Foraging in a Landscape Mosaic

Diet Selection and Performance of Free-ranging Cattle in Heathland and Riverine Grassland

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Proefschrift
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STELLINGEN

1. Verschillen in de beschikbaarheid van minerale nutriënten bepalen in belangrijke mate de habitatkwaliteit voor grote herbivoren.
   Dit proefschrift

2. Aangezien runderen gedurende het groeiseizoen niet in hun voedselopname worden beperkt door de beschikbare graastijd kunnen zij hun nutriëntenopname ook maximaliseren door voor kwaliteit in plaats van opnamesnelheid te kiezen.
   Dit proefschrift

3. De plukmethode ter simulatie van het dieet van grote herbivoren is goed bruikbaar, mits gekoppeld aan haptellingen en een gestratificeerde bemonstering van het voedselaanbod.
   Dit proefschrift

4. Ondanks de aantrekkelijkheid van 'satisfycing' als hypothetische foerageerstrategie, is het een slecht uitgangspunt bij veldonderzoek, omdat het nauwelijks te falsifiëren valt.
   D. Ward (1992). Oikos 63:312-317.
   P. Nonacs & L.M. Dill (1993). Oikos 67:371-375.

5. Bij het toepassen van lineaire programmeringstechnieken voor het voorspellen van de dieet- of habitatkeuze van grote herbivoren vormt de aanname van de maximalisatie van slechts één nutriënt bij een minimumeis voor de andere nutriënten een te grote simplificatie.

6. De voortdurende aandacht van plantenecologen voor de vraag of planten bij vraat overcompensatie in de jaarlijkse bovengrondse productie kunnen vertonen is niet alleen merkwaardig vanwege de geringe aanwijzingen ervoor, maar ook omdat de biologische betekenis van overcompensatie voor de plant uitermate onduidelijk is.
   A.J. Belsky, W.P. Carson, C.L. Jensen & G.A. Fox (1993). Evol. Ecol. 7:109-121.
   D.G. Milchunas & W.K. Lauenroth (1993). Ecol. Monogr. 63:327-366.

7. Bij het begrazingsbeheer in Nederlandse natuurgebieden worden verschillen tussen veerassen ten onrechte sterker benadrukt dan de habitatkwaliteit.

8. Nu er binnen de Europese Unie een steeds duidelijker ontwikkeling is naar schaalvergroting, wordt het de hoogste tijd deze ook op natuurgebieden toe te passen.

9. Voor een kansrijke opzet van grote natuurgebieden zijn niet alleen deskundigheid en een goede organisatie van belang maar is vooral ook ondersteuning vereist voor de ontwikkeling van alternatieve bestaansbronnen voor gedupeerde plaatselijke bevolking.

10. Bij het zoeken naar referentiebeelden voor natuurgebieden in Europa ten behoeve van het natuurbeheer dient men niet zo zeer een nauwkeurige reconstructie van de 'oernatuur' na te streven, dan wel een beter begrip van de processen die natuurlijke ecosystemen kenmerken.

11. De veramerikanisering van de westerse maatschappij is een voortzetting van de tendens tot behoud van juveniele kenmerken in de menselijke evolutie.

12. De wetenschap groeit met het beantwoorden van vragen, de wetenschapper groeit juist met het stellen ervan.

Stellingen behorende bij het proefschrift van M.F. Wallis de Vries: *Foraging in a landscape mosaic: Diet selection and performance of free-ranging cattle in heathland and riverine grassland.*
Wageningen, 24 mei 1994.

'Information consists of differences that make a difference.'

Gregory Bateson (1979). Mind and Nature - A necessary unity.

'Le boeuf, lui, ne dit rien. C'est un ruminant, un méditatif, un taciturne. Il ne dit rien, mais il n'en pense pas moins. Il réfléchit et se souvient.'

Michel Tournier (1980). Gaspard, Melchior et Balthasar.

To Pipo with his bold and cheerful nature
and to Calimero who finally proved right

Abstract

Wallis de Vries, M.F. 1994. Foraging in a landscape mosaic: Diet selection and performance of free-ranging cattle in heathland and riverine grassland. Doctoral thesis, Agricultural University, Wageningen, The Netherlands, 161 pp., English and Dutch summaries.

This thesis focuses on two main questions regarding the relation between a large herbivore, *Bos taurus*, and habitat quality: a) how do differences in habitat quality relate to nutrition and herbivore performance? and b) is herbivore foraging behaviour affected by habitat differences and can it be explained by optimal foraging theory? The study was carried out in the Netherlands using free-ranging steers in an experimental set-up with four combinations of two habitats of contrasting soil fertility: heathland and riverine grassland.

A hand-plucking method was developed to estimate forage quality and intake; calibration was carried out using oesophageally fistulated steers. Cattle performance was significantly affected by habitat quality. On heathland animals showed relatively low weight gains and slow fat accumulation coupled to high weight loss over winter. These impairments were caused by deficiencies in sodium and phosphorus which led to a reduced energy retention, bone resorption and pica behaviour. Animals on riverine grassland demonstrated a performance close to their growth potential. The treatments with combinations of habitats emphasized these differences.

Foraging selectivity increased with differences in forage quality and quantity and with spatial scale. Selectivity between short, tall and stemmy patches within two grassland communities was low but significant. Short and tall patches were preferred over stemmy patches. The preference for short patches was consistent with a daily intake maximization of digestible organic matter but not in agreement with instantaneous maximization. It is suggested that cognitive limitations reduce selectivity of cattle at lower spatial scales. At a higher scale level selection between landscape types was distinct and broadly agreed with model predictions assuming daily maximization for the intake of digestible organic matter, sodium and phosphorus.

Implications of the relation between habitat quality and herbivore performance are discussed with regard to nature conservation. Breed differences in cattle are of little consequence in mild climates. Fragmentation and uniformity of habitats are of much greater importance. It is argued that the habitat requirements of large herbivores should be used to develop guidelines for basic conditions to the design of nature reserves. Experiments using free-ranging domestic herbivores can elucidate these habitat requirements.

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Acknowledgements

The path that leads to such a thesis is full of twists and turns, with scores of significant events and happy, valuable, instructive or simply useful meetings along the way. Let me recall the ones that I found particularly important.

My first aspirations to become a biologist owe much to my parents who stimulated my inquisitiveness and showed me to care for more than human beings only. I remember with affection the long walks with my father in the dunes of Kennemerland, in search of the ever elusive cuckoo, and later the hikes in the mountains and our adventurous attempts to conquer the Roc d'Enfer. The lessons of biology at school were always utterly boring and seemed merely devoted to a an orderly but meaningless accumulation of lifeless facts. I was therefore relieved and delighted, when in the first years at the Agricultural University in Wageningen, Prof. J.W.M. Osse from the Department of Experimental Animal Morphology and Cell Biology, emphasized that the true inspiration of the biologist lies in the fascination for the living world. I want to thank Jaap Graveland, Michiel Hootsmans, Hubert Kivit, Peter Schippers and Peter van der Wateren to have kept this fascination alive over the years.

I am very grateful to Dr. Henk Doing who introduced me to the holistic approach of landscape ecology in the unforgettable setting of Feldis in Switzerland. Jan Bokdam and Dr. Chris Geerling gave me the opportunity to become captivated by the intriguing world of large herbivores and plant-animal interactions. This finally resulted in the present study. I am much indebted to Jan Bokdam and Prof. C.W. Stortenbeker from the former Department of Nature Conservation for their efforts to secure the opportunity to start the present research project and for their support in the elaboration of the project proposal and its realization.

This research was supported financially by Staatsbosbeheer (the Forest Service) and by the Ministry of Agriculture, Nature Conservation and Fisheries (Directorate of Nature, Forest, Landscape and Fauna, NBLF). I gratefully acknowledge Jacques Hendriks and Toon van der Ouderaa from the Forest Service and Hans Kampf and Hein Kuijper from NBLF for their enthusiastic support of the project. The help of Hein Kuijper was also essential in arranging the possibility to use the Karshoek as a study area. This beautiful and valuable area was the property of the late R.F.C. Baron Bentinck van Schoonheten. His favourable and cooperative attitude towards the project was of crucial importance. I appreciate that, following his unexpected death, his daughter Mrs. M. Baroness Bentinck van Schoonheten was willing to allow us to continue the investigations. K. Hekman and his family showed great care, interest and enthusiasm in looking after the animals in the Karshoek and keeping track of their whereabouts. During the field work we were always received with warmth and generous hospitality, for which I am extremely grateful. J.H. Eshuis and his wife furnished us with a comfortable lodging in Diffelen. I thank the Vereniging tot Behoud van Natuurmonumenten, notably Rob Lichthart and Chris Seegers, to have given us the opportunity to use the study area of the Doorwerthse Heide, where W.F. Aandeweg, Henk Hofman and Dick van der Kooij kept an eye on the animals. The Forest Service, through the efforts of L.A. Oldenkamp and Aart Minnen, kindly placed a large part of the Renkumse Benedenwaarden at our disposal as a riverine study area.

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The field work formed of course the most agreeable and inspiring part of the study. The friendly company of the steers, each with his own temperament, on a lazy summer afternoon, a rainy autumn day or a frosty winter morning will not be lightly forgotten. Maurits Gleichman from the Department of Terrestrial Ecology and Nature Conservation was my companion throughout the experiment for many long days of field work. We must each have recorded about a million bites! I greatly enjoyed his friendship and involvement in the project, and I look back with gratitude on our cooperation. Others also contributed to the field work: Arend Vermaat and the students Remco Schreuder, Sjoerd Althuizius and Raymond Kerckhoffs; all had their share in bringing together the evidence that produced this thesis.

A large part of the work consisted of chemical analyses of plant material in the lab. I owe many thanks to Tjakkie van der Laan, Monique Coenraats and Mariet Schalkoort for having converted the seemingly endless stream of samples to a rich source of information. R. van den Brink was very helpful for the provision of a freeze-drying facility at the Department of Animal Husbandry. P.G.M. Versteeg and C. Rijpma carefully drew the

vegetation maps from the study areas. Bobo Freeke and Alfred Timmer helped us with photographic documentation. I further thank the colleagues from the Department of Terrestrial Ecology and Nature Conservation and those from the library for providing a relaxed working atmosphere and assistance in many ways.

The grinding of data and observations, their arrangement into a meaningful perspective and the process of putting their story into writing - it was not really an easy task, and of course it should not be. I was lucky to be guided, criticized and stimulated by a number of sharp-witted people. I want to thank some of them in particular. The first I should mention is Prof. R.H. Drent. I feel a deep gratitude for having been enriched with the spirit that emanates from his approach to the study of ecology. I must confess that his comments often caused quite some upheaval in my plans and convictions, but after this had subsided their effect would be inspiring. Others from this 'Groningen school of ecology' also contributed considerably to the shaping of my views and attitudes in research: Dr. Joost Tinbergen, Sip van Wieren, the late Dr. Harm van de Veen and, last but not least, Prof. Herbert Prins. I was greatly enchanted by the views of Harm van de Veen, Sip van Wieren and Frans Vera on restoration ecology, which did much to change my ideas on nature conservation.

During the writing of the thesis I had great benefit from the numerous comments of critical and careful readers. I am glad and grateful that they did not lose patience with me when my ideas were still in a muddle. Prof. Herbert Prins and Prof. L 't Mannetje reviewed all the manuscripts and confronted me with fruitful suggestions from two different but also related disciplines, animal ecology and range management. The following people contributed to the improvement of various chapters: Sip van Wieren (Chapters 3 to 8), Maurits Gleichman (Chapters 3 and 7), Frans Vera (Chapters 7 and 8), Dr. G. Hof (Chapter 4), Jaap Graveland (Chapter 4), Dr. Bert Tolkamp (Chapter 7) and Jan Bokdam (Chapter 8). Mrs. E.M. Kok-Dieben kindly revised the English of various chapters.

At the closing of these acknowledgements I express my thanks to all my friends and family for having tolerated my somewhat unsocial behaviour of these last months. Finally, José, I want to thank you for a great many things, but I will only mention here how I value the moments we spent together observing the steers, trying to fathom their slow and thoughtful, but also curious and enterprising minds.

CHAPTER 1

General Introduction

Introduction

Habitat heterogeneity has long fascinated ecologists investigating the relations between animals and their food supply. Food resources in the natural landscape are typically distributed in a mosaic of patches of variable size and shape with a fluctuating quantity and quality of food. The decisions of the forager, confronted with this variation in space and time, can be placed in a functional context of optimal foraging in which the animal gains most by maximizing its nutrient intake over a certain time period. Since the pioneering work of MacArthur & Pianka (1966) a vast number of studies and experiments have contributed to the development of optimal foraging theory (reviewed in Pyke *et al.*, 1977; Pyke, 1984; Stephens & Krebs, 1986; Hughes, 1990). The physiological state of the animal and the adequacy of its information on the environment emerge as two essential factors to explain foraging behaviour. For large mammalian herbivores additional constraints are apparent. They have to satisfy requirements for various nutrients, which may not be available in the same type of habitat (Belovsky, 1978 and 1990). They also face an abundance of low-quality food in comparison to other animal groups. This necessitates long feeding times on a large number of food items which are slow to digest (Owen-Smith & Novellie, 1982). Moreover, the ability of large herbivores to sense different nutrients by taste or smell is apparently limited (Provenza & Balph, 1990; Illius & Gordon, 1990), so that they have to rely on acquired experience to make foraging decisions (Provenza & Balph, 1990).

There is an extensive body of knowledge on habitat preferences of wild herbivores (*e.g.* Sinclair & Norton-Griffiths, 1979; Skovlin, 1982; Halls, 1984; McNaughton & Georgiadis, 1986; Prins, 1987; Campan *et al.*, 1991; De Bie, 1991) and free-ranging domestic herbivores (*e.g.* Senft *et al.*, 1985; Putman, 1986; Gordon & Illius, 1989; Duncan, 1992; Smith *et al.*, 1992). It is also known that differences in available habitat are reflected in animal growth and condition (Klein, 1965 and 1970; Geist, 1978). However, the understanding of the causes and mechanisms to explain the field observations is hampered by environmental complexity. Recently, a number of simulation studies have addressed the selection of habitats by large herbivores (Roese *et al.*, 1991; Loza *et al.*, 1992; Turner *et al.*, 1993). Yet, these models have a predominantly exploratory character, as the used assumptions still lack enough support of evidence from field data. It thus appears necessary to conduct field experiments in order to gain insight into a) the relation between habitat quality and herbivore performance, and, b) the foraging strategy of the herbivore in a patchy environment. These two issues form the focus of attention in the following chapters.

The setting

This thesis reports on a field study using cattle (*Bos taurus*) as a large herbivore in two habitats of widely different soil fertility. These habitats, heathland and riverine grassland, are characteristic features of the landscape in Northwestern Europe. The study took place in the Netherlands, a low-lying part of Northwestern Europe containing the delta of three rivers: Rhine, Meuse and Scheldt. These rivers flow into the North Sea. The landscape of the mainland is largely shaped by the rivers, the sea, the influence of glaciation and periglacial processes during the Pleistocene, and the formation of peat bogs thereafter (De Bakker, 1979). Clays and eutrophic peat form the parent material in the lowlands. Sands, dystrophic peat and, occasionally, loess, make up the parent material in the higher regions, which reach a maximum elevation of 107 m above sea-level in the Veluwe. The soils of the lowlands generally have a high soil fertility, in contrast to the podzols and peat soils of the higher grounds. Over the centuries human land-use has converted most of the lower regions to grassland and the higher, sandy regions to heathland (De Bakker, 1979). The difference in soil fertility between lowland and higher areas was well-known to cause differences in animal productivity and performance of livestock before the advent of artificial fertilizers (*e.g.* Hengeveld, 1865; Russell *et al.*, 1956). Nowadays the heathlands have been largely afforested with Scots pine (*Pinus sylvestris*) and other exotic conifers or they have been 'improved' for land-intensive agriculture.

Wild herbivores have disappeared from the majority of these habitats. Instead, grazing often takes place by large domestic herbivores as a part of a management strategy to preserve or restore biological diversity (Gordon *et al.*, 1990; Bokdam & Wallis de Vries, 1992). In the Netherlands, the suitability of heathland and riverine grassland as year-round habitats for large herbivores has been the subject of debate since the management policy shifted in favour of a minimization of human interference. This debate formed the practical motive to start the present experiment on the relation between habitat quality and animal performance. The experiment lasted two years (May 1989 till July 1991).

It was decided to compare two different habitats in four combinations of availability:

- Heathland only
- Riverine grassland only
- Heathland and riverine grassland in combination (both habitats permanently available)
- Controlled habitat use with summer grazing in riverine grassland and winter grazing on heathland.

The first two treatments were set up to examine the differences in performance between habitats. The third treatment enabled the investigation of habitat preference of the animals. The fourth treatment involved a manipulation of habitat use by seasonal transportation of the animals to show the impact of a change in habitat. This choice of seasonal use of heathland and riverine grassland was motivated by knowledge of the dynamics in forage quality and availability. It was suggested that riverine grassland would be a favourable habitat in summer but an inferior habitat in winter, whereas the heathland would show less variation over the year (Bokdam & Wallis de Vries, 1992). The reverse combination of seasonal habitat use was therefore considered less informative than the present treatment. In all treatments the stocking rate was chosen so as to prevent quantitative food shortage through grazing impact.

The study areas

The climate of the Netherlands is cool and temperate. Mean annual temperature at the meteorological station in Wageningen, close to the study areas 'Doorwerthse Heide' and 'Renkumse Benedenwaarden', is +9.5 °C, with a minimum in January of +1.5 °C and a maximum in July of +17.4 °C (KNMI, 1972). Annual precipitation averages 775 mm with a maximum in August and a twofold difference between monthly maximum and minimum. The climate in the third study area 'Karshoek', as described by data from the meteorological station Dedemsvaart, is only slightly different with a mean annual temperature of +8.9 °C and annual precipitation of 750 mm. Data for the study period (Fig. 1.1) show that 1989 and 1990 were relatively warm and 1991 was close to the long-term average (+10.5 °C, +10.6 °C and +9.4 °C, respectively). The winter of 1990 was extremely mild, but in 1991 the winter was normal with a distinct cold spell in February. Spring temperatures rose early in all years, yet in 1991 the second half of April and all of May were exceptionally cold and both winter and spring were dry. The summers of both 1989 and 1990 were relatively dry, though 1990 was overall the wetter year.

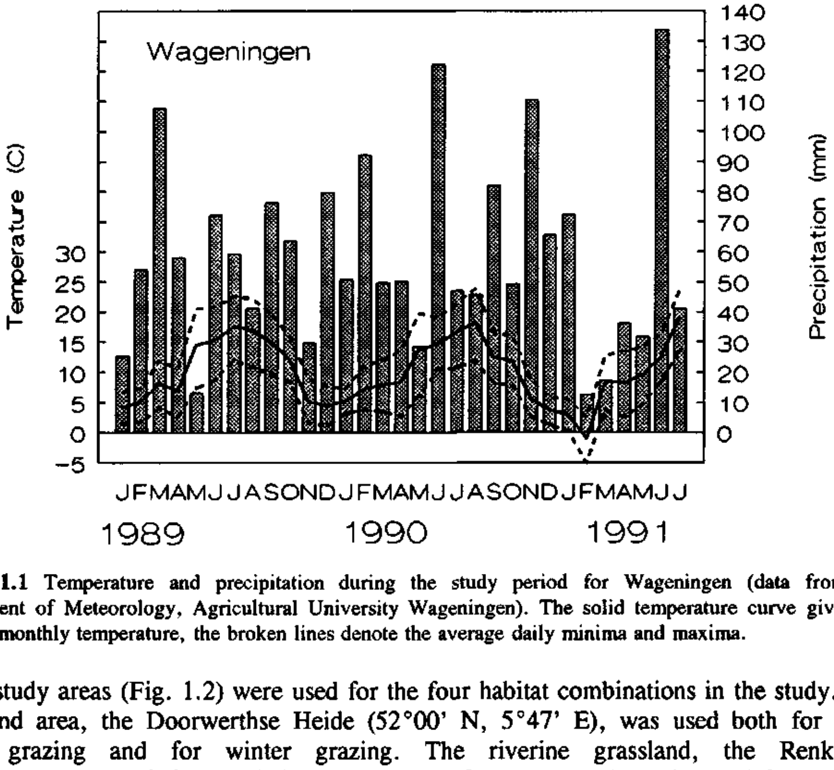


Figure 1.1 Temperature and precipitation during the study period for Wageningen (data from the Department of Meteorology, Agricultural University Wageningen). The solid temperature curve gives the average monthly temperature, the broken lines denote the average daily minima and maxima.

Three study areas (Fig. 1.2) were used for the four habitat combinations in the study. The heathland area, the Doorwerthse Heide (52°00' N, 5°47' E), was used both for year-round grazing and for winter grazing. The riverine grassland, the Renkumse Benedenwaarden (51°58' N, 5°43' E), was used for year-round grazing and for summer grazing. The combination treatment of heathland and riverine grassland was applied at the

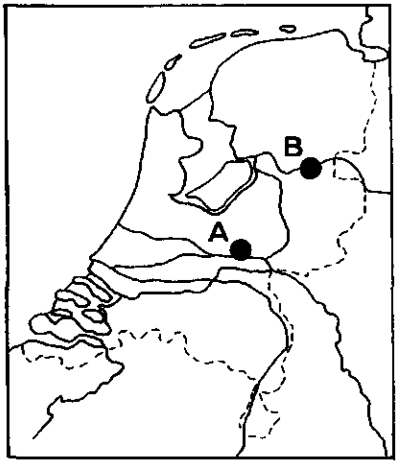


Figure 1.2 Location of the study areas in the Netherlands: A) Doorwerthse Heide and Renkumse Benedenwaarden, B) Karshoek.

Karshoek area (52°32' N, 6°32' E).

The difference in soil fertility between heathland and riverine grassland can be illustrated with data on the nutritive value of the main grass species (Table 1.1). The values for organic matter digestibility were comparable for low and high soil fertility, but the concentrations of nitrogen, phosphorus and calcium were clearly higher for the higher soil fertility. The nutrient concentrations of the grasses in the two riverine areas suggest that the soil fertility of the Renkumse Benedenwaarden is somewhat higher than in the riverine part of the Karshoek.

The vegetation in the study areas was mapped using recent aerial photographs (scale 1:18,000 enlarged to 1:2,500 or 1:5,000) and additional field measurements. Vegetation units were distinguished according to land form, vegetation structure and dominant plant species. The dry-weight-rank method ('t Mannetje & Haydock, 1963; Jones & Hargreaves, 1979) was used to describe the botanical composition of the grassland and heathland units more accurately; the species nomenclature follows Van der Meijden *et al.* (1990). The determination of botanical composition was carried out in three to four plots of 50x50 m^2 per vegetation unit. Within each plot 50 points (25x25 cm^2 quadrats) were sampled along a transect, at intervals of five paces. Three sampling periods (May, July and September 1989) were observed to account for seasonal variation within the growing season. In the study areas of the Doorwerthse Heide and Renkumse Benedenwaarden the dry-weight-rank method was used in combination with a double-sampling method of standing crop estimation (Haydock & Shaw, 1975) to adjust for differences in standing crop between measurement points.

Doorwerthse Heide

The Doorwerthse Heide is an area of heathland (50 ha) situated on an ice-pushed ridge (30 m above sea-level), dating from the Saalien glaciation (180,000-130,000 years Before Present). The parent material is of fluvio-glacial origin and sandy in texture with

Table 1.1 Annual mean and range for the nutritive value of hand-plucked samples of tall leafy grass in areas of different soil fertility: *Deschampsia flexuosa* in two areas with low soil fertility (Doorwerthse Heide and cover sand part of Karshoek) and *Agrostis stolonifera, A. capillaris* and *Lolium perenne* in two areas with high soil fertility (Renkumse Benedenwaarden and riverine point-bar of Karshoek). The samples were taken in 13 periods over two years. The range gives the minimum and maximum values.
(DOM = digestible organic matter, N = nitrogen, P = phosphorus, Na = sodium, Ca = calcium).

		Low Soil Fertility		High Soil Fertility	
		Doorwerthse Heide	Karshoek	Karshoek	Renkumse Benedenwaarden
DOM (% of dry matter)	mean	65.5	59.8	59.0	62.1
	range	(53.1-74.8)	(37.7-72.4)	(40.5-71.5)	(43.1-74.8)
N (")	mean	1.84	2.06	2.77	3.33
	range	(1.50-2.39)	(1.14-3.27)	(2.09-3.50)	(2.11-5.36)
P (")	mean	0.09	0.14	0.32	0.37
	range	(0.06-0.13)	(0.06-0.23)	(0.25-0.43)	(0.28-0.53)
Na (")	mean	0.02	0.02	0.06	0.07
	range	(0.01-0.03)	(0.00-0.05)	(0.02-0.20)	(0.03-0.14)
Ca (")	mean	0.15	0.17	0.38	0.60
	range	(0.09-0.18)	(0.12-0.25)	(0.27-0.58)	(0.38-0.75)

substantial amounts of gravel. The podzolized soils that have developed in this material carry a vegetation of dry heathland, dominated by *Calluna vulgaris* and *Deschampsia flexuosa* (Fig. 1.3). The occurrence of *Erica tetralix, Molinia caerulea* and, locally, *Carex nigra* and *C. panicea* indicates that the area was wetter early in the century, before it was drained by ditches. A strip of forest borders the heathland to the northern and eastern sides. Most of the older oak (*Quercus robur*) and pine (*Pinus sylvestris*) have been planted. Birch (*Betula pendula*) and Black cherry (*Prunus serotina*) have established spontaneously in the forest fringe but also in other parts of the area. On the western side the heathland is adjacent to arable fields to which slurry is applied. Airborne contamination with nutrients may have favoured the spread of *Deschampsia flexuosa*. The southern edge of the area looks down on a motorway.

Five vegetation units were distinguished in the area (Table 1.2): three units with a variable degree of dominance for *Calluna vulgaris* and *Deschampsia flexuosa*, one unit of vegetation dominated by *Molinia caerulea* and one unit of forest.

Prior to the grazing experiment, the management in the area consisted of cutting back birch and Black cherry in the open area to preserve the heathland aspect. Furthermore, most of the *Deschampsia flexuosa* vegetation was mown twice in the previous decade. For

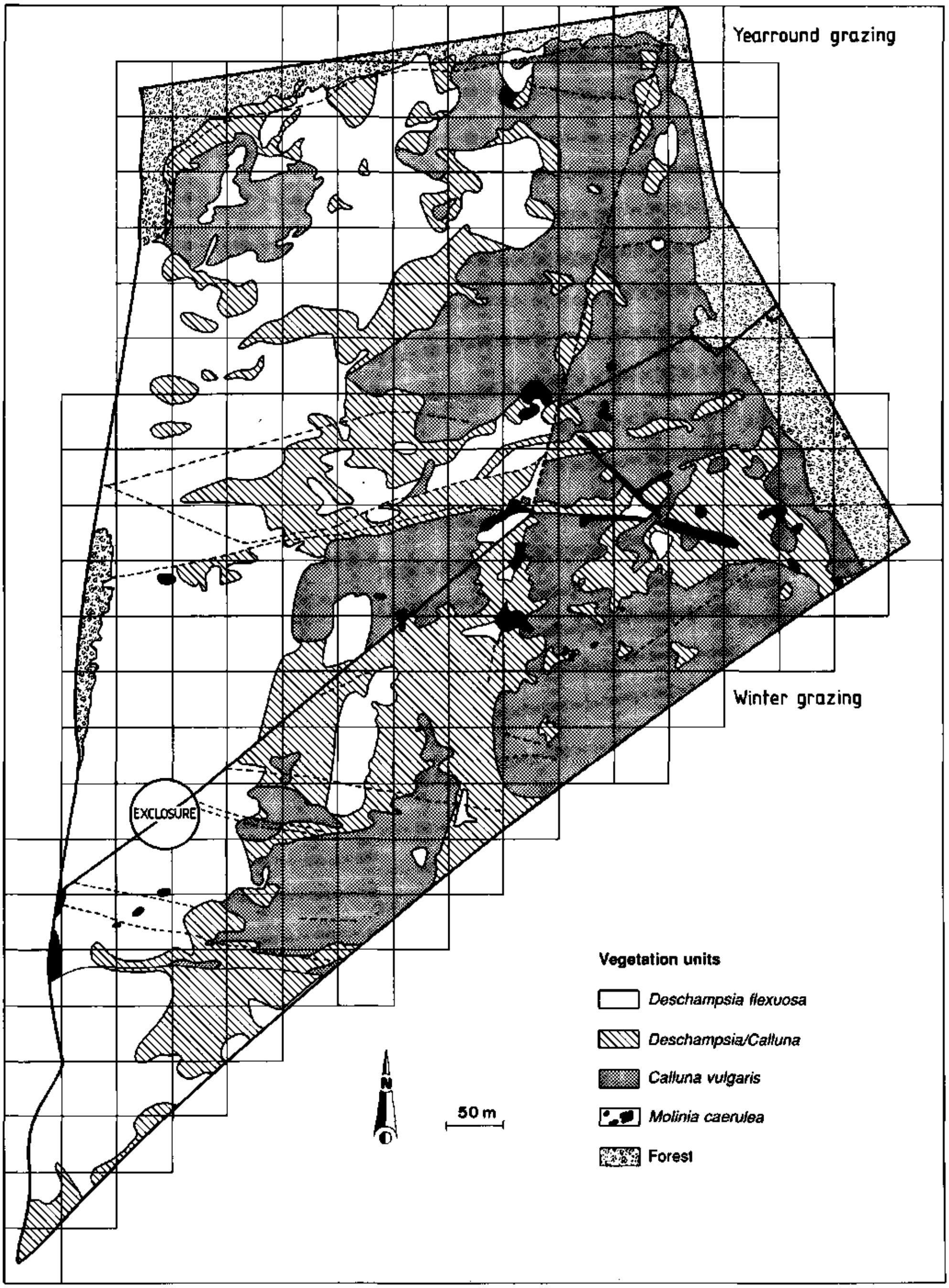


Figure 1.3 Vegetation units of the Doorwerthse Heide.

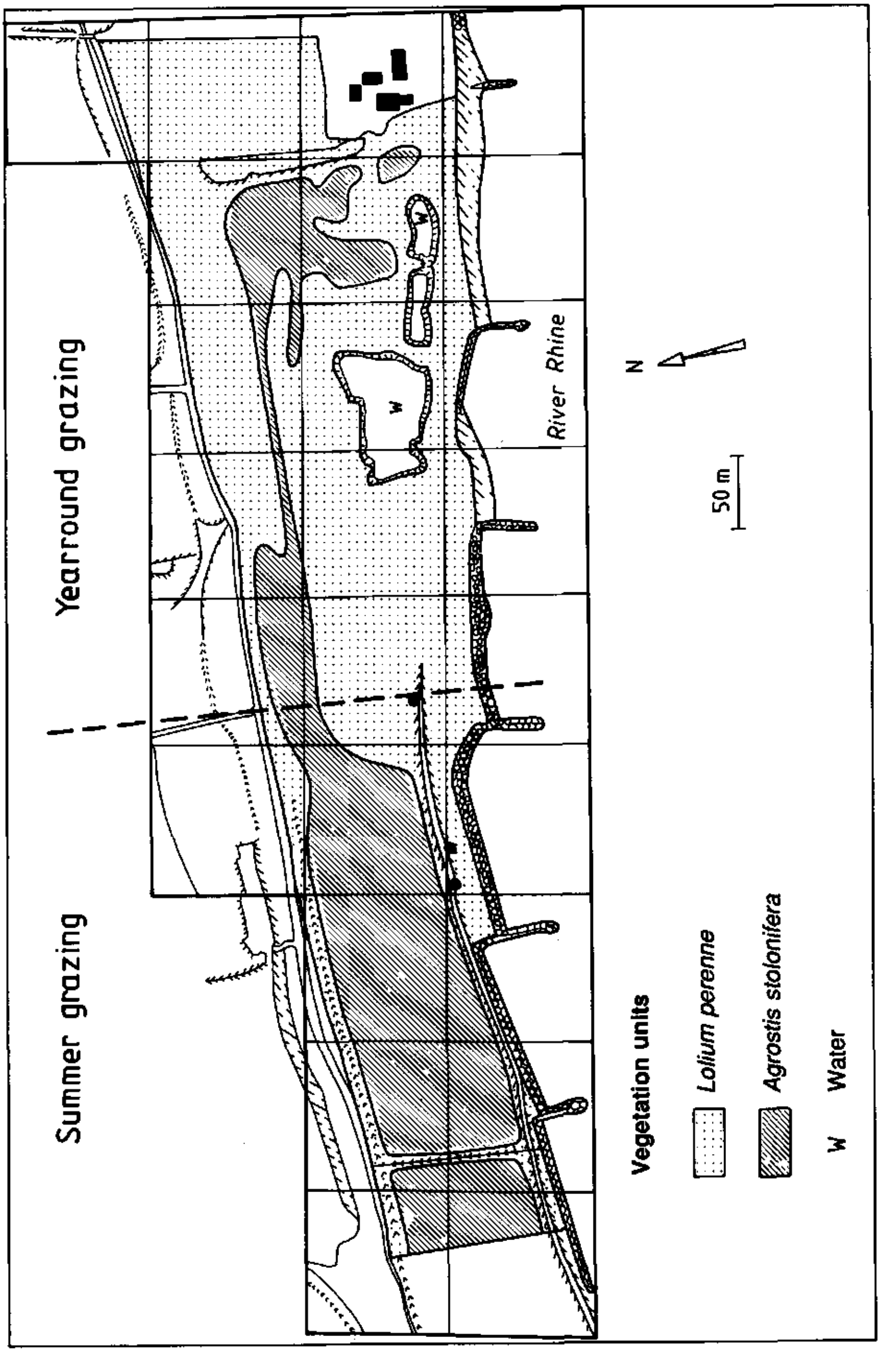


Figure 1.4 Vegetation units of the Renkumse Benedenwaarden. The vegetation unit of *Phalaris arundinacea* occurred in strips too narrow to be depicted.

the purpose of the experiment, the area was divided into two compartments by a fence running east-west (Fig. 1.3). The northern compartment (28 ha; including 1 ha without vegetation cover) was used for year-round grazing and the southern compartment (22 ha; including 0.3 ha without vegetation cover) for winter grazing (December-March); both compartments were stocked with five steers. No surface water is available in the area. Drinking water was therefore supplied in water tanks in the eastern part, near the fence between the two compartments.

Renkumse Benedenwaarden

This area of river forelands (14 ha), at an elevation of 7-12 m above sea-level, is situated 5 km southwest of the Doorwerthse Heide. It borders the river Rhine and is surrounded by pasture (Fig. 1.4). The river course has been fixed by the construction of a summer dike with perpendicular projections. Periods of flooding occur mostly during winter and in spring with the melting of snow in the Alps and lesser mountain ranges within the Rhine basin. Exceptional floods inundate the entire area, a few artificial levees excepted. During the study period two floods occurred, the highest leaving less than 1.5 ha free from water for a period of two weeks in February 1990.

The alluvial clay soil of this riverine area is calcareous and supports a productive grassland vegetation with a long history of land-use as summer pasture for dairy cows. Until the start of the experiment the grassland was regularly levelled and fertilized with slurry and artificial fertilizer. Woody vegetation is limited at present to a few trees of *Crataegus monogyna* and *Salix alba*. However, in the spring of 1989 seedlings of willow (*Salix spp.*) established on the sandy banks of the river following a rise in the water level. The two pools in the eastern part (0.4 ha) originated from former exploitation of clay. The northern border of the area consists of a canalized brook which discharges water from the sandy plateau to the north.

Three vegetation units were distinguished in the area (Table 1.2): a unit of *Lolium perenne* on higher grounds, a unit of *Agrostis stolonifera* characterized by *Alopecurus geniculatus* and *Rorippa sylvestris* in the depressions, and a unit of *Phalaris arundinacea* with tall grasses and herbs on the water's edge. Clones of *Cirsium arvense* spread rapidly in the grassland vegetation over the two years of the study, reaching a maximum cover in the *Lolium* unit of 31% in the second summer. The clones started to collapse in October and were reduced to a cover of less than 5% by the beginning of spring.

As in the heathland area, two compartments were made by erecting a north-south fence (Fig. 1.4). The eastern part (9 ha; including water) was used for year-round grazing and the western part (5 ha) for summer grazing (April-November) in combination with the winter grazing on heathland. Both compartments were stocked with five steers.

Karshoek

The area 'De Karshoek-Stegerense Veld' (abbreviated to Karshoek) covers 74 ha. It is situated at *ca.* 7 m above sea-level and at a distance of 100 km to the northeast of the other two study areas. The area and its vegetation have been described in more detail by Wallis de Vries (1991). The Karshoek borders the Vecht river and pastures in the South and forest plantations in the other directions (Fig. 1.5). The Vecht is a meandering river of some 200 km in length, draining part of the sand and peat plateaus of the eastern

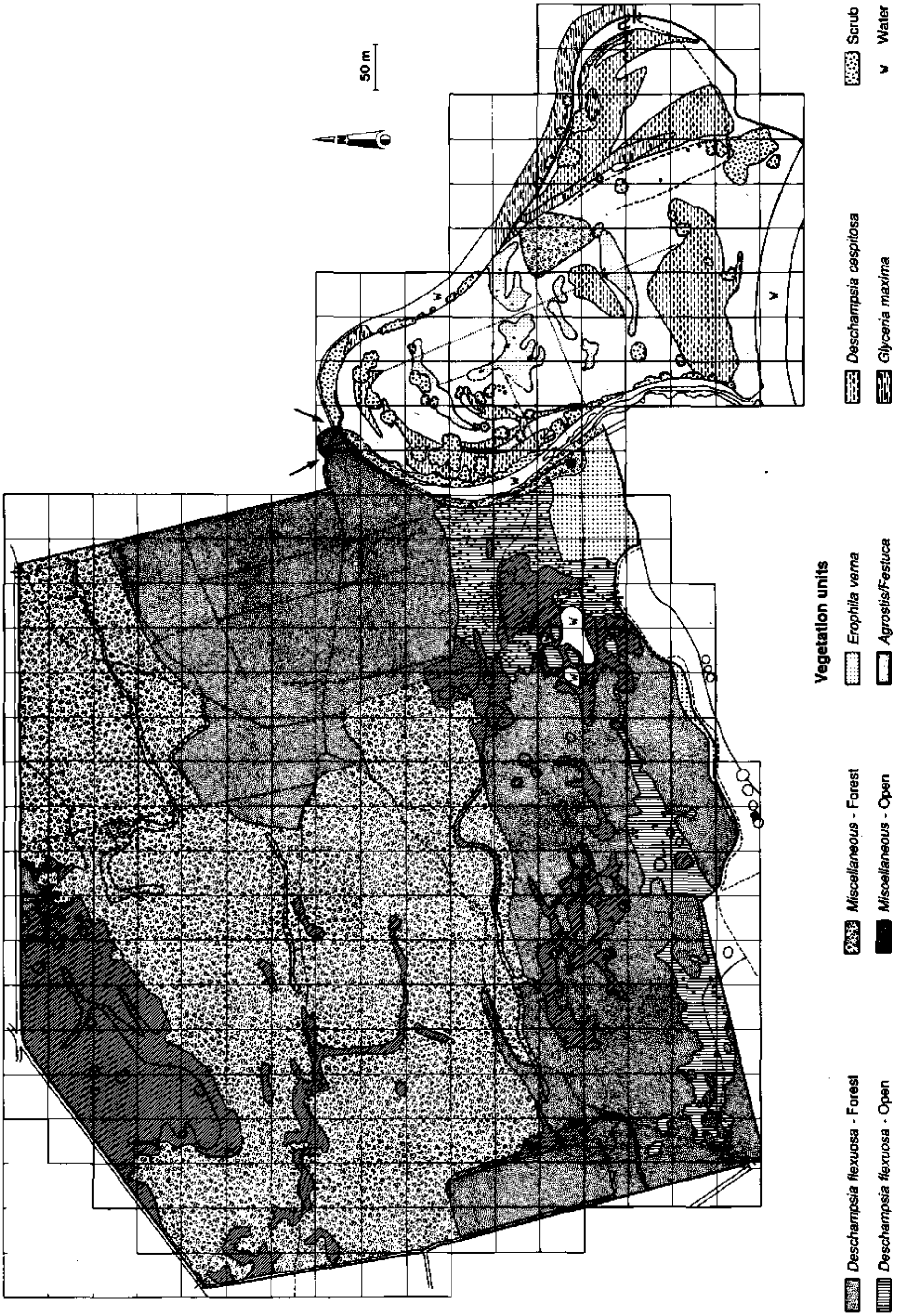


Figure 1.5 Vegetation units of the Karshoek. Note the two bridges at the northern end of the riverine part (see arrows), which connect the two landscape units: the riverine part in the east and the cover sand part in the west. The dots and small circles within units represent conspicuous trees and bushes.

Netherlands and northwestern Germany. Its volume is largely determined by rainfall. Floods do occur over relatively short periods and have become more frequent since the river was canalized and drainage of the surrounding land was increased. The regular fluctuations in the level of the river are controlled by several weirs. The canalization was carried out early in the 20th century, especially by cutting off a number of river bends at the upstream side. The downstream end of the bend remained connected to the river. The riverine part of the Karshoek (14 ha) consists of a point-bar encircled by the cut-off river bend (an additional 1.9 ha) with the canalized river to the south. The point-bar shows a typical pattern of alternating levees and depressions caused by the widening of the river meander and by dune formation. Locally, concretions of iron oxide have formed in the soil under influence of the high iron contents of the river water. The moist depressions have a sandy-loamy soil with a high organic matter content, the lower stream-bed ridges are drier and contain less loam and the dunes are dry and have poorly developed sandy soils. The point-bar has been used for centuries as a grazing ground for dairy cattle. In the southern part the dunes have been partly levelled and partly planted with pine (*Pinus sylvestris*). The use as pasture was intensified after 1945. The area was split up into five compartments, grazed in rotation mainly by heifers. Encroaching bushes and thistles were removed. The southern compartments received fertilization from artificial fertilizers and later on also from slurry. The enhanced production enabled hay-making once or twice a year in addition to the use for grazing.

The landscape of the river valley is embedded in a landscape of cover sand (60 ha) dating from the end of the Pleistocene. Moist podzolized soils have developed in the cover sand during the Holocene. The natural forests were converted to heathland by human land-use. Over-exploitation during the Middle Age impoverished the vegetation cover and turned the soil bordering the river valley into shifting sands. The resulting dunes were later colonized by bushes of *Juniperus communis*. A large part of this drier area of dunes was afforested with pine and a 1 ha-plot of oak (*Quercus rubra* and *Q. robur*) was planted during the 1920s. The heathland was used for sheep grazing until the 1930s and was then abandoned. Spontaneous establishment of pine gradually encroached upon the heath. The remaining heathland has been preserved by sod-cutting in 1982 and 1988.

Six vegetation units were distinguished in the riverine part and five units in the cover sand or so-called heathland part (Table 1.2). Within the riverine part the *Erophila verna* unit covers the dry river dunes. The vegetation is characterized by a number of annual species flowering in spring. The vegetation cover is fragile due to the often extreme summer drought. The *Agrostis capillaris/Festuca rubra* unit is the largest vegetation unit of the riverine part. It covers the ancient stream-bed ridges and the levelled dunes. Its diagnostic species are *Galium verum, Dianthus deltoides* and *Pimpinella saxifraga*. The *Deschampsia cespitosa* unit is a tussock grassland in depressions with a fluctuating water table. Inundation is frequent during winter. This unit is further characterized by the occurrence of *Festuca pratensis* and *Ranunculus repens*. The unit dominated by the tall grass *Glyceria maxima* occupies the wettest sites, gradually filling up the stagnant eutrophic water of the old river meander. Woody vegetation occurs in the Miscellaneous/Forest unit (0.4 ha, see below) and the Scrub unit. The latter is dominated on the drier parts by the shrub *Prunus spinosa*, which spreads by vegetative expansion,

Table 1.2 Description of the vegetation units in the three study areas. Dominant plant species represent more than 10% of available forage, accompanying species represent 5-10% of available forage.

Vegetation unit	Area (ha)	Geomorphology & Topography	Dominant species	Accompanying species
HEATHLAND				
Deschampsia	12.08[1]/ 4.48[2]	dry sandy/gravelly Pleistocene ice-pushed ridge	*Deschampsia flexuosa*	*Calluna vulgaris*
Deschampsia/Calluna	4.54/ 7.08	"	*Deschampsia flexuosa* *Calluna vulgaris*	
Calluna	7.72/ 8.24	"	*Calluna vulgaris*	*Deschampsia flexuosa* *Erica tetralix*
Molinia	0.22/ 0.35	"	*Molinia caerulea*	*Deschampsia flexuosa*
Forest	2.46/ 1.30	"	*Prunus serotina* *Pinus sylvestris* *Quercus robur*	*Betula pendula*
RIVERINE				
Lolium	6.75/ 1.63	drier Holocene riverine clay sediment	*Lolium perenne* *Elymus repens* *Agrostis stolonifera* *Cirsium arvense*	*Poa trivialis* *Ranunculus repens*
Agrostis	1.26/ 3.15	moist Holocene riverine clay sediment	*Agrostis stolonifera* *Ranunculus repens* *Poa trivialis*	*Elymus repens*
Phalaris	0.71/ 0.38	wet riparian zone	*Phalaris arundinacea*	*Salix spp.* *Glyceria maxima*

[1] Values mentioned first concern the year-round compartment.

[2] Values mentioned second concern the winter compartment on heathland and the summer compartment in the riverine area.

accompanied by the equally thorny *Rubus fruticosus* and *Rosa canina*. Oaks and *Sambucus nigra* establish in the centre of older scrub. Willow scrub (*Salix purpurea* and *S. cinerea*) occurs in the wetter depressions.

The units of the cover sand area (Table 1.2) have been roughly divided according to the distribution of forest and the occurrence of *Deschampsia flexuosa*, a potentially important forage species. The units with *Deschampsia flexuosa* cover the drier parts of the area including the dunes. *Prunus serotina* is a common shrub in most of the

(Table 1.2 continued)

Vegetation unit	Area (ha)	Geomorphology & Topography	Dominant species	Accompanying species
KARSHOEK				
Riverine part				
Erophila verna	0.90	dry river Holocene dunes	*Agrostis capillaris* *Poa pratensis* *Rumex acetosella*	*Festuca rubra* *Carex arenaria* *Agrostis vinealis*
Agrostis/Festuca	7.89	dry sandy/loamy Holocene river sediment	*Agrostis capillaris* *Poa pratensis* *Holcus lanatus*	*Festuca rubra* *Rumex acetosa*
Desch. cespitosa	3.19	moist loamy Holocene river sediment	*Agrostis stolonifera* *Deschampsia cespitosa* *Alopecurus pratensis* *Holcus lanatus*	*Lolium perenne* *Agrostis capillaris*
Glyceria maxima	0.44	wet riparian zone	*Glyceria maxima*	*Typha latifolia*
Scrub	1.20	dry/moist sandy/loamy Holocene river sediment	*Prunus spinosa* *Quercus robur*	*Sambucus nigra* *Salix purpurea*
Heathland part				
Desch. flexuosa/Forest	20.18	dry Pleistocene cover sand + dunes	*Deschampsia flexuosa* *Pinus sylvestris* *Prunus serotina*	*Betula pendula*
Desch. flexuosa/Open	3.73	"	*Deschampsia flexuosa* *Juniperus communis*	*Calluna vulgaris*
Quercus-Forest	1.15	"	*Quercus robur* *Quercus rubra*	
Miscellaneous/Forest	26.92	dry/moist Pleistocene cover sand	*Erica tetralix* *Molinia caerulea* *Pinus sylvestris*	
Miscellaneous/Open	8.31	" "	*Erica tetralix* *Molinia caerulea* *Calluna vulgaris*	

Deschampsia flexuosa/Forest unit and *Juniperus communis* is locally abundant in the *Deschampsia flexuosa*/Open unit. The Miscellaneous/Forest unit consists mainly of young, dense pine forest with little ground vegetation apart from some *Erica tetralix*, with the exception of 9 ha with *Molinia caerulea*. Some deciduous forest of alder (*Alnus glutinosa* and *A. incana*; 0.4 ha) without ground vegetation is also included in this unit. The *Quercus*-Forest has been distinguished as a separate unit, because of the availability of acorns in autumn. The Miscellaneous/Open unit is an assemblage of smaller units of moist heath (3.5 ha), dry heath (0.9 ha) and wet depressions (3.6 ha). The dry heath is dominated by *Calluna vulgaris* with *Cuscuta epithymum* as a characteristic species. The moist heath is dominated by *Erica tetralix* with *Calluna vulgaris* as an accompanying species and *Scirpus cespitosus, Drosera intermedia* and *Rhynchospora fusca* as diagnostic species. The wet depressions occur in the form of east-west running natural channels. They are mostly covered with a dense tussock vegetation of *Molinia caerulea* accompanied by *Erica tetralix*. The largest depression in the centre of the cover sand area has been dug out earlier this century and is now filled with a vegetation of *Eriophorum angustifolium, Juncus effusus* and *Carex rostrata*. Bare ground covers an additional 0.3 ha and surface water 0.2 ha.

Before the start of the experiment the cover sand area was fenced, the fencing within the riverine part was removed, and the construction of two bridges was begun to connect the two landscape types. Ten steers were released in the area in May. The bridges were finished by the second half of August 1989. The animals could range freely between the two areas thereafter. Drinking water was available on numerous points over the entire area.

The herbivore

Bos taurus, domestic cattle, was chosen as the species for the present study. This decision was based on four major arguments besides the practical motive that they occupy a central role as a large herbivore in the management of nature reserves in the Netherlands. First, using cattle has the important advantage that one can benefit from a large amount of knowledge on their nutritional requirements and growth performance under different conditions. Second, cattle are relatively easy to handle. Third, they can be approached close enough to allow detailed observations of grazing behaviour and fourth, their limited selective ability arising from the large dimensions of their mouth parts, increases the possibility to track diet selection in a complex vegetation. Furthermore, domestic herbivores generally offer greater opportunities to manipulate experimental conditions. These advantages have been exploited before in other studies (see for example references in Ungar & Noy-Meir, 1988; Provenza & Balph, 1990). There may be a disadvantage to use a domestic species which has been removed from its original environment and has been subject to artificial selection. Yet, in a review on the effects of domestication on behaviour, Price (1984) found that most differences between domestic and wild species are quantitative rather than qualitative in nature. The possible bias arising from the study of a domestic species is therefore not likely to be of fundamental importance.

Bos taurus is a large-bodied ruminant of the family *Bovidae*, tribe *Bovini*, which counts mainly species of comparable size: Banteng (*Bos banteng*), Gaur (*Bos gaurus*), Kouprey (*Bos sauveli*), Yak (*Bos grunniens*), American and European bison (*Bison bison* and *B. bonasus*), Water buffalo (*Bubalus bubalis*) and African buffalo (*Syncerus caffer*)

(Sinclair, 1977). The wild ancestor of the present-day cattle, the aurochs (*Bos primigenius*), became extinct in Poland in 1627 (Szafer, 1968). Domestic cattle are considered to belong to the same species as the aurochs (Epstein & Mason, 1984). Cattle, like most large *Bovini*, have evolved a complex digestive system which, in combination with their large size, enables them to digest the cell wall material of plants to an extent unparalleled by other herbivores (Van Soest, 1982; Hofmann, 1989). They are therefore well equipped to rely on grasses as a principle food resource. On the other hand they avoid woody plants and herbs with high contents of secondary plant compounds, especially tannins, since grazers are not well adapted to neutralize the reduction in digestion caused by these substances (Robbins *et al.*, 1987; Bernays *et al.*, 1989). The predominance of grasses in the diet of cattle simplifies the study of their nutrition, as secondary plant compounds will rarely play a significant role.

The cattle used in this study were steers of the Dutch Meuse-Rhine-Yssel (MRY) breed, a dual-purpose breed (both dairy and beef) which has been increasingly selected for milk production. The performance of MRY steers was compared against the performance of steers from an original beef breed, the Hereford, to evaluate possible breed differences. The two breeds were grazed together in the Karshoek area (five steers from each breed). Steers were chosen because they are intermediate in growth performance between bulls and cows (ARC, 1980) and because they are easy to handle. The animals were yearlings when the experiment started. They were housed in a stable with other steers of similar age in the six months preceding the experiment and weighed every fortnight. This allowed a selection of animals for body weight so that the different treatments received animals of comparable body weight. Initial treatment means for body weight were (± standard deviation, N=5): Heathland 314.8 ± 22.8 kg, Riverine 318.8 ± 37.5 kg, Combination of habitats MRY 316.6 ± 20.4 kg and Herefords 310.6 ± 31.0 kg, Controlled habitat use 316.4 ± 21.3 kg. All animals were treated annually against parasites to avoid any confounding effects of parasite load. It will be clear that there was no risk of predation for the animals. No form of supplementary feeding was given during the study period, with the exception of the provision of low-quality hay of *Molinia caerulea* (15 kg/day for one or two weeks) to the animals that were transported between heathland and riverine grassland, to facilitate their adaptation to the sudden change in diet. Shelter from adverse weather conditions was available in all study areas in the form of vegetation cover or land rises.

Outline of the thesis

Quantifying food intake and dietary quality presents a major difficulty when studying free-ranging herbivores. Yet, it is of crucial importance for the understanding of animal performance. This methodological problem is addressed in Chapter 2, which deals with the question how behavioural observations and indirect measurements can be used to estimate intake and nutritive value of the diet. The method selected relies on simulating bites by hand-plucking and integrating the information thus obtained on bite size and nutritive value with observations on biting rate and grazing time. A group of four oesophageally fistulated steers was used to test the hand-plucking method.

Chapter 3 provides a general overview of the results obtained on animal performance in the different habitat combinations. Information on body weight change and mineral status is presented to generate hypotheses on the functional processes behind the observed differences between treatments. The aspects of nutrition and foraging behaviour which may elucidate these processes are further investigated in the three subsequent chapters (Chapters 4-6).

In Chapter 4 the nutritional budget of steers in the different habitats is considered with respect to protein (nitrogen) and minerals in relation to energy intake and body condition. Special attention is given to the importance of minerals to explain patterns of body condition for both cattle and wild herbivores in habitats of low soil fertility.

Herbivores may modify their diet composition and, hence, their condition by selection for specific food resources. Cattle are known to be rather unselective grazers in a fine-grained vegetation, but they could be more selective between larger patches within a vegetation. The selection of foraging cattle between patches of different vegetation structure has been investigated for two grassland vegetation units. In Chapter 5 this patch selection is examined within the context of optimal foraging theory.

Foraging selectivity can differ between scale levels. Chapter 6 addresses the selection at a higher scale level between vegetation units in a landscape type and, finally, between landscape units in a landscape mosaic. A model is presented which predicts the habitat occupancy of grazing cattle under the assumption of nutrient maximization. The model predictions are tested using the data from the treatment with combined habitats.

Chapter 7 focuses on the differences between cattle breeds with regard to their adaptation and survival under free-ranging conditions. Physiological differences between breeds are reviewed. The comparison between MRY and Hereford steers in the present field study is used as a test case. The implications of breed differences for the choice of breed types in conservation areas are discussed.

The implications of insights emerging from this study for the practice of nature conservation are carried further in Chapter 8. Large wild herbivores are presented as keystone species in a variety of continental ecosystems. Their current status in Western Europe is reviewed, as an example of a region subject to a high degree of anthropogenic influence. The idea is then proposed to use the habitat requirements of large herbivores for the development of guidelines for the design of nature reserves.

The synthesis in Chapter 9 puts the findings from the entire study within an overall perspective: the challenge of the foraging herbivore to meet its nutritional requirements in a complex environment. The relevance of landscape and vegetation features to the herbivore is discussed in relation to its constraints in perceiving differences in forage resources. Emerging insights are used to give an outline of a foraging strategy of cattle which takes the cognitive limitations of the animal into account.

Plate 1. The heathland study area: the Doorwerthse Heide.

Plate 2. The riverine study area: the Renkumse Benedenwaarden (Photo J.M. Gleichman).

Plate 3. The cover sand landscape in the combination area, the Karshoek.

Plate 4. The riverine landscape in the combination area, the Karshoek (Photo J.M. Gleichman).

CHAPTER 2

Estimating Forage Intake and Quality in Grazing Cattle: A Reconsideration of the Hand-plucking Method

Summary

The hand-plucking method for estimation of bite size and nutritive quality was tested for steers grazing at low stocking rates on heathland and in riverine grassland. Vegetation height, standing crop and cover of distinct plant categories were determined in thirteen sampling periods over two years. In each period bite size was estimated with four oesophageally fistulated steers. Bite counts on different plant categories were made during sampling. The plant categories were sampled separately by hand-plucking and weighed to determine plucking size. Extrusa and hand-plucked samples were analyzed for concentrations of nitrogen and calcium.

Vegetation height was a more accurate predictor of plucking size than standing crop. A curvilinear relationship was derived between plucking size and bite size. The nutritive quality of extrusa and hand-plucked samples was not significantly different.

It is concluded that the application of the hand-plucking method appears promising when a stratified sampling approach to hand-plucking is followed. Future studies should examine operator-biases and how these can be minimized.

(submitted to the Journal of Range Management)

Introduction

The estimation of food intake and diet quality of wild herbivores is usually dependent on indirect, vegetation-based methods or on analysis of faeces or rumen contents (Putman, 1990). These methods are often inaccurate and may result in a considerably biased estimate. For domestic animals, which may be observed or captured easily, more appropriate methods have been developed (Corbett, 1978; Holechek *et al.*, 1982a; Bird *et al.*, 1984; Langlands, 1987). Intake can be estimated by determining faecal output and diet digestibility. The first quantity can be estimated by determining total faecal output or by regularly giving a known amount of an inert marker such as chromium oxide and measuring its dilution in a faecal sample. Diet digestibility can be satisfactorily estimated by *in vitro* digestibility determination using samples from oesophageally fistulated animals. Two alternative methods for the assessment of diet digestibility are the faecal index method and the *in vitro* digestibility determination of hand-plucked samples, taken to simulate the diet selected by the animal. The hand-plucking method is subject to a mostly unknown bias as the simulation of the grazing animal is likely to be imperfect. The faecal index method uses a relationship between the faecal content of an indicator, such as nitrogen, and diet digestibility. Serious drawbacks of this method are that the relation may vary between plant species, plant part, season and animal species. However, a number of studies have shown successful applications of faecal analysis for the determination of dietary contents of nitrogen and phosphorus (Holechek *et al.*, 1982a and 1985; Leslie & Starkey, 1985; Wofford *et al.*, 1985).

Oesophageally fistulated animals are widely used in studies of diet selection, as the extrusa samples offer the opportunity to assess bite size (Forbes, 1988) and the botanical composition of the diet (Holechek *et al.*, 1982b). However, their use for assessing the nutritive quality of the diet is limited. Salivary contamination considerably raises the contents of ash, sodium and phosphorus so as to preclude any accurate estimation of these constituents in the diet (Holechek *et al.*, 1982a; Langlands, 1987). Contents of nitrogen are altered by salivary contamination but do not differ on an organic matter basis (Little, 1972; Pinchak *et al.*, 1990). Concentrations of some minerals, calcium in particular, do not appear to be different in extrusa samples (Little, 1975; Pinchak *et al.*, 1990). The organic matter digestibility of extrusa samples is generally considered to be similar to the original feed, but several experiments have revealed significant differences between the two (Langlands, 1966; Holechek *et al.*, 1982a; Burritt *et al.*, 1987; Armstrong *et al.*, 1989). Extrusa organic matter digestibility in cattle is generally higher than the feed for values above 60-65% and lower for less digestible forage (Langlands, 1966; Armstrong *et al.*, 1989). Although the deviations remain limited to a maximum of around 2% (digestibility units) when applying regression formulas, the difference between feed and extrusa digestibility may be 5-10% for individual samples (Armstrong *et al.*, 1989). An experiment by Wallis de Vries (1990) gave similar results, although no significant differences between feed and extrusa digestibility could be demonstrated.

Extrusa samples thus may yield biased estimates of dietary quality for several components. Moreover, in heterogeneous vegetation extrusa samples usually consist of a mixture of plant parts and species. This hampers the study of diet selection as the quality and bite size of specific plant categories remains unknown. A solution to this problem can be found by recording grazing behaviour. Free *et al.* (1971) have shown that direct animal observations can be used to estimate the botanical composition of the diet. Simulation of the observed diet by hand-plucking (or by selective clipping) can then be considered for the investigation of the selection between forage items of different botanical and chemical composition. Hand-plucking could further be used to assess bite size and nutritive quality under range conditions.

Langlands (1974) found that hand-plucking underestimated digestibility and nitrogen content of sheep diets for low herbage quality and overestimated nutritive value when herbage quality was high. Also, nutritive value of hand-plucked samples varied between operators. Edlefsen *et al.* (1960) compared the composition of hand-plucked forage with extrusa from oesophageally fistulated sheep under range conditions. Differences in nitrogen and cellulose contents were not significant. A number of other constituents (ash, lignin, carbohydrates minus cellulose, gross energy and phosphorus) were significantly different but this was at least partly due to contamination with saliva. Van Rees (1984) collected hand-plucked and extrusa samples from two steers on three consecutive days in high-quality grassland. No significant difference in organic matter digestibility was found between the two sample types. These findings suggest that the method might be applied successfully with careful experimentation.

Earlier experiments reported by Wallis de Vries (1990), indicated that hand-plucking underestimated organic matter digestibility of cattle diets when an average pasture sample of about 100 simulated bites was compared with an extrusa sample. However, a trial using a refinement of the method closely predicted diet digestibility. The refinement consisted of sampling different plant categories separately and estimating diet digestibility according to the proportion of recorded bites on these categories. This chapter presents a more extensive test of the applicability of the hand-plucking method to assess bite size and nutritive quality of cattle diets.

Methods

Study sites

The grazing trials were conducted in two widely different vegetation types in a heathland area and a riverine area in the Netherlands. The heathland area, the formerly ungrazed Doorwerthse Heide (50 ha), is dominated by a vegetation of *Deschampsia flexuosa* and *Calluna vulgaris*. It was divided into two compartments, one grazed year-round (0.18 steers/ha) and one with winter grazing only (0.23 steers/ha from December to March). The riverine area, the Renkumse Benedenwaarden, is a river foreland of the Rhine river with a long history of use for pasturing livestock. The vegetation is dominated by *Agrostis stolonifera, Lolium perenne* and *Elymus repens*. The area was also split up into two compartments, one grazed year-round (0.57 steers/ha) and one with summer grazing only (0.96 steers/ha from April to November).

Experimental design

Thirteen experimental periods were planned at two month-intervals over two years, from May 1989 till May 1991. On each occasion two plots of 40x50 m^2 were sampled in all three currently grazed areas. Sampling plots were fenced off with electric wire on the sampling day.

Four oesophageally fistulated steers (aged *ca.* 13 months and weighing *ca.* 300 kg at the start of the first experiment) were used to collect samples from the selected diet. The animals were turned out in the area at least three days before experimentation. They were fasted *ca.* 4 hours prior to sampling to increase their willingness to graze. Samples were caught in a small bucket with soft plastic wings, strapped to the animal. Food recovery was ensured by fitting a foam plug in the animal's oesophagus. However, in two steers with a particularly large fistula the plug mostly fell out and was left therefore not used in these two animals; there was no evidence that this caused a reduction in the amount of food recovered. Each extrusa sample (50-250 g dry matter) required 5-10 minutes of grazing. On average 3.2 adequate samples were collected per plot.

The grazing behaviour of the animals was observed during sample collection, using the OBSERVER 2.0 computer programme (Noldus, 1991). Records were made of the biting frequency on different plant categories (Table 2.1). There were no significant differences in selection of the main plant categories between fistulated and non-fistulated steers (Schreuder, 1990). The plant categories were sampled by hand-plucking (50-100 pickings for each category) by the same operator over the entire experiment. The operator had been observing the grazing animals for at least two days before sampling. The samples were plucked between the thumb and a backward-bent forefinger, simulating the steers' grazing as close as possible.

Table 2.1 Plant categories distinguished on heathland and in riverine grassland.

Both areas:		
Short grass	:	leafy sward < 7 cm high
Tall grass	:	leafy sward > 7 cm high
Stemmy grass	:	sward with > 2 flowering stems/dm^2
Heathland only:		
Short *Molinia*	:	*Molinia caerulea* < 20 cm high
Tall *Molinia*	:	*Molinia caerulea* > 20 cm high
Other grasses	:	Various short broad-leaved graminoids
Short *Calluna*	:	*Calluna vulgaris* < 20 cm high
Tall *Calluna*	:	*Calluna vulgaris* > 20 cm high
Erica	:	*Erica tetralix*
Riverine grassland only:		
Phalaris	:	*Phalaris arundinacea*
Butomus	:	*Butomus umbellatus*
Cirsium	:	*Cirsium arvense*
Rumex	:	*Rumex obtusifolius* + *R. crispus*

In each experimental period the vegetation height and available standing crop for the three grass categories (*i.e.* short, tall and stemmy grass) in each compartment were measured in two (riverine grassland) or three (heathland) plot transects. Each transect consisted of 50 points, one every five meters, in ten parallel lines. At every point the plant category was recorded and vegetation height was measured with a tempex disc (*ca.* 8 g, 10 cm diameter) which was gently lowered onto the vegetation along a measuring-rod. A sample of the standing crop was taken every fifth point by clipping an area of 25x25 cm^2 down to a height of 2 cm or to the level of litter and dead plant material. At least four samples were clipped for each grass category (not enough material with flowering stems was available for clipping in May 1991 on heathland).

Sample analyses
The samples were stored in polythene bags at -20 °C. Extrusa samples were freeze-dried subsequently to prevent Maillard browning reactions, whereas hand-plucked and standing crop samples were oven-dried in a force-draught oven at 65 °C. All samples were weighed to determine respectively bite size, plucking size or standing crop. After grinding through a 1 mm sieve the extrusa and hand-plucked samples of six periods (May, July, September and November 1989, and January and May 1990) were analyzed for concentrations of total nitrogen (N on organic matter basis) and calcium (Ca on dry matter basis) to provide an estimate of nutritive quality. The laboratory procedures are described in Walinga *et al.* (1989). N and Ca were chosen because, as stated above, these constituents appear to be least affected by salivary contamination.

Statistical analysis
The data were pooled for the different vegetation types and compartments within the heathland and the riverine area, as these produced similar results. Since both areas differed widely in vegetation height and plant texture, which could influence the relation between plucking size and bite size, the data for heathland and riverine grassland were analyzed separately with respect to these parameters. Data on nutritive quality on the other hand, were pooled for both areas. This offered the possibility to extend the comparison between grazed and hand-plucked samples over a wider range of nutrient content. Moreover, there was no reason to assume that the comparison would differ between areas. All statistical analyses were carried out with the SAS (1985) computer package. Regression analysis was conducted to determine the effect of vegetation height and standing crop on plucking size.

Bite size was expressed relative to an estimated biting area to account for animal growth during the experiment. The biting area was calculated as a circle with the diameter of the incisor arcade breadth. This appears to be a realistic assumption for grassland vegetation of medium height (Illius, 1989). The arcade breadth of the fistulated animals (measured in late April of 1989 to 1991) increased linearly with live weight, although individual variation was apparent (Fig. 2.1). This relation allowed an estimation of arcade breadth on the basis of individual live weight, which was measured at each sampling period. An average plucking size corresponding to each extrusa sample was calculated by a weighted mean of plucking size for the different plant categories in accordance to their proportion in the bite count. The sample values and sample estimates of the different animals were averaged to give one data pair per plot. Regression analysis between plucking size and bite size was carried out for both vegetations separately.

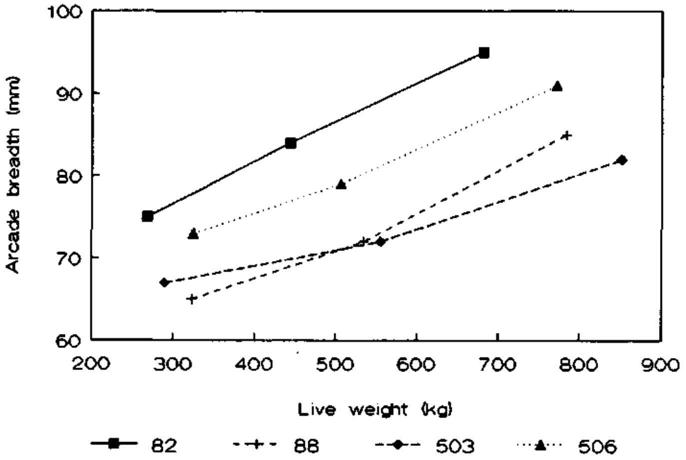


Figure 2.1 Incisor arcade breadth as a function of live weight in four oesophageally fistulated steers (numbered 82, 88, 503 and 506).

The regression line was forced through the origin, as it was assumed that cattle bite size and plucking size are zero under similar conditions.

Plot averages for the nutritive quality of the diet and the estimate from hand-plucked samples were compared by regression analysis. The required bite size estimates for the recognized plant categories were derived from the regression analysis between plucking size and bite size. A weighted estimate for the nutritive quality of the diet based on hand-plucked samples could thus be calculated for each sample.

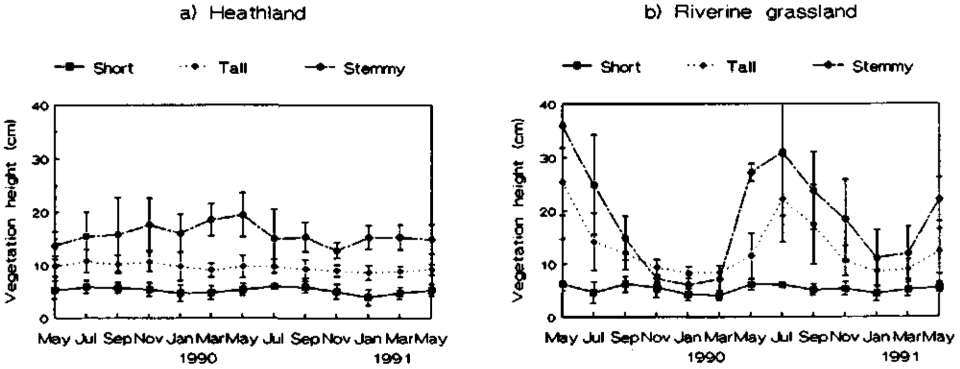
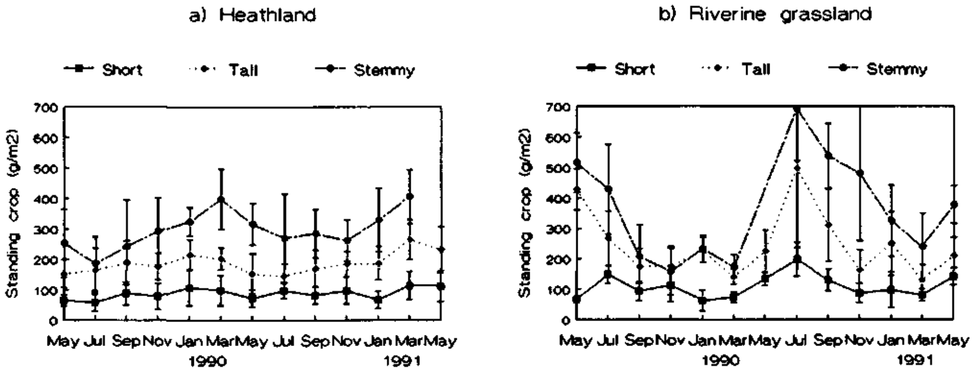


Figure 2.2 Vegetation height (± s.d.) for different plant categories (short grass, tall grass and grass with flowering stems) on a) heathland and b) riverine grassland from May 1989 to 1991.

Results

Vegetation height and standing crop

As expected, the peak height and standing crop in both areas were highest for grass with flowering stems, intermediate for tall grass and lowest for short grass (Figures 2.2 and 2.3). Vegetation height and standing crop were generally lower on heathland than in the riverine area. Furthermore, the pattern of change in both parameters was markedly different between the vegetations. On heathland the seasonal changes were very limited, in contrast to the riverine grassland, where both height and standing crop fell dramatically between July and March.


a) Heathland

b) Riverine grassland

Figure 2.3 Vegetation standing crop (± s.d.) for different plant categories (short grass, tall grass and grass with flowering stems) on a) heathland and b) riverine grassland from May 1989 to 1991.

Table 2.2 Regression equations describing the relation between plucking size (PS, g) and vegetation height (H, cm), and between plucking size and standing crop (SC, g/m²) for *Deschampsia flexuosa*-vegetation on heathland and for riverine grassland (95% confidence intervals indicated between brackets).

Heathland

$PS = 0.0825(\pm 0.0257)\,H - 0.00216(\pm 0.00110)\,H^2 - 0.229(\pm 0.128)$
$(R^2=0.880,\ d.f.=32,\ P<0.001)$
$PS = 0.00269(\pm 0.00094)\,SC - 2.71\ 10^{-6}(\pm 1.69\ 10^{-6})\,SC^2 - 0.0768(\pm 0.111)$
$(R^2=0.773,\ d.f.=32,\ P<0.001)$

Riverine grassland

$PS = 0.0820(\pm 0.0135)\,H - 0.00126(\pm 0.00039)\,H^2 - 0.220(\pm 0.091)$
$(R^2=0.864,\ d.f.=98,\ P<0.001)$
$PS = 0.00426(\pm 0.00089)\,SC - 3.59\ 10^{-6}(\pm 1.25\ 10^{-6})\,SC^2 - 0.235(\pm 0.122)$
$(R^2=0.765,\ d.f.=95,\ P<0.001)$

Vegetation height and standing crop showed high linear correlation coefficients in both heathland ($r=0.866$, d.f.$=48$, $P<0.001$) and riverine grassland ($r=0.921$, d.f.$=96$, $P<0.001$). The variation in plucking size, however, was better explained by vegetation height than by standing crop (Table 2.2). Due to the strong correlation between the two variables the bulk density (i.e. standing crop divided by height) did not show any significant correlation with plucking size.

Bite size estimation

The regression analysis revealed a close fit for a curvilinear relation between plucking size (PS, g; with 95% confidence intervals for parameters) and bite size per unit biting area (BS, mg/cm^2) (Fig. 2.4):

Heathland: $BS = 47.98(\pm 8.11)\ PS - 28.39(\pm 17.17)\ PS^2$ $R^2=0.779$, d.f.$=22$, $P<0.001$
Riverine : $BS = 34.87(\pm 4.48)\ PS - 17.53(\pm 7.57)\ PS^2$ $R^2=0.803$, d.f.$=26$, $P<0.001$

The quadratic term in the regression equation was significant for both heathland and riverine grassland ($P<0.01$ and $P<0.001$ respectively). Without the quadratic term the explained variation decreased respectively to 66.1% and 63.1%.

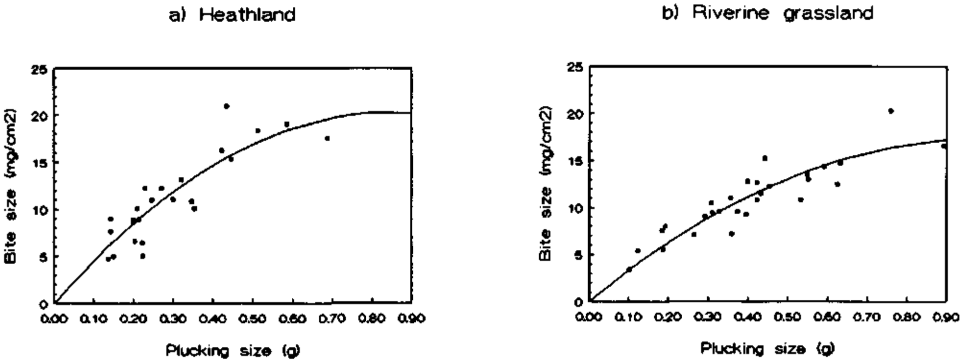


Figure 2.4 Bite size per unit biting area of oesophageally fistulated steers in relation to plucking size on a) heathland and b) riverine grassland (dots represent plot means, the line shows the regression equation given in the text).

Nutritive quality

The estimated contents of nitrogen and calcium (with 95% confidence intervals) were similar to the contents in the diet selected by the fistulated steers (Fig. 2.5):

N-diet $= 0.97(\pm 0.20)$ N-est. $+ 0.11(\pm 0.51)$ $R^2=0.751$, d.f.$=30$, $P<0.001$
Ca-diet $= 1.14(\pm 0.14)$ Ca-est. $- 0.04(\pm 0.06)$ $R^2=0.906$, d.f.$=29$, $P<0.001$

For both regressions the intercept was not significantly different from zero ($P>0.05$) and the regression coefficients were not significantly different from unity ($P>0.05$).

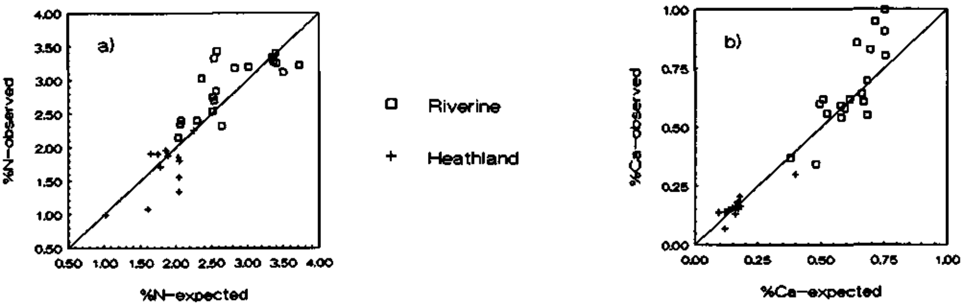


Figure 2.5 Comparison of diet quality as estimated by hand-plucking (expected) and as determined in extrusa samples from oesophageally fistulated steers (observed) for a) nitrogen (N) and b) calcium (Ca). Dots represent plot means from heathland and riverine grassland. The line indicates equality for oberved and expected values.

Discussion

General remarks

The results of this experiment show that hand-plucking can be used as a method to assess bite size and diet quality. This is in contrast to findings of Langlands (1974). The suitability of the hand-plucking method relies on sub-sampling of different plant categories and recording bite counts to adjust for diet selection, rather than taking a mixed sample of different plant categories. Furthermore, extensive familiarity with the grazing habits of the animal is a prerequisite. In this respect cattle will be easier to simulate than sheep, which are more selective grazers (Grant *et al.*, 1985 and 1987). This may have proved a handicap in the experiment by Langlands (1974). This author also pointed to the problem of differences between operators. These were not tested in the present study as the data were collected by one person only. However, calibration of the estimation of bite size and diet quality is advisable whenever possible, especially in heterogeneous vegetation.

Vegetation structure versus botanical composition for the estimation of diet selection

Botanical composition must be taken into account to differentiate between vegetation types. Within a botanically defined grassland type, distinction of the three plant categories on the basis of vegetation structure - short, tall and with flowering stems - appears a useful and practical method to quantify diet selection. It may seem more appropriate to distinguish separate plant species, even within a grassland type. However, the estimation of bite size would become much more difficult with bite counts on a species basis. In addition, the difference in nutritive quality between grasses of different growth stage is of the same magnitude as between different grass species on the same site (Hacker and Minson, 1981; Ulyatt, 1981; Norton, 1982; Koorevaar, 1986). Distinction between species would therefore not necessarily result in a more accurate estimate of diet quality.

In the riverine area, changes in botanical composition between years were significant for *Elymus repens* and *Agrostis stolonifera* (Wallis de Vries, unpubl.). Yet, there was no significant correlation between the cover of either of these species and changes in nutritive quality for nitrogen, phosphorus, calcium, sodium and organic matter digestibility. In contrast an ANOVA showed that there were significant differences between grass categories for all five nutrients examined ($P<0.05$; the difference for calcium was only significant at $P<0.10$). Thus, the distinction of grass categories appears more important than the differentiation of species. A practical argument in favour of the present approach is that cattle do not appear to discriminate actively between grassland species growing in a fine mixture (Grant *et al.*, 1985). It certainly is difficult for the observer.

Curvilinearity between plucking size and bite size
The relation between plucking size and bite size found in this study was of a curvilinear shape. Although based on one operator only, it may be argued that this type of relation could have a more general applicability. The curvilinearity results mainly from the choice of zero intercept. This seems justifiable on the ground that the allometric coefficient for bite weight declines on very short swards (Illius, 1989). The ability of cattle and a hand-plucking human to harvest grass then would converge, and it seems a fair assumption that the point of a zero harvest would be reached at a similar sward height (*ca.* 3 cm when extrapolating the regression between vegetation height and plucking size). Conversely, with increasing herbage availability cattle would tend to take relatively larger bites, favoured by the broader dental arcade and an extension of the reach by a sweep of the tongue, in comparison to the relatively small span of around half the size of a forefinger. With a further increase in sward height selectivity would become of greater importance, leading again to a convergence of bite size and plucking size.

Conclusion

The hand-plucking method offers potential for determining bite size and nutritive quality of grazing herbivores. The incorporation of stratified sampling of different plant categories in combination with observations on the selection between categories appears an essential improvement. The method should prove especially valuable in heterogeneous and sparsely grazed vegetations, where animals can demonstrate a considerable selectivity. Moreover, hand-plucked samples are free from the contaminants precluding reliable analyses for a number of parameters for nutritive quality in oesophageal extrusa or rumen samples. However, the method relies heavily on a calibration between operators and the study animal. Future studies should investigate the variation between operators and its minimization through the development of standard procedures.

The present method, including the calibration of bite size, has been used to estimate diet quality and bite size for various related vegetations. Details on the application are given in the Appendix to this chapter.

APPENDIX: Quantifying diet selection and bite size of cattle in the study areas

Recognized plant categories

In each study area a number of vegetation units were distinguished according to dominant plant species and topography (Chapter 1). Within each vegetation unit different plant categories were recognized. These were sampled as described earlier. Plant categories were used to record bite counts of the grazing steers. All different plant categories are listed in Table 2.3. Grass categories were sampled separately for each vegetation unit when botanical composition differed (*i.e.* in vegetation units with broad-leaved grasses).

Bite size estimation

The breadth of the dental arcade was measured only twice for each free-ranging animal (in July 1990 and April 1991), no individual relation between body weight and arcade breadth could therefore be determined. Instead, one relation was derived for all animals from all measurements, including those on the fistulated animals. The linear regression between live weight (LW, kg) and arcade breadth (AB, mm) was (with 95% confidence intervals):

$$AB = 0.0360(\pm 0.0088)\ LW + 59.8(\pm 5.7) \qquad (R^2=0.524;\ d.f.=60,\ P<0.0001)$$

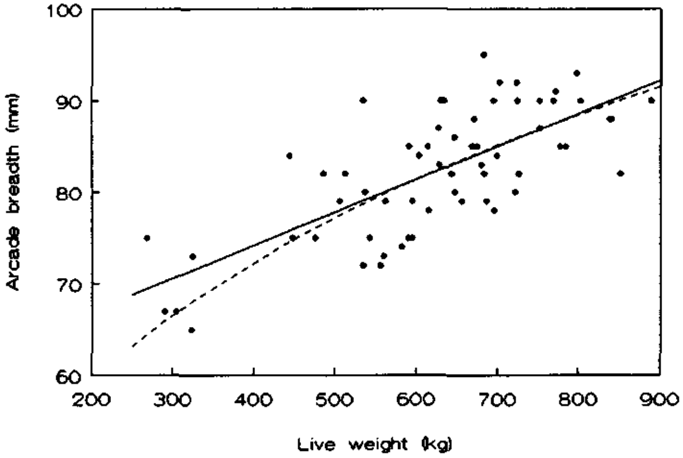


Figure 2.6 Incisor arcade breadth (AB) as a function of live weight (LW) for 25 steers measured in two subsequent years and for four oesophageally fistulated steers measured in three subsequent years. The *solid line* gives the calculated regression equation. The *broken line* shows the relation derived by Taylor *et al.* (1987): $AB = 7.8(LW/A)^{0.29}A^{0.36}$, with A=adult live weight in kg, estimated at 1050 kg for the present Meuse-Rhine-Yssel steers.

As shown in Figure 2.6, this regression line is not significantly different from the relation derived by Taylor *et al.* (1987), certainly not in the main range of 400-900 kg.

Table 2.3 **Plant categories distinguished in the three different study areas for recording bite counts of free-ranging steers (criteria for short, tall and stemmy categories are described in Table 2.1).**

Doorwerthse Heide	Renkumse Benedenwaarden	Karshoek
Heathland	*Riverine grassland*	*Heathland+Riverine grassland*
Monocots		
Short grass[1]	Short grass[2]	Short grass[1,2]
Tall grass[1]	Tall grass[2]	Tall grass[1,2]
Stemmy grass[1]	Stemmy grass[2]	Stemmy grass[1,2]
Short *Molinia*[2]	*Phalaris*[2]	*Molinia*[2]
Tall *Molinia*[2]	*Butomus*[2]	*Glyceria maxima*[2]
Other grasses[2]		*Deschampsia cespitosa*
Juncus effusus		*Juncus effusus*
		Juncus bulbosus
Herbs and ferns		
	Rumex	*Rumex*
	Cirsium	*Ceratocapnos claviculata*
		Dryopteris spp.
Dwarf shrubs		
Short *Calluna*		*Calluna*
Tall *Calluna*		*Erica*
Erica		
Browse		
Prunus serotina	*Salix spp.*	*Prunus serotina*
Betula pendula	*Crataegus monogyna*	*Prunus spinosa*
Rhamnus frangula		*Sambucus nigra*
Pinus sylvestris		*Pinus sylvestris*
		Picea spp.
		Betula spp.
Miscellaneous		
Acorns		Acorns
Fungi		Fallen leaves
Rabbit faeces		

1) Bite size estimated by regression equation for heathland (fine-leaved grasses)
2) Bite size estimated by regression equation for riverine grassland (broad-leaved grasses)

Arcade breadth of animals losing weight over winter was assumed to remain at the size corresponding to peak autumn weight. The regression equation was used to estimate the biting area for each individual, as in the fistulated animals.

The bite size of the grass categories and other monocots was estimated by the regression equation between plucking size and bite size per unit biting area found in the preceding study. In the case of unreliable plucking size due to lack of standardization during the first five periods, plucking size was estimated from the regression with vegetation height. An estimate for individual bite size was subsequently obtained by multiplication with the biting area for each animal. The regression derived for the riverine area was used to assess the bite size of broad-leaved grasses. The regression for the heathland area was used to estimate bite size for fine-leaved grasses and *Juncus bulbosus*. For plucking sizes greater than *ca.* 0.9 g, bite size was estimated to equal plucking size. This assumption was supported by results for eight extrusa samples with exceptionally large bite size (BS, g; range 0.76-1.81), which closely corresponded to plucking size (PS, g; 0.80-1.76; with 95% confidence intervals):

$$BS = 0.973(\pm 0.226)\,PS + 0.052(\pm 0.261) \qquad (R^2 = 0.949,\ d.f. = 6,\ P < 0.0001)$$

For a number of distinct plant species with smaller plucking size (herbs, dwarf shrubs and browse) the same assumption was followed, as bite size could be assessed more accurately by bite marks. Acorns and fungi (mostly *Panaeolus spp.*) were estimated to be taken one per bite, for rabbit faeces bite size was estimated at two pellets per bite.

Plate 5. An oesophageally fistulated steer grazing in riverine grassland.

Plate 6. Observations on grazing behaviour were carried out using a portable computer.

CHAPTER 3

Performance of Free-ranging Cattle in Contrasting Habitats

Summary

In a two year study body weight, mineral status and diet selection of cattle were recorded under extensive yearround grazing conditions in two semi-natural landscape types in the Netherlands. Groups of five Meuse-Rhine-Yssel (MRY) steers were allocated to four treatments: year-round grazing on heathland (H), idem in a riverine grassland (R), idem with H and R combined (H+R), winter grazing in H and summer grazing in R (H/R). In the H+R treatment five Hereford steers were added to compare the performance of a dual-purpose and a beef breed.

Final body weights were highest in R and H/R, slightly lower in H+R and 33% lower in H. Summer gains were lower and winter losses higher on H than in R, the losses being substantially greater in the colder winter. Differences between MRY and Herefords were negligible.

Herbage samples indicated that maintenance requirements were not met in H for sodium, phosphorus and calcium. The occurrence of pica behaviour also indicated mineral deficiencies in H. Blood serum concentrations of calcium, magnesium, sodium and copper were not different between treatments and met the requirement levels. Selenium seemed marginal in H+R. Phosphorus concentration decreased to a lower but steady level in H compared to R, H/R and H+R animals being intermediate. Saliva sodium/potassium ratios were variable but summer values indicated deficiencies in the H group.

The H+R animals frequently moved between the two habitat types. Use of the R habitat was heavier in summer than in winter. It is argued that a combination of habitats appears the only viable long-term management option without human interference.

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Introduction

European research on large herbivores has paid little attention to the relation between habitat quality and animal performance. Examples of such studies concern mainly red deer (*Cervus elaphus*)(Mitchell *et al.*, 1976; Staines, 1978; Clutton-Brock *et al.*, 1982; Iason *et al.*, 1986) and reindeer (*Rangifer tarandus*)(Skogland, 1985; Tyler, 1987). These and other studies (e.g. Sinclair, 1977; Belovsky, 1978; McNaughton, 1987; Thing *et al.*, 1987; Freeland & Choquenot, 1990) emphasize the importance of food quality on habitat use, individual survival and population dynamics. Wildlife habitats in Western Europe are generally under great human pressure and are typically fragmented by roads, urban and industrial areas and agricultural lands (Van Wieren, 1991). In the twelve countries of the European Union the surface covered by National Parks (meeting the IUCN criteria) larger than 100 km² comprises only 0.22% of the total land area. Seven out of the twelve nations do not even count a single National Park (Bibelriether & Schreiber, 1989). Thus, it appears that more extensive investigations of habitat-performance relations would not only benefit scientific objectives but also nature conservation goals.

In the Netherlands extensive cattle grazing in nature reserves has become a major management technique to preserve biological diversity (Thalen, 1984; Van Wieren, 1991). There is a growing tendency to minimize human interference. As domestic animals can be observed at close range and may be caught repeatedly with little effort, this offers a great opportunity to study the relation between diet selection and condition changes in detail. This chapter reports on the animal performance aspects of a two-year experiment with cattle in habitats of different soil fertility in the Netherlands.

Methods

Groups of five steers of the dual-purpose (dairy and beef) Meuse-Rhine-Yssel breed (MRY) were allocated to four treatments: (1) year-round grazing on heathland (H), (2) idem in a riverine grassland (R), (3) idem with H and R combined (H+R) in an area called 'Karshoek', (4) winter grazing (December-March) in H and summer grazing (April-November) in R (H/R) (Table 3.1). In the H+R treatment five Hereford steers were added to compare the performance of a dual-purpose and a beef breed. Animal densities were chosen so as to avoid a heavy grazing impact on the entire area. The H area (with a separate compartment for the winter grazing grounds of the H/R-animals) was situated on a Pleistocene ice-pushed ridge of low soil fertility on the Veluwe plateau. The R area (with a separate compartment for the summer grazing grounds of the H/R-animals) concerned fertile river-forelands of the Rhine river. The H+R area was situated along the Vecht river with more fertile sandy-loamy river deposits in the riverine part and poor cover sand deposits in the heathland part, which included a forested area.

The animals were just over a year old and weighed *ca.* 315 kg at the onset of the experiment. They were released in the areas in april 1989 and removed in july 1991. Although in both years winter flooding occurred in the riverine area, removal of the animals was not necessary. No supplements of any kind were given.

The animals were weighed at least every two months in summer and every month in

Table 3.1 Characteristics of habitat types.

	Area			
	Heathland	Riverine	Karshoek	
			Heathland	Riverine
Size (ha) yearround	28.1	8.7	60.4	13.9
H/R group	21.7	5.2		
Parent material	gravelly sand	alluvial clay	cover sand	alluvial sand/loam
Main food plants	*Deschampsia flexuosa* *Prunus serotina* *Calluna vulgaris* *Molinia caerulea*	*Agrostis stolonifera* *Elymus repens* *Lolium perenne* *Ranunculus repens*	*Deschampsia flexuosa* *Prunus serotina* *Molinia caerulea* *Erica tetralix*	*Agrostis capillaris* *Agrostis stolonifera* *Poa pratensis* *Holcus lanatus*

winter. Blood samples were taken on seven occasions and analyzed for contents of phosphorus (P), calcium (Ca), magnesium (Mg), sodium (Na), copper (Cu) and selenium (Se)(GSH-px) in the blood serum. Saliva samples were taken on four occasions and analyzed for Na and K. Grazing behaviour and diet composition were studied every two months for every treatment by recording bite selection in 10-minute focal observations during the entire daylight period for three days. Hand-plucked samples of different food classes were analyzed for mineral composition. The distribution of the H+R animals between the two habitat types was recorded on the basis of regular sightings (maximum of one morning and one afternoon record per day).

Results

Body weight changes

The change in body weights showed a clear annual cycle similar for all treatments (Fig. 3.1 a-b). High spring gains were followed by moderate gains in summer and fall, weight loss over winter and a rapid recovery at the start of grass growth. No difference emerged between MRY and Herefords in H+R.

Net weight gains were higher in R and H/R, followed by H+R (difference with R significant at $P<0.01$; with H/R not significant) and very much lower in H ($P<0.01$) (Fig. 3.2 a-b). This pattern was apparent in both years. The weight losses during winter were much higher in the colder winter of 1990/91 than in the exceptionally mild winter of 1989/90 ($P<0.01$) (Fig. 3.3 a-b). The H and H/R animals lost more weight than the R and H+R animals ($P<0.10$ and $P<0.01$ for the two years). The 1990/91 weight loss in

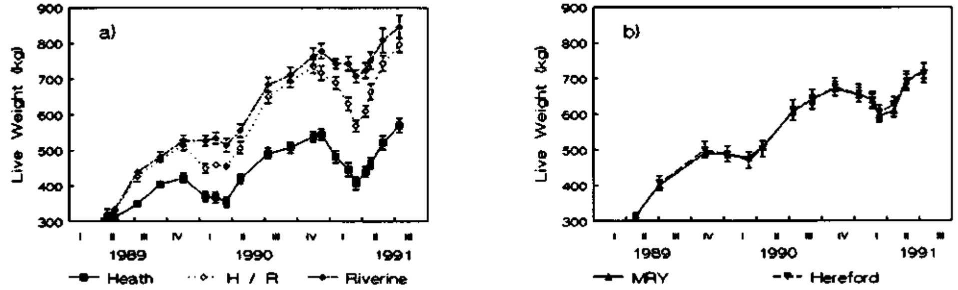


Figure 3.1 Live weight changes of steers (±s.e.) in (a) treatments H (heathland), H/R (winter heathland, summer riverine) and R (riverine grassland), (b) treatment H+R (heathland and riverine grassland combined).

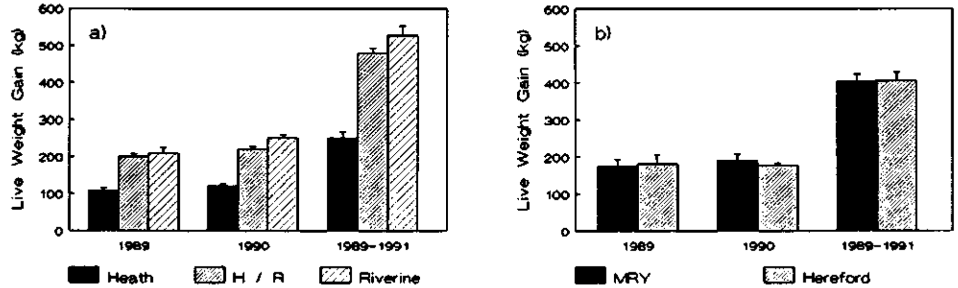


Figure 3.2 Net weight gains of steers (±s.e.) in (a) H, H/R and R treatments, (b) H+R treatment

the first two treatments amounted to respectively 25.3% and 22.7% (range 20.9-29.0%) of their peak weight in November, while in the latter two treatments it was 9.0% and 11.4% (10.6% for the Herefords). The smaller weight losses in 1989/90 represented 15.8%, 11.8%, 2.6%, 2.4% and 5.6% of the peak weight for respectively H, H/R, R, H+R (MRY and Herefords).

Pica behaviour

During the observation periods pica behaviour was observed frequently in H, whereas in the other treatments it was restricted to the occasional consumption of soil (mainly in late winter and early spring) and some chewing of plastic refuse. H-animals became fanatic in licking urine patches of rabbits and man; sweat would also be licked. They frequently chewed wood and occasionally consumed soil. In fall mushrooms were selected for and in winter faecal pellets of rabbits were eaten in large numbers. Most striking was the habit

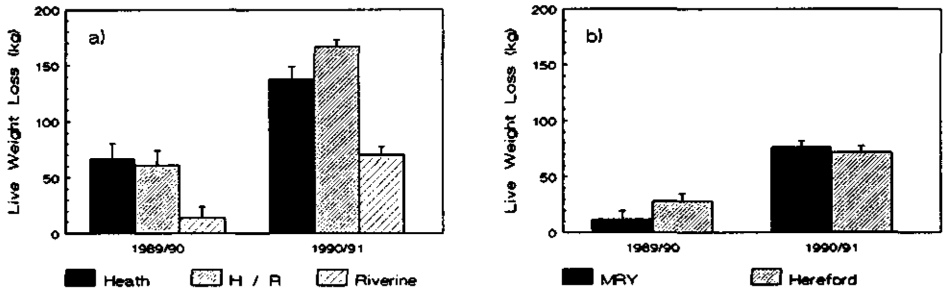


Figure 3.3 Winter weight loss of steers (±s.e.) in (a) H, H/R and R treatments, (b) H+R treatment

of ingesting non-food items such as plastic and feathers but also bones and even dead rabbits. In an experiment where rabbit legs and bones were presented to animals from all treatments, it appeared that only H-animals consumed these items, while other animals would frequently sniff or lick rabbit legs but never ingest them and bones would usually be plainly ignored; however, all animals would eat little pieces of plastic bag, apparently demonstrating their curiosity for strange objects (details in Chapter 4).

Mineral status

The hand-plucked herbage samples indicated that maintenance requirements (ARC, 1980) were not met in H for P, Ca and Na (Table 3.2). One H-animal was removed from the experiment in november 1990 after breaking its leg. Although this may have been due to a deficiency in P or Ca this could not be clearly established; unfortunately no bone analysis was carried out.

Table 3.2 Summer nutrient concentrations (%dry matter) in hand-plucked herbage samples from heathland and riverine grassland.

		Heathland	Riverine	Requirements Maintenance/Growth
Phosphorus	mean	0.13	0.35	0.20 / 0.22
	range	0.11-0.16	0.29-0.40	
Calcium	mean	0.16	0.65	0.25 / 0.40
	range	0.12-0.20	0.49-0.75	
Sodium	mean	0.02	0.08	0.07
	range	0.01-0.03	0.02-0.13	

Analysis of blood samples did not reveal any acute deficiencies (Table 3.3). Se levels were below the critical level for the MRY animals in H+R, which may be due to the Pleistocene sandy soils that are known to contain little Se (McDowell, 1985; Langlands, 1987). However, one would then expect H-animals to show Se deficiencies as well, which was not the case although their values clearly were lower than in H/R and R ($P<0.01$). In none of the apparently Se-deficient animals was there any outward sign or other indication of inferior condition.

There were no clear differences between treatments for levels of Ca, Mg, Na and Cu, although there was a tendency for the H animals to show higher Ca and Mg levels. P-levels were lower in H than in H/R and R ($P<0.10$ and $P<0.025$ respectively). In R and H/R the P-concentrations showed an annual cycle with generally lower values for the second treatment (Fig. 3.4 a). In contrast the P-level in H declined during the first year and remained constant throughout the second year. The P-levels in H+R fluctuated but showed a tendency to decline (differences between initial and final values were significant at $P<0.02$) (Fig. 3.4 b).

Table 3.3 Mineral content (±s.e.) of steer blood serum samples at the end of the experiment (after 770 days); H/R winter on heathland and summer on riverine grassland, H+R heathland and riverine grassland combined. Below the critical value deficiencies are probable (COMV, 1982)

Mineral	Critical Value	Treatment				
		Heathland	H/R	Riverine	H+R	
					MRY	Hereford
Phosphorus (mmol/l)	1.10	1.82±0.13	2.44±0.07	2.36±0.15	2.20±0.04	1.98±0.12
Calcium (mmol/l)	2.00	2.62±0.03	2.49±0.02	2.48±0.04	2.55±0.05	2.55±0.04
Magnesium (mmol/l)	0.78	1.22±0.05	0.99±0.01	1.03±0.03	0.99±0.04	1.09±0.04
Sodium (mmol/l)	135	137.8±1.2	140.6±0.5	138.5±0.8	140.0±1.0	141.2±1.3
Copper (μmol/l)	7.5	10.2±0.5	10.3±1.0	11.8±2.0	10.8±0.7	12.9±0.5
Selenium (U/l)	120	277±13	443±37	488±25	91±13	130±13

Saliva analysis gives a better indication of deficiencies for Na than blood serum samples (COMV, 1982). The contents of Na and K in saliva are complementary. The Na supply is adequate when Na>130 mmol/l and K<50 mmol/l; risks for disorders arise with Na concentrations of 45-90 mmol/l and K concentrations of 38-64 mmol/l (COMV, 1982). Na/K levels in saliva varied over the year in H and remained relatively constant in H/R and R (Fig. 3.5 a-b); less data were available for H+R, but these did not point to deficiencies. The H animals showed lower Na and higher K levels than the other animals in July 1990 and 1991 ($P<0.05$) but no treatment differences were apparent in November and March. The July values indicate an insufficient Na supply.

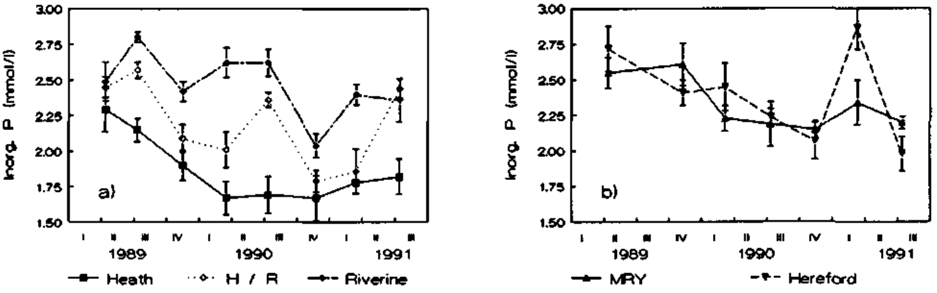


Figure 3.4 Phosphorus content (±s.e.) of blood serum samples of steers in (a) H, H/R and R treatments, (b) H+R treatment

Figure 3.5 Mineral content (±s.e.) of saliva samples of steers in H, H/R and R treatments for (a) Sodium and (b) Potassium

Habitat use in the H+R treatment

MRY and Herefords in H+R always stayed together in one herd. The animals frequently moved between the H and R areas. On average the animals spent 63.8% of the time in the R habitat. The R area was used more intensively during summer than in fall and winter ($P<0.002$) (Table 3.4). The H area was visited more frequently in the cold spring of 1991 than in the warm spring of 1990 ($P<0.02$).

Table 3.4 Herd sightings on Riverine grassland in the 'Karshoek' (H+R); the complement was spent on Heathland.

Season	% Sightings on Riverine grassland (± s.e.)	N
Spring (March-May)	66.3±9.4 1990: 85.5±7.8 1991: 47.1±2.9	6 3 3
Summer (June-September)	76.2±6.0	6
Autumn (October-November)	52.4±0.5	3
Winter (December-February)	54.6±3.3	6

The sighting percentage was calculated on a monthly basis;
N is the number of months, with 10.8 sightings per month on average.

Discussion

Over the two years of this study the animals in the riverine grassland showed the best performance with high weight gains, small winter losses and no apparent deficiencies. The animals on heathland did not suffer any fatal deficiencies (although the broken leg of one animal might be a result of calcium or phosphorus deficiency) but gained comparatively little weight and lost much over winter. Two animals lost 29% of their peak weight, which does seem close to the maximum. This relatively poor performance can probably be attributed to the low mineral content of the diet, especially calcium, phosphorus and sodium in combination with a low digestibility of the winter diet. A lack of minerals in the diet has frequently been observed to lead to a depressed intake and reduced growth (McDowell, 1985; Langlands, 1987). The observed forms of pica behaviour demonstrate that the animals reacted to the shortage of minerals. The craving for salt of sodium deficient animals is well-known (McDowell, 1985; Langlands, 1987), but the selective consumption of bones by the H animals may be a functional response as well, in order to obtain additional phosphorus and calcium; this was suggested earlier by Bazely (1989). Since they continued to grow it may be argued that the H animals were quite successful in utilizing the environment's limited resources and probably also in adjusting their metabolism (see ARC, 1980; Little, 1982).

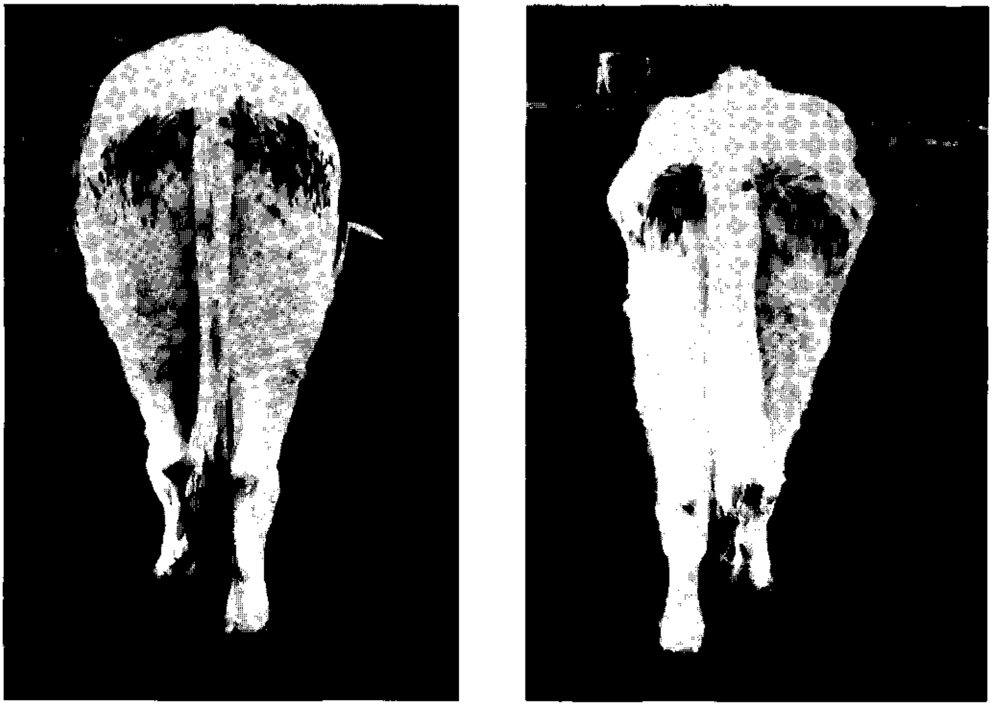
The H/R and H+R animals had an intermediate overall performance compared to the R and H animals. The H/R animals showed similar weight gains to the R animals, demonstrating a quick recovery of their substantial weight loss on heathland. The H+R animals had comparable weight gains to the H/R animals but a smaller weight loss over winter. Interestingly no difference in performance emerged between MRY and Herefords. Herefords clearly had more subcutaneous fat than the MRY, but it remains unclear as yet whether the two breeds differ in total fat storage capacity. From results of visual condition scores (Chapter 7) one would conclude that Herefords can stand longer periods of weight loss than MRY.

The lower gains of H+R compared to R may be explained by the somewhat poorer riverine grassland on sandy soil and the continued use of the heathland throughout the year. On the other hand the small winter loss compared to the H/R animals may also be attributed to the year-round availability of both habitats to the H+R animals, which thus could select from a broad range of food plants and avoid mineral shortage. In summer the high-quality grasses of the riverine grassland were preferred, with an occasional visit to the heathland to graze *Molinia caerulea* or *Deschampsia flexuosa* and browse *Prunus serotina*. In fall acorn mast, *Deschampsia flexuosa* and *Prunus serotina* attracted the animals to the heathland while the food quality in the riverine grassland declined. In winter the animals grazed *Deschampsia flexuosa* and *Erica tetralix* on heathland and the short sward and tall *Deschampsia cespitosa* tussocks in the riverine area. In the warm spring of 1990 the animals concentrated on the nutritious young grasses of the riverine grassland, while in the cold spring of 1991 the grass growth in the riverine grassland was late and the animals therefore continued to frequent the heathland. This shifting use of both habitats could not, of course, be displayed by the H/R animals. At least one of these animals showed adaptation problems to the change in diet when moved from the heathland to the riverine area in spring.

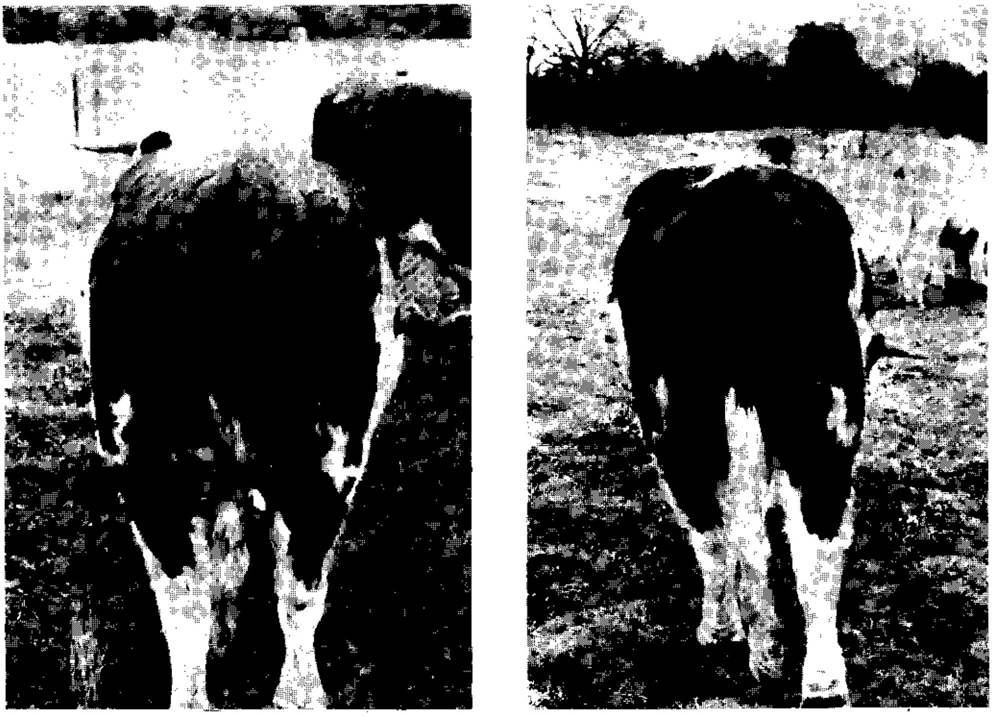
It is tempting to speculate on the performance of cattle populations when released in the wild in the heathland and riverine habitats. Although the latter habitat proved the best in this study, winter and spring flooding may render the area inaccessible for several weeks, compelling the animals to leave for other habitats. Moreover, in longer winters the availability of forage of acceptable digestibility may be so low that the animals would risk starvation (Bokdam & Wallis de Vries, 1992); this situation does seem rather exceptional however, as grass growth continues at temperatures little higher than freezing point. On heathland it can be expected that cows and calves would experience high mortality rates due to mineral deficiencies of especially phosphorus and sodium, as the demands of lactating and young growing animals are much greater than those of steers. Longer winters would very likely also take a heavy toll because of the limited build-up of fat reserves. The combination of habitats examined in the H+R treatment (and more conditioned in the H/R treatment) then seems to provide a complete habitat: the animals may benefit from the high-quality food in the riverine grassland and turn to the heathland when the river rises or the grass supply in the riverine area becomes inadequate.

Conclusion

Other studies have pointed to the need of large herbivore populations for seasonal migration between habitats (Jarman & Sinclair, 1979; Clutton-Brock *et al.*, 1982; Mc Naughton, 1987; Boyce, 1991; Klein, 1991; Penzhorn & Novellie, 1991). This finding should have important implications for the planning and assignment of wildlife reserves. The present study shows that the riverine grassland is an excellent habitat but that it may become unsuitable in winter, while heathland habitat offers an acceptable winter habitat. When heathland and riverine grassland are the main habitats available, a combination of habitats offering the opportunity for seasonal migration does seem the only viable long-term option for a naturally regulated cattle population.



Plates 7 and 8. On heathland body condition deteriorated considerably over winter: the condition score dropped from 3.0 in September 1990 (left) to 1.25 in March 1991 (right) for this animal.



Plates 9 and 10. Herefords showed a greater fat accumulation than the Meuse-Rhine-Yssel breed: condition score for this animal was 5.0 in September 1990 and 3.25 in March 1991.

Plate 11. Soil consumption occurred as a response to low mineral concentrations in the forage on heathland.

CHAPTER 4

Nutritional Limitations of Free-ranging Cattle: The Importance of Habitat Quality

Summary

The nutritional limitations of free-ranging cattle with regard to energy, nitrogen and minerals were examined in relation to variation in habitat quality. Twenty steers were allocated to four different treatments during two years: year-round grazing on heathland (H) with low soil fertility, year-round grazing on riverine grassland (R) with high soil fertility, summer grazing on riverine grassland (April-November) and winter grazing on heathland (December-March) (H/R), and year-round grazing in an area with heathland and riverine grassland combined (H+R). Forage intake and diet quality were quantified to calculate the nutritional budget for nitrogen (N), sodium (Na), phosphorus (P) and calcium (Ca). Energy intake was estimated from digestible organic matter intake. Condition of the animals was measured by live weight change, condition score, blood and saliva samples, fat reserve measurements with the deuterium oxide method, and rib bone analysis after slaughter.

Forage intake and quality showed significant monthly variation. Dry matter intake was lower in the H+R steers than for other treatments. Forage quality was significantly higher in riverine grassland than on heathland. Metabolizable energy-intake per unit gain was higher in H than for the other treatments, suggesting an impaired digestive efficiency. The nutrient balance was poorest in H, intermediate but always positive in the H/R and H+R treatments, and best in the R treatment. Requirements for the H animals were approximately met for N and Ca, but not for Na and P. As a consequence H animals showed various signs of malnutrition: lower weight gain and higher weight loss, apparent deficiencies of Na and P, lower condition scores and fat reserves, and pica behaviour (geophagia, osteophagia and carnivory).

The results of the study show that habitat quality was an important determinant of nutrition and animal performance. Conditions for cattle growth appear near-optimal in the riverine grassland in the absence of cold winters. In contrast, mineral deficiencies could lead to heavy winter mortality, osteomalacia and impaired reproduction in a population of free-ranging cattle on heathland. The recorded pica behaviour can be interpreted as a behavioural response to alleviate mineral deficiencies. It is argued that the impact of habitat differences with regard to nutrient availability also apply to populations of wild herbivores.

(submitted to Ecology)

Introduction

The influence of habitat quality on the performance of individuals has long been recognized for herbivores (Klein, 1965; Geist, 1978; Manseau & Gauthier, 1993). In large ungulate herbivores the individual performance is determined to a large extent by their food supply (Klein, 1970; Clutton-Brock *et al.*, 1982; Crawley, 1983; McNaughton, 1987), which can therefore be taken as a parameter for habitat quality. At low population densities relative to food abundance, the nutritive value of the food is the main nutritional determinant of the quality of a certain habitat type. Traditionally, energy and protein content have been viewed as the most important parameters for nutritive value (*e.g.* Prins & Beekman, 1989). Yet, an ever increasing amount of evidence points that minerals - particularly sodium and phosphorus - do govern the diet selection and body condition of large herbivores when soil fertility is predominantly low (Belovsky & Jordan, 1981; Freeland & Choquenot, 1990; McNaughton, 1988 and 1990; Ben-Shahar & Coe, 1992). The potential importance of these minerals as limiting agents in animal performance of domestic and wild herbivores has also been stressed in studies of feeding trials (Theiler *et al.*, 1927; Cohen, 1975; Agricultural Research Council (ARC), 1980; McDowell, 1985; Grasman & Hellgren, 1993), wildlife in captivity (Robbins, 1983) and rangeland studies (Cohen, 1975; Hyvarinen *et al.*, 1977; Gartner *et al.*, 1980; McDowell, 1985).

As the nutritive value of the food supply is a function of environmental variables, such as soil fertility, texture and moisture, environmental heterogeneity is a second important parameter of habitat quality (Forman & Godron, 1986; O'Neill *et al.*, 1988). However, there is no experimental evidence demonstrating how environmental heterogeneity and nutritive value interact to explain the variation in the condition of wild or free-ranging domestic (*i.e.* not commercially productive) herbivores. This chapter reports the findings of an experimental study which was conducted to assess the nutritional limitations of a large herbivore offered different combinations of habitat with low soil fertility and habitat with high soil fertility. The nutritional budget for minerals (sodium, phosphorus, and calcium), nitrogen and energy is examined to explain animal performance. Free-ranging cattle (*Bos taurus*) were used because their diet selection, intake and condition can be studied with relative ease and standards have been developed against which their performance may be compared.

Methods

Experimental Design

The low-fertility or poor habitat was represented by heathland, and the high-fertility or rich habitat by riverine grassland. Forage characteristics of both habitats have been described elsewhere (Bokdam & Wallis de Vries, 1992; Chapter 1).

During a two-year experiment twenty yearling steers of the Meuse-Rhine-Yssel breed were allocated to four different treatments in separate areas (matched for an average live weight of 315 kg in all treatments) Animal densities were chosen so as to prevent nutritional limitations through overgrazing. No supplements of any kind were given. All areas had an adequate supply of drinking water. The animals were treated annually against internal and external parasites to rule out any confounding effect of parasites on performance. The four treatments consisted of:

H : year-round grazing on heathland (28 ha),
R : year-round grazing on riverine pasture (9 ha),
H/R : winter grazing on heathland (22 ha; December-March) and summer grazing on riverine pasture (5 ha; April-November),
H+R: year-round grazing in an area with both heathland (60 ha) and riverine grassland (14 ha) available.

Thus, steers from two treatments were confined to an area either poor or rich in nutrients and the animals in the other two treatments were offered a combination of habitats, either with controlled transportation of the animals or with free-choice between habitats.

Study areas

All study areas were located in the Netherlands, within the cool temperate climate zone (for details see Chapter 1). The heathland site, the Doorwerthse Heide (52°00' N, 5°47' E, altitude 30 m), is situated on a Pleistocene ice-pushed ridge with sandy-gravelly parent material of low soil fertility. It is dominated by a vegetation of *Deschampsia flexuosa* and *Calluna vulgaris*. A minor part of the area is covered by young stands of *Quercus robur, Pinus sylvestris, Betula pendula* and *Prunus serotina*. The riverine site, the Renkumse Benedenwaarden (51°58' N, 5°43' E, altitude 8 m), consists of river forelands on fertile, heavy clay soil. It borders the river Rhine. The vegetation is dominated by pasture of *Lolium perenne, Agrostis stolonifera* and *Elymus repens*. The third site, the Karshoek (52°32' N, 6°32' E, altitude 7 m) is made up of two essentially different parts: a riverine area on sandy-loamy soil bordering the Vecht river, and a former heathland on Pleistocene cover sand of low soil fertility, partially turned to shifting sand during a period of overgrazing in past centuries. The heathland has been largely converted to pine forest (*Pinus sylvestris*), with a ground vegetation dominated by *Deschampsia flexuosa, Calluna vulgaris* and *Erica tetralix*. The riverine area consists of a vegetation mosaic dominated by grassland species: *Agrostis capillaris, A. stolonifera, Poa pratensis, Holcus lanatus* and *Festuca rubra*. Both parts are connected by a bridge over which the steers could move freely.

Measurements

The experiment started in May 1989 and ended in July 1991. Data were collected during thirteen periods of one week per treatment, every two months: May, July, September, November, January, March. In 1990 and 1991, the field work for the May period started two weeks earlier than in 1989.

Daily grazing times were estimated from vibra-recorders (Stobbs, 1970) fitted on neck collars to each individual animal for one week; readings could be calibrated by comparison with direct observations. Observations on foraging behaviour were made during three days for each treatment (four for H+R). These consisted of ten-minute focal animal observations during grazing, recording the bites taken of different plant categories. Plant categories included separate species of tall herbs and tussock grasses, dwarf shrubs, shrubs, trees and acorns (see Chapter 2). In grassland vegetation categories of mixed species were recognized according to sward structure: short leafy sward (<7 cm), tall leafy sward (>7 cm) and sward with flowering stems. Notes were also made on the ingestion of non-forage items (soil, rabbit faeces, plastic etc.). As many recordings per animal as possible were made during the entire daylight period. The data were collected using the OBSERVER 2.0 programme (Noldus, 1991). Most observations during the experiment were made by two observers, with occasional assistance of two more. Each observer had practised extensively prior to data collection.

Samples of each plant category were taken by hand-plucking by one observer. These were not significantly different in diet quality from samples collected from four oesophageally fistulated steers (Chapter 2). The same fistulated animals were used to convert plucking size of grassland plants to bite size through application of regression formulas including live weight as a size scaling factor (Chapter 2). For tall herbs, large tussock-forming graminoids and woody plants plucking size was supposed to equal bite size. Acorns were estimated to be consumed one per bite.

All samples were dried at 65°C, ground through a 1 mm sieve and analyzed for contents of total nitrogen (N), sodium (Na), phosphorus (P) and calcium (Ca) following procedures by Walinga *et al.* (1989). The organic matter digestibility was determined using the *in vitro* method of Goering & Van Soest (1970) with a sheep-cattle conversion factor for the standard samples, which were obtained from sheep (see Aerts *et al.*, 1984). The organic matter digestibility was converted to digestible organic matter (DOM), expressed on a dry matter basis.

Table 4.1 Visual condition scoring system (after Lowman *et al.*, 1976).

Score	Spinous processes	Ribs	Tail head
0	Very sharp	prominent	prominent
1	Sharp	less obvious	less obvious
2	Rounded	not obvious	some tissue cover
3	Only felt by firm pressure	invisible	some fat cover
4	cannot be felt	with beginning folds of fat	slight mounds of fat
5	cannot be felt	in folds of fat	buried in fat

In each period the animals were weighed without prior fasting and visually scored for body condition to the nearest 0.25 score (Table 4.1). The index used is linearly correlated with the amount of fat in the animal (Wright & Russel, 1984) and has also been adapted for free-ranging horses (Duncan, 1992). Similar condition score indices which have been demonstrated to correlate with body fat have been applied successfully to cattle (Fox *et* *al.*, 1988) and African buffalo (*Syncerus caffer*) (Prins, 1989). Blood samples were taken twice a year and analyzed for protein and mineral content. Saliva samples were collected on three occasions and analyzed for Na and potassium (K). Results for body weight changes, blood serum and saliva analyses have been presented by Wallis de Vries (1992; Chapter 3).

At the end of the experiment fat content was estimated with the plateau method using deuterium oxide (D_2O) (Prentice, 1990). The animals were injected with D_2O without prior fasting period. Subsequently, a blood sample was taken after 3.7-5.1 h and a second sample after 8.3-10.7 h. Analyses were carried out at the Centre for Isotope Research in Groningen, the Netherlands. The first blood sample yielded the higher D_2O concentrations and was therefore assumed to reflect a complete mixing of the injected D_2O in the animal's body water. This blood sample was then used to estimate total body water content. The estimate was corrected by 4% for D_2O loss through excretion and binding to protein. Lean mass was calculated by assuming a water content of 73% in the fat-free animal. Fat mass was estimated as live weight minus lean mass. As the method rests on assumptions concerning mixing time of D_2O and lean mass water content, the estimate of fat percentage should be treated as an index rather than as an absolute figure (H. Visser, pers. comm.).

The animals were slaughtered in July 1991. Analyses of bone mineralization and histomorphometry of the 12th rib were carried out according to procedures described in Van Mosel *et al.* (1991).

Calculations and Statistical Analysis

Nutritional budgets were calculated for each individual animal. Daily dry matter intake (in g DM/kg LW; DM = dry matter, LW = live weight) was estimated as the product of daily grazing time, biting rate and bite size per plant category. Dietary digestible organic matter (DOM in g/kg DM) was converted to metabolizable energy (ME in kJ/kg DM) by the following equations (with DCP for digestible crude protein in g/kg DM):

$$\mathrm{ME} = 15.06\,\mathrm{DOM} \qquad \text{for DOM/DCP} > 7$$

$$\mathrm{ME} = 14.02\,\mathrm{DOM} + 7.36\,\mathrm{DCP} \qquad \text{for DOM/DCP} < 7 \quad \text{(after Van Es, 1978)}$$

$$\text{with DCP} = 57.5\ \%\mathrm{N} - 38.7 \quad \text{(after Van Soest, 1982)}$$

Energy and nitrogen intakes were expressed on a metabolic weight basis ($LW^{0.75}$), whereas mineral intakes were expressed on a live weight basis, following ARC (1980) routine. Mineral and nitrogen requirements were determined according to the estimates for maintenance and growth from ARC (1980). For periods of weight loss the release of minerals and nitrogen was estimated by the product of their average concentration in the entire body as given by ARC (1980) and the recorded weight loss. The gross nutrient balance was calculated on a daily basis by subtracting requirements from intake. A separate balance was made up for the summer and the winter season (respectively April-November and December-March).

Energy requirements were not calculated, because changing body composition during periods of weight gain and loss, varying weather exposure and locomotion costs would only allow a crude guess. Instead energy intake has been expressed per unit net weight gain over the growing season (April-November).

Analysis of variance for repeated measurements was performed to determine treatment differences for various parameters between treatments and monthly periods using the SAS (1985) statistical package. The Kruskal-Wallis test was used for non-parametric data. Linear regression analysis was carried out to determine relationships between condition score and fat estimate.

Results

Forage intake and quality

The dry matter intake per unit live weight (DMI) was similar for three of the four different treatments (Table 4.2). The forage intake for the H+R steers was significantly lower than in the other three treatments ($P<0.05$), especially during summer. DMI was lower in the second year for all treatments as a consequence of increased body weights. There was a significant monthly variation ($P<0.0001$) with higher DMI in summer and lower values in winter (Fig. 4.1).

Table 4.2 Annual means of forage intake and diet quality for free-ranging steers in different habitat combinations of heathland (H) and riverine grassland (R) (DMI=dry matter intake in g/kg live weight, DOM=digestible organic matter, N=nitrogen, Na=sodium, P=phosphorus, Ca=calcium).
H: year-round heathland, R: year-round riverine grassland, H/R: winter heathland/summer riverine grassland, H+R: year-round heathland and riverine grassland combined.

Treatment	DMI (g/kg LW)	DOM	N	Na	P	Ca
		(in % of dry matter)				
H	21.4	63.6	1.95	0.02	0.10	0.17
H/R	21.4	61.4	2.52	0.06	0.30	0.46
R	21.4	62.5	3.07	0.08	0.36	0.64
H+R	19.3	63.7	2.40	0.05	0.26	0.32

Diet quality also showed a significant monthly variation ($P<0.0001$). Monthly maxima were reached in March or May and minima occurred mostly in January (Fig. 4.2). All pairwise treatment comparisons for the five diet quality parameters revealed significant differences ($P<0.01$, Table 4.2). The magnitude of the differences for DOM were small, however. Nitrogen and mineral concentrations were highest in the riverine area and lowest on heathland; this difference is illustrated by the shift in diet quality for the H/R animals between summer and winter range (Fig. 4.2). The diet of the H+R animals generally showed intermediate values to the riverine area and heathland.

Nutrient balance

Weight gains for the H steers were significantly lower than in the other treatments (Wallis

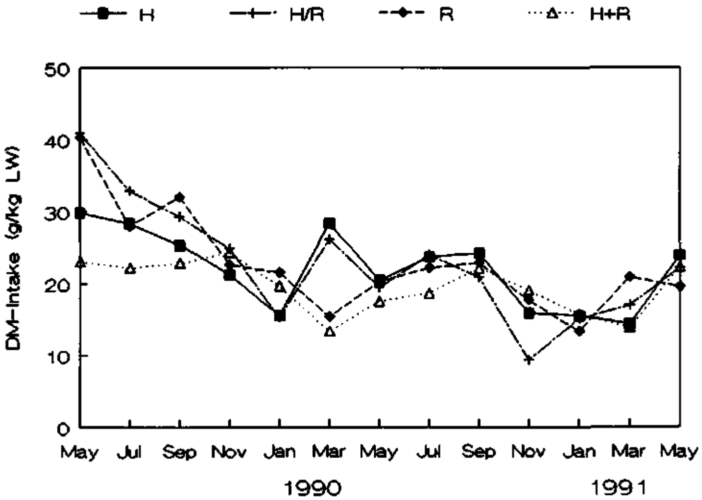


Figure 4.1 Daily dry matter intake per unit live weight for free-ranging steers on heathland (H), riverine grassland (R) and habitat combinations (H/R: winter/summer shift, H+R: year-round) in the course of two years.

de Vries, 1992; Chapter 3). The energy intake per unit weight gain during the growing season, however, was much higher in H animals compared to the others (Fig. 4.3). Therefore, the level of energy retention rather than the level of intake does seem to explain the lower weight gains on heathland.

Average daily gross balances for nitrogen and minerals (including weight changes) have been calculated for summer and winter of both years (Fig. 4.4 a-d). For all nutrients the H steers show a relatively poor balance in comparison to the R steers. The H+R treatment is intermediate and the H/R treatment reveals similar values to either H or R treatments depending on the season. The balance for the H animals appeared more favourable during winter, in the absence of growth and with available nutrients through the metabolization of weight losses. For the R and H+R treatments the difference in nutrient balance between summer and winter was less distinct.

With the exception of H, all steers reached a positive nutrient balance over the two years. The surplus was greatest in the riverine area. Despite its high requirements for growth, the R animals consumed around twice the required amount of minerals (183% for Na, 215% for P and 285% for Ca). On the other extreme, the H animals were almost able to meet their requirements for N (97%) and for Ca (92%), but clearly ingested insufficient amounts of P and Na (74% and 54% of requirements respectively).

Mineral status

An earlier analysis of results showed that Na/K ratios pointed to deficiencies in the H group for Na in summer but not in winter. Mineral content in blood serum did not

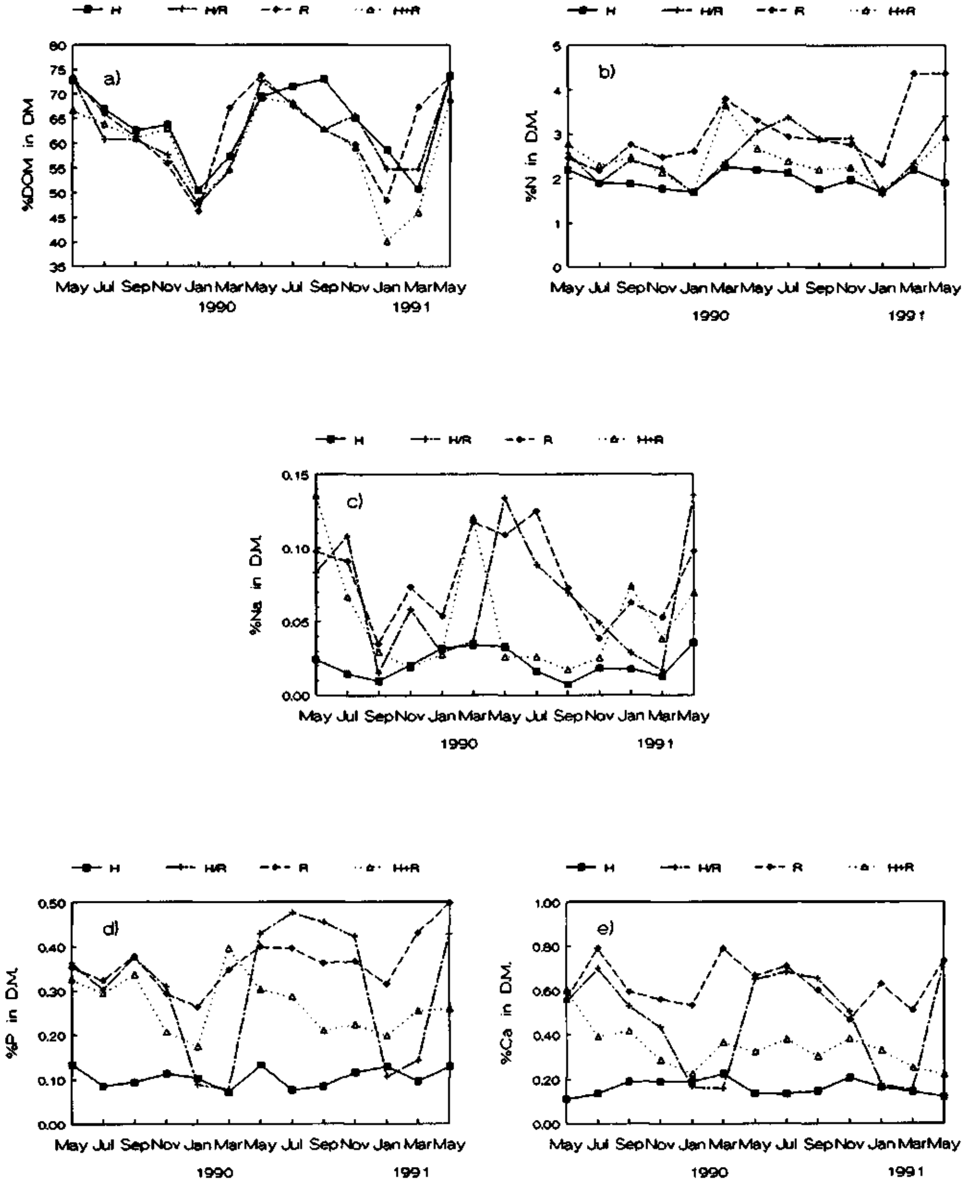


Figure 4.2 Diet quality for free-ranging steers on heathland (H) and riverine grassland (R) and habitat combinations (H/R: winter/summer shift, H+R: year-round) in the course of two years: a) digestible organic matter, b) nitrogen, c) sodium, d) phosphorus and e) calcium.

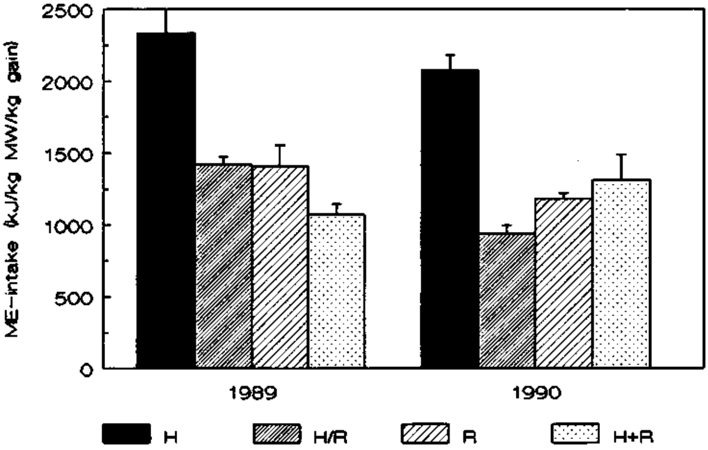


Figure 4.3 Intake of metabolizable energy (ME, kJ; ±s.e.) per kg metabolic weight per kg net weight gain during the growing season for free-ranging steers on heathland (H) and riverine grassland (R) in two years and habitat combinations (H/R: winter/summer shift, H+R: year-round).

Table 4.3 Bone analyses of free-ranging steers in different habitat combinations: heathland (H), riverine grassland (R) and combined habitats (H+R) after two years for bone ash percentage, osteoclast cover and percentage unmineralized bone (±95%-confidence limits). The P-value indicates the significance of treatment differences resulting from an ANOVA.

	%Bone ash cover	%Osteoclast cover	%Osteoblast bone	%Unmineralized
H	50.4±4.5	3.8±1.0	41.6±14.9	7.28±3.51
R	56.7±4.4	1.9±0.6	31.8±4.2	2.20±1.80
H+R	57.9±4.4	2.0±1.7	33.7±6.5	2.41±1.17
Treatment difference	P=0.020	P=0.014	N.S.	P=0.004

indicate deficiencies, although levels of inorganic-P were significantly lower in the H group than in other groups (Wallis de Vries, 1992; Chapter 3).

Analysis of bone material from the H, R and H+R steers has revealed further deviations in the first treatment (Table 4.3). Bone ash content was lower in the H treatment, while histological examination showed that osteoclast cover and the percentage of unmineralized bone were higher. Osteoclasts break down mineralized bone for remodelling purposes; this also occurs to alleviate P or Ca shortages (Jaworski, 1983). The cover of osteoblasts (bone building cells) was rather high and not significantly

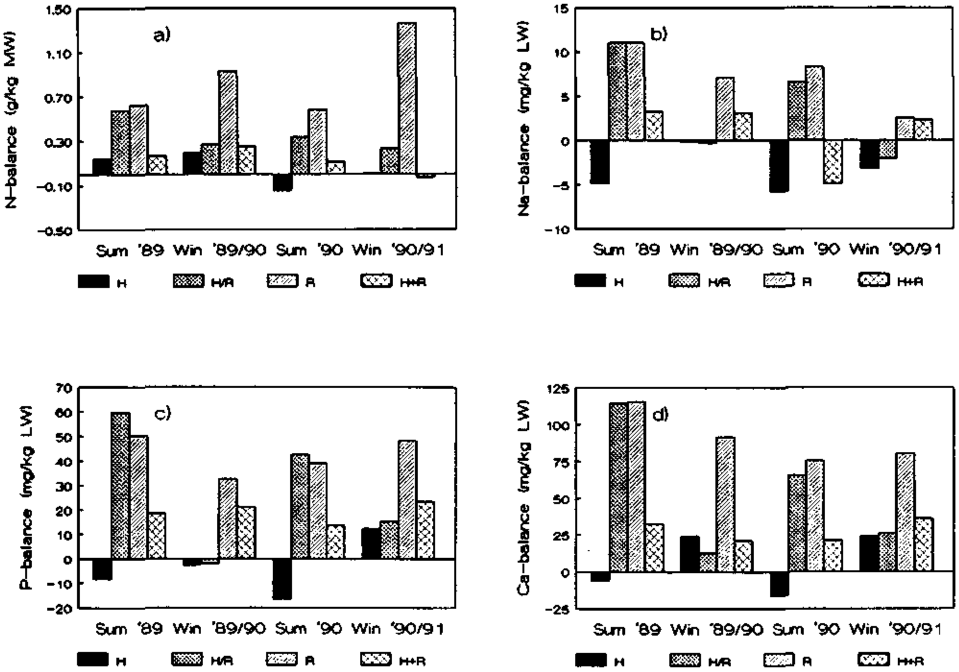


Figure 4.4 Mean gross daily nutrient balance in the summer season (April-November) and in winter (December-March) for free-ranging steers in heathland (H) and riverine grassland (R) and habitat combinations (H/R: winter/summer shift, H+R: year-round) in two years for a) nitrogen, b) sodium, c) phosphorus and d) calcium.

different between treatments, which reflects the relatively young age of the animals. Signs of osteomalacia were also observed in the field. Two animals of the H treatment developed a stiff gait; the first one during the first winter, the second one in the second spring. Although the first animal walked normally again after the summer, it broke its leg in november 1990 and was subsequently removed from the experiment (unfortunately no bone analysis was carried out on this animal).

Pica behaviour

Pica behaviour, the display of 'perverted appetite', is often a sign of mineral deficiency, mostly for Na and P (McDowell, 1985). The percentage occurrence of pica behaviour (licking of soil and urine patches; ingestion or chewing of wood, bone or plastic) during grazing observations was significantly different between treatments ($P<0.025$; Kruskal-Wallis test). Averaged over all observation periods it was more frequent in the H treatment (18.6%) and in the heathland part of the H+R treatment (19.3%) than in the R treatment (4.2%) and the riverine part of the H+R treatment (6.4%).

Consumption of rabbit faeces was frequently observed for the H steers. These contributed 1.1% to the average DM-intake, but faecal pellet intake was much higher during winter (3.1% of DMI on average), with two individuals relying up to 12.5% and 17.8% of DMI on faecal pellets in January of the second year. The nutritive value of rabbit faeces was not much higher than the average diet (2.05% N, 0.14% P, 0.03% Na, 0.28% Ca and 44.2% DOM). The inclusion of faecal pellets in the diet may be due to their relatively high intake rate in winter. Faecal pellet intake dropped radically with the onset of grass growth in spring. Intake of fungi occurred only in autumn and was limited to *ca.* 0.06% of DMI. Their availability was low but they appeared to be selected for. This could be expected in view of their high nutritive value (5.99% N, 1.00% P, 0.07% Na, 0.08% Ca and 74.8% DOM).

Steers of the H treatment also consumed bone pieces of dead rabbits. In September 1990, one of the H animals ate the entire body of a recently dead rabbit. This was again observed a few months later by another H individual. Subsequently, in the spring of 1991, different non-forage items were put in the path of all individuals when grazing, on at least two occasions. Small pieces of soft plastic were eaten by all individuals. However, when contaminated with rabbit blood the plastic was refused entirely. Fresh rabbit parts (including the bone) were sniffed, sometimes accompanied by 'flehmen' and sniff-yawning (Halder & Schenkel, 1972), but chewed and eaten by one H individual only. Fresh and cleaned bone was eaten by half of the H steers (the individuals which had been seen eating a dead rabbit). Finally, old rabbit bones, collected from rabbit burrows, were readily ingested by all H animals, but not even sniffed at by steers from the other treatments.

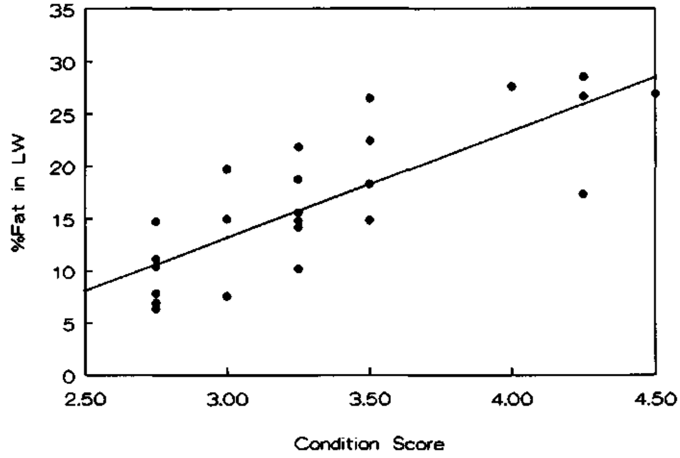


Figure 4.5 The relation between body fat percentage (live weight basis) and condition score in free-ranging steers (%Fat = 10.2 CSC - 17.4 ; R^2=0.64, d.f.=22, $P<0.001$)

Fat reserves

Fat reserves as determined at the end of the experiment by the deuterium oxide method were significantly different between treatments ($P<0.025$; Kruskal-Wallis test), which was mainly due to the low fat content of H animals (7.2%) relative to the other treatments (H/R 15.2%, R 19.4%, H+R 15.1%). There were significant positive relations between the estimate of fat content and condition score (Fig. 4.5).

Very low condition scores (1.7; range 1.25-2.00) were recorded for the H steers during the second, colder winter, when weight loss amounted to 25.3% (range 20.9-29.0%) of peak autumn weight (Wallis de Vries, 1992; Chapter 3). Extrapolation of the regression equation indicates the virtual exhaustion of fat reserves. Condition scores were continuously higher in the other treatments (Fig. 4.6).

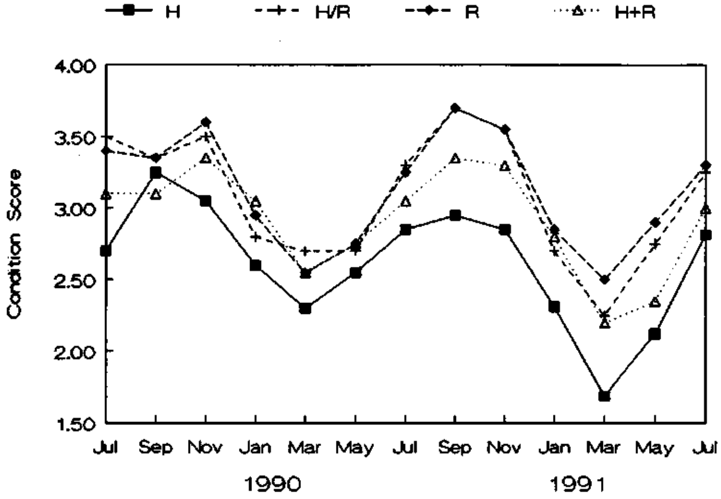


Figure 4.6 Condition scores for free-ranging steers on heathland (H) and riverine grassland (R) and habitat combinations (H/R: winter/summer shift, H+R: year-round) in the course of two years (s.e. varied between 0.05 and 0.15 score units).

Discussion

Animal performance

The analysis of the nutritional budget and performance of the steers in this study indicates clear differences between heathland and riverine habitats. Animals staying permanently on heathland showed the poorest performance. Their mineral balance was negative, especially for Na and P. Analysis of saliva samples indicated (periodic) deficiencies of Na. The high bone osteoclast cover and an incomplete bone mineralization suggests that the bone of these animals was gradually used up to meet mineral requirements. Pica behaviour indicated deficiencies of Na and/or P. Finally, H animals experienced low weight gains and high winter losses (Wallis de Vries, 1992; Chapter 3) and had lower fat reserves.

The R steers, grazing year-round on fertile riverine grassland, showed growth rates reflecting optimal conditions. Compared to MRY bulls in stall trials (Vos, 1969), the R steers reached 85% and 90% of the live weight of similarly aged bulls at the end of the first and second growing season respectively; at the end of the experiment this percentage had risen to 93%. Taking into account the slower growth rate of steers compared to bulls and the relatively unfavourable outdoor winter environment, these small differences indicate that the steers in the riverine area were close to their maximum physiological growth potential. Thus, the growth check during winter does appear to be compensated for in the course of summer. However, in cold winters the deterioration of digestibility could lead to a reduced forage intake and a much greater weight loss (Bokdam & Wallis de Vries, 1992).

The H/R and H+R steers showed an intermediate performance. This was to be expected as animals from both treatments suffered a mild nutritional stress by staying on heathland for part of their time, either forced or by their own choice. The reason why the H+R animals did not stay permanently in the riverine area may have been a higher energy intake rate on heathland, especially during winter (Chapter 6). In addition, the *in vitro* digestibility of riverine forage was lower in the H+R than in the R treatment (DOM 3% lower on average; Chapter 1). This difference also might explain the relatively low forage intake of the H+R animals during summer. For both the H/R and the H+R steers the nitrogen and mineral balances were positive. Their energy retention therefore does not seem to have been impaired by these nutrients.

In the case of the steers on heathland the following mechanism relating mineral shortage to energy metabolism may be hypothesized. Low concentrations of Na and P often depress food intake and growth rate (Cohen, 1975; Gartner *et al.*, 1980; McDowell, 1985). Although daily intake on heathland remained similar to the riverine area, growth rate proved to be much lower (Wallis de Vries, 1992; Chapter 3). A shortage of Na and P may depress the digestion in the rumen and thus reduce energy retention and growth. The importance of a constant salivary supply of Na and P to the rumen for optimal microbial activity has been noted repeatedly (Cohen, 1975; Kreulen, 1985; Reid & Jung, 1991). Lack of minerals could then explain the apparent excess of energy in the H steers: the actual energy value of the feed may have been much lower because of impaired digestion. Freeland *et al.* (1985) have proposed that tannins in the diet can lead to higher sodium losses in herbivores. However, it is unlikely that secondary plant compounds significantly worsened the sodium balance on heathland, as the diet of the steers consisted mainly of grasses and contained only 7% woody plants on average. Thus, the reduced digestive efficiency in H steers can explain their lower weight gains, smaller fat reserves and higher weight loss over winter. The equally high weight loss of the H/R steers (Wallis de Vries, 1992; Chapter 3) indicates that mineral body reserves cannot maintain an optimal rumen environment at low mineral intakes. The low diet digestibility and low weight loss for the H+R animals suggest that an even lower dietary energy content does not lead to high weight losses if coupled to a sufficient mineral intake (Fig. 4.2).

It may be speculated that Na and P would affect the survival and reproduction of free-ranging cattle on heathland. The low availability of these minerals appears to cause an insufficient build-up of fat reserves. The second winter during the study was normal for a mild temperate climate, yet the weight loss of H animals approached 30%, which is considered a critical value for successful recovery (Franzmann, 1985; Holechek & Herbel, 1986). Absolute weight loss was similar in the H/R steers (Wallis de Vries, 1992; Chapter 3), but their larger amount of reserves kept them in better condition (Fig. 4.6). The mineral requirements of lactating cows (450-500 kg, 10 l milk/day) for Ca correspond to a weight gain of 1 kg/day; for P this amounts to 1.5 kg/day and for Na requirements are twice those for gaining 1 kg/day (ARC, 1980). Thus, cow condition would rapidly deteriorate and allow even less accumulation of fat reserves. This would lead to high death rates in colder winters and insufficient condition for calf conception. Reduced fertility and abortion through a general loss of condition has been recorded in cattle suffering deficiencies in P and Na (Theiler *et al.*, 1927; Cohen, 1975; Gartner *et al.*, 1980; McDowell, 1985).

Pica behaviour as a functional response to deficiency

Pica behaviour has long been recognized as a sign for deficiency in Na and P (Green, 1925; McDowell, 1985). It also occurs in wild ungulates in various forms: geophagia and lick use by bovids, cervids, equids and others (Kreulen & Jager, 1984; Freeland & Choquenot, 1990; Guthrie, 1990); osteophagia in cervids, giraffe, one-humped camel and a number of antelopes; antler chewing in cervids; and even carnivory of live or dead lemmings, rabbits and birds by red deer, caribou and duiker (Grzimek, 1968; Kelsall, 1968; Sutcliffe, 1977; Furness, 1988; Stanley-Price, 1989; H. Klingel, pers. comm.). Various explanations have been put forward to interpret geophagia and lick use (Kreulen, 1985): it may prevent acidosis and disorders caused by secondary plant compounds by an increased buffering capacity, act as a lubricant for fibrous forage, provide extra minerals and stimulate the flow of saliva. The soil eaten on heathland consisted mainly of humose sand. Part of the geophagia is likely to have been induced by Na-enriched urine patches. A need for trace minerals (mainly copper, selenium and cobalt) might also have stimulated geophagia on heathland (see McDowell, 1985). However, this would not explain the chewing on stones, wood and plastic. Moreover, no deficiencies for trace minerals have been observed (Wallis de Vries, 1992; Chapter 3). In view of the observed mineral deficiency, it seems probable that the main cause for geophagia and the chewing on stones, wood and plastic on heathland was the stimulation of saliva flow, which contains high concentrations of Na and P and could thus relieve mineral shortage in the rumen. In this respect it is significant that H+R steers showed more pronounced pica behaviour on heathland than in the riverine area. This suggests that eating of soil is a direct response to the ingestion of forage with a low mineral content. Geophagia and chewing on stones has also been observed in cattle in an area with low soil fertility in the presence of NaCl supplementation (J.M. Gleichman, pers. comm.; S.E. Van Wieren, pers. comm.), which may suggest that deficiency of P alone also causes geophagia.

Osteophagia has been rarely interpreted as a functional response to phosphorus deficiency since this was first suggested by Green (1925), although Underwood (1981) hints at the possibility. While rodents and birds have proved to discriminate and select for Ca in a state of deficiency (Hughes & Wood-Gush, 1971; Hansson, 1990; J. Graveland, in prep.), Ca or P deficient livestock have not been shown to selectively consume mineral supplements when offered in powder form (Green, 1925; Gordon *et al.*, 1954; Coppock

Table 4.4 Average daily gross nutrient balance of free-ranging steers on heathland (H) including intake of non-forage items and the estimated use of body reserves required to cover mineral demands over the study period of 770 days.

	Consumed (mg/kg LW)		Required (mg/kg LW)	Balance (mg/kg LW)	Reserves (g)	% Use of Reserves (770 days)
	Forage	Soil, Bone & Water				
Na	4.7	0.9	8.8	-3.3	412.5	226
P	23.1	0.8	31.0	-7.1	2200	61
Ca	35.8	1.9	38.9	-1.3	3850	6.5

Intake of non-forage items has been estimated at 250 g soil, 2.5 g bone and 31 l drinking water for a mean live weight (LW) of 425 kg. Soil contained 0.04% Na and 0.06% P (J. Bokdam unpubl. data), bone was assumed to consist of 16% Ca, 8% P and 0.4% Na (ARC, 1980), analysis of drinking water revealed concentrations of 14 mg/l Ca, 9 mg/l Na and 0.37 mg/l P. Daily requirements were taken from ARC (1980). Initial body stores have been calculated from estimates by the ARC (1980) for body composition, on the basis of 315 kg live weight at the onset of the experiment. Reserves were assumed to be used with an efficiency of 100%, absorption of minerals from forage and non-forage was assumed according to ARC estimates (91% for Na, 58% for P and 68% for Ca).

et al., 1976). This has been viewed as evidence that herbivores cannot recognize Ca and P by taste and are therefore unable to select actively for these minerals (McDowell, 1985). Yet, herbivores may learn dietary differences by association (Provenza & Balph, 1990; Provenza, 1991). The unanimous consumption of plastic during the field experiment demonstrates the great curiosity of cattle. Bones and antlers are easily recognizable and contain high concentrations of Ca and P (ARC, 1980). By eating or chewing these out of curiosity, herbivores may learn to associate an alleviated deficiency with bone consumption. The world-wide occurrence of osteophagia in regions with low soil fertility suggests that it is one of the basic behavioural responses to counter mineral deficiency. Carnivory, as recorded in the H steers, is likely to be an extreme form of osteophagia (see Green, 1925; Underwood, 1981). The smell of blood is somehow repellant to the animals, and thus seems to prevent a ready acceptance of animal corpses. It may be speculated that this behaviour minimizes the risk of infection with parasites or diseases such as botulism, which is a common cause of mortality in herbivores eating bones from corpses (Green, 1925; McDowell, 1985; Stanley-Price, 1989). Old bleached bones do not appear to be a vector of botuline bacteria (Green, 1925). However, such selectivity for old bones would not prevent the animals from contracting spores of the extremely dangerous anthrax disease (Prins & Weyerhauser, 1987); the erratic and epidemic occurrence of this disease perhaps precludes animals to learn avoiding potential sources of infection.

The mineral sought after in osteophagia by herbivores is probably primarily P, as Ca deficiency is rare. Guthrie (1990) advocated that antler chewing is caused by Na deficiency. However, osteophagia and carnivory have also been recorded near the seashore (Sutcliffe, 1977; Furness, 1988), where Na deficiency is unlikely. Bone contains some 0.4% Na (ARC, 1980), which is more than ten times the plant concentration in poor environments. Yet, it is probably not enough: the amount of bone needed daily to balance the Na deficit in the H steers for example (Table 4.4), would be 340 g, which appears unrealistic. Much less bone (40 g) would be needed to cover the demands in P of the H animals. In the present case bone consumption was evidently not sufficient to prevent bone resorption and osteomalacia.

Mineral balance and condition
Despite the evidence of deficiencies all H animals survived the experiment but one which broke a leg (likely due to osteomalacia). This could be explained by the use of initial body stores and the uptake of nutrients from soil, bone and water. A corrected estimate of the average daily gross nutrient balance for the H steers has therefore been calculated (Table 4.4). The Na and Ca balances are altered substantially by including the intake of water and non-forage items; the P-balance remains relatively unchanged. Estimates of the percentage use of original body reserves show that only a small fraction (6.5%) of calcium reserves would be needed to cover the deficit. This percentage is much higher for P (61%) and more than twice (226%) the amount of body reserves would be required for Na. It appears reasonable, by analogy to weight loss, to estimate the available nutrient reserves at 30% of total body stores. Thus, the nutrient balance cannot be made to fit for Na and P. This suggests a higher absorption, a lower excretion or a lower requirement. Indeed, it has been found in balance trials that cattle given very low amounts of Na grew normally or only little less than control animals (Theiler *et al.*, 1927; Morris & Gartner, 1971). However, in the first experiment this resulted in abortion and in the second a number of physiological aberrations occurred. Similarly, two heifers given an extremely Ca- and P-deficient diet (0.06% P and 0.13% Ca) still gained 86 and 222 kg respectively over the first 9 and 21 months but died after 17 and 26 months (Theiler *et al.*, 1927). Thus, the animals may survive for rather long periods under deficiency but still function suboptimally in various ways. The observed deficiencies in the H steers point to a similar situation.

There seems to be a discrepancy between the sporadic reports of mineral deficiencies in wild herbivores (Robbins, 1983) and their relatively common occurrence in domestic herbivores (McNaughton, 1987). Wild herbivores usually occur in lower densities and in more diverse environments than livestock. This will increase the probability of finding a suitable nutrient source and thus prevent deficiencies. Moreover, selection pressure may promote an efficient use of scarce nutrients. In domestic animals, high densities, uniform ranges and selection for productivity under relatively optimal conditions tend to increase the chance of deficiencies under free-ranging conditions. Part of the discrepancy is also likely to be due to an underrepresentation of research on deficiencies in wild herbivores. Belovsky (1981a) has suggested a regulating function of Na-availability in the population dynamics of moose on Isle Royale. Studies on deer in environments with low soil fertility in Scotland have suggested mineral deficiencies to raise mortality and to lower reproduction success (Mitchell *et al.*, 1973; Iason *et al.*, 1986). Introduced reindeer on

South Georgia have shown considerable mortality through a jaw disease which could be associated with P-deficiency (Leader-Williams, 1988). Differences between wild and free-ranging domestic herbivores are therefore similar and probably more dependent on environmental conditions than on animal characteristics.

Conclusion

The present experiment revealed a major effect of habitat quality on the performance of steers. The animals restricted to the fertile riverine habitat thrived under near-optimal conditions. On heathland of low soil fertility deficiencies of Na and P were apparent. The combination of both habitats resulted in an intermediate performance without signs of deficiencies.

It may be postulated that mineral deficiency would seriously lower the population density of large herbivores in poor habitats by increased mortality and reduced reproduction rates from an inferior condition. Comparison of large herbivore population densities in areas with different nutrient availability in Africa support this hypothesis (Bell, 1982; De Bie, 1991). However, adaptation and behavioural responses to nutrient stress may reduce its negative effects to some extent. If so, the outcome could be a similar population density in low and high soil fertility habitats, yet with a different age structure and a decline in size of individuals, as noted by Klein (1965) and Geist (1971, 1978) in 'low quality' populations. More emphasis on mineral nutrition will be needed to clarify the impact of variation in mineral availability between habitats on the population level.

Plates 12 and 13. Two animals from the heathland treatment consumed rabbit corpses as a response to phosphorus deficiency (Plate 13 by J.M Gleichman).

CHAPTER 5

Foraging Strategy of Cattle in Patchy Grassland

Summary

We tested several strategies of foraging that grazing herbivores may adopt in a patchy habitat in relation to energy intake. The patch selection of cattle was investigated in an Agrostis/Festuca *grassland and in a* Lolium *grassland in thirteen observation periods over two years. Both grasslands were stocked with five yearling steers. Bite counts were made on patches of different vegetation structure: short, tall and mature stemmy grass. Bite size of each patch category was determined by hand-plucking. Samples of patch types were analyzed for organic matter digestibility, as a parameter for energy content.*

There was a large seasonal variation in relative patch cover and in forage characteristics. However, the differences between patches in bite size, bite rate and digestibility were consistent over time. In short patches digestibility was high, bite size was low and bite rate was high compared to stemmy patches. In tall patches digestibility was only little lower than in short patches and bite size and bite rate were intermediate between short and stemmy patches. The steers preferred the short and tall patches over the stemmy patches, despite a relatively low intake rate of digestible organic matter in the short patches.

Four hypotheses on foraging strategy were examined to explain the allocation of time or bites between patches: random allocation according to bites, random allocation according to grazing time, matching of time in proportion to digestibility, and matching of time in proportion to intake rate of digestible organic matter. The observed distribution of bites and time between patches was significantly different from the predictions of the various hypotheses. Patch choice was better explained by a random allocation of grazing time than by a random allocation of bites. Matching for digestible organic matter intake rate yielded the worst predictions of patch selection. Matching for digestibility gave the best explanation of patch selection, but the improvement compared to a random allocation of grazing time was not significant. The significance of the contribution of digestibility to patch selection may have been confounded by the effect of increased selectivity within tall patches.

The relation of the observed patch selection was discussed in relation to the maximization of energy intake rate. The selectivity of cattle was not pronounced, but it was consistent with a principle of maximization of energy intake on a daily basis instead of a short-term basis. Selectivity appeared to be constrained by the costs to search and discriminate between different forage resources. It is concluded that a flexible preference for short patches over tall patches and avoidance of stemmy patches provides a good approximation of energy intake maximization in a complex and changing environment.

(with C. Daleboudt, submitted to Oecologia)

Introduction

Grasslands often consist of patches of different vegetation structure, which vary in forage availability and nutritive value. Grazing causes a decline in biomass but an increase in nutritive value through the stimulation of regrowth (McNaughton, 1984). For foraging ungulates the selection between patches is the main tool by which they can manipulate forage intake rate and quality. This may be increasingly so for large grass and roughage feeders, such as cattle, which are less able to select from fine-grained vegetation within patches (Grant *et al.*, 1985 and 1987; Illius & Gordon, 1990). Patch selection is an important domain of optimal foraging theory (reviewed by Stephens & Krebs, 1986). Yet, it has been rather sparsely investigated in grazing ungulates (Illius, 1986; Bazely, 1988; Langvatn & Hanley, 1993). According to most models on optimal foraging the animal should maximize its long-term average intake rate of energy (or another essential nutrient) by making a trade-off between gains for energy intake from different patches and costs in time and energy for travel, searching and food handling (Stephens & Krebs, 1986). For grazing herbivores the application of these parameters is difficult: patch definitions need to consider the characteristics that are relevant to the herbivore, the travel time between patches is an intricate concept if patches form an uninterrupted mosaic such as in lightly grazed grasslands and, finally, the distinction of searching and handling time is impossible.

The key to a sensible definition of patches for grazing herbivores is the relation between sward characteristics and forage intake. Although different ungulate species vary in selectivity according to body size and mouth morphology (Illius & Gordon, 1987; Demment & Greenwood, 1988; Hodgson *et al.*, 1991), a general pattern for the response of intake to changes in the sward can be described (Hodgson, 1982; Forbes, 1988). Bite size is positively related to forage biomass and height (Allden & Whittaker, 1970; Illius, 1986; Penning, 1986; Forbes, 1988; Penning *et al.*, 1991; Burlison *et al.*, 1991) and to bulk density in thin and tall swards (Stobbs, 1973; Chacon & Stobbs, 1976; Forbes, 1988). Large bites require a greater mastication effort, which increases further with forage maturity (Demment & Greenwood, 1988; Penning et al., 1991). As bite rate is inversely related to mastication rate, bite rate steadily declines with bite size and maturity of the forage (Demment & Greenwood, 1988; Penning *et al.*, 1991; Illius, 1986). When experiencing forage depletion grazing animals may, within a limited range, compensate the intake reduction from lower bite size by increasing bite rate and grazing time. However, with progressive depletion of available forage the intake rate will be determined mainly by bite size, and therefore decrease (Allden & Whittaker, 1970; Chacon & Stobbs, 1976; Hudson & Nietfeld, 1985; Penning, 1986). When taking the additional effect of forage maturation into account, an optimum curve for the intake rate of digestible organic matter in relation to forage availability may emerge. Intake rate can decrease in mature swards with flowering stems because tall leafy swards are higher in digestibility and in bulk density, but only little lower in biomass (see Forbes, 1988). In conclusion, forage quantity (biomass, height or density) and maturity can be identified as the main determinants of patch quality for grazing herbivores.

The difficulty in distinguishing searching and handling times in herbivores has often been circumvented by comparing the short-term rate of nutrient intake between patches and considering this measure as a maximization criterion (*e.g.* Ungar & Noy-Meir, 1988). Clear evidence for intake rate maximization in grazing herbivores was found only in an experiment by Bazely (1988), in which sheep could choose between two patches differing widely in biomass and nutritive value. In the experiments by Illius (1986) and Langvatn & Hanley (1993) patch grazing time showed rather a matching pattern in proportion to patch intake rate. The significance of these results with respect to intake maximization is unclear. Constraints relative to the acquisition of information on patch differences or selection within patches might explain the observed reduction in patch selectivity. As suggested by Arnold (1987), the magnitude of patch differences could be important in determining the adopted strategy.

The present experiment examined the foraging strategy of cattle in a semi-natural context with a great variation in patch quality and availability: two grassland types grazed continuously over a two year period. The animals were therefore well acquainted with their environment. Changes in the vegetation over time were important but resulted purely from seasonal dynamics and grazing impact. Evidence suggested that different minerals played a role besides energy in determining the choice of habitat (Chapter 6). However, at the smaller scale of the vegetation unit the availability of minerals was less variable, hence we concentrated on energy intake for the purpose of this analysis. We tested a strategy of matching for energy intake rate against a strategy of matching for energy content and random foraging. The observed patch selection was discussed in relation to long-term energy intake rate maximization.

Methods

Study areas and animals

The experiment was conducted in two different study areas in the Netherlands: the Karshoek area (74 ha; 53°32' N, 6°32' E, altitude 7 m) and the Renkumse Benedenwaarden (9 ha; 51°58' N, 5°43' E, altitude 8 m) (see Chapter 1 for more details). In both areas the most frequently used vegetation unit was selected for the investigation of grazing behaviour. The vegetation unit studied in the Karshoek area was an *Agrostis/Festuca* grassland (8 ha in total), dominated by *Agrostis capillaris, Poa pratensis, Holcus lanatus* and *Festuca rubra.* In the Renkumse Benedenwaarden the vegetation consisted of a *Lolium* grassland (7 ha), dominated by *Lolium perenne, Agrostis stolonifera, Elymus repens* and *Poa trivialis.*

Both areas were stocked with five yearling MRY steers in May 1989 (in the Karshoek another five Hereford steers were added, but these will not be dealt with in this chapter). The animals grazed continuously in these areas until July 1991, without any kind of feed supplementation.

Measurements and observations

Vegetation measurements and animal observations were carried out in thirteen bimonthly periods. The observations in the *Agrostis/Festuca* grassland were always carried out two weeks earlier than in the *Lolium* grassland. Vegetation patch types were described using three grass categories and a tall herbs category. The grass categories were defined as short grass (<7 cm tall, no flowering stems), tall grass (>7 cm tall, no flowering stems) and stemmy grass (variable height, 3 or more flowering stems/dm^2). Vegetation height was measured with a tempex disc of 10 cm diameter (8 g) which was gently lowered onto the vegetation along a wooden rod. The tall herbs category comprised mainly *Cirsium arvense* and *Rumex obtusifolius*, but it will not be considered here, as it was rarely included in the diet: on average 0.6% and 1.2% of bites in the *Agrostis/Festuca* and *Lolium* grasslands respectively. Patch area was not determined as the size of individual patches but as the relative cover of the three grassy patch types. The cover of each patch type and the dominant plant species were determined during each period by walking transects of 250 paces, with a measurement point (10 cm diameter) at every fifth step. Nine transects were sampled in the *Agrostis/Festuca* grassland, seven in the *Lolium* grassland, four transects in both areas were sampled for botanical composition. The proportion of bare ground was low (0-5%) and was therefore excluded from the analysis.

Each patch type was sampled in every period by taking one hand-plucked sample to determine diet digestibility and estimate bite size. Hand-plucked samples were collected by one operator only and consisted of 50-100 pickings between thumb and forefinger, mimicking the steers as closely as possible. Experiments with oesophageally fistulated steers showed that diet quality was not different between hand-plucked and extrusa samples. Bite size was estimated from picking size by an empirically derived regression formula (Chapter 2). Correction for bite area (a circle with incisor arcade breadth as diameter) allowed bite size to be expressed as a vegetation-related characteristic independent of animal body size (in mg dry matter/cm^2 area). The fraction of digestible organic matter (DOM) in the dry matter was determined *in vitro* following procedures by Goering & Van Soest (1970) after drying at 65 °C and grinding through a 1 mm sieve. A sheep-cattle conversion factor (Aerts *et al.*, 1984) was applied to the standard samples, which were obtained from sheep. Differences in bite size and DOM between patch types, study areas and periods were analyzed by an ANOVA.

Observations of steer foraging behaviour were made in three to four days in each period using THE OBSERVER 2.0 computer programme (Noldus, 1991). As many records from the different steers were collected as possible during the entire daylight period. Observations consisted of 10-minute bite counts on the various plant patches recognized.

Analysis of foraging observations

Observation files were analyzed sequentially to determine biting rates for different patch types during periods of grazing activity. A minimum run of three consecutive bites on a patch was used as a threshold to include the sequence. Differences in bite rate between patch types, study areas and periods were analyzed by a split-plot ANOVA with individual steers as sub-units. Digestible organic matter intake rate was calculated as the product of DOM, bite size and bite rate.

Four hypotheses on foraging strategy were considered to account for the observed distribution of bites or grazing time between the three patch types:

H1a: random allocation of bites to patches, that is: the percentage bites per patch type is equal to the percentage cover per patch type;

H1b: random allocation of grazing time to patches, that is: the percentage grazing time per patch type is equal to the percentage cover per patch type. This hypothesis assumes that bite rate is a fixed response to the vegetation structure;

H2: matching of grazing time for digestible organic matter content (quality), that is: the percentage grazing time per patch type i ($t_{H2,i}$) is equal to the percentage cover per patch type i (c_i) weighted for DOM-content (DOM_i); the calculation of the predicted percentage $t_{H2,i}$ is as follows:

$$t_{H2,i} = 100\ (c_i\ DOM_i) / \sum_{i=1}^{3} (c_i\ DOM_i)$$

H3: matching of grazing time for energy intake rate, that is: the percentage grazing time per patch type i ($t_{H3,i}$) is equal to the percentage cover per patch type i (c_i) weighted for the intake rate of digestible organic matter ($DOMIR_i$); the calculation of the predicted percentage $t_{H3,i}$ is as follows:

$$t_{H3,i} = 100\ (c_i\ DOMIR_i) / \sum_{i=1}^{3} (c_i\ DOMIR_i)$$

These hypotheses were tested by multivariate analysis of the difference between observed and predicted percentages for the short and tall patch types only, the information on the proportion of the stemmy patch being the complement of the other two. Study area, year and month were considered as factors and animals as replicates. A significant difference (non-zero intercept) was the criterion to reject the hypothesis examined. All statistical analyses were performed using the SAS (1985) package. The deviation of observed from predicted proportions was examined in relation to patch type to compare the merit of the different hypotheses and examine the selectivity in the light of energy intake maximization.

Results

Patch characteristics

The botanical composition was quantitatively different between patches (Table 5.1). In the *Agrostis/Festuca* grassland *Agrostis capillaris, Poa pratensis, Lolium perenne, Phleum pratense* and *Achillea millefolium* showed a higher frequency percentage in the shorter patches than in the stemmy patches. The reverse was found for *Holcus lanatus, Elymus repens, Rumex acetosa* and *Alopecurus pratensis*. In the *Lolium* grassland the short patches contained relatively more *Lolium perenne, Poa trivialis* and *Trifolium repens*, whereas the stemmy patches contained more *Elymus repens*. The proportion of *Elymus repens* and *Agrostis stolonifera* increased in the *Lolium* grassland over the two years of the study in comparison with other species. For both study areas the tall patches were intermediate in species composition.

Table 5.1 Average frequency percentage of dominant plant species in short, tall and stemmy patches in *Agrostis/Festuca* and *Lolium* grassland during two years. The species nomenclature is according to Van der Meijden *et al.* (1990).

	Short	Tall	Stemmy
Agrostis/Festuca			
Agrostis capillaris	36.3	28.6	24.8
Poa pratensis	20.5	21.4	11.7
Holcus lanatus	5.9	23.6	29.0
Festuca rubra	4.9	10.1	8.4
Lolium perenne	9.0	2.4	2.0
Elymus repens	3.8	3.8	7.1
Phleum pratense	5.8	4.8	3.1
Rumex acetosa	1.9	1.9	6.6
Achillea millefolium	4.5	2.2	0.4
Alopecurus pratensis	0.8	0.4	4.3
Bromus hordeaceus	2.1	0.2	1.6
Rest	4.5	0.6	1.0
Lolium			
Lolium perenne	37.2	22.5	20.3
Agrostis stolonifera	24.1	26.6	19.0
Elymus repens	12.0	40.5	55.0
Poa trivialis	15.1	5.0	3.8
Ranunculus repens	2.5	2.5	0.2
Trifolium repens	7.1	1.2	0.0
Taraxacum officinale	0.7	1.4	0.0
Rest	1.3	0.3	1.7

Forage digestibility varied widely between months ($P<0.0001$), showing a clear seasonal pattern with a spring maximum and a winter minimum (Table 5.2). The lower values in the second winter, especially in March, reflect colder conditions. There was a difference between study areas ($P<0.0002$) with, on average, a 3-4% higher DOM-percentage in the *Lolium* grassland. The differences between patch types were highly significant ($P<0.0001$). The forage digestibility was highest in short patches, slightly lower in tall patches (1% DOM on average), and considerably lower in stemmy patches (7-8% DOM difference with tall patches on average). The variation in digestibility was more closely related to differences between patch types than to differences in the proportion of dominant plant species.

Bite size was consistently different between patch types ($P<0.0001$), the largest bites being observed in the stemmy patches and the smallest bites in the short patches (Table 5.2). The large bites for stemmy and tall patches in the *Lolium* grassland for January 1991 were associated with a cold spell during which much less selectivity was shown in the ingested material. Other seasonal effects were comparatively small. The two study

Table 5.2 Digestible organic matter (DOM), bite size per unit area and steer bite rate on short, tall and stemmy grass in *Agrostis/Festuca* and *Lolium* grassland during two years (s.e. standard error for 5 animals).

	1989				1990						1991		
	May	Jul	Sep	Nov	Jan	Mar	May	Jul	Sep	Nov	Jan	Mar	May
DOM (% in dry matter)													
Agrostis/Festuca													
Short	69.6	64.3	66.2	54.6	46.5	56.2	70.7	70.0	59.1	62.2	48.5	48.3	68.1
Tall	66.6	64.5	62.1	61.9	48.6	52.7	68.4	71.7	63.3	64.2	45.5	40.5	65.4
Stemmy	56.5	63.6	60.4	48.1	46.7	45.4	55.6	65.0	60.2	47.8	37.5	38.5	54.3
Lolium													
Short	72.5	64.9	63.7	56.7	48.5	68.7	73.7	69.0	57.7	60.5	54.9	72.4	73.5
Tall	73.6	59.7	62.8	56.3	47.8	68.1	74.8	68.8	65.3	63.1	43.1	63.1	73.6
Stemmy	73.7	59.0	55.2	54.2	38.0	54.1	73.7	63.9	56.5	51.4	37.5	35.6	64.7
Bite size (mg dry matter/cm^2)													
Agrostis/Festuca													
Short	8.4	7.6	5.4	5.4	5.1	3.0	3.9	6.3	5.2	4.7	3.5	3.2	3.8
Tall	13.7	10.1	10.5	9.1	10.7	8.4	9.1	11.8	11.8	11.6	9.4	11.7	10.1
Stemmy	15.9	13.9	17.0	16.7	16.5	12.3	16.7	13.1	15.7	16.0	17.3	16.4	14.1
Lolium													
Short	6.8	6.5	5.1	5.7	5.1	3.3	6.8	4.2	5.0	3.7	4.2	5.1	5.6
Tall	17.0	12.3	14.2	12.0	14.5	8.6	14.7	10.9	13.9	13.8	17.2	11.0	13.9
Stemmy	17.1	17.3	16.1	16.6	17.0	11.6	17.1	16.3	17.3	17.2	33.0	15.4	17.1
Bite rate (bites/min)													
Agrostis/Festuca													
Short	59.2	64.7	68.9	70.8	67.7	69.4	66.0	65.6	70.0	67.8	66.8	64.8	67.1
s.e.	4.5	1.6	2.5	1.8	2.1	2.2	2.1	2.3	1.7	1.7	2.6	3.4	2.0
Tall	52.0	61.7	64.0	64.9	55.3	72.1	64.0	62.3	62.4	59.1	60.2	60.6	64.5
s.e.	2.8	1.3	1.3	2.1	6.4	3.8	1.8	1.5	1.7	1.6	2.0	3.2	1.8
Stemmy	54.4	54.5	62.1	63.0	50.2	63.4	--	60.0	55.8	56.1	58.4	46.8	--
s.e.	4.4	3.2	4.0	2.6	5.8	3.2	--	2.9	2.0	3.6	3.4	2.3	--
Lolium													
Short	70.1	73.3	77.7	74.0	69.0	739	61.9	70.4	75.4	72.2	67.4	73.1	66.2
s.e.	1.3	1.4	2.5	1.9	3.1	2.6	3.3	2.0	2.9	2.4	3.8	2.8	3.2
Tall	59.5	57.2	65.8	63.8	65.5	66.9	54.4	63.2	61.5	53.0	51.6	64.3	56.5
s.e.	2.9	1.8	2.0	1.1	4.1	1.6	2.9	2.9	2.4	2.1	2.8	2.9	2.4
Stemmy	50.2	45.1	57.5	54.9	57.5	60.0	41.6	54.1	53.5	47.0	44.4	61.1	66.4
s.e.	2.6	0.9	2.3	2.4	2.9	3.3	5.5	2.6	2.6	2.7	2.3	5.0	4.8

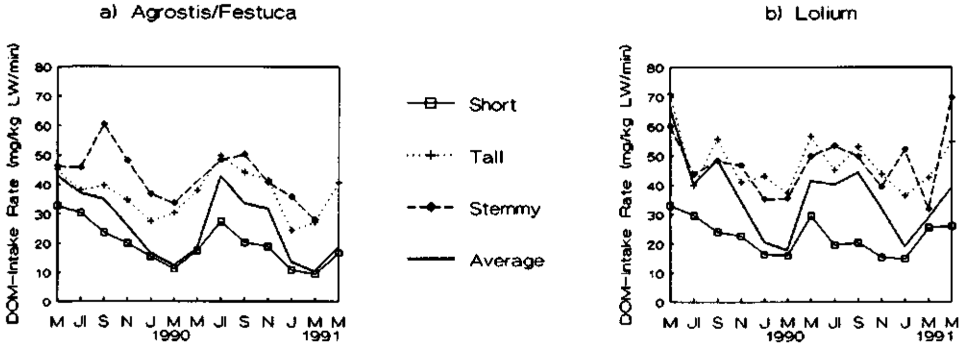
areas mainly differed with respect to the tall patches, for which larger bite sizes were observed in the *Lolium* grassland.

Bite size and bite rate (averaged over animals) were inversely related ($r=-0.79$, d.f.$=74$, $P<0.001$). Bite rate thus was high in short patches, intermediate in tall patches and low in stemmy patches (difference between patches significant at $P<0.0001$). The differences in bite rate between patch types were greater in the *Lolium* grassland than in the *Agrostis/Festuca* grassland ($P<0.0011$ for the interaction): bite rate was higher for short patches in the *Lolium* grassland, whereas the reverse applied to stemmy patches; there was little difference between study areas with regard to tall patches. The differences between animals within study areas were significant ($P<0.0001$). However, the ranking of animals according to bite rate was more clear-cut in the *Lolium* grassland than in the *Agrostis/Festuca* grassland.

The calculated intake rate of digestible organic matter (Fig. 5.1) was relatively low for short patches compared to the other two patches, which did not differ substantially. DOM-intake rate in the short and stemmy patches was comparable between study areas, but in the tall patches intake rate was generally lower in the *Agrostis/Festuca* grassland than in the *Lolium* grassland. Bite size was the main determinant of DOM-intake rate.

Patch cover and bite selection

The relative cover of the three patch types showed a clear seasonal pattern with an increase of the proportion of short grass after the growth peak in early summer (Fig. 5.2). Stemmy grass was only available to a significant extent during summer. Comparison of the two study areas shows an earlier increase of the cover of tall grass in May in the *Lolium* grassland. The increase of the percentage stemmy grass in this grassland between November and January resulted from leaf senescence and die-back in tall patches and in clones of *Cirsium arvense*, which were subsequently identified as stemmy patches.


a) Agrostis/Festuca

b) Lolium

Figure 5.1 Intake rate of digestible organic matter for three different patch types for a steer in a) *Agrostis/Festuca* grassland and in b) *Lolium* grassland over a period of two years (using a constant live weight of 500 kg with a corresponding bite area of 47.5 cm^2). The average DOM-intake rate over all three patch types, taking the relative cover of patch types into account, is marked as a thick line.

In both study areas the percentage of bites taken on short and tall patches was generally higher than the available cover proportion (Fig. 5.2). On stemmy patches the percentage of bites was consistently lower than the cover proportion. A multivariate analysis showed that individual differences between animals within study areas were significant ($P<0.025$). Yet, as the figures show, their magnitude was small.

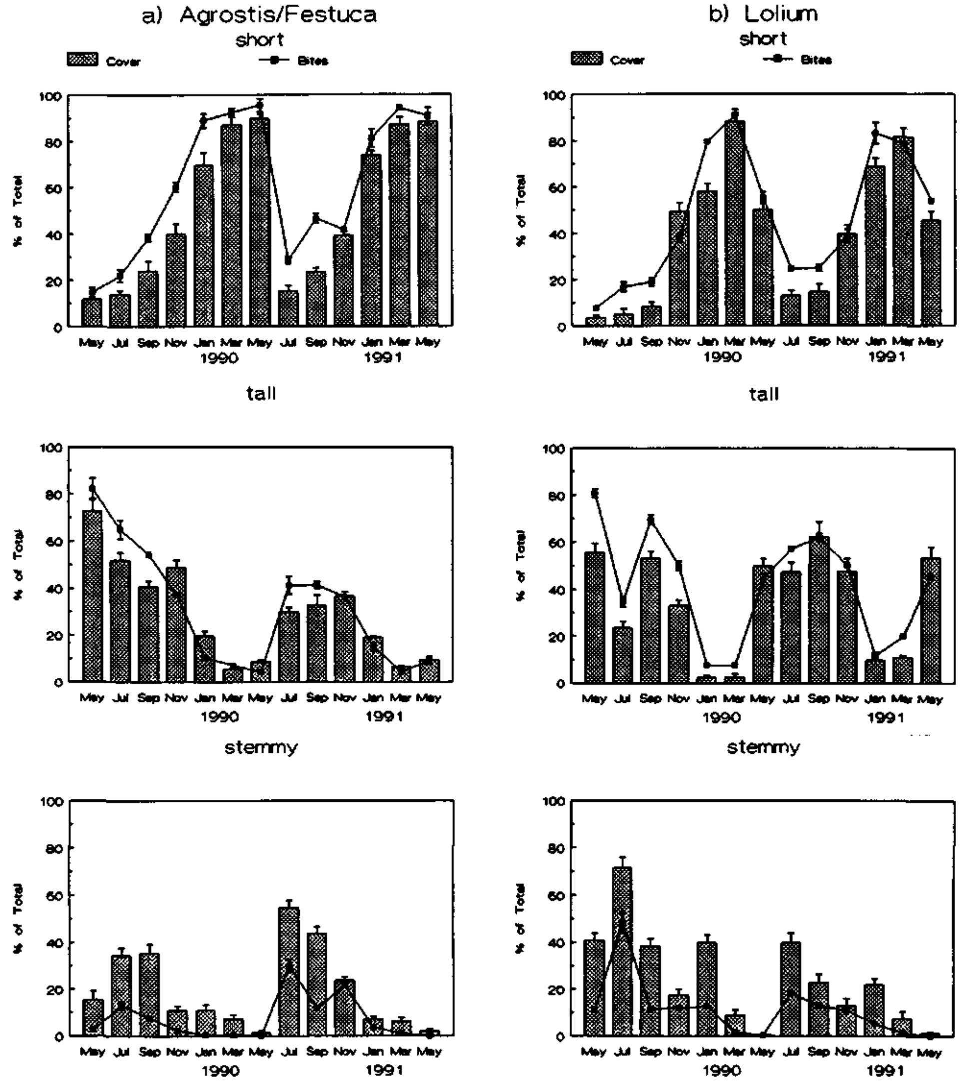
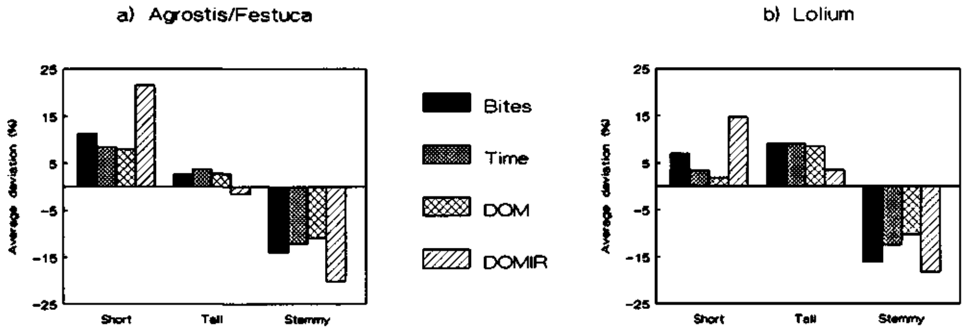


Figure 5.2 Distribution of patch cover and bites taken by steers over short, tall and stemmy patch types in a) *Agrostis/Festuca* grassland and in b) *Lolium* grassland (± standard error).

Testing foraging strategies

The observations showed a significantly different patch choice for all four hypotheses ($P<0.0001$). Differences between observed and predicted values varied significantly between months ($P<0.0001$, data not shown) and correlated especially with seasonal changes in patch cover. The differences between the two study areas were small. The apparent preference for short patches over stemmy patches could not be fully explained by considering relative patch cover, bite rate, DOM-content and bite size (Fig. 5.3).

Patch choice was better explained by a random allocation of grazing time (H1b, $F_{2,81}=172.0$) than by a random allocation of bites (H1a, $F_{2,81}=320.2$). Matching in proportion of DOM-intake rate (H3) yielded worse predictions of patch choice than random foraging ($F_{2,81}=429.6$). This was to be expected on account of the large influence of bite size on intake rate. The best predictions were obtained by assuming a matching of grazing time in proportion to DOM-content (H2, $F_{2,81}=133.9$). However, the *improvement of predictions from this hypothesis was not significant compared* to a random allocation of grazing time (H1b).


a) Agrostis/Festuca

b) Lolium

Figure 5.3 Average deviation of observed from predicted proportions of bites or grazing time on patches of short, tall and stemmy grass in a) *Agrostis/Festuca* grassland and in b) *Lolium* grassland for four foraging hypotheses. 'Bites' (H1a) random allocation of bites to patches, 'Time' (H1b) random allocation of grazing time to patches, 'DOM' (H2) matching of time in proportion to digestibility, and 'DOMIR' (H3) matching of time in proportion to intake rate of digestible organic matter.

Discussion

Differences between study areas and patch types

The *Lolium* grassland showed a higher DOM-content than the *Agrostis/Festuca* grassland. This presumably reflects differences in soil fertility, soil moisture and botanical composition. The difference was especially large in the transition from winter to spring, when grass growth started earlier in the *Lolium* grassland (Fig. 5.2). However, part of the difference arose from the later sampling date in this vegetation (12-13 days). The differences between the two areas with regard to bite size and bite rate were smaller than for DOM.

The differences between patch types were consistent and similar for both study areas. They agree with the results from other studies on the relation between sward characteristics and foraging behaviour, as reviewed by Forbes (1988). DOM-content and bite rate were comparatively high in short patches and bite size was relatively low. In tall patches the DOM-content was only little lower and bite size and bite rate were intermediate. Finally, in stemmy patches, the DOM-content and bite rate were lowest and bite size was highest. Differences in botanical composition were related to patch types, but were more quantitative than qualitative in nature. Species composition did not account for the recorded variation in digestibility and bite size. During field observations there was no indication that the steers selected between species within patches. We therefore consider the effect of botanical variation on foraging behaviour to be less significant than the larger differences in vegetation structure.

Selectivity

Although the steers demonstrated a significant degree of selectivity between patches, its magnitude was generally small. A random allocation of grazing time accounted for most of the variation in the proportion of bites taken on short, tall and stemmy patches. This result is in line with the findings of Illius (1986) and Illius *et al.* (1987) for grazing cattle in patchy pastures of *Lolium perenne* but contrasts with the observations by Bazely (1988), who found a strong preference of sheep in a sward of *Lolium perenne* for fertilized, tall patches of high nutritive value compared to unfertilized, shorter patches of low nutritive value. This discrepancy might be explained by the differences between patches. The patch differences were smaller in the studies by Illius. In the present study the greatest contrast existed between the short and tall patches *versus* the stemmy patches. The former were clearly preferred over the latter. This pattern was also found by Langvatn & Hanley (1993) for red deer (*Cervus elaphus*) grazing *Phleum pratense*.

A stronger degree of selection can be found when the differences between forage categories increase. Thus, clones of *Cirsium arvense* in the *Lolium* grassland were virtually excluded from the diet, although they made up 17-31% of the vegetation cover in summer. In a different study, Wallis de Vries (unpubl.) found that, on average, steers selected strongly against *Calluna vulgaris* and in favour of the more digestible *Deschampsia flexuosa* (Table 5.3). The number of bites per step was inversely related to the percentage cover of *Deschampsia flexuosa*, which is suggestive of a longer searching time with a decrease in the availability of the preferred species. *Calluna vulgaris* was only included in the diet in significant proportions when it achieved clear dominance in the vegetation. Grant *et al.* (1987) reported a comparable trend in selectivity in cattle and sheep grazing on Scottish heathland and blanket bog.

The dependence of selectivity on the difference between alternative forage categories was suggested earlier by Arnold (1987). The lesser selectivity displayed when the differences between species or patches are small can be explained by the reduced profitability from selection but also from an increased difficulty to discriminate between alternatives. Illius *et al.* (1992) have demonstrated carry-over effects of foraging behaviour in sheep between subsequent patches. They argued that sheep are subject to information constraints and modify their grazing behaviour with the acquisition of information during grazing. Decisions about a new patch would then be initially determined by information from the previous patch. Changing species preferences arising from previous grazing experience have also been found in sheep by Newman *et al.* (1992). Selectivity will be greater and less dependent on sampling with an increase in the difference between species or patches (Stephens & Krebs, 1986).

Table 5.3 Average forage availability and foraging behaviour of five steers in heathland vegetation units with different proportions of *Deschampsia flexuosa* (D) and *Calluna vulgaris* (C) in bi-monthly observations over a two year period (values with 95% confidence limits where appropriate; DOM digestible organic matter, d.m. dry matter).

	Deschampsia	*D/C*	*Calluna*
Proportion of unit (%area)	43.1	16.2	31.2
% Grazing time in unit	63.6±1.1	23.6±1.8	3.5±0.6
Bite rate (bites/min)	51.5±3.6	50.0±4.2	35.6±1.9
Bites/step	5.0±1.0	4.2±1.0	3.4±0.2
DOM-intake rate (g/min)	13.2±0.7	13.4±0.7	11.1±0.7
Diet digestibility (%DOM in d.m.)	66.0±0.9	65.4±0.8	58.4±1.1
Deschampsia flexuosa			
%cover	92.1±25.7	55.9±7.6	10.3±3.8
%bites	93.1±2.9	96.0±1.2	68.0±3.5
Calluna vulgaris[1]			
%cover	7.1±10.5	42.9±7.9	88.1±10.6
%bites	0.7±0.6	1.1±0.5	20.9±2.4

[1]Figures for *Calluna vulgaris* include smaller proportions of *Erica tetralix*.

Foraging strategy

We have chosen for the present analysis to examine the intake of DOM, a parameter for energy, as the foraging currency. This is a common approach when examining the diet selection of grazing ruminants. However, other nutrients could also have affected the selectivity of the steers (Chapters 4 and 6). To assess their potential effects we analyzed the three grass categories for contents of nitrogen, phosphorus, sodium, and calcium. The differences between grass categories for these nutrients were either not consistent (sodium and calcium) or followed the same pattern as in DOM (nitrogen and phosphorus). Taking sodium or calcium as foraging currency would generally predict a selection for larger bite size, which does not agree with the observations from this study. Nitrogen and phosphorus as currencies would yield similar results to the present analysis with DOM as a parameter for forage quality.

If the steers had been maximizing their short-term energy intake rate (H3) they would have selected either the tall or the stemmy patches and neglected the short patches. Yet, this clearly did not occur. The steers rather preferred the short patches. The observations were more in agreement with a random allocation of grazing time in proportion to patch cover (H1b) than with a random allocation of bites (H1a). This result indicates that differences in bite rate between patch types are important in determining the proportion of bites on a patch. As bite rate appears to be largely determined by vegetation structure and maturity, grazing time offers a better criterion to examine patch selection than the number of bites. The best explanation of the observed distribution of grazing time between patches was given by assuming a matching for digestibility (H2), although the improvement over the hypothesis of random allocation of grazing time was not significant. However, if we had considered the average DOM-content of each patch type instead of the selected DOM-content, the differences between patch types would have been greater due to the effect of senescence in the tall and stemmy patches (Wallis de Vries, unpubl. data for clipped material). H2 would then probably have yielded significantly more accurate predictions than found with the present approach. The small observed differences in DOM-content between short and tall patches thus are likely to result from within-patch selection in the more senescent tall patches. Selection on DOM-content can therefore still be expected to occur.

The greater preference for short over tall patches could have arisen from a greater time cost of selection within tall patches. This explanation does not seem to hold, because the DOM-intake rate in the tall patches was higher than in the short patches at only a slightly inferior digestibility. However, it may be that the difficulty to discriminate between adequate and inadequate forage within tall patches still presents a greater searching or recognition effort to the animal, even if this is not shown in the achieved intake rate. Selection for the relatively homogeneous short patches would reduce this cost, but what are the consequences of this preference for the intake of energy?

The seeming contradiction that selection on young material does not maximize short-term energy intake rate can be solved when extending the time horizon to a daily cycle. Lucas (1990) has pointed out that considering the appropriate time scale for the animal is important to understand foraging decisions. Maximizing short-term intake rate may not always be the optimal solution to achieve the goal of long-term average rate maximization (see also Stephens & Krebs, 1986). Beekman & Prins (1989) and Vulink & Drost (1991) have shown that bovines are commonly not limited in their daily forage intake by available time but rather by maximum voluntary intake ('gut fill'). It is well-known that food intake in ruminants increases with digestibility (Hodgson *et al.*, 1977; Armstrong *et al.*, 1986; Chapter 6), even though the mechanism is still poorly understood (Ketelaars & Tolkamp, 1992). Hence, if foraging time is not limiting, cattle can maximize their daily energy intake by selecting for the high digestibility and the lesser variability in short patches.

We evaluated the maximum voluntary intake from the different patches using a relation between diet digestbility and intake derived from field data by Hodgson *et al.* (1991) (Chapter 6). It appeared that on the short patches maximum voluntary intake was reached beyond a grazing time of 630 minutes in 8 out of 13 observation periods in the *Agrostis/Festuca* grassland and in 7 periods for the *Lolium* grassland. A grazing time of 630 minutes will rarely be exceeded in ruminants (Arnold & Dudzinski, 1978) and was the maximum group average recorded in this study. Cattle would therefore often still be time-limited if they concentrated solely on the short patches. This may be a reason to include the taller patches. If these differ little in quality from the short patch, then selectivity between patches may be reduced without compromising the maximization principle. The matching pattern for digestible protein intake rate found in red deer by Langvatn & Hanley (1993) instead of short-term intake rate maximization could have arisen from a similar trade-off between patch quality, grazing time and selectivity. In a complex and dynamic environment a flexible preference for short patches may therefore be a simple but optimal strategy to approximate maximization of daily energy intake.

Conclusion

The evidence for a preference for the short patches supports the view that grazing animals select for young growth and reject senescent plant material (McNaughton, 1984). We suggest that foraging strategies of large herbivores such as cattle are consistent with nutrient intake maximization but are constrained by searching and recognition costs on the availability of food resources. In this study, the preference for short patches approximated intake maximization on a daily basis. The inclusion of tall patches might be promoted by time-limitation and reduced by the required selectivity in the presence of senescent leaves of low quality. The inefficiency of this strategy with regard to grazing time may indicate that it is an application of a rule of thumb to select for green leaf, rather than an optimal weighing of estimated parameters for the different alternatives.

Plate 14. A mosaic of patches with different vegetation structure in *Agrostis/Festuca* grassland.

CHAPTER 6

Foraging in a Landscape Mosaic: Selection for Energy and Minerals in Free-ranging Cattle

Summary

Several studies have indicated the potential importance of nutrients besides energy in determining foraging decisions. A model was developed to test this idea, on the assumption of an intake maximization for different nutrients (energy, sodium and phosphorus). The model predictions were tested using field data on cattle grazing in a landscape mosaic of Pleistocene cover sand and riverine grassland. Observations on foraging behaviour, food intake and diet composition were collected in thirteen four-day periods over two years. Habitat selection was determined by comparing the proportion of grazing time in different vegetation units with the available area proportion of the units.

At a low scale level no habitat selection was apparent between the vegetation units of the riverine landscape. The Deschampsia flexuosa *unit was significantly selected for in the cover sand landscape. At the landscape level, the animals preferred the riverine landscape. The model revealed poor predictions of habitat occupancy at the low scale level. A much better prediction was obtained when vegetation units were combined on a higher scale level. The* Deschampsia flexuosa *unit provided a higher energy intake, whereas the intake of sodium was higher in riverine grassland. Phosphorus proved relatively insignificant in determining habitat occupancy. Based on energy maximization alone the model was a very poor predictor of habitat occupancy.*

It is argued that selection occurred mainly at the higher scale level. The incorporation of different nutrient constraints in foraging models can then prove fruitful to explain habitat occupancy. At the low scale level difficulties for the animal in assessing nutrient availability may result in a less selective foraging pattern. However, the costs of increased selectivity may be greater than the benefits.

(with P. Schippers, submitted to Oecologia)

Introduction

The selection by ungulates of a feeding station in an heterogeneous landscape has been tentatively described as a hierarchical decision process on different levels: the regional level, the landscape, the plant community and down to the individual plant (Senft *et al.*, 1987). The selection between plant communities in a landscape has been addressed in numerous studies on habitat use. As a good example, we refer to the description of the seasonal variation in the use of a landscape catena by large herbivores in the Serengeti, Tanzania (Jarman & Sinclair, 1979). On a regional scale these animals may show a migratory pattern of landscape use (Maddock, 1979). Such patterns of habitat selection have been related to various factors determining food availability: rainfall (Maddock, 1979), protein levels (Jarman & Sinclair, 1979; Ben-Shahar & Coe, 1992), and concentrations of sodium, phosphorus and magnesium (McNaughton, 1988 and 1989; Seagle & McNaughton, 1992; Ben-Shahar & Coe, 1992). Yet, the foraging strategy governing habitat selection remains less well understood (see McNaughton & Georgiadis, 1986). Models used to simulate habitat selection (*e.g.* Roese *et al.*, 1991; Loza *et al.*, 1992) often contain untested assumptions on feeding preferences and thus rather describe than explain the animal's behaviour.

Optimal foraging theory (reviewed by Stephens & Krebs, 1986) offers a framework to test hypotheses on diet selection. Patch models consider spatial variation in food availability and can therefore be used to predict foraging time in different habitats (Chapter 5). Most models used in optimal foraging theory use energy or protein as the currency to be maximized. While this may be a valid assumption in many cases (Belovsky, 1986; 1990), a number of studies on a variety of animal taxa (protozoans, birds, ruminants and humans) have suggested a selection for complementary nutrients (Rapport, 1980; Thompson *et al.*, 1987; Belovsky, 1990). The importance of minerals as a potential factor in the differentiation of habitat use, further advocates the consideration of a variety of nutrients in foraging models. Belovsky (1978) showed that moose (*Alces alces*) needed a certain amount of aquatic plants to satisfy the requirements for sodium, whereas terrestrial plants were more advantageous with respect to energy intake. It could be demonstrated that moose tended to maximize energy intake, while satisfying the sodium constraint. By incorporating the requirement for a nutrient besides energy the choice between two habitats could thus be explained. However, foraging animals usually face a variety of habitats. The question remains whether nutrient maximization can also explain habitat use in a more diverse environment.

In the present chapter we adopt a modelling approach to explain habitat selection of grazing cattle in a landscape mosaic with different nutrient availabilities. The term habitat is used in the sense of a spatially defined unit with a specific forage availability. Field data to test the model predictions were obtained from a grazing experiment with free-ranging cattle, which provided detailed estimates on food intake and habitat occupancy. Confounding influences of predation, parasites and long travel distances between different habitats were ruled out. Experimental evidence suggested that sodium and phosphorus were of potential importance in determining the digestive efficiency of cattle in the poor habitat (Chapter 4). We will therefore test a maximizing strategy for these nutrients along with energy.

Methods

Study area

Habitat occupancy and diet selection of free-ranging cattle were studied in a 74 ha study area called Karshoek (52°32' N, 6°32' E; altitude *ca.* 7 m), in the Netherlands. The area consists of a vegetation mosaic of a riverine grassland adjoining a Pleistocene cover sand area of low soil fertility. These two larger areas will be termed landscape units, as opposed to the lower scale level of vegetation units. A description of the main vegetation units and their surface area is given in Chapter 1.

The study area was stocked with five yearling Meuse-Rhine-Yssel steers and five yearling Hereford steers in April 1989. These were kept in the riverine landscape until August, when the entire area was made available to the animals. Grazing continued till June 1991. During this period the animals did not receive any kind of food supplements.

Field observations and measurements

The habitat occupancy and grazing behaviour of the steers were studied in thirteen bimonthly study periods of four days each. The animals were weighed in each period and fitted with a vibra-recorder (Stobbs, 1970) to estimate total daily grazing time. Regular sightings outside the study periods provided further information on the time spent in the riverine and the cover sand landscapes.

Direct observations on grazing behaviour were made during the entire daylight period. These consisted of ten-minute focal animal observations alternated with group recordings to record the activity and location of all animals. The focal animal data were collected using the OBSERVER 2.0 programme (Noldus, 1991). Bite counts on different plant categories (see Chapter 2 for details) were made in each vegetation. All recognized plant categories were sampled by hand-plucking. Bite size of each sample was estimated by calibration with oesophageally fistulated animals in a separate experiment (Chapter 2). All samples were dried at 65°C, ground through a 1 mm sieve and analyzed for dry matter contents of sodium (Na), phosphorus (P), calcium (Ca) following procedures by Walinga *et al.* (1989). Organic matter digestibility was determined *in vitro*, using the method of Goering & Van Soest (1970). As the available standard samples of known digestibility were from trials with sheep, a conversion to cattle values was performed by applying the regression equation of Aerts *et al.* (1984). Digestibility was finally represented as digestible organic matter (DOM in % of dry matter) and used as a parameter for energy.

The model

A FORTRAN model was developed in order to predict habitat occupancy. The model runs for a given number of days. It also predicts animal nutrient status, daily intake and grazing time, and vegetation standing crop. The model contains two main components: a vegetation and an animal component (Fig. 6.1). The model identifies the minimum nutrient (including DOM as an energy parameter). relative to the animal's requirements. The model animal represents an average individual from a population of a given size. This individual has to satisfy a given daily nutrient requirement in accordance to its given body weight and weight change. The animal is assumed to follow a foraging strategy of

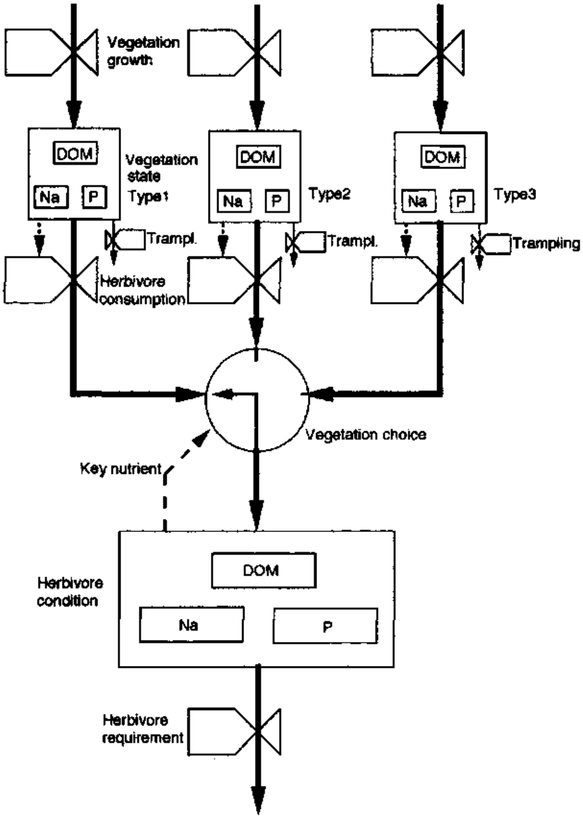


Figure 6.1 Representation of the model structure in a flow diagram: the choice of vegetation type (or unit) by the herbivore is the outcome of the dynamics linking vegetation state to herbivore condition.

nutrient maximization when choosing between vegetation units. Each vegetation unit is loaded with a certain area, available standing crop, plant productivity and nutrient content. The available standing crop determines the potential intake rate by the animal. The animal selects the vegetation with the highest intake rate for the minimum nutrient. After a grazing bout of a given time, the model animal evaluates its nutrient intake and selects anew. The standing crop is readjusted after each grazing bout. Standing crop reduction occurs by grazing and trampling (as a function of intake), taking into account the specific area of the vegetation unit and the animal density. Aboveground plant production is assumed to be unaffected by grazing.

Daily grazing time is supposed to be limited either by an absolute maximum or by maximum voluntary intake, determined by diet digestibility. When voluntary intake limits grazing time in a certain vegetation unit, its preference is lowered by multiplication with a

Table 6.1 Average forage intake rate and dietary quality for steers in different vegetations and observation periods in the Karshoek area.
(-- missing data, XX not available to the animals)

Observation periods		1	2	3	4	5	6	7	8	9	10	11	12	13
						1990						1991		
		May	Jul	Sep	Nov	Jan	Mar	Apr	Jul	Sep	Nov	Jan	Mar	Apr
Dry-matter intake rate (g/min)	*Agrostis/Festuca*	21.0	20.7	22.5	19.4	15.9	9.8	11.9	26.6	26.1	27.1	15.6	12.4	14.4
	Desch. cespitosa	19.9	21.9	26.4	26.8	17.0	14.7	17.3	24.2	26.2	28.6	29.9	15.9	18.8
	Erophila	--	21.5	26.1	22.5	12.0	10.8	9.3	28.4	22.8	31.3	17.0	8.0	13.1
	Glyceria	12.8	18.9	19.4	20.0	16.1	X	24.7	22.7	29.2	24.2	--	5.3	24.0
	Scrub	14.3	6.1	5.6	37.9	19.3	20.2	4.5	6.1	15.7	18.8	--	--	17.6
	Desch. flexuosa/Forest	X	X	--	33.0	24.4	--	24.8	26.0	35.7	22.7	25.3	21.0	28.9
	Desch. flexuosa/Open	X	X	--	24.1	31.0	--	12.6	20.2	--	16.3	13.3	9.8	21.2
	Quercus-Forest	X	X	X	25.0	14.7	X	X	X	--	X	X	X	X
	Misc./Forest	X	X	--	--	--	--	--	16.9	--	--	29.1	20.2	--
	Misc./Open	X	X	--	--	23.1	--	23.3	22.4	23.7	--	32.7	31.6	--
DOM (%d.m.)	*Agrostis/Festuca*	66.5	64.3	60.6	57.7	47.0	55.7	70.5	68.9	61.6	57.9	45.7	46.4	67.6
	Desch. cespitosa	66.8	61.3	51.9	59.2	47.2	53.3	67.7	68.0	59.5	60.6	40.7	41.9	66.0
	Erophila	--	64.1	61.4	54.9	45.1	55.0	69.9	60.6	55.3	60.5	44.7	48.6	68.0
	Glyceria	72.1	69.6	66.9	57.7	54.0	X	75.5	72.0	63.9	57.7	--	66.4	75.3
	Scrub	67.1	55.4	56.1	68.0	63.5	39.2	68.4	52.0	59.9	68.0	--	--	67.1
	Desch. flexuosa/Forest	X	X	--	65.0	48.1	--	67.9	69.3	65.7	60.2	45.4	50.4	70.5
	Desch. flexuosa/Open	X	X	--	65.7	49.5	--	69.3	69.5	--	69.5	58.8	37.8	69.5
	Quercus-Forest	X	X	X	68.2	63.5	X	X	X	--	X	X	X	X
	Misc./Forest	X	X	--	--	--	--	--	67.7	--	--	25.8	39.2	--
	Misc./Open	X	X	--	--	47.0	--	51.2	62.3	48.3	--	26.2	39.1	--

(Table 6.1 continued)

Observation periods		1 May	2 Jul	3 Sep	4 Nov	5 1990 Jan	6 Mar	7 Apr	8 Jul	9 Sep	10 Nov	11 1991 Jan	12 Mar	13 Apr
Na (ppm in d.m.)	*Agrostis/Festuca*	133	70	23	30	38	112	32	29	20	36	69	38	67
	Desch. cespitosa	180	76	41	52	35	234	25	29	20	36	65	58	58
	Erophila	--	10	17	38	51	154	31	20	16	41	57	53	39
	Glyceria	0	20	0	25	50	X	0	16	25	25	--	61	32
	Scrub	0	20	12	0	20	31	10	3	5	0	--	--	0
	Desch. flexuosa/Forest	X	X	--	6	12	--	20	11	13	0	46	9	62
	Desch. flexuosa/Open	X	X	--	20	28	--	20	10	--	0	47	16	20
	Quercus-Forest	X	X	X	7	20	X	X	X	--	X	X	X	X
	Misc./Forest	X	X	--	--	--	--	--	26	--	--	118	30	--
	Misc./Open	X	X	--	--	38	--	34	16	29	--	116	92	--
P (%d.m.)	*Agrostis/Festuca*	0.31	0.31	0.32	0.35	0.29	0.41	0.29	0.31	0.27	0.27	0.29	0.40	0.38
	Desch. cespitosa	0.36	0.29	0.32	0.39	0.17	0.28	0.37	0.39	0.27	0.27	0.25	0.34	0.39
	Erophila	--	0.23	0.25	0.33	0.26	0.38	0.33	0.24	0.21	0.33	0.24	0.30	0.32
	Glyceria	0.31	0.21	0.35	0.29	0.26	X	0.42	0.21	0.33	0.29	--	0.42	0.66
	Scrub	0.27	0.25	0.17	0.08	0.10	0.14	0.31	0.25	0.09	0.08	--	--	0.27
	Desch. flexuosa/Forest	X	X	--	0.13	0.13	--	0.18	0.11	0.12	0.12	0.20	0.20	0.18
	Desch. flexuosa/Open	X	X	--	0.10	0.12	--	0.15	0.06	--	0.12	0.19	0.20	0.15
	Quercus-Forest	X	X	X	0.10	0.10	X	X	X	--	X	X	X	X
	Misc./Forest	X	X	--	--	--	--	--	0.12	--	--	0.07	0.14	--
	Misc./Open	X	X	--	--	0.10	--	0.13	0.09	0.09	--	0.07	0.13	--

correction factor: the vegetation unit's specific maximum grazing time divided by the absolute maximum grazing time. With a change in standing crop, the vegetation preference changes in accordance with the change in intake rate.

Model input and parameters

The model was run for a grazing period of four days, which was similar to the length of the observation period. Vegetation input data on forage intake rate and quality are presented in Table 6.1. Missing data have been estimated from hand-plucked samples, interpolations and data from corresponding periods.

The surface areas of vegetation units (Chapter 1) were adjusted by subtracting bare ground and wet parts to arrive at effective foraging areas. The *Quercus*-Forest was only considered in November and January of the first year and in September of the second year, as no acorns or browse were available in other study periods. The *Molinia caerulea* dominated parts (unit of Miscellaneous Open) were only considered in the periods of July and September, as this species offered no green forage in other periods.

Annual plant production in the various vegetation units was estimated as indicated in Table 6.2. Daily production estimates were made assuming the growth curve used by Sibbald *et al.* (1979) for grassland and heathland. For *Glyceria maxima* the production curve was estimated from Westlake (1966). Browse and acorn production were assumed to reach peak values in May/June and October respectively.

Table 6.2 Annual aboveground plant production estimates of the vegetation units in the Karshoek area.

Vegetation unit	Aboveground plant production (g dry matter/m²/year)
Agrostis/Festuca	430[1,2]
Desch. cespitosa	630[2]
Erophila verna	200[2]
Glyceria maxima	1160[3]
Scrub	50[4]
Desch. flexuosa/Forest	225[1,2]
Desch. flexuosa/Open	130[1,2]
Quercus-Forest	mast 1989: 260[5] " 1990: 85[5]
Miscellaneous/Forest	100[1,2]
Miscellaneous/Open	200[1,2]

References: 1) Wallis de Vries (1989), 2) J. Bokdam (unpubl.)
3) Westlake (1966) 4) Bobek & Dzieciolowski (1972)
5) G. Groot Bruinderink (pers. comm.)

For each observation period initial standing crop values (SC, g/m²) for the various vegetation units were estimated from the measured dry matter intake rate (DMIR, g/min;

Table 6.1) through an empirically derived equation, which takes into account animal weight (LW, kg):

$$\mathrm{DMIR} = (0.027\ \mathrm{LW} + 22.5)(1 - e^{(-0.0075\ \mathrm{SC})})$$

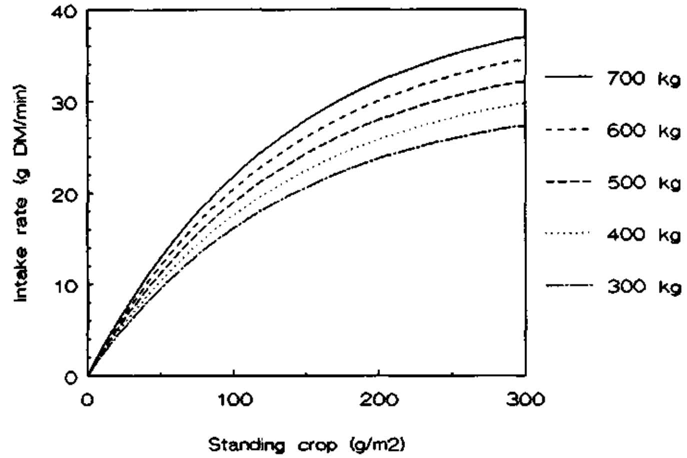


Figure 6.2 The assumed relation between vegetation biomass and dry matter intake rate for cattle of different body weight.

The equation has the same form (see Fig. 6.2) as the one suggested by Freer (1981). It is a simplification of a set of regression equations with quadratic shape relating biomass to plucking size, plucking size to bite size, and bite size to dry matter intake rate. No distinction was made between vegetation units. The first two relations have been examined more extensively in Chapter 2. The relation between bite size (BS, g) and intake rate was derived from data on three other groups of steers in riverine grassland and heathland (see Chapter 4):

$$\mathrm{DMIR} = 33.11\ \mathrm{BS} + 7.39 \quad (R^2=0.633,\ \mathrm{d.f.}=37,\ P<0.001)$$

The animals were supposed to graze in bouts of 15 minutes, corresponding to the interval of group recordings. After each bout the standing crop is readjusted, leading to a new dry matter intake rate following the equation above. The amount of biomass lost by trampling was estimated at 10% of consumption for most vegetation units (Van Deursen & Drost, 1990; T. Vellinga, pers. comm.). Higher values were assumed for more sensitive vegetations: 20% for the two *Deschampsia flexuosa*-units and 60% for the *Glyceria maxima*-unit.

The maximum daily grazing time was fixed at 630 minutes, which is within the range of 10-12 h mentioned by Arnold (1981). As a group average, this value was sometimes approached, but never exceeded, during this study (see Table 6.4). The limitation of grazing time by maximum voluntary intake was described as a function of digestibility. A regression equation between DOM (% of dry matter) and daily dry matter intake (DMI, g/kg LW) was derived from field trials by Hodgson *et al.* (1991) for cattle (cases with daily grazing times higher than 570 minutes were discarded to exclude time limitation; the dietary ash content was estimated according to the vegetation unit):

$$\text{DMI} = 0.52\ \text{DOM} - 12.25 \quad (R^2=0.841,\ \text{d.f.}=15,\ P<0.001)$$

The assumed daily animal dietary requirements for energy and minerals are given in Table 6.3. Daily requirements for digestible organic matter were estimated from field data for the study animals ($R^2=0.628$, d.f. $=11$, $P<0.001$). The estimate of 46.9 g DOM/kg LW$^{0.75}$ for maintenance compares well with the value of 44 g DOM/kg LW$^{0.75}$ given by Hodgson & Grant (1981).

Table 6.3 Daily nutrient requirements of cattle in relation to live weight (LW, kg) and daily weight change (DWC, kg/day).
The requirements for DOM have been derived from the present study (see text). The mineral requirements have been taken from ARC (1980), with a correction for mineral uptake from drinking water. Assumed water uptake was 26 l/day with a mineral content of 20 mg/l Na, 0.11 mg/l P and (Verdonschot, 1991).

DOM (g/day)	$(46.9 + 19.7\ \text{DWC})\ \text{LW}^{0.75}$
Na (g/day)	$0.0054\ \text{LW} + 1.65\ \text{DWC}$
P (g/day)	$0.0207\ \text{LW} + 12.7\ \text{DWC}$

Differences between vegetation units in heat loss through exposure were considered by applying formulas from Fox *et al.* (1988). However, the revealed increase of energy intake in exposed areas was small (a few percent), so that the effect of exposure was not included in the model. The extra costs in time and energy of moving between vegetations were likewise neglected in view of the small size of the study area: the animals could reach any location within 15 minutes walking time.

Statistical analysis

Habitat selection was assessed by testing the departures of habitat occupancy from surface area distribution. This was performed on two scale levels. On the lower scale level of vegetation units the chi^2-test was applied to the grazing time distribution between vegetation units within the riverine landscape and vegetation units within the cover sand landscape. The tests were carried out using the number of group observations in each period of four days, *i.e.* the average of locations for all individuals. In the riverine landscape the three smaller vegetation units were lumped together to avoid expected values of less than five, thus resulting in three classes. In the cover sand landscape the two *Deschampsia flexuosa*-units were grouped in one class and the two Miscellaneous units and the *Quercus*-forest were grouped in another, resulting in two classes (insufficient data were available for the September and March periods of the first year). On the higher scale level of the landscape the departure of the proportion of grazing time from the available surface area of riverine and cover sand landscapes was tested by comparing the observations with the expected binomial distribution according to surface area. The data for this distribution consisted of the number of group sightings on either landscape, with a maximum of one morning and one afternoon observation per day. No data were available for the first two periods, because the cover sand landscape was not accessible to the animals at that time.

The observation were compared with the model predictions on habitat occupancy for the pooled data of all periods. The correlation coefficient and the slope of the regression line between observed and predicted values were used as indices for the fit of the model; the expected value for both indices being one.

Results

Field data

Data on animal body weights, grazing time, food intake rate and food quality are given in Table 6.4. Compared to the calculated requirements, the animals appeared not to satisfy the requirements for DOM in seven of the thirteen periods and for Na in six periods. Requirements for P were met in all periods, however.

Habitat occupancy of vegetation units was different between the riverine and the cover sand landscape. Within the riverine landscape (Fig. 6.3 a) there was no significant difference between occupancy and surface area distribution in ten out of thirteen periods. Within the cover sand landscape (Fig. 6.3 b) habitat selection was much more pronounced, six out of nine periods revealing a significant departure from a random occupancy. In all these cases the *Deschampsia*-units were preferred to the Miscellaneous units. In the first November period the *Quercus*-forest was used extensively. A significant preference for this small unit could not be established, as it was grouped with the Miscellaneous units for the statistical test.

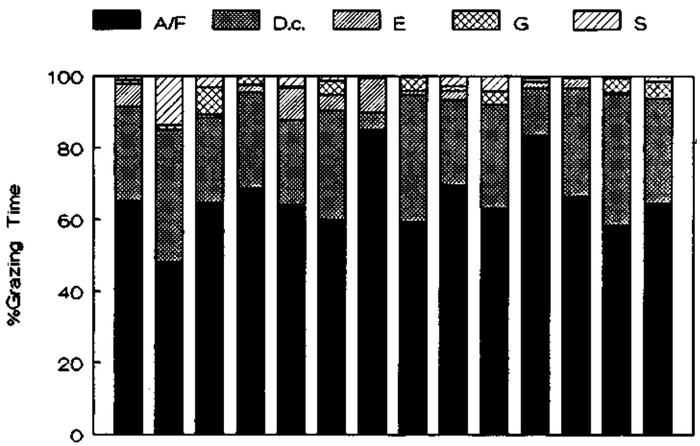
The proportion of time spent by the steers in the landscape units of the riverine landscape and the cover sand landscape was significantly different from the proportion of area available for all periods (Fig. 6.4). In every case the riverine landscape was preferred. A seasonal variation was apparent with a stronger preference for the riverine landscape in summer than in autumn and winter (see also Wallis de Vries, 1992; Chapter 3). In the first, mild spring the animals shifted sooner to the riverine landscape than in the second, drier and colder spring.

Model predictions

At the low scale level vegetation units the occupancy was poorly predicted by the model ($r=0.36$, slope 0.25, $n=112$). The model predicted a much more selective habitat occupancy than observed. We then decided to investigate whether the model could explain the habitat selection at a higher scale level of grouped vegetation units. The riverine landscape was subsequently treated as a single unit, the two *Deschampsia*-units were grouped together as a second unit, the two Miscellaneous units as a third unit, and, when acorns were available, the *Quercus*-forest as a fourth. The distribution of grazing time over these four larger vegetation units has been represented in Figure 6.4. Estimated food intake rate and dietary composition for these units were weighted according to the surface

Table 6.4 Average live weight, daily weight change, grazing time, forage intake rate and dietary quality for steers in different observation periods in the Karshoek area. Underlined nutrient concentrations indicate a shortage relative to requirements for maintenance and weight change.

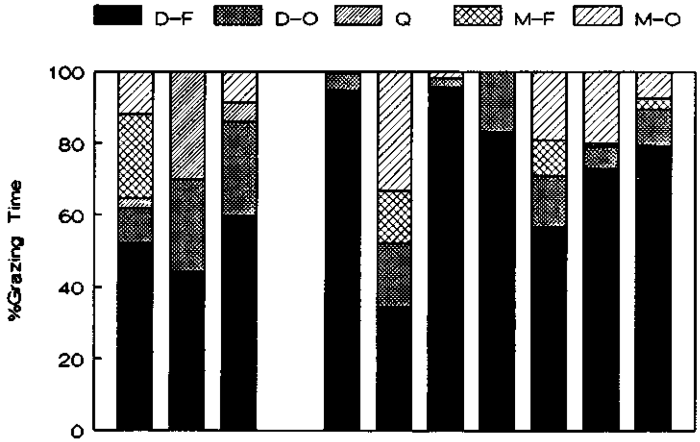
Observation periods	1	2	3	4	5	6	7	8	9	10	11	12	13
				1990						1991			
	May	Jul	Sep	Nov	Jan	Mar	Apr	Jul	Sep	Nov	Jan	Mar	Apr
Live weight (kg)	317	400	445	491	487	479	508	606	640	672	654	596	609
Weight change (g/day)	1240	990	720	330	-100	210	1030	952	560	110	-620	-460	1250
Grazing time (min/day)	368	437	458	469	462	627	573	448	489	504	415	460	629
Forage intake rate (g d.m./min)	19.8	20.3	22.2	25.5	20.7	10.2	15.6	25.3	29.0	25.4	24.8	18.0	21.6
Dietary quality													
DOM (%d.m.)	66.8	63.9	61.1	62.9	48.5	54.8	69.3	68.1	62.8	59.3	40.2	46.1	69.0
Na (ppm)	136	67	29	19	28	121	26	26	17	25	74	38	70
P (%d.m.)	0.33	0.29	0.34	0.21	0.18	0.40	0.30	0.29	0.21	0.22	0.20	0.26	0.26



a) Riverine

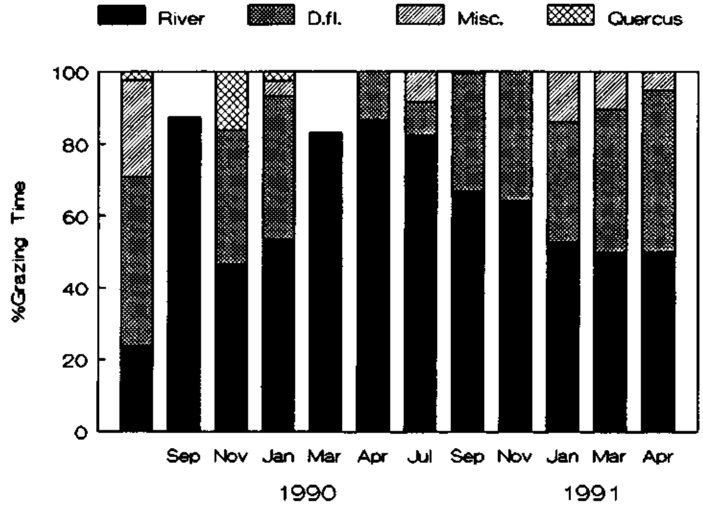
	May	Jul	Sep	Nov	Jan	Mar	Apr	Jul	Sep	Nov	Jan	Mar	Apr
	**	ns	ns	ns	ns	ns	*	ns	ns	***	ns	ns	ns
N observations	74	117	99	69	46	172	125	113	119	91	68	84	105

b) Cover sand



	Nov	Jan	Mar	Apr	Jul	Sep	Nov	Jan	Mar	Apr
	ns	***	--	***	ns	***	***	ns	*	***
N observations	36	50	--	42	22	23	17	38	40	86

Figure 6.3 Percentage grazing time for steers in different smaller vegetation units a) within the riverine landscape (A/F *Agrostis/Festuca*, D.c. *Deschampsia cespitosa*, E *Erophila verna*, G *Glyceria maxima*, S scrub) and b) within the cover sand landscape (D-F *Deschampsia flexuosa*-Forest, D-O *Deschampsia flexuosa*-Open, Q *Quercus*-Forest, M-F Miscellaneous-Forest, M-O Miscellaneous-Open). The left column gives the expected grazing time according to surface area distribution of the vegetation units. The number of observations is listed below, with the significance of the chi^2-test (* $P<0.05$, ** $P<0.025$, *** $P<0.005$).



	***	*	***	***	***	***	***	***	**	***	**
N observations	8	18	25	27	15	26	15	14	17	29	14

Figure 6.4 Percentage grazing time for steers in different larger vegetation units (see text); the riverine landscape is marked in black, the cover sand landscape comprises the other three units (Misc. = Miscellaneous). The left column gives the expected grazing time according to surface area distribution of the vegetation units. The number of observations per period is listed below, with the significance of the departure from a binomial distribution of grazing time between riverine and cover sand landscapes (* $P<0.05$, ** $P<0.025$, *** $P<0.005$). In the September and March periods of the first year not enough data were available to estimate the distribution within the cover sand landscape (see also Fig. 6.3 b).

area proportion of included vegetation units. The potential daily intake relative to requirements was usually highest in the *Deschampsia*-unit for DOM and in the riverine landscape for Na (Figures 6.5 a and 6.5 b). However, the DMIR in the riverine landscape was very low during winter (Fig. 6.5 c). An especially low potential DOM-intake was observed in the Miscellaneous unit, whereas in the first autumn the abundant acorn mast in the *Quercus*-forest allowed an even higher DOM-intake than the *Deschampsia*-unit.

The observed distribution of occupancy showed hardly any correlation with a random distribution according to surface area (r=-0.08, slope -0.12, n=34). This was to be expected on account of the preference for the riverine landscape. The model was first run with only DOM as the nutrient to be maximized. This resulted in an extreme selectivity of predicted habitat occupancy and again a very poor explanation of the observations (r=-0.17, slope -0.10, n=34). However, when with the three nutrients DOM, Na and P were simultaneously included in the model, the observations were much closer to the predictions (r=0.77, slope 0.54, n=34). Of the eleven observation periods examined, DOM was the sole predicted minimum nutrient (relative to requirements) in two cases, Na in four cases, a combination of DOM and Na in four cases, and a combination of DOM and P in a single case. The average diet corresponding to the predicted habitat occupancy reasonably satisfied the nutrient requirements: 94% for DOM, 98% for Na and 186% for P. The plot of observed against predicted habitat occupancy (Fig. 6.6) shows

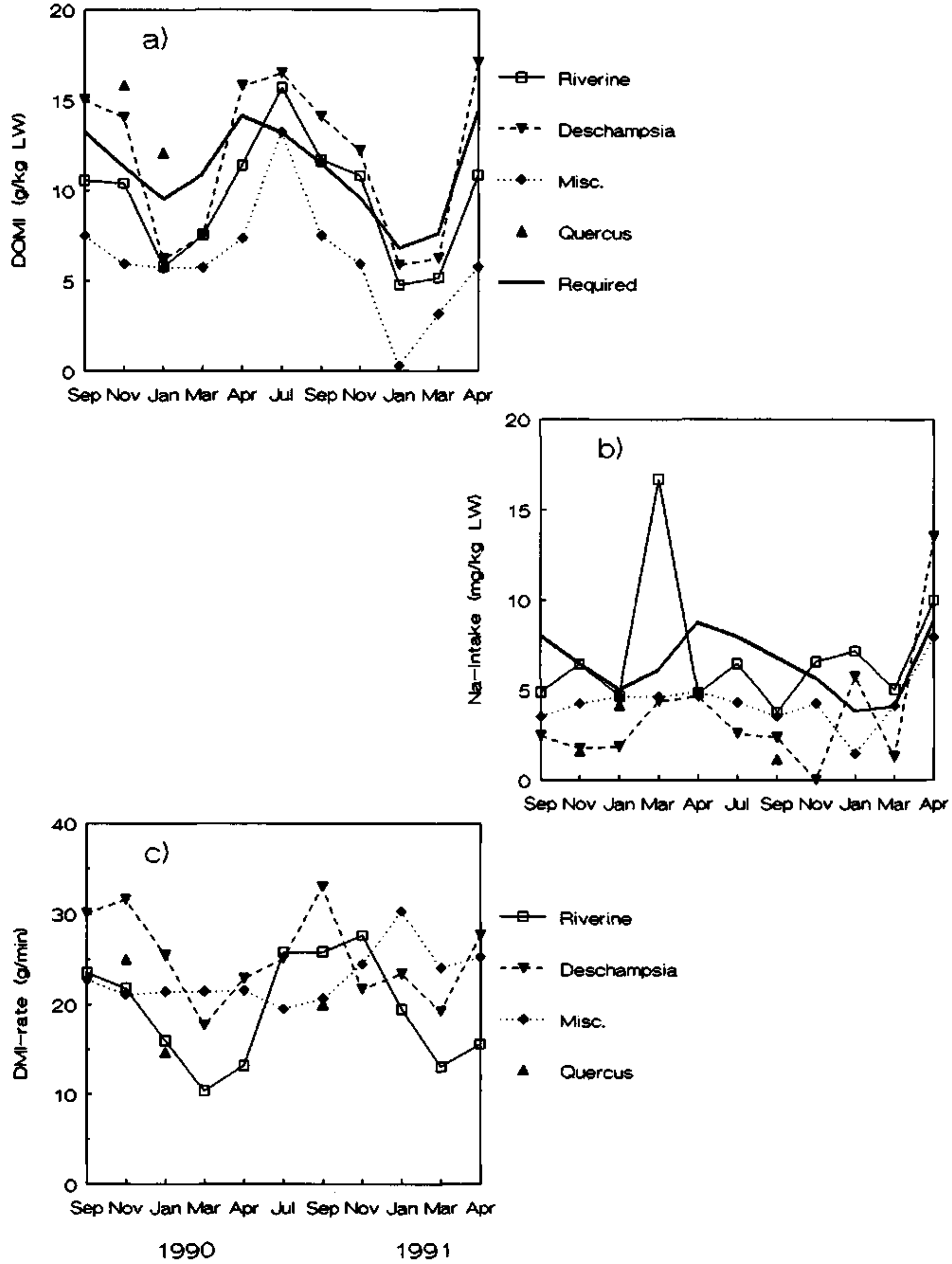


Figure 6.5 Potential daily intake of a) digestible organic matter and b) sodium (the solid line represents estimated requirements), and c) the dry matter intake rate for steers in different larger vegetation units (Misc. = Miscellaneous).

that the riverine landscape was generally chosen less than predicted by the model and the *Deschampsia*-unit was used more than predicted. The Miscellaneous unit was rarely included in either the predicted or the observed habitat occupancy. The observed occupancy still was generally less selective than predicted.

Model sensitivity

The model is sensitive to parameters affecting forage availability (production, consumption and trampling) and DMIR when the vegetation units are small or the run time is long. This affects model predictions on the scale of single vegetation units. On the higher scale level of composite vegetation units used later on, however, the influence of a change of 100% in food availability parameters on the model predictions is insignificant. The relation between available standing crop and DMIR is crude, but affects all vegetation units in a similar way, and thus will probably not greatly influence the model outcome.

Different assumptions on animal requirement could alter model predictions drastically. Lowering the requirements of the most frequent minimum nutrient, Na, by 35% led to an average 7% decrease in predicted occupancy of the riverine landscape. It did not result in an improved overall fit of the model, however (r=0.70, slope 0.56, n=34).

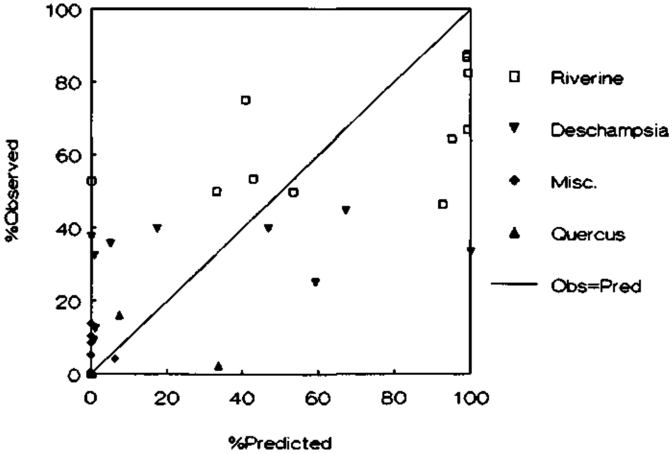


Figure 6.6 Plot of predicted habitat occupancy in larger vegetation units according to model predictions versus the actually observed occupancy (as a percentage of grazing time). The line denotes the equality of observed and predicted occupancy (Misc. = Miscellaneous).

Sensitivity of performance to habitat choice

The sensitivity of animal performance for the choice of habitat was evaluated by calculating the effect of a 20% change in the occupancy of the riverine landscape as compared to the model prediction. On average this 20% change in habitat choice resulted in only a 6% change in DOM-intake and a 16% change in Na-intake. A positive change in one nutrient was evidently accompanied by a negative change in the other. Depending on the difference in nutrient availability between habitats, the change in performance resulting from a suboptimal habitat choice may therefore be limited.

Discussion

Model assumptions and data input

The fundamental assumption of maximization of nutrient intake appears justified, as a lesser intake would have failed to satisfy energy and mineral requirements. The average observed daily grazing time was even longer than predicted (503 *versus* 465 minutes), which supports the maximization principle. Protein requirements could also be important for determining diet composition (see Prins & Beekman, 1989) and, hence, habitat occupancy. The nitrogen content in the diet of the study animals ranged between 1.7% and 3.7%, with an average of 2.4%. Their demands for crude protein (%CP = 6.25 %N) were satisfied in all seasons (Chapter 4). Protein was therefore not included as a separate factor in the model.

Predicted daily intake was constrained either by diet digestibility or by grazing time (in the case of low forage quantity). The relation between diet digestibility and potential daily intake used in the model is based on a limited data set of field trials. The use of digestibility as a determinant of maximum voluntary intake seems legitimate as significant linear relations between the two variables have been established for sheep (Armstrong *et al.*, 1986). Data from a study on free-ranging Highland cattle by Van Wieren (1992) (Fig. 6.7; R^2=0.710, d.f.=9, $P<0.01$) show a very similar result to the data from Hodgson *et al.* (1991), although the daily voluntary intake was slightly higher. The data from this study, with growing instead of adult animals, generally show a closer agreement to the data of Van Wieren (when excluding points with long daily grazing time). The

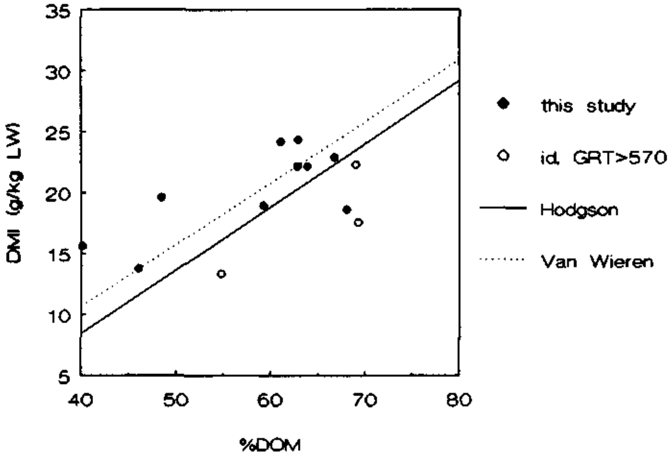


Figure 6.7 Relations between the percentage digestible organic matter and daily dry matter intake for cattle after data from Hodgson *et al.* (1991), Van Wieren (1992) and this study (closed circles). The open circles represent points with high daily grazing time (GRT>570 minutes).

overall impression is that the relation used in the model leads to an underestimation of voluntary intake. The difference in intercept does not change the model predictions concerning habitat occupancy, but the used equation does lead to a lower intake and thereby to a less favourable nutrient balance.

The model predictions on habitat occupancy are particularly sensitive to the input values concerning DMIR (which determines the initial biomass) and diet quality. DMIR is the product of biting rate and bite size. For the grassland vegetations these parameters have been estimated with reasonable accuracy through, respectively, large numbers of observations and calibration (Chapter 2). For the other vegetation units the values will be less accurate and may have reduced the fit of the model. This should be of less importance in the case of predictions for habitat occupancy on the higher scale level, as the differences between vegetation units were of greater magnitude. The values for diet quality can be considered as accurate, since the chemical analyses followed standard procedures and no significant differences were found between the diet selected by the animals and the estimate made by hand-plucking (Chapter 2). However, the values for Na have sometimes shown to be less reliable, although the general trend is clear and conform to expected values (Bokdam & Wallis de Vries, 1992).

Decision rules for habitat selection

The results of the field observations suggest that the cattle made choices on different scale levels. They showed an apparently random occupancy of vegetation units within the riverine landscape but on a landscape scale they clearly preferred the riverine landscape to the cover sand landscape. The model predictions on habitat occupancy at the higher scale level revealed that a maximization strategy for a combination of energy (DOM) and minerals (Na and P), gave a better explanation of the variation in habitat occupancy than by considering energy alone. This confirms the initial hypothesis that habitat occupancy during grazing can be governed by a variety of nutrient demands. The result is a more varied habitat occupancy than if only a single nutrient were to be maximized. The overestimation of the proportion grazing time in the riverine landscape probably follows from errors in parameters or input values. The observed habitat occupancy, however, was still more diverse than predicted by the present model. The random occupancy within the riverine landscape and the occupancy of the Miscellaneous units, though of relatively small importance, remain unexplained by the model.

An explanation for the apparent random occupancy of vegetation units must consider the ability of cattle, as a large herbivore, to discriminate between the availability of different nutrients. The random occupancy within the riverine landscape could be accounted for if the potential daily intake for the different vegetation units had been similar. But this was not the case: its average coefficient of variation was 15% for DOM and 41% for Na. However, as pointed out by Stephens & Krebs (1986) and Illius & Gordon (1990) the ability of large herbivores to smell or taste, and therefore recognize, the different required nutrients is limited. Moreover, food processing is relatively slow compared to the number of bites taken per day. Thus, it would be difficult for the animal to learn the feeding value of specific plants or vegetation patches from post-ingestive consequences. Foraging on a low scale level would then rely mostly on rules of thumb and frequent sampling (Illius & Gordon, 1990). This would lead to a more even habitat occupancy than expected if the animal had a perfect knowledge of its environment. A low, though clearly significant, degree of selection was also observed at a scale level below the vegetation unit, between patches differing in sward height and maturity (Chapter 5). At that low scale level the observed patch selection appeared to provide a good approximation of nutrient intake maximization. The apparently random habitat occupancy shown within the riverine landscape might also prove to contain an element of selection, if investigated in more detail. However, even if the occupancy of vegetation units were confirmed as being truly random, it could still reflect an optimal performance of the animal. That is, if discrimination errors are large or if the profits from a more selective use are small relative to the costs of acquiring sufficient information (see Yoccoz *et al.*, 1993; Chapter 5).

At a higher spatial scale level, differences between habitats will be greater and more predictable over time. Provenza & Balph (1990) and Provenza (1991) have shown that the ability of a number of mammals to learn by association from post-ingestive experience can have a clear effect on diet selection. Thus, herbivores may learn to discriminate habitats with different nutrient availabilities by experience and actively select an adequate diet or develop rules of thumb to this effect. Bailey *et al.* (1989) demonstrated that cattle are able to remember specific locations associated with a certain food reward. The differences between the riverine and the cover sand landscapes were clearly large enough to be recognized and to warrant a high degree of selectivity.

Conclusion

Differences in nutrient availabilities between vegetation or landscape units can be important in determining habitat selection during foraging. Optimal foraging models incorporating different nutrient constraints instead of one are more likely to explain the differentiated habitat occupancy observed in large herbivores. The success of such models probably increases with habitat variation, and thus with scale. In complex habitats, such as a landscape mosaic, habitat selection will depend not only on the currency the animal chooses but also on adequate knowledge of relative food availabilities and travel distances to food sources. Improvements in the explanation of habitat use in free-ranging herbivores will need to consider the animal's perception and its acquisition of information on the foraging environment. In particular, more emphasis should be placed on the role of sampling and experience. The importance of these factors has been established mainly from laboratory experiments and indirect field evidence (Provenza & Balph, 1990). The application of these insights to the study of herbivore foraging in a landscape mosaic now poses a challenge for further field experiments.

Plate 15. In the Karshoek the riverine landscape was preferred. Here the animals are basking in the sun on a winter day.

Plate 16. *Deschampsia flexuosa* provided a relatively high intake of digestible organic matter in the cover sand landscape of the Karshoek (Photo J.M. Gleichman).

Plate 17. In years with abundant mast acorns were included in the diet.

CHAPTER 7

Do Breed Differences in Cattle have Implications for Conservation Management?

Summary

A number of cattle breeds is being used for nature conservation purposes. The arguments for choosing a particular breed are often based on rather vague concepts such as sobriety and self-reliance. In this chapter a new set of more explicit biologically based criteria is developed. To this purpose vital characteristics for survival in the wild are identified using information on the cattle's wild ancestor, the aurochs, and contemporary wild bovines.

Growth pattern and energy metabolism are discussed as a background for a tentative reconstruction of aurochs characteristics. Important changes in these characteristics in the course of domestication are presented. Four main types of European cattle breeds are recognized: slow growing and late maturing work breeds, fast growing and late maturing beef breeds, early maturing beef breeds and early maturing dairy breeds.

The adaptation of these breed types for survival in the wild is evaluated using four criteria: energy requirement for maintenance, calving difficulty, maturation rate and so-called original traits. For seasonal grazing the breed differences hardly seem relevant. For yearround grazing breed differences have not yet proved to be biologically important. The evaluation suggests that work breeds and early maturing beef breeds appear the most appropriate. However, under climatically mild conditions only aesthetic arguments for a particular breed choice may prove relevant.

(adapted from a paper in De Levende Natuur [1993] 94, 142-149)

Introduction

In the Netherlands cattle have been introduced in dozens of nature reserves with the purpose of maintaining open vegetations or to develop them. Besides that, experiments are conducted with herds which are largely left to themselves for their subsistence, in analogy to wild herbivores. In most cases a clear choice is made for a particular breed type. Differences between breed types, however, have rarely been clearly established. The basis for the decision is therefore weak. In this chapter I will address the biological differences between breeds and their relevance for conservation management.

Only those cattle breed characteristics will be considered which are of importance to the management of nature reserves. These are predominantly the biological characteristics determining the survival of animals under natural circumstances. In practice, much cited criteria for the biological suitability of introduced cattle are self-reliance, robustness to winter conditions, sobriety, and the degree of suitability for different habitats. These criteria are rather vague, however, and difficult to evaluate without direct comparisons between breeds under field conditions. The lack of such studies allows a whole array of semi-truths to circulate, based on incidental observations and subjective interpretations. Some examples from management reports: modern breeds would hardly accumulate fat reserves; Scottish Highland cattle, Limousin and Hereford cattle would, in contrast to Galloway cattle, be unadapted to wetter areas; Dutch breeds would produce too much milk and so-called primitive breeds would be more sober, suffer less calving difficulties and need less veterinary care.

A successful introduction of cattle in a nature reserve, with the aim to minimize human interference, requires the fulfilment of the following conditions. The animals should accumulate enough fat reserves for the winter period, they should satisfy their requirements using the available forage in the area, the calving should take place without assistance and other veterinary care should also be superfluous. Moreover, requirements are set to the area in terms of size and food availability; no further attention will be devoted to these factors in this context. Furthermore, consideration could be given to 'original traits': morphological properties known from contemporary wild bovines and, through archaeological research, from the aurochs. Among these frame size, build, coat colour and horn type can be suggested. In order to assess the value of the named criteria, some background information is necessary.

Growth pattern and energy metabolism

In all mammals, the growth of different tissues follows a similar basic pattern (Bergström, 1974; Taylor, 1985): the neural system is developed first, followed by, respectively, bone, muscle and fat tissue. The greatest fat deposition therefore takes place at a later developmental stage. Fat is thus known as a so-called late maturing tissue. It accumulates first around the gut, then between the muscles, and last subcutaneously. This growth pattern varies according to the diet. Animals on a sober feeding regime will grow and fatten slower than animals on a high nutrition plane.

Breed differences can be largely accounted for by differences in the rate of physiological development. Larger breeds generally are late maturing, and therefore accumulate fat at a later age than smaller breeds. A similar difference exists between the sexes: bulls grow larger and fatten slower than cows.

The energetic maintenance requirement is higher for muscle tissue than fatty tissue, as a continuous turn-over of protein occurs in muscles (Webster, 1985). A higher energy requirement can also be caused by a larger proportion of active organs such as liver, kidneys, heart and guts (Solis *et al.*, 1988). The food intake shows a close correlation with the energy requirement. Animals with a higher requirement can reach a higher intake per unit of metabolic weight (Webster, 1985). Furthermore, both within and between breeds, a clear positive relationship is apparent between energy requirements for maintenance (basal metabolism), maximum voluntary intake and growth rate (Vercoe & Frisch, 1982; Ketelaars & Tolkamp, 1992). For animals with a higher basal metabolism, this results in faster growth at an abundant high-quality food supply. However, with a less digestible or limited food supply, the animals with a lower metabolic rate are at an advantage.

In colder regions and areas with a periodic food shortage, fat reserves constitute an important energy source. Nevertheless, the energy provision of herbivores during winter still relies heavily on a regular food intake. Even in Svalbard reindeer, which accumulate up to 30% of their body weight of (mainly subcutaneous) fat, the fat reserves account only for 25% of their energy requirements (Tyler, 1987). The fat stores appear essential as a buffer in times of raised energy expenditure, such as the rut or the lactation period (Mitchell *et al.*, 1976; Thing *et al.*, 1987; Tyler, 1987).

Fat also acts as an insulator, leading to reduced energy costs for an animal with more subcutaneous fat (Thompson *et al.*, 1983; Solis *et al.*, 1988). The insulating function of the fur is considered more important, however (Tyler, 1987).

The aurochs

What is known about the build and the energy metabolism of the ancestor of domestic cattle, the aurochs? The aurochs was a large animal, bulls measuring 175-200 cm at the withers and cows 150-170 cm. However, the species declined in size after the Pleistocene. Davis (1987) shows that an appreciable variation in size must have existed. He cites work of Grigson, who, for Holocene aurochs, estimated a height of 157 cm and 147 cm at the withers for bulls and cows respectively. The colour of the bulls was black with a white muzzle and a light back stripe, which sometimes extended to the flanks in the shape of a lighter zone. The cows were more of a reddish brown and the calves were born fully brown. Some variation in coloration, such as in the African buffalo (Sinclair, 1977), seems likely. The animals probably had a thinner summer coat and a thick winter coat.

Contemporary wild bovines belong to the genera *Bos* (yak, gaur, kouprey and banteng), *Bison* (American and European bison) and the less closely related genera *Syncerus* (African buffalo) and *Bubalus* (water buffalo and anoa) (Sinclair, 1977). Because of its large frame the aurochs, like its present-day relatives, was probably a late maturing animal. A large size offers a number of advantages: a higher digestive capacity, a reduced heat loss, a lower predation risk and the possibility of delivering larger calves, which have a higher survival probability.

The wild bovine species bison (*Bison bison*) and yak (*Bos grunniens*) have shown to possess a low basal metabolic rate and voluntary food intake, and to grow and fatten slowly during the first years of their life (Peters, 1958; Richmond *et al.*, 1977 and 1978; Christopherson *et al.*, 1979). The claim made by several authors (*e.g.* Peden *et al.*, 1974; Schaefer *et al.*, 1978), of a more efficient digestion in these species compared to domestic cattle, has never been definitely proved; weight differences between animal species and methodological flaws explain most of the reported differences (see Van Soest, 1982). The possibility remains, however, that a lower food intake leads to a more complete digestion. The low metabolic rate indicates an adaptation to a moderate food quality. Through their lower intake capacity, however, wild bovines grow slower than domestic cattle which have been selected for productivity.

Fat accumulation in wild bovines proceeds slowly in comparison with domestic bovines (Mason, 1984). This can partly be attributed to the difference in mature frame size and basal metabolism. In cervids of the temperate zone, fat reserves are also small compared to livestock (Wright & Russel, 1984; Tyler, 1987). In this case the difference in frame size cannot be the cause of the difference in reserves. The explanation can be found when considering the conditions under which livestock is kept. Natural, seasonal fluctuations in growth, with weight loss over winter, have been largely eliminated for livestock in Europe. This leads to a much greater build-up of fat reserves than in wild conspecifics. Domestic bovines therefore are often unnaturally fat in comparison to wild bovines.

It appears likely that the physiological characteristics mentioned for contemporary wild bovines, such as bison and yak, also applied to the aurochs. Like the aurochs, and probably even more so, these species are adapted to an environment with harsh winters and a food supply which deteriorates significantly under these circumstances.

Domestication of cattle

Many breeds of domestic cattle are smaller than the aurochs. Various explanations for the diminution in size have been put forward. Adaptation to a food supply restricted in quantity or mineral content can be cited as one of the main causes. This certainly seems to hold for the extremely small Iron Age cattle (Davis, 1987) and the formerly existing heathland cattle in the Netherlands (Hengeveld, 1865). Steehouwer (1987) proposes that domestic cattle have become smaller because, whether on purpose or accidentally, they have been selected for early maturity. Early maturity may have arisen by early reproducing animals getting a larger share in the herd. A second reason for the evolution towards early maturity may have been the disappearance of selection for 'bull traits'. In natural bovine populations the big, imposing bulls are most successful. This applies much less to cows and there may even be an advantage (for the farmer) in early maturity: cows will reproduce earlier at a small adult size.

During domestication coat colour variation increases, with a notably larger proportion of white (loss of pigment). This probably is a consequence of a certain degree of inbreeding (Mason, 1984). The coloration of Dutch 'witrikken' (white backs) and the

Park cattle of Chillingham provide examples of this phenomenon. The belted pattern of the Dutch Lakenvelder and the Belted Galloway represents a similar case. Hornlessness is another genetically determined characteristic which may be revealed by inbreeding (French *et al.*, 1966; Davis, 1987).

Breed types

Besides a differentiation in size, there has been a selection for production objective, which has led to separation in work, beef and dairy breeds (Epstein & Mason, 1984). Only the European breeds will be discussed here. We can distinguish four broad breed categories (Table 7.1):

I late maturing work breeds,
II late maturing beef breeds,
III early maturing beef breeds,
IV dairy breeds.

The late maturing work breeds represent the group considered as the most primitive. It encompasses the Iberian breeds (including the fighting cattle) and the Steppe cattle. These are large animals with many aurochs traits, such as big horns, slow growth and a brown calf colour (French *et al.*, 1966). It is unclear whether the scanty fat accumulation is a consequence of late maturity, inferior feed or climate. Work breeds were mainly kept as draught-animals, pulling carts or ploughs. Meat and milk constituted byproducts of lesser importance. The size of the draught-animals was an advantage in supplying power. Apart from this, selection on these animals probably followed no particular direction. The Scottish Highland cattle possibly have a similar history. This breed is also late maturing by its slow growth, but it has a small frame. The latter characteristic could be a result from an adaptation to the marginal food supply in the low fertility environment of the Scottish mountains.

In France and Northern Italy the circumstances for bovine productivity are more favourable, due to a mild climate and a fertile soil. The local original work breeds have been increasingly selected for meat production since the rise of the draught-horse. Examples are the Charolais, Limousin, Blonde d'Aquitaine, Piemontese and Chianina breeds. The last breed is the world's largest cattle breed, with bulls measuring up to 180 cm at the withers at a weight of over 1500 kg (Sambraus, 1987). Like the above-mentioned work breeds (excluding the Scottish Highland cattle) the French-Italian breeds are probably no or barely smaller than the aurochs. They are late maturing breeds with a notably fast growth rate, a high muscle/bone ratio and a late fat accumulation. The fast growth rate can be explained by the body composition on the one hand: a similar amount of energy produces more muscle mass than fat. On the other hand the faster growth rate appears related to a higher metabolic rate (Webster, 1985) and therefore a higher food intake than in the previous group. The endeavour to breed larger, fast growing animals has also increased calf weights, leading to a higher incidence of calving difficulties in this breed group, especially for calves carrying the double-muscling gene (Mason, 1971; Bülow-Olsen, 1980).

Early maturing beef breeds comprise the British Aberdeen Angus, the Hereford and the

Galloway; the last should possibly be considered as a hornless variation of the Scottish Highland cattle, selected for meat production. The high-quality feed given to cattle nowadays has turned early maturation to a disadvantage: according to the present demand for lean meat, the animals fatten too quickly, whereas the late maturing beef breeds yield a higher production of leaner meat (Mason, 1971; Bergström, 1974). When the animals mainly depend on roughage of lesser quality, however, the early maturing beef breeds gain advantage of their lower energy requirements and greater fat accumulation (or shorter finishing period).

Dairy breeds can be viewed as cattle with the most developed 'cow traits'. The animal type is also predominantly early maturing, and therefore fattening rapidly. The Jersey and the black-and-white Friesian may be cited as examples. The American Holstein Friesian is a black-and-white breed selected for a still higher milk production. Thanks to modern feeding methods it has also been successfully selected for a larger frame. The difference compared to beef breeds with respect to fat deposition concerns mainly its location: in dairy breeds fat accumulates more around the internal organs, whereas subcutaneous fat deposition is comparatively more important in beef breeds (Wright & Russel, 1984; Taylor & Murray, 1991). Another breed difference concerns the mass of active organs, such as the liver. This is clearly greater in dairy breeds than in beef breeds (Taylor & Murray, 1991). Both differences can be related to the higher metabolic activity brought about by milk production. The consequence is that dairy breeds have a higher energy requirement than beef breeds (Thompson *et al.*, 1983; Solis *et al.*, 1988).

The so-called Heck cattle cannot be classified in one of the four breed groups, as there is not enough information. These animals have many original external traits. The breed is not a reconstructed aurochs, as some pretend, but a new breed developed by the Heck brothers through crossing and selection; they have therefore been called Heck cattle by F. Vera. Many breeds have been used for its creation: Hungarian Steppe cattle, Scottish Highland cattle, Braunvieh from the Alps, Murnau-Werdenfelser, Angler, German black-and-white, Italian Podolian and Corsican cattle (Sambraus, 1987). The original genetic basis for this breed is therefore extensive. This does not imply, however, that the genetic variation is still great today; this would require closer study.

Practical experiences

What is the practical significance of differences in physical appearance and energy metabolism? Are there clear differences in the success of introducing various breeds in nature reserves? The answer to these questions is not easy, because scarcely any experiments have been done to clarify these matters.

If we look at feral cattle populations, it appears that these can maintain themselves without human interference. European cattle breeds have been left to themselves in climatologically vastly different areas: Australia, Colombia, the Seychelles, Spain, the Western Pyrenees, and islands off the coasts of Japan, New Zealand and Scotland (Epstein & Mason, 1984; Hall & Moore, 1986). In severe winters breed differences in fat reserves and coat thickness will probably determine body condition. This should only prove important for the rate at which the reserves are used up, however. The fact that

Table 7.1 Characterization of four groups of cattle breeds according to physical appearance and growth.

Group	Maturity	Growth Rate	Use	Fat Reserves (main storage)	Energy Requirement	Breeds	Height Withers		Live Weight	
							♂	♀	♂	♀
I	Late	Slow	Work	Subcutaneous?	Low	Spanish land breeds	148	136	890	530
						Steppe cattle	150	140	900	575
						Scottish Highland	132	115	550	425
II	Late	Fast	Work/Beef	Subcutaneous?	Average	Charolais	149	137	1250	800
						Limousin	150	137	1100	725
						Blonde d'Aquitaine	151	142	1125	775
						Piemontese	142	133	850	550
III	Early	Average	Beef	Subcutaneous	Low	Hereford	135	127	850	550
						Galloway	128	120	800	475
						Aberdeen Angus	130	120	850	500
IV	Early	Average	Dairy/(Beef)	Internal	High	Dutch Friesian	142	132	950	550
						Holstein Friesian	152	140	1100	650
						Meuse-Rhine-Yssel	142	132	1050	600
						Jersey	127	122	650	400

References: French et al. (1966), Sambraus (1987) cold *per se* is not a problem, has been sufficiently proved on the Wolfhezer Heide, the Netherlands (Bokdam *et al.*, 1986).

In nearly all grazed nature reserves in the Netherlands either summer grazing or year-round grazing with supplementation is applied. Therefore, breed differences in utilization of the food supply to get through the winter remain speculative. It is generally agreed upon that all breeds keep healthy during the growing season, as long as possible mineral deficiencies are prevented.

In most cases the problems caused by diseases and parasites are insignificant at low stocking rates (C. Holzhauer, pers. comm.). This is not surprising, since the risk for contamination is much smaller than in regular animal husbandry practice. In a population without regulation the load would probably be density dependent. Until now, however, there has been no indication of breed dependent differences in sensitivity to diseases and parasites.

In nature reserves calving occurs increasingly without assistance. This does not appear to cause problems. The experience on the Wolfhezer Heide shows that black-and-white cows calve in seclusion and leave the calf under cover, as has been observed in other feral cattle. The calf remains hidden and awaits the cow to suckle. Only after a few days does it join the herd (J.M. Gleichman, pers. comm.). The supposition that dairy breeds produce too much milk to suckle only their own calf, is only valid for cows which have been kept for milk production earlier. Veterinary care is almost exclusively needed for births of large calves from French-Italian breeds and their crosses (particularly Charolais) (Bülow-Olsen, 1980).

The Karshoek experiment

In order to compare two breeds with regard to growth and accumulation of body reserves, an experiment was carried out using a beef breed and a double-purpose breed (beef and dairy) with an emphasis on milk production: Herefords and Meuse-Rhine-Yssel cattle (MRY or Dutch red-and-white). These two breeds respectively represent the third and fourth breed groups.

The experiment was conducted in the area Karshoek-Stegerense Veld, along the Vecht river near Ommen (Province Overijssel). The area covers 75 ha with a varied vegetation composition: pine forest and dry to moist heathland on poor sandy soil, river dunes and acid to nutrient-rich grasslands along the Vecht river. During two years five Hereford and five MRY steers grazed in the area without any kind of supplementation. All animals were just over one year old at the onset. Every two months the condition and foraging behaviour of the animals were studied. The condition was determined by weight, external condition scores for fatness (Lowman *et al.*, 1976) and analysis of serum (twice a year) and saliva (incidentally) to determine mineral status. Foraging behaviour was monitored by collecting as many 10-minute observations as possible for each animal, during four consecutive daylight periods. Each observation consisted of recording the number of bites on different plant species and categories of different vegetation structure.

The results on live weight development and mineral status have been treated more extensively elsewhere (Wallis de Vries, 1992; Chapter 3). Neither the live weight nor the mineral status differed between the two breeds (Fig. 7.1). However, the Herefords were fatter (Fig. 7.2; $P<0.001$) and remained smaller: the height at the withers at the end of the experiment was 141.0±4.6 cm for MRY and 133.0±3.7 cm for Herefords (±s.d.; difference significant at $P<0.02$). The greater fatness of the Herefords not only concerned subcutaneous fat (as judged by the condition score) but also the fat percentage of total body weight, as estimated by measurements with deuterium oxide (methods described in Chapter 4): 15.1±4.2% and 25.4±4.6% for MRY and Herefords respectively (± s.d.; difference significant at $P<0.05$).

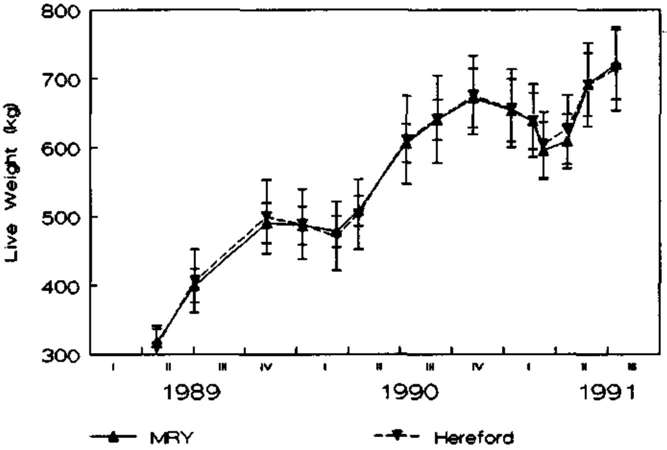


Figure 7.1 Live weights (± standard deviation) of MRY and Hereford steers in the Karshoek.

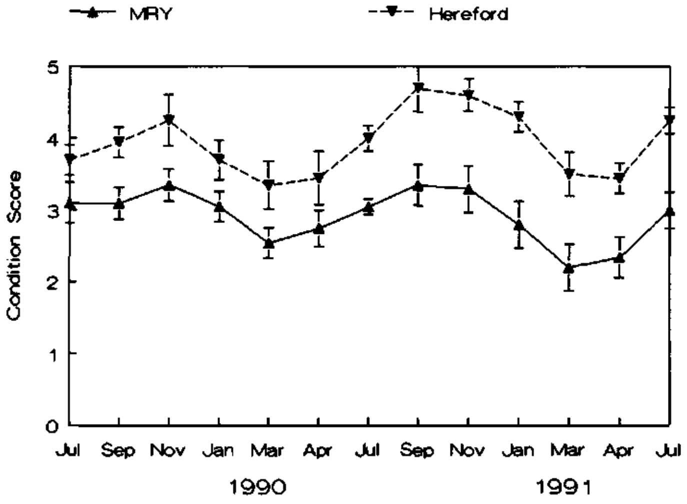


Figure 7.2 Condition scores (± standard deviation) of MRY and Hereford steers in the Karshoek.

The diet selection of the two breeds did not show much difference. The animals usually stayed together as a herd. In the forest both breeds consumed as much woody material (on average 12.5% of bites for MRY and 10.4% for Herefords). In the grassland, however, a different foraging behaviour was apparent. In the most frequently grazed vegetation, the unit of *Agrostis capillaris* and *Festuca rubra*, the MRY steers took more bites on short patches and less of the stemmy patches (Fig. 7.3). The proportion of the categories varied according to the seasonal change in the vegetation (Chapter 5). The difference between the breeds always remained small, but was significant over the entire experiment ($P<0.02$). In combination with data on digestibility and mineral contents of these plant categories (Chapter 5), these results indicate a higher dietary quality for MRY in comparison to Herefords.

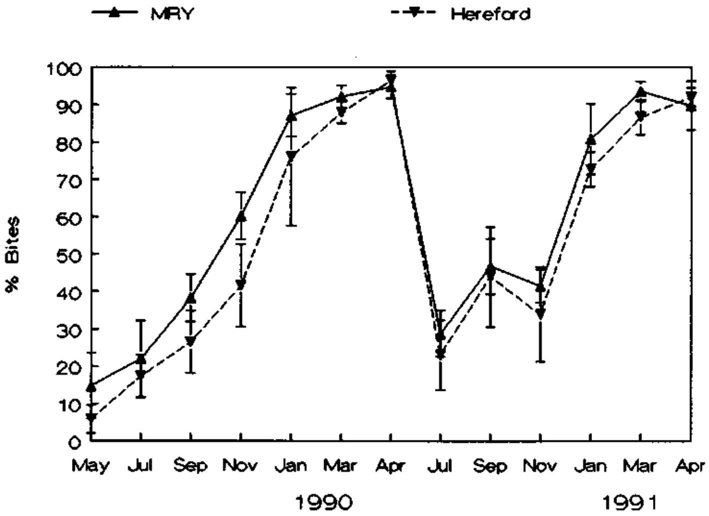


Figure 7.3 Percentage bites on short *Agrostis capillaris/Festuca rubra* sward (± standard deviation) of MRY and Hereford steers in the Karshoek experiment.

Interpretation of the Karshoek experiment

Can we explain these results in the light of the preceding review? And what are the implications for the suitability of both breeds? The higher dietary quality for the MRY could relate to the presumably higher maintenance requirements of this breed, which tends more towards a dairy breed than the Hereford and has a thinner skin and subcutaneous fat layer (Callow, 1961). The Herefords clearly suffered more from diarrhoea in spring; this has been remarked before by Barton (1966). They therefore would perhaps benefit from a lower dietary quality (see Prins & Beekman, 1989). Because of its larger adult frame the MRY breed would be expected to show a slower fat accumulation, a faster growth and a greater height at the withers. This is confirmed by the results concerning fat storage and withers height, but not by the weight development. The MRY should show a stronger negative impact from the suboptimal forage quality during winter as a consequence of their higher energy requirements for maintenance. They could compensate partly by opting for a higher dietary quality and food intake. The net result in terms of growth depends on the environmental conditions. It appears that the MRY have developed some growth retardation, but not so strong as for the Herefords to outweigh them. The priority for growth has led to a continued development of the skeleton of the former, thus still resulting in a greater frame than in the Herefords. A comparable fatness of the breeds would be expected if the experiment had continued until full maturation of the animals.

The Karshoek experiment therefore has produced results in line with the expectations. The breed differences are not sufficiently important, however, for justifying the conclusion that Herefords are better suited for year-round grazing than MRY. This could possibly be true in colder or poorer regions, but under prevailing conditions in the Netherlands, both breeds appear about equivalent.

Over the last two years black-and-white heifers have been grazing in the area. These also have stood the winter successfully without food supplementation. It should be borne in mind that the winters of 1991/92 and 1992/93 were relatively mild. In the coastal dunes of Duin en Kruidberg a group of Limousin cows has lived through the winter of 1992/93 in good condition without receiving supplements (H. Piek, pers. comm.). These results again show no definite breed differences with respect to body condition in winter.

Table 7.2 Appraisal of the four breed groups according to important conservation management criteria. (- negative, ± neutral, + positive)

Breed group:	Work	Late mature /Beef	Early mature /Beef	Dairy
Energy requirements	+	-	±	-
Calving difficulty	+	±	+	+
Maturation rate	+	+	-	-
Original traits	+	±	±	-

Discussion

In the preceding pages the differences between cattle breeds concerning their survival in nature reserves have been put in a biological perspective. The variation between individuals has been affected of old by farmers, whether accidentally or on purpose, thus eventually generating different breeds. It is not essential to consider the actual circumstances under which a particular breed is kept and productive. For nature conservation purposes insight into the biological characteristics is more relevant. This has scarcely received attention in the past.

In Table 7.2 an appraisal of the four distinguished breed groups has been given, based on important criteria for conservation management: energy requirements, calving difficulty, maturation rate and original traits (build, coat colour, horns). The first two criteria can be considered as a specification of the concept self-reliance, which still lacks a clear definition. The criteria maturation rate and original traits are somewhat questionable. They indicate the degree of similarity with the aurochs. These criteria could be viewed as indirect evidence for other functional characteristics that are important for survival. However, this argument remains speculative without further verification. A different justification for these criteria is that animals with more original traits are aesthetically more attractive in nature reserves. I think the combination of these two arguments provides sufficient support to maintain the criteria maturation rate and original traits. The influence of the animals on the vegetation has not been taken into consideration. There is no reason at present to assume that this will vary between breeds; although hornless breeds will probably have less impact on shrubs and young trees.

Conclusion

A final judgement of the suitability of various breeds for conservation management, based on the four above-mentioned criteria, is presently not possible. Objective comparative data are lacking. Only a rough appraisal can therefore be made, such as in Table 7.2. In general all breeds appear equally suitable for grazing during the summer season. In areas with a low forage quality the beef breeds and slow-growing, late maturing breeds are at an advantage. The greater calving difficulty should be taken into account when considering fast-growing, late maturing breeds.

This review is mainly focused on the circumstances in which human interference is minimal, *i.e.* year-round grazing without food supplementation. The expectation is that late maturing work breeds are the most suitable, followed by the early maturing beef breeds, the late maturing beef breeds and, finally, the dairy breeds. The first two groups have a relatively lower energy requirement for maintenance, which is an advantage for surviving the winter. Among the Dutch breeds the MRY, as the least specific dairy breed, seems the most suitable. Breed differences related to geographical origin and foraging behaviour appear small and therefore less important. Although genetic differences in mineral utilization do occur, it is unknown whether these are breed specific. If so, this could prove important in nutrient-poor areas like the Veluwe in the Netherlands.

In areas with a so-called nature development objective, dedomestication of cattle will be important. In such a situation, it could be important to choose a breed with a large genetic variation, allowing natural selection to take place. It is possible that Heck cattle have a good background in this respect. In the Oostvaardersplassen, a polder area on marine clay, the animals thrive at a low level of supplementation. Besides this, Heck cattle were not registered by law as livestock until now, increasing the possibilities to use them in nature reserves. However, it may prove that under the climatic conditions prevailing in the Netherlands, breed differences in cattle prove only relevant on aesthetic and not biological grounds. Research and practice will have to elucidate this matter.

Plate 18. In the Karshoek Herefords (right) showed a greater fat accumulation than the Meuse-Rhine-Yssel (MRY) breed: the condition score of the Hereford on the photo is 3.75 against 3.0 for the MRY (July 1990). Note the traces of wet faeces on the Hereford.

Plate 19. MRY appeared to select more for short grass patches than Herefords.

CHAPTER 8

Large Herbivores and the Design of Large-scale Nature Reserves in Western Europe

Summary

Nature conservation in densely populated areas, as in Western Europe, faces a continuous loss, isolation and fragmentation of suitable habitats for wild species. Conservation measures have not been able to counter this threat to natural diversity. A new concept for nature conservation thus seems required. Large herbivores require large tracts of land, they can have a significant influence on vegetation composition and may thus serve as an umbrella species group for other species of plants and animals. It is therefore proposed to use the habitat requirements of large herbivores as a key to the design of large-scale nature reserves.

The present status of nature reserves in the European Union concerning size distribution and the occurrence of large herbivores and their predators is reviewed. It is argued that an enlargement of existing reserves, a process-oriented management approach and a minimization of human influence may be the only option for the long-term preservation of wild plants and animals.

(submitted to Conservation Biology)

Introduction

Nature conservation management in regions with intensive land-use, such as in Western Europe, is focused to a large extent on the continuation of practices from former land-use systems. These include grazing, hay-making, burning, felling and turf cutting (Bakker, 1989; Morris, 1991; Peterken, 1991). Hunting may also be part of the management strategy or is often tolerated. The aim of such a conservation approach is in essence to preserve a high biodiversity. One may add that the reference for this biodiversity stems mainly from the semi-natural ecosystems of the past two centuries. Natural ecosystems, i.e. ecosystems with a minimum of human interference, are not the ultimate goal for conservation or restoration management in this line of thinking. This does appear sensible as the natural ecosystems in regions such as Western Europe have all but disappeared. Knowledge on their structure and functioning is therefore scarce, so that the wild flora and fauna present within the cultural landscape is an easier and more practical reference for conservation aims.

Over the last decades however, it has become clear that the threat to the existence of wild species of plants and animals cannot be stopped with the approach to conservation described above. Agriculture has been modernized and intensified considerably, thereby dramatically reducing its role in maintaining natural diversity. This has lead to an enormous loss, isolation and fragmentation of suitable habitats for wild species (Wilcove *et al.*, 1986; Green, 1989; Spellerberg, 1991). The maintenance of semi-natural reserves by the above-mentioned management practices often requires substantial labour inputs. The costs of traditional conservation management are therefore increasing ever more. A new approach to nature conservation thus seems required for regions under high human utilization pressure. In this chapter such an alternative is proposed from a biological perspective, by considering the habitat requirements of large herbivores as a key to a choice.

The significance of large herbivores to nature conservation

Large herbivores are present in most continental ecosystems. They can exert a major impact on their environment. In the present day the best illustration of the biological richness of an ecosystem under heavy herbivore pressure is given by African savannas like the Serengeti (Sinclair & Norton-Griffiths, 1979). In Lake Manyara National Park, Tanzania, the regeneration of *Acacia* woodlands has shown to be highly dependent on crashes in herbivore populations induced by diseases (Prins & Van der Jeugd, 1993). The question whether the natural herbivore fauna of the temperate regions in Eurasia would significantly alter the vegetation succession is still under debate (Thalen, 1984; Vera, 1988; Van Wieren, 1991). It has been hypothesized that the extinction in the late Pleistocene of most of the so-called megaherbivore fauna has led to a greater uniformity in vegetation composition and a wave of extinctions in the associated animal communities (Owen-Smith, 1987). However, in the form of domestic livestock large herbivores have continued to influence the landscape. Tubbs (1986) has shown that in analogy to Lake Manyara, the forest regeneration in the New Forest, England, has had a strong relation to a lowered grazing pressure over the past four centuries. Areas in Western Europe with a long history of traditional grazing management have shown to be biologically very rich (Pettersson, 1965; Persson, 1984; Tubbs, 1986; Bakker, 1989; Pott & Hüppe, 1991). A major explanation for this phenomenon appears to be the differential herbivore pressure on various parts of a grazed area. This has led to the application of controlled grazing management with cattle, ponies and sheep in nature reserves in Western Europe, and in the Netherlands in particular (Thalen, 1984; Bakker, 1989; Gordon *et al.*, 1990; Van Wieren, 1991).

Populations of large herbivores require comparatively vast areas of land (Forman & Godron, 1986; Eisenberg & Harris, 1989). Using a simple model Belovsky (1987) has predicted a required land area of 10,000-100,000 ha to ensure a 95% probability for the persistence of a herbivore population over one century. The associated minimum population size lies in the order of a few thousand. Soulé (1987) has warned against the application of such figures as a general standard. Yet, for the sake of simplicity I will use the value of 10,000 ha as a minimum threshold for a potentially adequate area size for a population of large herbivores. Such a tract of land should meet the requirements for food, water and shelter. Migration between different habitats may be a necessity in regions with a seasonal climate (Forman & Godron, 1986; Coughenour, 1991). Reserves then should include a summer and a winter range (Boyce, 1991; Klein, 1991; Albon & Langvatn, 1992) or a wet- and a dry-season range (Maddock, 1979; Fryxell & Sinclair, 1988; Williamson *et al.*, 1988). A parallel to these migrations can be seen in traditional livestock 'transhumance' in pastoralist systems (Ruiz & Ruiz, 1986; Coughenour, 1991). On a finer scale, there may be movements between landscape types with different nutrient availabilities (Seagle & McNaughton, 1992; Chapter 6).

The habitat requirements of large herbivores could serve as a standard for the formulation of an adequate design of nature reserves. In summary two main reasons support this argument. Firstly, large herbivores are a significant component of the ecosystem, often increasing habitat quality for other animals and plants. Secondly, viable populations of large herbivores require extensive areas of land. Thus, a suitable area for a specific herbivore population should meet the requirements for many wild plant and animal species. Large herbivores can therefore be considered as a 'keystone' or 'umbrella' species group. Their worldwide distribution has the advantage of a more general application of the concept.

Nature reserves in the European Union

The European Union offers a good example to illustrate the effects of high human pressure on the status of natural areas and herbivore populations. The IUCN categories for nature reserves offer a good standard for this purpose, as they are based mainly on differences in the degree of human influence on a reserve area. The IUCN system for categorizing reserves is not widely applied in the European Union. This may have resulted from the rejection of human pressure as a classification criterion. However, from a biological viewpoint, its application yields a clarifying picture.

Characteristic features of nature reserves in the European Union, compared to less intensively used regions of the world, are the low percentage of 'strict nature reserves' and 'national parks'(0.34% of the land area), in contrast to the relatively high percentage of 'managed nature reserves', 'protected landscapes' and 'natural monuments' (9.36% of the land area) (Table 8.1). The degree of human influence in the nature reserves of the European Union is therefore relatively high. Many national parks would not meet the standards used in North America and Africa. Four nations out of the twelve do not count even a single national park, and seven nations do not have any national park larger than 10,000 ha. Furthermore, also in four nations, the area proportion of nature reserves exceeding 10,000 ha is less than 60%. This figure would be still lower if the reserves smaller than 1,000 ha had been taken into account.

Table 8.1 Land area percentage of protected nature reserves in the European Union as compared to other regions in the world (Total refers to total land area of nations etc.).
The category 'National parks' used here comprises the IUCN categories I (strict nature reserves) and II (national parks), the category 'protected landscapes' comprises IUCN categories III (natural monuments), IV (managed nature reserves) and V (protected landscapes).

	%National Parks	%Protected Landscapes	%Reserves on Total	%Nat. Parks on Total	%>100km^2 on Total
Belgium	0	2.35	2.35	0	94.5
Denmark	0.31	9.14	9.45	3.3	57.7
France	0.50	9.20	9.71	5.2	97.8
Germany	0.04	15.69	16.72	0.2	82.9
Greece	0.46	0.36	0.82	56.1	43.9
Ireland	0	0.38	0.38	0	36.8
Italy	0.97	5.69	6.66	14.6	83.9
Luxemburg	0	0	0	--	--
The Netherlands	0.26	9.16	9.42	2.7	56.7
Portugal	0.04	5.54	5.57	0.7	96.1
Spain	0.24	6.70	6.94	3.5	91.8
United Kingdom	0	18.95	18.95	0	95.1
European Union[1]	**0.34**	**9.36**	**9.70**	**3.5**	**89.5**
Scandinavia[1]	**5.07**	**2.91**	**8.00**	**63.6**	**91.6**
Eastern Europe[1]	**1.06**	**3.35**	**4.41**	**24.0**	**89.1**
Asia[1,2]	**2.13**	**2.11**	**4.24**	**50.3**	**98.1**
North America[2]	**2.30**	**5.01**	**7.31**	**31.5**	**98.1**
South America[2]	**2.70**	**2.45**	**5.15**	**52.5**	**98.0**
Africa[1,3]	**2.59**	**1.20**	**3.80**	**68.4**	**99.5**
Oceania[2]	**3.73**	**1.91**	**5.64**	**66.1**	**94.4**
World Total[2]	**2.42**	**1.95**	**4.37**	**55.3**	**97.7**

References: 1) IUCN (1992), 2) IUCN (1990), 3) IUCN (1987)

Table 8.2 Distribution of area and number of protected nature reserves in the Netherlands over size classes.

Only those areas with any mentioned biological interest have been selected from the more extensive list referred to below. This excludes intensive farmland, monotonous forest plantations and private properties with mainly cultural values. The total area makes up 10% of the nation, which agrees reasonably with the figure in Table 8.1.

	Size in ha						
	0-1	1-10	10-10^2	10^2-10^3	10^3-10^4	$>10^4$	Total
%Area	0.01	0.26	6.73	43.16	46.09	3.74	374,025 ha
Number	21	125	401	313	59	1	920

Reference: Vereniging tot Behoud van Natuurmonumenten (1991)

In the Netherlands 50.2% of the total area of reserves is less than 1,000 ha in size, and only one (3.7%), a wetland, is larger than 10,000 ha (Table 8.2). It should be remarked that the fragmentation of reserves actually is lower as different reserves may be adjacent to each other; this will not greatly influence the overall picture, however.

The European Union includes 19 national parks larger than 10,000 ha. These are mostly found in marginal areas with respect to land-use: mountainous areas and wetlands. The presence of large herbivores and their predators in these areas and in the twelve nations is indicated in Table 8.3. Large predators have been eradicated or are threatened in most nations. The status of large herbivores is more favourable: most of the listed species still occur in large parts of their original range. The red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) have increased their distribution range over the last century, sometimes with the help of re-introductions (Rijksinstituut voor Natuurbeheer, 1983; Niethammer & Krapp, 1986). On the other hand the aurochs (*Bos primigenius*) and the tarpan (*Equus ferus ferus*) have become extinct, whereas European bison (*Bison bonasus*) and moose (*Alces alces*) have been eradicated in the territory of the European Union (Niethammer & Krapp, 1986). Mouflon (*Ovis ammon musimon*) and fallow deer (*Dama dama*) have been excluded from the present overview: the former must probably be considered as an early domesticated sheep reverted to a wild state and the distribution range of the latter is unclear due to human interference (Niethammer & Krapp, 1986).

It can be concluded that the original Holocene large mammal fauna of Western Europe is nowhere present in its total variety. At the scale of separate national parks it is apparent that the large mammal fauna is still far less complete. Yet most of the species still occur in the wild. As large grazers, domestic cattle (*Bos taurus*) and horses (*Equus ferus* forma *caballus*) may be considered as descendants and ecological substitutes of the aurochs an tarpan.

The loss of species through habitat destruction and hunting can also be illustrated for

Table 8.3 The presence of large mammal fauna in the European Union and in its National Parks larger than 10,000 ha (- eradicated, + present, R re-introduced, X outside the animal's distribution range, (+) occasional or remnant population, ? uncertain).

	Size (ha)	Habitat	Brown bear *Ursus arctos*	Wolf *Canis lupus*	Lynx *Lynx lynx* *+ L. pardina*	Red deer *Cervus elaphus*	Roe deer *Capreolus capreolus*	Wild boar *Sus scrofa*	Chamois *Rupicapra rupicapra*	Ibex *Capra ibex* *+ C. pyrenaica*
Belgium			-	-	-	+	+	+	X	X
Denmark			-	-	-	+	+	-	X	X
France			(+)	-	+/R	+	+	+	+	R
Camargue	13,120	Wetland	-	-	-	-	-	+	X	X
Ecrins	91,800	Alpine	-	-	-	-	+	+	+	R
Mercantour	68,500	Alpine	-	-	-	-	-	+	+	R
Pyrénées Occ.	45,700	Alpine	(+)	-	(+)	+	+	+	+	-
Vanoise	52,800	Alpine	-	-	-	-	+	+	+	R
Germany			-	(+)	(+)	+	+	+	+	R
Bayerischer Wald	13,100	Montane	-	(+)	(+)	+	+	+	X	X
Greece			+	+	+	+	+	+	+	-
Prespes	19,470	Mont/Wetl.	+	+	+	-	+	+	-	-
Vikos-Aoos	12,600	Montane	+	+	+	-	+	+	+	-
Ireland			-	-	-	+	X	-	X	X

Table 8.3 (continued)

	Size (ha)	Habitat	Brown bear *Ursus arctos*	Wolf *Canis lupus*	Lynx *Lynx lynx* + *L. pardina*	Red deer *Cervus elaphus*	Roe deer *Capreolus capreolus*	Wild boar *Sus scrofa*	Chamois *Rupicapra rupicapra*	Ibex *Capra ibex* + *C. pyrenaica*
Italy			+	+	?	+	+	+	+	+
Abruzzo	43,950	Montane	+	+	-	R	R	+	+	X
Arcipelago Toscano	67,500	Islands	X	X	X	X	X	X	X	X
Calabria	15,890	Montane	-	+	-	-	+	+	X	X
Dolomiti Bellunesi	31,000	Alpine	?	-	-	+	+	-	+	R
Gran Paradiso	70,000	Alpine	-	-	?	-	-	-	+	+
Sibillini	65,200	Montane	-	+	-	-	-	-	-	-
Luxemburg			-	-	-	+	+	+	X	X
The Netherlands			-	-	-	+	+	R	X	X
Portugal			-	+	+	+	+	+	-	-
Spain			+	+	+	+	+	+	+	+
Aigües Tortes	10,230	Alpine	-	-	-	+	-	+	+	+
Coto Donana	50,720	Wetland	-	-	+	+	-	+	X	X
Covadonga	16,920	Alpine	+	+	-	+	+	+	+	R
Ordesa	15,600	Alpine	-	-	-	+	+	+	+	+
Teide	13,570	Island	X	X	X	X	X	X	X	X
United Kingdom			-	-	-	+	+	-	X	X

References: Smit & Van Wijngaarden (1981); Niethammer & Krapp (1986); Bibelriether & Schreiber (1989) birds. The bird species listed in Table 8.4 have all disappeared within historic times from large parts of the European Union, leading to a typical discontinuous distribution in the area of Germany, The Netherlands, Belgium, England and most of France. The distribution range of the brown bear (*Ursus arctos*), wolf (*Canis lupus*), lynx (*Lynx lynx* and *L. pardina*) and red deer shows similar discontinuities to the listed bird species. The listed birds are characteristic for wetlands, remote areas and old-growth forests. The Pied flycatcher (*Ficedula hypoleuca*) and the Treecreeper (*Certhia familiaris*) could perhaps be added to the group of old-growth forest species, but their former distribution range is unknown. Twelve species with a more southern or more continental distribution have been excluded from the list. Some of these, such as the Griffon vulture (*Gyps fulvus*) and the Great bustard (*Otis tarda*) could perhaps be included because they are known to have had a more northern distribution in past centuries. A number of bird species, *e.g.* meadow birds such as the Godwit (*Limosa limosa*), has undoubtedly benefited from human land-use. Yet, these birds originate from natural habitats. They would therefore perhaps decline in numbers in natural areas but disappear only locally, in contrast to the species listed in Table 8.4, which have all but vanished from man-made habitats.

Table 8.4 Examples of European bird species with a discontinuous distribution range due to human activities. Species with a more southern or more continental distribution have been excluded from the list as their occurrence in natural ecosystems is unclear.

Wetlands	
Spoonbill	*Platalea leucorodia*
White stork	*Ciconia ciconia*
Greylag goose	*Anser anser*
Osprey	*Pandion haliaetus*
Montagu's harrier	*Circus pygargus*
Crane	*Grus grus*
Common sandpiper	*Tringa hypoleucos*
Remote areas, including forests	
Black stork	*Ciconia nigra*
Red kite	*Milvus milvus*
Short-toed eagle	*Circaetus gallicus*
Goshawk	*Accipiter nisus*
Golden eagle	*Aquila chrysaetos*
Peregrine	*Falco peregrinus*
Capercaille	*Tetrao urogallus*
Eagle owl	*Bubo bubo*
Nightjar	*Caprimulgus europaeus*
Raven	*Corvus corax*

References: Cramp (1977, 1980, 1983, 1985, 1988, 1992), Cramp & Perrins (1993)

Management of large herbivores in the Netherlands

Within the European Union The Netherlands are the most densely populated nation (400 inhabitants/km^2) with the most intensive land-use. As has been shown in Tables 8.1 and 8.2 the fragmentation of nature reserves in this country is extreme. This clearly has affected the management of large mammals. Large predators have been eradicated, but some species of large herbivores are present. Roe deer occur in most of the country. Large numbers of red deer and wild boar (*Sus scrofa*) are only present in the forested area of the Veluwe. The populations of large herbivores are largely regulated through hunting. Furthermore, supplementary feeding is widespread, as the land owners want to keep the animals in good condition and at high population densities in areas usually much smaller than 10,000 ha (Rijksinstituut voor Natuurbeheer, 1983; Anonymous, 1988); moreover, the food quality on the sandy area of the Veluwe is marginal (Bokdam & Wallis de Vries, 1992).

Table 8.5 Percentage of the number of grazed nature reserves in different size classes for two management organizations in the Netherlands: the Vereniging tot Behoud van Natuurmonumenten ('Natuurmonumenten') and Staatsbosbeheer (the Forest Service).

	Size in ha						
Management Organization	0-1	1-10	10-10^2	10^2-10^3	10^3-10^4	$>10^4$	Total number
'Natuurmonumenten'	0	19.4	57.0	20.8	2.8	0	75
Forest Service	0.8	28.6	59.4	11.2	0	0	126

References: H. Piek (pers. comm.), Vereniging tot Behoud van Natuurmonumenten (1991), Batterink (1984)

Management is still more intensive when free-ranging domestic herbivores are concerned, even when they are not commercially productive. The reserves where grazing by livestock occurs are usually small-sized: *ca.* 75% of the total number of grazed reserves covers less than 100 ha (Table 8.5), compared to 60% for all reserves (Table 8.2). Moreover they mostly consist of uniform habitats. About 75% of the reserves is situated either on areas with low soil fertility (poor sandy soils) or on areas with high soil fertility (clay and eutrophic peat soils) (Table 8.6). Both types often are incomplete habitats, leading to a hazardous animal performance. Mineral deficiencies occur on poor sandy soils (Bokdam & Wallis de Vries, 1992; Wallis de Vries, 1992; Chapters 3 and 4). Flooding, high ground-water levels and poor food digestibility in cold winters can render areas on clay and eutrophic peat soils temporarily unsuitable for herbivores (Bokdam & Wallis de Vries, 1992; J.Th. Vulink, pers. comm.). A combination of a fertile riverine area and a cover sand area of low soil fertility has proved successful for cattle. The best performance, however, was recorded in a riverine area with enough higher ground as a refuge against flooding (Wallis de Vries, 1992; Chapter 3). The consequence of the

Table 8.6 Percentage of the number of grazed nature reserves in different habitat types for two management organizations in the Netherlands.
Low fertility areas include fluvio-glacial sandy sediments, inland dunes and oligotrophic peat; intermediate fertility areas include coastal dunes, fluvio-glacial sandy-loamy and loess sediments, and natural levees in river valleys; high fertility areas include fluviatile and marine sediments and eutrophic peat (Bokdam & Wallis de Vries, 1992).

Management Organization	Soil fertility Low	Intermediate	High	Low+High
'Natuurmonumenten'	46.7	13.3	28.0	12.0
Forest Service	21.4	14.3	51.6	12.7

References: H. Piek (pers. comm.), Vereniging tot Behoud van Natuurmonumenten (1991), Batterink (1984)

incomplete nature of the habitats in most reserves and of their small size is that domestic herbivores can often be used only in a seasonal grazing system or with supplementary feeding during winter. This type of grazing management is promoted by the widely held, though ecologically incorrect, opinion of managers that loss of condition over winter is harmful to the animals.

It can be concluded that both free-ranging domestic and wild herbivores in the Netherlands are not subject to the natural limitations of the habitats in which they live. Instead they are mostly kept artificially in good condition and at a fixed animal density. Human impact on nature reserves in the Netherlands therefore remains high.

Discussion: new designs for nature reserves

The human impact on nature reserves described for the Netherlands can also be found in the large national parks of the European Union. The parks often constitute incomplete habitats for large herbivores, being situated in alpine areas or wetlands. In high mountains there often is a conflict between the interests of nature conservation and traditional farming. The farmers have their settlements, arable lands and hay-meadows in the valleys and use the alpine pasture for livestock grazing. Park boundaries typically exclude the valley areas. Thus, the seasonal altitudinal migration of large herbivores is seriously hampered. Moreover, livestock densities are often so high as to be detrimental to forest regeneration and wild herbivore populations (Stern, 1983; Bibelriether & Schreiber, 1989). The European national parks clearly are not the natural sanctuaries they are sometimes claimed to be, especially when compared to North American and African national parks.

It may be argued that human impact cannot or should not be excluded from parks in densely populated regions. Indeed, management practices derived from traditional land-use have proved successful for the preservation of a variety of wild plant and animal species (Bakker, 1989; Fry, 1991). Yet, for other species this has lead to extinction, as illustrated above. The increasing habitat loss and fragmentation moreover threatens many of the remaining species (Wilcove *et al.*, 1986; Green, 1989; Spellerberg, 1991). Recently, Dudley (1992) has pointed to the neglect of the severely threatened biological richness of primeval temperate forests. In Western Europe this neglect may very well originate from the tendency of conservation bodies to focus on man-made habitats. Human interference in conservation therefore does certainly not appear to guarantee the preservation of wild plants and animals. It seems that a more promising approach for that purpose would be to rely on ecosystems regulated by natural processes. This approach has also been advocated by Van de Veen (1985), Baerselman & Vera (1989) and Van Wieren (1991) and termed 'nature development'. Pickett *et al.* (1993) have described this concept of conservation biology as a result of the new system-oriented paradigm in ecology. Critics (*e.g.* Morris, 1991; Götmark, 1992) have responded that exclusion of human interference would lead to climax communities with a loss of species from earlier succession stages. However, this need not be true in an ecosystem where natural disturbance is allowed to interfere with succession.

The biodiversity in natural ecosystems often appears to depend on a certain amount of disturbance (*sensu* White & Pickett, 1985) such as fire, flooding, storms and herbivory (Hobbs & Huenneke, 1992). Choosing optimal sites and sizes of naturally regulated ecosystems for conservation will then depend on the presence of these disturbance agents. The abiotic disturbance will be characteristic for the specific ecosystem. Walker (1989) and Baker (1992) have argued that choosing the scale of the reserve is crucial in determining the amount of disturbance. However, as these authors also show, there is as yet little information on the scale of abiotic disturbance to provide a basis for management decisions. In the case of forest plantations Koop (1986) has outlined a management approach to restore the small-scale shifting succession mosaic.

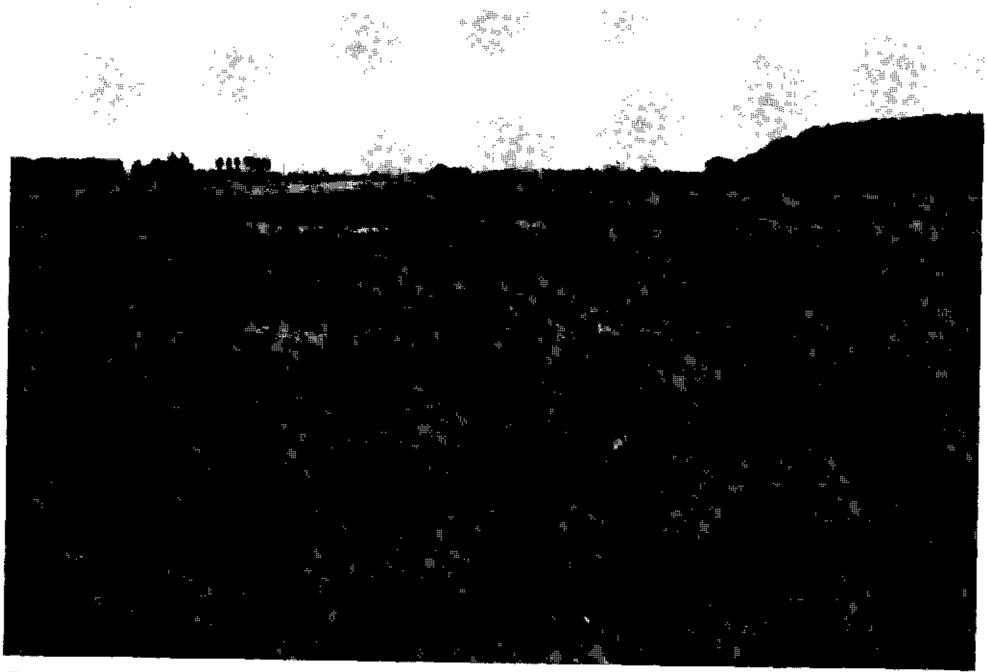
Herbivory is a type of biotic disturbance which may have profound effects on the structure and composition of an ecosystem (Norton-Griffiths, 1979; Hobbs & Huenneke, 1992; Prins & Van der Jeugd, 1993). Choosing the proper reserve scale thus also applies to the opportunities for the establishment of viable populations of large herbivores. The present analysis points to scale aspects in habitat quality. Adequate reserves for large herbivores should be of the size order of 10,000 ha or more and contain a suitable yearround habitat. In Western Europe this implies the inclusion of valleys in mountainous areas and in lowland areas the combination of riverine valleys and other riparian habitats with adjoining higher ground. The establishment of large nature reserves does not necessarily lead to the underestimation of the value of small managed reserves. As argued by Wilcove *et al.* (1986) and Spellerberg (1991) these could have an important function as connecting chains (and initially also as species reservoirs) in a network of large reserves. However, the evidence for the functioning of corridors between small reserves is still scarce and mainly concerns birds. Simulation studies by Gilpin (1991) have revealed that the probability for extinction increases drastically in a metapopulation created by habitat fragmentation. Large reserves are therefore a safer basis for conservation management.

It has been argued that large herbivores may be seen as a key to the design of large nature reserves. The basis for this argument is that they can play a significant role in shaping the landscape and that a viable population of large herbivores requires a varied and extensive area, suitable for most other species. This may not be true with respect to the larger carnivores, which usually have home ranges far larger than those of herbivores: a size order of 100,000 ha and more (Belovsky, 1987). The requirements of large carnivores may thus be the final bottleneck for the establishment of a complete ecosystem (McNaughton, 1989). This is certainly a valid argument. However, as carnivores are dependent on herbivore populations and as they do not have a similar direct impact on vegetation succession, it appears that the role of herbivores is of more primary importance for conservation measures. This is certainly the case where such large areas need to be newly established.

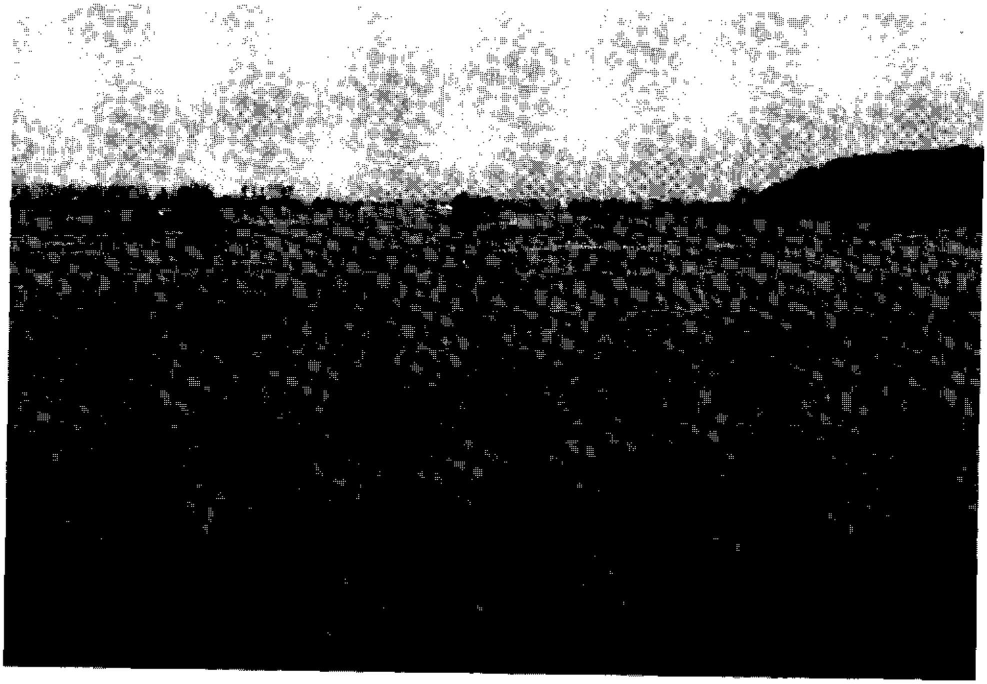
The nature reserve of the Oostvaardersplassen in the Netherlands provides a good example of an attempt at 'nature development' in a new area: a polder in a former sea arm. Although the area only covers 6,000 ha, the spontaneous colonization by a variety of birds has made the area renowned in little more than two decades (Vera, 1988). Herbivores play an important role in shaping the vegetation communities: greylag geese (*Anser anser*) prevent the reed (*Phragmites australis*) vegetation from encroaching, Heck cattle and konik horses, introduced ten years ago, maintain areas of open grassland in the drier parts. Roe deer have moved in the area by themselves and red deer have been released recently. Apart from the regulation of the water level, the initial seeding of grassland, and the introduction of the large herbivores, little human activity has affected the community succession in the area. The large herbivore populations are still growing, but it would prove a unique experiment in Europe not to interfere with population development once saturation densities have been reached.

Conclusion: what are the perspectives?

Is this view of nature conservation in Europe realistic for such a densely populated region? Present developments in agriculture suggest they can be (Green, 1989; Anonymous, 1992). In the European Union the growing surplus of agricultural production is presently forcing a reduction of the production capacity. One of the consequences of this development will be a significant change in land-use practice. This may prove positive or negative to the preservation of wild plants and animals, depending on the chosen policy. The economically soundest option appears to be the intensification of production on a smaller land area and the cessation of agricultural production on marginal lands. Various scenarios have been evaluated following this principle (Anonymous, 1992). It is concluded that all scenarios would lead to a reduction in the area needed for agriculture between 40% and 79%. This would result in a substantial increase of the available land for other uses, such as nature reserves. Baerselman & Vera (1989) have suggested how the concept of 'nature development' could be turned into policy. The present discourse emphasizes that the establishment of a network of large nature reserves with a minimization of human interference appears a prerequisite for the long-term preservation of wild species.



Plates 20 and 21. River floods can inundate virtually the entire area of a valley and thus mark especially the embanked river forelands as an incomplete habitat (Photos in the riverine study area).



CHAPTER 9

Synthesis: Defining a Foraging Strategy for Cattle in a Landscape Mosaic

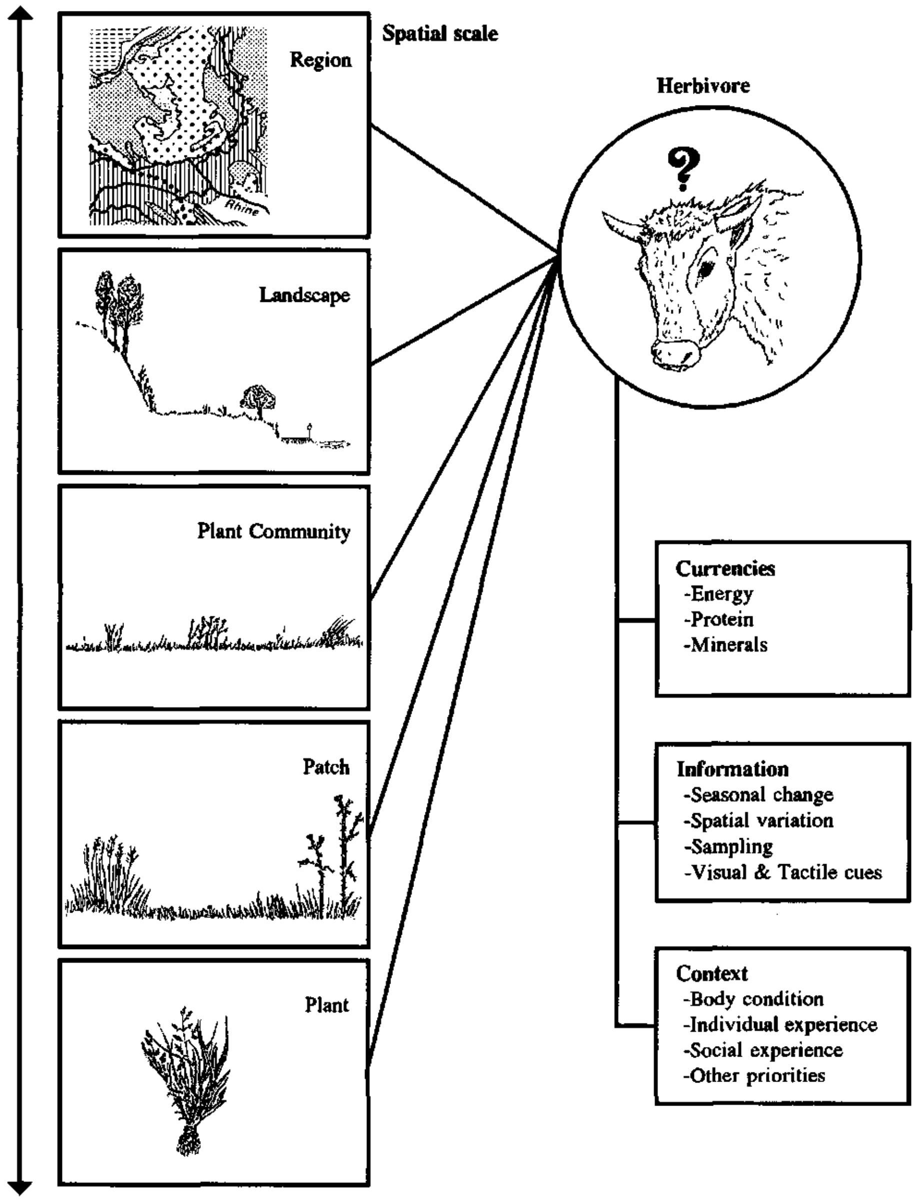
Introduction

In the previous chapters I have presented the trials faced by a large herbivore, *Bos taurus*, to maintain its body condition in different habitats. The importance of habitat quality for an adequate intake of minerals was addressed in Chapters 3 and 4. In habitats of low soil fertility, cattle are liable to suffer from deficiencies in sodium and phosphorus. These deficiencies decrease individual performance and may ultimately cause death and impaired reproduction. The animals may show adaptive responses to suboptimal nutrition by adjusting their metabolism (Chapter 7) or by changing their foraging behaviour (Chapters 5 and 6). The relation between habitat quality with regard to food resources and foraging behaviour has been investigated on different levels of spatial scale. At small scale levels the variation in food resources are mainly determined by local differences in soil formation, mesorelief, vegetation structure and plant species within a discrete part of the landscape. At a higher scale level food resources vary with other variables specific to a larger spatial hierarchy such as geological substrate, hydrology, altitude, and climatological conditions. The different nature of environmental variables in relation to spatial scale can be expected to have a fundamental impact on herbivore foraging decisions. Senft *et al.* (1987) first treated this issue from a theoretical viewpoint. In this synthesis, I venture to substantiate some of their considerations on foraging mechanisms and spatial heterogeneity with the insights emerging from the present study. The scheme presented in Figure 9.1 will be used as an organizing device to portray the foraging herbivore as an animal with certain physical characteristics, a social background and a number of behavioural priorities which has to meet specific nutritional requirements within this context. By weighing nutritional gains and time costs and using various sources of information the herbivore can reach an optimal decision for the allocation of foraging time to the different food resources in its environment.

The herbivore environment

The environment of free-ranging cattle, and other herd-living ungulates, can be viewed as a mosaic of spatial units at different scale levels on account of differences in geological substrate, geomorphological structure and landscape forming processes (Fig. 9.1) (Senft *et al.*, 1987; Stuth, 1991). The highest scale level, the region, comprises an assemblage of landscape units which may be used over the entire life of an animal or which are used by a herd over a longer period. As considerable distances may separate various parts of the region, the frequency with which a specific landscape unit is visited is rather low. Migration, whether seasonal or nomadic, is therefore the typical movement pattern

Figure 9.1 Scheme of spatial relations, currencies, information and context influencing foraging decisions of a large herbivore.



observed at this scale (Kelsall, 1968; Baker, 1978; Maddock, 1979; McNaughton, 1985; Albon & Langvatn, 1992). The driving force behind these migrations is usually a temporary change in forage availability, which forces the animals to exploit other parts of their range.

In the present study, the scale level was lower and allowed the cattle to move daily to all parts of their range. Two landscape units (the second scale level) were available to the animals from the Karshoek study area: heathland and riverine plain (Chapter 1). These landscapes were characterized by a different geological substrate of contrasting soil fertility. Within the landscape units a number of patchy plant communities (third scale level) could be distinguished. These communities differed with respect to abiotic features such as topography and soil type and with respect to biotic features such as botanical composition and vegetation structure. At the still lower fourth scale level, differences in growth stage, botanical composition and grazing impact led to the development of a dynamic pattern of patches of short, tall and stemmy grass. Within the riverine grassland communities this patch structure was especially clear (Chapter 5). Moreover, grass patches were complemented by clones of tall herbs such as *Cirsium arvense*. On heathland *Deschampsia flexuosa* and *Calluna vulgaris* formed a comparable mosaic of species.

From the fourth scale level of patches within plant communities upwards, foraging decisions centre upon the question whether to stay or to leave. Relevant parameters for these decisions are the distance and costs of travel, and the relative gain in food intake by staying or leaving. The actual process of food consumption takes place within the patch, at the fifth and lowest spatial scale of the food plant. It involves the selection of plant parts and species with an adequate nutritive value and intake rate.

The herbivore

The differentiation of large herbivores with respect to their diet and foraging behaviour is closely related to their ability to digest cell wall material (Van Soest, 1982; Hofmann, 1989; Duncan, 1992; Illius & Gordon, 1992). In Chapter 1 cattle have been characterized as large ruminants specialized in diets of high cell wall content, especially grasses.

Some additional comments can be made with regard to the influence of allometric relations in setting the limits to ruminant foraging opportunities. Illius & Gordon (1992) have shown that similar limitations appear to apply to the non-ruminant hindgut fermenters (*e.g.* equids, elephants and rhinos). Large ruminants have a relatively longer retention time of food in the digestive tract (scaling with body weight W as $W^{0.27}$) than smaller ruminants (Illius & Gordon, 1989). This increases digestive capacity in large ruminants because digestion rate shows little variation with body weight and the weight scaling exponent of intake compares favourably with the exponent for energy requirements at maintenance (Demment & Van Soest, 1985; Illius & Gordon, 1991). Large ruminants are therefore capable to forage less selectively on less digestible material with higher cell wall contents. On the other hand large herbivores have larger mouth parts and will thus be less able to select from a fine-grained vegetation (Illius & Gordon, 1990). Moreover, there is a size difference in grazing ruminants with respect to their ability to meet their maintenance requirements on short swards. Bite weight is a function of the breadth of the incisor arcade, which scales with a lower exponent for body weight ($W^{0.36}$) than the maintenance requirements for energy ($W^{0.73}$) (Illius & Gordon, 1987). On short swards biting area becomes restricted and becomes directly proportional to incisor arcade breadth (Illius & Gordon, 1987; Illius, 1989). This suggests that large grazing ruminants such as cattle should rather select between than within patches, and leave the shortest patches ungrazed.

Currencies and information

Herbivores need to satisfy nutritional requirements for energy, protein and minerals. These are the nutritional currencies which determine the foraging decisions. Maximization of these currencies is the most likely strategy for a wide range of herbivores (Belovsky, 1986). The content of energy and the major nutrients such as protein and phosphorus tend to co-vary in their availability and appear to be concentrated in young leaves (Owen-Smith & Novellie, 1982). However, maximization can become a difficult task when different key nutrients are not equally distributed between resources. This occurs when habitats vary in soil fertility (Chapters 1 and 6) or with an imbalance in nutrient contents, such as a protein excess in young growth (Prins & Beekman, 1989). Maximization is then subject to the constraint of achieving a balanced diet.

Maximization requires accurate information on potential food patches (Chapters 5 and 6). The animal cannot be assumed to have a perfect knowledge of its environment. Indeed, the animal's ability to collect adequate information is likely to present a major constraint on foraging decisions (Illius & Gordon, 1990). Sources of information on forage availability are the immediate surroundings and the animal's memory and experience. Seasonal changes in photoperiod, weather and forage may trigger migrations over longer distances. Information on the forage directly available is provided by visual and tactile cues (Arnold, 1981; Bazely, 1988). However, it appears that the animal needs to sample frequently to assess the forage characteristics more accurately (Illius & Gordon, 1990; Illius *et al.*, 1992). Learning by association may well be the most important method to develop a successful foraging strategy (Provenza & Balph, 1990; Provenza, 1991). The curiosity of cattle for new plants and strange objects is well known and may provide a clue to process of accumulating knowledge. The observation of osteophagia in the face of phosphorus deficiency could be an example of such a learning experience (Chapter 4), although its worldwide occurrence also hints at a genetic component. Experience is certainly of potential importance to select between foraging locations: Bailey *et al.* (1989) have shown that cattle are able to associate locations and food rewards. When released in their respective areas at the onset of this study, the steers from all treatments thoroughly explored the entire terrain available to them.

Context

The context of the foraging herbivore consists of the factors that indirectly affect its foraging decisions (Fig. 9.1). The body condition of the animal is a primary guide to its nutritional requirements. The suggestion by Prins & Beekman (1989) of a selection for a balanced diet by African buffalo (*Syncerus caffer*) to avoid nutritional disorders from an excess in protein and the above-mentioned example of pica behaviour (Chapter 4) are examples in which condition affects foraging behaviour. Another, more incidental observation concerns an individual in the Karshoek area that, in the spring of the second year, repeatedly moved away from the herd to forage on aquatic *Juncus bulbosus* (Na-content 0.80% of dry matter, *i.e.* sixteen times the dietary average; Chapter 4). It may be speculated that this individual discovered a new source of sodium in an habitat where sodium was scarce (Chapter 6). If this view is correct such a discovery could be marked as a step in an individual learning process on the distribution of resources.

The experience of individuals can thus offer solutions to the foraging requirements set by the animal's body condition. As an analogy to the 'memes' proposed by Dawkins (1976), individual experiences may be transferred between individuals living in a social system. The passing of information on foraging behaviour between mother and young can be an important stage in the acquisition of experience (Provenza & Balph, 1990). At a higher organization level, Prins (1987) has speculated that a herd of herbivores can be considered as a super individual through the accumulation over successive generations of information on its home range. This should prove a great advantage of social life in both complex and marginal habitats. An additional advantage of herd life with respect to foraging is that aggregation will enhance forage quality by inducing plant regrowth (McNaughton, 1984; Fryxell, 1991). These advantages are offset to some degree by the increased interference and competition between herd members. However, it appears that the negative effect of living in groups is inversely related to social status (Prins, 1987), so that high-ranking animals are least affected.

In the present study I used castrates separated from their mothers at an early age and living in small groups (five or ten individuals). Their acquisition of experience in foraging was limited to 25 months. As a consequence, the passing of information between generations by learning was absent. The steers usually grazed at an estimated interindividual distance of between five and twenty meters on average. Direct competition and interference between them was therefore low. Nevertheless, single individuals would rarely be more than 100 m distant from other group members. Moreover, the synchronization of activities between individuals was strong. In the Karshoek area this implied that shifting from the riverine landscape to the cover sand landscape (or vice-versa) was performed as a group. The animals had to cross a bridge to reach the other part of the area. The decision to head for the bridge would often be taken at some distance away (500 m). Prior to the crossing, however, the group would spend idling and ruminating for generally more than 30 minutes, standing on the bridge - seemingly ruminating about their choice: the bridge would rarely be crossed more than twice a day, so that it was an important decision indeed. It was often unclear whether a particular animal initiated the movement, although it would always require the 'consent' of the dominant steer and a low-ranking former dominant (that lost a horn in combat and subsequently tumbled in the group hierarchy). These observations of group relations suggest that herd life may even shape the foraging pattern of social herbivores living in small groups.

Other behavioural priorities include drinking, ruminating, resting, seeking shelter, avoiding predators and a variety of social interactions. These may interfere with the timing and location of foraging activities. In this study the selection of foraging locations was probably not much affected by other priorities, as the scale of the areas was small (Chapter 1).

Foraging decision rules

The challenge to the student of foraging behaviour is to unravel the animal's perception of its environment, the foraging objectives, and the mechanisms by which these objectives are attained. It is of great importance to identify the constraints relative to the animal's 'design', such as its ability to acquire information and to learn. These determine the potential of the animal to decide between alternatives. Seen in this light, the purpose of placing hypotheses on foraging strategies in the context of optimal foraging theory is not to test whether the animal behaves optimally (see Ollasson, 1987). This is so by definition, if one considers the animal as an evolutionary product with inherent limitations. Optimal foraging theory rather provides a basis one can use to test ideas on foraging animals with the ultimate goal of gaining understanding of the animal's behaviour (Stephens & Krebs, 1986). The testing of hypotheses has been given attention in Chapters 5 and 6. In the following section an integration of results and miscellaneous observations is attempted to broaden the functional picture of *Bos taurus* as a forager.

Patch selection

The patch was the lowest scale level investigated during the present study (Chapter 5). Modelling studies show that the variation within patches can be important to determine the overall profitability of a certain patch type (Illius, 1986; Ungar & Noy-Meir, 1988). It may be doubted, however, whether the grazing animal actually can exploit this variation to its full extent. The herbivore appears to need sampling before it can assess the value of a patch (Illius & Gordon, 1990; Illius *et al.*, 1992). It may therefore prove impossible to the animal to distinguish variation within patches. However, as argued in Chapter 5, selectivity may arise with an increase of within-patch variability (senescence or species composition).

At the level of the patch, the cattle in this study showed a significant but not very pronounced selectivity. Patches containing flowering stems were rejected in favour of short and, to some extent, tall leafy patches. The daily nutrient intake of large grazing ruminants is usually not likely to be limited by available time but rather by maximum voluntary intake (Beekman & Prins, 1989; Vulink & Drost, 1991; this study). Cattle can therefore afford to spend much effort on the shorter patches where the energy intake rate is low but quality is high. The advantage of such an apparent waste of time may be that the frequency of decision making is thereby considerably reduced. Grazing cattle usually take between 15,000 and 40,000 bites a day (Stobbs, 1973; Chacon & Stobbs, 1976; this study). Making a deliberate decision for each bite would require a tremendous amount of information processing and presumably present a significant time cost and loss of opportunity to forage on better and easily recognizable patches (see also Belovsky, 1981b). As discussed above, it appears that grazing herbivores cannot assess the nutritive potential of a bite without sampling. The animal may, however, use a rule of thumb to estimate digestibility by sensing fibrousness parameters (proportion of green leaf, woody material, ease of harvesting) (Prins, in prep.). It is thus more likely that the animal decides for bouts of bites in a particular patch. A selection for short patches then approximates a maximization strategy if grazing is continued up to maximum voluntary intake. The two major drawbacks of such a relatively simple foraging strategy are that it is not efficient with respect to time and that nutrient maximization may not be obtained if the short patches were not the best or if the intake rate was too low. The fact that the observed selectivity for short patches was not so pronounced could indicate a flexible patch choice to compensate on tall patches if short patches failed to satisfy the objective of maximization.

Allometric relations predict that large herbivores are at a disadvantage on short swards compared to smaller-sized animals. This disadvantage does not necessarily become apparent in the absence of interspecific competition or with an overall abundant food supply. Selection on short patches may then be favourable. However, a different situation arises when short patches predominate. In the present study this occurred in early spring on riverine grassland, when the available forage consisted mainly of very short material with a high protein content and digestibility. Bite size was very low and average daily grazing time rose to 630 minutes but voluntary intake was below its maximum (Chapter 5). Cattle thus indeed become time-limited in the face of a combination of low forage quantity with high quality. This combination may even lead to nutritional disorders. Symptoms of tympanites (bloat) and acidosis (Essig *et al.*, 1988) were recorded during the specified period in at least two individuals on riverine grassland. Acidosis has been observed in wild ruminants with a sudden increase in diet quality (Kreulen, 1985). The disorders presumably arose from the low content of fibre, and high concentrations of protein and soluble carbohydrates of the short material. The animals appeared to counter this ailment by geophagia (soil consumption) (see Kreulen, 1985), but there was no indication of a change in patch selection toward the consumption of standing dead material. In the Karshoek, Hereford steers selected slightly less on the short patches than MRY steers (Chapter 7). As Herefords probably have lower nutritional requirements than MRY, this may have been a reaction to avoid an excessive protein content in the diet.

Another exceptional situation concerns the winter period. The quality of available food is then often insufficient to satisfy maintenance requirements, resulting in a loss of weight and body condition (Chapters 3 and 4). The steers appeared to respond to these circumstances by a shift in foraging strategy: they included bulk forage of low digestibility in the diet (Bite size 1.7-4.2 mg dry matter/kg live weight, Digestible organic matter 25.8-48.0% of dry matter) which would be avoided at other times of the year. On heathland the consumption of *Calluna vulgaris* rose to a maximum in January and in the Karshoek area *Deschampsia cespitosa* tussocks, *Calluna vulgaris*, *Erica tetralix*, *Juncus effusus*, *Pinus sylvestris* and some deciduous browse were selected (Fig. 9.2). This change in selection was even more pronounced during periods with snow. In the riverine study area the animals then started to eat substantial amounts of stemmy grass (61.0% of bites, compared to 5.2% previously) and in the Karshoek 100% of bites were taken from low-digestibility bulk forage. This behaviour is related to conditions in which weight loss is inevitable, regardless of the foraging strategy. A similar change in forage selection has been observed in a number of studies (Bokdam *et al.*, 1986; Van Wieren, 1988 and 1992; Pfister & Adams, 1993). It is likely that with the increase of foraging costs by cold and decreasing forage availability, an energy saving strategy is beneficial to large herbivores (Soper, 1941; Malechek & Smith, 1976; Murray, 1991; Cuyler & Oritsland, 1993; Schmidt, 1993). Bulk forage can then be selected to minimize foraging time. Energy losses were also reduced by adopting a perpendicular position to the sun to absorb its heat. The animals further rely on their fat reserves for the supply of energy to bridge over the unfavourable period.

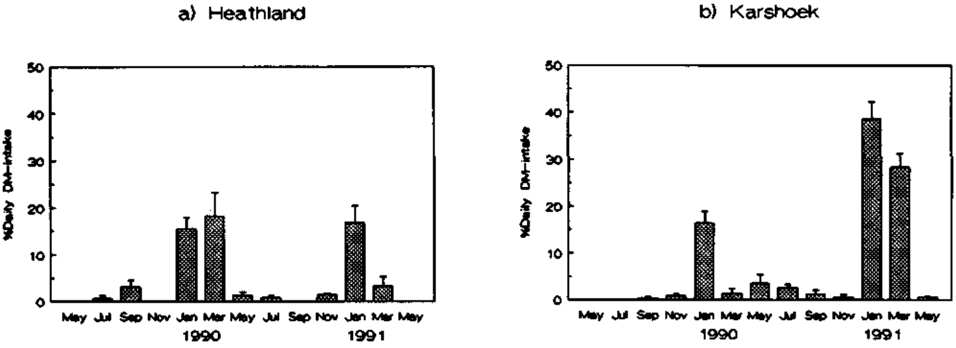


Figure 9.2 Percentage (± standard error) of bulk forage of low digestibility in the diet of steers at different times of the year for a) heathland (*Calluna vulgaris*, *Erica tetralix*) and b) the Karshoek area (*Deschampsia cespitosa* tussocks, *Calluna vulgaris*, *Erica tetralix*, *Juncus effusus*, *Pinus sylvestris*).

Selection between plant communities

The selection between plant communities was not always evident. Within the riverine landscape of the Karshoek selectivity could not be demonstrated, whereas the steers demonstrated a clear preference for the *Deschampsia flexuosa* communities in the cover sand landscape (Chapter 6). The steers on heathland also selected the communities containing a larger proportion of *Deschampsia flexuosa* (and a smaller proportion of *Calluna vulgaris*) (Chapter 5). Moreover, the animals on heathland were seen to select for extremely short patches with a significantly different botanical composition characterized by *Agrostis capillaris*, occurring around rabbit burrows and in a strip along the western fence. Bite size in these patches was extremely low (less than half the bite size on short *Deschampsia flexuosa*), but the concentrations of nitrogen (2.75%), phosphorus (0.23%) and calcium (0.25%) were substantially higher than in the average diet (Chapter 4); sodium concentration and digestibility were not much higher than the average. The limited availability of the *Agrostis* patches (*ca.* 0.7% of vegetation cover) resulted in an insignificant contribution to the overall diet (4.5% of bites on average, 1.5% of average intake).

The habitat occupancy shown in the riverine landscape was suboptimal from the viewpoint of nutrient maximization. It may be that the steers perceived this landscape as a single patchy community without clear nutritional differences. Indeed, the differences between communities were small when compared to the cover sand and heathland landscapes. In the latter case community choice was in agreement with predictions assuming nutrient maximization.

Selection between landscape units
In the Karshoek area two landscape units were distinguished: the riverine landscape and the cover sand landscape. These differed with respect to geomorphology, availability of minerals and botanical composition (Chapter 1). Both landscapes were used but there was a definite preference for the riverine part. This preference was lower in autumn and winter than during the rest of the year (Chapters 3 and 6). The partitioning of grazing time between both landscape units was best explained by a strategy of maximization for both energy and sodium. The availability of sodium was greater in the riverine landscape, that of energy was greater in the cover sand landscape. The forage intake rate of riverine forage declined to very low values over winter, rendering the cover sand landscape relatively more profitable.

In the other habitat treatments with restricted availability of habitats, the steers on heathland suffered most. This was attributed to an impaired digestion resulting from a lack of sodium and phosphorus (Chapters 3 and 4). In contrast to forage for bovines in tropical environments, which is often low in protein (Sinclair, 1977; Prins & Beekman, 1989), the availability of protein in the present experiment was always sufficient. Although no deficiencies occurred in the riverine study area, some negative effects from habitat restriction emerged as well. Low forage intakes were recorded during winter and early spring, the excessive nutritive value of the spring forage caused digestive disorders in a number of animals, and floods present another risk in riverine landscapes. Yet, in this study these limitations were not severe enough to cause a substantial loss in body condition of the steers.

Conclusion

Habitat quality, as described by the spatial heterogeneity in food resources, is not only an important factor in the performance of large herbivores (Chapters 3 and 4) but it also shapes their foraging decisions. Foraging cattle appear to select actively when distinct differences in nutritive value and intake rate exist between foraging plants, patches, plant communities and landscape units. At the level below the landscape, the preference for high nutritive value appeared the main criterion for selection, but the demonstrated preference was not pronounced and showed flexibility. No complete exclusion of patches within a grassland community or communities within a landscape type occurred, even when there were significant differences in quality. It is not sufficiently clear whether the low selectivity observed is a result of a lack of discriminatory ability, an optimal choice subject to an additional nutritional or time constraint, or an easy but slightly suboptimal strategy. The strategy outlined above does yield an approximation of maximization for daily energy intake if the quantity of available forage is sufficient. Although it is not a time-efficient strategy, it may be effective since forage intake by cattle appears only to be limited by available grazing time when food quality is high but the intake rate is low.

Acquiring reliable information on the foraging environment does seem to be more valuable at the higher scale level of the landscape. At this level differences in forage availability and nutrient content are of greater magnitude, more predictable and therefore more likely to be remembered and used by the animal. While nutrient maximization on the basis of energy alone can explain selectivity at lower scale levels, the availability of minerals proves an important additional factor for the selection between landscape units. The present study suggests that cattle combine a simple foraging strategy at a low scale level with their experience on the distribution of resources at the higher scale level to meet a variety of nutritional demands in an essentially patchy environment.

The mechanism of learning through consequences and passing-over of information between individuals and generations has the potential to generate a complex pattern of optimal resource exploitation. The partitioning of time between landscape units in the Karshoek area occurred in bouts of half a day up to several days. This suggests the possibility that cattle optimize habitat occupancy, over a longer time scale of at least a day. Indications for a longer time scale in optimizing forage intake have also been found in other studies (De Boer & Prins, 1989; Lucas, 1990). It has further been surmised that social herbivores 'manage' their food supply, so as to maximize nutrient intake by optimizing the return time to preferred food patches (Ydenberg & Prins, 1981; McNaughton, 1984; Prins, in prep.). This portrays the foraging herbivore as an actor in the process of vegetation development and succession. It is the significance of this role and how it is affected by habitat quality and spatial scale that will need to be emphasized in future studies on plant-animal relations in heterogeneous habitats.

Epilogue: Practical implications for nature conservation

Aside from its scientific significance, this work has clear bearings on the domain of nature conservation. The significance of breed differences was treated in Chapter 7 and the relation between large herbivores and the design of nature reserves was discussed in Chapter 8. Some further remarks may be made on the perspectives for large herbivores in heathland and riverine landscapes and their significance for restoration ecology.

The present work demonstrates that disregarding the connections between landscape systems raises artificial barriers for large herbivores. Given the opportunity, the animals would use a variety of communities and landscapes instead of the restricted areas they are usually offered. The possibilities to enlarge and to diversify existing nature reserves therefore deserves more attention. As it is, large herbivores will often be subject to the limitations of uniform systems: mineral deficiency on poor heathland landscapes, flooding and low winter forage availability in fertile riverine and related landscapes. Flooding was not a serious threat in the two years of this study. Yet, during a period of 29 days in February/March 1990 with a flood lasting for two weeks, the steers on the remaining 1-1.5 ha riverine grassland lost 0.7 kg/day, even though they were gaining weight in the periods before and after the flooding.

This is not to say that large herbivores should be excluded from uniform landscapes. Such a drastic solution should not be envisaged too rashly. A few comments may be useful to put the potential of these areas in a better perspective. The presence of large herbivores in uniform landscapes can be valuable enough to warrant further experiments on their performance in various habitats. The characteristics of different landscapes vary and may turn out to have local variation satisfying the needs of the animals. There is still insufficient knowledge on the adaptability of different herbivores, especially regarding conditions of low mineral availability but also with respect to winter survival in fertile habitats. Finally, practical limitations of small and uniform reserves for sustaining a population of large herbivores may be overcome by relatively small and simple measures. A few suggestions can be made. The provision of mineral blocks may be sufficient to prevent deficiencies in regions of low soil fertility. In riverine landscapes a limited area of land protected from inundation could settle the risks of flooding. The occurrence of inbreeding in small areas can be avoided by periodic introductions of males from another population.

However, any human interference in the management of populations of large herbivores will affect the natural dynamics of the herbivore numbers as well as their impact on the system. The exploration of possibilities to create nature reserves with a minimum of human interference and with boundaries set by natural landscape features, should receive the highest priority if we are to preserve the dynamics of natural systems and their characteristic species. Large herbivores can act as keystone species in restoration ecology by revealing habitat constraints through their behaviour and performance. In an early phase of developing new nature reserves, free-ranging domestic herbivores may serve as experimental models for the wild species which are to follow, hopefully...

Plate 22. In the Karshoek area the steers often idled before crossing the bridge joining the riverine and the cover sand landscapes (Photo J.M. Gleichman).

Plate 23. In winter time the steers included more low digestible bulk forage in their diet than at other times of the year; this steer is eating *Juncus effusus* (January 1990) (Photo J.M. Gleichman).

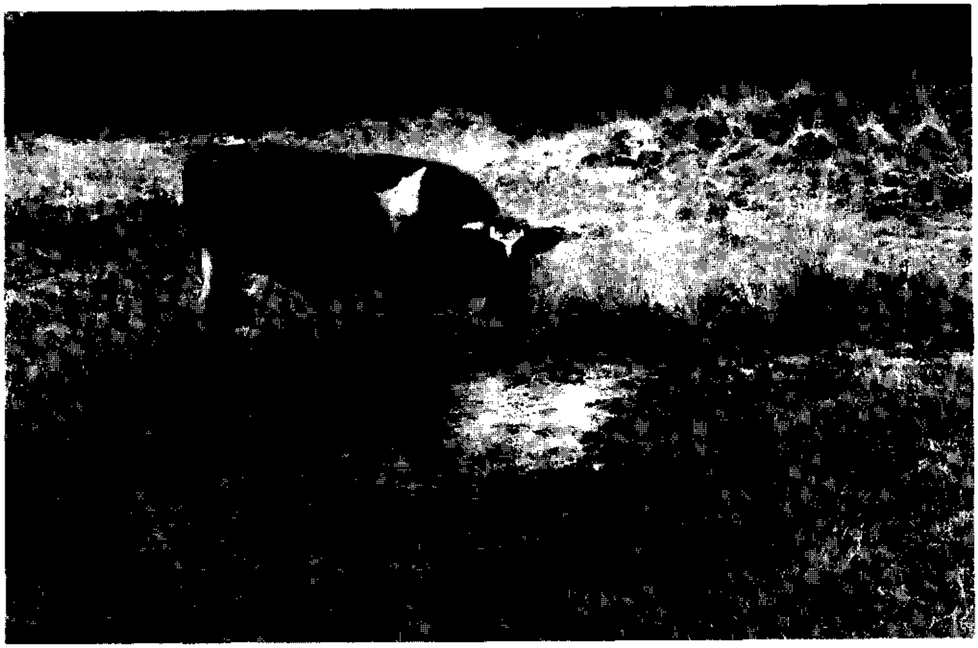


Plate 24. One of the steers in the Karshoek foraged on *Juncus bulbosus*, an aquatic plant with a high sodium concentration (April 1991) (Photo J.M. Gleichman).

Plate 25. On heathland the steers selected for extremely short *Agrostis capillaris* patches, with relatively high concentrations of minerals and protein.

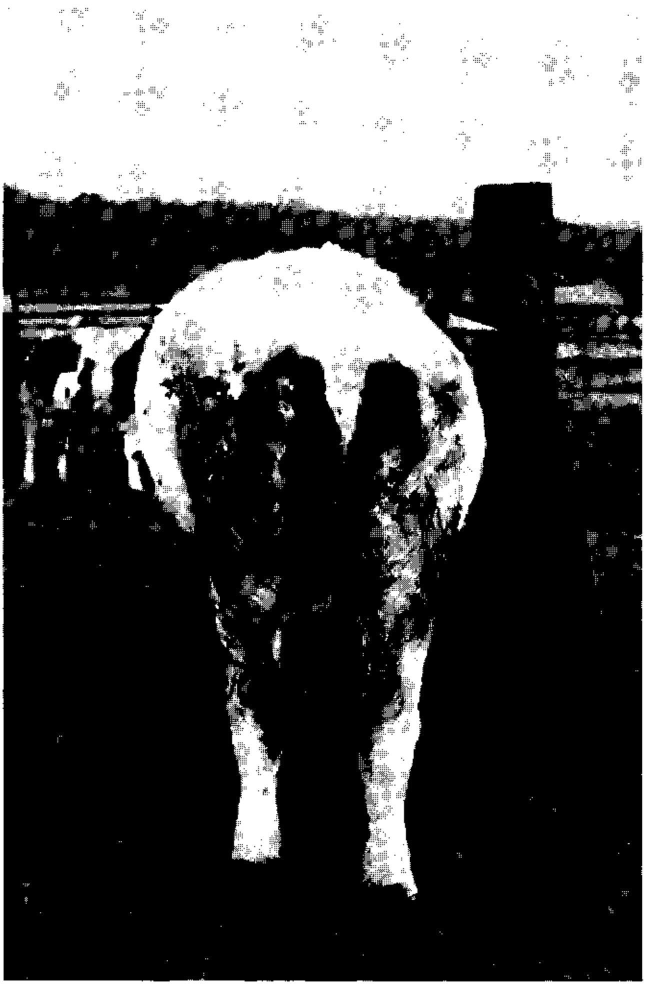


Plate 26. An animal from the treatment with controlled habitat use showing characteristic symptoms of bloat in the riverine area after being transferred from heathland in spring (May 1990).

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Summary

This thesis deals with the relation between habitat quality and the performance of a large mammalian herbivore, *Bos taurus*. Habitat quality has long been recognized as a significant factor determining herbivore growth and body condition. Yet, the mechanisms by which it affects wild animals remain poorly understood, because of the complexity of natural ecosystems. A key to a clearer definition of habitat quality can be found in the abundance, nutritive value and spatial distribution of the food supply. By foraging selectively the herbivore may make an optimal use of the heterogeneity of habitats to obtain the best feasible diet. Such selectivity should be most pronounced in an environment with a great contrast in food availability between habitat types. Based on these considerations the following two central questions underlying the study have been formulated:

a) how do differences in habitat quality relate to nutrition and herbivore performance?

b) is herbivore foraging behaviour affected by habitat differences and can it be explained by optimal foraging theory?

The study was carried over out a two-year period in two habitat types in the Netherlands: heathland and riverine grassland. These habitats contrast in soil fertility, which is also reflected in the nutritive value of the forage. Four combinations of the two habitats were examined in an experimental set-up to enable a good comparison and minimize confounding factors:

-Heathland only

-Riverine grassland only

-Heathland and riverine grassland in combination with free access to both habitats

-Controlled habitat use with summer grazing in riverine grassland and winter grazing on heathland.

All treatments involved year-round grazing. The first two treatments were designed to investigate the effect of habitat on performance. The third treatment enabled the study of habitat selection. The fourth treatment was a control treatment to show the impact of a change in habitat. The four treatments were studied in three study areas, which have been described in Chapter 1.

The heathland area, the Doorwerthse Heide (50 ha), was divided into a 28 ha compartment for the year-round treatment and a 22 ha compartment for the 'control' treatment. The vegetation was dominated by a mosaic of *Deschampsia flexuosa* and *Calluna vulgaris*, and bordered by forest. The riverine area, the Renkumse Benedenwaarden (14 ha), was also divided into two compartments, a 9 ha year-round part and a 5 ha part for the 'control' treatment. The vegetation of this study area was dominated by pasture of *Agrostis stolonifera, Lolium perenne* and *Elymus repens*. All three treatments were stocked with 5 yearling steers of the Meuse-Rhine-Yssel breed. The third study area, the Karshoek (74 ha), was used for the 'combination' treatment. It is an area along the Vecht river, with a 14 ha riverine part and a 60 ha cover sand part, which is comparable to the heathland area. The vegetation in the riverine area showed a variation according to topographical position. The largest vegetation unit was a grassland

with *Agrostis capillaris, Poa pratensis, Holcus lanatus* and *Festuca rubra* as dominating grasses. The area was stocked with 5 Meuse-Rhine-Yssel steers and 5 Hereford steers for the comparison of the performance of a dual purpose/dairy breed with a beef breed.

A number of reasons resulted in choosing for *Bos taurus*, domestic cattle, as the species for study. It is a good species for experiments because it is easy to handle, tame, relatively easy to study with regard to diet selection and there is a vast body of literature on its nutrition and performance. Cattle represent a large ruminant and a specialist grazer. These characteristics have been used in the management of nature reserves to influence vegetation development. This provided an additional practical motive to study cattle.

The thesis contains nine chapters. Chapters 2 to 8 have also been published or submitted for publication as separate articles. Chapter 2 describes the used methodology to estimate forage intake and diet quality in cattle. Chapters 3 and 4 consider the performance of the steers in the different habitat treatments and suggest an explanation for the observed differences based on the nutritional budget. Chapters 5 and 6 examine foraging behaviour in relation to food availability and spatial scale. Chapter 7 addresses the differences between cattle breeds and their significance for survival in nature. These have implications for nature conservation. Conservation aspects are treated further in Chapter 8, which considers the role of large herbivores in ecosystems as a background for the design of nature reserves. The final synthesis, Chapter 9, aims at an integration of insights on cattle as foragers in complex environments.

In Chapter 2 I examined the possibility to estimate forage intake and quality by means of an indirect method: behavioural observations and simulation of the diet by hand-plucking. Experiments were done in heathland and in riverine grassland. Observations on grazing behaviour allowed the determination of the type of forage selected and the biting rate. Bite size and nutritive value (concentrations of nitrogen and calcium) were estimated by simulating bites of steers on different forage types. Data on true bite size and nutritive value were obtained from extrusa samples of oesophageally fistulated steers. A good calibration of hand-plucking size was found by using regression analysis between true and estimated bite size. The concentrations of nitrogen and calcium were not significantly different between extrusa samples and hand-plucked samples. It was therefore concluded that the applied method of hand-plucking is suitable to determine forage intake and quality of cattle.

The overview of animal performance in Chapter 3 reveals a considerable effect of habitat quality. Summer weight gains were much higher in the riverine habitat than in the heathland habitat, the reverse was found for the weight loss over winter. Animals in the control treatment coupled high winter losses to high summer gains. In the combination treatment the steers had a low weight loss during winter, but the summer weight gains were somewhat lower than in the riverine treatment. The mineral status of the heathland animals indicated deficiencies in sodium and phosphorus. The importance of mineral deficiencies was analyzed in more detail in Chapter 4 by considering forage intake and diet quality. The animals in the riverine habitat appeared to suffer no significant limitations to realize their growth potential. Animals from the control treatment were observed to compensate quickly for their weight loss during winter. The slightly inferior performance of animals in the combination treatment compared to the riverine and control treatments is attributed to a lower soil fertility in the riverine habitat of the Karshoek area. It is concluded in this chapter that on heathland the lack of sodium and phosphorus led to an impaired growth and slower accumulation of fat reserves through a reduction of the digestion of forage in the rumen. Bone resorption is another negative effect on condition. The development of pica behaviour (the ingestion of non-forage items) on heathland can be interpreted as a behavioural response to alleviate the deficiencies by the stimulation of the saliva flow. The consumption of bones and animal remains proves to be a specific response to phosphorus deficiency.

The foraging behaviour of steers in patchy grassland was analyzed in Chapter 5. The theory of optimal foraging predicts that the animal maximizes its long-term average rate of energy intake. In the studied situation the rate of intake of digestible organic matter, a parameter of energy, was higher in tall and stemmy grass patches than in short patches. Forage from the short patches, on the other hand, was comparatively high in digestibility. The steers showed a low but significant selection for the short and the tall patches and avoided the stemmy patches. The preference for the high digestibility in the short patches was contrary to expectations for maximization of intake rate. Yet, this preference can be explained if maximization occurs on a daily basis and cattle are not limited in their food intake by grazing time but rather by voluntary intake. An exclusive preference for the short patches would often lead to time limitation and the inclusion of the tall patches may therefore be a necessity. It is suggested that patch selectivity in cattle is generally limited by the ability and the required costs to discriminate between patches. In a complex environment a flexible preference for short patches then provides a good approximation of energy intake maximization.

At a higher level of spatial scale the distribution of forage resources may show a different pattern and generate other modes of selectivity. In Chapter 6 habitat selection in the Karshoek was investigated at the level of plant communities and at the level of landscape units. Habitat occupancy was predicted using a foraging model assuming nutrient maximization for digestible organic matter, sodium and phosphorus. The observations showed that there was a significant preference for the riverine landscape over the cover sand landscape. This was broadly in agreement with the model predictions, which led to the expectation of a narrower selectivity. According to the model, the availability of sodium attracted the steers to the riverine landscape, whereas the higher intake rate of digestible organic matter favoured the cover sand landscape, especially in winter and early spring. Based on digestible organic matter intake alone the model was a very poor predictor of habitat occupancy. This confirms the idea, arising from the analysis of nutrition and performance, that minerals can play an important role in habitat selection. Within the cover sand landscape there was a clear preference for the communities with *Deschampsia flexuosa*. However, no significant community preferences were found within the riverine landscape. This disagreed with the predictions. It is argued that discrimination costs and abilities may also limit selectivity at the community level. At the landscape level the differences are more predictable and can be related by the animals to specific locations.

In the synthesis (Chapter 9) these considerations on herbivore foraging in relation to differences in spatial scale are put in a broader perspective. Cattle are portrayed as

foragers which appear to deal with the complexities of their environment by a mechanism of learning through consequences. The passing of learning experience over generations may be an important characteristic for social herbivores. It may create the opportunity for them to manipulate the quality of their food resources to their own benefit.

In the thesis I discuss several implications of insights on herbivore foraging and nutrition for nature conservation. Breed differences in cattle are reviewed in Chapter 7 with respect to their significance for the choice of a suitable large herbivore in projects on restoration ecology. It appears that breeds differ mainly in maturation rate and basal metabolic rate. Additional selection criteria are calving difficulty and so-called original traits. Present evidence, including the Karshoek experiment, suggests that breed differences would generally not have a significant effect on cattle survival in the wild under mild climatic conditions. The provision of suitable habitat conditions are probably much more important. In Chapter 8 it is concluded from a review of nature reserves in Western Europe that these do not generally meet the requirements for the establishment of large herbivore populations. Fragmentation and incompleteness of habitats appear to be the major threats for their subsistence. It is suggested that the habitat requirements for native large herbivores encompass the requirements of most local wild plant and animal species. Moreover, large herbivores may have an important role in terrestrial ecosystems through their impact on vegetation development. It is therefore advocated to use the habitat requirements of this species group as a guideline to basic conditions for the design of large nature reserves. In an epilogue to the synthesis (Chapter 9), the conclusion is reached that restricting habitat availability in nature reserves increases the risk to generate incomplete habitats for cattle and other large herbivores. It is proposed to use free-ranging domestic herbivores as experimental models in the study of habitat quality and herbivore performance.

Samenvatting

Foerageren in een landschapsmozaïek: voedselkeuze en conditie van vrij-grazende runderen op heide en rivierdalgrasland

Dit proefschrift gaat in op de relatie tussen habitatkwaliteit en de conditie van een groot herbivoor zoogdier, *Bos taurus*. Habitatkwaliteit staat reeds lang bekend als een factor van betekenis voor de bepaling van de groei en de conditie van herbivoren. Toch zijn de mechanismen waardoor habitatkwaliteit wilde dieren beïnvloedt slecht begrepen vanwege de complexiteit van natuurlijke ecosystemen. Een sleutel tot een duidelijker omschrijving van habitatkwaliteit kan worden gevonden in de kwantiteit, de voedingswaarde en de ruimtelijke verdeling van het voedselaanbod. Door selectief te foerageren kan de herbivoor de heterogeniteit van habitats optimaal benutten teneinde het best haalbare dieet te vergaren. Een dergelijke selectiviteit zou het sterkst tot uiting moeten komen in een omgeving met een groot contrast in voedselbeschikbaarheid tussen habitattypen. Gebaseerd op deze overwegingen zijn de volgende centrale vragen voor het onderzoek geformuleerd:

a) hoe houden verschillen in habitatkwaliteit verband met de voeding en de conditie van herbivoren?

b) verandert het foerageergedrag van de herbivoor door verschillen in habitat en biedt de theorie van optimaal foerageergedrag hiervoor een verklaring?

Het onderzoek werd uitgevoerd over een periode van twee jaar in twee habitattypen in Nederland: heide en rivierdalgrasland. Deze habitats zijn tegengesteld in bodemvruchtbaarheid, hetgeen wordt weerspiegeld in de voedingswaarde van het gewas. Vier combinaties van de twee habitats werden onderzocht in een experimentele proefopzet teneinde een goede vergelijking mogelijk te maken en de invloed van andere factoren te beperken:

-Heide alleen
-Rivierdalgrasland alleen
-Heide en rivierdalgrasland in combinatie met vrije beschikbaarheid van beide habitats
-Gecontroleerd habitatgebruik met zomerbegrazing in rivierdalgrasland en winterbegrazing op heide.

Alle behandelingen betroffen jaarrond begrazing. De eerste twee behandelingen waren bedoeld om de invloed van het habitat op de groei en de conditie te bestuderen. De derde behandeling maakte de studie van habitatselectie mogelijk. De vierde behandeling was een controle om de invloed van een verandering in habitat duidelijk te maken. De vier behandelingen werden in drie proefgebieden onderzocht. Deze zijn beschreven in Hoofdstuk 1.

Het heidegebied, de Doorwerthse Heide (50 ha), was verdeeld in een compartiment van 28 ha voor jaarrond begrazing en een compartiment van 22 ha voor de 'controle' behandeling. De vegetatie werd bepaald door een mozaïek van Bochtige smele

(*Deschampsia flexuosa*) en Struikhei (*Calluna vulgaris*) en omzoomd door een bos. Het rivierdalgebied, de Renkumse Benedenwaarden (14 ha), was eveneens verdeeld in twee compartimenten, een jaarrond gedeelte van 9 ha en een gedeelte van 5 ha voor de 'controle' behandeling. De vegetatie van het proefgebied werd bepaald door een weide van Fioringras (*Agrostis stolonifera*), Engels raaigras (*Lolium perenne*) en Kweek (*Elymus repens*). Alle drie behandelingen werden begraasd door 5 ossen van het Maas-Rijn-IJsselland (MRIJ) ras van een jaar oud. Het derde proefgebied, de Karshoek (74 ha), werd benut voor de 'combinatie' behandeling. Het betrof een gebied langs de Overijsselse Vecht, met een 14 ha groot rivierdalgedeelte en een dekzandgedeelte van 60 ha dat vergelijkbaar is met het heidegebied. De vegetatie van het rivierdalgebied vertoonde een variatie naar gelang de topografische ligging. De grootste vegetatie-eenheid was een grasland met Gewoon struisgras (*Agrostis capillaris*), Veldbeemd (*Poa pratensis*), Gestreepte witbol (*Holcus lanatus*) en Rood zwenkgras (*Festuca rubra*) als de dominerende grassen. Het gebied werd begraasd door 5 MRIJ ossen en 5 Hereford ossen ter vergelijking van de groei en de conditie van een dubbeldoel/melkras met een vleesras.

Een aantal redenen leidde tot de keuze van *Bos taurus*, het gedomesticeerde rund, als diersoort voor het onderzoek. Het is een goed proefdier omdat het handelbaar is, tam, relatief gemakkelijk te bestuderen ten aanzien van zijn voedselkeuze en er een uitgebreide hoeveelheid literatuur bestaat over zijn voeding, groei en conditie. Het gedomesticeerde rund is een typische grote herkauwer en een gespecialiseerde graseter. Deze eigenschappen zijn benut bij het beheer van natuurreservaten om de vegetatie-ontwikkeling te beïnvloeden. Dit leverde een bijkomend praktisch argument om rundvee te kiezen.

Het proefschrift bevat negen hoofdstukken. De hoofdstukken 2-8 zijn ook gepubliceerd of ter publicatie voorgelegd als afzonderlijke artikelen. Hoofdstuk 2 beschrijft de gebruikte methodologie om de voedselopname en de dieetkwaliteit voor runderen te schatten. Hoofdstukken 3 en 4 bestrijken de groei en de conditie van de ossen in de verschillende habitat behandelingen en opperen een verklaring voor de waargenomen verschillen op grond van de nutriëntenbalans. Hoofdstukken 5 en 6 gaan in op het foerageergedrag in verband met de voedselbeschikbaarheid en ruimtelijke schaal. Hoofdstuk 7 heeft betrekking op de verschillen tussen runderrassen en hun betekenis voor overleving in de natuur. Deze hebben gevolgen voor het natuurbeheer. Aspecten van natuurbescherming komen ook aan de orde in Hoofdstuk 8, dat de rol van grote herbivoren in ecosystemen beschouwd als achtergrond voor de inrichting van natuurreservaten. De uiteindelijke synthese, Hoofdstuk 9, richt zich op een integratie van inzichten over runderen als foeragerende herbivoren in een complexe omgeving.

In Hoofdstuk 2 onderzocht ik de mogelijkheid om de voedselopname en -kwaliteit te schatten met behulp van een indirecte methode: gedragsobservaties en simulatie van het dieet door een plukmethode. Er werden experimenten uitgevoerd in heide en rivierdalgrasland. Waarnemingen aan graasgedrag maakten het vaststellen van de voedselkeuze en de hapsnelheid mogelijk. De hapgrootte en de voedingswaarde (concentraties van stikstof en calcium) werden geschat door de happen van de ossen op verschillende gewastypen na te bootsen. Gegevens over de ware hapgrootte en de voedingswaarde werden verkregen uit extrusamonsters van slokdarmgefistuleerde ossen. Een goede ijking van plukgrootte werd gevonden door regressieanalyse tussen ware en geschatte hapgrootte. De concentraties stikstof en calcium waren niet significant verschillend tussen extrusa- en plukmonsters. Er werd hieruit geconcludeerd dat de toegepaste plukmethode bruikbaar is voor de bepaling van voedselopname en -kwaliteit bij runderen.

Het overzicht van groei en conditie in Hoofdstuk 3 laat een aanzienlijk effect van habitatkwaliteit zien. De gewichtstoename in de zomer was duidelijk groter in het rivierhabitat dan in het heidehabitat, het tegenovergestelde werd waargenomen voor de gewichtsverliezen in de winter. De dieren in de controle-behandeling paarden grote winterverliezen aan een grote gewichtstoename in de zomer. In de combinatie-behandeling vertoonden de ossen een klein gewichtsverlies over de winter, maar waren de toenamen in de zomer wat lager dan in de rivier-behandeling. De mineralenstatus van de dieren op de heide wees op tekorten aan natrium en fosfor. Het belang van mineralentekorten werd uitvoeriger geanalyseerd in Hoofdstuk 4 door de voedselopname en de dieetkwaliteit in beschouwing te nemen. De dieren in het rivierhabitat bleken geen beperkingen van betekenis te ondervinden voor de realisatie van hun groeipotentieel. Dieren van de controle-behandeling vertoonden een snelle compensatie voor de geleden gewichtsverliezen in de winter. De licht achterblijvende groei van de dieren in de combinatie-behandeling ten opzichte van de rivier- en de controle-behandeling wordt toegeschreven aan een lagere bodemvruchtbaarheid in het rivierhabitat van de Karshoek. Er wordt in dit hoofdstuk geconcludeerd dat op heide het gebrek aan natrium en fosfor leidden tot een verminderde groei en een vertraagde opbouw van vetreserves door een verlaging van de vertering van voedsel in de pens. Botafbraak is een ander negatief effect op de conditie. De ontwikkeling van pica-gedrag (het eten van materie anders dan gewas) op heide kan worden opgevat als een gedragsrespons teneinde de tekorten te verlichten door het opwekken van speekselafscheiding. Het opeten van botten en dierlijke resten blijkt een specifieke reactie te zijn, veroorzaakt door fosfortekort.

Het foerageergedrag van ossen in een graslandmozaïek werd in Hoofdstuk 5 geanalyseerd. De theorie van optimaal foerageergedrag voorspelt dat het dier zijn lange termijn gemiddelde van de snelheid van energie-opname maximaliseert. In de bestudeerde situatie was de opnamesnelheid van verteerbare organische stof, een parameter voor energie, hoger in plekken met hoog en stengelig gras dan in plekken met laag gras. Gras van de lage plekken had echter een relatief hoge verteerbaarheid. De ossen vertoonden een lage doch significante selectie voor de lage en de hoge plekken en meden de stengelige plekken. De voorkeur voor de hoge verteerbaarheid in de lage plekken was tegengesteld aan de verwachtingen op grond van maximalisatie van opnamesnelheid. Deze voorkeur kan echter worden verklaard als maximalisatie op dagbasis plaatsvindt en runderen niet in hun voedselopname worden beperkt door graastijd maar door vrijwillige opname. Een exclusieve voorkeur voor lage plekken zou vaak leiden tot een tijdsbeperking, zodat de opname van hoge plekken een noodzaak kan blijken te zijn. Er wordt gesuggereerd dat de selectiviteit tussen plekken bij runderen doorgaans wordt beperkt door het vermogen en de benodigde kosten voor het onderscheiden van verschillende plekken. In een complexe omgeving kan een flexibele voorkeur voor lage plekken aldus een goede benadering bieden van maximalisatie van de energie-opname.

Op een hoger ruimtelijk schaalniveau kan de verdeling van voedselbronnen een ander patroon laten zien en leiden tot andere typen van selectiviteit. In Hoofdstuk 6 werd de habitatselectie in de Karshoek onderzocht op het niveau van plantengemeenchappen en op het niveau van landschapstypen. De habitatbezetting werd voorspeld met behulp van een foerageermodel, uitgaande van nutriëntenmaximalisatie voor verteerbare organische stof, natrium en fosfor. De waarnemingen toonden dat er een significante voorkeur was voor het rivierlandschap boven het dekzandlandschap. Dit was globaal in overeenstemming met de modelvoorspellingen, die een engere selectiviteit deden verwachten. Volgens het model trok de beschikbaarheid van natrium de ossen tot het rivierlandschap aan, terwijl de hogere opnamesnelheid van verteerbare organische stof het dekzandlandschap bevoordeelde, vooral in de winter en het vroege voorjaar. Op grond van alleen de opname van verteerbare organische stof was het model een slechte voorspeller van habitatbezetting. Dit bevestigt het idee, voortkomend uit de analyse van voeding, groei en conditie, dat mineralen een belangrijke rol bij habitatselectie kunnen spelen. Binnen het dekzandlandschap was er een duidelijke voorkeur voor de gemeenschappen met Bochtige smele. Daarentegen werd er geen significante voorkeur voor plantengemeenschappen gevonden binnen het rivierlandschap. Dit was niet in overeenstemming met de voorspellingen. Er wordt betoogd dat de kosten en het vermogen tot onderscheiding wederom een beperking kan vormen voor de selectiviteit op het lagere schaalniveau. Op het landschapsniveau zijn de verschillen voorspelbaarder en kunnen de dieren deze koppelen aan specifieke locaties.

In de synthese (Hoofdstuk 9) worden deze beschouwingen over het foerageren van herbivoren in relatie tot verschillen in ruimtelijke schaal geplaatst in een breder verband. Runderen worden getypeerd als foeragerende dieren die met de complexiteit van hun omgeving blijken om te gaan door middel van een mechanisme van leren door gevolgen. Het doorgeven van leerervaringen tussen generaties kan een belangrijke karakteristiek vormen van sociale herbivoren. Het kan hen de gelegenheid bieden om de kwaliteit van hun voedselbronnen te manipuleren tot hun eigen voordeel.

In het proefschrift worden enige implicaties besproken van inzichten over de voeding en het foerageren van herbivoren voor de natuurbescherming. Rasverschillen bij runderen worden behandeld in Hoofdstuk 7 met betrekking tot hun betekenis voor de keuze van een geschikte grote herbivoor in natuurontwikkelingsprojecten. Het blijkt dat rassen voornamelijk verschillen in snelheid van rijping tot volwassenheid en in basaal metabolisme. Andere selectiecriteria zijn geboorteproblemen en zogenaamde wildkenmerken. Het huidige bewijsmateriaal, waaronder de Karshoekproef, rechtvaardigt de veronderstelling dat rasverschillen in het algemeen onder milde klimaatomstandigheden geen belangrijk effect sorteren op de overleving van runderen in het wild. Het voorzien in geschikte habitatcondities is waarschijnlijk veel belangrijker. In Hoofdstuk 8 wordt op grond van een overzicht van natuurreservaten in West-Europa geconcludeerd dat de reservaten in het algemeen niet voldoen aan de eisen voor de handhaving van populaties van grote herbivoren. Versnippering en incompleetheid van habitats lijken de belangrijkste bedreigingen voor hun overleving te zijn. Er wordt betoogd dat de habitateisen voor inheemse grote herbivoren de eisen van de meeste locale wilde plante- en diersoorten omspannen. Grote herbivoren kunnen bovendien een belangrijke rol spelen in terrestrische ecosystemen via hun invloed op de vegetatie-ontwikkeling. Daarom wordt ervoor gepleit de habitateisen van grote herbivoren te gebruiken als richtlijn voor randvoorwaarden voor de inrichting van grote natuurreservaten. In een epiloog van de synthese (Hoofdstuk 9) wordt de conclusie getrokken dat het beperken van de beschikbaarheid van habitats in natuurgebieden het risico vergroot dat incomplete habitats voor runderen en andere grote herbivoren ontstaan. Er wordt voor gepleit om vrij-grazende gedomesticeerde herbivoren te gebruiken als experimentele modellen bij de studie van habitatkwaliteit en de conditie van herbivoren.

List of Photographic Illustrations

(All photographs taken by the author or, where indicated, by J.M. Gleichman)

Curriculum Vitae

Michiel Frederik Wallis de Vries werd geboren op 27 augustus 1960 te Den Haag. Hij bezocht de middelbare school in Genève (Zwitserland) en in Zeist, alwaar hij aan het Christelijk Lyceum in 1978 het Atheneum-B diploma behaalde. Van 1978 tot 1986 studeerde hij biologie aan de Landbouwhogeschool te Wageningen. Doctoraalvakken werden gevolgd in het Natuurbeheer, de Vegetatiekunde & Plantenoecologie, de Dieroecologie en de Regionale Bodemkunde. De praktijkstage werd doorgebracht bij een wildbenuttingsproject in Burkina Faso. In 1986 behaalde hij het ingenieursdiploma, met lof. Van eind 1986 tot medio 1988 werd de vervangende dienstplicht als gewetensbezwaarde vervuld bij het Staatsbosbeheer. Gedurende deze periode verrichtte hij een onderzoek naar de produktie en de kwaliteit van het voedselaanbod voor runderen en paarden in natuurgebieden met schrale graslanden en heide.

Van 1988 tot 1992 volgde een aanstelling bij de Vakgroep Natuurbeheer van de Landbouwuniversiteit Wageningen als Assistent in Opleiding. Het onderzoek voor dit proefschrift werd in deze periode uitgevoerd. Voorts was hij betrokken bij diverse taken in het studentenonderwijs. In de winter van 1992/93 werd een korte opdracht uitgevoerd voor de Stichting Het Nationale Park De Hoge Veluwe, een evaluatie van de effecten van grofwild op de ontwikkeling van de vegetatie. Gedurende 1993 verbleef hij een half jaar in de steppe van Mongolië, als project-assistent verbonden aan een project van de Stichting Reservaten Przewalskipaard te Rotterdam dat financiële steun geniet van het Nederlandse Ministerie van Ontwikkelingssamenwerking. In Mongolië werd in het Hustain Nuruu Steppe Reservaat gewerkt aan de opzet en de uitvoering van ecologisch veldonderzoek, het opleiden van Mongoolse biologen en het adviseren bij de inrichting en het beheer van het reservaat. Sedert zijn terugkeer uit Mongolië is hij als gastmedewerker verbonden aan de Vakgroep Terrestrische Oecologie en Natuurbeheer van de L.U. Wageningen.

Michiel Frederik Wallis de Vries was born on 27 August 1960 in The Hague, The Netherlands. He followed secondary school in Geneva (Switzerland) and in Zeist (The Netherlands), where he graduated in 1978 at the Christelijk Lyceum. He studied biology from 1978 till 1986 at the Agricultural University Wageningen, The Netherlands. Graduate research was conducted in the disciplines Nature Conservation, Vegetation Science & Plant Ecology and Soil Science. A practical period was spent at a game cropping project in Burkina Faso. In 1986 he obtained his 'ingenieursdiploma' (with honours). From the end of 1986 till mid 1988 an alternative military service as conscience objector was fulfilled at the Forest Service. During this period he carried out research on the production and quality of forage for cattle and horses in nature reserves with acid grasslands and heathland.

From 1988 till 1992 an appointment followed as AIO (Ph.D. student) at the Department of Nature Conservation of the Agricultural University Wageningen. The study for this thesis was conducted during this period. He was furthermore involved in various tasks of graduate student education. In the winter 1992/93 a short evaluation of the effects of big game on vegetation development was carried out for the Foundation National Park 'De Hoge Veluwe'. During 1993 he stayed for half a year in the steppes of Mongolia as project assistant in a project of the Foundation Reserves Przewalski Horse in Rotterdam which is supported financially by the Ministry of Development Aid from the Dutch government. In the Hustain Nuruu Steppe Reserve in Mongolia he worked on the elaboration and initiation of ecological field research, the education of Mongolian biologists and as an advisor for the organization and management of the reserve. Since his return from Mongolia he works at the Department of Terrestrial Ecology and Nature Conservation of the Agricultural University Wageningen.