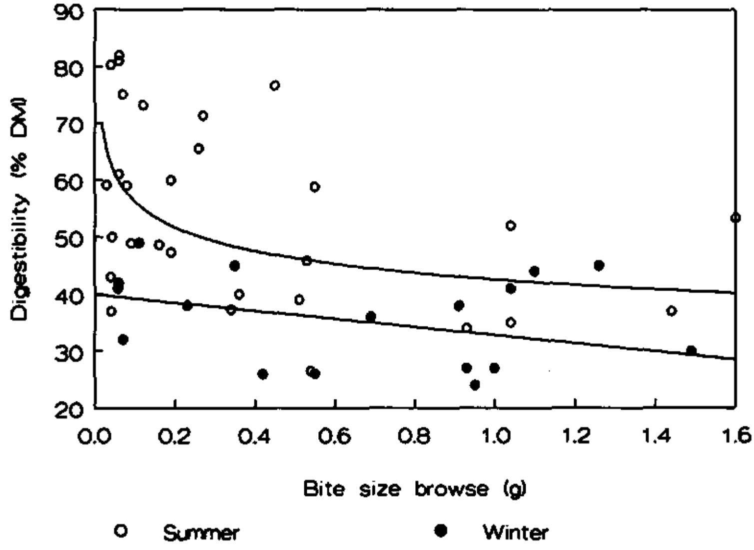

Fig 8.3. The relationship between browse bite size and digestibility.
Regression summer: Dig. = $42.57(\text{bite size})^{-0.12}$; $r^2=0.51$.
Regression winter: Dig. = $-7.12(\text{bite size})+39.94$; $r^2=0.48$.

Table 8.2. In vitro digestibility (%DM) of simulated bites from two bite size classes of grass and browse species (summer values).

	simulated bite size leaves <0.1 g	 leaves/twigs 0.1-0.5 g
Browse species		
Betula pendula	59.1	36.9
Frangula alnus	81.0	55.1
Quercus robur	70.5	51.2
Sorbus aucuparia	73.1	53.6
Grass species		
Deschampsia flexuosa	78.2	66.0
Holcus lanatus	77.5	69.2

quality when twigs are included in the bite (Hjeljord et al 1982). Hence, in the growing season, high quality browse is mainly to be found in small bites (figure 8.3).

These data confirm the prediction that browse species contain more cell solubles and have lower digestibilities than grass species. Furthermore browsers need to be selective in order to exploit browse optimally. Both specific adaptations and small body size thus facilitate browse usage.

Hofmann's classification

About 60 species of ruminants have been investigated morphologically and classified by Hofmann to date (Figure 8.1, Hofmann 1988). In all three classes both small and large species are present. When the species are grouped in distict BW classes (figure 8.4) it appears that most CS are of small BW, most GR are in the larger size classes while IF are intermediate. The anatomical and morphological investigations comprise a great many characteristics. In his principal work The Ruminant Stomach (Hofmann 1973) quantitive data on 25 characteristics related to internal stomach structure can be found for 26 African ruiminants. Five of these characteristics, that posed no problems of scaling with BW or were known to scale linearly with BW, were suitable for analysing class comparisons and BW relationships. These were: capacity of the reticulo-rumen, capacity of the omasum-abomasum, capacity ratio of the reticulo-rumen:omasum-abomasum, the papillae density in the ventral rumen wall, and the maximum

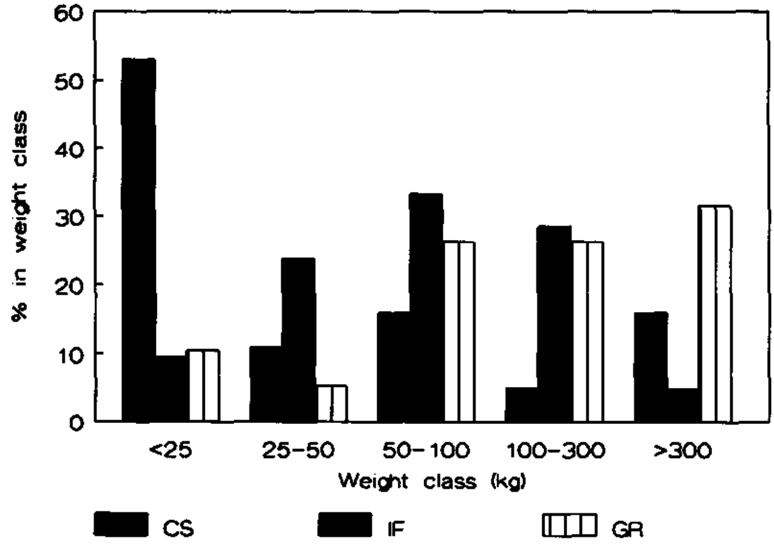

Fig 8.4. The distribution of the body weights of 25 ruminants belonging to CS, IF or GR over various weight classes. (Data: Hofmann 1973).

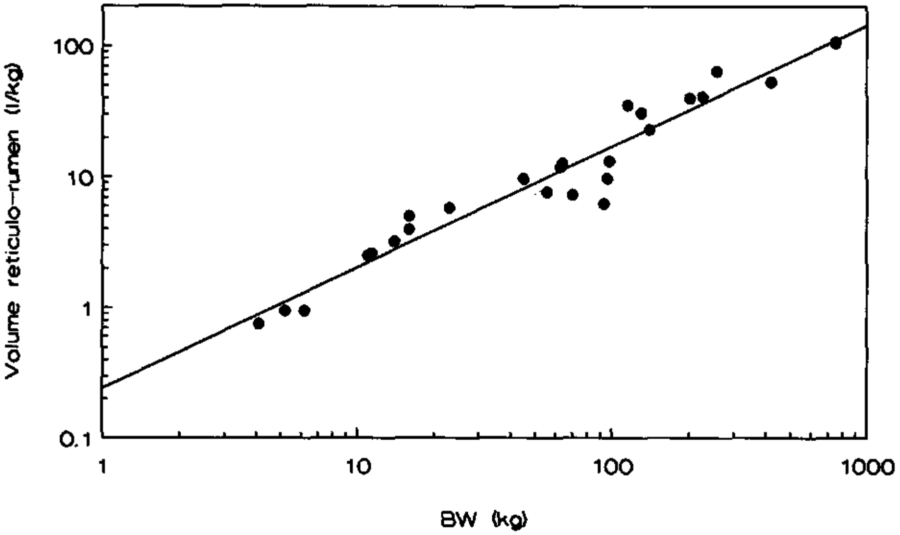

Fig 8.5. The relationship between the capacity of the reticulo-rumen (l/kg) and BW of 25 species of ruminants investigated by Hofmann (1973).

surface enlargement factor (SEF). Three of these factors are considered important and it was concluded that class differences were unidirectional: GR had larger reticulorumens than CS; the capacity of the abomasum was much larger in GR, and the surface enlargement factor was much larger in CS when compared to GR (Hofmann 1973). As Hofmann did not perform statistical analysis on his data both class differences and BW relationships of the mentioned characteristics were analysed here.

Class differences

For only one of the characteristics investigated significant differences between two classes were detected (table 8.3). The papillae density of CS differed from that of GR but not from IF. (NB. If, however, the very small CS (< 10 kg) Guenther's dik-dik, Kirk's dik-dik and the suni were excluded from the analysis the differences were not significant anymore). Except for pappillae density, class means for all other characteristics are surprisingly similar. The present analysis therefore does not warrant earlier conclusions made with respect to the stomach characteristics investigated here (Hofmann 1973).

Table 8.3. Means of 5 characteristics associated with inner gut structure in CS, IF and GR. (Source: Hofmann 1973, table 8.2). Class means with different superscripts differ significantly ($P<0.05$). (s.d.)

	n	CS	IF	GR
Volume reticulo-rumen (l/kg)	25	0.183 (0.08)	0.199 (0.05)	0.190 (0.07)
Volume omasum-abomasum (l/kg)	25	0.020 (0.01)	0.018 (0.01)	0.019 (0.01)
ret-rum:oma-abom	25	0.11 (0.03)	0.09 (0.02)	0.10 (0.01)
density rumen pap. (no/cm^2)	25	59.5^{a} (24.0)	46^{ab} (17.2)	34.2^{b} (13.8)
maximum surface enlargement factor	25	25.1 (8.8)	23.2 (9.3)	22.2 (9.3)

BW relationships

The regression analysis of five characteristics related to gut structure is given in table 8.4 while the relationship of the capacity of the reticulo-rumen with BW is also given in figure 8.5. The capacity of the rumen-reticulum and that of the omasum-abomasum were highly related to body weight. Pappillae density and surface enlargement factor showed a weaker correlation while no relationship between the ratio of the reticulo-rumen:omasum-abomasum and body weight was detected.

When comparing the class difference-approach with the BW-approach it must be concluded that the BW-approach explains the variation in the investigated characteristics much better than the class difference-approach.

Table 8.4. Regression analysis of five characteristics related to internal stomach structure. Data from Hofmann (1973). The regressor variable was body weight.
The regression took the form logY=a*logBW+b.

Response variable (Y)	Intercept (b)	Slope (a)	r^2	n	P
Vol. Ret-Rum	-1.421	0.925	0.94	25	$P<0.001$
Vol. Oma-Abom	-3.882	0.970	0.94	25	$P<0.001$
Ret-Rum:Oma-Abom	-	-	0.12	25	n.s.
Pap. density	4.572	-0.206	0.37	25	$P<0.001$
Surf. enl. factor	2.396	0.161	0.39	25	$P<0.001$

Diet choice

Based on adaptations related to the ability for selective feeding and gut morphology, and on the qualitive differences between grass forage and browse forage, it can be expected that CS are more browsers and GR are more grazers. Data on diet composition from most species indicated in figure 8.1 could be found in the literature (see appendix 1). The analyses were generally performed on the grass component because this was a more consistent category in the data set than the dicot part of the diet. Of the dicot part only the browse component is given.

Class differences

The average grass and browse content of the three classes differed significantly from each other (table 8.5).

Table 8.5. Average percentage grass and browse in the diet of CS, IF and GR. Means with different superscrips differ significantly ($P<0.01$). (For species data see appendix 1).

	n	% grass	(sd)	% browse	(sd)
CS	14	8.6^a	(3.3)	74.9^a	(11.8)
IF	19	50.1^b	(19.4)	35.8^b	(17.5)
GR	19	74.8^c	(10.7)	16.3^c	(10.5)

CS had much less grass in the diet than GR while IF were intermediate. In figure 8.1 Hofmann gave all the investigated species a place on the X-axis ranging from extreme CS on the left to extreem GR on the right. When the species are thus ranked (the middle of each 'species-line' was taken as reference point) and plotted against the average % grass in the diet (figure 8.6), the trend, again, is clear.

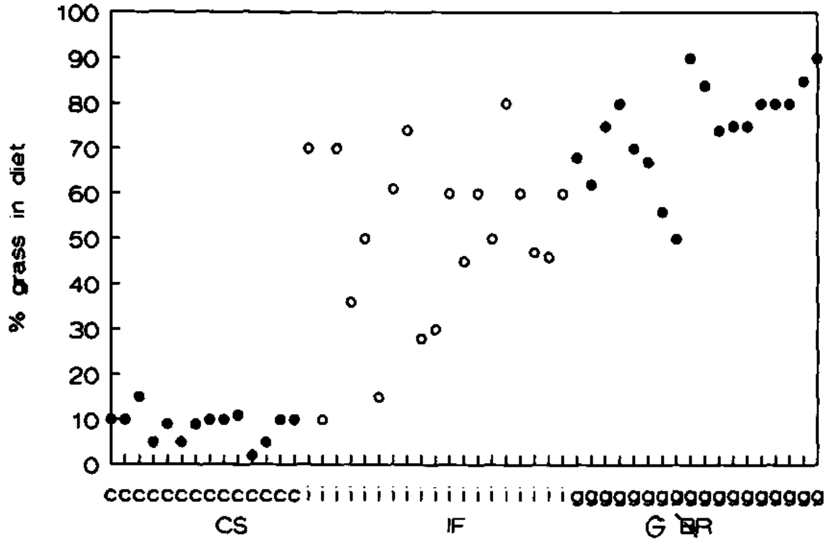

Fig 8.6. The average percentage grass in the diet of 51 species of ruminants belonging to different feeding styles. The species are ranked on the X-axis according to the more extreme CS being positioned on the left and the more extreme GR on the right as based on the classification of Hofmann (compare figure 8.1).

Figure 8.6 and the results in table 8.5 indicate that CS are obligate non-grass eaters while IF show most variation.

BW relationships

No relationship was found between the % grass in the diet and BW. Also when the regression analysis was performed on the classes separately neither class revealed a significant relationship (figure 8.7). The solid lines represent the fitted linear regression line.

In conclusion the results of the diet analyses show distinct differences in diet composition between classes and no relationship between diet choice and BW.

Digestive capacity

The described anatomical adaptations of the gut (Hofmann 1973, 1988, 1989) and the confirmed difference in diet choice (see above section) would implicate that GR are better adapted to a grass diet and hence would have higer capacity to digest cell walls than CS.

Class differences

Significant differences were detected between the digestive efficiencies of GR, IF and CS (figure 8.8, table 8.6).

Table 8.6. Comparison of slopes and intercepts of digestion curves of GR, IF and CS (figure 8.8)

comparison	n	slope	intercepts
GR-CS	105	$P<0.001$	$P<0.001$
IF-CS	83	$P<0.001$	$P<0.05$
GR-IF	128	n.s.	$P<0.01$

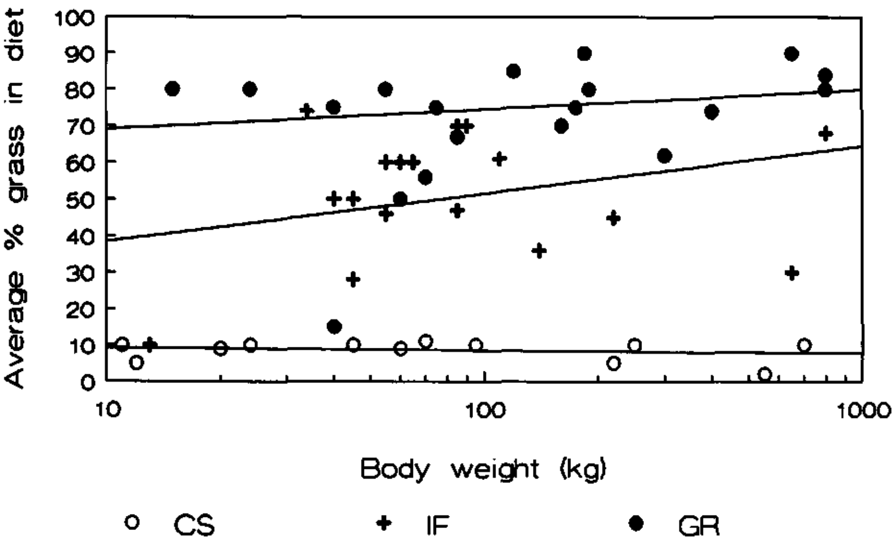

Fig 8.7. The relationship between the average percentage grass in the diet and BW of CS, IF and GR.

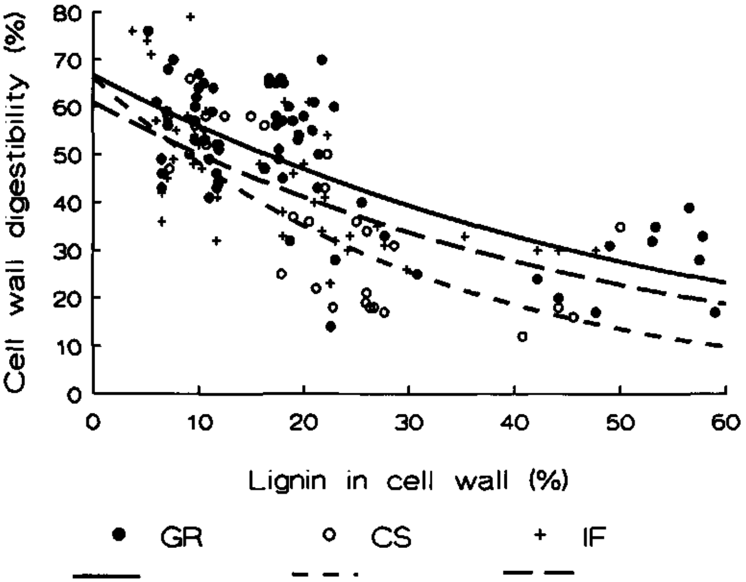

Fig 8.8. Relationship between cell wall digestibility and lignin in cell wall in CS, IF and GR.
Regression CS: $Y=66.3e^{-0.032X}$; $r^2=0.52$; $n=29$
Regression GR: $Y=66.7e^{-0.018X}$; $r^2=0.42$; $n=74$
Regression IF: $Y=60.9e^{-0.020X}$; $r^2=0.43$; $n=52$

Grass and roughage feeders were more efficient cell wall digesters than both intermediate feeders and concentrate selectors, while intermediate feeders were more efficient than concentrate selectors.

Although the general relationship between the lignin content of the cell wall and cell wall digestibility is quite good (Van Soest 1982), permitting the above method of comparing digestive efficiencies, the many data points represent a wide variety of feeds tested. Therefore only those digestion trials were selected where direct comparisons were made between species belonging to different feeding types. The results of these 'inter-feedingtype' comparisons are given in figure 8.9.

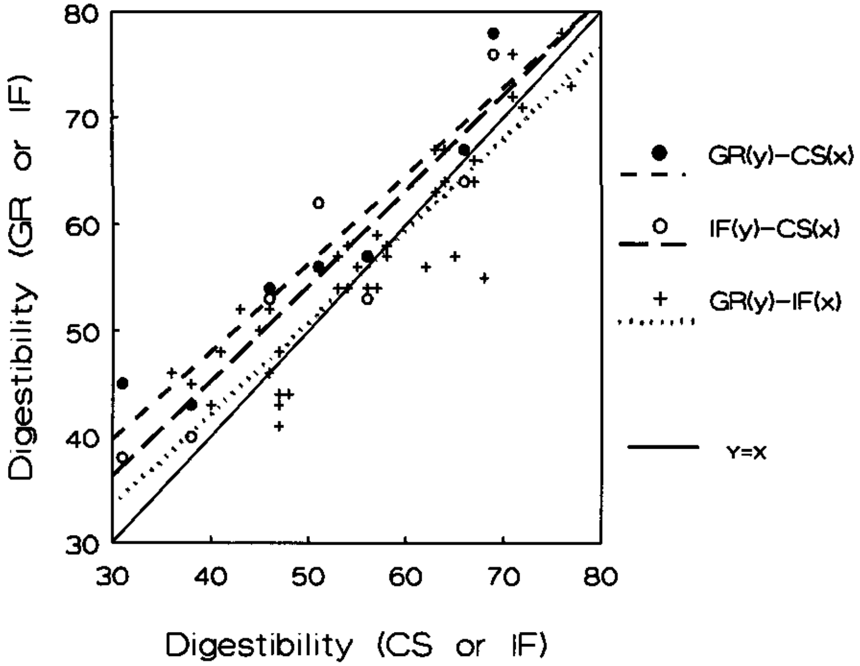

Fig 8.9. Results of direct comparisons with the same feeds of the in vivo digestion (DM) of GR(y) compared to CS(x), IF(y) compared to CS(x), and GR(y) compared to IF(x).
Dig GR=0.83(±0.127)Dig CS + 15.0(±6.66) ; r^2=0.90 ; n=6
Dig IF=0.90(±0.162)Dig CS + 9.38(±8.50) ; r^2=0.86 ; n=6
Dig GR=0.86(±0.063)Dig IF + 7.64(±3.54) ; r^2=0.82 ; n=42

The differences between GR and CS were greater than the differences between IF and CS while GR had higher digestive capacity than IF at lower digestibility while IF were slightly better at high digestibilities. There is a tendency that the differences between feeding types become smaller at higher digestibilities. The results of the direct comparisons are similar to those analysed above.

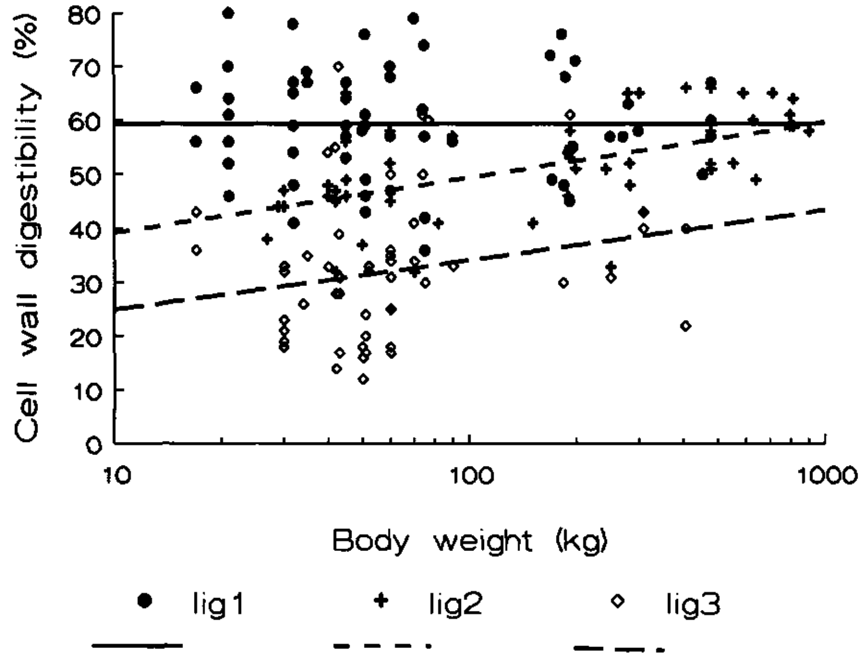

Fig 8.10. Relationship between cell wall digestibility and body weight in ruminants in three dietary quality classes (see text for further explanation). The fitted lines are only illustrative and do not indicate significance.

BW relationships

A possible effect of BW on cell wall digestibility was analysed by regressing cell wall digestibility on the natural logarithm of BW. No overall relationship was found between cell wall digestibility and BW. Because of the large variation in the chemical composition in the feeds tested, possible relationships within certain quality classes easily can be masked in the general relationship. Therefore the analysis was also performed on the three following quality classes:

lig1: % lignin in NDF < =10%; lig2: 10< % lignin in NDF < =20; lig3: % lignin in NDF > 20 (figure 8.10).

For both the highest (lig1) and the lowest (lig3) quality class no relationship between cell wall digestion and BW was found (r^2=0 and r^2=0.05 resp.). In the intermediate quality class a weak positive relationship was found (r^2=0.32).

Discussion

Grass and browse species differed in cell wall content and digestibility, a finding also reported by Demment & Van Soest (1985) and White & Trudell (1980). Furthermore it is clear that a high ability for selective feeding facilitates an efficient exploitation of browse. The results implicate that diet differences can be used to distinguish between ruminant feeding types.

The various tests that have been performed so far with regard to Hofmann's 'class hypothesis' vs the 'body weight-relationship hypothesis' are summarized in table 8.7. The overview suggests that more variables are explained by body weight than by class differences, although important class differences do exist.

Table 8.7. Summary of variables tested to date with regard to the Hofmann hypothesis and the body weight hypothesis.

Variable	Class diff.	BW	Ref.
Diet composition	Yes	No	This study
Fibre digestion	No	Yes	Robbins et al 1995
	Yes	No	This study
Parotid sal. gl. wght	Yes	Yes	Robbins et al 1995
Rumen ferm. rate	No	Yes	Gordon & Illius 1994
Hindgut ferm. rate	No	No	Gordon & Illius 1994
VFA production	No	Yes	Gordon & Illius 1994
Retention time	No	Yes	Gordon & Illius 1994
Liquid rumen flow rate	No	Yes	Robbins et al 1995
Cap. ret.-rumen	No	Yes	This study
Cap. omasum-abomasum	No	Yes	This study
Cap. ratio RR:OA	No	No	This study
Papillae density	Yes,partly	Yes	This study
Max. surface enlargem.	No	Yes	This study

Diet composition strongly favoured the class hypothesis while no body weight relationships were found. Given the already discussed qualitative differences between grass and browse it can be expected that also class differences in various variables related to digestive physiology will be found. The reported data on fibre digestion are conflicting but Robbins et al (1995) did use a much smaller data set (especially the grass and roughage feeders are under represented) than in the present study. Detecting class differences in fibre digestion in a large data base is even more difficult because of the large variation in the forages used and other sources of variation related to the carrying out of feeding trials. Furthermore the data set used in this study included the data used by Robbins et al (1995). A re-evaluation of the fibre digestion data points towards expected class differences in the capacity to digest cell walls, while no body weight relationship with fibre digestion was found. Variation in parotid salivary gland weight is both explained by feeding type and body weight. These findings have been adequately discussed by Robbins et al (1995).

The other variables in table 8.7 do not seem to be related to feeding style while most of them do bear a relationship with body weight.

The most remarkable finding of this study was that a number of variables that have been used by Hofmann (1973) to base his classification on did not reveal any class difference after statistical analysis while four of them were related to BW. As only 5 variables could be tested here while Hofmann based his classification on the analysis on many more variables, a rejection of his hypothesis based on gut-morphology is not realistic at the moment. As stated before, Hofmann has actually only classified ruminants and one can not speak of a clear hypothesis. A more proper approach to the adaptive syndromes as distinguished by Hofmann therefore would be to analyse many variables simultaneously in a principal component analysis. In this way possible classes can be revealed with a less descriptive and technically more justified method.

A number of reasons can be given to explain the conflicting results. First, there is agreement that for many variables only limited data were available (Gordon & Illius 1994, Robbins et al 1995). Second, many of the variables tested (rumen fermentation rate, hindgut fermentation rate, VFA production, retention time, capacity of the reticulo-rumen) are most likely to vary more with the type and quality of the diet consumed than with fixed animal species characteristics. Therefore care has to be taken in generalizing and extrapolating results from feeding trials. The most important explanation, however, lies in the interaction between the effects of class and BW. Although all three feeding type classes contain both small and large species it is clear that the majority of CS are small animals and the majority of GR are large while most IF are of intermediate BW (figure 8.4). This means that many parallels can be expected and that only parameters that bear no relationship with BW but that do show differences between classes are clear indicators for the existence of distinct feeding types. The only variables that meet these criteria are diet composition and fibre digestion. For those variables that are related to BW it is much more difficult to reveal any potential class difference, and many more data are then needed to discriminate between class effects and BW effects.

In conclusion the Hofmann classification still holds for diet composition and fibre digestion while for the other variables tested no class difference was found or the tests are (yet) inconclusive. As diet composition and fibre digestion both are affected by many animal character traits, at least three adaptive syndromes can be distinguished, this indicates that in 'exploiting' the green world natural selection has favoured an unique adaptive radiation within ruminants, each occupying a specific niche but all equally well adapted.

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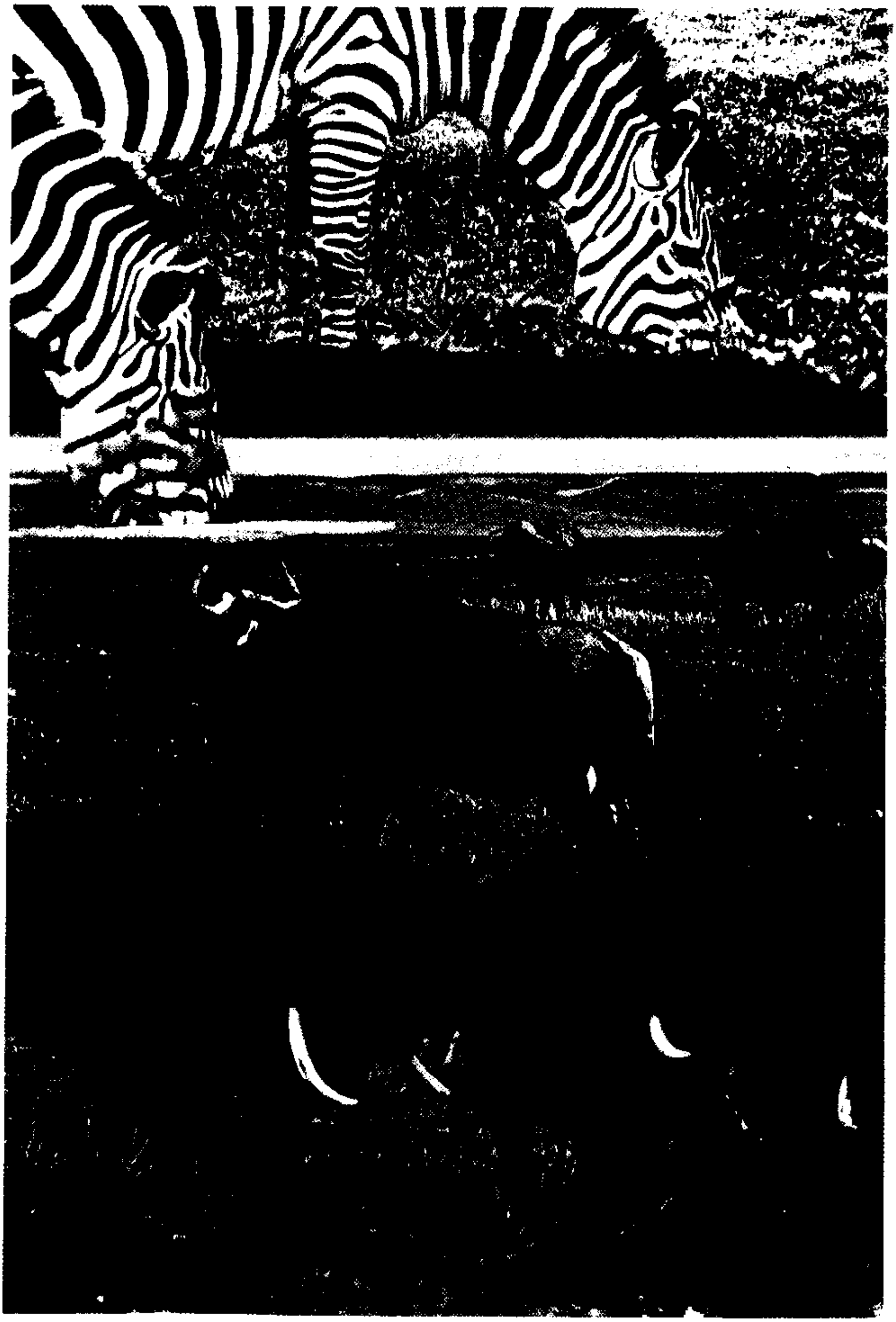
Appendix 1. Body weight and average grass and browse content of the diet of the studied ruminants.

Species		Weight (kg)	%Grass	%Browse	Ref.
Moschus moschiferus	musk deer	11	10	50	19
Muntiacus muntjak	muntjac	24	10	70	19
Dama dama	fallow deer	55	46	36	17
Axis axis	axis deer	85	70	20	19
Cervus unicolor	sambar	220	45	45	19
Cervus timorensis	rusa	65	60	25	19
Cervus duvauceli	barasingha	190	80	15	19
Cervus nippon	sika deer	45	50	40	17,13
Cervus elaphus	red deer	85	47	44	2,3,6,7,1
Cervus elaphus	wapiti	250	64	18	9,10,16,2
Capreolus capreolus	roe deer	20	9	73	2,5,11
Odocoileus virginianus	white-tailed	60	9	64	1,3,9
Odocoileus hemionus	mule deer	70	11	57	3
Alces alces	moose	550	2	90	3,5,18
Rangifer tarandus	caribou	140	36	37	3,8,23,29
Giraffa camelopardalis	giraffe	700	10	80	3,21
Antilocapra americana	pronghorn	40	15	44	3
Sylvicapra grimmia	greyduiker	12	5	85	21
Oreotragus oreotragus	klipspringer	12	5	90	21
Raphicerus campestris	steenbok	13	10	70	21
Ourebia ourebia	oribi	15	80	10	21
Tragelaphus strepsiceros	greater kudu	220	5	80	3,21
Tragelaphus imberbis	lesser kudu	95	10	80	3,21
Tragelaphus scriptus	bushbuck	45	10	70	21
Taurotragus euryceros	bongo	250	10	80	21
Taurotragus oryx	eland	650	30	60	3,21
Bubalus bubalus	water buffalo	800	80	10	19
Syncerus caffer	african buffalo	650	90	5	3,21,31
Bos taurus	ox	400	74	14	3,17,22,2
Bison bison	bison	800	84	11	3,24,27
Bison bonasus	wisent	800	68	13	3
Alcelaphus buselaphus	hartebeest	175	75	20	3,21
Damaliscus lunatus	topi	120	85	10	3,21
Connochaetes taurinus	wildebeest	185	90	5	3,21
Oryx gazella	oryx	160	70	20	21
Kobus ellipsiprymnus	waterbuck	190	80	10	3
Kobus kob	kob	75	75	15	21
Redunca redunca	bohor reedbuck	55	80	10	21
Gazella granti	Grant's gazelle	40	50	50	3,21
Redunca fulvorufula	mountain reedbuck	24	80	10	21
Antilope cervicapra	black buck	40	75	20	21
Litocranius walleri	gerenuk	40	15	80	21
Aepyceros melampus	impala	55	60	40	3,21
Capricornis sumatraensis	serow	90	70	20	20
Rupicapra rupicapra	chamois	34	74	8	30
Oreamnos americanus	mountain goat	110	61	10	3
Capra ibex	ibex	60	60	40	20
Capra hircus	domestic goat	45	28	58	3,4,22
Ovis canadensis	bighorn	85	67	20	3,14
Ovis dalli	dall sheep	70	56	22	3
Ovis aries	domestic sheep	60	50	23	3,4,7,22
Ovibos moschatus	muskox	300	62	26	3,12,25

1:Blair & Brunett 1980; 2:Borowski & Kossak 1975; 3:Breymeyer & Van Dyne 1980; 4:Bullock 1985; 5:Cederlund et al 1980; 6:Collins et al 1978; 7:Colquhoun 1971; 8:Helle 1981; 9:Hobbs et al 1983; 10:Hobbs et al 1981; 11:Jackson 1980; 12:Klein & Bay 1990; 13:Mann 1983; 14:Miller & Gaud 1989; 15:Mitchell et al 197

16:Nelson 1982; 17:Putman 1986; 18:Risenhoover 1989; 19:Schaller 1967; 20:Schal
21:Skinner & Smithers 1990; 22:Squires 1982; 23:Staaland & Punsvik 1980;
24:Telfer & Cairns 1980; 25:Thing 1984; 26:Van de Veen 1979; 27:Waggoner & Hink
28:Wallis de Vries 1994; 29:Wright 1980; 30:Perle & Hamr 1985; 31:Prins 1996.



CHAPTER 9

UNGULATES: TRENDS IN EVOLUTION, DISTRIBUTION AND COMMUNITY STRUCTURE

CHAPTER 9

Introduction

In this chapter various aspects of ungulate ecology are explored. As mammals, ungulates are a highly diverse group and so they have been since mid-Tertiary times. During a long epoch major changes have taken place. One of the most striking is the steady increase of the number of species of ruminants relative to that of the non ruminants. Below some mechanisms are discussed that may have influenced the outcome of this process.

Although a diverse group, ungulates are not evenly distributed over the face of the earth. Distribution patterns are highly skewed towards the tropics, and the possible reasons for this and other aspects of ungulate distribution are discussed.

Locally ungulate communities can be very rich in species. This poses important questions as to how so many species manage to live together. How different are they and what is the smallest amount of difference needed for co-existence to take place?

Evolutionary trends

Although the first mammals already appeared in Triassic times (Colbert & Morales 1994) the first major radiation took place at the beginning of the Cenozoic after the great reptiles died out at the close of the Cretaceous period. Except for the Proboscidea, elephants and their relatives, all other hoofed mammals are thought to have originated from a primitive group of hoofed mammals, the Condylarths. From the earliest ungulates, Protogulatum (late Cretaceous) to the present day Bison the history of the ungulates is marked by a coming and going of a large number of families, genera and species. Neverteless two general phases of development can be distinguished. An early phase during Paleocene and Eocene times, when primitive ungulates in great variety spread over the earth. These ancient ungulates began to decline during Eocene times. At the same time the modern ungulates were arising to evolve in ever increasing diversity and complexity from about the beginning of the Eocene epoch to present times.

The extant species of ungulates are not evenly distributed across the various orders, suborders and families (table 9.1; the Sirenidae (sea cows) and the Hyracoidae (hyraxes) are not included in the analyses). By far the most of the 176 species recognized are found in the family of the bovids, within the suborder of the ruminants. Also the deer family (Cervidae) is a large group of species. Although a number of families now contain only a few species, this has not always been the case. Originating sometime during early and middle Eocene times, the Proboscideans flowered during the mid and late Cenozoic to produce a great diversity of large giants that spread all over the world. One group, the Mastodonts, believed to be ancestral to the elephants, thrived in the

Pleistocene on most continents. Various species of mammoths lived until the very end of the Pleistocene epoch. Then they became extinct and only two species survived into modern times.

Table 9.1. Classification of extant ungulates.

Order	Suborder	Family	N Species
Proboscidea	Euelephantoidea	Elephantidae	2
Perissodactyla	Hippomorpha	Equidae	6
	Ceratomorpha	Tapiridae	4
		Rhinocerotidae	5
Artiodactyla	Suina	Suidae	10
		Dicotylidae	2
		Hippopotamidae	2
	Tylopoda	Camelidae	4
	Ruminantia	Tragulidae	4
		Giraffidae	2
		Cervidae	32
		Bovidae	103

Although it has been suggested that man has caused or enhanced mammoth extinction in the Ice Age (Martin & Klein 1984) the proboscideans as a group were already declining and the modern elephants are actually the last representatives of a group probably on its way to extinction within the next few thousand years (Colbert & Morales 1994).

From an ancestral form Hyracotherium (Eohippus from the Eocene), the perissodactyls developed along various paths of adaptive radiation, reaching the height of their evolution in middle Tertiary times when they were the dominant ungulates in the world. The evolution and radiation of the horses into a bewildering array of species and genera during the Oligocene and Miocene epoch is especially well known. But also the rhinoceroses were numerous in the Tertiary and according to Prothero & Schoch (1989) the rhinos were the largest and ecologically most diverse group of perissodactyls in the Miocene. The modern tapirs are in some respects the most primitive of the living perissodactyls (Norman 1994). They have retained the four toes on the front feet and the three toes on the hind feet, so characteristic of early Eocene members of the order. Tapirs were prominent in the Ice Age faunas of North America and Eurasia but disappeared there at the end of the Pleistocene but survived in the tropics. The perissodactyls are already in the decline for several million years, and now must be regarded as an order of mammals that, in spite of the high specialization among some of its members, is on its way to extinction (Colbert & Morales 1994). Slowly but steadily these hoofed mammals gave way to the dominant ungulates of present times, the artiodactyls.

Although the first artiodactyls, like the first perissodactyls, appear in the early Eocene, they do not radiate as a group before middle and late Cenozoic times. Compared to the other suborders the members of the Suina (pigs, peccaries and hippos) share generally more primitive characters (Colbert & Morales 1994). The pigs and peccaries originate in early Oligocene age and branched along numerous lines of adaptive radiation as they evolved through the middle and late Cenozoic. A number of lines died out during the Pleistocene epoch. Hippopotamuses do not appear in the fossil record until late Miocene times. During the Pleistocene they were widespread throughout Eurasia and Africa while now they are much restricted in their distribution.

The first tylopods (camels and llamas) appear in late Eocene times in North America. A number of lines evolved through the Cenozoic with varying degree of developmental progress. The presentday llamas represent camels in essentially a Miocene stage of evolution, and the large camels represent the culminating phase of the central camelid line of development (Colbert & Morales 1994). At the end of the Tertiary several camelid branches died out.

The last groups of artiodactyls to discuss belong to the suborder Ruminantia. The tragulids are very small primitive ruminants and resemble in many ways what a ruminant ancestor could have been like. They date back to Eocene times but were common in the Oligocene fauna. The remaining three families of artiodactyls (deer, giraffes and bovids) are true ruminants. The giraffes and the deer are closely related while the bovids are the most advanced and the dominant group of ungulates at present.

The success of the ruminants

The present dominance of bovids and cervids within the group of ungulates has been ascribed to their superior digestive system of pregastric fermentation combined with the rumination mechanism. The complex stomach of pregastric fermenters makes longer retention of the food possible with the result that the food can be more thoroughly digested. Therefore they are more efficient and require less food than species without a complex stomach (Van Soest 1994). Another important advantage of pregastric fermentation is a relaxation of the requirements for B vitamins and amino acids. Also secondary compounds can be detoxified in the forestomach and it might well be that this is one of the priciple advantages for the evolution of a more complex stomach (Van Soest 1994). A disadvantage of pregastric fermentation is the need for a certain minimal energetic quality of the food because otherwise a prolonged retention time can become a serious limiting factor. Chewing the cud increases the efficiency of the digestive process and it has the additional advantage that less time has to be spend foraging.

Are nonruminants indeed less efficient? Very few comparative studies have been carried out between ruminants and nonruminants and little is known of the digestive capacities of the tapirs, rhinos, hippos and camelids. Elephants have a low digestive capacity (Hackenberger 1987, in Van Soest 1994) but their efficiency has to be related to body size as large bodies do not have to be as efficient as small bodies. Most comparisons within similar weight classes have been made between equids and bovids (notably cattle). In all studies equids had a lower digestive efficiency than the ruminants (Foose 1982, Duncan 1992, Chapter 5). Food intake was generally higher in equids especially with feeds of low digestibility (Duncan et al 1990, Duncan 1992, Chapter 5). The higher food intake is an important compensation mechanism for a lower digestive efficiency and it has been proposed that equids, by eating more, can more than compensate the low efficiency (Janis 1976, Duncan et al 1990, Duncan 1992). Although in a number of comparative studies equids indeed had a higher digestible dry matter intake (Johnson et al 1982, Foose 1982), van Wieren (Chapter 5) found a lower digestible dry matter intake in equids when compared to cattle in feeding trials with four very different feeds. The matter thus is not settled in this respect but nevertheless we can speculate that the present dominance of the bovids and cervids in species richness is the result of competitive displacement, and that the displacement is strongly related to a more efficient system of food gathering and food processing. If competitive displacement has occurred, this more efficient system has ultimately resulted in higher net population growth rates of ruminant species. Although very little is known of actual population growth rates of most species we are able to compare ruminant and nonruminant species with respect to a few crucial life history traits: the age at sexual maturity and the potential number of young that can be produced per year.

Differences in life history traits

Net population growth rate (r) is influenced by many life history traits and all of them are highly variable depending on the ecological circomstances (Stearns 1995). Direct comparisons between ungulate species or fylogenetic groups with respect to population performance have never been carried out and also we have no information on what happened in the past. Nevertheless it would be important to be able to compare relevant life history traits of succesfull groups (the real ruminants, Ruminantia) with those of the apparently less succesfull groups (nonruminants). Data were collected of two life history traits that could be assessed such as to reveal species-specific values to make comparisons possible. These traits were: age at sexual maturity, and number of young produced per year. The values for both traits are supposed to be realistic when favourable ecological conditions prevail and growth rates at r_{max} (or close to r_{max}) are possible. A possible third life history trait, maximum life span, was not analyzed because most data are based on zoo-records that are not likely to be average species-specific estimates.

Both age at sexual maturity and number of young produced are principal life history traits (Stearns 1995), but age at sexual maturity has to be considered as one of the most important. According to Cole (1954) age at sexual maturity is a dominant variable in the evolution of rate of population increase, while Stearns (1995) notes that 'age at sexual maturity is pivotal, for fitness is often more sensitive to changes in this trait than to changes in any other'. That small differences in this trait between related species can have large consequences has been amply demonstrated by McCullough (1987) in a comparison between mule deer and white tailed deer. There are three advantages in maturing early (Stearns 1995):

1. A higher probability of survival to maturity because the juvenile period is shorter;
2. The offspring are born earlier;
3. An earlier start of reproducing.

The data on which the analyses are based are given in appendix 1.

Two groups of ungulates were compared. One group consisted of the recent and succesfull (real) ruminants (tragulids, giraffids, cervids and bovids), the other consisted of the nonruminants. In the latter group the suids are not included because their basic life history strategy is considered to be different from all other groups in their seeming to be more r selected species (with a relative large number of young per year and early maturation relative to size); the suids are presented separately.

As both traits scale allometrically with body size (Stearns 1995), taking the form $Y=aX^b$), the data were transformed using natural logarithms. Group differences in slope and intercepts were tested using analysis of covariance with 'group' as covariate (SAS 1995), the relationship taking the form: $\ln Y=a*\ln BW + b$.

As both groups are not equally well distributed across the whole body weight range and especially no nonruminants are found in the smaller body weight range, analyses were performed for three different size ranges: 2-4000 kg; 50-4000 kg; and 50-1000 kg. All comparisons yielded the same results, and only the comparisons of the 50-4000 kg range are presented in figure 9.1b and 9.2b. The fitted regressions for the various separate ungulate families (including the suids) are given in figure 9.1a and 9.2a.

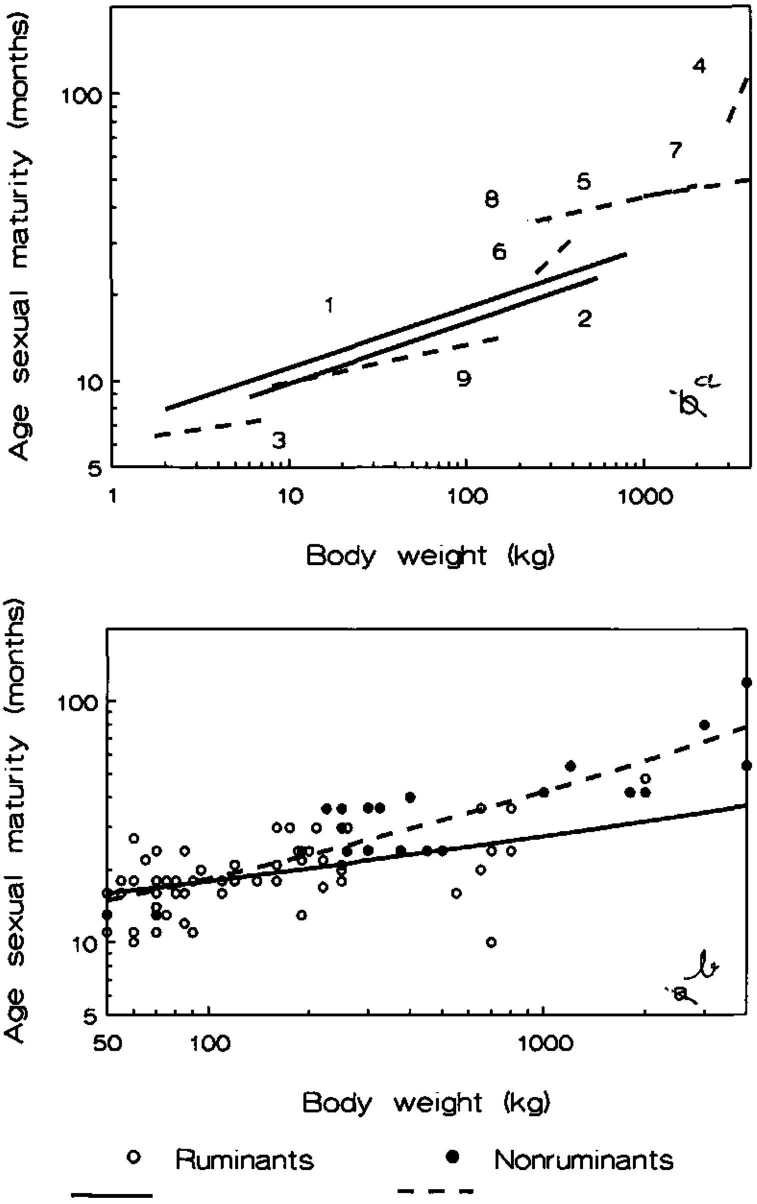


Figure 9.1. The relationship between age at sexual maturity and body weight in ungulates. a: ungulate families (1 = Bovidae, 2 = Cervidae, 3 = Tragulidae, 4 = Elephantidae, 5 = Hippopotamidae, 6 = Equidae, 7 = Rhinocerotidae, 8 = Tapiridae, 9 = Suidae); b: ruminants and nonruminants (suids excluded);

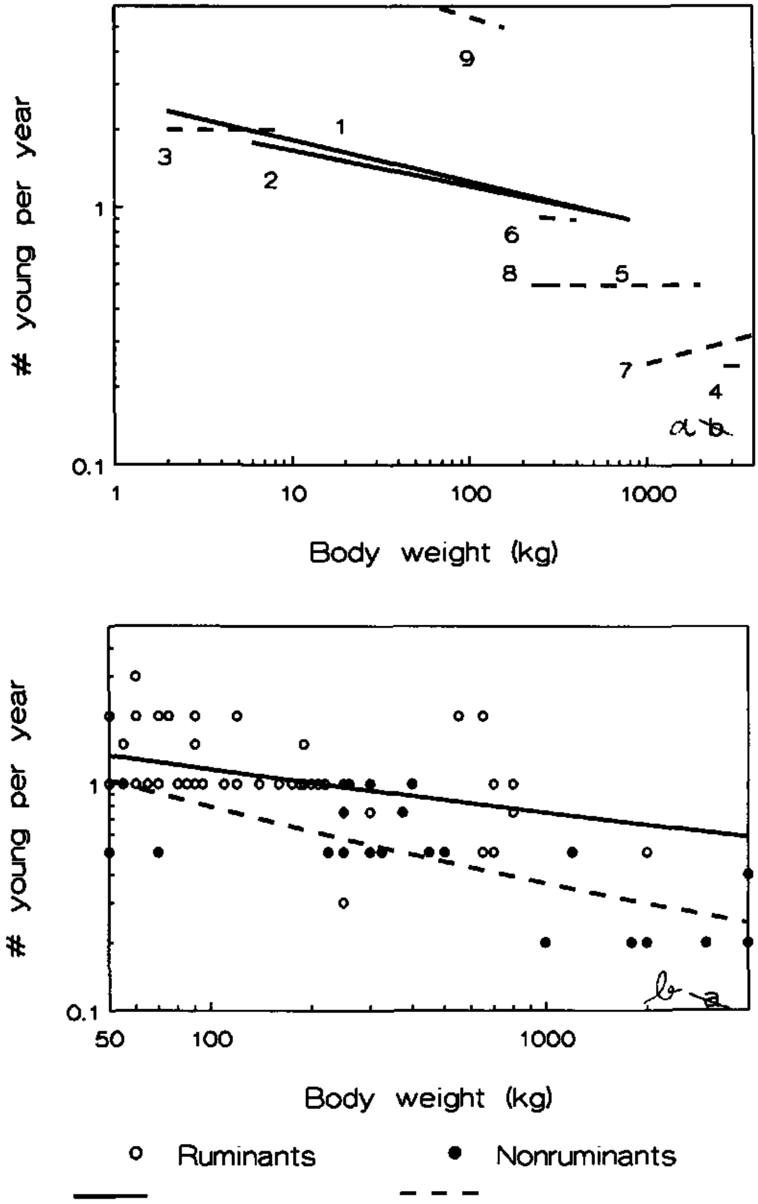


Figure 9.2. The relationship between maximum number of young produced per year and body weight in ungulates. a: ungulate families (1 = Bovidae, 2 = Cervidae, 3 = Tragulidae, 4 = Elephantidae, 5 = Hippopotamidae, 6 = Equidae, 7 = Rhinocerotidae, 8 = Tapiridae, 9 = Suidae); b:ruminants and nonruminants (suids excluded);

Age at sexual maturity differed significantly between the two groups (figure 9.1b), both in slope ($F=76.8$, $P<0.001$) and in elevation ($F=13.0$, $P<0.001$). On average ruminants mature earlier than nonruminants, the differences becoming pronounced in the larger body weight range. The results also confirm the general notion that age at sexual maturity increases with body weight. The regression equation for the ruminants is: ln'age'= 0.156lnBW + 2.182 ($r^2=0.25$, $P=0.001$, $n=71$), and for the nonruminants: ln'age'= 0.366lnBW + 1.243 ($r^2=0.74$, $P=0.001$, $n=22$).

The two groups differed significantly in the number of young that can be produced per year (figure 9.2b), both in slope ($F=90.0$, $P<0.001$) and elevation ($F=31.0$, $P<0.001$). Ruminants produce on average more young per year than nonruminants of similar body weight. The figures confirm the general pattern of a decrease in the number of young produced with increasing body weight.
The regression equation for the ruminants is:
ln'N young'= -0.167lnBW + 0.933 ($r^2=0.18$, $P=0.01$, $n=71$), and for nonruminants:
ln 'N young'= -0.391lnBW + 1.41 ($r^2=0.46$, $P=0.001$, $n=22$).

The results indicate that the modern ruminants have a potentially higher reproductive capacity than the nonruminants (excluding the suids). This would give them a clear competitive advantage if all other life history traits remaining equal. To what extent this is and was the case is not known. Nevertheless the found differences in these crucial life history traits could have played an important role in the replacement of the generally older nonruminant groups by the recent ruminant families. As has been discussed earlier it is tempting to attribute the likely difference in performance to differences in food processing efficiency of the two groups. Although this matter still has to be settled it need not be the only explanation. As the nonruminants generally are belonging to the older families it is also possible that the differences are related to phylogeny. Older forms might experience lineage-specific constraints through the fixation of form and function in the traits that characterize the lineage (Pagel & Harvey 1988, in Stearns 1995).

Distribution

Ungulates are not evenly distributed over the face of the earth. In figure 9.3 ungulate faunas of four continents are presented in the form of a cenogram, whereby species are ranked according increasing weight in a group. Most ungulate species are found in Africa (85) and only very few in both North America (11) and South America (16). Part of the explanation of this unequal distribution is the much more severe extinctions that ocurred in North America, South America and Europe during the Pleistocene

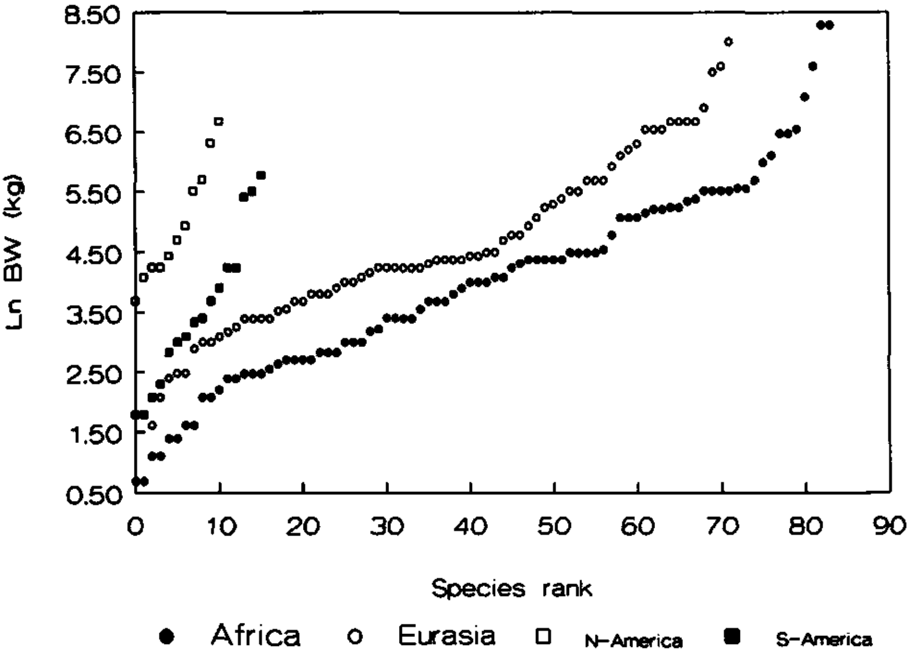


Figure 9.3. Relationship between body weight and species body weight rank, in ungulates from Africa, Eurasia, North-America (N-Am), and South-America (S-Am).

(Colbert & Morales 1994). The exact reasons for these selective extinctions are not yet known. The relative very high species richness in Africa is not a phenomenom of all times. In the past frequent movements occurred of groups between continents and much of the modern fauna of artiodactyls in Africa represent an influx from Europe and the Orient during late Pliocene and Pleistocene times (Colbert & Morales 1994). The species richness of Eurasia is mainly confounded to Southeast Asia while Europe has a species richness comparable to that of North America. In fact many species and genera from Europe an North America have a circumpolar distribution. In Europe and North America very large and very small ungulates are absent. In the large faunas of Africa and Eurasia the distribution is not completely regular (figure 9.3), the slope of the curve being steeper at both the small and the large body weight end. This pattern will be discussed in more detail below. In the larger size range a conspicuous difference between Africa and Eurasia is caused by the presence of a number of large bovids (banteng, yak, aurochs, gaur, kouprey, water buffalo, wisent) in the later continent.

Figure 9.4 reveals the distribution of ungulate species across the major climatic and habitat zones. By far the most species are found in the tropics, and fewest in cold environments (including high mountain areas). The group of ungulates is quite evenly distributed across major habitats (forest:60, ecotone:55, open habitat: 61 species). In the tropics more species are found in forests while in cold environments almost all species are from open areas. The latitudinal gradient is very well known: highest species richness in the tropics, deceasing towards the poles for most life forms (Rosenzweig 1995). Of the number of explanations given for this trend two are believed to be of great importance here: area and productivity. The positive relationship between area and species richness is well known (Rosenzweig 1995). Terborg (1973, in Rosenzweig 1995) calculated the area of the major latitudinal zones and found that the tropics covered more area (roughly double!) than any other zone. The very high diversity of ungulates in Eastern Africa partly reflects the large area of tropical grassland in that area. It is generally believed that diversity (for many taxa) is highest at intermediate

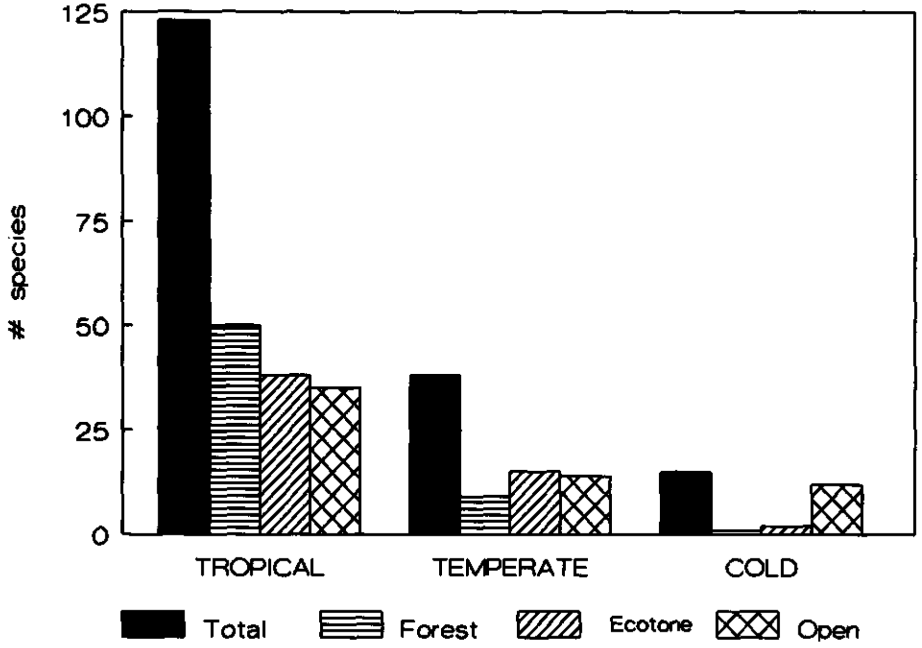


Figure 9.4. Frequency distribution of ungulates across major habitats in the tropics, temperate- and cold climates.

productivity levels (Begon et al 1995). This phenomenom has not really been explained and according to Rosenzweig (1995) the 'explanation remains murky'. To what extent this principle also operates in ungulate distribution is not clear. In areas with very high productivities, forests generally prevail and here we can expect fewer ungulate species in an assemblage because fewer food niches are expected to be available for ungulates. The high diversity of East Africa is undoubtfully related to very high productivity levels (vulcanism), combined in some areas (Serengeti) with natural 'treelessness'. We can really speak of parts of Eastern Africa as being hot-spots for ungulate diversity and biomass. The diversity of ungulates is very likely strongly related to a high plant diversity, providing a wide array of feeding niches, while plant diversity is related to habitat and resource heterogeneity.

The distribution of the major feeding styles across latitude and habitat is given in figure 9.5. Four feeding styles were distinguished. Omnivores and frugivores (very small ungulates (< 10 kg) are mainly frugivorous (Hofmann 1973)), browsers (who mainly consume leaves and twigs of dicots), grazers (mainly consumers of monocots), and intermediate feeders (who both graze and browse). The highest percentage of omnivores/frugivores is found in the tropics while in cold environments they are absent (figure 9.5a). In temperate environments intermediate feeders prevail while in cold environments half of the species are grazers. The differences between these distributions are difficult to explain except for the absence of omnivores/frugivores in cold environments (fruits and seeds, if available, only during a limited period of the year). The distribution across habitat types is quite predictable. Most forest species are omnivore/frugivore or browser (for obvious reasons). Most grazers are found in the open areas while the ecotone (here defined as areas with significant cover of both woody species and grasses) distribution is much more similar to that of open areas than of forests.

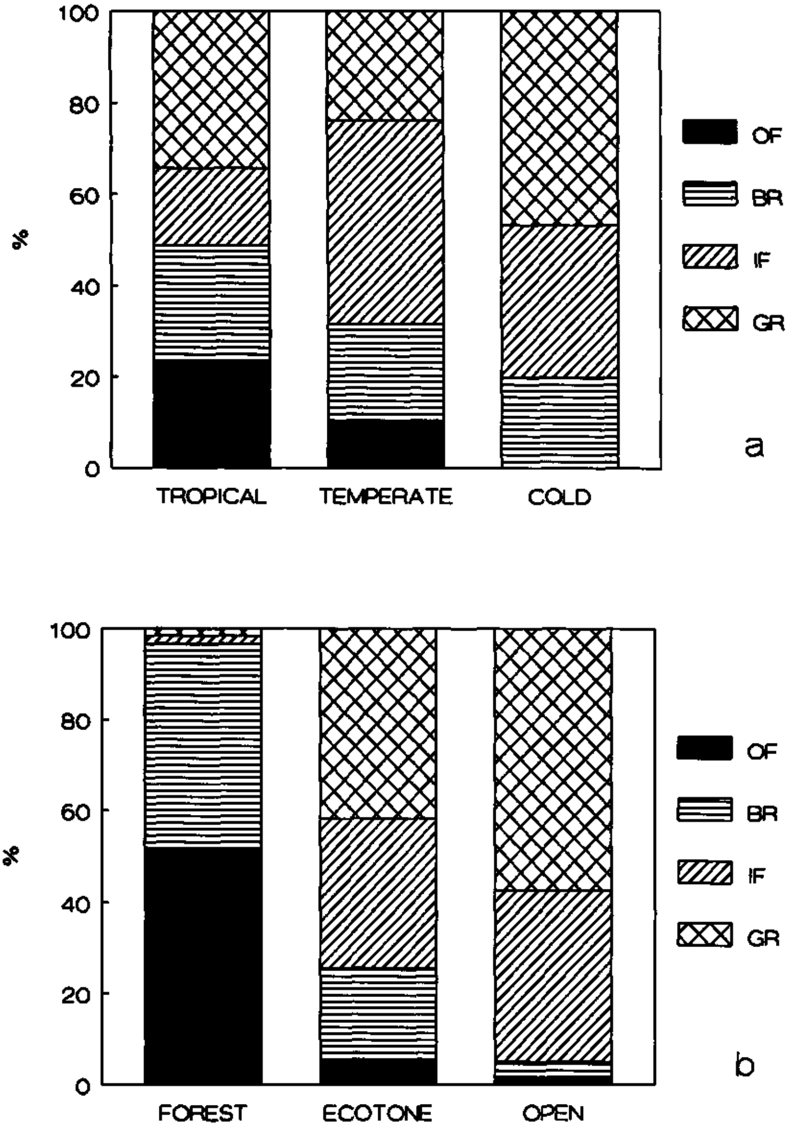


Figure 9.5. Distribution of ungulate feeding styles across climatic region (a) and habitat (b).

Body size distribution

The body size distribution of all ungulates is given in figure 9.6. Such log normal distribution has been reported for many taxa and groups (Hutchinson & MacArthur 1959, Van Valen 1973, Schoener & Janzen 1968), although frequently the distribution has a skewed right tail (Stanley 1973) which is absent here. Size distributions are generally given for whole taxa or large groups but also in local ungulate communities size distributions appear to have an optimum at intermediate body sizes (figure 9.7). Much has been speculated about this unimodal shape of the curve. As most ecological parameters scale allometrically with body size, we might expect a decrease in the number of species with increasing size. Larger species need more space (have larger home ranges), have lower densities and therefore populations of large species are composed of fewer individuals than small species (Peters 1987). Furthermore larger species also face higher extinction rates and lower rates of evolutionary change (Stanley 1973, Fowler & MacMahon 1982). May (1978) presented a distribution of all living animal species (of which he could find information) (figure 9.8). Peters (1987) and probably also May interprete this pattern as the number of species declining with increasing body size, with the left tail being unreliable estimates because small species are not so well classified. as large ones. Their interpretation thus follows intuition. Rosenzweig (1995) however, in discussing the generally found size distributions, interpretes the pattern by stating that 'it too, appears unimodel'. The decrease on the left hand side of the curve still remains to be explained.

The ungulate curve probably reflects an optimum size for exploiting the green world. Intake rate (both instantaneous and on larger time scales) and food processing capacity determine to a large extent the potential for herbivores to exploit their food resources. Small herbivores need high quality food items and have a relatively low capacity to digest plant fibre. Digestive capacity is high in large bodied animals but they need a bulky vegetation because of their high absolute intake rates. It can be expected that to be able to utilize fibrous plants properly, herbivores need to have certain minimal size (Van Soest 1994) and that therefore it is unlikely that there are many species of small ungulates. Ungulates smaller than 10 kg are mainly frugivores. Furthermore it can be

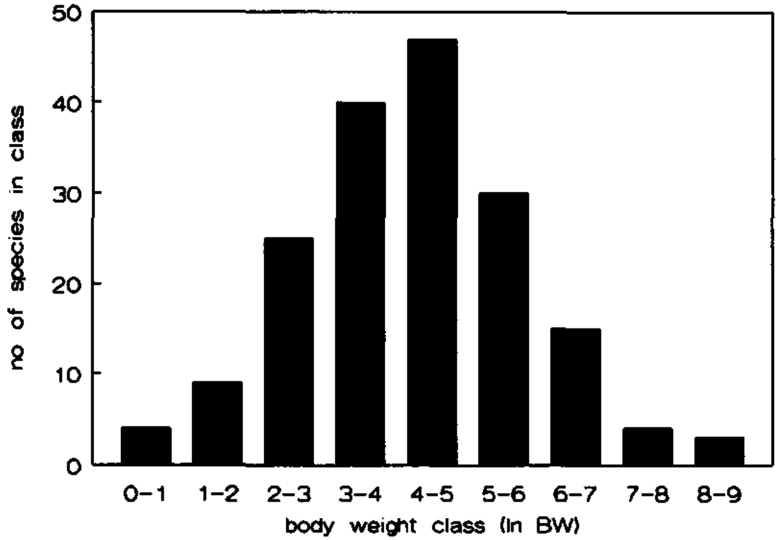


Figure 9.6. Frequency distribution of ungulates species in the world across body weight classes.

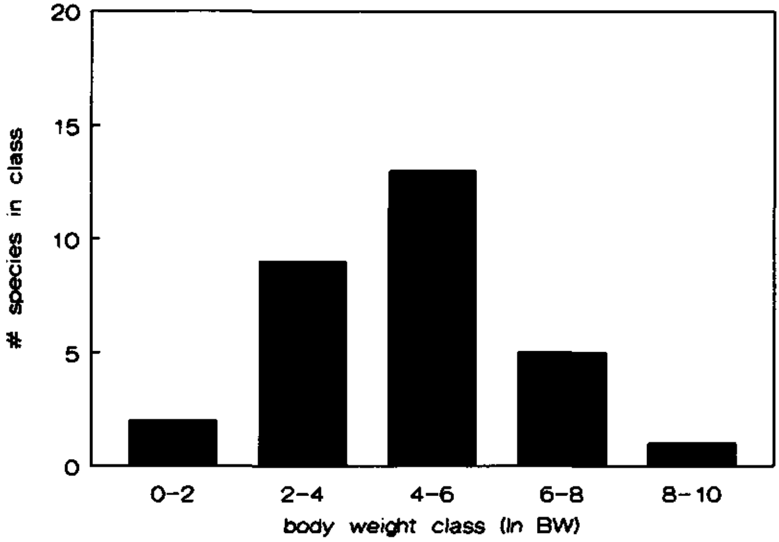


Figure 9.7. Frequency distribution of ungulates species in Serengeti N.P. (East Africa). Source: Williams et al 1994.

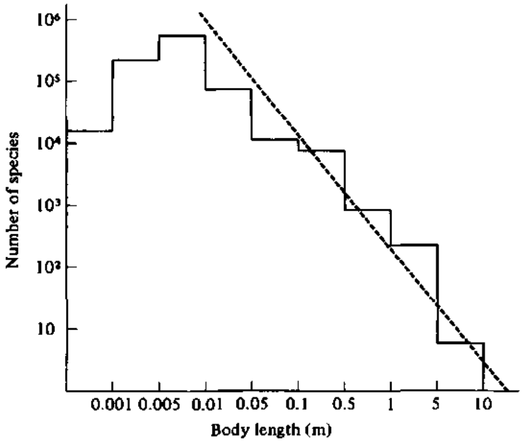


Figure 9.8. The size distribution of animal species (May 1978). The dotted line through the upper tail of the histogram approximates the decline of species number with length.

expected that the high quality food items needed by very small herbivores are generally scarce, limiting niche space for small species. Very large species of herbivores need bulk and are therefore not able to exploit medium to low ranges of vegetation biomass. It seems that, relative to the overall structure and composition of the vegetation (bite size ranges), medium sized herbivores have the best of both worlds. They have a potentially high digestive capacity and have access to a large array of different biomasses which they can exploit. The variation in plant species and vegetation structure on that level has made further specialization possible in feeding style. In figure 9.9 the size distribution of five different feeding styles is given. The (real) ruminants dominate the medium size classes. Most importantly, it can be seen that the medium body size classes are the most diverse in feeding styles.

It can be concluded that the green world as it presents itself can best be exploited by and provides the greatest number of different feeding niches to ungulates of medium body size. If the unimodal size distribution of ungulates represents a general pattern, it can be expected that cenograms of large faunas do have 'gaps', revealing itself as steeper parts of the curve at low and high body size, and that it is not necessary to suggest that in these ranges species are 'missing' (Prins & Olff, in press).

Community structure

Ungulates are a diverse group of species, both globally and (mainly in Africa and Southeast Asia) locally. The sometimes many species living sympatrically poses the intriguing question of how all these species within a guild can co-exist. Is there no competition between some species? Theory predicts that competing species can only co-exist as the result of niche differentiation of their realized niches. The question then becomes what the limit is to the similarity of competing species or in other words: how much dissimilarity is minimal needed for co-existence? So far very few answers have been generated to this question for all systems studied (Begon et al 1995). May and MacArthur (1972, in Rosenzweig 1995) state that no rules can be given to how close species niches can be, while Abrams (1983, in Begon et al 1995) concludes that no number can be attached to limiting similarity and that we can only say it exists.

It has been suggested that body size can be used to explain the co-existence of similar species (Hutchinson 1959). If the size difference between similar species becomes large enough niche differentiation can become pronounced enough for co-existence to take place. How exactly this is brought about is unclear but it is generally thought that it is related to a differential use of the food resource base. Hutchinson (1959) was the first to give evidence for some minimal size difference in various groups of animals (insects, seed eating birds) and he found that the weight ratio of adjacent species in guilds was approximately 2 (as calculated from an average lenght-ratio of 1.3). Similar weight ratios have later also been reported for cuchoo-doves, bumblebees and African tree squirrels (summarized by Begon et al 1995). Little work has been carried out in ungulate communities. Maiorama (1990) studied size distributions on continental and regional scales and found a general periodicity in the size distributions of herbivores such that numbers peaked in size classes that were a fourfold difference with adjacent peaks. She contributed this periodicity to competitive size displacement. A periodicity however is not supported by the data presented here (and also rejected by Prins & Olff (in press) while furthermore we have to look more to sympatrically living faunas in order to study the mechanism behind co-existence properly. Prins & Olff (in press) noted that the weight ratios presented so far were mainly from seed eating species. Seeds are discrete food items and they speculate that for (grass eating) herbivores average weight ratios might be less than 2 because of grass being a more complex and continuous food resource that is furthermore also

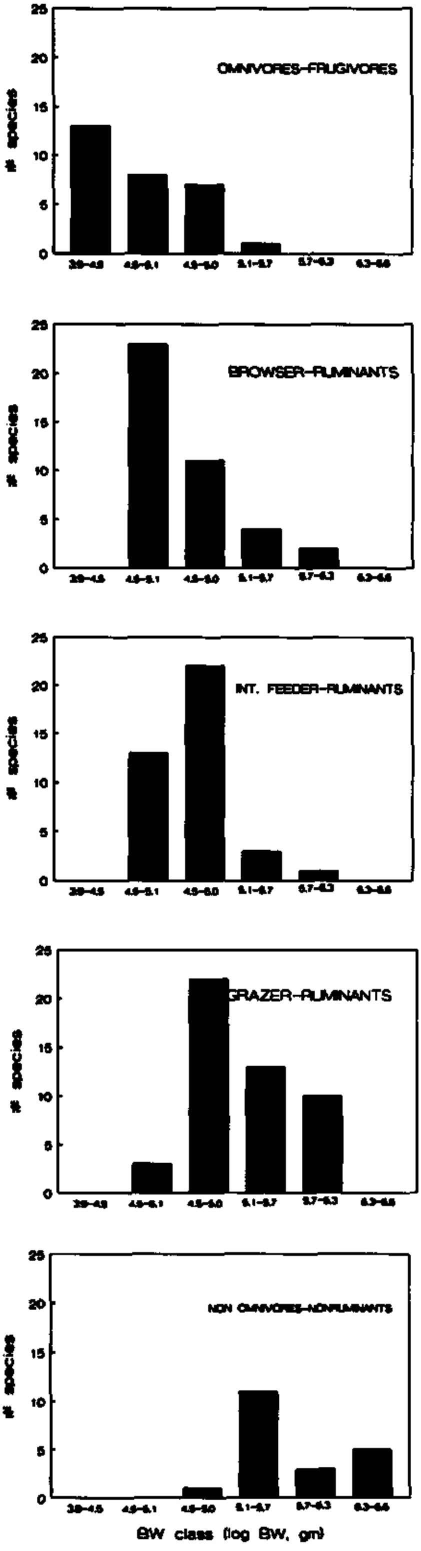


Figure 9.9. Body size distribution of ungulate groups with different feeding ecology.

affected and modified by the grazing process. Because of these considerations facilitation can take place permitting more herbivore species to co-exist than in situations with more discrete food items. Although we can thus expect average weight ratios to be smaller than 2 in rich ungulate communities we still don't know how small size differences can or must be and how important body size really is in explaining coexistence of similar species.

Figure 9.10 and figure 9.11 present cenograms and average weight ratios (WR) of ungulate assemblages on various scales and in different localities.

Figure 9.10 makes clear that WR of local ungulate communities in North America (Yellostone N.P.) and Europe (Bialowieza N.P.) are close to 2 because of a low species richness. The ungulate community of Mole N.P. (Ghana) represents a reconstruction based on historical data of the former species richness (Hekman-Leenders 1996). This park in West Africa is now much impoverished. The lowest WR are found in East Africa (Ruaha N.P. in Tanzania is given as an example). Average WR < 1.5 frequently occur in many parts of Africa.

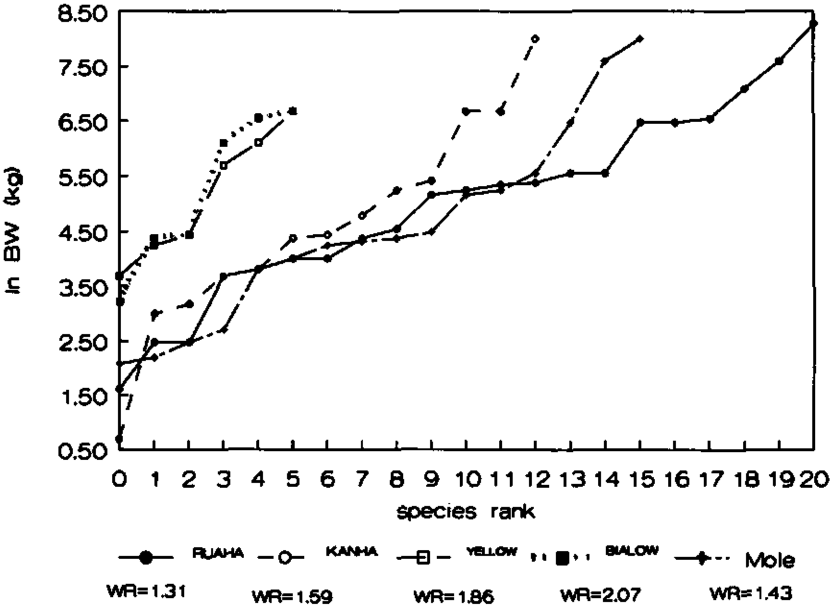


Figure 9.10. The relationship between body weight and species weight rank, and average weight ratio, of ungulate assemblages in some national parks: Ruaha (Tanzania), Kanha (India), Yellowstone (N-America), Bialowieza (Poland), Mole (Ghana).

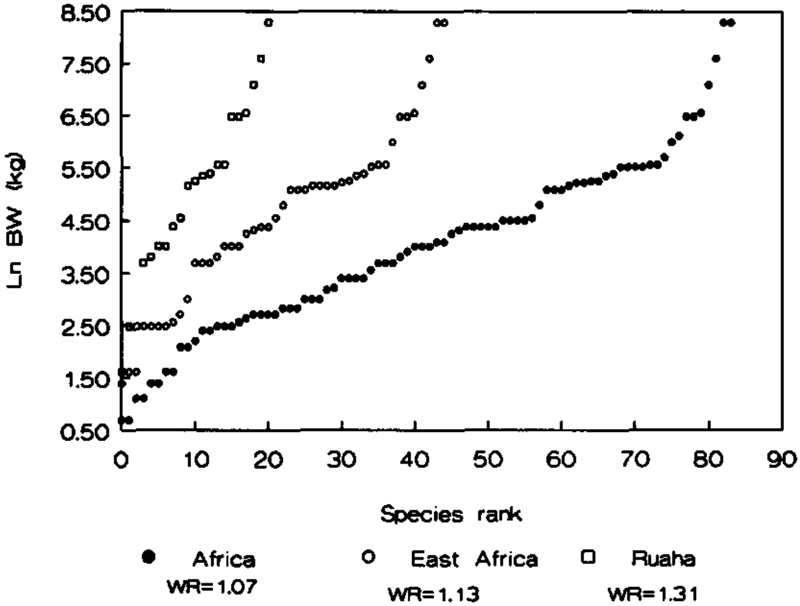


Figure 9.11. The relationship between body weight and species weight rank, and average weight ratio, of ungulate assemblages in Africa, East Africa and Ruaha N.P. (Tanzania).

Figure 9.11 illustrates the well known species richness-area relationship: a smaller area contains fewer species than a larger one (Rosenzweig 1995). This relationship poses the question what should be the minimum area to study competition and niche separation in ungulates. Focussing on East Africa there are no real geografic barriers to dispersal, indicating we have to focus on large areas. Because no general rules exist for this problem I have taken the size of the larger parks as minimum areas for the struggle between ungulate species to take place on an evolutionary time scale. This means that all species within such an area can potentially interact. Having (more or less) defined area we have to define the guilds within which competition is likely to occur. Two important denominators of niche space are used here: habitat (spatial differentiation) and pricipal food choice (resource partitioning). Three habitat types have been distinguished but as the ecotone zone is frequently used by both (a number of species) from the open plains and by species from the forest two major habitats have been distinguished: open-ecotone habitat (OE) and forest-ecotone habitat (FE). Within the group of herbivores three feeding styles are frequently distinguished: browsers, grazers and intermediate feeders (Chapter 8). As intermediate feeders feed both on browse and grass they are potentially competitors with both browsers and grazers. Therefore two main feeding styles can be distinguished: browsers-intermediate feeders (BI) and grazers-intermediate feeders (GI). In this way four different guilds are apparent with ecologically similar species who can interact within the same biome. Cenograms and average weight ratios of the four guilds of a large area in East Africa (the Serengeti) are presented in figure 9.12.

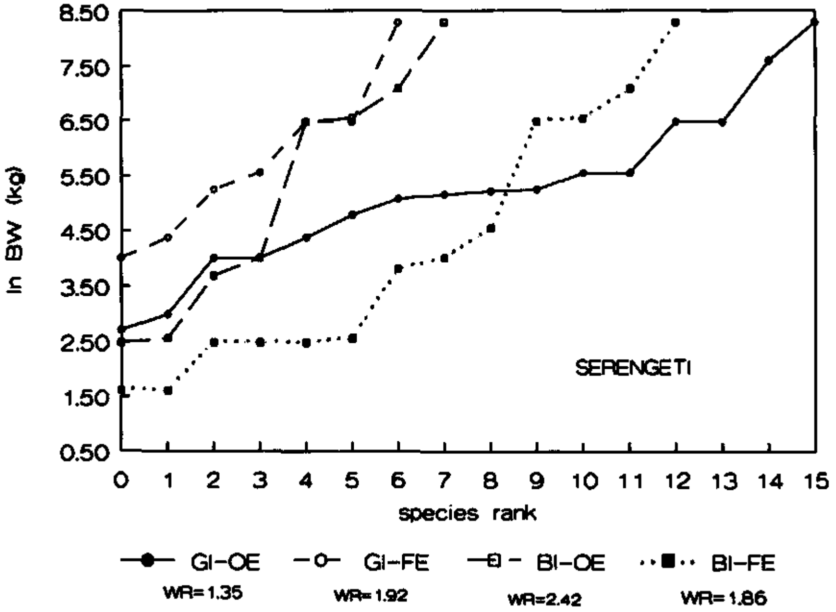


Figure 9.12. The relationship between body weight and species weight rank, and average weight ratio, of different guilds of ungulates in Serengeti N.P.(GI:Grazers-Int. Feeders, BI:Browsers-Int. Feeders, OE:Open habitat-Ecotone, FE:Forest-Ecotone).

The average weight ratio is highest for browser-intermediate feeders in the open-ecotone habitat and lowest for the grazer-intermediate feeders in the open-ecotone habitat. The highest density of species within a guild is thus found in the 'grazer' community on the African savanna. This was predicted by Prins & Olff (in press) and the prediction holds in the light of the present data, even taken into consideration that they did not distinguish between habitat and that their guild of 'grazers' contained 13 species of ungulates that are almost obligate browsers. The high incedence of species packing within the grazers of the savanna has been attributed to intergrazer facilitation

(Prins & Olff in press). Although facilitation is probably part of the explanation there is still very little prove that facilitation really takes place in the sense that fitness is increased in species that are facilitated. It is also likely that the number of different feeding niches is higher in the open areas when compared to more forested areas while also the effect of area can not be excluded.

The average weight ratio only tells us something about the distribution across the whole weight range involved and is thus not giving insight in the pattern of weight relationships of groups of species within a limited size range. Yet is here that we can expect the most intense competition and that we can study what the real limiting similarity might be. Therefore cenograms of two major guilds for three large parks in in East Africa are presented in figure 9.13.

In the 'browser' group (figure 9.13a) the pattern is quite regular in the higher weight range but in the lower weight range it can happen that five species of the same weight occur together! In the 'grazer' group (figure 9.13b) it frequently occurs that within the medium size range the weight ratio between two or more adjacent species is close to 1. Thus in either guild groups of species occur that are ecologically very similar, while it can be expected that the species within such a group are potentially severe competitors. Table 9.2 gives an overview of which similar species within a guild occur together in a number of national parks, of similar large size, in East Africa (and frequently do so in other parks in the region, Williams et al 1994).

The results indicate that weight ratios as such offer no explanation for the co-existence of similar species within a guild and that, at least for ungulate communities, a Hutchinson 'rule' does not exist. What then can be the explanation for the co-existence of similar species? In the first place there may be subtle differences in habitat preferences that do not show in the present classification of only two habitat types. In the second place the resource partitioning may be more refined than so far known, yet for a number of species combinations such a differentiation is not evident.

A well known combination is the one of zebra-wildebeest. They are of the same size, forage on the same grasses, and frequently associate in mixed groups. These and similar cases are difficult to explain. In the case of zebra and wildebeest it is possible that competition is severe and that the system is still in a transition phase with the zebra slowly disappearing from the system, although there seems to be no evidence to substantiate this claim. It is also possible that similar species co-exist in some sort of dynamic equilibrium. Even if they have similar food habits and occupy the same habitat they still may differ in their response to resource use. If the environment is patchy, heterogenous or unpredictable competitive superiority may switch from time to time

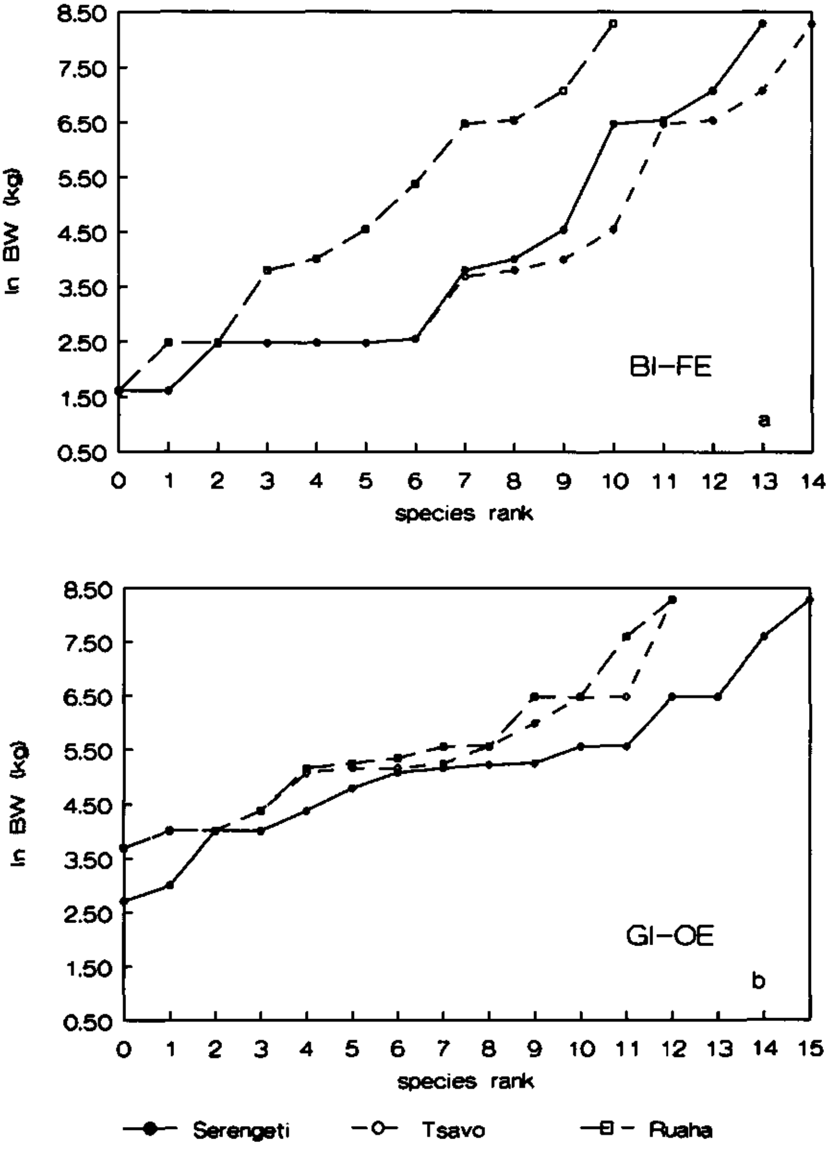


Figure 9.13. The relationship between body weight and species weight rank, and average weight ratio, of two guilds of ungulates in three large parks in East Africa. a: Browsers-Intermediate Feeders in Forest-Ecotone habitat (BI-FE); b: Grazers-Intermediate Feeders in Open-Ecotone habitat (GI-OE).

Table 9.2. Groups of similar species within guilds occurring sympatrically in the Serengeti N.P., Tsavo N.P. and Ruaha N.P., East Africa. (BW, kg).

SERENGETI	TSAVO	RUAHA
	browsers	
Blue duiker (12)	Blue duiker (12)	Blue duiker (12)
Red Duiker (12)	Red duiker (12)	Bush duiker (12)
Bush duiker (12)	Bush duiker (12)	Klipspringer (12)
Klipspringer (12)	Klipspringer (12)	
Steenbok (12)	Steenbok (12)	
	grazers	
Chanler's reedbuck (55)	Oryx (160)	Kongoni (175)
Bohor reedbuck (55)	Kongoni (175)	Jackson's hartebeest (175)
	Hunter's hartebeest (175)	Waterbuck (190)
Oryx (160)	Waterbuck (190)	Sable antelope (210)
Kongoni (175)		
Waterbuck (190)		Zebra (259)
		Roan antelope (260)
Wildebeest (230)		
Zebra (259)		
Roan antelope (260)		

from the one species to the other, locking them in a kind of quasi equilibrium with no conclusive outcome. To what extent this really happens we do not know but it is of great importance to study the major life history traits and general population dynamics of similar species living sympatrically over longer periods. To reveal the minimum dissimilarity necessary for co-existence of ungulates in guilds, it would be awarding to focus research on the species listed in table 9.2, or on comparable groups of similar species. For this further understanding of co-existence and competition, food digestion studies as carried out in the present thesis are, I am sure, indispensable.

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Appendix 1. Body weight, age at sexual maturity (AGE), number of young per year (YOUNG), diet preference (OM=omnivorous, BR=browser, GR=grazer, IF=intermediate feeder), distribution (AF=Africa, EA=East Asia, NA=North America, SA=South America), habitat choice (F=forest, E=ecotone, O=open landschape, TR=tropical, TE=temperate, CO=cold environment) of ungulates of the world. References: Eisenberg 1981, Haytenorth et al 1994, Lekagud & McNeely 1977, Macdonald & Barrett 1993, Oliver 1993, Walker 1968, and references mentioned in appendix 1 of chapter 8).

	BW kg	AGE months	YOUNG N	DIET	REGION	HABITAT
Chevrotain	8	8	2	OM/BR	AF	F/TR
Kantjil	5	7	2	OM/BR	EA	F/TR
Mousedeer	2	5	2	OM/BR	EA	F/TR
Meminna	2	10	2	OM/BR	EA	F/TR
Muskdeer	11	10	2	BR	EA	E/CO
Chinese muskdeer	12	10	2	BR	EA	E/CO
Muntjac	24	10	1.5	BR	EA	F/TR
Reeves muntjac	18	10	1.5	BR	EA	F/TR
Bornean yellow muntjac	22	10	1.5	BR	EA	F/TR
Black muntjac	26	10	1.5	BR	EA	F/TR
Tufted deer	40	14	1	IF	EA	E/TE
Fallow deer	55	16	1	IF	EA	O/TE
Hogdeer	50	16	1	IF	EA	E/TE
Chital	85	16	1	GR	EA	E/TR
Sambar	220	22	1	IF	EA	E/TR
Rusa	65	22	1	GR	EA	E/TR
Barasingha	190	22	1	GR	EA	O/TR
Eld 's deer	110	16	1	GR	EA	E/TR
Sika deer	45	16	1	IF	EA	E/TE
Rred deer	85	12	1	IF	EA/NA	E/TE
Pere David's deer	160	18	1	GR	EA	O/TR
Waterdeer	12	6	4	BR	EA	F/TE
Roe deer	20	14	3	BR	EA	F/TE
White-tailed deer	60	10	3	BR	NA	F/TE
Muledeer	70	14	2	BR	NA	F/TE
Marsh deer	30	16	1	IF	SA	O/TR
Peruvian guemal	40	16	1	IF	SA	O/TE
Huemul	70	16	1	IF	SA	E/TE
Red brocket	20	10	1.5	BR	SA	F/TR
Grey brocket	17	10	1.5	BR	SA	F/TR
Brocket	8	10	1.5	BR/OM	SA	F/TE
Grey dwarf brocket	10	10	1.5	BR/OM	SA	F/TR
North pudu	6	10	1.5	BR/OM	SA	F/TE
South pudu	6	10	1.5	BR/OM	SA	F/TE
Moose	550	16	2	BR	EA/NA	F/CO
Caribou	140	18	1	IF	EA/NA	O/CO
Okapi	250	36	0.3	BR	AF	F/TR
Giraffe	700	10	0.5	BR	AF	E/TR
Pronghorn	40	15	2	BR	NA	O/TE

	BW kg	AGE months	YOUNG N	DIET	REGION	HABITAT
Grey duiker	12	11	2	BR	AF	F/TR
Maxwell's duiker	8	11	2	BR/OM	AF	F/TR
Black duiker	17	11	2	BR	AF	F/TR
Zebra duiker	15	11	2	BR	AF	F/TR
Ogylby's duiker	15	11	2	BR	AF	F/TR
Jentink's duiker	60	11	2	BR	AF	F/TR
Redflanked duiker	9	11	2	BR/OM	AF	F/TR
Blackstriped duiker	17	11	2	BR	AF	F/TR
Yellow backed duiker	70	11	2	BR	AF	F/TR
Whitebellied duiker	17	11	2	BR	AF	F/TR
Blackfronted duiker	15	11	2	BR	AF	F/TR
Harvey's duiker	14	11	2	BR	AF	F/TR
Abbott's duiker	50	11	2	BR	AF	F/TR
Red duiker	12	11	2	BR	AF	F/TR
Royal antilope	2	18	2	BR/OM	AF	F/TR
Pygmy antilope	4	18	2	BR/OM	AF	F/TR
Suni	5	18	2	BR/OM	AF	F/TR
Salt's dikdik	3	7	1.5	BR	AF	F/TR
Red-bellied dikdik	3	7	1.5	BR/OM	AF	F/TR
Swayne's dikdik	2	7	1.5	BR/OM	AF	F/TR
Guenther's dikdik	4	7	1.5	BR/OM	AF	F/TR
Kirk's dikdik	5	7	1.5	BR/OM	AF	F/TR
Beira	11	10	2	BR	AF	E/TR
Klipspringer	12	12	2	BR	AF	E/TR
Grysbok	11	6	2	BR	AF	E/TR
Steenbok	13	6	2	BR	AF	E/TR
Oribi	15	12	2	GR	AF	O/TR
Greater kudu	220	17	1	BR	AF	F/TR
Lesser kudu	95	20	1	BR	AF	F/TR
Mountain nyala	190	24	1	IF	AF	E/TR
Nyala	90	11	1	BR	AF	E/TR
Sitatunga	80	16	1	IF	AF	E/TR
Bushbuck	45	11	2	BR	AF	F/TR
Bongo	250	20	1	BR	AF	F/TR
Eland	650	20	2	IF	AF	E/TR
Nilgai	120	18	2	GR	EA	E/TR
Anoa	200	24	1	GR	EA	E/TR
Waterbuffalo	800	24	1	GR	EA	E/TR
African buffalo	650	36	0.5	GR	AF	E/TR
Gaur	800	24	1	GR	AE	E/TR
Banteng	700	24	1	GR	EA	E/TR
Kouprey	800	24	1	GR	EA	E/TR
Aurox	700	24	1	GR	EA	E/TE
Yak	700	24	0.5	GR	EA	O/CO
Bison	800	36	0.75	GR	NA	O/TE
Wisent	800	24	1	GR	EA	E/TE
Hartebeest	175	30	1	GR	AF	O/TR
Topi	120	21	1	GR	AF	O/TR
Bontebok	60	27	1	GR	AF	O/TR
Black wildebeest	230	24	1	GR	AF	O/TR

	BW kg	AGE months	YOUNG N	DIET	REGION	HABITAT
Common wildebeest	230	24	1	GR	AF	O/TR
Roan antilope	260	30	1	GR	AF	E/TR
Sable antilope	210	30	1	GR	AF	E/TR
Bluebuck	160	30	1	GR	AF	O/TR
Oryx	160	21	1	GR	AF	O/TR
Addax	90	18	1.5	GR	AF	O/TR
Waterbuck	190	13	1.5	GR	AF	E/TR
Kob	75	13	2	GR	AF	E/TR
Lechwe	90	18	1	GR	AF	E/TR
Nile lechwe	80	18	1	GR	AF	O/TR
Reedbuck	80	18	1	GR	AF	O/TR
Bohor reedbuck	55	18	1	GR	AF	O/TR
Mountain reedbuck	24	18	1	GR	AF	O/TR
Vaal rhebok	25	13	2	IF	AF	O/TR
Dama	55	18	1	IF	AF	O/TR
Mountain gazelle	30	12	2	IF	AF	O/TR
Dorcas gazelle	20	18	2	IF	AF	O/TR
Slenderhorned gazelle	30	18	1	IF	AF	O/TR
Soemmerings gazelle	40	18	1	GR	AF	E/TR
Red-fronted gazelle	35	18	2	IF	AF	O/TR
Grant's gazelle	40	18	1	IF	AF	O/TR
Thomson 's gazelle	20	12	2	GR	AF	O/TR
Speke's gazelle	20	12	2	IF	AF	O/TR
Goitred gazelle	30	18	2	IF	EA	O/TE
Tibetan gazelle	30	18	1	IF	EA	O/CO
Mongolean gazele	45	18	2	IF	EA	O/CO
Blackbuck	40	12	1	GR	EA	O/TR
Gerenuk	40	12	2	BR	AF	E/TR
Dibatag	30	12	2	IF	AF	O/TR
Springbuck	30	7	2	IF	AF	O/TR
Impala	55	16	1.5	IF	AF	E/TR
Chiru	30		1	IF	EA	E/TE
Saiga	45	8	3	BR	EA	O/TE
Goral	30	30	2	IF	EA	E/TE
Serow	90	18	2	GR	EA	E/TE
Takin	250	18	1	BR	EA	E/TE
Chamois	34	24	1	GR	EA	O/CO
Mountain goat	110	18	1	GR	NA	O/CO
Ibex	60	18	1	IF	EA	O/CO
Markhor	70	18	2	IF	EA	E/TE
Dagestan tur	80	18	1	GR	EA	O/TE
Wild goat	35	11	2	IF	EA	O/TE
Aoudad	75	18	2	IF	EA	O/TE
Tahr	90	18	1	IF	EA	E/TE
Bharal	55	18	1	GR	EA	O/CO
Argali	120	18	2	IF	EA	E/TE
Bighorn sheep	85	24	1	IF	NA	O/TE
Dall sheep	70	24	1	IF	NA	O/TE
Snow sheep	70	24	1	IF	EA	O/CO
Urial	70	18	2	GR	EA	O/CO

	BW kg	AGE months	YOUNG N	DIET	REGION	HABITAT
muskox	300	24	0.75	GR	EA/NA	O/CO
Fourhorned antilope	20	8	2	IF	EA	E/TR
Collared peccary	22	12	3	OM	SA	E/TR
White-lipped peccary	28	14	3	OM	SA	E/TR
Warthog	80	17	4	GR	AF	E/TR
Forest hog	160	16	5	GR	AF	F/TR
Bushpig	80	17	6	OM	AF	F/TR
Wild boar	80	12	6	OM	EA	F/TE
Pygmy hog	8	10	5	OM	EA	E/TR
Java warty pig	70	12	6	OM	EA	F/TR
Bearded pig	80	14	6	OM	EA	F/TR
Sulawesi warty pig	70	12	5	OM	EA	F/TR
Philippine warty pig	70	14	7	OM	EA	F/TR
Babirusa	80	7	7	OM	EA	F/TR
Common hippo	2000	48	0.5	GR	AF	O/TR
Pygmy hippo	250	36	0.5	OM	AF	O/TR
African wild ass	250	30	1	GR	AF	O/TR
Mountain zebra	300	24	1	GR	AF	O/TR
Grevy's zebra	400	40	1	GR	AF	O/TR
Common zebra	259	24	1	GR	AF	O/TR
Kiang	375	24	0.75	GR	EA	O/CO
Przewalski horse	250	21	0.75	GR	EA	O/TE
Indian elephant	3000	80	0.2	GR	EA	E/TR
African elephant	4000	120	0.2	IF	AF	E/TR
Black rhino	1200	54	0.5	BR	AF	E/TR
White rhino	4000	54	0.4	GR	AF	E/TR
Sumatran rhino	1000	42	0.2	BR	EA	F/TR
Pantzer rhino	2000	42	0.2	IF	EA	E/TR
Java rhino	1800	42	0.2	IF	EA	F/TR
Malayan tapir	300	36	0.5	BR	EA	F/TR
Lowland tapir	250	36	0.5	BR	SA	F/TR
Central American tapir	325	36	0.5	BR	SA	F/TR
Andes tapir	225	36	0.5	BR	SA	F/TE
Two-humped camel	500	24	0.5	GR	EA	O/TE
Dromedary	450	24	0.5	GR	AF/EA	O/TR
Guanaco	70	13	0.5	GR	SA	E/TE
Vicugna	50	13	0.5	GR	SA	O/TE

SUMMARY

Digestive strategies in ruminants and nonruminants

In the introduction the taxonomy and evolutionary history of ungulates is shortly described and the importance of the group for mankind is stressed. Two large groups of ungulates are distinguished: the Perissodactyls (odd-toed ungulates) and the Artiodactyls (even-toed ungulates). Horses, zebras and rhinos are examples of odd-toed ungulates. At present it is a small group comprising 14 species. The even-toed ungulates are a much larger group (ca 165 species) and most of them are ruminants. Pigs, antilopes, deer, cattle, goats and sheep belong to this group. The Perissodactyls once were the dominant group but the Artiodactyls start dominating from the Pleistocene onwards. De first ungulates probably were small consumers of leaves and fruits and were forest dwelling animals. Later species increase in body size and become adapted to the utilization of cellulose-rich grasses which start developing in the Miocene. The development of pregastric fermentation combined with the rumination mechanism appears to be a succesfull strategy and has probably induced an extensive radiation within the ruminants. Half a billion wild ungulates populate the world together with five billion domesticated animals. The importance of ungulates for man is not so much food consumption but mainly the provision of power, and dung for fuel and as a source for nutrients.

The importance of large herbivores for nature conservation is the subject of chapter 2. It is made clear that the different kinds of herbivores exert different kinds of effects on vegetation composition and vegetation structure. Most important, however, is animal density. High densities retard succession and may facilitate other smaller herbivores. Very high densities generally have negative effects on other fauna.

Chapter 3 investigates if the phenomenom of a lower voluntary food intake in the winter, as is found in wild ruminants of temperate and arctic climates, also occurs in free-grazing domestic (Highland) cattle. The available evidence indicates it does. Although the mechanism of this phenomenom is well known its ultimate causation is not clear. It is argued that it might be the result of a longterm trade-off between the energetic gain of the consumption of food (of a certain quality), against the costs in terms of the production of free oxygen radicals as the result of food consumption.

The potential use of an internal marker, indigestible acid detergent fibre (IADF), to predict the digestibility of plants, is studied in chapter 4. During feeding trials with goats, sheep, wild boar and pigs, using very different types of feeds, digestibility was estimated with the total faecal collection method and the IADF-method. A good relationship was found between both methods and it was concluded that IADF can act as a adequate predictor of digestibility.

Sheep and goats are compared in chapter 5. Earlier feeding trials have demonstrated very little differences in digestive capacity between the two species. Nevertheless sheep are classified as 'grass and roughage feeders' and goats as 'intermediate feeders'. As browse normally is not used in feeding trials, and differences are expected especially with this feeding type, feeding trials were carried out with browse being an important part of the diet. Differences in food intake and digestibility were small with highly digestible feeds. Browse diets were better digested by the sheep but food intake and passage rate were much higher in the goats. This result is in line with the expectation as based on morphology and anatomy.

Chapter 6 describes feeding trials carried out with representatives of four different digestive strategies: Highland cattle ('grass and roughage feeder'), Red deer ('intermediate feeder'), Roe deer ('concentrate selector') and Konik horses ('hindgut fermenter'). Different types of feeds were tested: Grass-seed straw, grass hay, alfalfa and willow (leaves and twigs). The ponies had lower digestive efficiencies than the ruminants. Of the ruminants the Roe deer had lowest digestive capacity and the cattle the highest. Red deer took an intermediate position both with respect to digestibility and food intake. The various ways with which the ruminants were able to extract nutrients from the feeds was in line with predictions based on morphological and anatomical classification.

The possible role of fibre in the feeding ecology of Wild boar was studied in chapter 7. Increasingly Wild boar are not supplementary fed anymore in Western Europe. Recent work on non-supplementary fed boar has made clear that fibre-rich plants like grasses can be an important component of the winter-diet in mast-poor years. This raises the question to what extent boar which (like man) is an omnivore, is capable of utilizing fibre-rich plants. A domesticated race, the Meishan pig, was included for comparison. A number of feeds (acorns, grasspellets and grass-seed straw) were better digested by the Wild boar while the Meishan consumed more from the grass hay, grass pellets and the grass-seed straw. It was calculated that Wild boar (and domesticated pigs) can keep maintenance while eating grasses with cell wall contents no less than 55%.

In chapter 8 some predictions that followed from Hofmann's classification of the ruminants in 'grass and roughage feeders', 'intermediate feeders' and 'concentrate selectors' were tested with respect to fibre digestion and diet choice. It was analyzed if variation in fibre digestion, diet choice, (and some of Hofmann's morphological parameters) was best explained by either class differences or body weight. For both fibre digestion and diet choice class differences could be detected while no relationship was found with body weight. Class differences were found in only one of five morphological parameters tested while two had a weak relationship with body weight. Class differences therefore do exist but the classes can best be regarded as adaptive syndromes being the result of many interacting variables.

The last chapter (9) pays attention to the evolution, distribution and community ecology of ungulates. Significant differences in two important life history traits were detected between two groups of ungulates: the successfull recent ruminants (Ruminantia) and the disappearing older families (rhinos, equids, elephants, tapirs). Members of the second group, relative to body weight, reach sexual maturity at a later age and produce fewer young per year than those of the first group.

Most of the 176 species of ungulates are found in the tropics and much less in the temperate and cold climates. Probable reasons are the relatively large area of the tropics and the optimum relationship that exist between productivity and species diversity.

Community structure was studied in East African ungulate assemblages. Here many species frequently occur sympatrically and the question can be put how all these species manage to co-exist and if competition is occurring between similar species. Within a community of ungulates on the level of a large national park different guilds can be distinguished that differ in habitat preference and diet choice. Between these guilds no competition is expected to take place. Within a guild combinations of ungulates with similar body weights and similar ecology frequently occur. Between these species competition is possibly heavy unless important niche differences, which are yet unknown, do exist permitting co-existence to take place. Detecting these differences would bring about a better understanding of how species-rich ungulate communities are structured and regulated.

SAMENVATTING

Verteringsstategieën bij herkauwers en niet-herkauwers

In de inleiding wordt aandacht geschonken aan de taxonomie en de evolutie van hoefdieren en het belang van deze groep voor de mens. Er zijn twee grote groepen van hoefdieren: de Perissodactyla (onevenhoevigen) en de Artiodactyla (evenhoevigen). Onder de onevenhoevigen vinden we de paarden, zebra's, ezels en de neushoorns. Deze groep bestaat heden ten dage uit 14 soorten. De groep van de evenhoevigen bevat veel meer soorten (ca 165) waarvan het merendeel herkauwers zijn. In deze groep horen o.m. de varkens, antilopen, hertachtigen, runderen, geiten en schapen thuis. De onevenhoevigen waren ooit de dominante groep maar de evenhoevigen, met name de herkauwers, gaan domineren in het Pleistoceen. De eerste hoefdieren waren waarschijnlijk kleine blad- en vruchteneters die in het bos leefden. Later ontstaan grotere soorten en vinden aanpassingen plaats aan de fermentatie van cellulose-rijke grassen die ontstaan en zich sterk uitbreiden in het Mioceen. Het ontstaan van de voormaagfermentatie gekoppeld aan het herkauwmechanisme blijkt een succesvolle strategie en is wellicht mede een reden voor een sterke radiatie binnen de herkauwers.

Er zijn naar schatting ongeveer een half miljard wilde hoefdieren in de wereld en meer dan vijf miljard gedomesticeerde. Het belang van herbivoren voor de mens zit hem niet zo zeer in de bijdrage aan de voedselkonsumptie maar veel meer in de bijdrage aan niet-voedsel kategorieën als het leveren van trekkracht en mest voor gebruik als brandstof en nutriëntenbron.

Het belang van grote herbivoren voor het natuurbeheer is het onderwerp van hoofdstuk 2. Duidelijk wordt hier ook dat verschillende soorten herbivoren heel verschillende effekten met zich mee brengen. In de resterende hoofdstukken wordt vooral aandacht besteed aan vergelijkende verteringsfysiologie waarbij vertegenwoordigers van verschillende 'verteringsstrategieën' met elkaar worden vergeleken. De inspiratie voor dit werk vindt zijn oorsprong in de ideeën van R. Hofmann en die van P. van Soest. Hofmann heeft de herkauwers ingedeeld in drie groepen. Deze indeling berust voornamelijk op morfologische verschillen van het maagdarmkanaal. Vanuit deze verschillen heeft Hofmann (en anderen) geëxtrapoleerd naar allerlei aspekten van de verteringsfysiologie. Zo zouden 'concentrate selectors', in tegenstelling tot 'grass and roughage feeders', relatief slechte celwandverteerders zijn maar een relatief hoge voedselopname kunnen realiseren omdat bij deze groep een hoge passagesnelheid van het voedsel mogelijk is. Deze claims zijn tot nu toe nog nauwelijks onderzocht en er is zeker nog maar weinig vergelijkend onderzoek gedaan. Een van de verdiensten van van Soest is geweest dat hij een analysetechniek heeft ontwikkeld waarbij de plant als voedselbron voor herbivoren goed kan worden gekarakteriseerd. Deze techniek behelst in eerste instantie het scheiden van plantmateriaal in een celinhoud- en een celwandgedeelte, terwijl in volgende stappen de samenstelling van de celwand verder wordt geanalyseerd. Hierbij is de bepaling van het ligninegehalte van groot belang. De kombinatie van het totale celwandgehalte, tesamen met het ligninegehalte, bepaalt in hoge mate de potentiële verteerbaarheid van de plant. De 'van Soest analyse' is dus een belangrijk hulpmiddel voor het verkrijgen van inzicht in de verteringscapaciteit (van celwanden) van allerlei soorten herbivoren.

Zoals gezegd wordt in hoofdstuk 2 de rol die grote herbivoren kunnen spelen in het natuurbeheer behandeld. Dit vanuit de opvatting dat in de natuurlijke referentie grote herbivoren een successie naar een (tamelijk) gesloten bos vermoedelijk niet tegen kunen houden in de meeste situaties. Met hulp van de mens zijn echter vele situaties gekreëerd waarbij de dichtheden kunstmatig werden verhoogd. Als de dichtheid toeneemt verandert eerst de soortensamenstelling van het bos. Bij nog hogere dichtheden wordt de bosverjonging sterk vertraagd en uiteindelijk kan een geheel open landschap ontstaan. Bij niet te hoge dichtheden kunnen soortenrijke parklandschappen ontstaan (wood-pasture, hudelandschaft). Deze landschappen, die mee door menselijk ingrijpen in stand worden gehouden, hebben honderden jaren lang west Europa gedomineerd. In graslanden leidt een niet te intensieve begrazing tot een struktuurrijke vegetatie en een hogere diversiteit in plantensoorten in vergelijking met maaien of niets doen. Een vrij hoge begrazingsintensiteit kan vergrassing van de heide tegengaan en een versnelling teweeg brengen in de nutriëntencyclus. Er wordt een aantal voorbeelden gegeven van begrazingseffekten op de overige fauna. Deze kunnen zowel positief als negatief zijn. Een negatief voorbeeld is het vertrappen van nesten van weidevogels door vee bij een hoge veebezetting. Een positief voorbeeld is de toename van het aantal nakomelingen van hindes op het eiland Rhum als gevolg van het facilitair graasgedrag van geïntroduceerde Schotse hooglanders. Het hoofdstuk besluit met een pleidooi voor het doen laten ontstaan van meer natuurlijker ecosystemen waarbij populaties zoogdieren en populaties planten elkaar vrijelijk kunnen beïnvloeden. Dit is alleen mogelijk in grote aaneengesloten gebieden.

In hoofdstuk 3 wordt onderzocht of het bij wilde herkauwers optredende verschijnsel van een lagere vrijwillige voedselopname in de winter ook voorkomt bij vrijgrazende Schotse hooglanders. Er zijn sterke aanwijzingen dat dit inderdaad het geval is. Hoewel het mechanisme achter dit verschijnsel wel bekend is (het berust op een endogene fysiologische ritmiek die in gang wordt gezet door daglichtvermindering), is de uiteindelijke oorzaak nog niet duidelijk. Het wordt beargumenteerd dat het wel eens het resultaat zou kunnen zijn van een lange termijn trade-off tussen de energetische opbrengst van het consumeren van voedsel van een bepaalde kwaliteit, tegenover de kosten in termen van de produktie van vrije zuurstof radikalen die voedselconsumptie met zich mee brengt.

In hoofdstuk 4 wordt onderzocht in hoeverre een interne merkstof, het zogenaamde 'indigestible acid detergent fibre (IADF)', kan worden gebruikt om verteerbaarheid van voeders te schatten. Tijdens voerproeven met geiten, schapen, wilde zwijnen en varkens, waarbij ook heel verschillende voeders werden getest, werd de verteerbaarheid bepaald door middel van totale mestopvang en door middel van de 'IADF'-methode. Het bleek dat er een goede relatie bestaat tussen de resultaten van beide methoden zodat geconcludeerd werd dat IADF een goede voorspeller kan zijn van verteerbaarheid.

In hoofdstuk 5 worden schapen en geiten met elkaar vergeleken. De zeer vele vergelijkende voerproeven die al eerder met deze soorten zijn uitgevoerd laten nauwelijks een verschil zien in verteringscapaciteit. Toch worden deze soorten door Hofmann in verschillende categoriën ingedeeld. Schapen zijn geklassificeerd als 'grass and roughage feeders' en geiten als 'intermediate feeders'. Op basis van dit verschil zouden er verschillen in vertering verwacht mogen worden, in ieder geval bij sommige voedertypen. Vooral bij het benutten van houtige gewassen kunnen verschillen verwacht worden maar dit soort planten wordt zelden gebruikt in voederproeven. Vandaar dat de experimenten werden uitgevoerd met houtachtigen als een belangrijk bestanddeel van het rantsoen. Het bleek dat er weinig verschil was in voedselopname en verteerbaarheid van die rantsoenen die een hoge verteerbaarheid hadden. De rantsoenen rijk aan houtachtigen (bladeren en twijgen van populier en wilg) werden echter beter verteerd door schapen maar de geiten hadden een veel hogere voedselopname en een kortere passagesnelheid.

Hoofdstuk 6 beschrijft voerproeven die zijn uitgevoerd met vertegenwoordigers van vier verschillende verteringsstrategieën: Schotse hooglandrunderen ('grass and roughage feeders'), edelherten ('intermediate feeders'), reeën ('concentrate selectors') en Konik ponies (een niet-herkauwende dikke darm verteerder). Er werden uiteenlopende voeders getest: graszaadhooi, grashooi, stro, lucerne en wilg (blad en twijg). De ponies hadden een lagere verteringscapaciteit dan de herkauwers. Deze lagere efficiëntie konden ze gedeeltelijk compenseren door een hogere voedselopname te realiseren. Van de herkauwers hadden de reeën de laagste verteringscapaciteit en de runderen de hoogste. Gemiddeld nam het edelhert een tussenpositie in, zowel wat betreft de vertering als de voedselopname. De verschillende wijze waarop de herkauwers in staat waren om energie uit het voedsel te halen stemden overeen met de voorspelling op basis van karakteristieken van het maagdarmkanaal.

De mogelijke rol die ruwvezel kan spelen in de voedseloecologie van het wilde zwijn wordt onderzocht in hoofdstuk 7. In toenemende mate worden wilde zwijnen niet meer bijgevoerd in de vrije natuur. Recent onderzoek aan niet-bijgevoederde wilde zwijnen heeft duidelijk gemaakt dat vezelrijke planten als grassen een belangrijk bestanddeel vormen van het winterdiëet in jaren dat er weinig of geen eikels en beukenoten zijn. Dit roept de vraag op in hoeverre zwijnen die (evenals de mens) omnivoor zijn, in staat zijn dit soort vezelrijke produkten te benutten. Een gedomesticeerd ras, het Meishan varken, werd bij de proef betrokken. Een aantal voeders (eikels, grasbrok en graszaadstro) werden beter verteerd door het wilde zwijn terwijl de Meishans meer aten van een drietal produkten (grashooi, grasbrok en graszaadstro). Berekend werd dat wilde zwijnen (en gedomesticeerde varkens) in hun energie-onderhoud kunnen voorzien door het eten van grassen waarvan het celwandgehalte niet hoger is dan 55% en waar voldoende eiwit in zit.

In hoofdstuk (8) wordt Hofmann's klassifikatie van de herkauwers in drie typen onder de loep genomen. Zoals gezegd zouden de gevonden morfologische verschillen ook een aantal specifieke implikaties hebben voor verteringsfysiologie en voedseloecologie. In de voorafgaande hoofdstukken wordt dit ook grotendeels bevestigd. Recentelijk echter is de Hofmann indeling sterk bekritiseerd. Analyses van een aantal aspekten met betrekking tot verteringsfysiologie brachten de critici tot de conclusie dat de veronderstelde klasseverschillen niet bestonden en dat de gevonden variatie het best werd verklaard door het lichaamsgewicht. Deze kritiek noopte tot een heranalyse van een aantal belangrijke aspekten waarbij, naast de eigen gegevens, ook zoveel mogelijk gegevens uit de literatuur werden verzameld. De geanalyseerde aspekten betroffen de verteringskapaciteit en de dieetkeus. Daarnaast werden ook een deel van Hofmann's morfologische variabelen statistisch getoetst omdat Hofmann zelf dat nooit gedaan heeft.

Steeds werd per variabele gekeken of er klasseverschillen bestonden en of er een relatie gevonden worden met het lichaamsgewicht. Het resultaat was dat er zowel voor de verteringscapaciteit (voor celwanden) als voor de dieetkeus klasseverschillen konden worden aangetoond, terwijl er geen relatie was met het lichaamsgewicht. Merkwaardigerwijs bleek er maar bij één van de vijf morfologische variabelen een significant klasseverschil te bestaan terwijl twee van de vijf sterk en twee andere iets zwakker gerelateerd waren aan het lichaamsgewicht. Daar Hofmann zijn indeling baseerde op veel meer dan vijf karakteristieken is het niet goed mogelijk om op basis van deze resultaten zijn indeling te verwerpen. Eigenlijk heeft Hofmann herkauwers slechts geklassificeerd, en daarvoor veel variabelen gebruikt, waardoor er niet gesproken kan worden van een duidelijk hypothese. Hofmann beschrijft aanpassingssyndromen en dit maakt het lastig om per variabele te onderzoeken of klasseverschillen wel bestaan. Een betere benadering zou zijn om de vele variabelen tegelijkertijd te analyseren middels een principale componenten analyse. Op deze manier kunnen mogelijke klassen zichtbaar gemaakt worden op basis van een minder beschrijvende en meer analytische methode.

Daar dieetcompositie en verteringscapaciteit beide beinvloed worden door veel dierkarakteristieken kan men zeggen dat er tenminste drie aanpassingssyndromen kunnen worden onderscheiden. Dit impliceert dat natuurlijke selectie heeft geleid tot een unieke radiatie in de herkauwers, allemaal even goed aangepast en elk een specifieke nis bezettend.

In het laatste hoofdstuk (9) wordt aandacht besteed aan de evolutie, verspreiding van hoefdieren en aan de opbouw van hoefdiergemeenschappen. Onderzocht wordt of er verschillen bestaan in belangrijke aspekten van de reproduktie-snelheid tussen succesvolle recente groepen hoefdieren, de herkauwers (Ruminantia), en de 'langzaam uitstervende oudere' hoefdierfamilies (o.a. neushoorns, tapirs, paardachtigen en olifanten). Inderdaad bereiken vertegenwoordigers van de laatste groep , relatief ten opzichte van hetzelfde lichaamsgewicht, later de sexuele volwassenheid en kunnen ze minder jongen per jaar produceren. Deze nadelen kunnen mee een bijdrage hebben geleverd aan het verliezen van de concurrentieslag met de herkauwers.

Van de 176 soorten hoefdieren komen de meeste soorten voor in de tropen en veel minder in de gematigde en de koude streken. Azië en Afrika herbergen de meeste soorten terwijl in Europa, Noord Amerika en Zuid Amerika slechts weinig soorten voorkomen. De redenen hiervoor moeten gezocht worden in enerzijds het grote areaal dat de tropen beslaan en anderzijds in de optimumrelatie zoals die bestaat tussen soortsdiversiteit en produktiviteit van de vegetatie.

Vooral in Oost Afrika kunnen er tientallen soorten hoefdieren in een gebied samen voorkomen. Omdat het allemaal planteneters zijn kan de vraag gesteld worden of er ook concurrentie optreedt tussen sommige soorten. Bekeken is hoe hoefdier-gemeenschappen zijn opgebouwd op het niveau van een groot nationaal park. Er kunnen binnen zo'n gemeenschap verschillende groepen onderscheid worden die duidelijke verschillen vertonen in habitatpreferentie en voedselkeus. Tussen deze groepen is weinig concurrentie te verwachten. Binnen een groep komen echter frequent combinaties van soorten voor met eenzelfde lichaamsgewicht en die ook verder ecologisch gezien veel op elkaar lijken. Tussen deze soorten is concurrentie te verwachten tenzij er toch nog verschilen blijken te bestaan die zodanig groot zijn dat samenleven goed mogelijk is. Het opsporen van deze verschillen zou een beter begrip mogelijk maken van de structuur en het functioneren van soortenrijke hoefdiergemeenschappen.

DANKWOORD

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Dr. Rory Putman kindly corrected the greatest part of the English text but by doing so, also came up with many valuable suggestions for improving the contents.

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Dan is daar Marjolein. En zij is er nog steeds!

CURRICULUM VITAE

Sipke Egbert van Wieren werd geboren op 6 juli 1951 te Surhuisterveen. In 1968 behaalde hij het VWO diploma aan het Ichthus College te Drachten. In hetzelfde jaar begon hij met de studie Biologie aan de Rijksuniversiteit in Groningen. In 1977 werd het doctoraal examen afgelegd met als hoofdvakken Ethologie en Plantenoecologie. Van 1977 tot 1978 was hij verbonden aan de Rijksuniversiteit in Groningen waar hij onderzoek deed aan de populatiedynamica van het Spitsbergen rendier, na deel te hebben genomen aan een Spitsbergen expeditie in 1977 (REES'77). In 1979 en 1980 deed hij bij het toenmalige Rijksinstituut voor Natuurbeheer onderzoek naar de biologie van de gewone zeehond in het Nederlandse waddengegied. In 1981 en 1982 hield hij zich bij het Staatsbosbeheer bezig met het opstellen van een beheers- en inrichtingsplan voor het Nationaal Park Schiermonnikoog in oprichting. Van 1982 tot 1987 deed hij, als onderzoeker verbonden aan het Instituut voor Milieuvraagstukken van de Vrije Universiteit te Amsterdam, onderzoek naar de begrazingseffecten van Schotse hooglandrunderen op de Veluwe. In 1988 wederom werkzaam bij het Rijksinstituut voor Natuurbeheer werd onderzoek verricht naar de effecten van begrazing van hoefdieren op bos-(heide)gebieden. Vanaf 1989 tot heden is hij, eerst als onderzoeker, en vanaf 1995 als universitair docent verbonden aan de vakgroep Terrestrische Oecologie en Natuurbeheer van de Landbouwuniversiteit te Wageningen. Het grootste deel van de werkzaamheden ten behoeve van dit proefschrift is verricht in het kader van het 'Nationaal Bosbegrazingsexperiment 1990-1995'.